

ORIGIN AND HISTORY OF THE  
ERINACEINAE AND BRACHYERICINAE  
(MAMMALIA, INSECTIVORA)  
IN NORTH AMERICA

THOMAS H. V. RICH

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# CONTENTS

Abstract .....	5
Introduction .....	6
Acknowledgments .....	10
Nomenclature and Methods of Measurement .....	11
Abbreviations .....	13
Systematics .....	15
Subfamily Erinaceinae, Fischer von Waldheim, 1817 .....	15
Tribe Erinaceini, Fischer von Waldheim, 1817 .....	15
<i>Untermannerix</i> , New Genus .....	15
<i>Untermannerix copiosus</i> , New Species .....	16
Tribe Amphechinini, New .....	24
<i>Parvericius</i> , Koerner, 1940 .....	26
<i>Parvericius montanus</i> , Koerner, 1940 .....	27
<i>Amphechinus</i> , Aymard, 1850 .....	31
<i>Amphechinus horncloudi</i> (J. R. Macdonald, 1970), Rich and Rasmussen, 1973 .....	31
? <i>Amphechinus</i> .....	33
Tribe Uncertain .....	34
<i>Stenoechinus</i> , Rich and Rasmussen, 1973 .....	34
<i>Stenoechinus tantalus</i> , Rich and Rasmussen, 1973 .....	34
<i>Untermannerix</i> or <i>Amphechinus</i> , Species Indeterminate .....	35
<i>Parvericius</i> or <i>Stenoechinus</i> , Species Indeterminate .....	35
Erinaceinae, Genus and Species Indeterminate .....	35
Subfamily Brachyericinae, Butler, 1948 .....	36
<i>Brachyerix</i> , Matthew, 1933 .....	36
<i>Brachyerix macrotis</i> , Matthew, 1933 .....	36
<i>Brachyerix incertis</i> (Matthew, 1924), Rich and Rich, 1971 .....	41
<i>Brachyerix</i> cf. <i>B. incertis</i> .....	43
<i>Metechinus</i> , Matthew, 1929 .....	44
<i>Metechinus nevadensis</i> , Matthew, 1929 .....	44
<i>Metechinus amplior</i> , New Species .....	49
<i>Metechinus</i> sp. ....	70
Localities .....	70
Discussion and Conclusions .....	80
Method of Cladistic Analysis .....	80
Data Analyzed for Determination of Character Polarity .....	84
Alterations to the Present Taxonomy of the Erinaceinae and Brachyericinae .....	93
The Hypothetical, Primitive Morphotypes of the Erinaceinae and Brachyericinae ...	95
History and Phyletic Relationships Within the Erinaceinae and Brachyericinae ...	99
Relationship of the Adapisoricidae and Other Erinaceidae to the Brachyericinae and Erinaceinae .....	107
Literature Cited .....	111





## ABSTRACT

Modern Erinaceidae include the familiar hedgehog, *Erinaceus europaeus*, the archetypical primitive placental mammal in the minds of many biologists. Now restricted to the Old World, the family flourished in North America during the Miocene when three subfamilies were present there.

Restricted to North America, the Brachyericinae seem to have originated on that continent. Both North American genera of Amphechinini (new tribe of the Erinaceinae) are well known in the Old World in earlier Oligocene deposits and hence appear to have immigrated into North America just before their first appearance there in the early Miocene.

Area of origin of the Erinaceini may be interpreted as (1) unspecified within Holarctica plus the Ethiopian Region or (2) as external to Holarctica, depending on how the evidence is weighed. The sudden appearance of the tribe over the extent of Holarctica plus the Ethiopian Region at the beginning of the Miocene and the existence of an adequate structural ancestor in North America immediately prior to the time of initial appearance suggests the first interpretation. Counter to this, the presence in the Oligocene of a derived sister group of the Erinaceini (i.e., the Amphechinini) suggests that the tribe existed by that time, probably in an area where adequate collections from that epoch have not been made, e.g., Africa. Van Couvering (1972) has suggested that many forms which suddenly appear in the Miocene record of Europe without known precursors may have existed in Africa during the Oligocene and migrated only after the two continental blocks met in the mid-Cenozoic. Because the African Oligocene record of small mammals is so pitifully poor and a plausible reason exists for expecting that the Erinaceini existed there during that epoch, the second hypothesis appears more probable at this time.

Once established in North America in the early Miocene, both the Erinaceinae and Brachyericinae had relatively uneventful histories. Least eventful was that of the Amphechinini, one

species (*Parvericius montanus*) appearing to be conspecific with forms known in the Oligocene of Asia and the other species (*Amphechinus horncloudi*) differing only slightly from its Old World predecessors and contemporaries in that genus. Although *A. horncloudi* did not survive the Ari-kareean when it first appeared, *P. montanus* persisted with little noticeable change from that age through the Barstovian. Only one species of Erinaceini is recognized, *Untermannerix copiosus* (new), which appeared in the Barstovian and persisted until the Clarendonian with no noticeable change.

More complex was the history of the Brachyericinae. Both genera have two species of markedly different size. In each, the smaller species appears to suddenly replace the larger. In the case of *Metechinus*, the evidence for this abruptness is equivocal but for *Brachyerix* it is highly compelling.

Most useful in the analysis of the data has been the cladistic method as outlined by Hennig in his 1966 work. It was a fundamental tool in the development of the more plausible second hypothesis of the history of the Erinaceini outlined above.

Determination of primitive and derived states or polarity of a given character, a fundamental problem of the cladistic method, was made by analyzing the distribution of the different states among the several groups recognized in an initial, credible higher phylogenetic hypothesis. Character states widely scattered in a haphazard pattern among the groups were regarded as primitive; ones found in only a few groups, particularly when thought to be closely related, were regarded as derived. In cases where the pattern was ambiguous, by restricting the sample examined to forms known prior to an arbitrary geologic epoch, it was often possible to determine polarity in this subset. Because in this procedure one is examining the forms that would have been available had one lived at that earlier, arbitrary date, the methodological pitfalls are no different from examining the total sample including modern forms.

## INTRODUCTION

Today only two families of the order Insectivora are known in North America, the Talpidae (moles) and Soricidae (shrews). However, during the latter part of the Mesozoic and throughout the Cenozoic, several other families of that order existed there. One of these was the Erinaceidae, whose members are presently restricted to the Old World. During the Miocene, representatives of all three subfamilies of that family were to be found in North America, two of which form the basis of the present report. The first subfamily, the Erinaceinae, contains five living genera, the best known being the common European hedgehog, *Erinaceus europaeus*, which is covered with sharp dermal spines as are all other members of this group. During the Miocene, three genera of erinaceines inhabited North America. The second subfamily, the Brachyericinae, containing two genera and now extinct, was a North American endemic. Although undoubtedly insectivores, the skulls of specimens in this subfamily are remarkably similar in size and morphology to those of smaller species of the carnivore *Mustela*. The third subfamily, mentioned briefly in this report, is the Galericinae, known today only from southeastern Asia where four living genera are found. In North America, this subfamily only occurs in Miocene deposits where two genera are recorded: *Lanthanotherium* and *Ocajila*.

In addition to these three subfamilies, members of the Adapisoricidae and the Plesiosoricidae as recognized by Van Valen (1967) have been placed within the Erinaceidae by previous workers (e.g., Simpson, 1945). Although the ancestry of the Erinaceidae probably is to be found in the heterogeneous assemblage that is the Adapisoricidae of Van Valen, it seems a more useful procedure now to recognize the advanced pattern of dental construction common to all the restricted Erinaceidae as compared with that of the Adapisoricidae by separating these two groups at equivalent taxonomic rank rather than submerging the adapisoricids as a subfamily within the erinaceids or

distributing them among the other subfamilies. By a similar argument, the Plesiosoricidae appear to stand apart from the group of three subfamilies that are here recognized as erinaceids and should be separated from them at least at the rank that unites them; i.e., the familial rank.

Recognition of the presence of the Erinaceidae in North America has come painfully slowly and with a few false starts. Matthew played a principal role in this history. He first recognized the existence of the family in North America on the basis of the new genus and species he named and described in 1903, *Proterix loomisi* from the lower Poleslide Member of the Brule Formation in South Dakota. Although Matthew regarded *Proterix* as a member of the Erinaceinae, the most recent reviewer of the genus was uncertain as to its proper subfamilial assignment (see Gawne, 1968).

In a faunal list for the Loup Fork beds of South Dakota published by Matthew the following year (Matthew and Gidley, 1904, p. 245), there is an entry with the tantalizingly vague designation "Insectivore, gen. indet." No specimen number was given, but a mandible not assigned a number until more than a half-century later appears, based on the label associated with it, to possibly have been the specimen in mind when the entry was made. I regard this mandible (AMNH 86930) as a specimen of the erinaceine *Untermannex copiosus*, new genus and new species. (See p. 16 of this report.)

In 1924, Matthew described yet another specimen that has subsequently come to be thought an erinaceid. Collected in Barstovian deposits at Thomson's Quarry B in Nebraska, this specimen was made the type for a new species, *Talpa ?incerta*, the query reflecting Matthew's doubt as to the proper placement of the species. Wilson (1960) questioned the familial assignment of this species, eight years later Hutchison (1968) correctly identified it as an erinaceid, and finally it was recognized as a separate species of *Brachyerix* Matthew (in Matthew and



Mook, 1933) by Rich and Rich (1971); i.e., *B. incertis*.

In 1929 Matthew described *Metechinus nevadensis* from the Clarendonian (medial and late Miocene) deposits in Fish Lake Valley, Nevada. He regarded *M. nevadensis* as an erinaceine erinaceid, a position to which he also assigned *Brachyerix macrotis* from the Miocene Deep River beds of Montana when he named and described that species and genus in 1933 (see Matthew and Mook, 1933).

Friant (1934) regarded *Brachyerix* and *Metechinus* as erinaceines in which the reduction of  $M^3$  had been taken to its logical extreme, the complete loss of the tooth.

McGrew (1938) briefly mentioned a second specimen of *Metechinus*, an edentulous jaw from Clarendonian (late Miocene) deposits in Nebraska. Webb (1969) again mentioned this specimen but added nothing to McGrew's terse comments.

In his review of *Palaerinae*, a junior synonym of *Amphechinus*, Viret (1938) summarized the previous history of investigation of the genus. He regarded *Erinaceus* as derived from a stock independent of *Amphechinus* because of two advanced features of the latter that precluded it from an ancestral position: enlarged anterior incisors and reduced  $P^2$  (*Ibid.*, p. 28).

Based on dental characters, Viret (1940, p. 65) recognized an affinity between *Metechinus* and the Erinaceinae. His ideas of the relationships are explicitly expressed in a chart where *Metechinus* is shown as splitting from the stock that gave rise to *Erinaceus* and *Amphechinus* before that group subdivided into the separate branches that gave rise to those two genera.

The presence of the Erinaceinae in North America was not established until 1940 when Koerner proposed *Parvericius montanus* from the Miocene Deep River beds of Montana as a new species and genus which he regarded as being similar to *Erinaceus*. The single specimen on which *P. montanus* was based remained the only recognized erinaceine from North America for 30 years.

In 1941 Meade named *Metechinus marslandensis* on the basis of a jaw fragment

from Miocene deposits of Nebraska. Meade's species was subsequently synonymized with *Brachyerix macrotis* by Rich and Rich (1971). In his paper Meade speculated on the possibility of *Proterix* as an ancestral form to *Metechinus* and compared *Metechinus nevadensis* with *Brachyerix macrotis*.

In 1942 Henshaw described *Metechinus fergusoni* from Barstovian deposits of Nevada. Rich and Rich (1971) recently synonymized *M. fergusoni* with *Brachyerix incertis*.

Bohlin (1942) described two species he named *Palaeoerinaceus minimus* and *Palaeoerinaceus kansuensis* from the late Oligocene deposits of Taben-buluk, Kansu, China. Rich and Rasmussen (1973) have subsequently synonymized the former species with *Parvericius montanus* and tentatively regard the latter as a synonym of *P. montanus*. Bohlin, in the same paper, voiced the objection originally raised by Viret to regarding *Amphechinus* as in the lineage ancestral to *Erinaceus*, namely the enlarged incisors of *Amphechinus*.

Hürzeler (1944) named and described a new genus and species from the Aquitanian (early Miocene) of Europe: *Dimylechinus bernoullii*. He thought this species to be closely related to *Palerinaceus edwardsi* and explicitly rejected the notion of a close relationship with *Metechinus nevadensis*.

Simpson (1945) placed *Brachyerix* and *Metechinus* in the Echinisoricinae and *Parvericius* and *Palaeoerinaceus* in the Erinaceinae. His allocation of the genera within the Erinaceidae was only tentative for as he noted:

The subdivision of recent forms [of erinaceids] into two subfamilies is also well established, but the division of the various fossil genera between the two is dubious in the extreme, and the allocations of these genera in this classification, although not purely capricious, are not to be taken too seriously. There were really more than two lines of descent, and the data do not yet show just how they should be grouped. This is particularly true of the American forms, which are themselves a complex group and which do not fall into a geographic unit. (*Ibid.*, pp. 177-178.)

Butler (1948, p. 488), seeing a similarity

between *Parvericius* and *Amphechinus*, suggested that *Parvericius* might be properly an erinaceine but included it with *Brachyerix* and *Metechinus* in his new tribe Brachyeri-  
cini within the Neurogymnurinae in his formal classification of the Erinaceidae. This action was taken because of the supposed reduction of  $M^3$  of *Parvericius montanus* from the condition known in *Amphechinus edwardsi*, which was thought to indicate alliance with *Metechinus* and *Brachyerix* which lack that tooth. However, subsequent examination of the type specimen of *P. montanus* indicates that its  $M^3$  is not reduced (Rich and Rasmussen, 1973, p. 4). Butler considered the Neurogymnurinae (including the Brachyeri-  
cini) as having had a history separate from the Erinaceinae since the Eocene. His reasons for allying *Neurogymnurus* with *Brachyerix* and *Metechinus* were the similarities seen in the structure of the mastoid region. In the same paper, Butler (1948, p. 486) formally synonymized *Palaeoerinaceus* and *Palaeoscaptor* with *Amphechinus*. By invoking a secondary reduction in the size of the anterior upper and lower incisors, Butler (1948, p. 487) regarded *Amphechinus* as a suitable ancestor for the modern Erinaceinae.

Two isolated upper molars identified by Galbreath (1953) as *Brachyerix* sp. cannot now be assigned to this genus. One, thought by Rich and Rich (1971) to be *Metechinus nevadensis*, is referable to *Metechinus amplior*, new species, and the other may not be an insectivore.

Butler (1956b) described a new erinaceine genus with three new species (*Gymnurechinus leakeyi*, *G. camptolophus*, *G. songhorensis*) plus a new species of the previously known erinaceine genus *Amphechinus* (*A. rusingensis*) from the early Miocene of East Africa. *Gymnurechinus* was regarded by Butler as a primitive member of the lineage which gave rise to the living erinaceines (and thus a member of the Erinaceini as that term is used here). Because of the existence of *Gymnurechinus* with its reduced anterior upper and lower incisors, Butler abandoned his position that *Amphechinus* was ancestral to the modern erinaceines and accepted the ear-

lier conclusion of Viret (1938) and Bohlin (1942) that *Erinaceus* and *Amphechinus* represent two different lineages within the Erinaceinae.

An isolated lower molar from the Hemingfordian lower Pawnee Creek Formation identified by Wilson (1960) as an  $M_2$  of *Metechinus* cf. *M. marslandensis* and in Rich and Rich (1971) as an  $M_1$  of *Amphechinus* now appears to be an  $M_1$  of either *Parvericius* (a genus regarded as a junior synonym of *Amphechinus* by Rich and Rich, 1971, following Van Valen, 1967) or *Stenoechinus* Rich and Rasmussen (1973).

An extensive collection of isolated teeth of *Brachyerix macrotis* from Hemingfordian deposits (early Miocene) of Wyoming was described by Reed (1960) under the name *Metechinus marslandensis*.

James (1963) identified a fragment of a molar of *Metechinus* from the Clarendonian Caliente Formation in Cuyama Valley, California.

Van Valen in his classification of the Insectivora discussed the relationships of all the brachyeri-  
cines and erinaceines then known in North America: *Brachyerix*, *Metechinus*, and *Parvericius* (Van Valen, 1967, p. 273). He rejected Butler's allying *Brachyerix* and *Metechinus* with *Neurogymnurus* and instead thought that *Brachyerix montanus* (a *lapsus calami* by Matthew, 1933 [in Matthew and Mook, 1933] for *Brachyerix macrotis*) appeared to have been derived from *Proterix*, whereas *Metechinus nevadensis* and *Metechinus fergusonii* were thought to be at least morphologically derivable from *Parvericius montanus*. Van Valen's statements concerning the position of *Parvericius* are somewhat confusing. He asserts that *Parvericius* was probably derived from the North American Oligocene genus *Proterix* in one paragraph and in the next that *Parvericius* was "an immigration of *Amphechinus*," a genus previously known in the Oligocene and Miocene of the Old World. So similar did Van Valen regard *Amphechinus* and *Parvericius* that he synonymized the latter genus with the former.

McKenna and Holton (1967) described a new erinaceoid genus and species from Mon-



golia which they named *Exallerix hsandagolensis* and grouped it with *Brachyerix*, *Metechinus*, and *Dimylechinus* in Butler's tribe Brachyericini which they raised to subfamilial rank within the Erinaceidae. Although accepting Butler's action in 1948 synonymizing *Palaeoerinaceus* with *Amphechinus*, they rejected the synonymy of *Palaeoscaptor* with *Amphechinus*. *Exallerix* and the later brachyericines were regarded as an offshoot from the early Erinaceinae; i.e., from *Palaeoscaptor* and *Amphechinus*.

Voorhies (1969) listed but did not describe material of *Metechinus* from Barstovian or Clarendonian deposits of Nebraska.

Sulimski (1970) described specimens he designated as *Amphechinus* (*Palaeoerinaceus*) cf. *minimus* (Bohlin, 1942). Rich and Rasmussen (1973) transferred these specimens to *Parvericius montanus* along with the material originally designated *Palaeoerinaceus minimus* by Bohlin (1942).

J. R. Macdonald (1970) described a second North American erinaceine species, *Palaeoerinaceus horncloudi*, from the Monroe Creek Formation of South Dakota. This species was subsequently transferred to *Amphechinus* by Rich and Rasmussen (1973) following Butler's 1948 synonymizing the two genera.

Rich and Rich (1971) reviewed the genus *Brachyerix*. In that paper they synonymized *Metechinus marslandensis* with *Brachyerix macrotis*, transferred *Talpa incerta* Matthew (1924) to *Brachyerix*, and placed *Metechinus fergusonii* in synonymy with *Brachyerix incertis*. In their discussion and conclusions, they noted that the European *Dimylechinus* was perfectly adequate as a direct ancestor to the North American *Brachyerix* and *Metechinus*, that neither of the last two genera could be derived from the other, and that *Exallerix* was a poorly known form, similar to other brachyericines in the few details available.

L. J. Macdonald (1972) has recently described additional material of *Amphechinus horncloudi* (under the name *Metechinus marslandensis*) together with the first specimens of *Parvericius montanus* from the Monroe Creek Formation of South Dakota.

Rich and Rasmussen (1973) described a new genus and species of erinaceine from Arikareean (early Miocene) deposits in southwestern Montana, *Stenoechinus tantalus*, as well as added records of occurrence to species previously known in North America: *Parvericius montanus*, and *Amphechinus horncloudi*. In addition, Rich and Rasmussen synonymized *Palaeoerinaceus minimus* and tentatively synonymized *Palaeoerinaceus kansuensis* with *Parvericius montanus*. They concluded that *Parvericius* and *Amphechinus* probably immigrated into North America near the beginning of the Miocene because both genera were present in Asia during the Oligocene. The area of origin for *Stenoechinus* they regarded as Holarctica, the genus having originated from an unidentified group in either North America or the Old World.

Storer (1975) has found isolated teeth of *Parvericius montanus*, *Untermannerix copiosus*, *Brachyerix* cf. *B. incertis*, and possibly *Amphechinus* from the medial Barstovian (medial Miocene) of Saskatchewan.

On the basis of a single isolated  $M_2$ , Rich and Patton (1975) recorded the possible presence of *Amphechinus* in the Arikareean Buda local fauna of Florida.

Martin (1976) identified a number of specimens from the medial Hemingfordian Batesland Formation of South Dakota as *Parvericius* sp. cf. *P. montanus*. This record has not been verified by me.

The present investigation has made it possible to select among many of the conflicting interpretations made by earlier workers. It now appears that the suggestion originally made by Viret (1938) of two distinct lineages within the Erinaceinae is valid. This view is formally integrated into the taxonomy of the subfamily by the recognition of two tribes; the Erinaceini Fischer von Waldheim (1817) which includes all the living members of the subfamily plus *Mioechinus* Butler (1948), *Gymnurechinus* Butler (1956b), *Postpalerinaceus* (Crusafont and Villalta, 1947) Butler (1956b), and *Untermannerix*, new genus; and the Amphechinini new, which includes *Amphechinus* Aymard (1850), *Palaeoscaptor* Matthew and Granger (1924), *Parvericius*

Koerner (1940), and *Dimylechinus* Hürzeler (1944). The tribal assignment of *Stenoechinus* Rich and Rasmussen (1973) is uncertain. The Amphechinini are distinguished from the Erinaceini by the presence of enlarged anterior upper and lower incisors.

*Dimylechinus*, although superficially similar to *Brachyerix* and *Metechinus*, now seems to be allied with *Amphechinus* as Hürzeler (1944) originally concluded. Because of the specialized construction of  $P_4$ , *Dimylechinus* is far removed from a position close to the ancestral lineage which gave rise to *Brachyerix* and *Metechinus*. They, in turn, are too specialized in a number of features to be considered as close to the ancestry of *Dimylechinus*.

*Exallerox*, although superficially similar to *Brachyerix* and *Metechinus*, appears to possess some specialized features which indicate that what likenesses are present are more readily explained by convergence than close phyletic affinity. The position of this genus within the erinaceoids is doubtful.

Revision of the present paper was essentially completed in the Austral autumn of 1974. Germane papers and specimens that have subsequently come to my attention have been incorporated, but owing to my geographic isolation it has not been feasible to keep fully abreast of later development in the topics covered.

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A visit to Europe in the fall of 1971 greatly helped in evaluating the relationships between North American forms and their European relatives. A primary reason for the success of this visit was the generous assistance provided by many persons at the different institutions I visited: Drs. Johannes Hürzeler and Burkart Engesser, Naturhistorisches Museum, Basel, Switzerland; L. Ginsburg, Donald E. Russell, and Emile Heintz, Institut de Paléontologie, Paris, and Alan J. Charig, the late W. Roger Hamilton, and Mr. Jeremy Hooker, Department of Paleontology, British Museum (Natural History).

Mrs. Jean West of Milwaukee, Wisconsin, suggested the specific name for *Metechinus amplior*, new species, Mrs. Mary Lee Vickers typed the manuscript with assistance from Mrs. Linda M. Hunt. Miss Camilla Hewitt of New York carefully read an advanced version of the manuscript and suggested many editorial changes.

#### NOMENCLATURE AND METHODS OF MEASUREMENT

Descriptions of the skulls and mandibles made in this paper follow the nomenclature of Butler (1948) except where noted. In de-

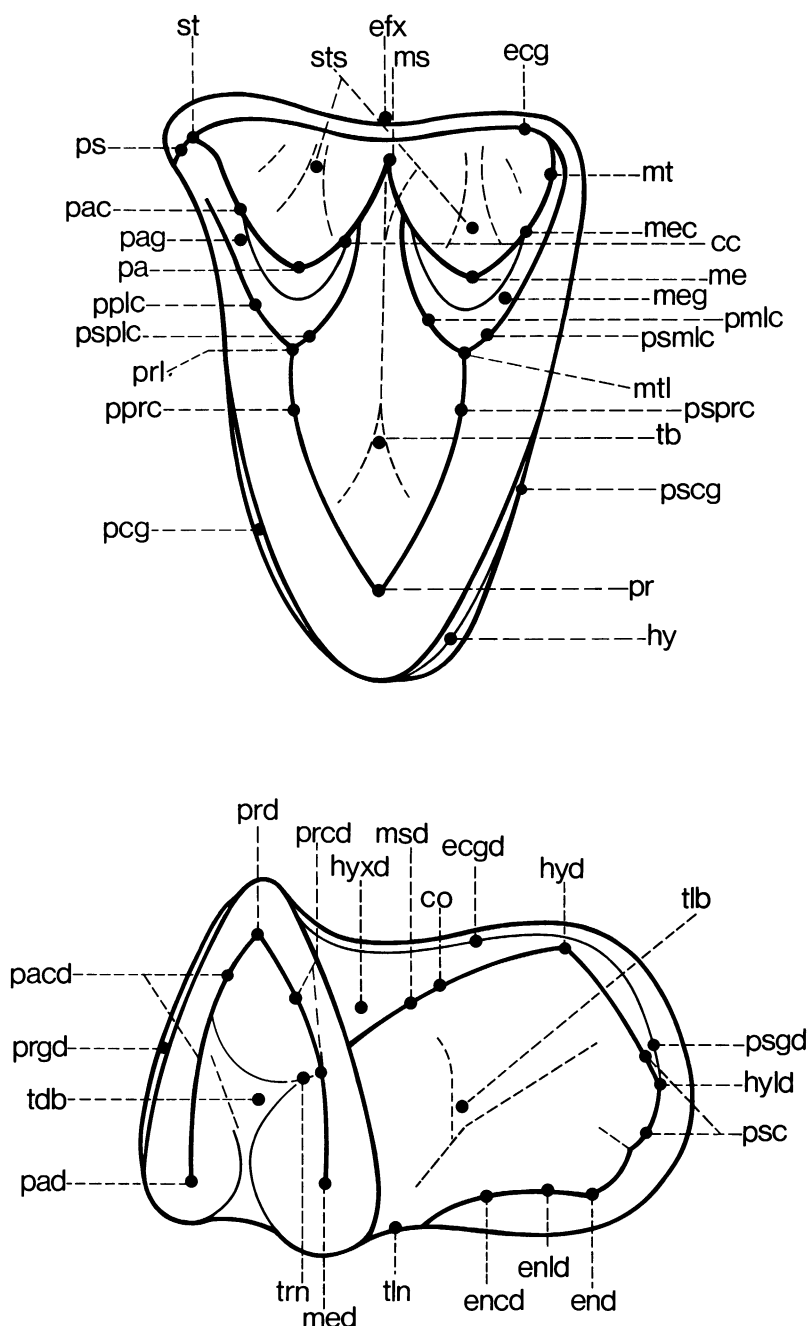


FIG. 1. Hypothetical upper and lower molars, illustrating the tooth nomenclature used in this paper. *Abbreviations:* cc, centrocrista (divisible into the postparacrista and premetacrista); co, cristid obliqua; ecg, ectocingulum; ecgd, ectocingulid; efx, ectoflexus; encd, entocristid; enld, entoconulid; end, entoconid; hy, hypocone; hyd, hypoconid; hyld, hypoconulid; hyxd, hypoflexid; me, metacone; mec, metacrista (or postmetacrista); med, metaconid; meg, metacingulum; ms, mesostyle; msd, mesoconid; mt, metastyle; mtl, metaconule; pa, paracone; pac, paracrista (or preparacrista); pacd, paracristid; pad, paraconid; pag, paracingulum; pcg, precingulum; pmlc, premetaconule crista; pplc, preparaconule cris-



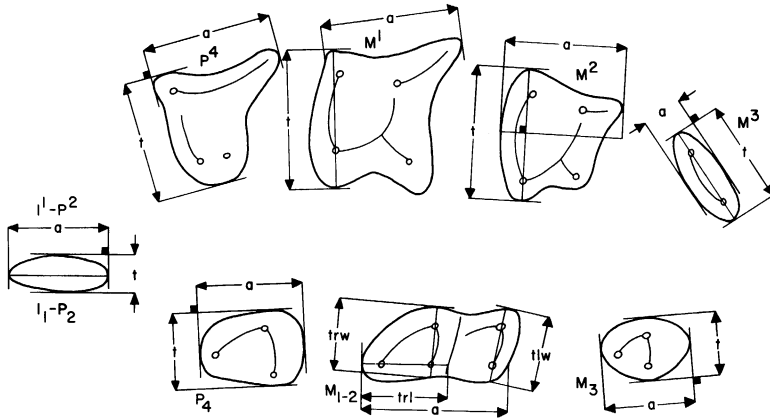


FIG. 2. Occlusal view of erinaceid dentition showing points between which measurements were taken. *Abbreviations:* a, anteroposterior diameter; t, transverse diameter; tr l, trigonid length; tr w, trigonid width. For  $I^1-P^4$ ,  $M^3$ ,  $I_1-P_4$ , and  $M_3$ , the transverse diameter, t, is defined 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. (From Rich and Rasmussen, 1973, fig. 1.)

tails of the structure of the auditory region, notably the ectotympanic, Van der Klaauw (1931) was followed because Butler did not describe this area with sufficient elaboration. For the teeth, the nomenclature outlined by Szalay (1969) for primitive eutherian mammals was followed (see fig. 1). Measurements of the teeth were made following the system given in Rich and Rasmussen (1973) (see fig. 2).

## ABBREVIATIONS

### INSTITUTIONS

ACM, Amherst College Museum  
AMNH, Department of Vertebrate Paleontology,  
American Museum of Natural History  
AMNH(CA), Formerly the Department of Comparative Anatomy, collection now included in catalogue of specimens in the Department of

Mammalogy, American Museum of Natural History  
AMNH(M), Department of Mammalogy, American Museum of Natural History  
CM, Carnegie Museum  
F:AM, Frick Collection, American Museum of Natural History  
FMNH, Field Museum of Natural History  
KU, Museum of Natural History, the University of Kansas  
LACM, Los Angeles County Museum of Natural History  
LACM(CIT), California Institute of Technology collection in the Los Angeles County Museum of Natural History  
MPUM, Museum of Paleontology, University of Montana  
RAM, Ray Alf Museum, Webb School, Claremont, California  
ROM, Royal Ontario Museum, Toronto  
SDSM, Museum of Geology at the South Dakota School of Mines and Technology, Rapid City

←  
ta; pprc, preprotocrista; pr, protocone; prcd, protocristid; prd, protoconid; prl, paraconule; prgd, precingulid; ps, parastyle; pscd, postcristid; pscg, postcingulum; psdg, postcingulid; psmc, postmetaconule crista; pspc, postparaconule crista; pspcr, postprotocrista; st, stylocone; sts, styler shelf; tb, trigon basin; tdb, trigonid basin; tlb, talonid basin; tln, talonid notch; trn, trigonid notch. (Redrawn from Szalay, 1969, fig. 1.)

T. b., Taben-buluk collection, Paleontological Museum, Uppsala, Sweden<sup>1</sup>  
 TTU, The Museum, Texas Tech University, Lubbock  
 UCM, University of Colorado Museum  
 UCMP, University of California Museum of Paleontology, Berkeley  
 UMMP, University of Michigan Museum of Paleontology  
 UNSM, University of Nebraska State Museum  
 USGS(PSB,D), United States Geological Survey, Paleontology and Stratigraphy Branch, Denver  
 UW, Department of Geology, University of Wyoming  
 YPM, Yale Peabody Museum  
 Z. Pal., Palaeozoological Institute, Polish Academy of Sciences, Warsaw

#### ILLUSTRATIONS

AL, alisphenoid  
 AN, angle  
 Ap, anterior process  
 B, bulla  
 BO, basioccipital  
 BWCpb, bullar wall (compact bone)  
 CD, condyle  
 CF, condylar foramen  
 CP, coronoid process  
 CRF, carotid foramen  
 EAM, external auditory meatus  
 EF, ethmoid foramen  
 EFN, exit for facial nerve (VII)  
 EJ, external jugular vein  
 EO, exoccipital  
 EO(POP), paroccipital process of exoccipital  
 EST, exit for stapedial artery  
 EUST, eustachian canal  
 F, facial branch of nerve VII  
 FC, facial canal (=Fallopian canal)  
 FM, foramen magnum  
 FO, fenestra ovalis  
 FOR O, foramen ovale  
 FR, frontal  
 FrC, foramen for canal of unknown purpose  
 F VR E, foramen for Vidian ramus of promontory artery to enter tympanic region  
 F VR L, foramen for Vidian ramus of promontory artery to leave tympanic region  
 H, hypoglossal nerve (XII)

Hdm, head of malleus  
 HF, hypoglossal foramen  
 I, incus  
 IC, internal carotid artery  
 IF, infraorbital foramen  
 IP, interparietal  
 JF, jugular foramen  
 JI, internal jugular vein  
 JU, jugal  
 LF, lacrimal foramen  
 M, maxilla  
 MA, malleus  
 MAS, mastoid  
 ME, meatus  
 MF, mental foramen  
 Mn, manubrium of malleus  
 Mp, muscular process of malleus  
 M V, mandibular branch of nerve V  
 N, nasal  
 N IX, X, XI, cranial nerves IX, X, XI  
 OC, occipital  
 OCC, occipital condyle  
 OF, optic foramen  
 ONF, orbitonasal foramen  
 OS, orbitosphenoid  
 P, promontorium  
 PA, promontory artery  
 PAL, palatine  
 PAR, parietal  
 PER, periotic  
 PGF, postglenoid foramen  
 PM, premaxilla  
 PS, periotic spur  
 RI, ramus inferior of stapedial artery  
 RIE, exit for ramus inferior of stapedial artery  
 RS, ramus superior of stapedial artery  
 S, sphenoid  
 SMF, stylomastoid foramen  
 SO, supraoccipital  
 SOF, suboptic foramen  
 SPF, sphenorbital foramen  
 SQ, squamosal  
 ST, stapes  
 STR, strut  
 SVR, strut for Vidian ramus of promontory artery  
 TEJ, tube for external jugular vein  
 TFC, tube for facial canal  
 TM V, tube for mandibular branch of trigeminal nerve  
 TPA, tube for promontory artery  
 TSA, tube for ramus inferior of stapedial artery  
 UF, unidentified foramen  
 VF, Vidian foramen  
 VR, Vidian ramus of promontory artery

<sup>1</sup> All the Taben-buluk collection has been permanently transferred to the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, Peoples Republic of China.

## SYSTEMATICS

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

KNOWN DISTRIBUTION: Stampian? (?35 my., early Oligocene)—Recent, Europe; Aquitanian (20 my., early Miocene)—Recent, Africa; 32 my. (medial Oligocene)—Recent, Asia; medial Arikarean—late Clarendonian (23–10 my., early to late Miocene), North America.

DIAGNOSIS: Distinguished from the Brachyericinae by the presence of three, not two, upper premolars; the hypocone being lower, rather than equal or taller than the protocone on  $P^1$ ; presence of a postcingulum on the lower molars; zygomatic arch shallow; and greater development of the mandibular angle; from other members of the Erinaceidae except the Brachyericinae and *Proterix* by the presence of two lower incisors; from other members of the Erinaceidae except *Proterix* by the presence of two lower premolars; from other members of the Erinaceidae by the presence on  $P_4$  of a paraconid nearly as tall as the protoconid<sup>2</sup>; from other members of the Erinaceidae by the absence of a well-developed talonid on  $M_3$  if that tooth is present; from other members of the Erinaceidae except the Brachyericinae and *Hylomys* by the development of the palatine posterior to the transverse crest of the palate.

TRIBE ERINACEINI FISCHER VON  
WALDHEIM, 1817

KNOWN DISTRIBUTION: Burdigalian (18 my., early Miocene)—Recent, Europe;

Aquitanian (20 my., early Miocene)—Recent, Africa; Pleistocene (2 my.)—Recent, Asia; Barstovian—Clarendonian (16–10 my., medial to late Miocene), North America.

DIAGNOSIS: Distinguished from the Ampechinini by the presence of small  $I_1$  and  $I^1$ .

UNTERMANNERIX, NEW GENUS

ETYMOLOGY: *Untermann*, in honor of the late Mr. and Mrs. George E. Untermann of Vernal, Utah; *erix*, Latin, hedgehog.

TYPE: *Untermannerix copiosus*, new species.

KNOWN DISTRIBUTION: Barstovian—Clarendonian (16–10 my., medial to late Miocene), western North America.

DIAGNOSIS: Distinguished from *Mioechinus* and the modern erinaceines by the size of  $P^3$  being greater than  $P^2$ ; from *Palaeoscaptor* by absence of a metacone on  $M^3$ ; from *Gymnurechinus* by the presence of only one root on  $P_2$ ; from *Stenoechinus* by the paraconid being only slightly lower than the protoconid on  $P_4$ ; from *Ampechinus*, *Dimylechinus*, *Mioechinus*, *Palaeoscaptor*, and *Postpalerinaceus* by the presence of relatively anteroposteriorly compressed trigonids on the anterior two lower molars, particularly  $M_1$ ; from *Gymnurechinus*, *Palaeoscaptor*, and *Stenoechinus* by complete absence of a postcingulum or talonid on  $M_3$ ; from *Dimylechinus* by presence of  $M^3$  and  $M_3$ ; from living erinaceines (*Erinaceus*, *Atelerix*, *Aethechinus*, *Paraechinus*, and *Hemiechinus*) by a solid rather than fenestrated palate; from the living erinaceines, *Mioechinus*, and *Postpalerinaceus* by the greater length of the palate relative to its width; from *Ampechinus*, *Dimylechinus*, *Gymnurechinus*, *Palaeoscaptor*, *Paraechinus*, and *Parvericius* by the nearly vertical anterior edge of the ascending ramus; from *Ampechinus*, *Dimylechinus*, and *Palaeoscaptor* by a greater elevation of the condyle; from all the other Erinaceinae by the relatively reduced angle on the mandible.

<sup>2</sup> The erinaceine *Stenoechinus tantalus* has a low paraconid on  $P_4$ . See discussion on p. 105.



FIG. 3. *Untermannerix copiosus*, new genus and new species, type, F:AM 76703. Palatal view of skull. Found 2 feet above Blue-Gray Ash in the Pojoaque Member of the Tesuque Formation, central Pojoaque Bluffs, NE  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , SE  $\frac{1}{4}$ , sect. 36, T. 20 N, R. 8 E, Santa Fe County, New Mexico (35° 55' 11" N, 106° 02' 31" W).  $\times 4.5$ .

### *Untermannerix copiosus*, new species

Figures 3–7

ETYMOLOGY: *Copiosus*, Latin, abundant, in reference to the numerous specimens of this species that are available.

TYPE: F:AM 76703, muzzle of skull with complete dentition and both mandibles complete except for left lower incisors and left ascending ramus. (See figs. 3–7.)

TYPE LOCALITY AND STRATIGRAPHIC POSITION: (See Localities, section 52.)

DIAGNOSIS: Only named species of genus.

REFERRED MATERIAL: F:AM 76705, left maxilla fragment with  $M_1$ – $M_3$ . (See Localities, section 50.)

F:AM 76717, fragmentary left ramus with  $M_3$  and alveoli for  $M_1$ – $M_2$ , missing horizontal ramus anterior to  $M_1$  and most of ascending ramus. F:AM 76716, left mandible fragment with  $M_2$  and alveolus for  $M_3$ , missing hori-

zontal ramus anterior to  $M_2$  and ascending ramus. (See Localities, section 51.)

F:AM 76719, crushed muzzle of skull with complete dentition but incisors and canines heavily worn or extensively damaged, right mandible with  $I_1$ ,  $P_2$ , and  $M_1$ – $M_3$  damaged and lacking the angle and condyle, and left mandible with incisors, canine, and  $M_3$  damaged and posterior part of jaw absent. (See Localities, section 57.)

F:AM 76718, left mandible fragment with  $M_1$  and extensively damaged  $M_2$  trigonid. (See Localities, section 35.)

F:AM 76720, right  $P^3$ – $M^1$  in maxilla fragment. F:AM 76721, right  $M^1$  in maxilla fragment. F:AM 76722, left  $M_2$  with mandible fragment. F:AM 76723, isolated right  $M_2$ . F:AM 95183, isolated right  $M^2$ . (See Localities, section 53.)

AMNH 86930, mandible fragment with  $P_3$ –



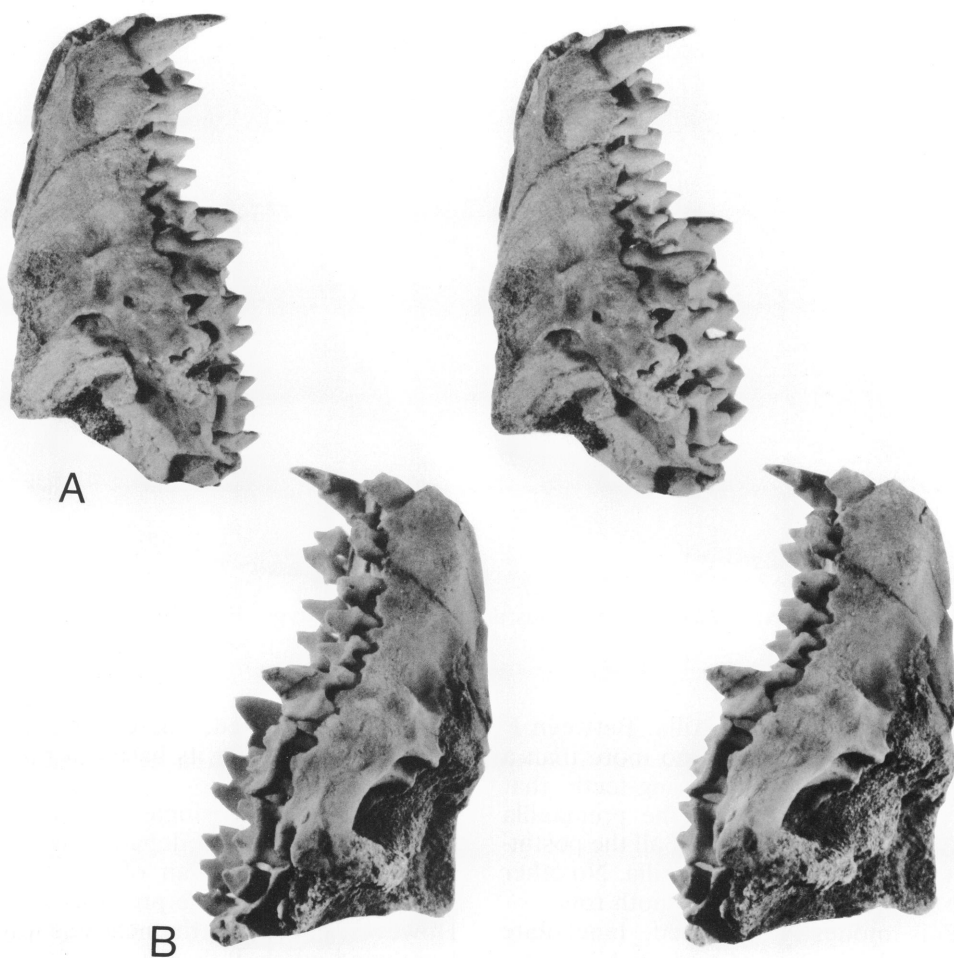


FIG. 4. *Untermannex copiosus*, new genus and new species, type, F:AM 76703. A. Right lateral view of skull. B. Left lateral view of skull.  $\times 4.5$ .

$M_1$  and badly damaged trigonid of  $M_2$ . (See Localities, section 47.)

F:AM 76734, isolated left  $M_2$ . F:AM 76735, isolated right  $P_4$ . F:AM 76737, isolated left  $M^2$ . F:AM 76738, isolated right  $M^2$ . UMMP V61025, isolated left  $M^2$ . UMMP V61028, isolated right  $M^2$ . UMMP V61030, isolated right  $P_4$ . UMMP V61032, isolated left  $M^1$ . (See Localities, section 39.)

F:AM 76740, isolated right  $M_2$ . UMMP V61023, isolated right  $P^4$ . UMMP V61024, isolated right  $M^3$ . (See Localities, section 40.)

UNSM 45201, isolated right  $M_1$ . UNSM

45203, two left and four right  $M_2$ s. UNSM 45219, one left and one damaged right  $M_1$ . UNSM 45220, isolated right  $M^2$ . UNSM 45301, partial right mandible with damaged  $P_4$  and  $M_1$  and alveoli of  $C_1$ - $P_2$ . UNSM 45302, one left and one right  $M^1$ . UNSM 45303, right  $M^2$ . (See Localities, section 42.)

UMMP V55722, isolated right  $M_1$ . (See R. L. Wilson, 1968, fig. 12a-b.) (See Localities, section 63.)

ROM 7632, isolated right  $M^2$  (see Storer, 1975, fig. 2c). TTU 5014, isolated left  $P^4$ . (See Localities, section 37.)

UPPER DENTITION: Three upper incisors



FIG. 5. *Untermannerix copiosus*, new genus and new species, type, F:AM 76703. Dorsal view of skull.  $\times 4.5$ .

are implanted in the premaxilla. Between  $I^3$  and  $C^1$  is a short diastema, no more than a third the length of the bordering teeth, that marks the contact between the premaxilla and maxilla. Behind this point, all the postincisors are implanted in the maxilla. No other diastemata are present in the tooth row.

$I^1$ : This modestly recurved, lanceolate tooth extends downward and slightly anterior so that it departs about 10 degrees from the vertical. Its length below the alveolar border is about twice that of the succeeding upper incisor. In cross section, this tooth has the outline of a mediolaterally compressed oval with the leading edge rounded and the trailing edge sharp. The single root of this tooth is confined to the premaxilla and terminates above  $P^3$ . The root of this tooth is about three-fifths as long as the crown.

$I^2$ - $P^2$ : These four teeth have a common pattern that each departs from to some degree. All are mediolaterally compressed and have a single, prominent cusp, the paracone, which has a well-developed crest on its posterior side extending dorsally to a weak metastyle (except  $I^2$  which lacks a metastyle). All but  $I^3$  have a parastyle and all but

$I^2$  are double rooted. There is a slight inflation of the crown at its base but no distinct cingula are present.

$I^2$ : As the only single-rooted tooth,  $I^2$  might be expected to depart most radically from the common plan of the four teeth grouped together in the previous paragraph. However, except for the near equality of its length and width, it does not deviate too far. The outline of the tooth in occlusal view is elliptical. The tooth is displaced somewhat medially from the tooth row towards the midline of the skull.

$I^3$ : Unlike the other three teeth grouped together here for descriptive purposes, the paracone is directly below the anterior root of this tooth, rather than beneath its center. Consequently, the profile of the crown in lateral view departs the most radically of the four from bilateral symmetry. Instead of being a single straight segment that terminates at the parastyle as in the other three teeth, the anterior edge of  $I^3$  is composed of two straight segments that meet in such a way as to give the leading edge of the tooth a convex appearance. The outline of the tooth in occlusal view is nearly rectangular.

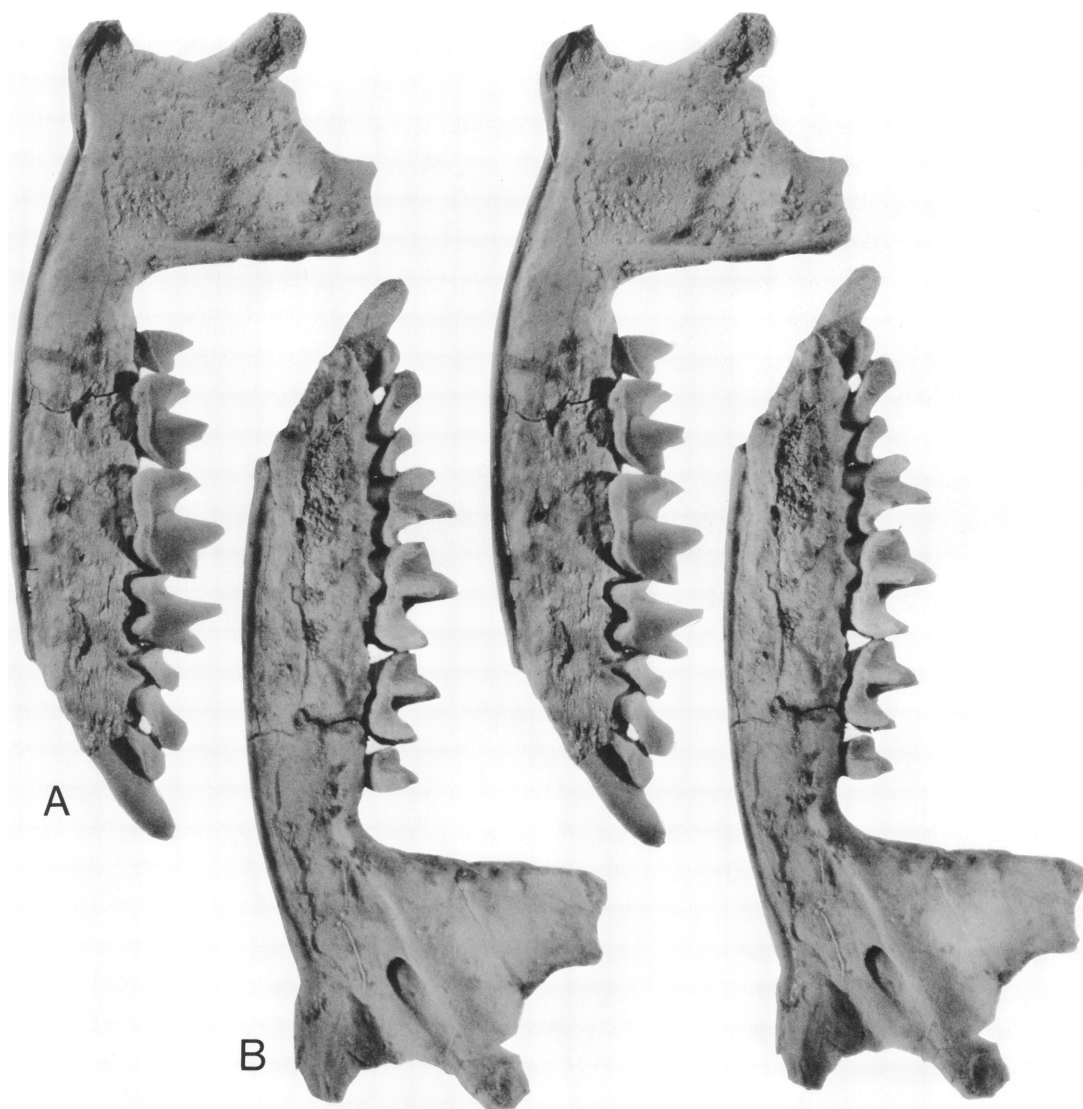


FIG. 6. *Untermannerix copiosus*, new genus and new species, type, right mandible, F:AM 76703. A. Lateral view. B. Medial view.  $\times 4.5$ .

In length, width, and height  $I^3$  is greater than  $I^2$ .

$C^1$ : Of the four teeth grouped together here, the canine requires the least addition of information to complete its description. Its outline in occlusal view is irregular but may be visualized as an oval with the broad end anterior.

$P^2$ : In its own way, this tooth departs as radically as  $I^3$  from the general appearance of the four teeth described here together. It is unique among them in having a relatively elongate metacrista linking the weak metastyle with the paracone. Its outline in occlusal view is irregular but is approximated by an oval with the broad end posterior.

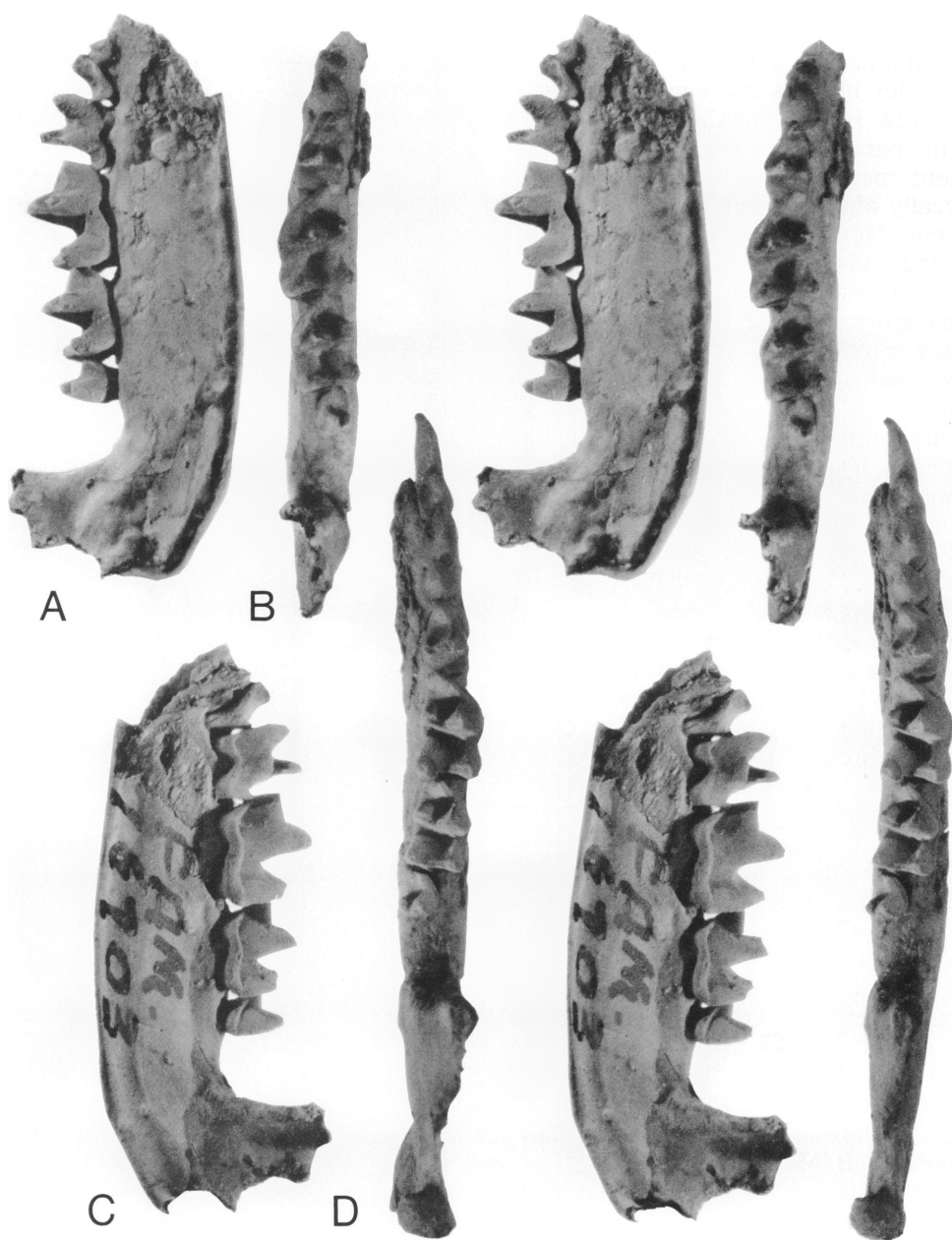


FIG. 7. *Untermannerix copiosus*, new genus and new species, type, F:AM 76703. A. Medial view of left mandible. B. Occlusal view of left mandible. C. Lateral view of left mandible. D. Occlusal view of right mandible.  $\times 4.5$ .

Beginning with  $I^3$  and continuing through to  $P^3$ , the tips of the paracones of the successive teeth are progressively more dorsal.

$P^3$ : In numerous respects,  $P^3$  is a miniature replica of  $P^4$  behind it. The straight buccal border of the tooth is directed anteromedi-



ally so that it forms an angle of 45 degrees with the midline of the skull. The anterior and posterior borders are concave and the lingual border is convex. Along the posterior side of the paracone is a crest that meets the prominent metacrista which extends posterobuccally along the midline of the metastylar spur. No sign of a metastyle is to be seen at the end of the metacrista. The protocone is somewhat less than half the height of the paracone and medial to it. Behind the protocone is a flat surface that dips posterodorsally. This surface lacks any trace of a hypocone.

P<sup>4</sup>: This tooth is several times larger than the preceding P<sup>3</sup>. The height of the paracone, tallest and most prominent cusp on the tooth, is only slightly less than the length of the tooth. One-third the height of the paracone, the protocone is lingual and slightly anterior to that cusp, as in modern hedgehogs. The hypocone is a somewhat smaller and shorter cusp than the protocone and posterolingual to it. Linking these two cusps is a low crest but no such ridge links either of them to the buccal structures of the tooth. Behind the hypocone is a small planar surface that dips steeply posterodorsally. Although no parastyle is present, a prominent parastylar spur is developed on the anterior side of the base of the paracone. Developed as a prominent blade on the strong metastylar spur, the metacrista projects laterally and somewhat posteriorly from the base of the paracone, terminating marginally without developing a distinct metastyle. No distinct cingula are present except for a short buccal cingulum between the protocone and hypocone. In order of decreasing diameter, the three roots of the tooth are developed above the protocone-hypocone, metacrista, and paracone-parastylar spur.

M<sup>1</sup>: Largest tooth in the skull, M<sup>1</sup> is slightly broader and somewhat longer anteroposteriorly than P<sup>4</sup>. The height of the paracone, tallest of the four principal cusps, is half the length of the tooth. Posterior to the paracone and nearly as tall, the metacone is the second tallest cusp on the tooth. Third tallest cusp on the tooth, the protocone, is lingual and slightly anterior to the paracone. Posterolin-

gual to the protocone is the lowest of the four principal cusps, the hypocone. As is true of modern hedgehogs, the protocone and paracone are closer to one another than the hypocone and metacone. No trace of a paraconule is present. On two specimens from the same locality, F:AM 76720 and 76721, a prominent metaconule is present. On the other specimens this cusp is not clearly developed. Situated at the buccal end of the precingulum is a small parastyle that is linked to the paracone by a short paracrista. From the metacone, the metacrista extends posterobuccally for a distance equal to one-third the tooth length. Narrow cingula are present almost continuously along the perimeter of the tooth. In occlusal view, the anterior border is straight and the buccal, posterior, and lingual borders concave. The metastylar spur forms a prominent projection posterobuccally away from the body of the tooth, whereas the parastylar spur is a much weaker anterior projection. Separate roots are developed above the paracone-parastyle and metacone-metastyle regions but it is not clear whether one anteroposteriorly elongated root is developed above the protocone-hypocone region or if there are two roots, one above the protocone and a second above the hypocone.

M<sup>2</sup>: In basic pattern, this tooth is not altogether different from the somewhat larger M<sup>1</sup>. The relative heights and basal dimensions of the four principal cusps are the same but the metacone has shifted its position medially so that it is posterolingual rather than posterior to the paracone. This shift is reflected by all the structures in the posterobuccal region of the tooth for the metastylar spur projects posteriorly rather than posterobuccally and is reduced; the buccal border of the tooth is not subparallel to the midline of the skull but rather is directed posteromedially and forms an angle with the midline of 35 degrees. Similarly, the parastylar spur has shifted so that it projects buccally rather than anteriorly, the parastyle being further buccal relative to the paracone. Cingula are present but weaker, particularly on the lingual and buccal sides of the tooth.

M<sup>3</sup>: This tooth is basically a mediolaterally elongated blade with the protocone at one end and the somewhat lower paracone at the other, the two joined together by a straight crest. Along the rear margin of this tooth a weak postcingulum is developed. A prominent root is developed above the protocone and a somewhat smaller one is present above the paracone.

LOWER DENTITION: I<sub>1</sub>: In length, this tooth is similar to modern Erinaceini, the distance from the tip of the crown to the alveolar border of the tooth being only about one and two-thirds the similar measurement on I<sub>2</sub>. At the border of its alveolus, this tooth is elliptical in cross section, the mediolateral and minor axis being three-fourths the length of the major axis. The buccal side of the crown is convex but the medial side is nearly flat.

I<sub>2</sub>, C<sub>1</sub>, P<sub>2</sub>: In general plan, these teeth are quite similar although C<sub>1</sub> is noticeably larger than the other two. Extending anteriorly from the single root, the crown overlaps the preceding tooth. Near the anterior end of the tooth is a crest along the midline that terminates posteriorly at the protoconid. In height, the protoconid is about one-fourth, or in the case of C<sub>1</sub>, about one-third, the length of the tooth. Along the lingual border and, except for I<sub>2</sub>, along the posterior border is a weak ridge.

P<sub>4</sub>: This tooth is much larger than the preceding three teeth. Most prominent of the cusps is the protoconid; its height is equal to the tooth length. Somewhat lower and smaller in basal dimensions than the protoconid, the paraconid is, nonetheless, quite well developed, its basal-apical axis being anterodorsally inclined. In lateral view, a deep V-shaped notch separates the two cusps. Located on the midline of the tooth, the paraconid is anterolingual to the protoconid. Smallest and lowest of the trigonid cusps, the metaconid is appressed against the postero-medial side of the base of the protoconid. Greatest breadth of the tooth occurs in the region of the short talonid. Along the posterior margin of the talonid is a low ridge near the center of which is developed a small cuspsule. Continuous with this ridge is a nar-

row cingulum along the buccal margin of the tooth. This tooth is double rooted.

M<sub>1</sub>: The length of the trigonid is three-fourths its width and almost half the length of the tooth. Tallest of the trigonid cusps and greatest in basal dimensions is the protoconid. Intermediate in height, the metaconid is lingual and slightly anterior to the protoconid. Linking the two cusps is a protolophid that, when viewed posteriorly, has an acute V-shaped profile. The paralophid extends anterolingually from the protoconid to the lowest cusp on the trigonid, the paraconid. In lateral view, the paralophid has a V-shaped profile, the angle between the two segments being obtuse but close to a right angle and the lingual segment that terminates at the paraconid is nearly horizontal. Placed at the anterolingual corner of the tooth, the paraconid in lingual view is anterodorsally inclined at an angle of about 30 degrees with respect to the vertical metaconid.

Width of the talonid is slightly greater than that of the trigonid. Entoconid and hypoconid are placed at the extreme posterior corners of the tooth. Taller of the talonid cusps, the entoconid 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 which is directed dorsomedially so that it terminates lingually midway between the hypoconid and entoconid just below the crest of the postcristid. 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<sub>2</sub>: Because this tooth is quite similar to M<sub>1</sub> in general morphology, a detailed description is unnecessary but a few points of difference are noted in the following two paragraphs.

In length and width, this tooth is about five-sixths the size of M<sub>1</sub>. No distinct paracoid is present, the paralophid terminating lingually without any noticeable swelling. For the lingual one-fourth of its length, the paralophid is directed lingually, not anterolingually. In posterior view, the V-shaped notch of the protolophid is obtuse.

Despite the fact that the talonid is equal or slightly narrower, not slightly wider than the trigonid, the hypoconid position is still somewhat more buccal than that of the protocoid. The buccal cingulum terminates anteriorly at the forward edge of the prevallid and posteriorly opposite the base of the hypoconid, being separated from the posterior cingulum by a short gap.

As is the case with M<sub>1</sub>, no specimen is available with the alveoli of this tooth exposed.

M<sub>3</sub>: This single-rooted tooth contrasts markedly with the more anterior molars for it lacks a talonid and the trigonid is anteroposteriorly expanded, the length being nearly half again as great as the width. Although the protoconid is no taller, it is greater 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 on the lingual end of the paralophid marks the presence of the paracoid. As in the more anterior molars, in lateral view the paralophid has a V-shaped profile, the two limbs of which meet at nearly right angles, and the lingual segment is nearly horizontal. 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.

As is true of the more anterior molars, no alveoli of this tooth are exposed.

FACE: As is typical of erinaceids, the nasals were long and narrow. Posteriorly, the nasals contact the frontals, anteriorly, they do not extend quite as far forward as the pre-

maxillae. The premaxilla is firmly attached to the maxilla behind it. The premaxilla-maxilla suture passes between I<sup>3</sup> and C<sup>1</sup> and curves upward and backward from there. No trace of a separate lacrimal bone is present. An extension from the weak supraorbital crest passes forward and downward around the lacrimal foramen and then turns posteriorly onto the crest of the zygoma. The opening of the lacrimal foramen is directed posteriorly but is visible in lateral view as in *Erinaceus* and *Amphechinus*.

Only the anterior end of the zygomatic arch formed by the maxilla is preserved. There the dorsoventral depth of the root is similar to that seen in *Erinaceus* and *Amphechinus*. On the anterolateral face of the arch is a shallow excavation for the insertion of snout musculature as in smaller species of the Galericinae. Forming the ventral border of this excavation is a well-defined ridge.

PALATE: Most of the palate is formed by the maxilla, the premaxilla accounting only for the region immediately adjacent to the incisors and anterior and lateral to the palatine fissures. At the posterior end of the palate is a triangular fenestrated palatine. Two fenestra are present in the palatine anterior to the transverse crest and to the left of the midline on F:AM 76703; the larger posterior one faces ventrally; the smaller anterior one is at the rear of a shallow anteroposteriorly directed groove and faces forward into this groove. The transverse crest extends unbroken across the rear of the palate opposite M<sup>3</sup>s. Piercing the transverse crest anteroposteriorly near its lateral extremes are the posterior palatine foramina. The palatine was developed behind the transverse crest for only a short distance.

Although *Untermannerix* has an elongated snout when compared with *Erinaceus* the positions of structures on the face and in the orbit of the skull are the same relative to the tooth row. The anterior opening of the infraorbital foramen is above the juncture between P<sup>3</sup> and P<sup>4</sup>; the anterior end of the orbit is above M<sup>1</sup>; and the base of the zygomatic arch is opposite M<sup>1</sup> and M<sup>2</sup>.

ORBITOTEMPORAL REGION: Only the maxilla is known in its entirety in this area. The

anterodorsal part of the alisphenoid and the anteroventral corner of the orbitosphenoid are preserved. None of the orbital fenestra that commonly pierce these two bones are to be seen but neither bone extends into a region where such fenestra are to be expected.

**MANDIBLE:** Beneath  $P_4$  is an anteroposteriorly elongated mental foramen. The angle projects for a short distance behind the main body of the jaw and is slightly inflected. The unfused midline symphysis of the mandible extends posteriorly to beneath  $P_3$ . The dorsal boundary of the symphysis dips posteriorly at an angle of 15 degrees with respect to the dorsal edge of the mandible. At its anterior end, the symphysis covers the entire medial surface of the mandible while it covers a progressively decreasing amount posteriorly. In the ventral region of the midline symphysis is a faint depression that may have been the site for the insertion of the geniohyoideus muscle. This groove appears to become larger anteriorly but the anteroventral region of the symphysis was not preserved on any of the specimens available.

The ascending ramus lies slightly labial to the midline of the mandible. Its anteroposterior length measured from the condyle is somewhat more than twice the maximum depth of the jaw. Until abruptly terminated by the horizontal, moderately concave dorsal edge, the anterior border of the ascending ramus extends almost vertically with no indication of curving posteriorly with height. On the leading edge of the ascending ramus is a sharp lateral flange that forms the anterior margin of the masseteric fossa. The central third of the flange projects posteriorly rather than laterally from the ascending ramus so that the most anterior part of the masseteric fossa is not visible in lateral view. On the medial side of the ascending ramus is a ridge that extends posterodorsally from the anteroventral corner of the ascending ramus to the condyle. The strength of this ridge remains constant over its entire length. Immediately beneath this ridge and midway between the anterior and posterior borders of the ascending ramus is the mandibular foramen, which is level with the tooth row. The condyle is well above the level of the tooth row. In posterior view, the margin of the

mandible tapers gradually from a maximum thickness at the condyle to a knife-edge thinness immediately above the angle. Above the condyle, the posterior border of the ascending ramus is as thin as a knife-edge. 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.

**REMARKS:** Because of the few specimens known of *Untermannerix copiosus*, elaborate statistical analysis of the sample is not justified. However, a few comments do seem in order. The largest  $M^2$  known (F:AM 76705) has an anteroposterior diameter 1.24 times that of the smallest (F:AM 76719). Specimens of only four other individuals are known and none is more than 1.14 times the smallest. However, with only a total of six individuals represented, it would be unjustified to separate F:AM 76705 from the other specimens at the specific rank on the basis of size alone. As pointed out by Simpson, Roe and Lewontin (1960, pp. 89–95) such extremes are to be expected in measurements of biological specimens belonging to a single species even when the coefficient of variation is small.

In the form of  $M^2$ , there are specimens with the buccal border of the tooth only slightly concave and others with a deep concavity; there are some with the metacrista directed posteriorly and others with it directed posterobuccally. With the small samples available, it is not possible to determine whether these differences are of specific significance or not. However, comparison with large samples of the modern European hedgehog, *Erinaceus europaeus*, suggests that the range of variation seen among these fossil specimens is no greater than that which occurs within a single, modern species.

Other teeth of this species, when compared with one another, reveal a similar pattern of variability between the specimens although the degree of difference is not as great as in the case of  $M^2$ .

#### TRIBE AMPHECHININI, NEW

**KNOWN DISTRIBUTION:** Stampian?—Vindobonian (?35–14 my., early? Oligocene—medial Miocene), Europe; Aquitanian—



TABLE 1  
Skull Measurements (in Millimeters) of *Untermannerix copiosus*

	F:AM 76703 (type)	F:AM 76705	F:AM 76719	F:AM 76720
Length, premaxilla border to post-palatine crest	14.8	—	—	—
Width of palate including M <sup>1</sup>	11.6	—	12.5	—
Width of muzzle at infraorbital foramen	8.7	—	10.5	—
Anteroposterior distance from anterior rim of orbit to infraorbital foramen				
Left	1.8	—	—	—
Right	1.8	—	—	1.9
Length, I <sup>1</sup> –M <sup>3</sup>				
Left	16.7	—	—	—
Right	16.3	—	—	—
Length, I <sup>3</sup> –M <sup>3</sup>				
Left	14.2	—	15.4	—
Right	13.8	—	—	—
Length, P <sup>4</sup> –M <sup>3</sup>				
Left	8.6	—	8.8	—
Right	8.8	—	—	—
I <sup>1</sup> , anteroposterior diameter				
Left	1.4	—	1.3	—
Right	1.4	—	1.2	—
I <sup>1</sup> , transverse diameter				
Left	1.0	—	0.9	—
Right	0.9	—	0.8	—
I <sup>2</sup> , anteroposterior diameter				
Left and Right	1.1	—	—	—
I <sup>2</sup> , transverse diameter				
Left and Right	0.8	—	—	—
I <sup>3</sup> , anteroposterior diameter				
Left	1.4	—	—	—
Right	1.3	—	—	—
I <sup>3</sup> , transverse diameter				
Left and Right	0.9	—	—	—
C <sup>1</sup> , anteroposterior diameter				
Left	1.5	—	1.6	—
Right	1.4	—	1.5	—
C <sup>1</sup> , transverse diameter				
Left	0.9	—	0.9	—
Right	0.9	—	1.0	—
P <sup>2</sup> , anteroposterior diameter				
Left	1.5	—	1.3	—
Right	1.5	—	1.2	—

TABLE 1—(Continued)

	F:AM 76703 (type)	F:AM 76705	F:AM 76719	F:AM 76720
P <sup>2</sup> , transverse diameter				
Left	0.9	—	0.9	—
Right	0.9	—	1.0	—
P <sup>3</sup> , anteroposterior diameter				
Left	1.7	—	1.6	—
Right	1.7	—	—	1.5
P <sup>3</sup> , transverse diameter				
Left	1.6	—	1.5	—
Right	1.6	—	—	1.6
P <sup>4</sup> , anteroposterior diameter				
Left	3.0	—	2.7	—
Right	3.0	—	2.7	2.7
P <sup>4</sup> , transverse diameter				
Left	2.7	—	2.9	—
Right	2.7	—	2.7	2.9
M <sup>1</sup> , anteroposterior diameter				
Left	3.0	3.4	3.0	—
Right	3.1	—	2.9	3.1
M <sup>1</sup> , transverse diameter				
Left	3.4	3.8	3.2	—
Right	3.3	—	3.1	3.3
M <sup>2</sup> , anteroposterior diameter				
Left	2.3	2.9	2.2	—
Right	2.4	—	2.2	—
M <sup>2</sup> , transverse diameter				
Left	2.8	3.7	3.0	—
Right	3.0	—	3.2	—
M <sup>3</sup> , anteroposterior diameter				
Left	0.8	—	0.8	—
Right	0.9	1.0	—	—
M <sup>3</sup> , transverse diameter				
Left	1.9	—	2.2	—
Right	1.9	2.4	—	—

Vallesian (20–11 my., early to late Miocene), Africa; ?32–?25 my. (medial—late Oligocene), Asia; medial Arikarean—late Barstovian (23–12.5 my., early to medial Miocene), North America.

DIAGNOSIS: Distinguished from the Erinaceini by the presence of an elongated I<sub>1</sub> and I<sup>1</sup>.

INCLUDED GENERA: *Amphechinus*, *Dimylechinus*, *Palaeoscaptor*, and *Parvericius*.

PARVERICIUS KOERNER, 1940

TYPE: *Parvericius montanus* Koerner, 1940.

TABLE 2  
Measurements (in Millimeters) of TTU 5014, Left P<sup>4</sup> of *Untermannex copiosus*

Anteroposterior diameter	2.6
Transverse diameter	2.6

KNOWN DISTRIBUTION: ?30–?25 my. (late Oligocene), Asia; medial Arikareean—late Barstovian (23–12.5 my., early to medial Miocene), North America.

DIAGNOSIS: Distinguished from *Palaeoscaptor* and *Stenoechinus* by the greater length of M<sup>1</sup> relative to its width; from *Palaeoscaptor* by absence of a metacone on M<sup>3</sup>; from *Gymnurechinus* by the presence of only one root on P<sub>2</sub>; from *Stenoechinus* by the paraconid being only slightly lower than the protoconid on P<sub>4</sub>; from *Amphechinus*, *Dimylechinus*, *Mioechinus*, *Palaeoscaptor*, and *Postpalerinaceus* by an anteroposteriorly compressed M<sub>1</sub> trigonid; from *Gymnurechinus*, *Palaeoscaptor*, and *Stenoechinus* by complete absence of a postcingulum or talonid on M<sub>3</sub>; from *Dimylechinus* by presence of M<sup>3</sup> and M<sub>3</sub>; from *Erinaceus*, *Atelerix*, *Aethechinus*, and *Hemiechinus* by the posteriorly inclined anterior edge of its ascending ramus; from *Amphechinus*, *Dimylechinus*, and *Palaeoscaptor* by greater elevation of the condyle; and from *Untermannex* by a relatively elongate angle on the mandible.

*Parvericius montanus* Koerner, 1940  
*Parvericius montanus* Koerner, 1940, p. 841.  
*Palaeoerinaceus minimus* Bohlin, 1942, p. 23.  
*Amphechinus* (*Palaeoerinaceus*) cf. *minimus* Sulimski, 1970, p. 64.

TYPE: YPM 13956, right maxilla fragment with P<sup>3</sup>–M<sup>3</sup> complete except for lingual halves of P<sup>3</sup>–<sup>4</sup>. (See Koerner, 1940, pl. 1, fig. 1a; Rich and Rasmussen, 1973, fig. 12a.)

TYPE LOCALITY AND STRATIGRAPHIC POSITION: (See Localities, Section 67.)

DIAGNOSIS: Only known species of genus.

REFERRED MATERIAL: T. b. 235, partial right mandible with nearly unworn P<sub>4</sub>–M<sub>3</sub>, and alveoli for C<sub>1</sub> and P<sub>2</sub> (type specimen of *Palaeoerinaceus minimus* Bohlin, 1942), (see Bohlin, 1942, figs. 3d, 6c, c', c'', 7e, e'; pl. 1, figs. 4, 7). T. b. 207, anteroventral part of ascending ramus and posterior part of horizontal ramus including alveolus for M<sub>3</sub>. T. b. 248, partial mandible missing anterior half of horizontal ramus, angle and dorsal tip of ascending ramus with alveoli for M<sub>2</sub> and M<sub>3</sub> (see Bohlin, 1942, fig. 3f). T. b. 561, edentulous mandible fragment with alveoli for C<sub>1</sub>–M<sub>3</sub>, lacking region anterior to C<sub>1</sub> and posterior to M<sub>3</sub> (see Bohlin, 1942, figs. 3e, e', 6d). (See Localities, Section 2.)

Z. Pal. MgM-III/24, partial right mandible with M<sub>2</sub> and M<sub>3</sub> (see Sulimski, 1970, fig. 2f, pl. 19 fig. 5). Z. Pal. MgM-III-25, partial right mandible with M<sub>1</sub>, M<sub>2</sub>, and posterior root of P<sub>4</sub> (see Sulimski, 1970, fig. 2e, pl. 19, fig. 6). Z. Pal. MgM-III/26, partial right mandible with P<sub>4</sub>–M<sub>2</sub> (see Sulimski, 1970, fig. 2d, pl. 19, fig. 7). (See Localities, Section 1.)

SDSM 64173-1 isolated right M<sub>1</sub>, . . .-2 isolated right M<sub>1</sub>, . . .-3 specimen destroyed, . . .-4 isolated left M<sub>1</sub>. SDSM 64174, isolated left M<sup>2</sup>. (See Localities, Section 4.)

LACM 23512, one isolated left M<sup>1</sup> and one isolated right M<sup>1</sup> plus a fragment of a third right upper molar. LACM 23513, isolated right P<sub>4</sub>. LACM 23514-1 isolated right M<sub>1</sub>, . . .-2 isolated right M<sub>1</sub>, and . . .-3 isolated

TABLE 3  
Measurements (in Millimeters) of Upper Molars of *Untermannex copiosus*

	F:AM 76721 Right M <sup>1</sup>	F:AM 76738 Right M <sup>2</sup>	F:AM 95813 Right M <sup>2</sup>	UMMP V61024 Right M <sup>3</sup>	UMMP V61025 Right M <sup>2</sup>
Anteroposterior diameter	3.1	2.3	2.5	0.9	2.4
Transverse diameter	3.5	2.9	3.4	2.0	3.0

TABLE 4  
Mandible Measurements (in Millimeters) of *Untermannerix copiosus*

	F:AM 76703	F:AM 76703	AMNH 86930	F:AM 76717	F:AM 76718	F:AM 76719	F:AM 76719	F:AM 76722
	Left (type)	Right (type)				Left	Right	
Mandible depth below P <sub>4</sub> anterior root	2.6	2.7	3.1 <sup>a</sup>	—	—	2.9	3.1	—
Mandible depth below M <sub>1</sub> anterior root	3.0	3.1	2.9 <sup>a</sup>	—	—	3.1	—	3.0
Mandible depth below M <sub>2</sub> posterior root	3.3	3.0	—	—	2.8	3.7	—	—
Mandible depth below M <sub>3</sub> root	3.3	3.0	—	4.1	—	—	—	—
M <sub>1-3</sub> , length	7.3	7.3	—	—	—	7.8 <sup>b</sup>	—	—
I <sub>1</sub> , depth at alveolar rim	—	1.1	—	—	—	—	1.0	—
I <sub>1</sub> , transverse diameter	—	0.9	—	—	—	—	0.8	—
I <sub>2</sub> , anteroposterior diameter	—	1.3	—	—	—	—	—	—
I <sub>2</sub> , transverse diameter	—	1.1	—	—	—	—	—	—
C <sub>1</sub> , anteroposterior diameter	—	1.9	—	—	—	—	2.0	—
C <sub>1</sub> , transverse diameter	1.2	1.2	—	—	—	—	1.0	—
P <sub>3</sub> , anteroposterior diameter	1.5	1.3	1.5	—	—	1.4	1.3	—
P <sub>3</sub> , transverse diameter	1.2	1.2	1.1	—	—	1.1	—	—
P <sub>4</sub> , anteroposterior diameter	2.2	2.3	2.2	—	—	2.5	2.5	—
P <sub>4</sub> , transverse diameter	1.4	1.5	1.7	—	—	1.6	1.6	—
M <sub>1</sub> , anteroposterior diameter	3.2	3.3	2.9	—	3.0	3.3 <sup>b</sup>	—	—
M <sub>1</sub> , trigonid length	1.6	1.6	1.5	—	1.6	1.5 <sup>b</sup>	—	—
M <sub>1</sub> , trigonid width	2.2	2.2	1.8	—	1.9	2.2	—	—
M <sub>1</sub> , talonid width	2.3	2.3	1.9	—	2.0	2.3	—	—
M <sub>2</sub> , anteroposterior diameter	2.6	2.7	—	—	—	2.8	—	2.9
M <sub>2</sub> , trigonid length	1.4	1.4	—	—	—	1.4	—	1.5
M <sub>2</sub> , trigonid width	1.9	2.0	—	—	—	2.1	—	2.1
M <sub>2</sub> , talonid width	1.9	1.9	—	—	—	2.1	—	2.0
M <sub>3</sub> , anteroposterior diameter	1.3	1.3	—	1.5	—	—	—	—
M <sub>3</sub> , trigonid width	0.9	0.9	—	1.3	—	—	—	—

<sup>a</sup> Minimum measurement owing to damage.  
<sup>b</sup> Measurement suspect owing to damage.

left M<sub>1</sub>. SDSM 64182-2 isolated right M<sup>1</sup>, . . . -6 isolated left M<sub>1</sub>, and . . . -8 isolated right M<sub>2</sub> (see figs. 4a, b, and c, respectively,

in Macdonald, 1972). (See Localities, Section 3.)

SDSM 7889, isolated right M<sup>2</sup>. (See Localities, Section 44.)

ROM 7624, isolated right M<sub>2</sub> (see Storer, 1975, fig. 2g). ROM 7628, isolated right talonid of M<sub>1</sub> (see Storer, 1975, fig. 2e). ROM 7626, lingual half of isolated left M<sup>1</sup>. ROM 7629, isolated left M<sup>1</sup> (see Storer, 1975, fig. 3a). ROM 7630, isolated right M<sup>2</sup> (see Storer, 1975, fig. 3c). ROM 7631, isolated left M<sup>2</sup> (see Storer, 1975, fig. 3b). ROM 7671, isolated left P<sub>4</sub> (see Storer, 1975, fig. 2a).

TABLE 5  
Measurements (in Millimeters) of P<sub>4</sub>s of  
*Untermannerix copiosus*

	F:AM 76735	UMMP V61023	UMMP V61030
Anteroposterior diameter	2.2	2.1	2.0
Transverse diameter	1.7	1.7	1.5

TABLE 6  
Measurements (in Millimeters) of Lower Molars of *Untermannerix copiosus*

	F:AM 76716	F:AM 76723	F:AM 76734	F:AM 76740	UMMP V55722
	M <sub>2</sub>	M <sub>2</sub>	M <sub>2</sub>	M <sub>2</sub>	M <sub>1</sub>
Anteroposterior diameter	3.1	2.8	2.7	2.8	3.1
Trigonid length	1.6	1.3	1.5	1.6	1.6
Trigonid width	2.1	2.0	1.9	2.0	1.9
Talonid width	2.1	2.1	1.8	2.0	2.1

ROM 7673, isolated right talonid of M<sub>1</sub> (see Storer, 1975, fig. 2f). ROM 7679, right M<sub>3</sub> in mandible fragment with alveoli for M<sub>2</sub> and anteroventral region of masseteric fossa (see Storer, 1975, fig. 2h). (See Localities, Section 37.)

MPUM 1551, right mandible with highly worn P<sub>4</sub>-M<sub>3</sub>, tip of I<sub>1</sub> root, fragment of C<sub>1</sub>, P<sub>3</sub> alveolus, horizontal ramus complete from C<sub>1</sub> to base of leading edge of the ascending ramus. (See Localities, Section 10.)

UCM 29507, isolated left M<sub>1</sub>. (See Localities, Section 24.)

UCM 29853, isolated right M<sub>1</sub>. UCM 29955, left mandible with M<sub>1-3</sub>, posterior half of rear alveolus of P<sub>4</sub>, horizontal ramus complete from rear alveolus of P<sub>4</sub> to base of leading edge of ascending ramus. (See Localities, Section 26.)

UCM 32772, right mandible fragment with worn M<sub>2</sub> and alveolus for M<sub>3</sub>. (See Localities, Section 25.)

UW 4065, isolated right M<sub>2</sub>. (See Localities, Section 19.)

F:AM 76704, complete left mandible, edentulous except for P<sub>4</sub>. F:AM 76724, left mandible fragment with M<sub>2</sub>. F:AM 76725, right mandible fragment with M<sub>2-3</sub>. F:AM 76726, left mandible fragment with M<sub>2-3</sub>. F:AM 76727, right edentulous mandible fragment. F:AM 76728, right edentulous mandible fragment. F:AM 76729, isolated left M<sup>1</sup>. F:AM 76730, isolated left M<sup>1</sup>. F:AM 76736, buccal half of isolated left P<sup>4</sup>. F:AM 95180, fragment of right, edentulous mandible with alveoli for M<sub>2-3</sub>; horizontal ramus not preserved anterior to M<sub>2</sub>; angle and ascending ramus not preserved. UMMP V56569, left mandible lacking only P<sub>2</sub> and angle. UMMP V57331, left mandible fragment with I<sub>1</sub>, C<sub>1</sub>, P<sub>4</sub>; alveoli for I<sub>2</sub>, P<sub>3</sub>, M<sub>1</sub>; anterior alveolus for M<sub>2</sub>; and lacking the region posterior to the alveolus for the forward root of M<sub>2</sub>. UMMP V61026, isolated left M<sup>1</sup>. UMMP V61027, isolated right M<sub>2</sub>. UMMP V61029, isolated left M<sub>1</sub> (this specimen appears to have been etched by acid). UMMP V61031, isolated right M<sub>2</sub>. UMMP V61033, isolated

TABLE 7  
Measurements (in Millimeters) of the Upper Dentition of *Parvericius montanus*<sup>a</sup>

	F:AM 76729	F:AM 76730	F:AM 76736	F:AM 76737	LACM 23512- 18	ROM 7629	ROM 7630	ROM 7631	UCM 30850	SDSM 7889
P <sup>4</sup> , anteroposterior diameter	—	—	2.1	—	—	—	—	—	—	—
M <sup>1</sup> , anteroposterior diameter	2.1	—	—	—	—	2.0	—	—	2.0	—
M <sup>1</sup> , transverse diameter	2.3	2.1	—	—	2.2	2.4	—	—	2.5	—
M <sup>2</sup> , anteroposterior diameter	—	—	—	1.7	—	—	1.7	1.6	—	1.5
M <sup>2</sup> , transverse diameter	—	—	—	2.2	—	—	2.2	2.2	—	2.2

<sup>a</sup> Specimens previously mentioned in Rich and Rasmussen (1973, table 6) are not listed in this table.

TABLE 8  
Mandible Measurements (in Millimeters) of *Parvericius montanus*<sup>a</sup>

	F:AM 76724	F:AM 76725	F:AM 76726	F:AM 76727	F:AM 76728	F:AM 95180	LACM 23513	ROM 7671	ROM 7679	UCM 29171	UCM 32772
Mandible depth below M <sub>1</sub> anterior root	—	—	—	—	2.1	—	—	—	—	2.1	—
Mandible depth below M <sub>2</sub> posterior root	2.0	2.5	2.3	2.3	2.4	—	—	—	—	—	1.5
Mandible depth below M <sub>3</sub> root	—	2.4	2.3	2.0	2.3	2.5	—	—	2.3	—	1.5
P <sub>4</sub> , anteroposterior diameter	—	—	—	—	—	—	1.5	1.4	—	1.4	—
P <sub>4</sub> , transverse diameter	—	—	—	—	—	—	1.0	1.1	—	0.9	—
M <sub>1</sub> , anteroposterior diameter	—	—	—	—	—	—	—	—	—	2.1	—
M <sub>1</sub> , trigonid length	—	—	—	—	—	—	—	—	—	1.0	—
M <sub>1</sub> , trigonid width	—	—	—	—	—	—	—	—	—	1.2	—
M <sub>1</sub> , talonid width	—	—	—	—	—	—	—	—	—	1.3	—
M <sub>2</sub> , anteroposterior diameter	1.9	1.9	1.9	—	—	—	—	—	—	—	1.5
M <sub>2</sub> , trigonid length	1.0	1.0	—	—	—	—	—	—	—	—	0.8
M <sub>2</sub> , trigonid width	1.4	1.4	—	—	—	—	—	—	—	—	1.0
M <sub>2</sub> , talonid width	1.3	1.3	—	—	—	—	—	—	—	—	0.9
M <sub>3</sub> , anteroposterior diameter	—	0.8	0.8	—	—	—	—	—	0.9	—	—
M <sub>3</sub> , trigonid width	—	0.7	0.7	—	—	—	—	—	0.6	—	—

<sup>a</sup> Specimens previously mentioned in Bohlin (1942), Sulimski (1970), and Rich and Rasmussen (1973, table 7) not listed in this table.

right P<sub>4</sub>. UMMP V61034, isolated right M<sup>1</sup>. (See Localities, Section 39.)

UMMP V61022, isolated left M<sub>1</sub>. (See Localities, Section 40.)

UCM 30850, isolated right M<sup>1</sup>. (See Localities, Section 13.)

UCM 29171, right mandible fragment with worn P<sub>4</sub>, M<sub>1</sub> and trigonid of M<sub>2</sub>. (See Localities, Section 27.)

DESCRIPTION: One additional bit of information can be added to the description of this species by Rich and Rasmussen (1973): a single, anteroposteriorly elongated lingual root is present beneath the protocone and hypocone on M<sup>2</sup>. Otherwise, the comments of Rich and Rasmussen will not be elaborated upon.

REMARKS: Isolated M<sub>1</sub>s and M<sub>2</sub>s of *Parvericius montanus* and *Stenoechinus tantalus* cannot be distinguished from one another by any criterion known to me. On the other hand, P<sub>4</sub> and M<sub>3</sub> of these two species may be readily distinguished. If M<sup>1</sup> and M<sup>2</sup> tentatively regarded as *S. tantalus* by Rich and Rasmussen (1973, pp. 14–16) are correctly

identified, these teeth, too, are quite distinct in the two species. At the present time, the presence of *P. montanus* has been established by the presence of at least one of these diagnostic teeth at seven different localities in North America and *S. tantalus* is similarly known at two. The two species are not known to occur together at any of these localities. As a matter of practicality, the isolated M<sub>1</sub>s and M<sub>2</sub>s that might belong to either species have been placed in the species which is known to occur at the same locality.

SPECIMENS INCORRECTLY REFERRED TO *Parvericius*: L. Macdonald (1972) identified a collection of isolated teeth from ant-hills derived from the early Miocene Monroe Creek Formation of South Dakota. At the time she did her work, no specimens of the mandible of *Parvericius montanus* had been recognized. Therefore, her proper assignment of the majority of lower molars which she referred to this species was a commendable effort. However, two lower molars she placed in this species now appear to belong elsewhere. SDSM 64182-4 (see L. Macdon-

TABLE 9  
Measurements (in Millimeters) of Isolated Lower Molars of *Parvericius montanus*<sup>a</sup>

	LACM 23514-1, M <sub>1</sub>	LACM 23514-2, M <sub>1</sub>	LACM 23514-3, M <sub>1</sub>	ROM 7624, M <sub>2</sub>	ROM 7628, M <sub>1</sub>	ROM 7673, M <sub>1</sub>	SDSM 64173-1, M <sub>1</sub>	SDSM 64173-2, M <sub>1</sub>	SDSM 64173-4, M <sub>1</sub>	SDSM 64182-6, M <sub>1</sub>	SDSM 64182-8, M <sub>2</sub>	UW 4065, M <sub>2</sub>
Anteroposterior diameter	2.3	2.3	—	1.8	—	—	2.2	—	2.1	2.1	1.7	1.9
Trigonid length	1.2	1.2	1.1	1.0	—	—	1.1	1.1	1.1	1.1	0.9	0.9
Trigonid width	1.5	1.6	1.5	1.2	—	—	1.2	1.3	1.4	1.3	1.2	1.4
Talonid width	1.5	1.5	—	1.2	1.5	1.6	1.2	—	1.5	1.4	1.2	1.4

<sup>a</sup> Specimens previously mentioned in Rich and Rasmussen (1973, table 7) not listed in this table.

ald, 1972, fig. 4d) is an M<sub>5</sub> of *Peratherium* sp. LACM 23515-4 is a slightly damaged lower molar of a non-erinaceid, perhaps a talpid.

Martin identified a number of specimens from the Batesland Formation of western Bennett County, South Dakota as *Parvericius* sp. cf. *P. montanus*. He regards this lithic unit as medial Hemingfordian (Martin, 1976, pp. 94–96). The one figured specimen of his sample (SDSM 7538, see Martin, 1976, fig. 3a) is clearly not an erinaceid M<sup>1</sup> owing to the presence of a prominent metaconule; perhaps it is a plesiosoricid. I have been unable to examine the other specimens referred to *P. montanus* by Martin and thus cannot comment on the correctness of their assignment to the species although certainly it is to be expected in the Batesland Formation.

#### AMPHECHINUS AYMARD, 1850

TYPE: *Amphechinus arvernensis* (de Blainville, 1840).

KNOWN DISTRIBUTION: Stampian?—Vindobonian (?35–14 my., early? Oligocene—medial Miocene), Europe; Aquitanian—Vallesian (20–11 my., early to late Miocene), Africa; ?32–?25 my. (medial—late Oligocene), Asia; medial Arikareean—medial Barstovian (23–14 my., early to medial Miocene), North America.

DIAGNOSIS: Distinguished from *Palaeoscaptor* and *Stenoechinus* by the greater length of M<sup>1</sup> relative to its width; from *Pa-*

*laeosaptor* by absence of a metacone on M<sup>3</sup>; from *Gymnurechinus* by the presence of only one root on P<sub>2</sub>; from *Stenoechinus* by the paraconid being only slightly lower than the protoconid on P<sub>4</sub>; from *Aethechinus*, *Atelerix*, *Erinaceus*, *Gymnurechinus*, *Hemiechinus*, *Paraechinus*, *Parvericius*, and *Stenoechinus* by an anteroposteriorly elongated trigonid on M<sub>1</sub>; from *Gymnurechinus*, *Palaeoscaptor*, and *Stenoechinus* by absence of a talonid or postcingulum on M<sub>3</sub>; from *Dimylechinus* by presence of M<sup>3</sup> and M<sub>3</sub>; from *Erinaceus*, *Atelerix*, *Aethechinus*, and *Hemiechinus* by the posteriorly inclined anterior edge of its ascending ramus; from *Aethechinus*, *Atelerix*, *Erinaceus*, *Gymnurechinus*, *Hemiechinus*, *Paraechinus*, *Parvericius*, *Postpalerinaceus*, and *Untermannerix* by the lesser elevation of the condyle; and from *Untermannerix* by a relatively elongate angle on the mandible.

*Amphechinus horncloudi*  
(J. R. Macdonald, 1970),  
Rich and Rasmussen (1973)

*Palaeoerinaceus horncloudi* J. R. Macdonald, 1970, p. 20.

*Amphechinus horncloudi* Rich and Rasmussen, 1973, p. 22.

TYPE: SDSM 62113, fragment of right mandible with P<sub>2</sub>–M<sub>1</sub>, damaged C<sub>1</sub>, roots of I<sub>1–2</sub>, and anterior root of M<sub>2</sub>. (See J. R. Mac-



donald, 1970, fig. 5; Rich and Rasmussen, 1973, fig. 7b).

TYPE LOCALITY AND STRATIGRAPHIC POSITION: (See Localities, Section 3.)

DIAGNOSIS: Distinguished from other species of *Ampechinus* by the talonid being greater in width than the trigonid on  $P_4$ .

REFERRED MATERIAL: SDSM 6278, fragment of left ramus with damaged  $M_1$ , alveoli for  $P_4$ ,  $M_2$ , and  $M_3$ . (See Localities, Section 5.)

SDSM 64172, isolated right  $M^1$  (see L. Macdonald, 1972, fig. 5b). (See Localities, Section 4.)

LACM 23510, isolated left  $M^1$ . LACM 23511, one isolated left  $M_2$  and one isolated right  $M_2$ . SDSM 64180, left  $P^4$  (see L. Macdonald, 1972, fig. 5a). (See Localities, Section 3.)

KU 18097, left maxilla fragment with  $P^3$ ,  $P^4$  (except metacrista),  $M^1$ , and anterior alveoli of  $M^2$  (see Rich and Rasmussen, 1973, fig. 8). KU 18405, right  $P^4$  fragment. (See Localities, Section 11.)

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. (See Rich and Rasmussen, 1973, fig. 7c, 9.) (See Localities, Section 7.)

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 right palate behind  $P^2$ ; casts of olfactory bulbs, chambers for ethmoturbinals, and left maxillary sinus exposed. (See Rich and Rasmussen, 1973, fig. 10.) (See Localities, Section 6.)

UCM 30735, isolated left  $P_4$ . (See Localities, Section 12.)

UNSM 11674, left mandible fragment with  $I_1$ ,  $P_4$ ,  $M_2$ , and  $M_3$ ; alveoli for  $I_2$ ,  $C_1$ ,  $P_2$ , and  $M_1$ ; and lacking angle and dorsal part of ascending ramus. (See Localities, Section 14.)

DESCRIPTION: Except for  $M_2$ , all known elements of this species have been described by Rich and Rasmussen (1973) and their comments are not repeated here.

$M_2$ : The length of the trigonid is nearly two-thirds the length of the tooth. The length

TABLE 10  
Measurements (in Millimeters) of  $M^1$  of  
*Ampechinus hornclaudi*

	LACM 23510	SDSM 64172
Anteroposterior diameter	—	3.1
Transverse diameter	3.7	3.4

of the trigonid is five-sixths its width. Subequal in height with the metaconid, the paraconid is noticeably larger in basal dimensions. The metaconid is lingual to the protoconid and the two cusps are linked by a protolophid that, when viewed posteriorly, has a right angle V-shaped profile. Except for a slight swelling at the anterior tip of the paralophid, there is no sign of a paraconid in occlusal view. The paralophid extends anterolingually from the protoconid, terminating anterior and slightly buccal to the metaconid. In lateral view, the paralophid has a V-shaped profile, the angle between the two segments being obtuse but close to a right angle, and the lingual segment that terminates at the paraconid is nearly horizontal. Placed at the anterolingual corner of the tooth, the paraconid in lingual view is anterodorsally inclined at an angle of about 70 degrees with respect to the vertical metaconid.

Width of the talonid is four-fifths that of the trigonid. Entoconid and hypoconid are placed at the extreme posterior corners of the tooth. Taller of the talonid cusps, the entoconid is approximately equal to the paraconid in height. The entoconid is posterior to the metaconid and the hypoconid is slightly more lingual than the protoconid. In anterior view, the buccal margin of the protoconid is straight and that of the hypoconid is buccally convex. Extending anterolingually from the hypoconid, the cristid obliqua abuts against the posterior wall of the trigonid at a point slightly lingual to the tip of the protoconid. A low entocristid closes the talonid basin lingually. A well-developed narrow cingulum is developed along the entire length of the prevallid. Behind the hypoconid, the postcingulum is inclined dorsomedially so

TABLE 11  
Mandible Measurements (in Millimeters) of *Amphechinus horncloudi*<sup>a</sup>

	SDSM 62113 (type)	LACM 23511-1	LACM 23511-3	SDSM 6278	UCM 30735	UNSM 11674
Mandible depth below P <sub>3</sub>	—	—	—	—	—	4.8
Mandible depth below M <sub>1</sub> anterior root	4.0	—	—	—	—	5.6
Mandible depth below M <sub>2</sub> posterior root	—	—	—	—	—	6.0
Mandible depth below M <sub>3</sub> root	—	—	—	4.8	—	5.8
P <sub>3</sub> , anteroposterior diameter	2.7	—	—	—	—	—
P <sub>3</sub> , transverse diameter	1.1	—	—	—	—	—
P <sub>4</sub> , anteroposterior diameter	2.5	—	—	—	2.7	2.9
P <sub>4</sub> , transverse diameter	2.0	—	—	—	1.7	2.0
M <sub>1</sub> , anteroposterior diameter	3.6	—	—	—	—	4.9 <sup>b</sup>
M <sub>1</sub> , trigonid length	2.1	—	—	—	—	—
M <sub>1</sub> , trigonid width	2.3	—	—	—	—	—
M <sub>1</sub> , talonid width	2.3	—	—	2.4	—	—
M <sub>2</sub> , anteroposterior diameter	—	2.7	—	—	—	3.4
M <sub>2</sub> , trigonid length	—	1.7	—	—	—	2.0
M <sub>2</sub> , trigonid width	—	2.0	1.9	—	—	2.7
M <sub>2</sub> , talonid width	—	1.6	1.6	—	—	2.1
M <sub>3</sub> , anteroposterior diameter	—	—	—	—	—	1.2
M <sub>3</sub> , trigonid width	—	—	—	—	—	1.1

<sup>a</sup> KU 18162, mentioned previously in Rich and Rasmussen (1973, table 4), is not listed in this table.  
<sup>b</sup> Maximum estimate, measurement is from the posterior edge of P<sub>4</sub> to anterior edge of M<sub>2</sub>.

that it terminates at the apex of the postcris-  
tid midway between that cusp and the ento-  
conid.

?*AMPHECHINUS*  
FORM 1

MATERIAL: ROM 7625, isolated right M<sub>1</sub>  
talonid (see Storer, 1975, fig. 3e). ROM 7627,  
isolated left talonid (see Storer, 1975, fig.  
3d). (See Localities, Section 37.)

REMARKS: In all comparable aspects,  
these two specimens are indistinguishable  
from the talonid of M<sub>1</sub> of *Amphechinus horn-*  
*cloudi*. The similarity is so great that noth-

TABLE 12  
Talonid Width (in Millimeters) of M<sub>1</sub> of  
*?Amphechinus*

ROM 7625	ROM 7627
2.4	2.4

ing can be added or need be changed in the  
description of the talonid of M<sub>1</sub> of *A. horn-*  
*cloudi* in Rich and Rasmussen (1973) to make  
it applicable to these specimens. No other  
erinaceine known from North America has  
such a large talonid on the lower molars.

Molar talonids of brachyericines, unlike  
these specimens, lack a postcingulum.

FORM 2

MATERIAL: UF 18417, isolated right M<sub>2</sub>.  
(See Localities, Section 15.)

TABLE 13  
Measurements (in Millimeters) of UF 18417, M<sub>2</sub>  
of *?Amphechinus*

Anteroposterior diameter	2.7
Trigonid length	1.6
Trigonid width	1.7 <sup>a</sup>
Talonid width	1.6

<sup>a</sup>Minimum estimate, actual width slightly greater.

REMARKS: This specimen has been described and compared at length by Rich and Patton (1975) and their comments are not repeated here. It is sufficient to note that this tooth is quite similar in size as well as morphology to LACM 23511-1, an isolated  $M_2$  of *Amphechinus horncloudi* from the Monroe Creek Formation of South Dakota mentioned above.

# TRIBE UNCERTAIN

*STENOECHINUS* RICH AND RASMUSSEN, 1973

TYPE: *Stenoechinus tantalus* Rich and Rasmussen, 1973.

KNOWN DISTRIBUTION: Medial Arikarean—Hemingfordian (23–16 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  $M^1$  relative to its length; from *Amphechinus*, *Dimylechinus*, *Palaeoscaptor*, and *Parvericius* by a shorter  $I_1$  root; from all other erinaceines by a reduced paraconid lower than the metaconid and markedly lower than the protoconid; from *Amphechinus*, *Dimylechinus*, *Mioechinus*, *Palaeoscaptor*, and *Postpalerinaceus* by an anteroposteriorly compressed  $M_1$  trigonid; from *Aethechinus*, *Amphechinus*, *Atelerix*, *Erinaceus*, *Hemiechinus*, *Mioechinus*, *Paraechinus*, *Parvericius*, and *Postpalerinaceus* by the presence of a prominent postcingulum on  $M_3$ ; from *Palaeoscaptor* by a talonid on  $M_3$  reduced to a prominent postcingulum; and from *Dimylechinus* by the presence of  $M_3$ .

# *Stenoechinus tantalus*

Rich and Rasmussen, 1973

TYPE: 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  $M_1$ . (See Rich and Rasmussen, 1973, fig. 2a-c.)

TYPE LOCALITY AND STRATIGRAPHIC POSITION: (See Localities, Section 11.)

TABLE 14  
Measurements (in Millimeters) of Lower Dentition  
of *Stenoechinus tantalus*<sup>a</sup>

	UCM 26754	UCM 27162	UCM 27702	UCM 31938
Mandible depth below				
$M_2$ posterior root	—	—	1.8	—
$P_4$ , anteroposterior diameter	—	1.2	—	—
$P_4$ , transverse diameter	—	1.0	—	—
$M_1$ , anteroposterior diameter	2.5	—	—	—
$M_1$ , trigonid length	1.5	—	—	1.2
$M_1$ , trigonid width	1.3	—	—	1.3
$M_1$ , talonid width	1.5	—	—	—
$M_2$ , anteroposterior diameter	—	—	1.6	—
$M_2$ , trigonid length	—	—	0.8	—
$M_2$ , trigonid width	—	—	1.1	—
$M_2$ , talonid width	—	—	1.0	—

<sup>a</sup> Specimens mentioned previously in Rich and Rasmussen (1973, table 2) not listed in this table.

DIAGNOSIS: Only known species of genus.

REFERRED MATERIAL: KU 18002, left mandible fragment with  $P_4$ ,  $M_1$ , and that part of the mandible immediately below these two teeth (see Rich and Rasmussen, 1973, fig. 3). KU 18003, right mandible fragment with  $M_2$ , alveolus for  $M_3$ , 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 (see Rich and Rasmussen, 1973, fig. 4b). KU 18342, edentulous left mandible fragment with alveoli for  $M_2$  and  $M_3$ , 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  $M_2$  and  $M_3$ , lacking horizontal ramus anterior to  $M_1$  and all of mandible behind  $M_3$  alveolus. KU 18359, isolated right  $M^1$  (see Rich and Rasmussen, 1973, fig. 4a). KU 18404, isolated right  $M_1$  trigonid. (See Localities, Section 11.)

KU 18406, left mandible fragment with  $M_{1-3}$ , lacking ascending ramus and horizontal ramus anterior to  $M_1$ . (See Localities, Section 9.)

TABLE 15

Talonid width (in Millimeters) of ROM 7672,  $M_1$  of *Untermannerix* or  $M_2$  of *Amphechinus*

1.9
-----

UCM 26754, isolated left  $M_1$ . UCM 27162, left  $P_4$  in mandible fragment. UCM 31938, isolated left  $M_1$ . UCM 27702, mandible fragment with  $M_2$  and single alveolus for  $M_3$ . (See Localities, Section 28.)

DESCRIPTION: The Montana material of this species has been described by Rich and Rasmussen (1973, pp. 9–16) and their comments are not repeated here. Comparison of the Colorado material is given below in the Remarks section.

REMARKS: The presence of *S. tantalus* at the Slump (Fence) locality is established by UCM 27162, a mandible fragment containing a  $P_4$ . This tooth is similar to that of KU 18002 from the Tavenner Ranch locality no. 2 in that the protoconid is slender and its height is approximately one and one-fourth times the length of the tooth. The paraconid is missing but the cross sectional area of its base is small and the point of bifurcation between it and the base of the protoconid is even lower than on KU 18002. Taken together with the fact that the anterior edge immediately above the forward root which forms the base of the paraconid is more anteriorly inclined on this specimen than in KU 18002, it appears that the paraconid on this tooth was even lower than the already remarkably low condition of that cusp on KU 18002 and quite unlike any other erinaceine.

*Untermannerix* or *Amphechinus*,  
Species indeterminate

MATERIAL: ROM 7672, isolated right  $M_1$  or  $M_2$  talonid (see Storer, 1975, fig. 3f). (See Localities, Section 37.)

REMARKS: In all comparable features including size, this specimen cannot be distinguished from either the talonid of  $M_2$  of *Amphechinus horncloudi* or the talonid of  $M_1$  of *Untermannerix copiosus*.

TABLE 16

Measurements (in Millimeters) of KU 9988, isolated  $M_1$  of *Parvericius* or *Stenoechinus*

Anteroposterior diameter	2.3
Trigonid length	1.2
Trigonid width	1.3
Talonid width	1.4

*Parvericius* or *Stenoechinus*,  
Species indeterminate

MATERIAL: KU 9988, isolated left  $M_1$ . (See Wilson, 1960, fig. 13a, b.) (See Localities, Section 18.)

REMARKS: This specimen has had a checkered taxonomic history, having been allied with *Metechinus marslandensis* by Wilson (1960, p. 21) and with *Amphechinus* by Rich and Rich (1971, p. 44). It can be distinguished from  $M_1$  of either *Parvericius montanus* or *Stenoechinus tantalus* only by the presence of a prominent notch in the middle of the paralophid. This notch is reminiscent of the condition seen in some members of the Plesiosoricidae (e.g., *Plesiosorex*, *Met-erix*) and unlike erinaceids. However, on the plesiosoricids the notch is much narrower. In addition, this unworn tooth lacks any sign of a hypoconulid, which further militates against its being placed among the plesiosoricids.

ERINACEINAE,

Genus and Species indeterminate

MATERIAL: KU 18396, isolated right  $M^2$ . (See Rich and Rasmussen, 1973, fig. 17.) (See Localities, Section 8.)

DESCRIPTION: This specimen has been recently described by Rich and Rasmussen (1973, pp. 45–46) and their comments are not repeated here.

TABLE 17

Measurements (in Millimeters) of  $M^2$  of  
Erinaceinae, Genus and Species indeterminate,  
KU 18396

Anteroposterior diameter	1.5
Transverse diameter	2.4

REMARKS: This enigmatic specimen was accidentally destroyed since its description by Rich and Rasmussen (1973). The only information that may be added to the comparisons made by them is that *Parvericius montanus* differs from this specimen just as *Palaeoscaptor acridens* was previously known to do in that the postprotocrista and postmetaconule crista form one continuous crest rather than two short crests quite distinct from one another. Thus, this specimen remains as distinctive from other erinaceids as previously noted.

#### SUBFAMILY BRACHYERICINAE BUTLER, 1948

KNOWN DISTRIBUTION: Late Arikareean or Hemingfordian—Clarendonian (21–10 my., early—late Miocene), North America.

DIAGNOSIS: Distinguished from all other members of the Erinaceidae except the Ampechinini by enlarged  $I^1$  and  $I_1$ ; from all other members of the Erinaceidae by the presence of only two upper premolars and one lower premolar, height of the hypocone on  $P^4$  equal to or greater than that of the protocone, absence of a postcingulum on the lower molars, greater reduction of the mandibular angle, deep zygomatic arch, and ectotympanic completely enclosed within the auditory bulla; from all other members of the Erinaceidae except the Erinaceinae and *Proterix* by the presence of only two lower incisors; from all members of the Erinaceinae by the weak paraconid on  $P_4$ ; from all other members of the Erinaceidae except *Dimylechinus*, *Ampechinus*, *Palaeoscaptor* and some but not all specimens referred to *Mioechinus* and *Atelerix* by an anteroposteriorly expanded trigonid on  $M_1$ ; from all other members of the Erinaceidae except *Dimylechinus* by the absence of  $M^3$  and  $M_3$ ; and from all members of the Erinaceidae except the Erinaceinae and *Hylomys* by the development of the palatine posterior to the transverse crest of the palate.

#### BRACHYERIX MATTHEW, 1933

*Brachyerix* Matthew, 1933, in Matthew and Mook, 1933.

TYPE: *Brachyerix macrotis* Matthew, 1933 (Matthew and Mook, 1933).

KNOWN DISTRIBUTION: Late Arikareean or Hemingfordian—late Barstovian (21–12 my., early—medial Miocene), North America.

DIAGNOSIS: Distinguished from *Metechinus* by smaller size; nearly parallel lateral margins of basicranium (in ventral view), not converging posteriorly at large angle; larger, more inflated auditory bullae closer to one another; flange separating posterior and concave lateral surfaces of squamous region of zygoma; expansion of ventral tips of interparietal anteriorly between parietal and mastoid; lower partition formed by mastoid between stylomastoid and jugular foramina; postmetaconule crista joined to metacone rather than separated by a prominent notch on  $M^1$ ; trigonid of  $M_1$  more expanded anteroposteriorly; and anteroposterior diameter of  $M_2$  shorter relative to that of  $M_1$ .

#### *Brachyerix macrotis* Matthew, 1933

Figures 8–11

*Brachyerix macrotis* Matthew, 1933, in Matthew and Mook, 1933, p. 2, fig. 1, "*Brachyerix montanus*," *lapsus calami* by Matthew.

*Metechinus marslandensis* Meade, 1941, p. 43.

"*Brachyerix loomisi*," *lapsus calami* by Butler, 1956b, p. 72, table 10.

TYPE: AMNH 21335, uncrushed skull with right  $P^4$ – $M^2$ , left  $P^4$ ,  $M^2$ , roots of  $C^1$ ,  $P^3$ , and  $M^1$ ; and missing the premaxillae, central regions of the zygomae, anterior part of the nasals, and the anteropalatal region of the maxillae. (See Rich and Rich, 1971, figs. 3 and 4.)

TYPE LOCALITY AND STRATIGRAPHIC POSITION: (See Localities, Section 65.)

DIAGNOSIS: Larger species of genus; strong lingual cingulum on  $P^3$  extending from parastyle to posterior side of paracone; no  $P^3$  protocone.

REFERRED MATERIAL: FMNH P26399, type of *Metechinus marslandensis* Meade, 1941. Partial left mandible with  $M_{1-2}$ . (See Localities, Section 30.)

PU 16229, uncrushed skull lacking inci-

sors, right  $M^2$ , and zygomatic arches. (See Localities, Section 66.)

UCMP 86137, nearly complete, uncrushed skull with  $P^4$ – $M^2$ ; lacking only the nasals, premaxillae, and the anterior regions of the maxillae; associated with lower jaws complete on one side if not the other except for  $I_2$  and tip of  $I_1$  (see Rich and Rich, 1971, figs. 6–11). UCMP 94718, partial, uncrushed skull with most of snout except premaxillae, left  $C^1$ – $P^4$ , right  $P^3$ – $M^2$ , and right lateral and dorsal walls of braincase. UCMP 102634, partial right side of skull with  $C^1$ – $M^2$ , zygomatic arch, and lateral wall of braincase. UCM 21547, 29351, 29397, 29395, 29957, 29958, 29971, 29972, 32770, nine isolated right  $M_1$ s. UCM 21541, 21551, 29426, 29758, 32769, five isolated left  $M_1$ s. (See Localities, Section 24.)

“... A.C.M. Nos. 10459–10460, 10462–10482, 11325, 11315–11321, 11427–11430; R.O.M. Nos. 2078, 2079; U.W. 1072, 1073, 1075 [the actual University of Wyoming specimen numbers are U.W. Nos. 1702, 1703, 1705]; C.N.H.M. [=FMNH] Nos. PM 2130–2135, 2108–2124. These numbers include numerous isolated specimens of  $P^4$ – $M^2$  and  $M_{1-2}$ ” (Reed, 1960, p. 5). Reed originally referred these specimens to *Metechinus marslandensis*. CM 14959, right jaw with four posterior teeth, alveolus for a small tooth between broken anterior end of jaw and four posterior teeth; root of enlarged incisor; jaw broken posteriorly immediately behind  $M_2$  (see Rich and Rich, 1971, fig. 12). KU 18005, left mandible fragment with  $P_4$ ,  $M_1$ , missing those parts of the mandible anterior and posterior to these two teeth. (See Localities, Section 25.)

F:AM 74965, crushed skull with right  $C^1$ – $M^1$ , roots of  $M^2$ , left  $M^{1-2}$ , roots of  $P^4$ ; and missing the premaxillae and anterior part of the nasals (see Rich and Rich, 1971, fig. 13). (See Localities, Section 21.)

F:AM 74964, left mandible with worn  $M_{1-2}$ ; alveoli for three small teeth between  $I_1$  and  $M_1$ ; cross section of alveolus for enlarged  $I_1$ ; mandible broken posteriorly at mandibular foramen, anteriorly immediately in front of  $I_2$ . (See Localities, Section 22.)

F:AM 76693, left mandible with  $M_2$ , alveoli for four teeth anterior to  $M_2$ , broken anteriorly immediately in front of  $I_2$  alveolus exposing cross section of enlarged  $I_1$  alveolus, and lacking coronoid process and angle. (See Localities, Section 23.)

F:AM 76695, edentulous jaw with alveoli for  $M_{1-2}$ , broken anteriorly through the anterior root of  $M_1$  and posteriorly behind the posterior root of  $M_2$ . (See Localities, Section 16.)

F:AM 76713, left mandible with  $M_{1-2}$ , root of  $I_1$ , alveoli for  $I_2$ ,  $C_1$ , and  $P_4$ . F:AM 76714, right mandible fragment with  $M_{1-2}$ . (See Localities, Section 17.)

USGS(PSB,D) Fossil Vertebrate Specimen D719A, left mandible with worn  $M_{1-2}$ ; alveoli for three small teeth anterior to  $M_1$ ; cross section of enlarged incisor; mandible broken posteriorly a short distance behind  $M_2$ , anteriorly through alveolus of  $I_2$ . (See Localities, Section 29.)

UNSM 11675, right mandible fragment with  $P_4$ – $M_2$ ; alveoli for  $I_1$ – $C_1$ ; lacking dorsal and posterior parts of the ascending ramus. (See Localities, Section 20.)

DESCRIPTION: This species was described by Rich and Rich (1971) and their comments are not repeated here. Subsequent discoveries and re-examination of previously known material, however, has brought to light one modification to the description of the basicranial region and four to the tympanic region.

BASE OF THE CRANIUM: On the external surface of the medial wall of the bulla, immediately anterodorsal to the medial end of the sulcus for the eustachean canal is the opening for a small canal that passes dorsally into the braincase. On figure 17a in Rich and Rich (1971), this foramen is the prominent one at the base of the tip of the arrow labeled EUST, the sulcus for the eustachean canal being the lightly indicated, broad depression immediately lateral to this foramen. This foramen is labeled UF in figure 11a of this report. Such a canal is not present in modern erinaceids although the bone in this region may be perforated by tiny foramina that appear to end blindly.

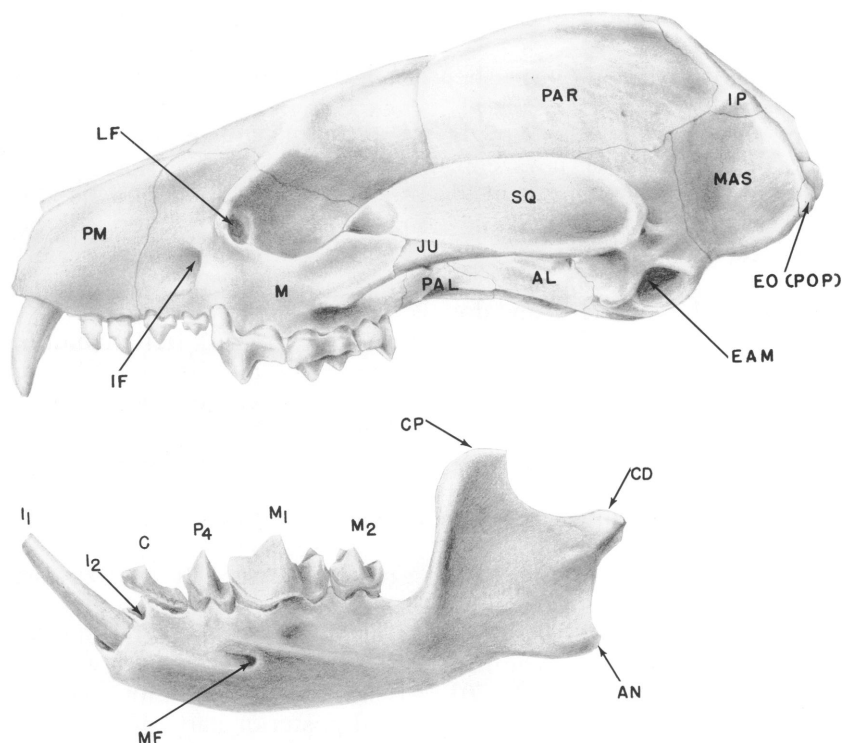


FIG. 8. *Brachyerix macrotis*, reconstruction of skull and mandible in lateral view based on AMNH 21335 (type specimen), F:AM 74965, UCMP 86137, a specimen of *Metechinus nevadensis*, UCMP 29600 (type specimen) and two specimens of *Metechinus amplior*, F:AM 74923 (type specimen) and UMMP V57332. (Modified from Rich and Rich, 1971, fig. 1.) Approximately  $\times 4$ .

**TYMPANIC REGION:** Rich and Rich (1971, p. 35) described the ventral, horizontal surface of the auditory bulla of *Brachyerix macrotis* as being a distinctly double-walled structure with a layer of cancellous bone separating two layers of compact bone. However, in *Metechinus amplior*, new species the ectotympanic occupies approximately the same position as what was interpreted as the inner wall of compact bone in *B. macrotis*. If this structure in *B. macrotis* is correctly interpreted as the ectotympanic, then that bone is completely enclosed ventrally by the bulla formed by the sphenoid and periotic, being exposed to view only at the external auditory meatus where the most lateral parts of this element may be seen. The suture between the sphenoid and periotic can

be seen running mediolaterally in the roof of the tympanic cavity just anterior to the promontorium on PU 16229, a specimen unavailable to Rich and Rich at the time of their original study. Medially, the suture curves to a posteromedial orientation and is visible on the crest of a strut that abuts the medial wall of the bulla.

Rich and Rich (1971, p. 37) reported that the stapedia artery passed out of a bony tube, through the stapes, and into another tube. On PU 16229, the stapedia artery passed through the obturator foramen of the stapes enclosed in a delicate bony intercrural canal. The presence or absence of a bony intercrural canal may have been a feature subject to individual variation in *Brachyerix macrotis* as Doran noted in a number of mod-



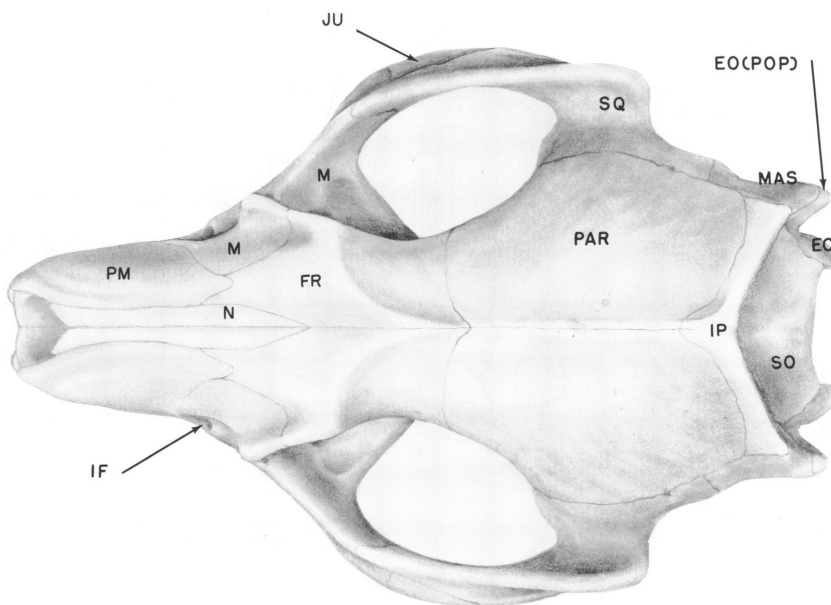


FIG. 9. *Brachyerix macrotis*, reconstruction of skull in dorsal view based on same specimens as used for figure 8. (Modified from Rich and Rich, 1971, fig. 2a.) Approximately  $\times 4$ .

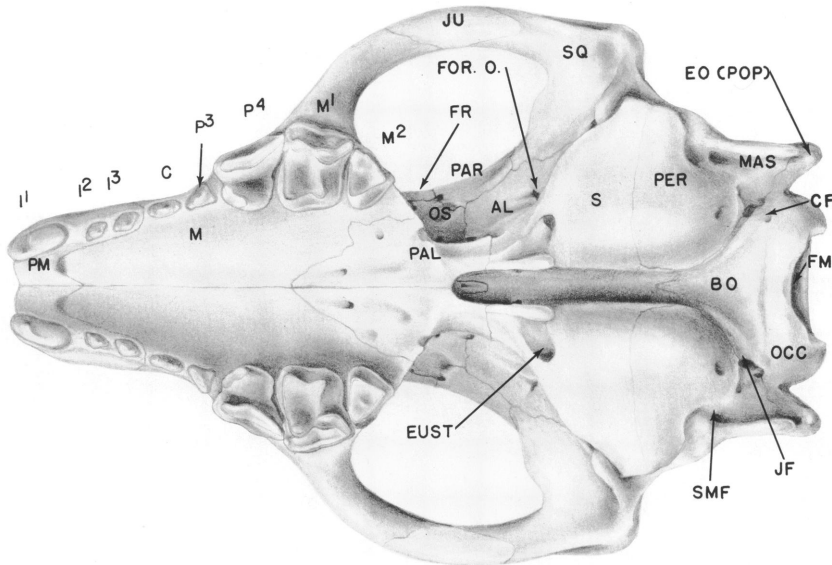


FIG. 10. *Brachyerix macrotis*, reconstruction of skull in ventral view based on same specimens as used for figure 8. (Modified from Rich and Rich, 1971, fig. 2b.) Approximately  $\times 4$ .

ern rodent species (*Dipus aegyptius*, *Capromys pilorides*, *Dasyprocta aguti*, *Cavia caprera*, see Doran, 1879, pp. 414–417).

An incision into the tube for the Vidian ramus (TVR in fig. 17a, Rich and Rich, 1971) on AMNH 21335 revealed that the “tube”

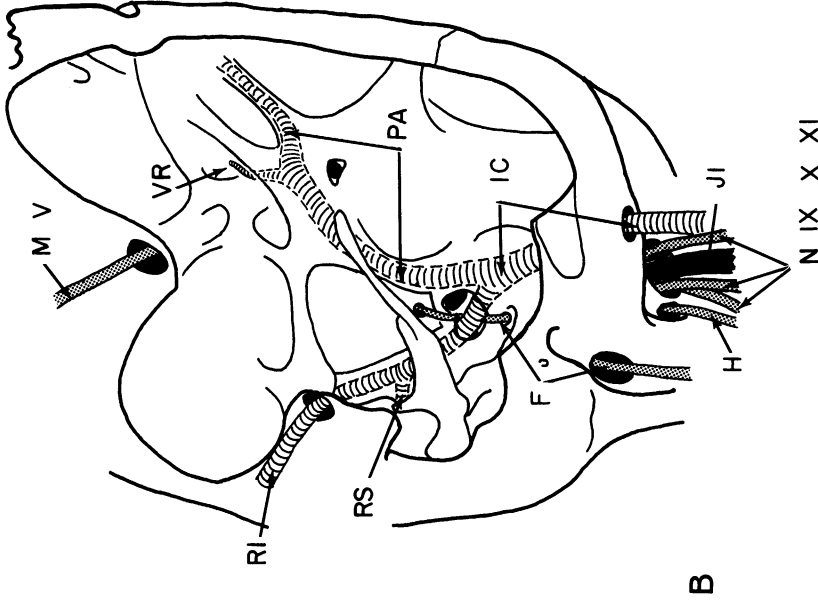
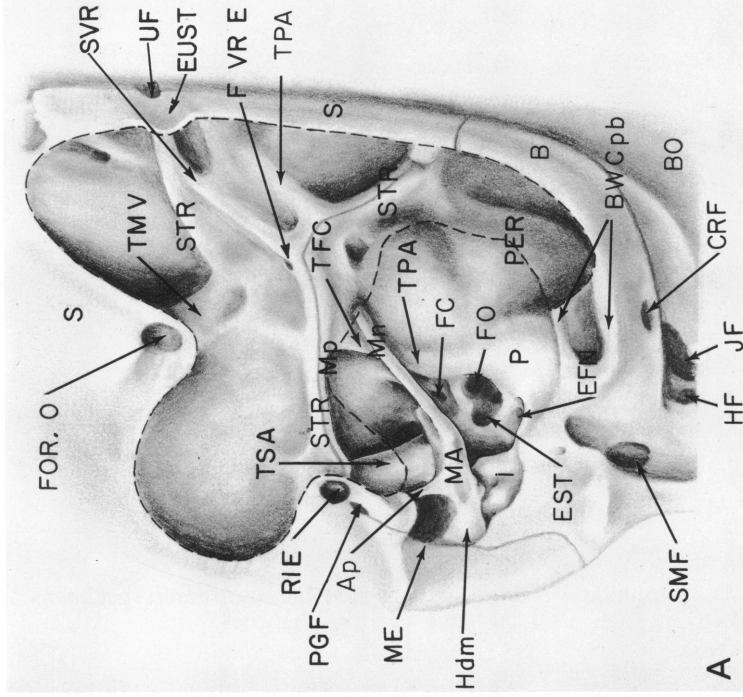


FIG. 11. *Brachymeris macrotis*. A. Reconstruction of right tympanic region in ventral view based on AMNH 21335 (type specimen), and PU 16229. B. Reconstruction of arteries, veins, and nerves of the tympanic region. (Tracing of B placed over A will give a clearer idea of the relationships between the structures portrayed in each figure.) (Modified from Rich and Rich, 1971, fig. 17.) Approximately  $\times 10$ .

TABLE 18  
Skull Measurements (in Millimeters) of  
*Brachyerix macrotis*<sup>a</sup>

	PU 16229	UCMP 94718	UCMP 102634
Width of palate including M <sup>1</sup>	12.3	12.8 <sup>b</sup>	—
Width of postorbital constriction	7.3	8.2	—
Width between orbits <sup>c</sup>	9.4	10.0	—
Width of muzzle at infraorbital foramen	8.6	8.2	—
Width of braincase (at level of top of zygomatic arch)	16.9	17.8 <sup>d</sup>	—
Anteroposterior distance from anterior rim of orbit to infraorbital foramen			
Left	2.2	2.0	—
Right	2.4	1.8	—
Length upper cheek teeth, P <sup>4</sup> –M <sup>2</sup> , right	—	7.9	7.2
C <sup>1</sup> , anteroposterior diameter			
Left	1.5	1.6	—
Right	1.5	—	1.5
C <sup>1</sup> , transverse diameter			
Left	0.8	0.9	—
Right	0.7	—	0.9
P <sup>3</sup> , anteroposterior diameter			
Left	1.5	1.5	—
Right	1.5	1.6	1.4
P <sup>3</sup> , transverse diameter			
Left	0.9	0.8	—
Right	0.9	0.9	0.8
P <sup>4</sup> , anteroposterior diameter, right	3.3	3.9	3.0
P <sup>4</sup> , transverse diameter			
Left	2.6	—	—
Right	2.4	2.7	2.2
M <sup>1</sup> , anteroposterior diameter, right	—	3.0	2.7
M <sup>1</sup> , transverse diameter, right	3.0	3.4	3.1

	PU 16229	UCMP 94718	UCMP 102634
M <sup>2</sup> , anteroposterior diameter, right	—	—	1.7
M <sup>2</sup> , transverse diameter			
Left	2.1	—	—
Right	—	2.6	2.1

<sup>a</sup> Specimens previously mentioned in Rich and Rich (1971, table 2) not listed here.

<sup>b</sup> Measurement from right M<sup>1</sup> to midline doubled.

<sup>c</sup> Difficult to repeat measurement because method of taking measurement was not explicitly stated in Matthew, 1929. Here the measurement was taken across top of skull between supraorbital processes.

<sup>d</sup> Measurement from right wall of braincase to midline doubled.

was not hollow, thus the Vidian ramus could not have passed through this strut. For this reason, the same structure is here referred to as the strut for the Vidian ramus (SVR in figure 11a). Examination of PU 16229 revealed a small foramen near the point where the Vidian ramus had been thought to bifurcate from the promontory artery. A slight groove in the strut formerly thought to contain the Vidian ramus indicates that it ran forward along the ventral surface of that strut. No foramen has been found in the anterior part of the auditory region for the exit of the Vidian ramus from that chamber into the braincase. A revised reconstruction of the arteries, veins, and nerves of the tympanic region is given in figure 11b.

*Brachyerix incertis* (Matthew, 1924),  
Rich and Rich, 1971  
Figure 12

*Talpa incerta* Matthew, 1924, p. 74.

*Metechinus fergusonii* Henshaw, 1942, p. 101.

TYPE: AMNH 18891, right mandible with M<sub>2</sub>; alveoli for M<sub>1</sub> and enlarged incisor; and missing posterior and dorsal parts of ascending ramus, angle, and horizontal ramus anterior to M<sub>1</sub>. (See Rich and Rich, 1971, fig. 18.)

TABLE 19  
Mandible Measurements (in Millimeters) of  
*Brachyerix macrotis*<sup>a</sup>

	F:AM 76713	F:AM 76714	KU 18005	UNSM 11675
Mandible depth below C <sub>1</sub> <sup>b</sup>	—	—	—	4.6
Mandible depth below M <sub>1</sub> anterior root	3.3	3.0	3.8	4.2
Mandible depth below M <sub>2</sub> posterior root	3.2	3.3	—	4.7
M <sub>1-2</sub> length	6.3	6.3	—	7.7
P <sub>4</sub> , anteroposterior diameter	—	—	1.7	1.8
P <sub>4</sub> , transverse diameter	—	—	1.4	1.4
M <sub>1</sub> , anteroposterior diameter	3.9	3.9	3.7	4.8
M <sub>1</sub> , trigonid length	2.5	—	2.2	2.9
M <sub>1</sub> , trigonid width	1.7	1.8	1.9	2.1
M <sub>1</sub> , talonid width	1.8	—	2.1	2.2
M <sub>2</sub> , anteroposterior diameter	2.4	2.3	—	3.2
M <sub>2</sub> , trigonid length	1.1	1.4	—	1.6
M <sub>2</sub> , trigonid width	1.4	1.5	—	1.9
M <sub>2</sub> , talonid width	1.2	1.1	—	1.7

<sup>a</sup> Specimens previously mentioned in Rich and Rich (1971, table 3) not listed here.

<sup>b</sup> In Rich and Rich (1971, table 3), this same measurement is described as "Mandible depth below anterior part of P<sub>2</sub>."

TYPE LOCALITY AND STRATIGRAPHIC POSITION: (See Localities, Section 33.)

DIAGNOSIS: Smaller species of genus; weak lingual cingulum on P<sup>3</sup> extending from parastyle to small protocone on posterior side of paracone; protocone present on P<sup>3</sup>.

REFERRED MATERIAL: LACM(CIT) 2817, type of *Metechinus fergusonii* Henshaw, 1942. Fragment of left maxillary with P<sup>4</sup> and parts of two alveoli belonging to M<sup>1</sup> preserved. As originally described by Henshaw (1942, p. 101), the specimen also included, "part of the alveoli for two incisors, C. [and] the roots of P<sup>3</sup>? . . ." (see Henshaw, 1942, pl. 2 fig. 1). LACM(CIT) 2818, [possibly from the same individual as the type of *Metechinus fergusonii* Henshaw, 1942, LACM(CIT) 2817 (Henshaw, 1942, p. 101)], left lower jaw with two anterior alveoli, P<sub>4</sub>-M<sub>2</sub>, and lower posterior region of the ramus

(see Henshaw, 1942, pl. 2 fig. 2). As originally described, a third anterior alveolus was preserved on this specimen (Henshaw, 1942, p. 101). (See Rich and Rich, 1971, fig. 19.) (See Localities, Section 48.)

F:AM 74954, fragmentary skull with the posterior region of the left palate, anterior part of the left zygoma, entire basicranium, lateral aspect of the postorbital region and the squamosal, most of the left supraoccipital and basioccipital regions, left P<sup>3-4</sup>, posterior root of left C<sup>1</sup>, and alveoli of left M<sup>1-2</sup>. (See Localities, Section 32.)

F:AM 76712, right mandible complete except for angle and condyle, with M<sub>1-2</sub>, roots of P<sub>4</sub>, alveoli of I<sub>2</sub> and C<sub>1</sub>, and I<sub>1</sub> lacking apex. (See Localities, Section 56.)

KU 23498, horizontal ramus of left mandible complete except for region posterior to anterior alveolus of M<sub>2</sub>, with I<sub>1-2</sub> and M<sub>1</sub>, alveolus for C<sub>1</sub> and forward alveolus of M<sub>2</sub>. CM 27727, fragment of left horizontal ramus with M<sub>1-2</sub>, and incomplete alveoli for I<sub>1</sub>, C<sub>1</sub>, and P<sub>4</sub>. CM 10877, left M<sub>1</sub> with that part of horizontal ramus directly below the tooth. CM 27718 and 27719, two left M<sub>2</sub>s and fragments of horizontal rami posterior to those teeth. KU 28396, edentulous partial right horizontal ramus with alveoli for M<sub>2</sub> and posterior root of M<sub>1</sub>. CM 27720 and KU 28397, two isolated right M<sub>1</sub>s. CM 27721, isolated left M<sub>1</sub>. CM 27722 and KU 28395, two isolated right M<sub>2</sub>s. KU 28394, isolated left M<sub>2</sub>. CM 27725, right maxilla with C<sup>1</sup>, P<sup>4</sup>, M<sup>1</sup>, and alveoli for P<sup>3</sup>. CM 27726, left maxilla fragment with C<sup>1</sup> and P<sup>3</sup>. KU 28392, isolated right P<sup>4</sup>. CM 27723 and 27724, two isolated right M<sup>1</sup>s. KU 28393, isolated left M<sup>2</sup>. (See Localities, Section 43.)

DESCRIPTION: F:AM 76712 and KU 23498 further confirm the succinct description of this species given in Rich and Rich (1971, p. 43) as being the same as *Brachyerix macrotis* in all parts preserved except the few features mentioned in the diagnosis. The enlarged I<sub>1</sub> may be seen for the first time on these two specimens.

I<sub>2</sub>: Previously unknown in either species of *Brachyerix*, the I<sub>2</sub> is present on KU 23498. Extending anteriorly from the root, the

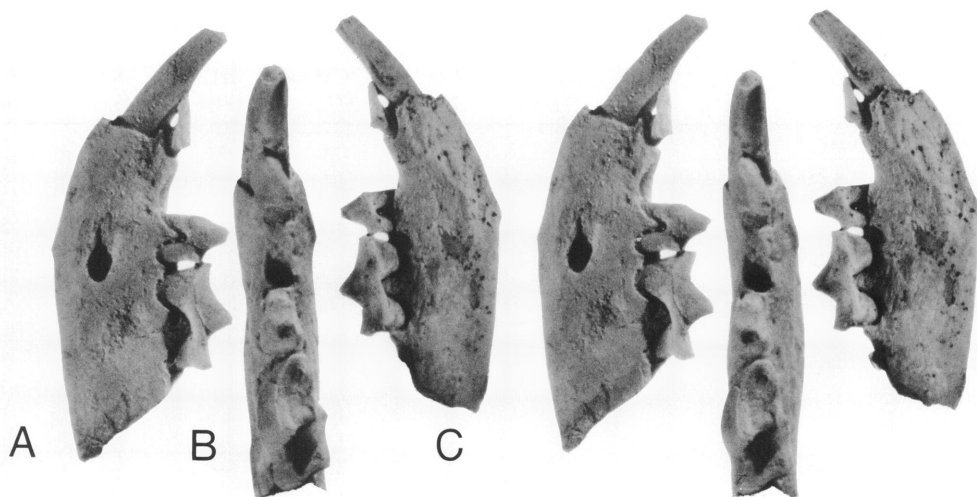


FIG. 12. *Brachyerix incertis*, KU 23498, left mandible fragment, from the Madison Valley Formation at the Anceney locality (KU Mont. loc. 34), SE  $\frac{1}{4}$ , SE  $\frac{1}{4}$ , NW  $\frac{1}{4}$ , sect. 13, T. 2 S, R. 3 E, Gallatin County, Montana (45° 39' 51" N, 111° 18' 01" W). A. Lateral view. B. Occlusal view. C. Medial view.  $\times 4.5$ .

crown of this tooth overlaps  $I_1$ . Directed anteroposteriorly along the midline of the tooth is a low ridge. No distinct cusp is developed anywhere on this tooth. In occlusal view, the outline of the tooth is roughly an isosceles triangle, the height of which is approximately double the length of the base and the apex is directed anteriorly.

*Brachyerix* cf. *B. incertis*

**MATERIAL:** ROM 7633, isolated left  $M_2$  (see Storer, 1975, fig. 2b). ROM 7634, isolated right  $M_2$  (see Storer, 1975, fig. 2a). ROM 7678, right  $M_2$  talonid. (See Localities, Section 37.)

**REMARKS:** These specimens are virtually identical with  $M_2$  of *Brachyerix incertis* but are noticeably smaller than even that diminutive species. The specimens have been recently described by Storer (1975).

**SPECIMENS INCORRECTLY REFERRED TO *Brachyerix*:** L. J. Macdonald (1972) allocated a group of specimens found on anthills derived from the early Miocene Monroe Creek Formation of South Dakota to *Brachyerix macrotis*. Re-examination of the ma-

terial on which this allocation was based indicates that the specimens should be regarded as *Amphechinus horncloudi* (see p. 32).

Other specimens erroneously referred to *Brachyerix* were discussed by Rich and Rich (1971, p. 44).

TABLE 20  
Measurements (in Millimeters) of the Upper  
Dentition of *Brachyerix incertis*<sup>a</sup>

		Antero- posterior Diameter	Transverse Diameter
CM 27723, $M^1$		2.1	2.6
CM 27724, $M^1$		2.5	2.9
CM 27725,	$C^1$	1.3	0.5
	$P^4$	2.7	2.0
	$M^1$	2.2	2.6
CM 27726,	$C^1$	1.1	0.6
	$P^3$	1.2	0.7
KU 28392, $P^4$		2.6	2.2
KU 28393, $M^2$		1.5	1.9

<sup>a</sup> Specimens previously mentioned in Rich and Rich (1971, table 2) not listed here.

TABLE 21  
Mandible Measurements (in Millimeters) of *Brachyerix incertis*<sup>a</sup>

	CM 27718	CM 27719	CM 27727	KU 23498	KU 28396	F:AM 76712
Mandible depth below C <sub>1</sub> <sup>b</sup>	—	—	—	2.7	—	2.7
Mandible depth below M <sub>1</sub> anterior root	—	—	—	2.9	—	3.0
Mandible depth below M <sub>2</sub> posterior root	2.0	2.6	—	—	2.5	3.0
M <sub>1-2</sub> , length	—	—	4.7	—	—	5.1
I <sub>2</sub> , anteroposterior diameter	—	—	—	1.4	—	—
I <sub>2</sub> , transverse diameter	—	—	—	0.9	—	—
P <sub>4</sub> , anteroposterior diameter	—	—	—	1.3	—	—
P <sub>4</sub> , transverse diameter	—	—	—	1.0	—	—
M <sub>1</sub> , anteroposterior diameter	—	—	2.9	2.7	—	3.1
M <sub>1</sub> , trigonid length	—	—	1.6	1.6	—	2.0
M <sub>1</sub> , trigonid width	—	—	1.1	1.3	—	1.6
M <sub>1</sub> , talonid width	—	—	1.3	1.3	—	1.8
M <sub>2</sub> , anteroposterior diameter	1.9	2.0	2.0	—	—	2.1
M <sub>2</sub> , trigonid length	1.0	1.2	1.0	—	—	1.2
M <sub>2</sub> , trigonid width	1.1	1.1	1.0	—	—	1.4
M <sub>2</sub> , talonid width	0.8	0.8	1.0	—	—	1.1

<sup>a</sup> Specimens previously mentioned in Rich and Rich (1971, table 3) not listed here.

<sup>b</sup> In Rich and Rich (1971, table 3), this same measurement is described as "Mandible depth below anterior part of P<sub>2</sub>."

#### METECHINUS MATTHEW, 1929

##### *Metechinus* Matthew, 1929.

TYPE: *Metechinus nevadensis* Matthew, 1929.

KNOWN DISTRIBUTION: Early Barstovian—Clarendonian (16–10 my., medial–late Miocene), North America.

DIAGNOSIS: Distinguished from *Brachyerix* by larger size; lateral margins of basicranium (in ventral view) converging posteriorly at large angle rather than nearly parallel; smaller, less inflated auditory bullae further separated from one another; absence of flange separating posterior and flat lateral surfaces of squamous region of zygoma; ventral tips of interparietal not intercalated between parietal and mastoid; taller partition formed by mastoid between stylomastoid and jugular foramina; postmetaconule crista not joined to metacone but rather separated by a prominent notch on M<sub>1</sub>; trigonid of M<sub>1</sub> more anteroposteriorly compressed; and anteroposterior diameter of M<sub>2</sub> longer relative to that of M<sub>1</sub>.

#### *Metechinus nevadensis* Matthew, 1929

*Metechinus nevadensis* Matthew, 1929, p. 95.

TYPE: UCMP 29600, uncrushed, partial skull with right I<sup>3</sup>, C<sup>1</sup>, P<sup>4</sup>–M<sup>2</sup>; left C<sup>1</sup>, P<sup>4</sup>–M<sup>2</sup>; alveoli for P<sup>3</sup>s; missing anterior part of premaxillae, central region of right zygoma, ventral and posterior walls of braincase including tympanic region; associated with fragments of lower mandibles including left anterior part ascending ramus, left P<sub>4</sub>–M<sub>1</sub> and that part of mandible directly below these two teeth, and right mandible with M<sub>1-2</sub> lacking that part of horizontal ramus anterior to M<sub>1</sub>, ascending ramus above the level of the tooth row, and posterior part of angle. (See Matthew, 1929, pls. 7, 8.)

TYPE LOCALITY AND STRATIGRAPHIC POSITION: (See Localities, Section 61.)

DIAGNOSIS: Distinguished from *Metechinus amplior*, new species by the smaller size of the skull, greater width to length ratio of skull, posterior palatine foramen developed on the maxilla-palatine suture rather than

TABLE 22  
Measurements (in Millimeters) of Isolated Lower  
Molars of *Brachyerix incertis*<sup>a</sup>

	Antero- pos- terior Diam- eter	Tri- gonid Length	Tri- gonid Width	Talonid Width
CM 10877, M <sub>1</sub>	3.0	1.7	1.3	1.2
CM 27720, M <sub>1</sub>	2.7	1.6	1.1	—
CM 27721, M <sub>1</sub>	3.0	1.8	1.5	1.5
KU 28397, M <sub>1</sub>	3.0	1.9	1.3	1.6
CM 27722, M <sub>2</sub>	1.8	0.9	0.9	0.6
KU 28394, M <sub>2</sub>	2.0	1.0	1.0	0.9
KU 28395, M <sub>2</sub>	2.1	1.1	1.1	0.9

<sup>a</sup> Specimens previously mentioned in Rich and Rich (1971, table 3) not listed here.

medial to it, crest between protocone and hypocone on P<sup>4</sup>, lingual border of lower molars markedly concave between metaconid and entoconid rather than straight, and buccal borders of lower molars markedly concave between protoconid and hypoconid rather than nearly straight.

UPPER DENTITION: I<sup>3</sup>: All the major structures on this tooth are arranged along a single anteroposterior axis. The paracone is conical in form and its base is two-thirds the length of the tooth. In lateral view the anterior side of the paracone is slightly convex, and the posterior side is straight. At the anterior end of the tooth is a well-developed paracrista and an even stronger metacrista is present at the posterior end. The single root displays no indication of bifurcation.

C<sup>1</sup>: Smaller than I<sup>3</sup>, this double-rooted tooth has a conical paracone, the base of which occupies the entire crown except for a low, weak cingulum along the anterior margin and an even weaker, low cingulum along the posterior margin.

P<sup>3</sup>: This tooth is not preserved on the single specimen available but on the basis of the alveoli, it appears to have been noticeably smaller than C<sup>1</sup>, unlike *Brachyerix macrotis*. Curiously, there appear to have been three roots on the left P<sup>3</sup> and only two on the right.

P<sup>4</sup>: This tooth is several times larger than

TABLE 23  
Measurements (in Millimeters) of M<sub>2</sub> of  
*Brachyerix* cf. *B. incertis*

	ROM 7633	ROM 7634	ROM 7678
Anteroposterior diameter	1.8	1.8	—
Trigonid length	1.1	1.1	—
Trigonid width	1.1	1.2	—
Talonid width	0.8	0.9	0.8

the preceding P<sup>3</sup>. The height of the paracone, tallest cusp on the tooth, is about nine-tenths the length of the tooth. One-fourth the height of the paracone, the protocone is lingual and slightly anterior to that cusp, as in modern hedgehogs. The hypocone is posterolingual to the protocone, subequal in height to that cusp but somewhat larger in basal dimensions. The two cusps are linked to one another by a well-developed crest but neither is linked in that manner to any of the buccal structures of the tooth. Behind the hypocone on the lingual side of the tooth is a small, slightly concave surface. No parastyle is present, and the elongated metacrista terminates posteriorly without a distinct metastyle. No buccal cingulum is present but there is a well-developed precingulum along the anterior side of the base of the paracone. The number and condition of the roots cannot be determined.

M<sup>1</sup>: Largest tooth in the skull, M<sup>1</sup> is broader and slightly more anteroposteriorly compressed than P<sup>4</sup>. Height of the paracone, tallest of the four principal cusps, is half the length of the tooth. The paracone is anterobuccal to the metacone and although the bases of the two cusps are confluent, no distinct centrocrista links them together. In contrast, on M<sup>1</sup> of modern hedgehogs the paracone is anterior or anterolingual to the metacone. Second tallest cusp on the tooth, the metacone has a steep anterior side and a more steeply dipping posterior one. Third tallest and most lingual cusp on the tooth, the protocone is lingual and somewhat anterior to the paracone. Its base projects medially beyond the body of the tooth. Posterobuccal to the protocone is the lowest of the four prin-



cial cusps, the hypocone. The hypocone and metacone are closer to the midline of the tooth than the protocone and paracone. Such is the condition of  $M^2$  on some modern hedgehogs but never  $M^1$ . 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, for no paraconule is present. In anterior view this loph has a broad inverted U-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 extending posterolingually to the hypocone and the other, the postmetaconule crista, buccally toward the metacone from which it is separated by a prominent notch. No metaconule is developed on this tooth. Situated at the buccal end of a short precingulum present along the anterior side of the paracone base is a small parastyle. It is so closely appressed to the anterobuccal side of the paracone that there is no room for the development of a paracrista. From the metacone, the metacrista extends posterobuccally for a distance equal to one-fourth the tooth length. No ectocingulum is present along the buccal margin of the tooth.

The number and condition of the roots cannot be determined on this specimen.

$M^2$ : The metacone and hypocone form a short mediolaterally oriented blade with slight swellings at either end that mark the presence of the two cusps. Support for the identification of this blade as a combined metacone and hypocone is to be found when the lower dentition is manually placed in occlusion with the upper. In that condition, the blade extends along the rear of the talonid of  $M_2$  from a position directly behind the entoconid (where the hypocone would be expected to occlude) to a position directly behind the hypoconid (where the metacone would be expected to occlude). Posterolingual to the paracone, the hypocone-metacone is posterobuccal to the protocone. The protocone is lingual to the paracone. Heights of the four cusps are subequal and about one-half the length of the tooth. Moderately

deep, the trigon basin is bordered by a low postprotocrista between the protocone and hypocone-metacone. Highest of the crests, the preprotocrista forms a continuous wall between the protocone and paracone. Linking the paracone and hypocone-metacone is a crista with an inverted U-shaped profile in labial view. Anterior to the paracone is a short precingulum but no trace of an ectocingulum is present.

LOWER DENTITION:  $P_4$ : Only the protoconid is developed as a distinct cusp; its height is one and one-fifth times the tooth length. Nearly the entire area of the crown is covered by the base of this cusp. At the anterior extreme of the tooth is a tiny cusplule. A narrow postcingulum is developed along most of the rear margin of the tooth. No buccal or lingual cingula are present nor is there any trace of a bulge in the side of the protoconid where either the metaconid or paraconid might be expected. The greatest breadth of the tooth is where the narrow postcingulum meets the base of the protoconid. No specimen displaying the alveoli of this double-rooted tooth is known.

$M_1$ : The length of the trigonid is half the length of the tooth. The width of the trigonid is subequal to its length. As in other brachyricines, the prevallid is expanded anteriorly. Lowest of the trigonid cusps, the paraconid is anterior to the metaconid, the bases of the two cusps separated by a deep cleft. The protoconid is posterobuccal to the paraconid. Linking the two cusps is the paralophid, which in lateral view has a broad V-shaped profile and in occlusal view is somewhat buccally convex. Tallest of the trigonid cusps, the protoconid is two-thirds as tall as the tooth is long. The metaconid is anterolingual to the protoconid, and the bases of the two cusps are connate.

Width of the talonid is slightly greater than that of the trigonid. Situated at the extreme posterior corners of the talonid are the hypoconid and entoconid. Although tallest of the talonid cusps, the entoconid is lower than the paraconid. The hypoconid lies slightly more labial than the protoconid. Extending anterolingually from the hypoconid, the cristid obliqua abuts against the posterior wall

of the trigonid at a point below the protoconid. Because the entocristid is weak, the talonid basin is open lingually. A short, weak labial cingulum is present beneath the protoconid. In occlusal view, the buccal border of the tooth from the protoconid to the hypoconid and the lingual border from the metaconid to the entoconid are deeply concave rather than nearly straight, the condition generally seen in erinaceids.

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

$M_2$ : This tooth is about three-fourths as long as  $M_1$ . The trigonids of the two teeth are subequal in width but the talonid width of  $M_1$  is nearly one and one-half times that of  $M_2$ . The trigonid length is half the total length of the tooth. The prevallid is not as expanded anteriorly as on  $M_1$ , the length of the trigonid being three-fourths its width. Lowest of the three trigonid cusps, the paraconid is anterobuccal to the metaconid, and the bases of the two cusps are separated by a deep cleft. The protoconid is posterobuccal to the paraconid. Linking the two cusps is a paralophid that in lateral view has a broad V-shaped profile and in occlusal view is straight. Subequal in height to the metaconid, the protoconid is three-fifths as tall as the tooth is long. The metaconid is lingual and slightly anterior to the protoconid, and the bases of the two cusps are joined by a short protolophid.

The talonid is four-fifths the width of the trigonid. Tallest of the talonid cusps, the entoconid is markedly taller than the paraconid and nearly as tall as the metaconid. Both the hypoconid and entoconid are closer to the midline of the tooth than are the metaconid and protoconid. No hypoconulid is present. Extending anterolingually from the hypoconid, the cristid obliqua abuts against the posterior wall of the trigonid at a point slightly lingual to the protoconid. Best developed on the anterior side of the entocoid, the entocristid is lowest immediately posterior to the trigonid. The labial cingulum extends the length of the prevallid.

This tooth is double rooted as are  $P_4$  and  $M_1$ . The single specimen with  $M_2$  preserved has been broken between  $M_1$  and  $M_2$  and re-

joined. If the orientation of the long axes of the two molars with respect to one another is accurate, they were subparallel. Alveoli of this tooth are not visible on either available mandible.

**FACE:** The zygoma is elevated toward its posterior end and, in contrast to modern hedgehogs, is deep except where it joins the body of the squamosal. The dorsal profile is straight back to the level where the zygomatic arch passes into the body of the squamosal, rising to its maximum height at that point. Behind that point, the dorsal profile is horizontal and again straight.

As is typical of erinaceids, the nasals were long and narrow, tapering posteriorly and finally terminating between the left and right frontal bones opposite the anterior end of the orbit. Due to damage at the anterior end of the single available specimen, it is impossible to determine how far forward the nasals extended relative to the premaxilla. Unlike *Brachyerix macrotis*, the premaxilla remained firmly attached to the maxilla behind it even in death. The maxilla-premaxilla suture begins ventrally between  $C^1$  and  $I^3$  and forms an irregular arc that curves upward and backward. Premaxilla-frontal contact occurred but the extent cannot be determined due to slight crushing in this region. No trace of a separate lacrimal is present. The supraorbital crest is strong, and an extension from it passes anterior to the lacrimal foramen, enclosing it within the orbit before turning posteriorly along the crest of the zygoma. Construction of this crest is similar to that of smaller species of the Galericinae (=Echinosoricinae).

The anterior end of the zygomatic arch is formed by the maxilla. If a jugal was present as a separate element near the middle of the zygomatic arch, it has been lost on the single specimen available. A deep excavation into the anterior face of the zygomatic arch probably served as a site for the origin of the snout musculature as in the smaller species of the Galericinae.

**PALATE:** Most of the palate is formed by the maxilla, the premaxilla contributing only in the area immediately adjacent to the upper incisors. The suture between the premaxilla

and the maxilla extends anteromedially from immediately anterior to the canine. Two-thirds the distance from the margin of the palate to the midline is a palatine fissure that deeply incises the anterior border of the maxilla. If the palatal region of the maxilla is complete, the length of the palate from the anterior border of the maxilla to the transverse crest near the posterior end of the palate is 18.1 mm. The palate extends for a short distance behind the transverse crest, as in the modern Erinaceinae and *Hylomys*.

The palatine-maxilla suture passes through a notch in the transverse process homologous to the posterior palatine foramen. Projections from the transverse process nearly meet and bridge these notches ventrally. The relatively lateral position and development of the posterior palatine foramina as notches is similar to the condition found in erinaceines and unknown in galericines.

Extending posteriorly to a small foramen, a slight groove is developed on either side of the midline at the anterior end of the palatine. Presumably this groove is homologous to the more extensive one found in galericines, in which the palatine nerve and artery lie. Three or four additional small foramina can be seen in each palatine. The bones of the palate are as thick and solid as those of the galericines. No vacuities typical of the erinaceines are present in the palate.

The shortening of the skull that has occurred in *Metechinus nevadensis* is reflected in the position of the teeth relative to the orbital region. Only slightly forward of its position in living hedgehogs, the infraorbital foramen is above the center of  $P^3$ . This foramen lies above the anterior end of  $M^1$  in *Echinosorex* and *Podogymnura* and above the juncture between  $P^4$  and  $P^3$  in all other living erinaceids. The anterior end of the orbit lies above the anterior end of  $P^4$ . In *Echinosorex* and *Podogymnura*, the orbit is above the juncture between  $M^1$  and  $M^2$  and is over  $M^1$  in the remaining modern hedgehogs. The base of the zygomatic arch in *M. nevadensis* is opposite  $M^1$  only, not above  $M^1$  and  $M^2$  as in most modern erinaceids or more fully over  $M^2$  as on *Echinosorex* and *Podogymnura*.

**ORBITOTEMPORAL REGION:** Extensive crushing has occurred in this region on the single available specimen, so only a few comments are possible. Most of the anteromedial wall of the orbit appears to have been formed by the maxilla. Sutures have been obscured by the extensive crushing so the relative contributions of the palatine, frontal, orbitosphenoid, alisphenoid, and parietal to the wall of the orbit are unclear. The positions of the orbitonasal, sphenorbital, suboptic, optic, and orbitosphenoid foramina cannot be determined although some foramina can be seen but not identified due to the damage in the orbitotemporal region.

**BASE OF THE CRANIUM AND TYMPANIC REGION:** Due to damage of the specimen in the posterior region of the skull, little can be said about it except that the postglenoid was present and low, and the squamosal formed the dorsal edge of the external auditory meatus.

**CRANIAL ROOF AND POSTERIOR SURFACE:** The postorbital process is stronger than in any living hedgehog. As in all Recent erinaceids except *Hylomys* and *Neotetracus*, the maxilla and parietal are well separated. Closest resemblance in the pattern and relative sizes of the temporal and sagittal crests is to be found in the larger species of Recent hedgehogs. Both crests are strongly developed and meet midway between where the sagittal plane intersects the nasal-frontal and frontal-parietal sutures. Delicate sculpturing covers most of the parietal. More subdued sculpturing is to be found on the lateral surfaces of the squamosal and mastoid.

No trace of the interparietal bone remains on the specimen. The ventral part of the lambdoid crest is preserved on the right side and indicates that the complete structure was quite strong unlike modern hedgehogs and similar to *Brachyerix*. Unlike any modern hedgehog, the mastoid has expanded posterolaterally to form a prominent lambdoid crest that is nonetheless somewhat weaker than the posteriorly directed one in *Brachyerix*.

The squamous region of the zygomatic arch may be envisioned as two tabular bars meeting at right angles. Projecting laterally

from the body of the skull, the first bar is parallel to the frontal plane. Along its posterior face is a groove in the bottom and slightly medial to the center of which is a small foramen. Beginning at the distal end of the laterally directed bar and extending anteriorly is a second tabular bar which is parallel to the sagittal plane. Unlike *Brachyerix macrotis*, the lateral surface of this bar is flat, not concave, and no flange sharply separates this flat surface from the posterior side of the first bar.

**MANDIBLE:** The mental foramen lies below the anterior root of M<sub>1</sub>. The anterior extreme of the dorsal margin of the angle is preserved and indicates that the angle protruded at least somewhat posteriorly beyond the adjacent margin of the jaw, unlike *Brachyerix macrotis*. Along the leading edge of the ascending ramus is a strong lateral flange forming the anterior margin of the masseteric fossa. A ridge begins at the base of the leading edge of the ascending ramus on its medial side and extends toward the condyle, becoming weaker posteriorly, and finally disappearing about halfway there. Immediately ventral to this ridge is the mandibular foramen, which is level with the tooth row and is about one-third the distance from the anterior to the posterior edge of the ascending ramus. The condyle lies slightly above the level of the tooth row. In posterior view, the margin of the mandible tapers gradually from maximum thickness at the condyle to a minimum immediately above the condyle. A ridge extending anteroventrally from the condyle forms the posteroventral border of the masseteric fossa.

**Metechinus amplior**, new species  
Figures 13–17

**ETYMOLOGY:** *Amplior*, Greek, larger, in reference to the greater size of this species relative to *Metechinus nevadensis*.

**TYPE:** F:AM 74923, crushed skull lacking posterior part of left zygomatic arch, crowns of both I<sup>1</sup>s, left I<sup>3</sup>, and right I<sup>2</sup>–P<sup>2</sup>. (See figs. 13–14; also see Rich and Rich, 1971, fig. 14.)

**TYPE LOCALITY AND STRATIGRAPHIC POSITION:** (See Localities, Section 50.)

TABLE 24  
Skull Measurements (in Millimeters) of UCMP  
29600, Type of *Metechinus nevadensis*

Width across zygomatic arches	30.4 <sup>a</sup>
Width of palate including M <sup>1</sup>	17.0
Width of postorbital constriction	10.9
Width between orbits <sup>b</sup>	12.8 <sup>c</sup>
Width of muzzle at infraorbital foramen	10.9 <sup>c</sup>
Width of braincase (at level of top of zygomatic arch)	18.7 <sup>c</sup>
Anteroposterior distance from anterior rim of orbit to infraorbital foramen	
Left	2.0
Right	2.1
Length upper cheek teeth, P <sup>4</sup> –M <sup>2</sup>	
Left	10.7
Right	10.8
I <sup>3</sup> , anteroposterior diameter, left	1.7
I <sup>3</sup> , transverse diameter, left	1.2
C <sup>1</sup> , anteroposterior diameter	
Left	2.0
Right	1.6
C <sup>1</sup> , transverse diameter	
Left	0.9
Right	1.0
P <sup>4</sup> , anteroposterior diameter, right	4.2
P <sup>4</sup> , transverse diameter	
Left	3.4
Right	3.4
M <sup>1</sup> , anteroposterior diameter	
Left	3.8
Right	3.9
M <sup>1</sup> , transverse diameter	
Left	4.9
Right	4.9
M <sup>2</sup> , anteroposterior diameter	
Left	2.8
Right	2.6
M <sup>2</sup> , transverse diameter	
Left	4.0
Right	3.9

<sup>a</sup> Distance from left zygomatic arch to midline was doubled.  
<sup>b</sup> Difficult to repeat measurements because method of taking measurement was not explicitly stated in Matthew, 1929. Here the measurement was taken across top of skull between supraorbital processes.  
<sup>c</sup> Measurement suspect because of distortion.

TABLE 25  
Mandible Measurements (in Millimeters) of  
UCMP 29600, Type of *Metechinus nevadensis*

	Left	Right
M <sub>1-2</sub> , length	—	8.6
P <sub>1</sub> , anteroposterior diameter	2.0	—
P <sub>4</sub> , transverse diameter	1.3	—
M <sub>1</sub> , anteroposterior diameter	5.0	5.1
M <sub>1</sub> , trigonid length	2.6	2.6
M <sub>1</sub> , trigonid width	2.9	2.8
M <sub>1</sub> , talonid width	3.0	2.9
M <sub>2</sub> , anteroposterior diameter	—	3.7
M <sub>2</sub> , trigonid length	—	1.8
M <sub>2</sub> , trigonid width	—	2.6
M <sub>2</sub> , talonid width	—	2.0

DIAGNOSIS: Distinguished from *Metechinus nevadensis* by the greater size of the skull, lesser width to length ratio of skull, posterior palatine foramen developed medial to the maxilla-palatine suture rather than on it, absence of crest between protocone and hypocone on P<sup>4</sup>, lingual border of lower molars nearly straight between metaconid and entoconid rather than markedly concave, and buccal borders of lower molars nearly straight between protoconid and hypoconid rather than markedly concave.

REFERRED MATERIAL: UCMP 50121, fragment of right (not left, *contra* James, 1963, p. 65) M<sup>2</sup> including the paracone (see James, 1963, fig. 24). (See Localities, Section 58.)

F:AM 76711, right mandible fragment with M<sub>2</sub>, lacking coronoid process and horizontal ramus anterior to M<sub>1</sub> alveoli. (See Localities, Section 34.)

F:AM 76701, left M<sub>1</sub> with small mandible fragment attached. F:AM 76706, badly crushed skull lacking both zygomatic arches and retaining only left P<sup>3-4</sup>, M<sup>2</sup> and right partial P<sup>4</sup>, and partial M<sup>1</sup>. F:AM 76709, left P<sup>4</sup> and M<sup>1</sup> in maxilla fragment. F:AM 94233,

crushed skull, lacking region anterior to the premolars, orbital region, and most of the parietals and supraoccipitals; retains left P<sup>3</sup>-M<sup>2</sup>, and right P<sup>2</sup>-M<sup>2</sup>. (See Localities, Section 50.)

F:AM 74925, left mandible complete except for crown of I<sub>1</sub> and coronoid process (see fig. 15). (See Localities, either Section 36 or 50.)

F:AM 95182, fragmentary skull with right P<sup>4</sup> and M<sup>1</sup> associated with nearly complete horizontal ramus of right mandible lacking only angle and ventral margin below M<sub>2</sub>, with I<sub>1</sub>-M<sub>2</sub>, tip of I<sub>1</sub> missing and M<sub>2</sub> badly damaged. (See Localities, Section 55.)

F:AM 76710, right mandible with P<sup>4</sup> and lacking coronoid process. (See Localities, Section 54.)

F:AM 74924, fragmentary left maxilla with P<sup>4</sup>-M<sup>1</sup> plus anteroexternal root of M<sup>2</sup>. (See Localities, Section 62.)

F:AM 76708, right mandible with M<sub>2</sub> and partial M<sub>1</sub>, lacking coronoid process and horizontal ramus anterior to M<sub>1</sub>. (See Localities, Section 64.)

F:AM 74921, nearly complete, slightly crushed skull with I<sup>1</sup>-I<sup>2</sup>, P<sup>3</sup>-M<sup>2</sup>; lacking the basicranium and anterior part of the nasals. F:AM 74922, left maxilla with M<sup>1-2</sup>. F:AM 76696, fragmentary skull and anterior part of left lower jaw. F:AM 76697, isolated right M<sub>1</sub>. F:AM 76698, incomplete right mandible with M<sub>1-2</sub>. F:AM 76699, isolated right M<sub>1</sub>. F:AM 76700, left edentulous mandible. F:AM 76715, edentulous partial skull lacking both zygomatic arches and premaxillae. F:AM 94234, isolated left M<sub>1</sub>. F:AM 94235, isolated right M<sub>1</sub>. F:AM 94236, isolated right M<sub>1</sub>. (See Localities, Section 31.)

UCMP 29211, left mandible fragment with M<sub>1</sub>, lacking ascending ramus and horizontal ramus anterior to M<sub>1</sub>. UCMP 29212, right mandible fragment with M<sub>2</sub>, lacking ascending ramus above condyle and horizontal ra-

→

FIG. 13. *Metechinus amplior*, new species, type, F:AM 74923. A. Palatal view of skull. B. Dorsal view of skull. Found in the Santa Cruz Red layer near the middle of the Pojoaque Member of the Tesuque Formation, SW ¼, sect. 28 or NW ¼, sect. 33, T. 21 N., R. 9 E., Rio Arriba County, New Mexico (36° 01' N., 105° 59¾' W.). ×2.



A



B



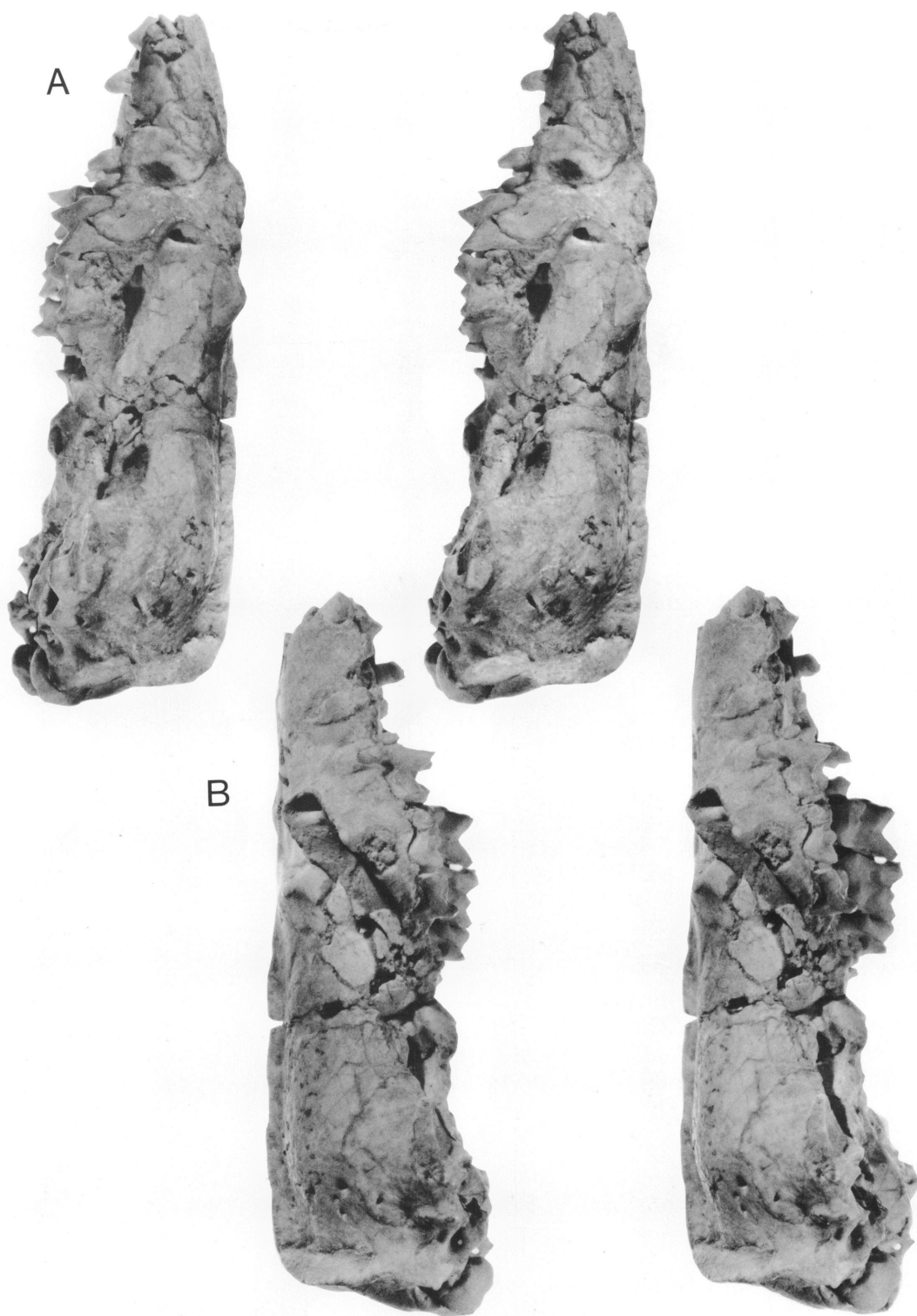


FIG. 14. *Metechinus amplior*, new species, type, F:AM 74923. A. Left lateral view of skull. B. Right lateral view of skull.  $\times 2$ .



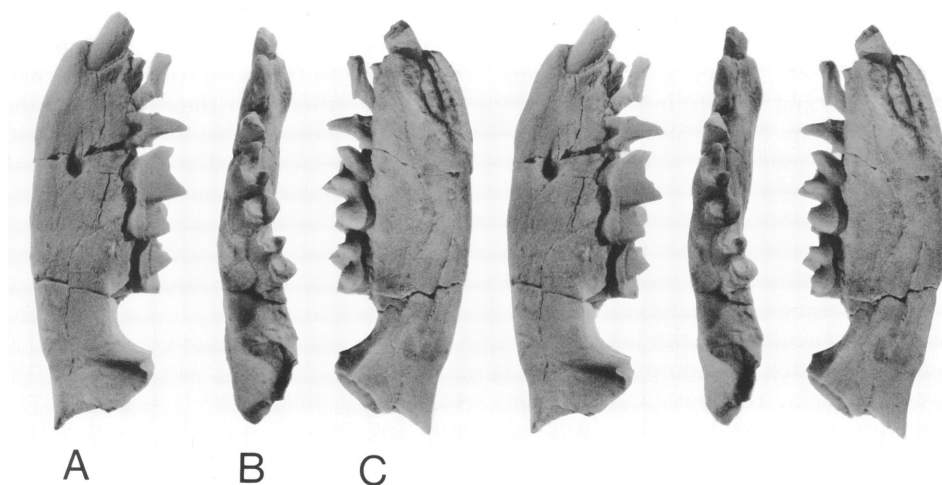


FIG. 15. *Metechinus amplior*, new species, F:AM 74925. A. Lateral view of left mandible. B. Occlusal view. C. Medial view. Found either in the Santa Cruz Red layer near the middle of the Pojoaque Member of the Tesuque Formation somewhere in the following area: SW  $\frac{1}{4}$ , sect. 28; NW  $\frac{1}{4}$ , sect. 33, N  $\frac{1}{2}$ , sect. 32, T. 21 N, R. 9 E, Rio Arriba County, New Mexico (36° 01' N, 106° 00' W), or at White Operation Quarry near the middle of the Skull Ridge Member of the Tesuque Formation, NE  $\frac{1}{4}$ , NE  $\frac{1}{4}$ , sect. 9, T. 20 N, R. 9 E, Santa Fe County, New Mexico (35° 56' 18" N, 105° 56' 54" W).  $\times 2$ .

mus anterior to  $M_2$ . UCMP 36162, right edentulous mandible fragment with alveoli for  $M_{1-2}$ , lacking ascending ramus and horizontal ramus anterior to  $M_1$ . UCMP 36163, right premaxilla with  $I^{1-3}$ , teeth complete except for the tip of  $I^1$ . UCMP 36164, isolated left  $M^1$ . UCMP 36165, left  $M^1$  in a small fragment of maxilla including base of zygomatic arch. (See Localities, Section 41.)

F:AM 76731, isolated left  $M_1$ . F:AM 76732, isolated right  $M_1$ . F:AM 76733, isolated left  $M_2$ . UMMP V57329, partial skull with left  $P^4$ – $M^2$  and right  $M^{1-2}$ , lacks snout and basicranium. (See Localities, Section 39.)

F:AM 76741, isolated left  $M^2$ . (See Localities, Section 40.)

UMMP V57332, right maxilla and premaxilla with  $I^{1-2}$ ,  $P^{3-4}$ , and three alveoli in between for  $I^3$  and  $C^1$ ; left premaxilla fragment with broken  $I^1$ , and  $I^{2-3}$ ; right mandible fragment with  $M_2$ , lacking part of jaw anterior to  $M_2$ . (See Localities, Section 60.)

UNSM 45133, isolated left  $M_2$ . UNSM 45151, incomplete right mandible with  $M_{1-2}$  and alveoli for  $P_4$ . UNSM 45152, incomplete

right mandible with  $P_4$ – $M_2$  and alveoli for  $I_1$ – $C_1$ . (See Localities, Section 42.)

UMMP V26955, partial right mandible with  $P_4$ . (See Localities, Section 46.)

KU 9175,  $M^1$  in maxilla fragment. Previously, this specimen has been identified as *Brachyerix* sp. by Galbreath (1953, p. 92) and *Metechinus nevadensis* by Rich and Rich (1971, p. 44). AMNH 48998, skull fragment with left  $M^1$  and partial  $M^2$ . (See Localities, Section 38.)

UCM 34441, right  $P_4$  and  $M_1$  plus that part of mandible directly below those two teeth. (See Localities, Section 49.)

UPPER DENTITION:  $I^1$ : This tooth was a large, single-rooted, highly mediolaterally compressed incisor that curved upward and backward above  $I^2$  and  $I^3$  as far posteriorly as the premaxilla-maxilla suture. On UCMP 36163, the only specimen where the base of the root may be observed, it is constricted but not fully closed, suggesting that that individual was immature and a closed root was the adult condition. A prominent, concave, posteriorly facing wear surface is present from the tip to the base of the posterior side

of this same specimen. Similar wear can be seen in living erinaceids. The crown of the right I<sup>1</sup> on F:AM 74921 appears to have been broken during life and subsequently abraded before death as can be seen on the same tooth in a modern specimen of *Echinosorex gymnurus albus* (AMNH(M) 103886).

I<sup>2</sup>: Short diastema separate this diminutive tooth from the incisors in front and behind. The single root is anteroposteriorly elongated and has two vertical grooves, one on the medial side and a second on the lateral. The crown was mediolaterally compressed with a single major cusp, the paracone, in the middle of the anteroposteriorly directed crest that extends the length of the tooth. At each end of this crest near the base of the crown is a small cusp.

I<sup>3</sup>: In morphology, this tooth is practically a duplicate of the preceding I<sup>2</sup>. It is somewhat larger and the posterior basal cusp behind the paracone is more prominent and part of a well-developed cingulum along the rear of the tooth. The root of this tooth is either elongated with vertical grooves as in I<sup>2</sup> or circular in outline with no sign of bifurcation.

C<sup>1</sup>: This tooth is mediolaterally compressed to such an extent that all the major structures are arranged along a single anteroposterior axis. The paracone is bladelike in form and its base is two-thirds the length of the tooth. Both the anterior and posterior sides of the paracone are straight when viewed laterally. Truncating the apex of the cusp is a wear facet parallel to the frontal plane. A well-developed paracrista is developed on the anterior side of the tooth and an even stronger metacrista is present on the posterior side. As in most erinaceids, this tooth is double rooted. In contrast to *Brachyerix macrotis*, this tooth is markedly larger, rather than subequal to P<sup>3</sup> in size.

P<sup>3</sup>: The base of the paracone occupies the central half of the tooth. Both anterior and posterior edges of the paracone are straight. When unworn, the apical height of the paracone was about equal to the length of the tooth. The metastyle is smaller and lower than the paracone, and the two are linked by

a metacrista. Along the posterior side of the tooth is a cingulum that extends from the metastyle to the posterolingual corner of the tooth. Smaller than the metastyle, the parastyle is not joined by a crista to the paracone. One specimen (F:AM 76696) has a small protocone on it that is linked by a basal cingulum with the parastyle. All other specimens display a medial bulge in the protoconal region but lack both a protocone and a basal cingulum.

P<sup>3</sup> may be either double or triple rooted. In those specimens where three roots are developed, the largest is above the parastyle and the other two, which are subequal in strength, overlie the metastyle and protocone or protoconal region. Where only two distinct roots are present, it is owing to the apparent fusion of the latter two, equally strong roots.

P<sup>4</sup>: This tooth is several times larger than the preceding P<sup>3</sup>. The height of the paracone, tallest cusp on the tooth, is about four-fifths the length of the tooth. One-third the height of the paracone, the protocone is lingual and slightly anterior to that cusp, as in modern hedgehogs. Posterolingual to the protocone is the somewhat larger hypocone which is either subequal in height or somewhat taller. No crest links these cusps either to one another or to the buccal structures of the tooth. Behind the hypocone on the lingual side of the tooth is an extensive, nearly planar surface. No parastyle is present, and the elongate metacrista terminates posteriorly without a distinct metastyle. Between the metacrista and the base of the paracone on F:AM 76693 is a well-developed carnassiform notch. This is not an artifact of preservation because it is present on both the right and left P<sup>4</sup>. F:AM 94233 is heavily worn but appears to have vestiges of such a notch whereas F:AM 76696, which is less worn, has no indication of a carnassiform notch. No buccal cingulum is present but a well-developed precingulum is present along the anterior side of the base of the paracone. Three roots are present on the tooth. Two of them are subequal in strength and anteroposteriorly elongated, one above the metacrista,

the other above the protocone and hypocone. The third root is the weakest and is above the paracone.

M<sup>1</sup>: Largest tooth in the skull, M<sup>1</sup> is slightly broader and somewhat shorter to somewhat longer anteroposteriorly than P<sup>4</sup>. Height of the paracone, tallest of the four principal cusps, is half the length of the tooth. The paracone is anterobuccal to the metacone, the two cusps are linked together by a low centrocrista, and their bases are confluent. In contrast, on M<sup>1</sup> of modern hedgehogs the paracone is anterior or anterolingual to the metacone. Second tallest cusp on the tooth, the metacone has a steep anterior side and a more steeply dipping posterior one. Third tallest and most lingual cusp on the tooth, the protocone is lingual and somewhat anterior to somewhat posterior to the paracone. Its base projects for a short distance medially beyond the body of the tooth. Posterobuccal to the protocone is the lowest of the four principal cusps, the hypocone. The hypocone and metacone are closer to the midline of the tooth than the protocone and paracone. Such is the condition of M<sup>2</sup> on some modern hedgehogs but never M<sup>1</sup>. Linking the anterobuccal corner of the protocone and the anterolingual corner of the paracone are the well-developed preprotocrista and preparaconule crista. The preprotocrista in anterior view has a broad inverted U-shaped profile. At its buccal end adjacent to the paracone base, the preprotocrista meets the preparaconule crista at a high point along the loph formed jointly by these two cristae. This high point may be homologous with the paraconule but there is no sign of a distinct cusp having been developed in that area. The postprotocrista is directed posterobuccally from the protocone. This crista divides at a point lingual to the anterior edge of the metacone, one branch extending posterolingually to the hypocone and the other, the postmetaconule crista, buccally toward the metacone from which it is separated by a marked notch. No metaconule is developed on this tooth. Situated at the buccal end of a short precingulum present along the anterior side of the para-

cone base is a small parastyle. It is so closely appressed to the anterobuccal side of the paracone that there is no room for the development of a paracrista. From the metacone, the metacrista extends posterobuccally for a distance equal to one-fourth the tooth length. Between the posterior tip of the metacrista and the parastyle is a weakly developed ectocingulum, segments of which are undeveloped on various specimens.

Three roots were present on this tooth, an anteroposteriorly elongated, bladelike one above the protocone and hypocone, and two smaller, crudely semicircular roots, one above the paracone and the other over the metacone.

M<sup>2</sup>: The structure that will be referred to as the metacone-hypocone hereafter in this description occurs as a mediolaterally elongate blade in some individuals and as a single conical cusp in others. Where it occurs as a single conical cusp, it occludes behind the talonid on M<sub>2</sub> midway between the entoconid and hypoconid, a position midway between where the hypocone and metacone would be expected to occlude were each developed as a distinct cusp. Including the metacone-hypocone, there are three distinct cusps on this tooth, the others being the protocone and paracone. Posterolingual to the paracone, the hypocone-metacone is posterobuccal to the protocone. The protocone is lingual to the paracone. Heights of the three cusps are subequal and about one-half the length of the tooth. Moderately deep, the trigon basin is bordered by a low postprotocrista between the protocone and hypocone-metacone. Highest of the crests, the preprotocrista forms a continuous wall between the protocone and paracone. Linking the paracone and hypocone-metacone is a crista with a broad, inverted U-shaped profile in labial view. A prominent ectocingulum is present buccal to the paracone. Anterior to the paracone is a short precingulum.

LOWER DENTITION: I<sub>1</sub>: On the single specimen where this tooth is unbroken (F:AM 76696), its tip is slightly worn and its length above the alveolus is 7.5 mm. In cross section, the crown of the tooth is nearly circular

except for the medial side which is straight. In contrast, the root is mediolaterally compressed and elliptical in cross section. Beneath  $I_2$ , the dorsoventral axis is one and one-fifth times the length of the mediolateral axis. At this same point the dorsoventral axis is half the depth of the jaw. The dorsal border is almost imperceptibly concave and the ventral border is convex. In a pattern typical of gliriform teeth,  $I_1$  curves from an orientation parallel to the ventral margin of the mandible at its posterior extreme to an anterodorsal direction below  $I_2$ . The roots of  $I_2$ ,  $C_1$ , and  $P_4$  extend downward lateral to the  $I_1$  root. The posterior tip of  $I_1$  root is close to the anterior root of  $M_1$ . On the one specimen where the posterior tip of  $I_1$  root could be observed (F:AM 76696), the root was open.

$I_2$ : Extending anteriorly from the root, the crown overlaps  $I_1$ . Lying on the midline of this tooth near the anterior end is the protoconid. Its height is about one-fourth the length of the tooth. Along the midline of the tooth near its posterior end is a short, low crest. The root of this tooth is directed posteroventrally and is nearly circular in cross section with a diameter of 1.0 mm. The depth of the alveolus is greater than 1.4 mm. All measurements of  $I_2$  alveolus given here were made on F:AM 76696.

$C_1$ : This tooth and  $I_2$  are similar in morphology. The protoconid is slightly taller, its height being approximately one-third the length of the tooth. The crest at the rear of the tooth parallel to the midline is somewhat longer and is joined by a second crest that extends lingually along the posterior border of the talonid. Extending posterolingually from the tip of the protoconid is a third crest.

Elliptical in outline, the alveolus for this single-rooted tooth has a major axis mediolaterally directed and 1.2 mm. in length and a minor axis 1.0 mm. long. Depth of the alveolus is unknown.

$P_4$ : This tooth is shorter, broader, and taller than  $C_1$ . Only the protoconid is developed as a distinct cusp; its height is one to one and one-fourth times the tooth length. Nearly the entire anterior two-thirds of the tooth is covered by the base of this cusp. Along

the anterolateral and anteromedial sides of the base of the protoconid is a basal cingulum which may be quite broad or so narrow as to be barely perceptible. No distinct paraconid is developed on this cingulum nor is there any other trace of that cusp. No bulge is present in the base of the protoconid at its posterolingual corner nor is there any other trace of the metaconid. Along the rear of the base of the protoconid is developed a narrow postcingulum that is nearly horizontal and extends from the medial to the buccal side of the tooth.

On no specimen of this double-rooted tooth are the alveoli exposed.

$M_1$ : The length of the trigonid is half to three-fifths the length of the tooth. The width of the trigonid is subequal to its length. As in other brachyricines, the prevallid is expanded anteriorly. Lowest of the trigonid cusps, the paraconid is anterior to the metaconid, and the bases of the two cusps are separated by a deep cleft. The protoconid is posterobuccal to the paraconid. Linking the two cusps is the paralophid, which in lateral view has a broad V-shaped profile and in occlusal view is somewhat buccally convex. Tallest of the trigonid cusps, the protoconid is two-thirds as tall as the tooth is long. The metaconid is anterolingual to the protoconid, and the bases of the two cusps are connate.

Width of the talonid is slightly greater than equal to one and one-fifth times that of the trigonid. Situated at the extreme posterior corners of the talonid are the hypoconid and entoconid. Although tallest of the talonid cusps, the entoconid is lower than the paraconid. The hypoconid lies slightly more labial than the protoconid. Extending anterolingually from the hypoconid, the cristid obliqua abuts against the posterior wall of the trigonid at a point below the protoconid. Because the entocristid is weak, the talonid basin is open lingually. A labial cingulum extends from a point buccal to the paraconid to another point buccal to the hypoconid. As in most erinaceids, in occlusal view, the buccal border of the tooth from the protoconid to the hypoconid and the lingual border from the metaconid to the entoconid are nearly straight.

Between the alveoli of the double-rooted  $M_1$  is a thick partition with a prominent dorsoventral crest on the anterior side and a second, somewhat weaker crest on the posterior side. Anterior alveolus is roughly triangular in outline and posterior alveolus, rectangular. Dimensions of the anterior alveolus of F:AM 76700 are 1.8 mm. mediolaterally and 2.2 mm. anteroposteriorly. Dimensions of the posterior alveolus of the same specimen are 2.2 mm. mediolaterally and 2.3 mm. anteroposteriorly.

$M_2$ : This tooth is about three-fourths as long as  $M_1$ . The trigonids of the two teeth are subequal in width but the talonid width of  $M_1$  is nearly one and one-half times that of  $M_2$ . The trigonid length is half the total length of the tooth. The prevallid is not as expanded anteriorly as on  $M_1$ , the length of the trigonid being three-fourths its width. Lowest of the three trigonid cusps, the paraconid is anterobuccal to the metaconid, and the bases of the two cusps are separated by a deep cleft. The protoconid is posterobuccal to the paraconid. Linking the two cusps is a paralophid that in lateral view has a broad V-shaped profile and in occlusal view is straight. As tall or taller than the metaconid, the protoconid is three-fifths as tall as the tooth is long. The metaconid is lingual to the protoconid, and the bases of the two cusps are joined by a short protolophid.

The talonid is four-fifths to seven-eighths the width of the trigonid. Tallest of the talonid cusps, the entoconid is markedly taller than the paraconid and nearly as tall as the metaconid. Both the hypoconid and entocoid are slightly closer to the midline of the tooth than are the metaconid and protoconid. No hypoconulid is present. Extending anterolingually from the hypoconid, the cristid obliqua abuts against the posterior wall of the trigonid at a point below the protoconid. Best developed on the anterior side of the entoconid, the entocristid is lowest immediately posterior to the trigonid. The labial cingulum extends the length of the prevallid.

This tooth is double rooted as are  $P_4$  and  $M_1$ . Unlike those two anterior teeth, the midline is not subparallel to the long axis of the mandible but forms an angle of 13–19 de-

grees in the occlusal plane, and the talonid is posterolingual to the trigonid. The posterior alveolus is elliptical in outline and anteroposteriorly elongated. Its major axis is 1.8 mm. in length, its minor axis is 1.2 mm. in length on F:AM 76710.

**FACE:** The zygoma is elevated toward its posterior end and, in contrast to modern hedgehogs, is deep except where it joins the body of the squamosal. The dorsal profile is straight and rises to a maximum height at its posterior end where the sagittal crest joins the occipital crest.

As is typical of erinaceids, the nasals were long and narrow, their posterior end tapering to a point between the left and right frontal bones opposite the anterior end of the orbit. Owing to damage at the anterior end of all the skulls available, it is impossible to determine how far forward the nasals extended relative to the premaxilla. Unlike the case in *Brachyerix macrotis*, the premaxilla remained firmly attached to the maxilla behind it even in death. The maxilla-premaxilla suture begins ventrally between  $C^1$  and  $I^3$  and forms an irregular arc that curves upward and backward. Contact between the premaxilla and frontal was extensive, equal to the width of the nasals in that region. No trace of a separate lacrimal is present on any specimen. The supraorbital crest is strong, and an extension from it passes anterior to the lacrimal foramen, enclosing it within the orbit before turning posteriorly along the crest of the zygoma. Construction of this crest is similar to that of smaller species of the Galericinae (=Echinosoricinae).

The anterior end of the zygomatic arch is formed from the maxilla. Confined to the narrow space below the maxilla and squamosal near the center of the arch, the jugal is a small triangular element similar to that of erinaceines. A deep excavation into the anterior face of the zygomatic arch probably served as a site for the origin of the snout musculature as in the smaller species of the Galericinae.

**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

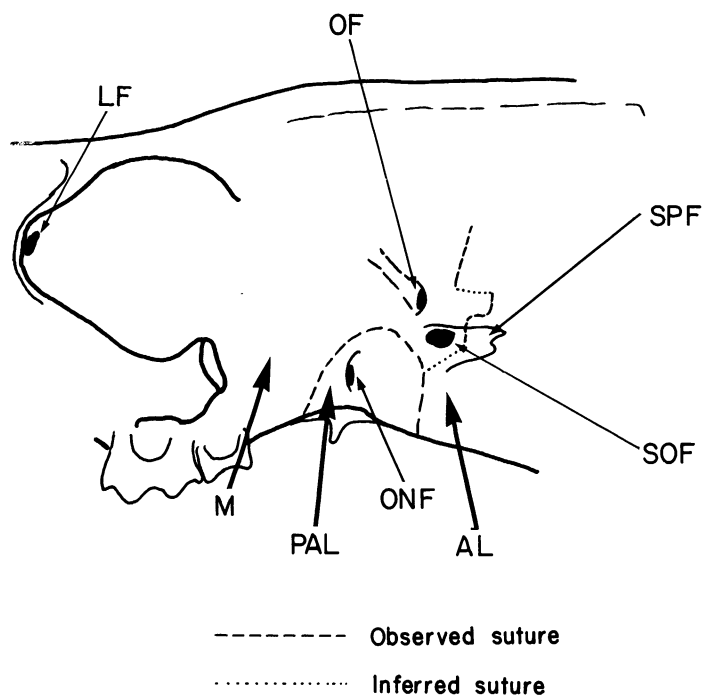


FIG. 16. *Metechinus amplior*, new species, diagrammatic reconstruction of left orbitotemporal region of skull in lateral view based on F:AM 74923 (type), and 74921. Approximately  $\times 3$ .

extends as far forward as the anterior side of  $I^2$ . Because all specimens are at least slightly damaged along the anterior border of the palatine, the absence of palatine fissures in this region is probably due to the state of preservation because these structures are generally present in erinaceids. If the palatal region of the maxilla is complete in the least distorted specimen (F:AM 74921), the length of the palate from the anterior border of the maxilla to the transverse crest near the posterior end of the palate is 23.6 mm. The palate extends for a short distance behind the transverse crest, as in the modern Erinaceinae and the galericine *Hylomys*.

Notches homologous to the posterior palatine foramina are developed in the transverse crest medial to the palatine-maxilla suture. Projections from the transverse crest extend toward one another but fail to meet, leaving these notches open ventrally. The position of the posterior palatine foramina is

duplicated in the galericines, but development as notches rather than holes is found only in some erinaceine genera.

Extending posteriorly to a small foramen, a slight groove is developed on either side of the midline at the anterior end of the palatine. Presumably this groove is homologous to the more extensive but weaker groove found in galericines, in which the palatine nerve and artery lie. In addition to the small foramen just mentioned, as many as three more may pierce the palatine. The bones of the palate are as thick and solid as those of the galericines. No vacuities typical of the erinaceines are present in the palate.

The shortening of the skull that has occurred in *Metechinus amplior* is reflected in the position of the teeth relative to the orbital region. The infraorbital foramen is above the center of  $P^3$ , the anterior end of the orbit lies above the anterior end of  $P^4$ , and the base of the zygomatic arch is opposite  $M^1$ .

**ORBITOTEMPORAL REGION:** Damage is so extensive on the five skulls of this species available to me that a complete description of this region is not now possible. What information is presented here is gleaned from a composite reconstruction based on F:AM 74921 and F:AM 74923 (see fig. 16).

Most of the anteromedial wall of the orbit appears to have been formed by the maxilla. Because of an absence of sutures, the relative contributions of the frontal, orbitosphenoid, alisphenoid, and parietal to the posteromedial wall of the orbit are unclear. The palatine contribution is a small one.

As in the modern galericines, the orbitonasal foramen is situated in the palatine near the transverse palatine crest and the suture with the maxilla, and is well separated from the sphenorbital foramen. Contrary to a statement in Rich and Rich (1971, p. 32), the condition in *Brachyerix macrotis* is similar, and unlike that in modern erinaceines. There is no direct evidence as to the position of the ventral half of the orbitosphenoid-alisphenoid suture on any available specimen of *Metechinus amplior*. The position of the suture shown in figure 16 between these two bones was drawn on the assumption that the position of the suboptic foramen relative to the orbitosphenoid was the same as in *Brachyerix macrotis* and other erinacids; i.e., in the posteroventral corner of that bone. As is the case with the suboptic foramen, the precise position of the optic foramen with respect to the boundaries of the orbitosphenoid is unknown. The optic foramen is anterodorsal to the suboptic foramen. Extending anterodorsally from the optic foramen is a groove that terminates anteriorly at a position dorsal to the orbitonasal foramen. Most certainly, the failure to observe ethmoid foramina was not owing to their absence in the animals when alive but to the poorly preserved state of the region surrounding the orbitosphenoid-frontal suture on all available specimens. As in *Hylomys* and *Neotetracus*, the sphenorbital foramen is immediately posterior to the suboptic foramen. Unlike *Brachyerix macrotis*, there is no distinct crest merging with the dorsal edge of the sphenorbital foramen and extending anterodorsal-

ly, passing above the optic foramen. Posterodorsal to the optic foramen is a depression that is similar to ones seen in various modern genera.

In contrast to *Brachyerix macrotis*, no sign can be seen of a groove extending posteriorly from the sphenorbital foramen, passing above the external pterygoid process of the alisphenoid and below the foramen ovale before terminating at the anterolateral corner of the auditory bulla. No signs of openings for the alisphenoid canal are present although this structure is commonly found in modern hedgehogs. As in living erinaceids, the foramen rotundum is not distinct from the sphenorbital foramen, and the foramen ovale is large and immediately anterior to the auditory bulla.

**BASE OF THE CRANIUM:** Although the precise position of the relevant suture is obscured by damage, it is clear that both the palatine and alisphenoid bones form the internal and external pterygoid processes as in all modern erinaceids. The external pterygoid process passes posteriorly into a sharp crest that extends laterally along the anterior edge of the auditory bulla and terminates just medial to the postglenoid process from which it seems to be separated by a shallow notch. This entire ridge appears to be formed by the alisphenoid with no contribution from the squamosal. In Rich and Rich (1971, p. 34), I incorrectly interpreted a much blunter ridge apparently homologous to this one as the tympanic wing of the sphenoid (=alisphenoid and basisphenoid combined). This ridge alone is not the entire sphenoid or even alisphenoid contribution to the auditory bulla and thus the term was improperly employed. With regard to the true tympanic wing of the alisphenoid, I then asserted that Butler (1948, p. 456) had confused the condition found in the two subfamilies of living erinaceids as to whether the tympanic wing of the alisphenoid extended as far laterally as the postglenoid process. Butler stated that in the Galericinae (=Echinosoricinae), the tympanic wing extends as far laterally as the postglenoid process and in the Erinaceinae, the tympanic wing stops short of the postglenoid process. I stated that the condition of the two

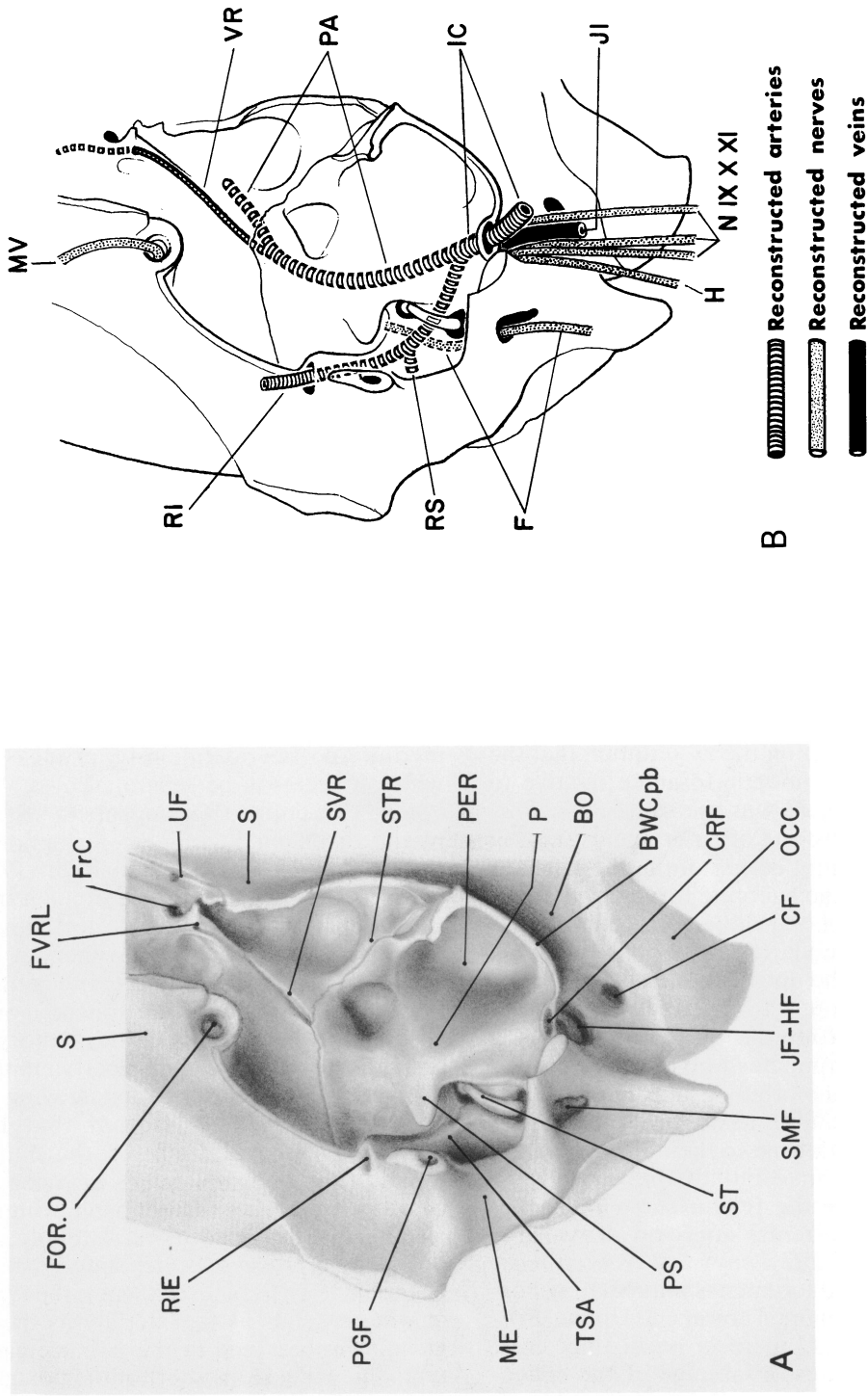


FIG. 17. *Metachinus amplior*, new species. A. Reconstruction of right tympanic region in ventral view based on the left and right tympanic regions of F:AM 74923 (type), 76715, and 94233. B. Reconstruction of arteries, veins, and nerves of the right tympanic region. (Tracing of B placed over A will give a clearer idea of the relationships between the structures portrayed in each figure.) Approximately  $\times 6$ .



subfamilies had been inadvertently reversed. Re-examination of the material shows that we both erred, I to a greater degree, for although a crest may extend close to the vicinity of the postglenoid process in the *Galericinae*, near the postglenoid process this crest is formed not by the alisphenoid but by the squamosal in both subfamilies of living *Erinaceidae*; thus it is incorrect to say that the tympanic wing of the *alisphenoid* is adjacent to the postglenoid process. The pterygoid is not present as a distinct ossification and is fused to the alisphenoid without any trace of a suture. No trace can be seen of a small venous foramen that is found near the posterior end of the groove between the internal and external pterygoid process in living hedgehogs. However, the poor preservation of all specimens in this area prevents a definite conclusion.

*Metechinus amplior* lacks the deep groove in the base of the skull that is terminated posteriorly by the basisphenoid pit which is the hallmark of the modern *erinaceines*.

On the external surface of the medial wall of the bulla, immediately anterodorsal to the medial end of the sulcus for the eustachian canal, is the opening for a small canal that passes dorsally into the braincase (UF in fig. 17a). Such a canal is not present in modern *erinaceids* although the bone in this region may be perforated by tiny foramina that appear to end blindly.

As in the *erinaceines*, the condylar foramen is a single opening at the base of a small pit close to the occipital condyle. Unlike the *galericines*, the condyle is not emarginated by the condylar foramen.

The stylomastoid foramen, opening at the posterior part of the lateral margin of the auditory bulla, is elongated anterolaterally and separated from the external auditory meatus by a partition formed wholly or in part by the mastoid. Whether there is a periotic contribution to this partition is unclear because no suture between that bone and the mastoid can be seen in the area in question on any of the specimens available owing to damage. Unlike the case in *Brachyerix macrotis*, the hypoglossal and jugular foramina do not ap-

pear to be separated from one another. This may be due to postmortem damage. Situated adjacent to the posterior end of the auditory bulla, the jugular-hypoglossal foramen is an anteroposteriorly elongated depression. Together, the jugular-hypoglossal foramen and this depression cover the same area as the jugular and hypoglossal foramina on the basicranium of *B. macrotis*. The stylomastoid and jugular-hypoglossal foramina are separated by a partition formed by the mastoid which is pierced by a canal. Presumably, this canal was occupied by the auricular branch of the vagus nerve (X), which in *Canis familiaris* links the main branches of the vagus (X) and facial (VII) nerves in this region of the skull (Miller et al., 1964, fig. 10-16). There is no ledgelike process extending anteromedially from the jugular foramen along the margin of the bulla to its posteromedial corner.

**TYMPANIC REGION:** Bullae are broader than long, well separated, and flask-shaped. All walls of the bulla are single layers of compact bone. Processes of the alisphenoid, basisphenoid, tympanic, and periotic form the auditory bulla. The anterior wall of the bulla is formed by the alisphenoid which appears to be separated laterally from the basisphenoid by a poorly defined suture on two specimens (F:AM 74923 and 76715) immediately behind a low ridge along the anterior edge of the ventral surface of the auditory bulla between the lip of the external auditory meatus and the medial opening of the eustachian canal. This suture, if correctly identified, is fused medially. The anterior two-thirds of the ventral and medial walls of the auditory bulla are formed by the basisphenoid, whereas the periotic forms the posterior third of these same partitions.

The eustachian tube passed out of the auditory bulla through a foramen near the anteromedial corner of the bulla and continued anteromedially for a short distance across the front of the bulla in a well-defined groove or sulcus. Although no specimen can be cited as unequivocally demonstrating the presence of internal pterygoid processes ventrally bridging the medial end of the sulcus for

the eustachian tube, F:AM 76706 does appear to possess the anterior bases of such processes, the actual processes presumably having been broken off.

Except for *Paraechinus*, the structure of the tympanic roof is quite unlike that in any of the modern erinaceids. It is divided into a series of pockets separated from one another by hollow and solid struts and the promontorium. The hollow struts serve as passageways for the arterial blood supply and the facial nerve. The Vidian ramus of the promontory artery is attached for part of its length to the ventral surface of one of the solid struts. Other solid struts do not appear to serve as pathways for blood vessels or nerves. A flat plate projects laterally from the petrosal immediately anteroventral to the fenestra ovalis (PS in fig. 17a). No other known erinaceid has a comparable structure. In the dorsal roof of the tympanic cavity can be seen clearly the suture between the periotic and sphenoid where it is directed mediolaterally immediately anterior to the promontorium. Medially the suture curves to a posteromedial orientation and is visible on the crest of a strut that abuts the medial wall of the bulla.

The internal carotid artery entered the tympanic cavity at the rear through the carotid foramen in the periotic. Immediately after entering, the artery bifurcated into two branches, the stapedia and promontory branches of the internal carotid artery. Leaving the promontorium, the stapedia artery passed through the obturator foramen of the stapes enclosed in a bony intercrural canal. Still enclosed in bone, the stapedia artery passed anterodorsolaterally into a recess that opens into the braincase. The posteroventral lip of this recess is formed by the bony tube enclosing the anterior vertical semicircular canal which surrounds the subarcuate fossa, the recess being anterodorsal to that fossa. Bifurcation of the stapedia artery occurred in this recess, the superior ramus passed into the braincase and the inferior ramus entered another bony tube that carried it ventrally along the anterior edge of the epitympanic recess. Four bones contribute to the walls of this bony tube of the inferior ramus: dorsal-

ly, petrosal; posteroventrally, tympanic; anteroventrally, alisphenoid; and ventrolaterally, squamosal. The inferior ramus exits the tympanic region through a foramen at the posterolateral corner of the tympanic wing of the alisphenoid. Enclosed in a tube, the promontory artery continued forward across the promontorium and bifurcated into a large medial branch that entered the braincase medial to the point of bifurcation and a smaller lateral branch, the Vidian ramus. The Vidian ramus emerged onto the roof of the auditory cavity from a bony tube at the periotic-sphenoid suture and continued anteriorly along the ventral crest of a strut, finally leaving the auditory cavity through a foramen near the anterior end of that cavity (F VR L in fig. 17a). In its passage forward into the braincase, the canal which contained the Vidian ramus joined a much larger canal and together extended forward to emerge into the ventral floor of the braincase at a point dorsal to the anteromedial corner of the bulla. This larger canal can be traced for only a short distance posterior to the point of juncture with the Vidian ramus. It passes posteriorly in the medial wall of the bulla and hence medial to the Vidian ramus. The foramen where this canal passed anteriorly into the sphenoid can be clearly seen (FrC in fig. 17a). What purpose this canal may have served remains a mystery. Conceivably, it could have terminated as a blind pocket. Presumably, if the palatine branch of nerve VII was present and similar to living erinaceids, it left the auditory cavity and entered the braincase through the same foramen as the Vidian ramus. However, no foramen can be seen on the periotic-sphenoid suture lateral to that for the Vidian ramus where the palatine branch of nerve VII would have entered the auditory cavity to pass anteriorly if it had a pattern similar to living erinaceids.

From the point where the facial branch of nerve VII left the braincase through a foramen in the internal auditory meatus, passed posteriorly through the auditory chamber, and finally emerged from that chamber at its posterior margin via the stylomastoid foramen, the nerve was completely enclosed by

a continuous bony canal. The canal passed posteriorly immediately lateral to the fenestra ovalis and crossed but did not open into the canal for the stapedial artery, so that the facial nerve passed immediately dorsal to that artery. There is no sign of an opening to the facial canal immediately anterior or posterior to the fenestra ovalis, nor is there a swelling or tube on the roof of the auditory cavity to mark its passage except behind the bony intercrural canal that was enclosed by the stapes.

The mandibular branch of nerve V was enclosed in a tube in the anterior part of the tympanic cavity and exited through the foramen ovale. The fenestra rotunda is immediately posteromedial to the fenestra ovalis, faces posterolaterally and opens into a small recess bounded laterally by the tube for the facial nerve and posteriorly by the anterior wall of the stylomastoid foramen. In figure 17a, the fenestra ovalis is covered by the dorsal end of the anterior crus of the stapes.

Some cylinders and ridges in the tympanic cavity seem to have carried no nerves or vessels. Two major struts occur near the midline of the skull. One lies medial to the promontorium and the other lies medial to the strut that carried the Vidian ramus. Unlike *Brachyerix macrotis*, there is no transverse cylinder from the anterior end of the stapedial tube to the promontory tube, nor is there a second strut medial to the Vidian ramus or an additional strut farther anterior along the midline of the skull.

The tympanic cavity has expanded anteriorly above the posterior part of the palatines, anteriorly into the sphenoid, laterally into the squamosal, posteriorly behind the promontorium into the periotic, and dorsally into the braincase along the midline.

The tympanic ring is firmly attached to the sphenoid and periotic. The crista tympanica is quite strong and the recessus meatus acustica externi increases gradually in width from the tips of the anterior and posterior legs to the maximum at the ventral extreme of the tympanic near the sphenoid-periotic suture. Except for the most dorsal part of the tympanic, it is completely enclosed within the auditory bulla, a condition found elsewhere

only in Tupaiidae (Szalay, 1972, p. 64), *Lepictitis* (McKenna, 1966, p. 12), and *Brachyerix* among the known Insectivora. The anterior leg forms the ventral part of the posteromedial wall of the bony tube for the inferior ramus of the stapedial artery. The posterior leg of the tympanic ring covers a small area of the posterior lip of the external auditory meatus.

Only a short gap separates the spinae tympanicae anterior and posterior, indicating that the pars tensa and flaccida of the tympanic membrane were nearly separated from one another. The spina tympanica anterior is quite close to the posterior tip of the anterior leg of the tympanic. Even closer are the spina tympanica posterior and the anterior tip of the posterior leg of the tympanic.

In the region of the sulcus malleolaris on the medial side of the anterior leg of the tympanic ring there is no space for the tympanic plate of the malleus if that element was developed to a degree remotely similar to living erinaceids and has been lost from all available specimens. However, in the left auditory region of one specimen (F:AM 76715), there is a structure which is tubular in appearance and immediately adjacent and anteromediodorsal to the anterior leg of the tympanic. No sign of a suture exists between this structure and the periotic. Part or all of this structure may be the otherwise missing tympanic plate of the malleus. If only partly formed by the malleus, then some fraction of the medial region of this tubular structure is contributed by the periotic. No indication exists of exposure on the anterior surface of the bulla of the anterior tip of the tympanic plate of the malleus between the tympanic and alisphenoid.

Except for the possible tympanic plate of the malleus described above, that bone along with the incus is unknown in *Metechinus amplior*. Not all of the stapes can be seen where this bone is preserved (F:AM 76715) for the intercrural canal in its passage through the obturator foramen of the stapes obscures the posterior crus and the posterior part of the footplate. The head is markedly narrower than the shoulders of either crura. Along the lateral side of the head is a deep

groove. The diameter of the anterior crus decreases as the footplate is approached.

**CRANIAL ROOF AND POSTERIOR SURFACE:** The postorbital process is stronger than in any living hedgehog. As in all Recent erinaceids except *Hylomys* and *Neotetracus*, the maxilla and parietal are well separated. Closest resemblance in the pattern and relative sizes of the temporal and sagittal crests is to be found in the larger species of Recent hedgehogs. Both crests are strongly developed and meet immediately posterior to the point where the nasal-frontal suture intersects the sagittal plane and far forward of the point where the sagittal plane cuts the frontal-parietal suture. Delicate sculpturing covers most of the parietal and the lateral surfaces of the mastoid and squamosal, as it does on the skull of *Brachyerix macrotis*. The prominence of this sculpturing is variably developed on different specimens, strong on one, weak on another, barely discernible on a third.

The interparietal bone forms the dorsal part of the occipital crest and extends laterally to contact the mastoid. As in modern hedgehogs and unlike *Brachyerix macrotis*, the interparietal is not expanded anteriorly between the parietal and the mastoid at its ventral extreme. Rich and Rich (1971, p. 39) stated that the occipital crest on *B. macrotis* expanded anteriorly between the parietal and mastoid; it would have been more accurate to say that the interparietal was so developed. Unlike any modern hedgehog, the mastoid has expanded posterolaterally to form a prominent lambdoid crest that is nonetheless somewhat weaker than the posteriorly directed one seen in *Brachyerix*. As in modern erinaceids and unlike the condition found in *B. macrotis*, parts of the rim of the stylomastoid foramen can be seen in lateral view because there is no flange of mastoid lateral to it to obscure the view. The occipital process is appressed against the much larger mastoid process so that only a single crest is present.

The squamous region of the zygomatic arch may be envisioned as two tabular bars meeting at right angles. Projecting laterally from the body of the skull, the first bar is

parallel to the frontal plane. Along its posterior face is a groove slightly medial to the center of which is a small foramen. Beginning at the distal end of the laterally directed bar and extending anteriorly is a second tabular bar parallel to the sagittal plane. Just as in *Metechinus nevadensis* and unlike *Brachyerix macrotis*, the lateral surface of this bar is flat, not concave, and no flange sharply separates this flat surface from the posterior side of the first bar.

The posterior face of the skull is relatively flat and slopes posteroventrally, departing farther from the vertical than in modern erinaceids but not to the degree seen in *Brachyerix macrotis*. No sign of the suture between the exoccipital and supraoccipital bones could be found on any of the available specimens. The oval outline of the foramen magnum is transversely elongate, the dorsal edge rising well above the condyles as in modern hedgehogs except *Echinosorex*. Unlike erinaceines, there is no emargination of the supraoccipital along the midline by the foramen magnum.

**WALLS OF THE BRAINCASE:** On the internal surface of the periotic three distinct foramina and one fossa are present. Their arrangement is extremely similar to that in modern hedgehogs. The two smallest and most posterior are the foramina for the cochlear and endolymphatic ducts. The foramen for the cochlear aqueduct is directly anterior to the hypoglossal canal in the exoccipital. Lateral and dorsal to it is the foramen for the endolymphatic duct. Anterior to both are the large internal auditory meatus and the subarcuate fossa, the latter being the largest, most laterally and dorsally placed of the four openings. Although it is not possible to examine the extreme ventrolateral region of the internal auditory meatus, the morphology of the internal surface of the periotic in general and the rim of the internal auditory meatus in particular are so similar to the conditions found in living erinaceids that there seems to be no reason to doubt that the facial nerve (VII) and the two branches of the auditory nerve (VIII) entered the periotic from the braincase via the internal auditory meatus. The posterior and dorsal parts of the rim of

the subarcuate fossa are somewhat swollen owing to the presence of the anterior semicircular canal which in these regions lies immediately under the surface of the bone. In a similar manner, the ventral rim of the fossa is swollen by the presence of the vestibule of the semicircular canal system.

No suture between the basisphenoid and alisphenoid is evident on the floor of the braincase, thus the collective term sphenoid is employed here. Near the midline can be seen two small foramina, the points of entrance into the braincase of two small arteries: anteriorly, near the palatine-sphenoid suture is the foramen for the Vidian ramus; posteriorly, near the sphenoid-basioccipital suture is the foramen for the promontory artery. Approximately midway between these two foramina but lateral to a line joining them is the large opening for the short tube through which the mandibular branch of the trigeminal nerve (V) passes out of the braincase. The opening for this tube on the lateral surface of the skull is the foramen ovale.

On the lateral wall of the braincase there is a small area of squamosal between the sphenoid and periotic. Passage for the retroglenoid artery from the braincase was through a prominent foramen that led into a short tube directed ventrally which passed lateral to the anterior area of the epitympanic recess and finally exited the skull through the postglenoid foramen. A prominent groove on the medial surface of the lateral wall of the sphenoid passes posteriorly from the suture with the orbitosphenoid. Near its posterior end, the groove curves ventrally and joins another groove and together they pass into the tube for the retroglenoid vein. This second groove is preserved for only a short distance on all the available specimens. It was directed dorsally from the point of juncture with the first groove. A probable hypothesis is that these two grooves mark the pathways of two branches of the retroglenoid vein.

**MANDIBLE:** The mental foramen lies below the posterior root of  $P_4$ . Beneath  $P_4$  is a wide groove that extends anterodorsally from the mental foramen. Beneath the posterior root of  $P_4$  the jaw is deepest. It rapidly becomes shallower both anteriorly and pos-

teriorly from that point. Unlike *Brachyerix macrotis*, the angle protrudes well beyond the adjacent margin of the jaw although not to the degree seen in any modern erinaceids.

Extending forward from beneath the anterior end of  $M_1$ , the unfused symphysis occupies the ventral three-fifths of the mandibular medial surface. The dorsal border of the symphysis is nearly straight and subparallel to the ventral border, diverging somewhat anteriorly. No groove or other depression is present on the symphyseal surface to mark the site of insertion for the geniohyoideus muscle.

The ascending ramus lies slightly labial to the midline of the mandible. Its anteroposterior length measured from the condyle is almost twice the maximum depth of the jaw. Up to the height of the condyle, the anterior edge of the ascending ramus is straight and nearly vertical; above this, the ascending ramus is unknown. A strong lateral flange on the leading edge of the ascending ramus forms the anterior margin of the masseteric fossa. A ridge near the base and on the medial side of the ascending ramus extends from near the anterior edge of the ascending ramus posterodorsally toward the mandibular condyle becoming weaker posteriorly. Immediately ventral to this ridge is the mandibular foramen, which is level with the tooth row and is about one-third the distance from the anterior to the posterior edge of the ascending ramus. The condyle lies slightly above the level of the tooth row. In posterior view, the margin of the mandible tapers gradually from maximum thickness at the condyle to a minimum thickness immediately above the angle. A ridge extending anteroventrally from the condyle forms the posteroventral border of the masseteric fossa.

F:AM 74925 appears to be an unusual mandible in that when viewed from a dorsal vantage point, the horizontal ramus has a pronounced anteromedial curve (see fig. 15b). This contrasts markedly with the practically straight rami seen in the two other nearly complete rami of *Metechinus* that are available and the rami of *Brachyerix* and those of other subfamilies of erinaceids. This distortion does not seem to be an effect of

TABLE 26  
Skull Measurements (in Millimeters) of *Metechinus amplior*

[illegible]

TABLE 26—(Continued)

	F:AM 74923 (Type)	F:AM 74921	AMNH 48998	F:AM 74922	F:AM 74924	F:AM 76693	F:AM 76696	F:AM 76709	F:AM 76741	F:AM 94233	UCMP 36163	UCMP 36164	UCMP 36165	UMMP V57329	UMMP V57332	F:AM 95182
I <sup>2</sup> , anteroposterior diameter <sup>a</sup>																
Left	1.8	—	—	—	—	—	—	—	—	—	1.8	—	—	—	1.7	—
Right	1.7	1.8	—	—	—	—	—	—	—	—	—	—	—	—	1.7	—
I <sup>2</sup> , transverse diameter <sup>a</sup>																
Left	1.5	—	—	—	—	—	—	—	—	—	1.3	—	—	—	1.1	—
Right	1.1	1.1	—	—	—	—	—	—	—	—	—	—	—	—	1.0	—
I <sup>3</sup> , anteroposterior diameter, left	—	—	—	—	—	—	—	—	—	—	2.0	—	—	—	1.8	—
I <sup>3</sup> , transverse diameter, left	—	—	—	—	—	—	—	—	—	—	1.5	—	—	—	1.3	—
C <sup>1</sup> , anteroposterior diameter																
Left	2.2	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Right	—	2.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C <sup>1</sup> , transverse diameter																
Left	1.3	0.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Right	—	0.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P <sup>8</sup> , anteroposterior diameter																
Left	1.4	—	—	—	—	1.6	—	—	—	1.8	—	—	—	—	—	—
Right	1.7	1.9	—	—	—	—	1.8	—	—	1.6	—	—	—	—	1.8	—
P <sup>8</sup> , transverse diameter																
Left	1.1	—	—	—	—	1.3	—	—	—	0.9	—	—	—	—	—	—
Right	1.1	1.3	—	—	—	—	1.4	—	—	0.9	—	—	—	—	1.3	—
P <sup>4</sup> , anteroposterior diameter																
Left	5.1	4.3	—	—	5.2	4.8	—	5.0	—	5.2	—	—	—	4.8	—	—
Right	5.1	4.5	—	—	—	—	4.9	—	—	4.9	—	—	—	4.9	4.6	5.1
P <sup>4</sup> , transverse diameter																
Left	4.1	4.2	—	—	4.3	4.3	—	4.2	—	4.2	—	—	—	4.1	—	—
Right	4.2	4.2	—	—	—	—	3.9	—	—	4.3	—	—	—	4.1	4.4	4.3

TABLE 26—(Continued)

	F:AM 74923 (Type)	F:AM 74921	AMNH 48998	F:AM 74922	F:AM 74924	F:AM 76693	F:AM 76696	F:AM 76709	F:AM 76741	F:AM 94233	UCMP 36163	UCMP 36164	UCMP 36165	UMMP V57329	UMMP V57332	F:AM 95182
M <sup>1</sup> , anteroposterior diameter																
Left	4.8	4.3	4.7	5.2	5.2	—	—	4.8	—	4.4	—	4.4	4.7	4.8	—	—
Right	4.7 <sup>a</sup>	—	—	—	—	—	5.3 <sup>a</sup>	—	—	4.7	—	—	—	4.7	—	4.6
M <sup>1</sup> , transverse diameter																
Left	5.3	4.6	4.5	5.5	5.5	—	—	5.4	—	5.0	—	4.7	5.2	5.3	—	—
Right	5.2 <sup>a</sup>	—	—	—	—	—	5.4	—	—	5.4	—	—	—	5.2	—	5.3
M <sup>2</sup> , anteroposterior diameter																
Left	2.9 <sup>a</sup>	—	—	3.3	—	3.2	—	—	3.4	3.0	—	—	—	2.9	—	—
Right	3.3	3.5	—	—	—	—	3.5	—	—	—	—	—	—	—	—	—
M <sup>2</sup> , transverse diameter																
Left	4.4	—	3.8	4.6	—	4.3	—	—	4.5	3.8	—	—	—	3.8	—	—
Right	4.4	4.0	—	—	—	—	4.3	—	—	3.8	—	—	—	—	—	—

<sup>a</sup> Distance from midline to zygomatic arch was doubled.<sup>b</sup> Measurement suspect because of distortion.<sup>c</sup> Minimum value due to damage.<sup>d</sup> Difficult to repeat measurement because method of taking measurement was not explicitly stated in Matthew (1929). Here the measurement was taken across top of skull between supraorbital processes.<sup>e</sup> Distance from supraorbital process to midline was doubled.<sup>f</sup> Distance from muzzle to midline was doubled.<sup>g</sup> Maximum value due to damage.<sup>h</sup> Measurement made at base of crown.



TABLE 27  
Mandible Measurements (in Millimeters) of *Metechinus amplior*

	F:AM 74925	F:AM 76696	F:AM 76697	F:AM 76698	F:AM 76699	F:AM 76700	F:AM 76701	F:AM 76708	F:AM 76710	F:AM 76711	F:AM 95182	
Mandible depth below anterior part of C <sub>1</sub>	5.0	—	—	—	—	—	—	—	5.4	—	5.4	
Mandible depth below M <sub>1</sub> anterior root	6.2	—	—	5.9	—	6.2	—	—	—	—	5.8	
Mandible depth below M <sub>2</sub> posterior root	6.2	—	—	7.0	—	6.1	—	5.3	5.7	6.0	—	
M <sub>1-2</sub> , length	9.4	—	—	10.3	—	—	—	—	—	—	—	
I <sub>2</sub> , anteroposterior diameter	—	—	—	—	—	—	—	—	—	—	2.3	
I <sub>2</sub> , transverse diameter	—	—	—	—	—	—	—	—	—	—	1.8	
C <sub>1</sub> , anteroposterior diameter	3.1	3.2	—	—	—	—	—	—	—	—	2.9	
C <sub>1</sub> , transverse diameter	1.7	1.9	—	—	—	—	—	—	—	—	2.0	
P <sub>4</sub> , anteroposterior diameter	2.3	2.7	—	—	—	—	—	—	2.2	—	2.4	
P <sub>4</sub> , transverse diameter	2.9	2.1	—	—	—	—	—	—	2.1	—	1.8	
M <sub>1</sub> , anteroposterior diameter	5.3	—	5.0	6.1	5.8	—	—	—	—	—	6.0	
M <sub>1</sub> , trigonid length	2.8	—	2.9	3.4	3.2	—	—	—	—	—	3.7	
M <sub>1</sub> , trigonid width	3.2	—	2.8	3.5	3.1	—	3.1	—	—	—	3.0	
M <sub>1</sub> , talonid width	3.8	—	3.2	3.9	3.6	—	3.7	—	—	—	3.8	
M <sub>2</sub> , anteroposterior diameter	4.0	—	—	4.1	—	—	—	4.1	—	4.3	—	
M <sub>2</sub> , trigonid length	2.0	—	—	2.3	—	—	—	2.2	—	2.3	—	
M <sub>2</sub> , trigonid width	2.6	—	—	2.9	—	—	—	2.6	—	2.5	—	
M <sub>2</sub> , talonid width	2.3	—	—	2.6	—	—	—	2.1	—	2.0	—	
	F:AM 76731	F:AM 76732	F:AM 76733	F:AM 94234	F:AM 94235	F:AM 94236	UCM 34441	UCMP 29211	UCMP 29212	UCMP 36162	UMMP V26995	UMMP V57332
Mandible depth below anterior part of C <sub>1</sub>	—	—	—	—	—	—	—	—	—	—	—	—
Mandible depth below M <sub>1</sub> anterior root	—	—	—	—	—	—	6.2	—	—	—	—	—
Mandible depth below M <sub>2</sub> posterior root	—	—	—	—	—	—	—	4.5	4.5	5.5	5.3	—
M <sub>1-2</sub> , length	—	—	—	—	—	—	—	—	—	—	8.1 <sup>a</sup>	—
I <sub>2</sub> , anteroposterior diameter	—	—	—	—	—	—	—	—	—	—	—	—
I <sub>2</sub> , transverse diameter	—	—	—	—	—	—	—	—	—	—	—	—
C <sub>1</sub> , anteroposterior diameter	—	—	—	—	—	—	—	—	—	—	—	—
C <sub>1</sub> , transverse diameter	—	—	—	—	—	—	—	—	—	—	—	—
P <sub>4</sub> , anteroposterior diameter	—	—	—	—	—	—	2.3	—	—	—	2.0	—
P <sub>4</sub> , transverse diameter	—	—	—	—	—	—	2.0	—	—	—	1.6	—
M <sub>1</sub> , anteroposterior diameter	—	—	—	5.7	5.6	5.6	5.9	5.1	—	—	—	—
M <sub>1</sub> , trigonid length	—	—	—	3.0	3.1	3.3	3.3	2.8	—	—	—	—
M <sub>1</sub> , trigonid width	3.1	2.5	—	3.2	3.1	3.3	3.4	2.8	—	—	—	—
M <sub>1</sub> , talonid width	3.4	2.9	—	3.6	3.3	3.6	3.5	2.9	—	—	—	—
M <sub>2</sub> , anteroposterior diameter	—	—	2.7	—	—	—	—	—	3.9	—	—	3.9
M <sub>2</sub> , trigonid length	—	—	1.5	—	—	—	—	—	2.2	—	—	2.1
M <sub>2</sub> , trigonid width	—	—	1.7	—	—	—	—	—	2.2	—	—	—
M <sub>2</sub> , talonid width	—	—	1.7	—	—	—	—	—	2.1	—	—	2.2

<sup>a</sup>Estimated from alveoli.

the processes of preservation for although the specimen is broken at two points, the curvature is continuous rather than owing to abrupt changes of direction at the sites of breakage. Nor is there any indication of malocclusion in the dentition nor any other effect that might be expected to be present if this were a pathological condition.

REMARKS: In his discussion of UCMP 50121, a fragment of  $M^2$  from the Cuyama Valley area of California that he referred to as *Metechinus* sp., James (1963, p. 66) noted that it probably belonged to the same species as UCMP 36164 and 36165 from Nebraska (both are here regarded as *Metechinus amplior*, new species) rather than *Metechinus nevadensis*. James thought it significant that this specimen differed from *M. nevadensis* in being greater in size, having a larger angle between the anterior and posterior margins of the tooth, and a position of the parastyle adjacent to rather than separated from the anterior border of the tooth (James, 1963, pp.

65–66). He could not explicitly compare this specimen with UCMP 36164 and 36165 because these specimens lack  $M^2$ , which indicated to him that a larger species of *Metechinus* existed. Comparison with presently available specimens of  $M^2$  of *M. amplior* shows that of the three particular features noted by James, only size appears to be a consistent difference separating this species and *M. nevadensis*. In that one feature, James's specimen is clearly allied with *M. amplior*.

#### *Metechinus* sp.

Voorhies listed *Metechinus* sp. as part of the Verdigre fauna. (See Localities, Section 45.)

An edentulous mandible (UCMP 28860) from the Gordon Creek Quarry has been identified as *Metechinus* sp. by McGrew (1938) and Webb (1969). (See Localities, Section 59.)

## LOCALITIES

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

Figure 18 graphically summarizes the North American stratigraphic data presented in this report.

### MEDIAL OR LATE OLIGOCENE

1. Nareen Bulak ( $44^{\circ} 52' N$ ,  $97^{\circ} 21' E$ ), Mongolia (Sulimski, 1970, pp. 64–65, 68–69; Gradziński, Kaźmierczak, and Lefeld, 1969, pp. 58–59).

### LATE? OLIGOCENE

2. Taben-buluk ( $39\frac{1}{2}^{\circ} N$ ,  $94\frac{4}{5}^{\circ} E$ ), western Kansu, China (Bohlin, 1942, p. 7; 1946, pp. 242–248).

### ARIKAREEAN

3. SDSM V6229 (=LACM 1871) ( $43\frac{1}{3}^{\circ} N$ ,  $102\frac{1}{4}^{\circ} W$ ), Shannon County, South Dakota, Monroe Creek Formation.<sup>3</sup>

4. SDSM V6215 (=LACM 2008) ( $43\frac{1}{4}^{\circ} N$ ,  $102\frac{1}{4}^{\circ} W$ ), Shannon County, South Dakota, Monroe Creek Formation.<sup>3</sup>

5. SDSM V6210 ( $43\frac{1}{4}^{\circ} N$ ,  $102\frac{1}{3}^{\circ} W$ ), Shannon County, South Dakota, Monroe Creek Formation.<sup>3</sup>

6. Cabbage Patch locality 2 (KU-Mt-9) (=MV6504-5, Rasmussen, MS, pp. 131–132) ( $46^{\circ} 38' 45'' N$ ,  $113^{\circ} 02' 47'' W$ ), Granite County, Montana, middle Cabbage Patch beds.

7. Cabbage Patch locality 3 (KU-Mt-11) (=MV6617, Rasmussen, MS, p. 140) ( $46^{\circ} 37'$

<sup>3</sup> More precise locality information is on file at the Museum of Geology, South Dakota School of Mines and Technology, Rapid City, and at the Los Angeles County Museum of Natural History.

50° N, 113° 01' 37" W), Powell County, Montana, middle Cabbage Patch beds.

8. Cabbage Patch locality 4 (KU-Mt-12) (=MV6504-4, Rasmussen, ms, pp. 131-132) (46° 38' 39" N, 113° 02' 42" W), Granite County, Montana, middle Cabbage Patch beds.

9. Cabbage Patch locality 13 (KU-Mt-46) (46° 38' 42" N, 113° 02' 42" W), Granite County, Montana, middle Cabbage Patch beds.

10. Bert Creek locality 2 (=MV6504-2, Rasmussen, ms) (46° 38' 45" N, 113° 02' 42" W), Granite County, Montana, middle Cabbage Patch beds.

11. Tavenner Ranch locality 2 (KU-Mt-21) (=locality 1, Wood and Konizeski, 1965, p. 462) (46° 27' 27" N, 112° 49' 25" W), Powell County, Montana, upper Cabbage Patch beds.

12. (45<sup>1</sup>/<sub>5</sub>° N, 106<sup>7</sup>/<sub>8</sub>° W), near Yampa, Routt County, Colorado.<sup>4</sup> From a lithic unit tentatively regarded as the Split Rock Formation (Robinson, 1972, p. 234). In that general area of Colorado is a sequence of Tertiary basalt flows, many of which have been radiometrically dated (see Larson, Ozima, and Bradley, 1975). The Split Rock Formation near Yampa is interbedded with some of the lowest and consequently oldest of these flows (Larson, personal commun., 1975). In table I of Larson et al. (1975), the dates on the oldest parts of the sequence close to Yampa are 21.4 my. on the third flow from the exposed base of the south side of Turret Peak and 23.0 my. on the lowest exposed flow just north of Little Trappers Lake. In Evernden et al. (1964, p. 178) sample KA 481 from the late Arikareean lower Harrison Formation at Agate Springs National Monument was dated at 21.3 my.

13. Hole in the Rock (42° 27' N, 103° 42' W), Sioux County, Nebraska, anthill formed from sediments derived from the Harrison Formation.

14. (42° 40' N, 104° 05' W), one-half mile (=5/6 km.) north of Van Tassell, Niobrara County, Wyoming, Harrison Formation.

15. Buda local fauna (29<sup>3</sup>/<sub>4</sub>° N, 82<sup>1</sup>/<sub>2</sub>° W), Alachua County, Florida. An Arikareean age

for the Buda local fauna is suggested by a preliminary analysis of the total assemblage of mammalian material (Frailey, 1979).

#### ARIKAREEAN OR HEMINGFORDIAN

16. (42° 29' N, 103° 42<sup>1</sup>/<sub>2</sub>' W), 5 to 7 miles (8 to 11 km.) northeast of Agate, Sioux County, Nebraska. In this area, only the Marsland Formation (=Upper Harrison of Peterson, 1906) and the Harrison Formation are known to crop out (Galusha, personal commun., 1970).

#### HEMINGFORDIAN

17. (42° 33' N, 103° 47<sup>1</sup>/<sub>2</sub>' W), about 13 km. north of Agate, Sioux County, Nebraska, Marsland Formation.

18. Quarry A of Wilson (1960) (40° 54' N, 103° 14' W), Logan County, Colorado, Pawnee Creek Formation. Quarry A is part of the basis for the Martin Canyon local fauna. *Merychius elegans* occurs at Martin Canyon (Schultz and Falkenbach, 1947, p. 202) and Wilson (1960, p. 14) noted that specimens of *Merychius* were numerous at the level of Quarry A. If the specimens Wilson noted are referable to *M. elegans*, then the fauna of Quarry A is temporally equivalent to that of the Runningwater Formation (Cook, 1965, p. 6) of Nebraska (=Upper Marsland *sensu* Schultz and Falkenbach, 1947; see Cook, 1965, p. 6). An unconformity separates Quarry A from the underlying *Merycochoerus* Quarry of Matthew (1901) (Wilson, 1960, p. 13). Specimens regarded as *Merycochoerus proprius magnus* by Schultz and Falkenbach (1940, pp. 288-289) were collected from the *Merycochoerus* Quarry. This same subspecies is restricted to the Marsland Formation in northwestern Nebraska (Schultz and Falkenbach, 1940, p. 286); therefore, the fauna from Quarry A can be no older than that of the Marsland.

19. Marsland Quarry (42° 22' 35" N, 103° 18' 42" W), Box Butte County, Nebraska, Runningwater Formation. Marsland Quarry was regarded as in the Runningwater Formation of Cook (1965) by Yatkola (1978, p. 49). He reduced the rank of this lithic unit to

<sup>4</sup> More precise locality information is on file at the University of Colorado Museum, Boulder.

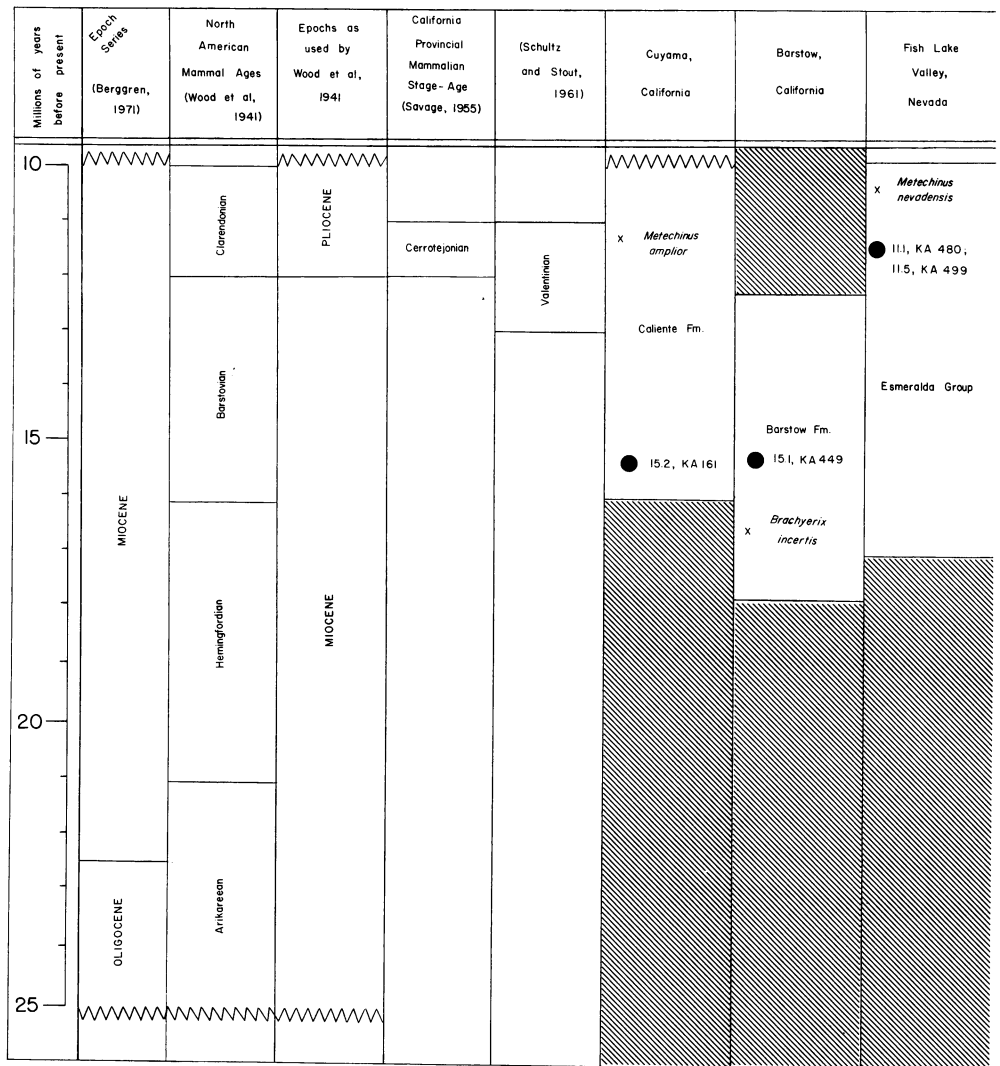


FIG. 18. (On 3 consecutive pages.) Correlation chart showing stratigraphic position of the occurrences of the Brachyericinae and Erinaceinae in North America. Unconformities are indicated by hatched areas and units that continue above or below the limits of the chart are bounded by a sawtoothed line.

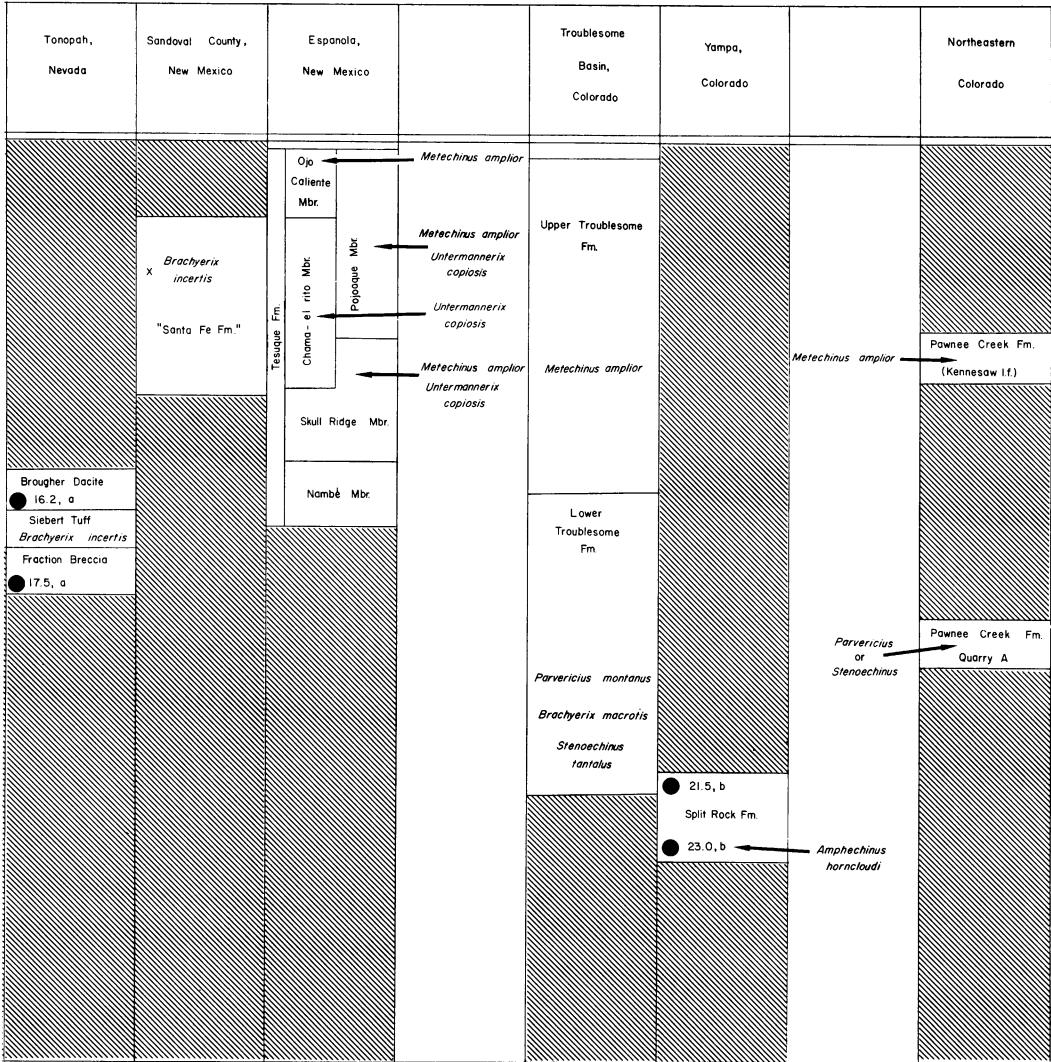
a member and placed it at the top of the Marsland Formation (Yatkola, 1978).

20. North branch of Cottonwood Creek ( $42^{\circ} 31\frac{1}{2}'$  N,  $103^{\circ} 04'$  W),  $8\frac{1}{2}$  miles ( $=13\frac{1}{2}$  km.) northwest of Dunlap, Dawes County, Nebraska, Runningwater Formation.

21. Foley Quarry ( $42^{\circ} 23' 59''$  N,  $103^{\circ} 01' 32''$  W), Box Butte County, Nebraska, Red

Valley Member of the Box Butte Formation (Galusha, 1975, pp. 53, 55).

22. Sand Canyon ( $42^{\circ} 32' 15''$  N,  $102^{\circ} 52' 00''$  W), Dawes County (erroneously recorded as Box Butte County in Rich and Rich, 1971, p. 15), Nebraska, Red Valley Member of the Box Butte Formation (Galusha, 1975, pp. 53, 55).

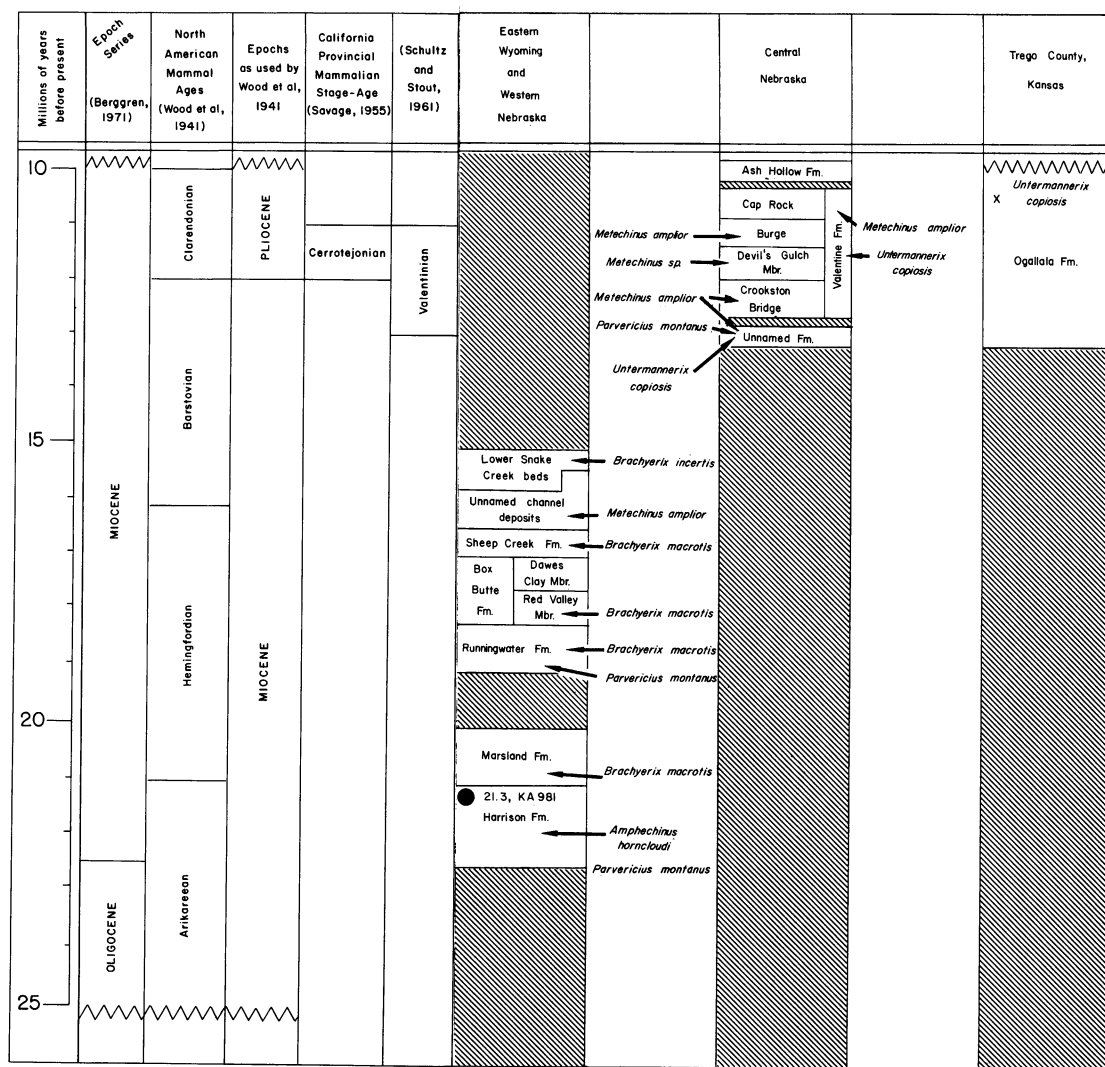


Where the faunal list for a formation is preceded by an "X," this indicates the temporal placement of the fauna within the temporal boundaries of the formation. Otherwise, the temporal limits of the fauna are no more precise than those of the formation in which it is found.

23. Greenside Quarry (42° 10½' N, 103° 43¾' W), Sioux County, Nebraska, lower Sheep Creek Formation (Skinner, Skinner, and Gooris, 1977, pp. 325, 342).

24. Split Rock local fauna (UCMP locality V69190), (42° 26' 35" N, 107° 33' 30" W), Fremont County, Wyoming, upper porous sandstone sequence of the Split Rock Formation

of Love (1961, p. 14; 1970, p. 77). In 1968, Robinson (ms, p. 83) was of the opinion that the upper porous sandstone sequence was equivalent in age to the Sheep Creek Formation of western Nebraska, and perhaps to lithic units immediately below but definitely above the Marsland Formation. This inference was based on the presence of *Brachy-*



Where physical dates have been made, a period, followed by the age in millions of years, followed by the source, is given. If the source is Evernden et al. (1964), the sample number is given, e.g., KA

*crus* sp. which is known in the Sheep Creek and Olcott formations, *Mesogaulus novellus* known only from the Sheep Creek Formation, and hypsodont equids which are recorded only from the Sheep Creek and younger formations in the western Nebraska sequence. Table 28 gives the stratigraphic position where known of the specimens relative to unit 2 of Love's (1961, p. 19) section of the Split Rock Formation, a prominent white tuff.

25. Same as 24 except latitude and longitude:  $42^{\circ} 26'_{10}''$  N,  $107^{\circ} 33'_{13}''$  W.

26. Same as 24 except latitude and longitude:  $42^{\circ} 26' 54''$  N,  $107^{\circ} 33' 08''$  W.

27. Blue Jaw Face locality ( $40^{\circ}_{16}'$  N,  $106^{\circ}_{10}'$  W), Grand County, Colorado, lower part of the Troublesome Formation.<sup>5</sup>

<sup>5</sup> The presence of *Merycochoerus matthewi*, *Merycochoerus proprius*, and *Mesogaulus* cf. *M. paniensis* in the lower part of the Troublesome Formation sug-



TABLE 28  
Stratigraphic Position of *Brachyerix macrotis* and *Parvericius montanus* at Split Rock<sup>a</sup>

Taxa	Specimen number	Position above (+) or below (-) prominent white tuff in meters	Element or elements
<i>B. macrotis</i>	UCM 29971, 29972	ca. +52-+59	Two M <sub>1</sub> s
<i>B. macrotis</i>	UCMP 86137	ca. +40	Nearly complete skull with jaws
<i>B. macrotis</i>	UCMP 94718, 102634	ca. +40	Two partial skulls
<i>B. macrotis</i>	UCM 21541, 21547, 21551, 29957, 29958, 32770	ca. +35-+59	Six M <sub>1</sub> s
<i>B. macrotis</i>	UCM 29395, 29397	+9-+59	Two M <sub>1</sub> s
<i>B. macrotis</i>	UCM 29426	+6-+59	One M <sub>1</sub>
<i>B. macrotis</i>	UCM 29351	+1.6-+59	One M <sub>1</sub>
<i>P. montanus</i>	UCM 32772	+1.6-+59	One M <sub>2</sub>
<i>B. macrotis</i>	UCM 32769	-1-+59	One M <sub>1</sub>
<i>B. macrotis</i>	UCM 29758	-5-+59	One M <sub>1</sub>
<i>P. montanus</i>	UCM 29507	-5-+59	One M <sub>1</sub>

<sup>a</sup> Specimens of *Brachyerix macrotis* and *Parvericius montanus* in stratigraphic order within the upper porous sandstone sequence of the Split Rock Formation, measured relative to the prominent white tuff (unit no. 2) in the section of Love (1961) on p. 19. Specimens with an upper stratigraphic range of +59 meters were found as float and thus could conceivably have come from as high as that relative to the white tuff, for that elevation is the local topographic high. See text for further discussion.

McKenna dated June 1967, said that when he published on the new species in 1941, he regarded it as derived from the Marsland Formation which was considered "to be those beds younger than Upper Harrison and older than Sheep Creek." He further stated that "in view of revisions in stratigraphy in that area since then I'm sure one should check the locality to determine the formation from which it [*M. marslandensis*] most likely came." The restricted Marsland (=Upper Harrison of Peterson, 1906), the Running-water Formation, and rocks containing a Sheep Creek equivalent fauna all crop out in the area designated by Meade. On the basis of Meade's description, it is impossible to determine from which of these three rock units his specimen was collected.

#### HEMINGFORDIAN OR BARSTOVIAN

31. Observation Quarry (42° 41' 25" N, 102° 50' 25" W), Dawes County, Nebraska, unnamed channel deposit considered to be temporally as early as post-Sheep Creek For-

mation and pre-Lower Snake Creek (=Olcott Formation of Skinner, Skinner, and Gooris, 1977) on the basis of the entire fauna (Galusha, personal commun., 1972) or as late as the upper part of the Lower Snake Creek (=Olcott Formation) on the basis of the equids (Skinner, personal commun., 1972).

#### BARSTOVIAN

32. Steepsides Quarry (35° 01' 55" N, 117° 03' 25" W), San Bernardino County, California, Barstow Formation approximately 1000 ft. [=305 m.] below the Skyline Tuff. The fauna recovered from this quarry is similar to that in the Lower Snake Creek beds (=Olcott Formation of Skinner, Skinner, and Gooris, 1977) of Sioux County, Nebraska (Galusha and Tedford, personal commun., 1969).

33. Thomson's Quarry B of 1921 (42° 9½' N, 103° 43½' E), Sinclair Draw, Sioux County, Nebraska, Lower Snake Creek beds (=Olcott Formation of Skinner, Skinner, and Gooris, 1977). Skinner, Skinner, and Gooris



(1977, p. 346) gave the type locality of *Brachyerix incertis* (Matthew, 1924) Rich and Rich, 1971, as Trojan Quarry, not Thomson's Quarry B of 1921 as reported in Matthew (1924, p. 74).

34. Skull Ridge (35° 57' N, 105° 59½' W), Santa Fe County, New Mexico, Skull Ridge Member of the Tesuque Formation.<sup>6</sup>

35. South Skull Ridge (35° 55½' N, 105° 59½' W), Santa Fe County, New Mexico, Skull Ridge Member of the Tesuque Formation.<sup>6</sup>

36. White Operation Quarry (35° 56' 18" N, 105° 56' 54" W), Santa Fe County, New Mexico, near the middle of the Skull Ridge Member of the Tesuque Formation (see Galusha and Blick, 1971, fig. 17, for details of stratigraphic position of White Operation Quarry).<sup>6</sup>

37. Kleinfelder Farm locality (49½° N, 106° W), near Rockglen, Saskatchewan, Wood Mountain Formation. The fauna from this locality is regarded as, "just older than the Norden Bridge local fauna and thus is uppermost Barstovian (Upper Miocene), just older than the basal beds of the Valentine Formation . . . ." (Storer, 1975, p. 127).

38. Kennesaw local fauna (40° 59' N, 103° 28' W), Sand Canyon, Logan County, Colorado, upper Pawnee Creek Formation. Galbreath (1953, p. 37) regarded the Kennesaw local fauna as slightly older than the Niobrara River local fauna which was collected from the Crookston Bridge Member of the Valentine Formation (Skinner, Skinner, and Gooris, 1968, p. 404).

39. Egelhoff Quarry (42° 48' 01" N, 100° 03' 10" W), Keya Paha County, Nebraska, unnamed lithic unit that unconformably overlies the Rosebud Formation and in turn is unconformably overlain by the Valentine Formation (Tedford, personal commun., 1972).

40. Norden Bridge Quarry (42° 47' 08" N, 100° 02' 04" W), Brown County, Nebraska, same lithic unit as previous locality (Egelhoff Quarry).

<sup>6</sup> The Skull Ridge Member of the Tesuque Formation is considered to be of Barstovian Age by Galusha and Blick (1971, p. 110).

41. Fort Niobrara (UCMP locality V3218) (42° 52' 25" N, 100° 29' 35" W), Cherry County, Nebraska, Crookston Bridge Member of the Valentine Formation (Skinner, Skinner, and Gooris, 1968, p. 405).

42. Myers Farm (UNSM locality Wt-15A) (40° 01¾' N, 98° 32½' W), Webster County, Nebraska, in sediments considered as equivalent to the Valentine Formation (Schultz, Martin, and Corner, 1975, p. 4). R. G. Corner (personal commun., 1976) has stated that, "The [Myers Farm] fauna compares well to the Crookston Bridge and Railroad Quarry local faunas as well as Egelhoff and Norden Bridge local faunas."

43. Anceney (KU Mont. loc. 34) (45° 39' 51" N, 111° 18' 01" W), Gallatin County, Montana, Madison Valley Formation. Dorr (1956, pp. 72-73) regarded the fauna from Anceney as late Barstovian in age. This fauna is presently being reviewed by John Sutton.

44. South Bijou Hill (SDSM V731) (43° 29¼' N, 99° 19' W), Charles Mix County, South Dakota, "Fossils and barite 'rock rose' zone" (see section in Skinner and Taylor, 1967, fig. 1c) of the Fort Randall Formation. Skinner and Taylor (1967, pp. 45-46) when considering the age of the fauna from the Fort Randall Formation stated that it "in part, represents the hiatus between the Lower Snake Creek [=Olcott Formation of Skinner, Skinner, and Gooris, 1977] and Lower Valentine formations."

#### BARSTOVIAN OR CLARENDONIAN

45. Verdigre Quarry (42° 29' 01" N, 98° 08' 17" W), Knox County, Nebraska, Valentine Formation. Fauna is similar to that known from the lower part of the Devil's Gulch Member of the Valentine Formation (Skinner, Skinner, and Gooris, 1968, p. 407).

46. Near the midpoint of the boundary between sections 17 and 20, T. 95 N., R. 74 W. (43° 02' 15" N, 99° 37' 15" W), Tripp County, South Dakota. Within a distance of one mile (=1.61 km.) of the locality given in the University of Michigan records, only three formations are shown on the geologic map of the area by Stevenson, Skogstrom, and

Harksen (1959): Pierre (Cretaceous), Valentine (Miocene), and Ash Hollow (Miocene). Thus it seems likely that the specimen was found either in the Valentine or Ash Hollow Formation.

47. A fragmentary mandible of *Untermannix copiosus* (AMNH 86930) has the following data associated with it: "U. Miocene[,] L. White R., S.D.[,] Gidley 1903." AMNH 86930 was not assigned that number, nor did it have any other number associated with it until more than half a century after Matthew and Gidley's report on the 1903 expedition to the Little White River area of South Dakota. This specimen may be the insectivore referred to in their faunal list for the Loup Fork beds (Matthew and Gidley, 1904, p. 245). In any event, the specimen most probably came from rocks Gidley referred to as Loup Fork beds for only that lithic unit was regarded as Upper Miocene in Matthew and Gidley's report (Matthew and Gidley, 1904, p. 241). The Loup Fork beds, as the term was used by Gidley in the Little White River area (43° N, 101° W), Bennett and Todd counties, South Dakota, are now placed in the Valentine and Ash Hollow formations (Skinner, personal commun., 1972).

48. Tonopah local fauna (LACM(CIT) location 172) (38° 11' 09" N, 117° 15' 20" W), Nye County, Nevada, Siebert Tuff (Davis, Kleinhampl, and Ziony, 1971). Details of the geographic location of this site are given by Henshaw (1942, p. 82). This local fauna has a disputed age. "Henshaw [1942, pp. 95–99] believed that some of the mammals in the Tonopah local fauna were more primitive than those found in the Burge Member of the Valentine Formation of Nebraska, more advanced than those in the 'Niobrara River fauna' collected by the University of California, and very similar to forms from the upper part of the Barstow Formation. Lewis (1964, p. 21) suggested that the Tonopah local fauna was similar to that in Frick's (1937) First Division of the Barstow Formation and stated that both faunas were of latest Miocene age. Beryl Taylor (personal commun., 1969) believes that Henshaw's *?Aepyccamelus*

*stocki*<sup>7</sup> and *Aelurodon wheelerianus asthenostylus* are more advanced than related forms from the Lower Snake Creek fauna but similar to forms occurring stratigraphically as high as the Valentine Formation; *?A. stocki* is similar to forms in those members of the Valentine Formation stratigraphically below the Burge Member" (Rich and Rich, 1971, p. 48). The Siebert Tuff is bracketed by the Brouther Dacite with a KA date of  $16.2 \times 10^6$  years BP and the Fraction Breccia with a KA date of  $17.5 \times 10^6$  years BP (Kleinhampl and Ziony, 1967). This time interval is poorly represented in the data presented by Evernden et al. (1964) concerning the ages of sites where land mammal fossils have been discovered in North America but it suggests a position near the Hemingfordian-Barstovian boundary.

49. Junction locality (40½° N, 106½° W), Grand County, Colorado, upper part of the Troublesome Formation.<sup>8</sup> *Hesperolagomys* is found both at this locality and in the Fish Lake Valley fauna from the Esmeralda Group of Nevada (see Localities, Section 61) (Robinson, personal commun., 1974).

50. Santa Cruz collection locality area 5 (see fig. 2 of Galusha and Blick, 1971) (36° 01' N, 105° 59¼' W), Rio Arriba County, New Mexico, Santa Cruz Red layer near the middle of the Pojoaque Member of the Tesuque Formation.<sup>9</sup> (See fig. 9, Galusha and

<sup>7</sup> Macdonald (1956, pp. 198–199) substituted the name *Aepyccamelus* for *Alticamelus* Matthew, which he considered a *nomen vanum* (Rich and Rich, 1971, p. 48).

<sup>8</sup> More precise locality information is on file at the University of Colorado Museum, Boulder.

<sup>9</sup> "The fossils [of the Pojoaque Member] have proved to be forms currently assigned approximately Valentine and Clarendon equivalents. The fossil taxa represented include many forms not commonly included in the Clarendonian, but the 'fit' is better with a Valentinian . . . and Clarendonian concept of North American Land-Mammal Ages than with either the preceding Barstovian or the succeeding Hemphillian" (Galusha and Blick, 1971, p. 64). Valentinian is used by Galusha and Blick for the "segment of time represented by the fauna of the Valentine Formation as revised by Skinner, Skinner, and Gooris (1968, p. 404)" (Galusha and Blick, 1971, p. 12).

Blick, 1971, for more precise information on the stratigraphic position of the Santa Cruz Red layer.)

51. (35° 59' N, 106° 05' W), either Santa Fe or Rio Arriba counties, New Mexico, Pojoaque Member of the Tesuque Formation.<sup>10</sup>

52. Central Pojoaque Bluffs (35° 55' 11" N, 106° 02' 31" W), Santa Fe County, New Mexico, three-fifths m. above the Blue-Gray Ash shown in the section of the Pojoaque Member of the Tesuque Formation figured by Galusha and Blick (1971, fig. 21).<sup>10</sup>

53. Jacona Microfauna Quarry (35° 54' 55" N, 106° 04' 14" W), Santa Fe County, New Mexico, Pojoaque Member of the Tesuque Formation.<sup>10</sup>

54. Vicinity of Espanola (36° N, 106° W), either Santa Fe or Rio Arriba counties, New Mexico, presumably from the Pojoaque Member of the Tesuque Formation.<sup>10</sup>

55. Third Wash or Arroyo Morada (36° 01' N, 105° 59' W), Rio Arriba County, New Mexico, probably from one of the white ash layers in the upper part of the Skull Ridge Member<sup>11</sup> of the Tesuque Formation or an ashy bed in the overlying Pojoaque Member<sup>10</sup> (Galusha, 1974, personal commun.).

56. Red Cliff Prospect (35° 25' 40" N, 106° 49' 25" W), main fork of Canyada Piedra Parada, Sandoval County, New Mexico, Middle Red Member of the Santa Fe Formation as used by Bryan and McCann (1937). The site is stratigraphically at the level corresponding to the "Reddish brown sand" above the unconformity within the Santa Fe Formation equivalent (see fig. 3b, Galusha, 1966). Galusha considers the lithic unit where the Red Cliff Prospect occurs as equivalent to the middle of the Pojoaque Member of the Tesuque Formation and Valentinian in age (Galusha, personal commun., 1971).

57. Chama-el Rito collecting locality (area 17 in fig. 2 of Galusha and Blick, 1971) (36° 16' N, 106° 11' W), Rio Arriba County, New Mexico, Chama-el Rito Member of the Tesuque Formation, considered to be of Val-

entinian or Clarendonian age by Galusha and Blick (1971, p. 110).

#### CLARENDONIAN

58. Hedgehog Quarry (UCMP locality V-5656) (34° 49' 16" N, 119° 20' 09" W), Ventura County, California, in the "reddish-brown mudstone in middle part of Caliente Formation, 212 feet [=64.6 m.] below top of red beds in red-bed lithofacies" (James, 1963, p. 135). James included the specimens from Hedgehog Quarry in his Mathews Ranch fauna to which he assigned an early Clarendonian age (James, 1963, p. 146).

59. Gordon Creek Quarry (UCMP locality V-3313) (42° 46' 15" N, 100° 39' 35" W), Cherry County, Nebraska, Burge Member of the Valentine Formation (Skinner, Skinner, and Gooris, 1968, pp. 407-408; Webb, 1969, p. 178).

60. Jefferson Ranch (42° 40' 16" N, 99° 45' 58" W), Brown County, Nebraska, Burge Member of the Valentine Formation.

61. Fish Lake Valley fauna (UCMP locality V-2804) (37° 55' N, 118° 05' W), 11.6 km. north of Chiatovich Ranch, Esmeralda County, Nevada, Esmeralda Formation. Stock (1926) described and Mawby (1968) commented upon two specimens of *Hypohippus* from this locality (UCMP 27116 and 27117) that are quite similar to others, as yet undescribed, in the collection of the American Museum of Natural History from the Cap Rock Member of the Ash Hollow Formation of northwestern Nebraska.

62. Conical Hill Quarry (36° 09' 10" N, 106° 14' 55" W), Rio Arriba County, New Mexico, lower Ojo Caliente Sandstone Member of the Tesuque Formation. The Ojo Caliente Sandstone Member is considered to be Clarendonian by Galusha and Blick (1971, p. 70).

63. WaKenney local fauna (UMMP locality UM-K6-59) (39° 04' 55" N, 99° 45' 31" W), Trego County, Kansas, Ogalalla Formation. R. L. Wilson considers the WaKenney local fauna as similar to the Clarendon local fauna of Texas among others, and most similar to the Beaver local fauna of the Laverne Formation of Oklahoma (R. L. Wilson, 1968, p. 77).

<sup>10</sup> See footnote 9.

<sup>11</sup> See footnote 6.

### MIocene, UNDIFFERENTIATED

64. (35½° N, 106° W), near Santa Fe, Santa Fe County, New Mexico, Santa Fe Group. The rocks of the Santa Fe Group range in age from Hemingfordian to Hemphillian (Galusha and Blick, 1971, p. 110).

65. (46° 37' N, 111° 03' W), east of the Smith River and seven miles southeast of Fort Logan, Meagher County, Montana, Deep River beds.<sup>12</sup>

66. (42½° N, 103½° W), 1 mile east of the Smith River and two miles north of Buckingham Ranch, Meagher County, Montana, Deep River beds.<sup>12</sup>

67. (46° 39' N, 111° 05' W), Meagher County, Montana, Deep River beds.<sup>12</sup>

It would be premature to regard the maps in figures 19 and 20, indicating the localities

where the specimens of the Erinaceinae and Brachyericinae have been found in North America, as being as sophisticated as a distribution map for the taxa represented. Too many North American Miocene localities lack a thoroughly collected small mammal component to their faunas to assume that even the general picture of the distribution of the various taxa is reasonably established. In several instances, the record is based on a single specimen, in one extreme case on a small fraction of one tooth. The record of occurrence of the known taxa will surely be widely extended when the Miocene localities of North America are more thoroughly collected with the recovery of small mammals as a specific objective. Thus, the meaningful resolution of distribution data is on the continental scale.

## DISCUSSION AND CONCLUSIONS

### METHOD OF CLADISTIC ANALYSIS

In attempting to understand the phyletic relationships of the Erinaceinae and Brachyericinae, an analysis was made following

<sup>12</sup> The type specimen of *Brachyrix macrotis*, AMNH 21335, was reportedly found within a few hundred m. of the following specimens [most reported by Mook (Matthew and Mook, 1933)]: *Brachycrus laticeps* (AMNH 21321 and 21322), *Promerycochoerus* (AMNH 21338), *Dromomeryx* (AMNH 21239), *Subdromomeryx antilopinus* (AMNH 21311), and *Cranioceras kinseyi* (AMNH 21317). The assemblage is from at least three stratigraphic levels. Elsewhere, *Promerycochoerus* is restricted to the Arikareean. Whereas *Brachycrus* occurs in both Hemingfordian and Barstovian rocks, *Subdromomeryx* is known only from Hemingfordian sediments. *Dromomeryx* is restricted to the Barstovian; *Cranioceras* is known only from the Valentine Formation of late Miocene age.

Most of the above taxa that seem to indicate the mixing of temporally distinct elements have been reported repeatedly from the Deep River beds. Thus, one may generalize and say that to know a specimen is from the Deep River beds means that its age may be from Arikareean to Barstovian or possibly later unless additional information is available.

the basic tenet of the cladistic method as propounded by Hennig (1966) and his advocates. Simply stated, this concept requires that groups be related by the presence of shared derived character states. Fundamental to this technique is the assumption that if two groups share a derived or advanced character state that a third group lacks, this is evidence that the most recent common ancestor of the first two groups had the derived character state and this common ancestor is not shared by the third group. Presumably, at some point after the common ancestor of all three groups had speciated, the lineage that gave rise to the first two groups acquired the derived character state and all members of the lineage ancestral to the third group retained the more primitive condition as is known to be the case in their descendant, the third group. Hence, the third group is more distantly related to the first two groups than they are to one another; i.e., these first two groups are sister groups in Hennig's terminology. By extension of this process and consideration of a constellation of characters, it is possible to arrive at a hypothesis of relationships based on shared de-

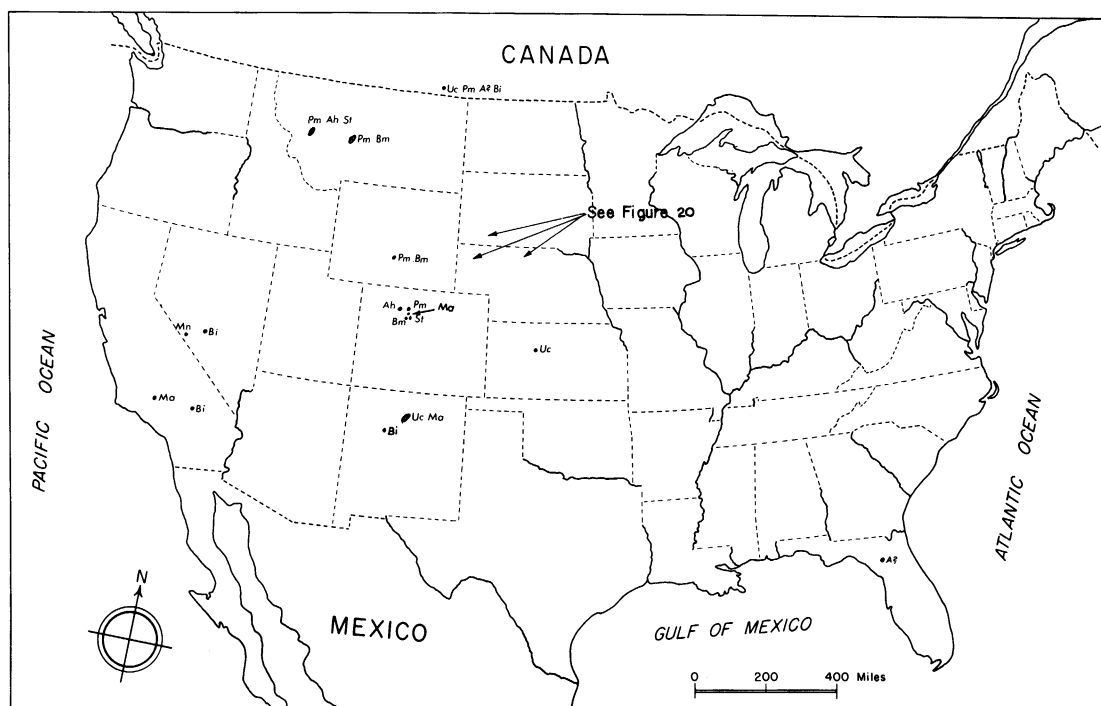


FIG. 19. Maps showing geographic position of the occurrences of the Brachyericinae and Erinaceinae in North America exclusive of the Nebraska-South Dakota region (see figure 20 for map of that area). Names of the taxa have been abbreviated as follows: A, ?*Amphechinus*; Ah, *Amphechinus horncloudi*; Bi, *Brachyerix incertis*; Bm, *Brachyerix macrotis*; M, *Metechinus* sp.; Ma, *Metechinus amplior*; Mn, *Metechinus nevadensis*; Pm, *Parvericius montanus*; PS, *Parvericius* or *Stenoechinus*; St, *Stenoechinus tantalus*; Uc, *Untermannerix copiosus*.

rived character states which is presumed to be a best estimate of the actual phyletic relationships of the groups under consideration.

A fundamental criticism that has been directed against this methodology is that of circularity. For in order to construct the phylogenetic hypotheses, it is necessary to be able to distinguish which of any two states of a given character is the more advanced or derived and which, the more primitive; i.e., estimate the polarity of a character. But to determine character polarity, most workers agree,<sup>13</sup> requires a knowledge of at least the broad outlines of the phylogeny of the group

being studied.<sup>14</sup> Hence at first sight the process appears hopelessly circular.

One way out of this dilemma is to find a preliminary phylogenetic hypothesis established on other principles and sufficiently close to the true phyletic pattern to serve as a starting point. With such a hypothesis in hand, it becomes possible to estimate the polarity of at least some characters. This in turn allows for refinement of the phylogenetic hypothesis which in turn permits estimation of polarity of yet more characters as well as checking on the estimates of previous ones. Thus by reiteration, the phylogenetic

<sup>13</sup> For a dissenting opinion, see Brundin (1972, p. 117).

<sup>14</sup> For a description of how character polarity may be determined using a phylogenetic hypothesis, see pp. 83–84, this report.

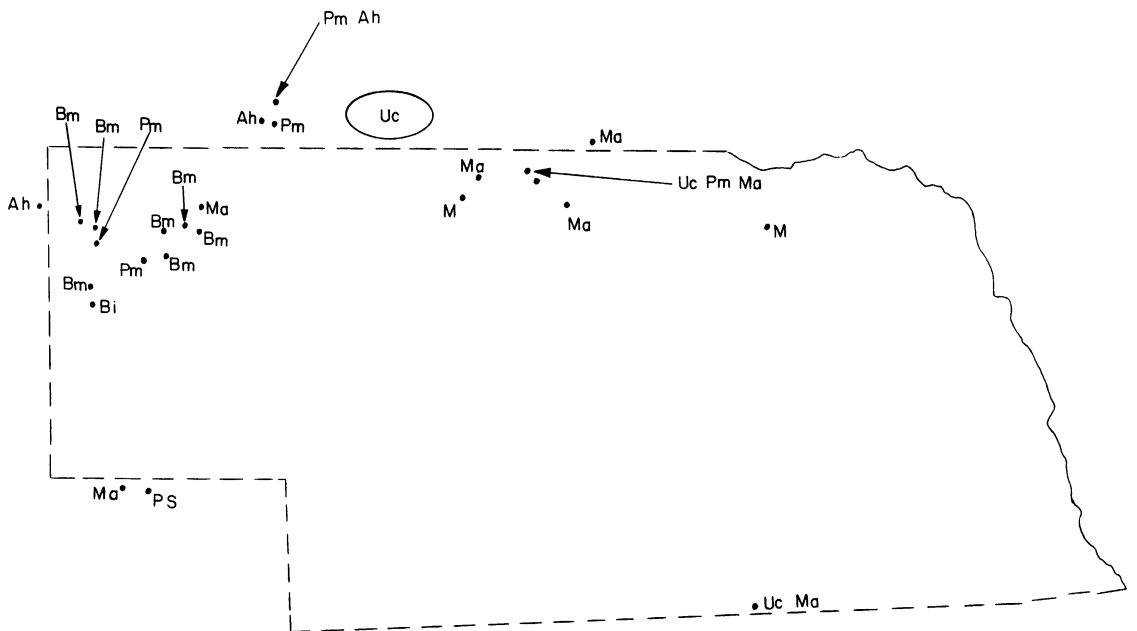


FIG. 20. Map showing geographic position of the occurrences of the Brachyericinae and Erinaceinae in Nebraska and South Dakota. See figure 19 for abbreviations of taxa.

hypothesis and character polarity estimates may be improved.

Efforts of many earlier and modern workers have produced a group of detailed phylogenetic hypotheses of the Insectivora and Deltatheridia that although they differ in particulars, preserve for the most part the same general pattern. That this group of hypotheses was not arrived at by strict application of the principles outlined by Hennig but rather by the interaction of a plexus of many different implicit and explicit philosophical outlooks, theories, and data is freely admitted.

To best justify one of these phylogenetic hypotheses as an adequate starting point for an analysis using the method of Hennig, given that it was not arrived at by rigid application of his methodology, would require not only the chronicling of the earlier classifications and phylogenetic hypotheses that have been put forth since at least the time of Linnaeus (see Simpson, 1945, and Gregory, 1910, for such reviews of the Mammalia) but also to trace in detail this underlying plexus

of ideas and information used to formulate these concepts. Understanding of this plexus is necessary in order to be sure that the phylogenetic hypothesis is based on logical premises consistent with modern biological theories. To adequately do so is a task far beyond the scope of this paper if it is to be done properly. To do a less than comprehensive review would most likely result in a travesty on historical technique of the kind described so wryly by Gould (1973, p. 322): "The past can stage no active protest; it is available for our use in any way we choose. At worst we rape it by extracting distorted sentences to suit our present purposes. At best, we understand it aright and enlighten our current proceedings. Somewhere in between, we may simply misrepresent it. . . ."

Admitting that such an investigation is beyond my ambition, there are still two considerations (albeit somewhat weaker!) suggesting that any one of the modern phylogenetic hypotheses for the Insectivora and Delta-

theridia can serve as an adequate basis to begin an analysis.

The first is that because the chosen hypothesis is only a starting point for a reiterative technique that eventually should yield a better estimate of the actual phylogenetic relationships, it is not necessary that there be no errors. To my knowledge, there is no method of deciding just how close to the actual phylogeny the initial hypothesis must be in order that reiteration between estimates of character polarity and phylogenetic hypotheses will converge on the actual conditions rather than spurious limits. To do this in actual practice of course presupposes surmounting another theoretical problem, that of being able to measure just how far the initial hypothesis is from the actual pattern of cladistic events.

Second, a theoretical investigation by Raup and Gould (1974) has demonstrated that a phylogeny can be rather accurately inferred by clustering techniques based on shared character states without a knowledge of polarity. In this study, Raup and Gould, with the aid of a computer, developed a series of hypothetical cladistic patterns using tables of random numbers to make decisions as to when lineages would branch and become extinct. In addition, independent of the cladistic decisions, at every branch point an imaginary morphology of 10 characters was altered using random numbers to determine whether or not changes were to be made. They were then able to analyze the taxa produced, attempt to cluster them on a morphological basis, form a phylogenetic hypothesis and check it against the cladistic pattern that produced the taxa. In this manner, they demonstrated, for their stochastic model at least, that a reliable relationship exists between the cladistic pattern and the pattern to be inferred on the basis of similarity of morphology independent of a knowledge of the polarity of characters. The results of this study suggest that knowledge of character state polarity is necessary only to refine a hypothesis of phylogenetic relationships, not to discover the gross pattern.

Although a theoretical demonstration of the relationship between phylogeny and mor-

phology such as that by Raup and Gould (1974) has not been attempted earlier, intuitively, many workers have anticipated those results and acknowledged their reasonableness (e.g., Simpson, 1961, p. 53; Brundin, 1966, p. 22).

For an initial phylogenetic hypothesis for the Insectivora and Deltatheridia, I chose to initially follow Van Valen's (1967) arrangement. Although there are other recent treatments of these two orders that would have served just as adequately as a starting point for this analysis, the choice was not wholly arbitrary. Figure 7 in Van Valen (1967) graphically expresses not only his opinion of the phylogenetic relationships between the various subdivisions of the Insectivora and a few other groups but also boldly conveys the uncertainty with which these opinions were held in a manner seldom seen elsewhere in the literature.

In principle, transformation of Van Valen's phylogenetic hypothesis, cast as it is in an ancestor-descendent mode, into a cladistic one framed in a sister group relationship pattern was a straightforward process. However, the number of separate sister group cladistic hypotheses derivable is the product of the number of possible ancestral groups indicated for each taxon of Van Valen. For just the insectivore groups shown in figure 7 of Van Valen (1967), 9216 such hypotheses could be constructed. In practice, it was unnecessary to consider this many phylogenetic hypotheses because the most intractable problems were questions requiring a detailed understanding of the phylogenetic relationships among only a few of the families and subfamilies being considered. Therefore, the number of permutations of the phylogenetic hypothesis necessarily considered was reduced to manageable proportions.

As the data are finally presented in tables 29–31, Van Valen's systematic scheme and phylogenetic hypothesis have been modified to conform with the final results of this study. However, reference to Van Valen's (1967) paper gives the original arrangement if desired.

Once the phylogenetic hypothesis of Van Valen had been accepted as a starting point,

the next step was to determine which conditions of each character were primitive and which advanced for the Insectivora and Del-tatheridia. The primary criterion for this determination was the distribution of the character states within the sample examined. The common ancestor of the Insectivora and Del-tatheridia gave rise to a number of lineages that divided repeatedly to ultimately result in the several genera and species recognized. Derived states for a given character were acquired by descendant species of this original ancestor. In turn, the descendants of the species with the derived character were species more closely related to one another than to other members of the two orders and were typified by the presence of this derived state unless further evolution of the character changed it once again. Depending on the amount of parallelism in acquiring derived character states, it is to be expected therefore, that derived character states will be confined to one or a few subdivisions at some taxonomic level within the two orders, whereas primitive states will be scattered about in a haphazard pattern. By a haphazard pattern, it is meant that the primitive states often will be found shared by taxonomic subdivisions within the two orders that do not show any special phylogenetic affinity on the basis of the ongoing phylogenetic hypothesis.

In many instances, the uncommon character states useful in this study were seen almost exclusively only in a few members of the Erinaceoidea, thus making the interpretation of the primitive and derived character states a straightforward procedure. Generally, the conclusions about character polarity reached here agreed with those made by previous workers such as Patterson and McGrew (1937), Viret (1938, 1940), Bohlin (1942), Butler (1948, 1956a, 1956b), McDowell (1958), McKenna and Simpson (1959), McKenna (1960), Russell (1964), and Szalay (1969).

In some instances, however, there were ambiguities that could only be resolved by examining the biases of the samples. For example, the presence of a hypoconulid on

M<sub>1-2</sub> is generally regarded as a primitive feature and yet approximately half the super-generic groups lacked this cuspule on the anterior lower molars. At face value, this seems to be a character whose polarity cannot be determined. However, had a worker lived at the end of the Eocene and examined only that part of the sample available to him then, the evidence would seem quite clear; only a few groups scrutinized would have lacked a hypoconulid, and hence the absence of that cusp would have been interpreted as a derived trait. It has been argued that one cannot use the temporal assignment of specimens to determine the primitive character state for a given character (e.g., Schaeffer, Hecht, and Eldredge, 1972, pp. 33-35, 37, 42-43). The difficulty is that one may have a specimen from a species that had acquired a derived state early and another, later species closely related but not a direct descendant that had retained a primitive character state. This problem poses a valid objection if the attempt to determine polarity is confined to what is believed to be a single lineage. However, if one considers a case of what is assumed to be a number of lineages and the phylogenetic hypothesis is cast in terms of sister group relationships rather than assuming ancestor-descendant ones, in principle the method of analysis for estimating character polarity as outlined on pp. 81-82 is the same no matter whether one considers Recent plus all fossil forms of a group or just fossil forms older than an arbitrary date. If a pattern emerges where none was before in the distribution of a given variable by division of a sample on the basis of another variable, this is not throwing data away but ordering it in a useful manner.

#### DATA ANALYZED FOR DETERMINATION OF CHARACTER POLARITY

In attempting to utilize the method of Hennig to understand the phyletic relationships within each of these subfamilies and to relate them to other insectivores including one another, a survey was made of approximate-



TABLE 29  
Characters Examined in 100 Genera of Insectivora and Deltatheridia

Character	← More Primitive Character States			More Derived Character States →	
	A	B	C	D	E
1. Size of I <sup>1</sup>	Small	Large	—	—	—
2. Number of upper premolars	5	4	3	2	1
3. Size of P <sup>3</sup> relative to P <sup>2</sup>	Much greater	Greater	Equal	Lesser	P <sup>2</sup> or P <sup>3</sup> absent
4. Height of hypocone relative to protocone on P <sup>4</sup>	Hypocone absent	Much lower	Lower	Equal	Greater
5. Number of lingual roots on M <sup>1</sup>	1	2	—	—	—
6. Paraconule present on M <sup>1</sup>	Yes	No	—	—	—
7. Metaconule present on M <sup>1</sup>	Yes	No	—	—	—
8. Metacone on M <sup>3</sup>	Yes	No	M <sup>3</sup> absent	—	—
9. Size of I <sub>1</sub>	Small	Large	—	—	—
10. Number of lower incisors	3	2	1	—	—
11. Number of lower premolars	4 or more	3	2	1	—
12. Number of roots on P <sub>2</sub>	2	1	P <sub>2</sub> absent	—	—
13. Paraconid on P <sub>4</sub>	Very low or absent	Low	Tall	—	—
14. M <sub>1</sub> trigonid	Anteroposteriorly compressed	Moderately expanded	Greatly expanded	—	—
15. M <sub>1</sub> trigonid	Vertical	Inclined anteriorly	—	—	—
16. M <sub>1</sub> trigonid	Tall	Short	—	—	—
17. Hypoconulid present on M <sub>1</sub>	Yes	No	—	—	—
18. Number of roots on M <sub>3</sub>	2	1	Tooth absent	—	—
19. Talonid on M <sub>3</sub>	Well-developed talonid present	Postcingulum present	Postcingulum absent	Tooth absent	—
20. Hypoconulid present on M <sub>3</sub>	Yes	No	M <sub>3</sub> talonid absent	—	—
21. Length to width ratio of palate	High	Low	—	—	—
22. Presence of palatine behind transverse process	No	Yes	—	—	—
23. Fenestration of palate	None	Slight	Extensive	—	—
24. Posterior border of zygomatic arch joins body of maxilla opposite	Posterior to space between M <sup>2</sup> and M <sup>3</sup>	Space between M <sup>2</sup> and M <sup>3</sup>	Middle of M <sup>2</sup>	Space between M <sup>1</sup> and M <sup>2</sup>	Metacone of M <sup>1</sup>
25. Development of angle on mandible	Prominent	Reduced	—	—	—

ly 50 characters in 100 insectivoran and deltatheridian genera. Characters were selected that held promise of being available for examination in a high percentage of fossil specimens, had been mentioned in previous

discussions of erinaceid or insectivore relationships, and could be readily evaluated without extended analysis of individual specimens. Only those characters which have proved to be useful in the subsequent anal-

TABLE 30  
Specimens and Literature References Used in  
Cladistic Analysis<sup>a</sup>

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Literature or specimens examined given after species name.
Order Insectivora
Suborder Proteutheria
Superfamily Tupaiioidea
Family Leptictidae
Subfamily Procerberinae
(1) <i>Leptonysson basiliscus</i> , AMNH 35295
(2) <i>Leptictidium auderiense</i> , Tobien (1962)
Subfamily Leptictinae
(3) <i>Palaeictops multicuspis</i> , AMNH 14741
<i>P. bridgeri</i> , AMNH 56032
(4) <i>Prodiacondon puercensis</i> , AMNH 16748
(5) <i>Diacondon bicuspis</i> , AMNH 4802
(6) <i>Leptictis haydeni</i> , Scott and Jepsen (1936)
<i>Leptictis</i> sp., 3704
RAM 3575
Subfamily Gypsonictopinae
(7) <i>Gypsonictops hypoconus</i> , AMNH 58764
<i>G. illuminatus</i> , Lillegraven (1969)
Family Zalambdalestidae
(8) <i>Zalambdalestes grangeri</i> , Kielan-Jaworowska (1969)
<i>Zalambdalestes</i> sp., Kielan-Jaworowska (1969)
Family Tupaiidae
Subfamily Tupaiinae
(9) <i>Tupaia javanica</i> , AMNH(M) 107595
Family Pantolestidae
(10) <i>Propalaeosinopa diluculi</i> , AMNH 35701, 35704
<i>P. thompsoni</i> , AMNH 33897, 33909
(11) <i>Palaeosinopa veterrima</i> , AMNH 15092, 16822
(12) <i>Pantolestes</i> sp., cast of YPM 13525 (AMNH 93645)
<i>P. natans</i> , Matthew (1909)
Family Pentacodontidae
(13) <i>Aphronorus fraudator</i> , AMNH 35624, 35636, 35642
(14) <i>Protentomodon ursivialis</i> , AMNH 22164, 22184
Superfamily uncertain
(15) <i>Kennalestes gobiensis</i> , Kielan-Jaworowska (1969)

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TABLE 30—(Continued)

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Suborder Macroscelidea
Family Macroscelididae
Subfamily Macroscelidinae
Tribe Macroscelidini
(16) <i>Elephantulus fuscipes</i> , AMNH(M) 49541
<i>E. rupestris</i> , AMNH(M) 165126
(17) <i>Macroscelides proboscideus</i> , AMNH(M) 89055
(18) <i>Petrodromus tetradactylus</i> , AMNH(M) 115781
Tribe Rhynchocyonini
(19) <i>Rhynchocyon cirnei</i> , AMNH(M) 49461
Suborder Dermoptera
Superfamily Mixodectoidea
Family Mixodectidae
(20) <i>Mixodectes pungens</i> , AMNH 3997, 16012, 16593
<i>M. malaris</i> , AMNH 833
(21) <i>Elpidophorus elegans</i> , AMNH 33899, 33900, 35963
(22) <i>Eudaemonema cuspidata</i> , AMNH 35829, 35830, 35834, 35838, Szalay (1969)
Superfamily Galeopteroidea
Family Galeopteridae
(23) <i>Cynocephalus variegatus</i> , AMNH(M) 107136
Suborder Erinaceota
Superfamily Erinaceoidea
Family Adapisoricidae
Subfamily Geolabidinae
(24) <i>Stilpnodon simplicidens</i> , AMNH 35690, 35692
(25) <i>Hyracolestes ermineus</i> , AMNH 20425
(26) <i>Centetodon praecursor</i> , McKenna (1960)
(27) <i>Myolestes</i> sp., AMNH 12054, 12063, 12378
<i>M. dasypelix</i> , Matthew (1909)
Cf. <i>M. dasypelix</i> , McKenna (1960)
(28) <i>Geolabis marginalis</i> , McKenna (1960)
Subfamily Adapisoricinae
(29) <i>Mckennatherium libitum</i> , Van Valen (1965)
(30) <i>Leptacodon tener</i> , AMNH 17179
<i>L. ladae</i> , AMNH 35954
(31) <i>Adunator lehmani</i> , Russell (1964)

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TABLE 30—(Continued)

(32) <i>Adapisorex abundans</i> , Russell (1964) <i>A. gaudryi</i> , Russell (1964)	(53) <i>Hylomys surillus</i> , AMNH(M) 102533
(33) <i>Paschatherium dolloi</i> , Russell (1964)	(54) <i>Neotetracus sinensis</i> , AMNH(M) 115513
(34) <i>Messelina tenera</i> , Tobien (1962)	Subfamily Erinaceinae
(35) <i>Ictopidium tatalgolensis</i> , Sulimski (1970)	Tribe Erinaceini
(36) <i>Tupaiaodon morrissi</i> , AMNH 19134 <i>T. ? minutus</i> , AMNH 19135	(55) <i>Gymnurechinus leakyei</i> , Butler (1956b) <i>G. camptolophus</i> , Butler (1956b) <i>G. songhorensis</i> , Butler (1956b)
Subfamily Creotarsinae	(56) <i>Untermannerix copiosus</i> , specimens listed on pp. 16–17 of this report
(37) <i>Litolestes notissimus</i> , AMNH 33830, 33831, 33841, 33938, 33944	(57) <i>Postpalerinaceus vireti</i> Butler (1956b), Crusafont (personal commun., 1975), Crusafont and Clois (1974), Crusafont and Villalta (1948)
(38) <i>Xenacodon mutilatus</i> , Matthew and Granger (1921)	(58) <i>Atelerix albiventris</i> , AMNH(M) 119126
(39) <i>Talpavus siegfriedti</i> , AMNH 22157, 22179, 22194, 22231	(59) <i>Hemiechinus megalotis</i> , AMNH(M) 170226
(40) <i>Creotarsus lepidus</i> , AMNH 16169	(60) <i>Mioechinus oeningensis</i> , Butler (1948) <i>M. sansanensis</i> , Butler (1948)
(41) <i>Dormaalius vandebroeki</i> , Quinet (1964)	(61) <i>Protechinus salis</i> , Lavocat (1961)
(42) Cf. <i>Entomolestes nitens</i> , AMNH 48175–48177, 48189	(62) <i>Erinaceus europaeus</i> , AMNH(M) 42562, 149412, 160470
(43) <i>Scenopagus edenensis</i> , McGrew (1959) <i>S. mcgrewi</i> , McKenna and Simpson (1959)	Tribe Amphechinini
(44) <i>Macrocranion tupaiaodon</i> , Tobien (1962)	(63) <i>Palaeoscaptor acridens</i> , AMNH 22080, 59707, 59729, 85734, Trofimov (1960)
(45) <i>Sespedectes singularis</i> , cast of LACM(CIT) 150 1785	(64) <i>Parvericius montanus</i> , specimens listed in Rich and Rasmussen (1973) and pp. 27–30 of this report
Subfamily Nyctitheriinae	(65) <i>Amphechinus edwardsi</i> , Viret (1938), Hürzeler (1944) <i>A. horncloudi</i> , specimens listed in Rich and Rasmussen (1973) and pp. 31–32 of this report
(46) <i>Nyctitherium celatum</i> , AMNH 15103 <i>N. serotinum</i> , AMNH 56060	(66) <i>Dimylechinus bernoullii</i> , Hürzeler (1944)
Family Erinaceidae	Tribe uncertain
Subfamily Galericinae	(67) <i>Stenoechinus tantalus</i> , specimens listed in Rich and Rasmussen (1973) and pp. 34–35 of this report
Tribe Galericipini	Subfamily Brachyericinae
(47) <i>Galerix exilis</i> , AMNH 10499, 10516, Butler (1948)	(68) <i>Brachyerix macrotis</i> , specimens listed in Rich and Rich (1971) and on pp. 36–37 of this report <i>B. incertis</i> , specimens listed in Rich and Rich (1971) and on pp. 41–42 of this report
Tribe Neurogymnurini	
(48) <i>Neurogymnurus cayluxi</i> , MNHN QU 8690 (figured by Filhol, 1884, pl. 1 fig. 9a, 13), MNHN MC 8730, MNHN QU 8697, Butler (1948)	
Tribe Echinosoricini	
(49) <i>Lanthanotherium</i> sp. F:AM 74969, 74973, 74984, 74990–74992, 76631	
(50) <i>Ocajila makpiyahe</i> , Macdonald (1963)	
(51) <i>Podogymnura truei</i> , AMNH(M) 164482	
(52) <i>Echinosorex gymnurus</i> , AMNH(M) 103884, 103886	

TABLE 30—(Continued)

<p>(69) <i>Metechinus nevadensis</i>, UCMF 29600, specimen listed on p. 44 of this report <i>M. amplior</i>, specimens listed on pp. 49–53 of this report</p> <p>Subfamily uncertain</p> <p>(70) <i>Proterix loomisi</i>, Gawne (1968) <i>P. bicuspis</i>, Gawne (1968)</p> <p>Family Dimylidae</p> <p>Subfamily Plesiodimylinae</p> <p>(71) <i>Plesiodimylus chanteri</i>, Müller (1967)</p> <p>Family Talpidae</p> <p>Subfamily Talpinae</p> <p>Tribe Urotrichini</p> <p>(72) <i>Neurotrichus gibbsi</i>, AMNH(M), 31171</p> <p>Tribe Talpini</p> <p>(73) <i>Talpa europaea</i>, AMNH(M) 163286</p> <p>Tribe Condylurini</p> <p>(74) <i>Condylura cristata</i>, AMNH(M) 135390</p> <p>Tribe Scalopini</p> <p>(75) <i>Scapanus latimanus</i>, AMNH(M) 37447</p> <p>(76) <i>Scalopus</i> sp., AMNH(CA) 208</p> <p>Family uncertain</p> <p>(77) <i>Exallerox hsandagolensis</i>, AMNH 22083</p> <p>Superfamily Soricoidea</p> <p>Family Plesiosoricidae</p> <p>(78) <i>Meterix</i> sp., F:AM 74920, 74929, 76651</p> <p>Family Nesophontidae</p> <p>(79) <i>Nesophontes edithae</i>, AMNH 14174</p> <p>Family Soricidae</p> <p>Subfamily Crocidurinae</p> <p>Tribe Crocidurini</p> <p>(80) <i>Crocidura occidentalis</i>, AMNH(M) 86800</p> <p>(81) <i>Paracrocidura schoutedeni</i>, AMNH(M) 180953</p> <p>Tribe Scutisoricini</p> <p>(82) <i>Scutisorex conicus</i>, AMNH(M) 48474</p> <p>Subfamily Soricinae</p> <p>Tribe Soricini</p> <p>(83) <i>Sorex cinereus</i>, AMNH(M) 127965</p> <p>Tribe Blarinini</p> <p>(84) <i>Blarina brevicauda</i>, AMNH(CA) 1405</p>	<p>Order Deltatheridia</p> <p>Suborder Hyaenodonta</p> <p>Superfamily Palaeoryctoidea</p> <p>Family Palaeoryctidae</p> <p>Subfamily Didelphodontinae</p> <p>(85) <i>Acmeodon secans</i>, AMNH 4063, 16599</p> <p>(86) <i>Gelastops parvus</i>, AMNH 35225– 35227</p> <p>(87) <i>Avunculus didelphodonti</i>, AMNH 35297</p> <p>(88) <i>Didelphodus absarokae</i>, AMNH 4228, 4229, 15700, 16825</p> <p>Subfamily Palaeoryctinae</p> <p>(89) <i>Palaeoryctes puercanensis</i>, AMNH 15923</p> <p>Family Micropternodontidae</p> <p>(90) <i>Sarcodon vetus</i>, AMNH 21732</p> <p>Family Didymoconidae</p> <p>(91) <i>Didymoconus colgatei</i>, AMNH 21627, 21651</p> <p>Suborder Zalambdodonta</p> <p>Superfamily Tenrecoidea</p> <p>Family Tenrecidae</p> <p>Subfamily Potamogalinae</p> <p>(92) <i>Potamogale velox</i>, AMNH(M) 51319</p> <p>Subfamily Oryzorictinae</p> <p>(93) <i>Microgale ?talazzci</i>, AMNH(M) 100711</p> <p>(94) <i>Limnogale mergulus</i>, AMNH(M) 100688</p> <p>Subfamily Tenrecinae</p> <p>(95) <i>Setifer setosus</i>, AMNH(M) 170612</p> <p>(96) <i>Hemicentetes semicaudatus</i>, AMNH(M) 100777</p> <p>(97) <i>Echinops telfairi</i>, AMNH(M) 100754</p> <p>Family Solenodontidae</p> <p>(98) <i>Solenodon paradoxus</i>, AMNH(M) 77745</p> <p>Superfamily Chrysochloroidea</p> <p>Family Chrysochloridae</p> <p>(99) <i>Neamblysomus gunningi</i>, AMNH(M) 54364</p> <p>(100) <i>Chrysochloris asiatica</i>, AMNH(M) 167963</p>
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" Arranged with slight modification according to the  
classification of Van Valen (1967).

ysis are tabulated in table 31. Characters that were found not to be useful were those in which only a single state was noticed or proved difficult to evaluate. In tables 29–31 and all subsequent discussion, a given character is identified by the same number and a given character state of that character by the same letter. For any one character, the character states were designated in alphabetical order with character state A as the most primitive.

Many of the characters listed in table 29 were difficult to evaluate and further explanation of the criteria used to determine the character states beyond what is on the table is needed.

Character 1, size of  $I_1$ ; character 9, size of  $I_1$ : if the first incisor was judged to be no longer than that of *Erinaceus europaeus* relative to the teeth behind it, then the specimen was allocated to the category "small or absent."

Character 13, height of the paraconid on  $P_4$ : the paraconid was described as "very low or absent" if there was no trace of that cusp or its presence was barely discernible. If the cusp was nearly as tall as the protoconid, it was described as "tall." Intermediate specimens were described as "low." There was little problem deciding in individual cases between the categories "tall" and "low" for the differences between specimens in these two categories were quite sharp. Greater difficulties were encountered between the "very low or absent" and "low" categories for several intermediates were found between the extremes which were readily separable into these two categories.

Character 14, degree of anteroposterior expansion of  $M_1$  trigonid: attempts to measure the angle between the prevallid and postvallid of the trigonid with a goniometer have yielded unsatisfactory results. The prevallid and postvallid surfaces are not flat planes but rather subtly depart from this ideal with slight but complex curves, which make it difficult to achieve repeatable measurements of sufficient accuracy to discriminate between the character states recog-

nized here. One can argue that because this angle cannot be measured mechanically to the degree recorded, the results listed are worthless. However, a second examination of a number of specimens results in an almost perfect reassignment of them into the same three groups as the initial categorization leading one to suspect that the character can be meaningfully divided into the states used here. In fact, it is quite possible that a greater number of subdivisions could be resolved consistently in this manner. Certainly the character state "greatly expanded" could be further subdivided as evidenced by the diagnosis of *Brachyerix* where it is separated from *Metechinus* by the greater degree of expansion of the trigonid of  $M_1$  although both are listed as having it "greatly expanded" in table 31. No verbal description of the boundaries of these character states is possible. One can only reconstruct the author's basis for making these judgments by examining the same material and deciding at that point whether the categories used here were consistently recognized. This is an unsatisfactory procedure, but none seems better under the circumstances.

The length to width ratio of the trigonid was not considered to be an adequate substitute for the angle between the prevallid and postvallid because in some teeth the angle is relatively great because the paraconid is shifted buccally, but the ratio is low.

Character 15, orientation of the trigonid of  $M_1$ : if the posterior edge of the posterolingual corner of the trigonid in lingual view was no more inclined anteriorly than in *Erinaceus europaeus*, the trigonid was described as "vertical." No attempt was made to measure this character with a goniometer, again because of markedly different results when specimens were measured twice. Efforts to judge this character merely by visual comparison with *E. europaeus* were less satisfactory than efforts to measure the degree of expansion of the trigonid of  $M_1$ , for specimens were not as consistently placed in the same groups. However, study of this character and character 16, height of the trigonid

TABLE 31  
**Character States of 100 Genera of Insectivora and Deltatheridia**  
 (See tables 29 and 30 and text for explanation of data presented here)

Character Number	(1) <i>Leptonysson</i>	(2) <i>Leptictidium</i>	(3) <i>Palaeictops</i>	(4) <i>Prodiacodon</i>	(5) <i>Diadodon</i>	(6) <i>Leptictis</i>	(7) <i>Gypsonictops</i>	(8) <i>Zalambdalestes</i>	(9) <i>Tupaia</i>	(10) <i>Propalaeosinopa</i>	(11) <i>Palaeosinopa</i>	(12) <i>Pantolestes</i>	(13) <i>Aphronorus</i>	(14) <i>Protentomodon</i>	(15) <i>Kennalestes</i>	(16) <i>Elephantulus</i>	(17) <i>Macroscelides</i>
1	—	—	—	—	A	A	—	—	B	—	—	—	—	—	A	A	A
2	—	—	—	B	B	B	—	B	C	B?	—	B	—	—	B	B	B
3	—	—	—	A	A	A	—	A	A	B	B	—	—	—	A	B	B
4	—	—	—	B	C	B	A	A	A	A	A	A	A	—	A	E	D
5	—	—	—	A	A	A	A	A	A	A	A	A	—	—	A	B	B
6	—	—	—	A	A	A	A	A?	B	A	A	B	A	—	A	B	B
7	—	—	—	A	A	A	A	A?	B	A	A	B	A	—	A	B	B
8	—	—	—	B	A	A	A	A	A	A	A	A	A	—	A	C	C
9	—	A?	A	A	A?	A	—	—	B	A	—	—	—	—	A	A	A
10	—	A	A	—	A	A	—	A	A	A?	—	—	—	—	A?	B	B
11	—	A	A	A	A	A	A	A	B	A	A	A	—	—	A	A	A
12	B	A	A	A	A	A	A	A	B	A	A	A	A	—	A	A	B
13	—	B	B	A	B	B	A	B	B	A	A	A	A	—	A	B	B
14	A	A	A	A	A	A	A	A	B	A	A	—	A	B?	A	C	C
15	A	A	A	A	A	A	A	A	A	A	A	—	A	A	A	B	B
16	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A
17	A	A	A	A	A	A	A	A	B	A	A	—	A	A	A	A	B
18	A?	—	A	A	A	A	A	A	A	A	A	—	A	A	A	B	C
19	A	—	A	A	A	A	A	A	A	A	A	—	A	A	A	C	D
20	A	—	A	A	A	A	A	A	B	A	A	—	A	A	A	B	C
21	—	—	—	A	—	A	—	A	A	A	A	A	—	—	A	A	A
22	—	—	—	A	—	A	—	A	A	—	—	—	—	—	—	A	B
23	—	—	—	A	—	A	—	—	A	—	—	A	—	—	—	C	C
24	—	—	—	—	A	A	—	B	A	A	A	—	—	—	—	C	C
25	A	—	—	—	A	A	—	—	A	A	—	—	—	—	—	A	A

of  $M_1$ , did reveal that there are a large number of erinaceoids characterized by a low, anteriorly inclined  $M_1$  trigonid, two advanced character states. Therefore, despite the imprecision of deciding which character state more properly described a given specimen, the character is employed here because it seems to have utility in distinguishing a significant number of erinaceoids.

Character 16, height of the trigonid of  $M_1$ : if the height of the metaconid above the lowest point on the entocristid was as great or greater than in *Erinaceus europaeus* relative

to the width of the trigonid, the trigonid of  $M_1$  was described as tall.

Character 19, degree of development of a talonid on  $M_3$ : if an entoconid, hypoconid, and entocristid were present on the tooth, it was described as having a "well developed talonid present." If the tooth lacked any or all of those structures but had any trace of a postcingulum behind the trigonid, it was described as having a "postcingulum present." Those described as "postcingulum absent" consisted of a trigonid with no structures present behind the postvallid.

TABLE 31—(Continued)

Character Number	(18) <i>Petrodromus</i>	(19) <i>Rhynchocyon</i>	(20) <i>Mixodectes</i>	(21) <i>Elpidophorus</i>	(22) <i>Eudaemonema</i>	(23) <i>Galeopithecus</i>	(24) <i>Stilpnodon</i>	(25) <i>Hyracolestes</i>	(26) <i>Centetodon</i>	(27) <i>Myolestes</i>	(28) <i>Geolabis</i>	(29) <i>Mckennatherium</i>	(30) <i>Leptacodon</i>	(31) <i>Adunator</i>	(32) <i>Adapisorex</i>	(33) <i>Paschatherium</i>	(34) <i>Messelina</i>
1	B	A	B	B	—	A	—	—	—	—	B	—	—	—	—	—	—
2	C	C	C	B	B	C,D	—	—	—	—	A	—	—	—	—	—	C
3	A	A	B	B	B	A	—	—	—	—	A	—	—	A	—	—	B
4	A	A	A	A	A	A	—	—	—	—	A	—	A	B	A	—	—
5	B	A	A	A	B	A	—	—	—	—	B	—	A?	A	—	A	A
6	B	B	A	A	A	A	—	—	—	—	B?	—	A	A	A	A	A
7	B	B	A	A	A	A	—	—	—	—	B?	—	A	A	A	A	A
8	A	A	A	A	A	A	—	—	—	—	A	—	A	A	A	—	A
9	A	A	B	—	—	A	A?	—	—	—	A	—	—	—	—	—	—
10	B	A	B	—	B	B	—	—	—	—	A	—	—	—	A	—	—
11	A	A	B	A	A	B	A	—	—	A	A	—	—	A	A	A	—
12	A	A	B	B	B	A	A	—	—	A	A	—	—	A	A	A	—
13	A	A	A	C	A	A	A	B	B	—	A	—	B	B	A	B	B
14	B	B	A	A	A	A	B	B	A	A	B	A	A	A	A	A	A
15	A	A	A	A	B	B	B	A	A	A	A	B	A	B	A	A	B
16	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A
17	B	B	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A
18	A	A	A	A	A	A	A	—	A	A	A	A	A	A	A	A	A
19	A	A	A	A	A	A	A	—	A	A	A	A	A	A	A	A	A
20	B	B	A	A	A	A	A	—	B?	A	B	A	A	B	A	A	A
21	A	A	A	—	—	B	—	—	—	—	A	—	—	—	—	—	—
22	A	A	—	—	—	A	—	—	—	—	A	—	—	—	—	—	—
23	C	A	A	—	—	A	—	—	—	—	A	—	—	—	—	—	—
24	A	A	A	A	A	A	—	—	—	—	B	—	—	—	B	—	—
25	A	A	—	—	—	B	—	—	—	—	A	—	—	—	—	—	—

Character 20, length to width ratio of palate: at the beginning of this survey, an attempt was made to measure this ratio numerically but was abandoned. In many cases, fossil specimens were not complete enough to make the same measurements in many of them, and yet it could be readily seen that the condition in the Brachyericinae and advanced Erinaceinae was highly unusual relative to the remainder of the Insectivora. Therefore, it was decided to relax the procedure in order to obtain a wider sample to establish this difference in at least a crude manner.

In order to achieve the breadth of cover-

age desired and yet avoid examining an unduly large number of specimens, the analysis was carried out at the generic rather than the specific level. The majority of extinct insectivore genera represented in the collections of the Department of Vertebrate Paleontology, American Museum of Natural History, together with a number of fossil genera described in the literature were included in the sample. In addition, a number of modern genera (but not all available) from the Department of Mammalogy, American Museum of Natural History, were examined. There was a bias in the quantity of specimens examined toward members of the Erinaceidae

TABLE 31—(Continued)

Character number	(35) <i>Ictopidium</i>	(36) <i>Tupaiaodon</i>	(37) <i>Litolestes</i>	(38) <i>Xenacondon</i>	(39) <i>Talpavus</i>	(40) <i>Creotarsus</i>	(41) <i>Dornaiulus</i>	(42) <i>Entomolestes</i>	(43) <i>Scenopagus</i>	(44) <i>Macrocranium</i>	(45) <i>Sespedectes</i>	(46) <i>Nyctitherium</i>	(47) <i>Galerix</i>	(48) <i>Neurogymnurus</i>	(49) <i>Lanthanotherium</i>	(50) <i>Ocajila</i>	(51) <i>Podogymnura</i>
1	—	—	—	—	—	—	—	—	—	A	—	—	A	A?	—	—	A
2	—	B	—	—	—	—	—	—	B	B	—	—	B	B	B	—	C
3	—	A	B	—	—	—	—	—	B	B	—	—	A	—	B	—	A
4	—	B	A	—	—	—	—	—	B	A	—	—	C	B,C	C	—	C
5	—	A	A?	—	—	—	—	—	A	A	—	A?	A	A	A	—	B
6	—	B	A	—	—	—	—	A	A	A	—	A	B	B	B	—	B
7	—	A	A	—	—	—	—	A	A	A	—	A	A	A	A	—	A
8	—	A	A	—	—	—	—	—	—	A	—	—	A	A	A	—	A
9	B	A	A?	A	—	—	A	—	—	A	—	—	B	A	B	—	A
10	A	A	A	A	—	A	A	—	—	A	—	A	A	A	A	—	A
11	B	—	B	A	—	B	B	A	—	A	—	A	A	A	A,B	—	B
12	B	—	A	A	—	A	B	A	—	B	—	A	A	A	B	—	B
13	B	B	B	A	B	B	A	A	—	A	A	B	C	A	A	—	B
14	A	A	A	A	A	A	—	A	A	B	A	A	B	B	B	—	B
15	A	A	B	—	B	B	—	A	B	B	B	A	A	B	A	—	A
16	A	A	B	—	B	B	—	B	A	A	B	A	B	B	B	—	B
17	B	A,B	A	A	A	A	—	A	A	A	B	A	B	B	B	—	B
18	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
19	A	A	A	A	A	A	—	A	A	A	A	A	A	A	A	A	A
20	B	A	A	A	A	—	—	A	A	A	A	—	B	B	B	B	B
21	—	A	—	—	—	—	—	—	—	A?	—	—	A	A	—	—	A
22	—	—	—	—	—	—	—	—	—	—	—	—	—	A	—	—	B
23	—	—	—	—	—	—	—	—	—	—	—	—	A	A	—	—	A
24	—	C	B	—	—	—	—	B	—	—	—	—	B	B	B	—	A
25	—	—	—	—	—	—	A	—	—	—	—	—	A	A	—	—	A

and Adapisoricidae, because on the basis of previous opinion, it seemed probable *a priori* that the closest affinities of the Erinaceinae and Brachyericinae were to be found with taxa previously placed in those two families.

Once the polarity of the various characters was established (see table 29), an attempt was made using shared derived character states to relate the various genera that had either been previously placed in the Erinaceinae or Brachyericinae or appeared on the basis of personal study to share many of the character states frequently cited as typifying one or both of them. In some cases, two taxa were considered to have shared a common ancestor not shared with a third taxon not

simply on the basis of shared derived character states but rather in possessing two distinct but recognizably more derived states than found in the third taxon. For example if three taxa have successively more derived states A, B, and C, respectively for a given character, this is evidence that the second and third taxa shared a common ancestor with state B that is not shared with the first taxon. Presumably none of the ancestors of the first taxon ever possessed a state for the character in question more advanced than A.

The result of this analysis has been visually summarized in the cladogram given in figure 21. This arrangement is not the only one possible but it does satisfy two criteria



TABLE 31—(Continued)

Character number	(52) <i>Echinosorex</i>	(53) <i>Hylomys</i>	(54) <i>Neotetracus</i>	(55) <i>Gymnurechinus</i>	(56) <i>Untermannerix</i>	(57) <i>Postpalerhinaceus</i>	(58) <i>Atelerix</i>	(59) <i>Hemiechinus</i>	(60) <i>Mioechinus</i>	(61) <i>Protechinus</i>	(62) <i>Erinaceus</i>	(63) <i>Palaeoscaptor</i>	(64) <i>Parvericius</i>	(65) <i>Amphechinus</i>	(66) <i>Dimylechinus</i>	(67) <i>Stenoechinus</i>	(68) <i>Brachyerix</i>
1	A	A	A	A	A	A	A	A	A	A	A	B	—	B	—	—	—
2	B	B,C	B,C	C	C	C	C	C	C	C	C	C	—	C	C	—	D
3	A	D	B	B	B	B	C	D	C	—	C	A	—	B	B	—	E
4	C	C	C	C	C	C	C	C	—	C	C	C	C	C	—	—	E
5	B	B	B	A	A	A	A	A	A	A	A	A?	A	A	—	—	A
6	A	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B
7	A	A	A	A	A,B	B	A	A	A	B	A,B	A	B	A,B	B	B	B
8	A	A	A	B	B	B	B	B	B	B	B	A	B	B	C	—	C
9	A	A	A	A	A	A	A	A	A	A	A	B	B	B	B	—	B
10	A	A	A	B	B	B	B	B	B	B	B	A,B	B	B	B	—	B
11	A	A	A,B	C	C	C	C	C	C	C	C	B,C	C	C	C	—	D
12	B	B	B	A	B	—	B	B	—	B	B	A,B	B	B	B	—	C
13	B	A	A	C	C	C	C	C	C?	C	C	C	C	C	C	B	A
14	B	C	B	B	B	B?	B,C	B	B,C	B	B	C	B	C	C	B	C
15	A	A	A	B	A	A	A	A	—	—	B	A	A	A,B	A	A	A
16	A	A	B	A	A	A	A	A	—	—	A	A	A	A	A	A	A
17	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
18	A	A	A	A,B?	B	B <sup>a</sup>	B	B	B	B	B	A	B	B	C	A	C
19	A	A	A	B,C	C	C <sup>a</sup>	C	C	C	C	C	B	C	C	D	B	D
20	B	B	B	B,C	C	C <sup>a</sup>	C	C	C	C	C	B	C	C	C	B	C
21	A	A	A	A	A	B	B	B	—	—	B	A	—	A	A	—	B
22	B	B	A	B	B	—	B	B	B	—	B	—	—	B	B	—	B
23	A	B	B	A	A	—	B	B	C	—	C	—	—	A	A	—	A
24	A	C	B	C	C	C	C	C	—	C	C	C	D	D	D	—	D
25	A	A	A	A	B	—	A	A	—	A	A	—	A	A	A	—	B

that commend it for serious consideration: (1) it requires the least amount of parallelism of any arrangement attempted, and (2) no reacquisition of a primitive character state is hypothesized after a derived state was achieved.

### ALTERATIONS TO THE PRESENT TAXONOMY OF THE ERINACEINAE AND BRACHYERICINAE

*Exallerix hsandagolensis* McKenna and Holton, 1967, is based upon a single, partial mandible from the medial Oligocene of Mongolia. Although the characters listed in table 31 suggest the placement of *Exallerix* where

it is shown in figure 21, two characters not tabulated in the survey suggest that the genus is only remotely related to *Brachyerix* and *Metechinus*. On no other insectivore specimen examined was there a prominent ridge for the masseter? muscle on the lateral side of the horizontal ramus of the mandible, nor were denticles similar to those on I<sub>1</sub>, P<sub>4</sub>, and M<sub>1</sub> of *E. hsandagolensis* observed. These rare or unique features within the Insectivora suggest that when *Exallerix* is better known, it may prove to be as aberrant a form as one of the more exotic members of the Dimylidae and perhaps deserving recognition as a distinct subfamily or family. For the moment, the best course seems to be to

TABLE 31—(Continued)

Character number	(69) <i>Metechinus</i>	(70) <i>Proterix</i>	(71) <i>Plesiodimylus</i>	(72) <i>Neurotrichus</i>	(73) <i>Talpa</i>	(74) <i>Condylura</i>	(75) <i>Scapanus</i>	(76) <i>Scalopus</i>	(77) <i>Exallaxis</i>	(78) <i>Meterix</i>	(79) <i>Nesophontes</i>	(80) <i>Crociodura</i>	(81) <i>Paracrociodura</i>	(82) <i>Scutisorex</i>	(83) <i>Sorex</i>	(84) <i>Blarina</i>	(85) <i>Acmeodon</i>
1	B	B?	—	B	A	A	B	B	—	—	A	B	B	B	B	B	—
2	D	C,D	B	C	B	B	B	B	—	—	C	C	C	B	B,C	B	—
3	E	B	C	C	C	C	B	B	—	—	B,C	D	B	D	D	D	—
4	D,E	C	A	A	A	A	A	A	—	C	A	A	C	C	C	C	—
5	A	A	B	A?	A	A	A	A	—	A	A	B	B?	B	B?	B?	—
6	B	B	B	B	B	B	B	B	—	B	B	B	B	B	B	B	A?
7	B	A	B	B	B	B	B	B	—	A	B	B	B	B	B	B	B?
8	C	A	B	A	A	A	A	A	—	—	A	A	A	A	A	B	—
9	B	B	A	A	A	A	A	A	B	B	A	B	B	B	B	B	—
10	B	A,B	A	A	A	A	A	B	B	B	A	C	C	C	C	C	—
11	D	B,C	B	C	A	A	A	B	C	B	B	C	C	C	C	C	B
12	C	B,C	B	B	A	A	B	B	B	B	A	B	B	B	B	—	A
13	A	A	A	A	B	B	A	A	A	B	A	A	B	A	A	C	B
14	C	A	C	C	C	C	B	A	C	A	B	C	A	C	C	C	B
15	A	B	—	A	B	B	A	B	A	A	A	A	B	A	A	B	A
16	A	B	—	A	A	A	A	A	A	A	B	A	A	A	A	B	A
17	B	B	B	B	B	B	B	B	B	A	B	B	B	B	B	B	—
18	C	A	C	A	A	A	A	A	C	A	A	A	A	A	A	A	—
19	D	A	D	A	A	A	A	A	D	A	A	A	A	A	A	A	—
20	C	B	B	B	B	B	B	B	C	—	B	B	A	B	B	B	—
21	B	B	—	A	A	A	A	A	—	B	A	A	A	A	A	A	—
22	B	A	—	A	A	A	A	A	—	A?	A	A	A	A	A	A	—
23	A	A	—	A	B	B	B	A	—	A	A	B	A	A	A	A	—
24	D,E	C	—	A	A	A	B	B	—	C	B	B	B	B	A	B	—
25	B	A	—	A	A	A	A	A	—	A	A	A	A	A	A	A	—

regard the genus as *Erinaceoidea incertae sedis*.

*Dimylechinus bernoullii* Hürzeler, 1944, was originally allied with *Amphelchinus* and thus placed in the Erinaceinae by Hürzeler (1944). Later workers followed this allocation until McKenna and Holton (1967) transferred *D. bernoullii* to the Brachyericinae. Rich and Rich (1971) followed this assignment. As a result of the analysis presented in figure 21 based on the data in table 31, it appears that Hürzeler's original allocation was correct. Of the 25 characters tabulated in table 31, the Brachyericinae may be distinguished from all the Erinaceinae except *D. bernoullii* by eight derived character states. Because *D. bernoullii* has lost the

third molars, the Brachyericinae may be separated from that species by three fewer derived character states. However, it does not seem prudent to ally *D. bernoullii* with the Brachyericinae merely because the gulf between is somewhat narrower for the three derived character states that tend to support such an allocation are not unique within the Insectivora. On the other hand, *D. bernoullii* does possess the one derived character state of the Erinaceinae that distinguishes them not only from the Brachyericinae but from all other Insectivora as well, namely the enlarged paraconid on P<sub>4</sub>.

Although *Amphelchinus* has long been regarded as an unusual erinaceine because of its enlarged first incisors and thus possibly

TABLE 31—(Continued)

Character number	(86) <i>Gelastops</i>	(87) <i>Avunculus</i>	(88) <i>Didelphodus</i>	(89) <i>Palaeoryctes</i>	(90) <i>Sarcodon</i>	(91) <i>Didymoconus</i>	(92) <i>Potamogale</i>	(93) <i>Microgale</i>	(94) <i>Limnogale</i>	(95) <i>Setifer</i>	(96) <i>Hemicentetes</i>	(97) <i>Echinops</i>	(98) <i>Solenodon</i>	(99) <i>Neamblysomus</i>	(100) <i>Chrysochloris</i>
1	—	—	—	—	—	—	B	B	B	B	A	B	B	B	B
2	—	—	—	—	—	—	B,C	C	C	C	C	D	C	B,C	B,C
3	—	—	B	B	—	—	A	B	A	A	—	E	B	A	A
4	—	—	A	A	—	—	A	A	A	A	A	A	A	A	A
5	—	—	A	A	—	A	A	A	A	A	A	A	A	A	A
6	—	—	A	B	—	—	B	B	B	B	B	B	B	B	B
7	—	—	A	B	—	—	B	B	B	B	B	B	B	B	B
8	—	—	A	B	—	—	A	B	B	B	B	B	B	B	B
9	—	—	A	—	—	—	A	A	A	A	A	A	A	A	A
10	—	—	A	—	—	—	A	A	A	A	A	B	A	A	A
11	A	A	A	B	A	A	B	B	B	B	B	C	B	B	B
12	A	A	A	B	A	A	B	A	B	A	A	A	A	B	B
13	B	B	B	A	B	B	B	B	B	B	B	B?	B	A	A
14	B	A	B	A	B	B	A	B	B	A	C	A	A	A	A
15	B	—	A	A	A	A	A	A	A	A	A	A	A	A	A
16	B	—	A	A	A	A	A	A	A	A	A	A	A	A	A
17	A	A?	A	A	A	A	B	B	B	B	B	B	B	B	B
18	A	—	A	A	—	—	A	A	A	A	A	A	A	B	B
19	A	—	A	A	—	—	A	A	A	B	B	B	A	C	C
20	—	—	A	A	—	—	B	B	B	B	B	B	B	B	B
21	—	—	A	B	—	—	A	A	A	A	A	A	A	A	A
22	—	—	—	A	—	—	A	A	A	A	A	A	A	A	A
23	—	—	—	A	—	—	A	A	A	A	A	A	A	A	A
24	—	—	—	—	—	—	A	A	A	B	A	A	B	B	B
25	—	—	—	—	—	—	A	A	A	A	B	A	B	A	A

" Crusafont (personal commun., 1975) said this to be the character state on an  $M_3$  he tentatively refers to *Postpalerinaceus*.

representing a separate lineage within the subfamily (e.g., Viret, 1938; Bohlin, 1942; Butler, 1956b), this conception of its phyletic position has never been recognized in any scheme of classification. Because the lower dentition of *Parvericius* is now adequately known and *Dimylechinus* has been returned to the Erinaceinae, including *Palaeoscaptor*, there are now four genera in the Erinaceinae that have enlarged first incisors. This is a derived character state and is regarded as an adequate basis for recognizing the tribe Amphechinini within the Erinaceinae. All the other members of the Erinaceinae are placed

in the tribe Erinaceini Fischer von Wal-dheim, 1817.

THE HYPOTHETICAL, PRIMITIVE  
MORPHOTYPES OF THE  
ERINACEINAE AND  
BRACHYERICINAE

After the internal geometry of the phylogenetic relationships within each of the sub-families had been worked out, an attempt was made to construct a hypothetical, primitive morphotype for each subfamily. This was done by generally assuming that the most

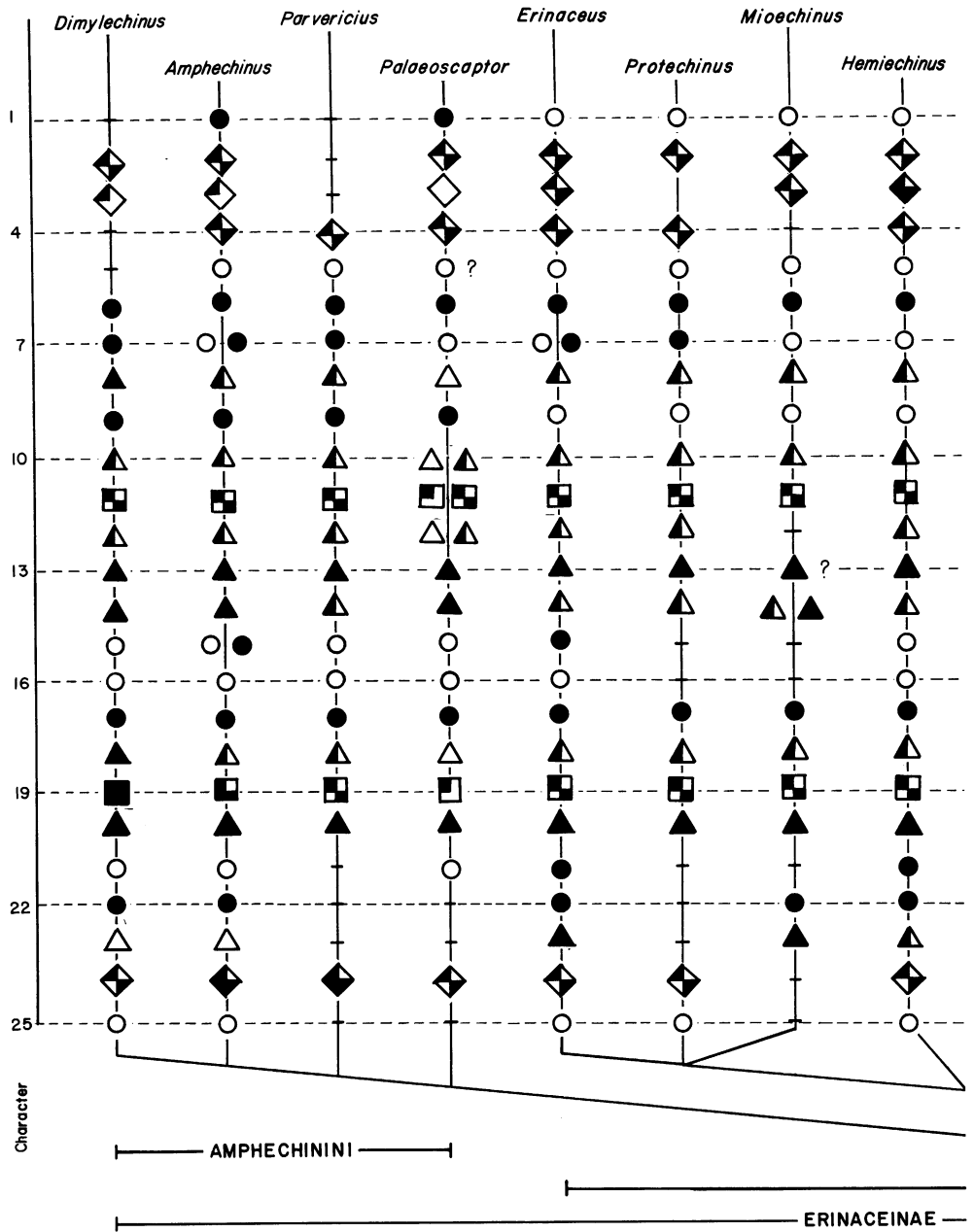
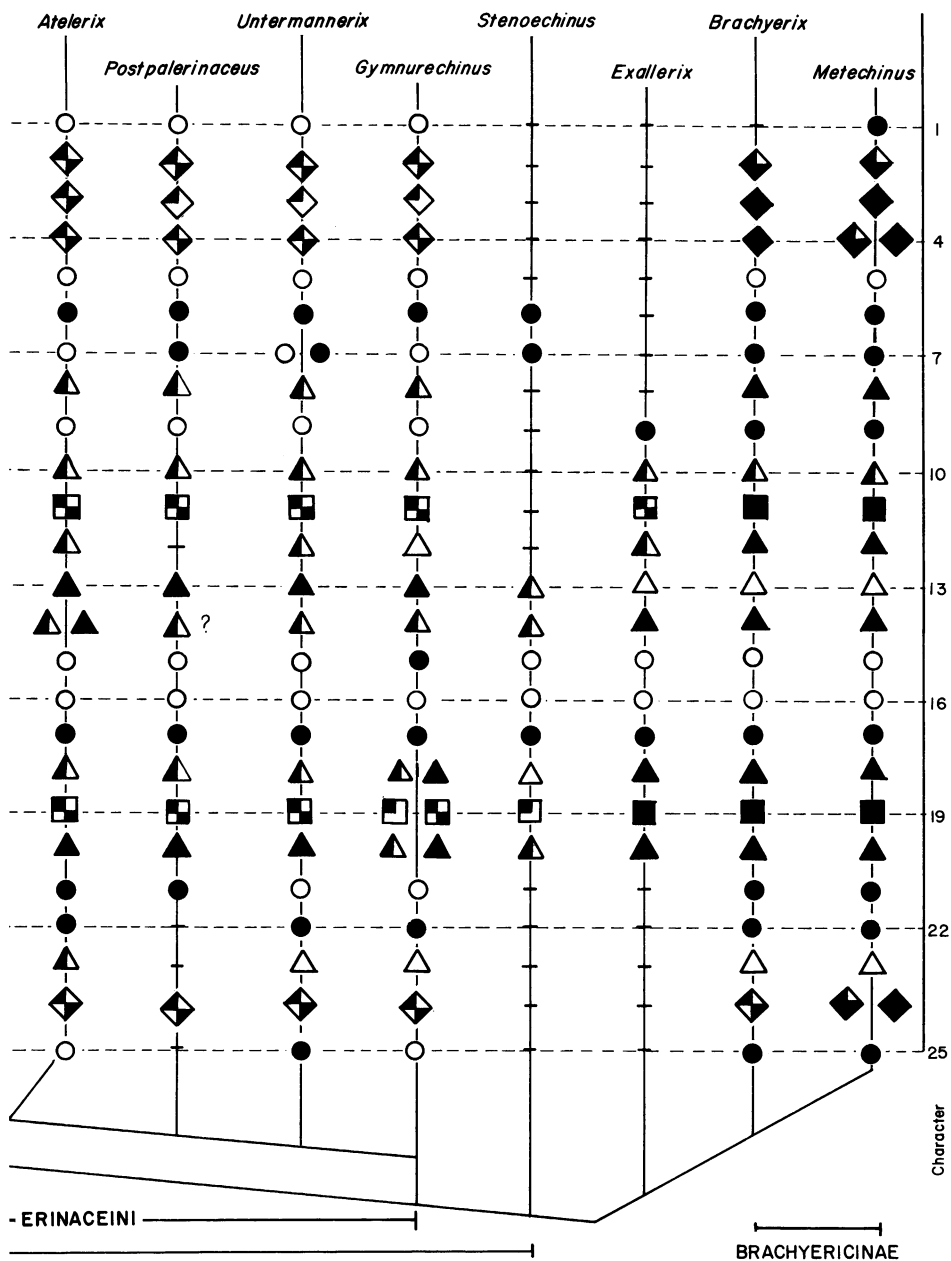


FIG. 21. Cladogram illustrating hypothesis of relationships among the Erinaceinae and Brachyeri- cinae based on the presence of shared, derived character states. In order to conserve space on this chart, the characters are listed by number in columns at the extreme lefthand and righthand margins of the diagram. These numbers correspond to those used to identify the characters in tables 29–31. The characters used in this analysis are briefly described in table 29 and further discussed on pp. 89–91. Specimens and figures of each genus examined are listed in table 30. Character states of each genus are tabulated in table 31.

On this diagram, the state or states of each character known for a genus are indicated by how much the symbol representing the character is shaded. More derived character states are more shaded as



indicated below. When more than one character state for a given character is known for a genus, both character states are indicated by a pair of symbols. Where no symbol for the character is present on the chart, the character is unknown in the genus.

More derived →

- Characters with 2 states ○ ●
- Characters with 3 states △ ▲ ▴
- Characters with 4 states □ ■ ▣ ▤
- Characters with 5 states ◇ ◆ ◆ ◆ ◆

TABLE 32  
Hypothetical, Primitive Morphotypes of the Erinaceinae and Brachyericinae

Character	Erinaceinae <sup>a</sup>		Brachyericinae
	Erinaceini	Amphechinini	
1. Size of I <sup>1</sup>	A, Small	B, Large	B, Large
2. Number of upper premolars		C, 3	D, 2
3. Size of P <sup>3</sup> relative to P <sup>2</sup>	B, Greater	A, Much greater	E, P <sup>3</sup> absent
4. Height of hypocone relative to protocone on P <sup>4</sup>		C, Lower	D, Equal
5. Number of lingual roots on M <sup>1</sup>		A, 1	A, 1
6. Paraconule present on M <sup>1</sup>		B, No	B, No
7. Metaconule present on M <sup>1</sup>		A, Yes	B, No
8. Metacone present on M <sup>3</sup>	A, Yes	B, No	C, M <sup>3</sup> absent
9. Size of I <sub>1</sub>	A, Small	B, Large	B, Large
10. Number of lower incisors		B <sup>b</sup> , 2	B, 2
11. Number of lower premolars		C <sup>b</sup> , 2	D, 1
12. Number of roots on P <sub>2</sub>		A, 2	C, P <sub>2</sub> absent
13. Paraconid on P <sub>4</sub>		C, Tall	A, Very low or absent
14. M <sub>1</sub> trigonid		B, Moderately expanded	C, Greatly expanded
15. M <sub>1</sub> trigonid		A, Vertical	A, Vertical
16. M <sub>1</sub> trigonid		A, Tall	A, Tall
17. Hypoconulid present on M <sub>1</sub>		B, No	B, No
18. Number of roots on M <sup>3</sup>		A, 2	C, Tooth absent
19. Talonid on M <sub>3</sub>		B, Postcingulum present	D, Tooth absent
20. Hypoconulid present on M <sub>3</sub>		B, No	C, M <sub>3</sub> talonid absent
21. Length to width ratio of palate		A, High	B, Low
22. Presence of palatine behind transverse process		B, Yes	B, Yes
23. Fenestration of palate		A, None	A, None
24. Posterior border of zygomatic arch joins body of maxilla opposite		C, Middle of M <sup>2</sup>	D, Space between M <sup>2</sup> and M <sup>3</sup>
25. Development of angle on mandible		A, Prominent	B, Reduced

<sup>a</sup> If the states of a character for the hypothetical, primitive morphotype of the Erinaceini and Amphechinini are the same, the state is listed once under the Erinaceinae; otherwise, separately under each tribe. Where the tribes differ, the hypothetical primitive morphotype of the Erinaceinae would be the same as that of the more primitive tribe for the particular character under consideration.

<sup>b</sup> See p. 99 of text for discussion of one specimen of *Palaeoscaptor acridens* with three lower incisors and three lower premolars.

primitive condition for each character found in any member of each subfamily was the character state of this hypothetical construct. The utility of this construct was an aid to identifying the groups most closely related to each of the subfamilies. Table 32 gives the hypothetical, primitive morphotype for the Brachyericinae and each tribe of the Erinaceinae.

The hypothetical, primitive morphotype common to both subfamilies is merely the combination of the most primitive character states for each character listed in table 32.

One exception to the general assumption that the most primitive condition seen in any member of the subfamily was to be consid-

ered as the condition of the hypothetical, primitive morphotype was the number of lower incisors and premolars in the Erinaceinae. One specimen of *Palaeoscaptor acridens* from the medial Oligocene Hsanda Gol Formation of Mongolia (AMNH 22080, see figs. 6, 7a in Rich and Rasmussen, 1973) has three lower premolars and probably had three lower incisors. No other specimen of an erinaceine has more than two of each type of tooth including the following specimens of *P. acridens* from the same formation and locality: AMNH 19139, 19142, 59751. Reduction in the number of these teeth is considered to be an advanced condition. Supporting the hypothesis that AMNH 22080 is an anomalous individual is the fact that the additional third incisor is a diminutive tooth, much smaller than  $I_1$  and apparently much smaller than  $I_2$  on the basis of the space in the mandible for that tooth. Likewise,  $P_2$  and  $P_3$  are small, single-rooted teeth in contrast to the larger, double-rooted  $P_2$  on all other erinaceines, which lack a  $P_3$ .

The hypothetical, primitive morphotype of the Erinaceinae is more advanced than that of the Brachyericinae in one character, the presence of a tall paraconid on  $P_4$ . In sharp contrast, the hypothetical, primitive morphotype of the Brachyericinae is more advanced than that of the Erinaceinae in seventeen of the 25 characters listed in table 31. If the hypothetical, primitive morphotype of the Amphechinini is compared with that of the Brachyericinae, two derived character states are shared between them that are not possessed by that of the Erinaceini: enlargement of the upper and lower first incisors. However, enlargement of the first incisors is known elsewhere in the Insectivora, whereas the enlarged paraconid on  $P_4$  is unique to the Erinaceinae. For these reasons and the many derived character states of the Brachyericinae not shared with the Amphechinini, the enlargement of the first incisors in the two groups is regarded only as an example of parallelism rather than indicating a closer phylogenetic relation than that between the Amphechinini and Erinaceini.

Comparison of the hypothetical, primitive morphotypes of the Erinaceinae and Bra-

chyericinae with other insectivore genera revealed that in every case, the hypothetical, primitive morphotypes of these two subfamilies shared more derived character states with one another than either did with these other genera. The relationships of the Brachyericinae and Erinaceinae with other groups of erinaceids and adapisoricids are further discussed on pages 107–110.

#### HISTORY AND PHYLETIC RELATIONSHIPS WITHIN THE ERINACEINAE AND BRACHYERICINAE

Of the three groups central to this report, the Brachyericinae, Amphechinini, and Erinaceini, the last is the most difficult to interpret as to its history on the North American continent. The widespread presence of the Amphechinini in Oligocene deposits of Europe and Asia and its complete absence in North America during that epoch make it reasonable to assume that the group immigrated to North America at the beginning of the Miocene, a time of widespread interchange of small, terrestrial mammals between the Old World and the New World after an almost complete absence of interchange during the Oligocene (R. W. Wilson, 1968). By contrast, the restricted Brachyericinae are known only from North America and probably arose there either directly from the adapisoricids or from a primitive erinaceine similar to *Stenoechinus*.

The difficulty with the Erinaceini is owing to conflicting evidence from their apparent close relationship as the primitive sister group to the Amphechinini and their later appearance than that tribe in the geologic record. Because of the difficulties raised by these considerations, it is only after extended consideration of the problem that the area of origin of the Erinaceini can be justifiably hypothesized as being external to North America. Hence, a detailed review of this question is warranted here.

Two hypotheses as to the relationships and history of the Erinaceini can be made with the presently available data. These hypotheses are not mutually exclusive, and

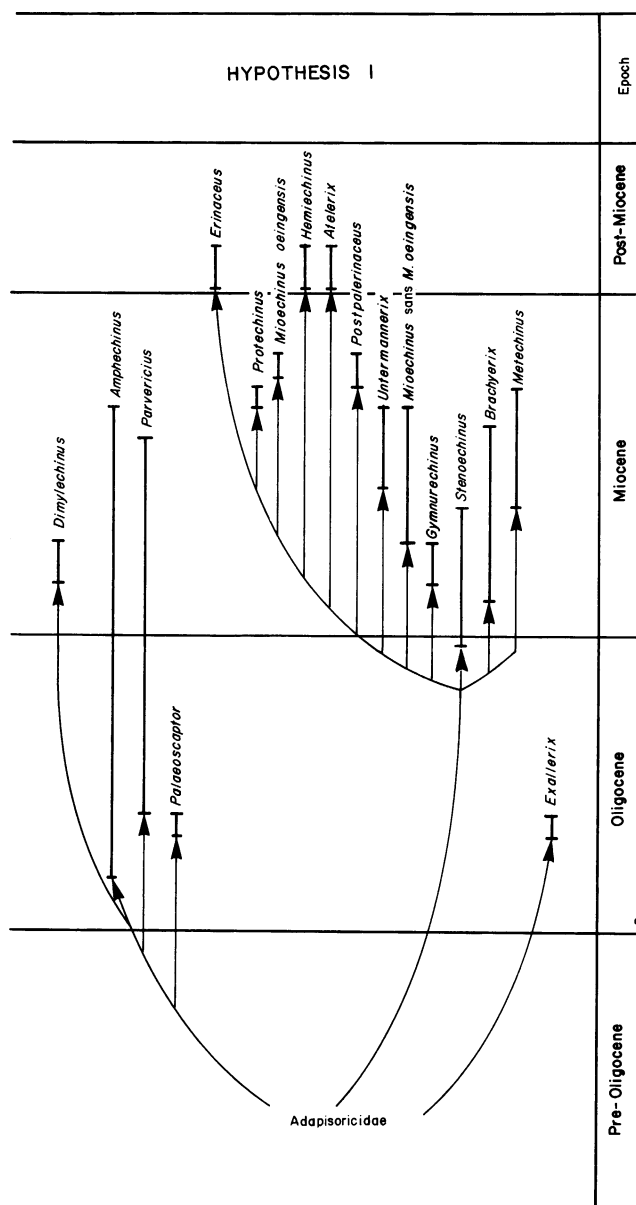
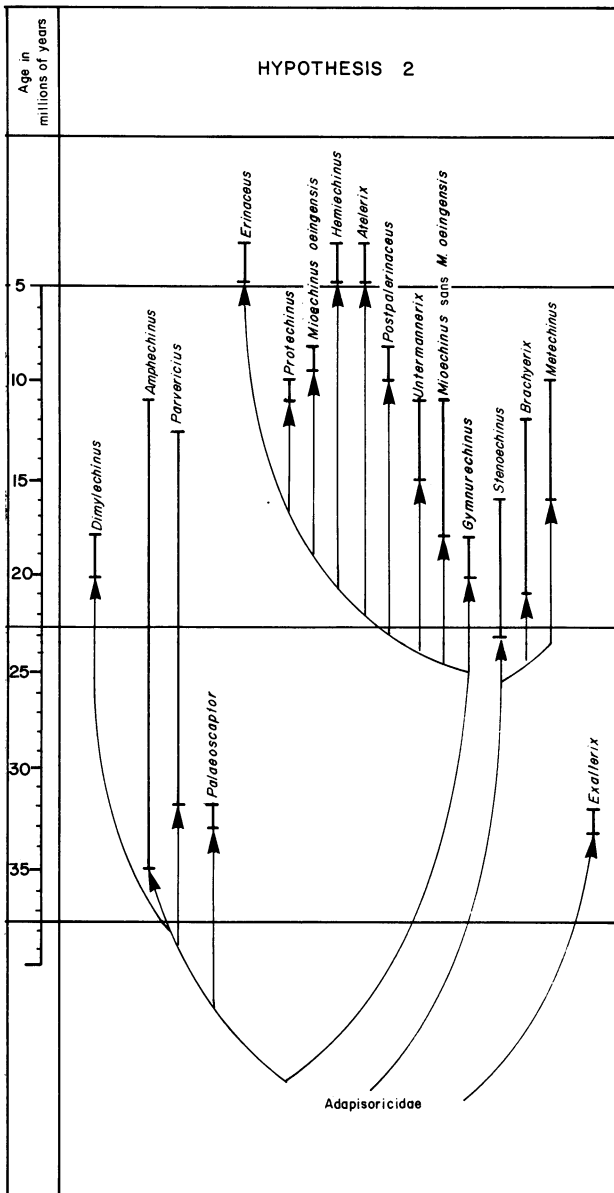


FIG. 22. Two hypotheses of the phylogenetic relationships among the Brachyericinae and Erinaceinae. In the first hypothesis, it is assumed that the Erinaceini (*Gymnurechinus* and its derived sister groups) did not evolve until immediately before their appearance in the fossil record, and their derivation from the Adapisoricidae was therefore completely independent of the derivation of the Amphexchinini. In the second hypothesis, it is assumed that the Erinaceini and Amphexchinini share a common ancestor that would be recognized as an erinaceine, hence the Erinaceini must have existed as an independent group when the Amphexchinini first appear in the fossil record.





Despite the unfortunate effect of giving the illusion of an example of "phylogenetic capture," the arrangement of the genera on the lefthand and righthand sides of the diagram is the same in order to facilitate comparisons of the two hypotheses. In addition, this arrangement of genera is nearly identical to that in figure 21 in order to facilitate comparisons between the results of the analysis of derived character states and the hypotheses of phylogenetic relationships presented here.

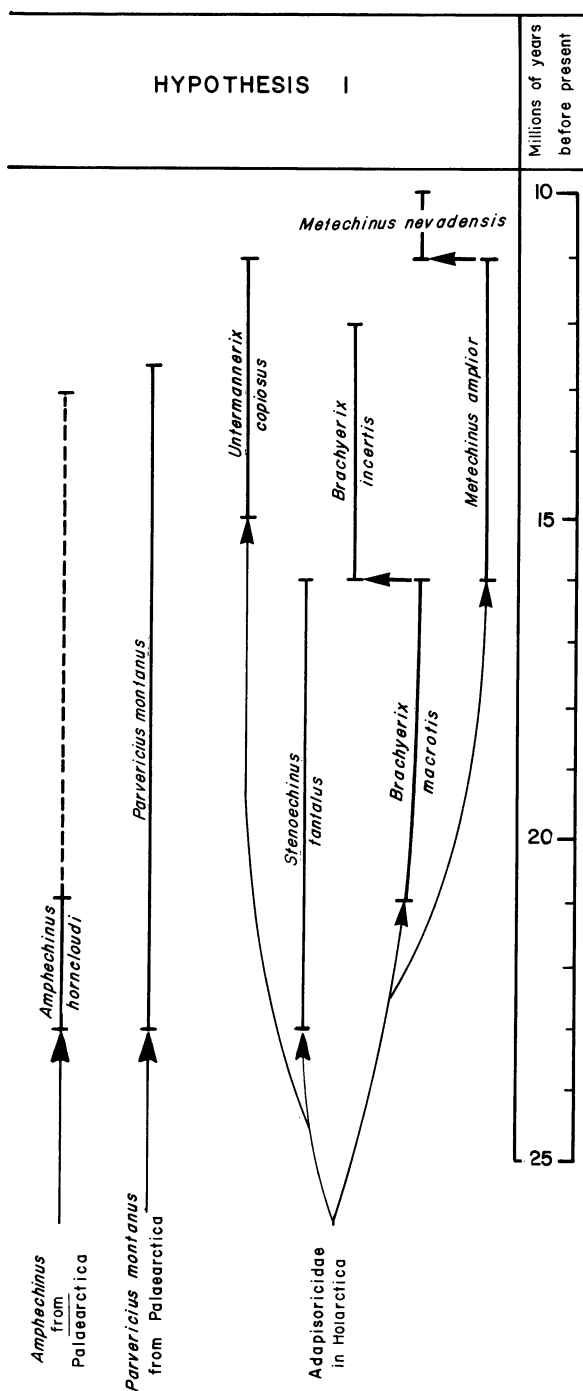
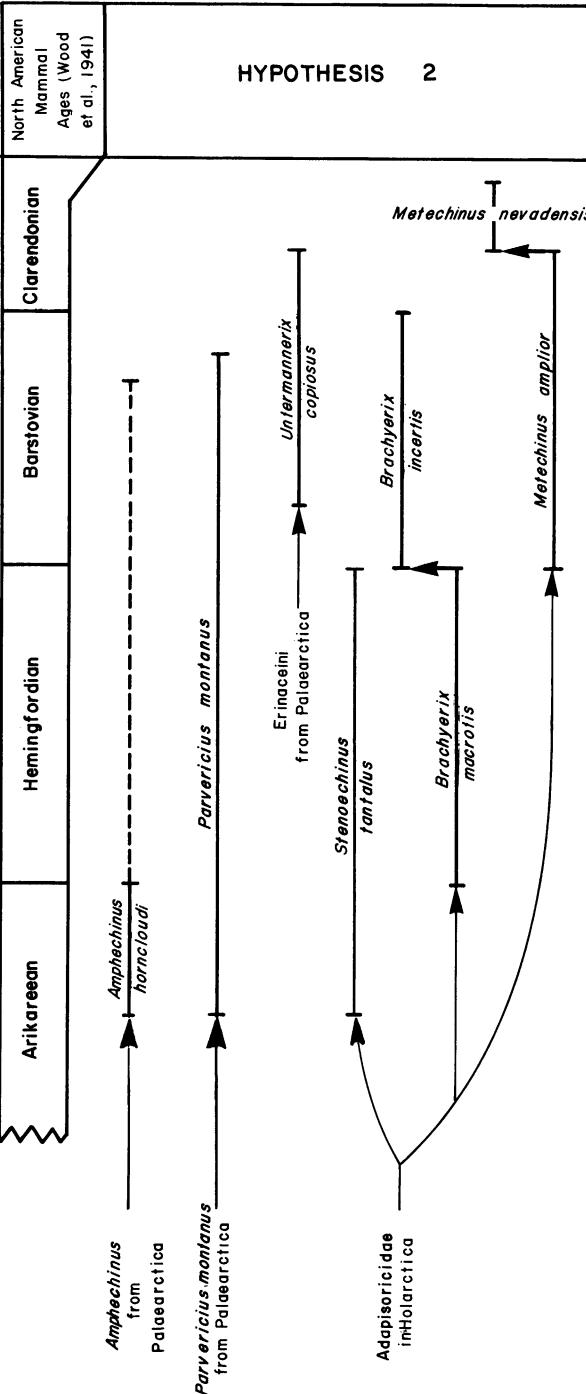


FIG. 23. Two hypotheses of the geographic history of the Brachyericinae and North American Erinaceinae. For each species, the chronological range in North America is indicated, and the identifica-



tion and geographic location of the ancestral group is given as precisely as possible. The assumptions of the two hypotheses are the same as those outlined in figure 22.

both may be partially correct, for they merely represent the plausible extremes of a spectrum of possibilities. In the first hypothesis, the time of origin of the group is assumed to be near the beginning of the Miocene when the tribe first appears in the Aquitanian of Africa in the form of *Gymnurechinus*. Slightly later, the presence of *Mioechinus* in the Burdigalian of Europe marks the first appearance of the tribe on that continent, whereas the earliest record in North America is *Untermannerix* from Barstovian deposits. Under this hypothesis, the place of origin of the tribe is no more precisely specified than Holarctica plus the Ethiopian Region.

In the second hypothesis, the Erinaceini are assumed to have appeared by the early Oligocene, probably in Africa or possibly North America and then spread into the rest of Holarctica plus the Ethiopian Region near the beginning of the Miocene.

Within the Erinaceini, there is striking agreement between the order of appearance of the several genera predicted by the cladogram method as propounded by Hennig (1966) and his advocates and the order of appearance of these genera in the fossil record (compare figs. 21 and 22). Only *Mioechinus* is an exception. This genus is based on three species, each of which is known from a single, incomplete specimen. One is a skull crushed dorsoventrally so that it is well known only in ventral view; the other two are jaw fragments. The specimen which shows the advanced feature (presence of a basisphenoid pit), which places the genus in its derived position, is the latest occurrence of the genus, *Mioechinus oeningensis* from the Tortonian of Europe. If that species alone is considered, the temporal position of the genus in figure 22 is not anomalous with its position on the cladogram (fig. 21).

That the order of appearance of the Erinaceini in the temporal sequence is close to that predicted by the cladogram suggests that the time of appearance of these various advanced character states which formed the basis for the cladogram was not long before they appear in the known record. Otherwise, one must postulate that the agreement seen is owing merely to chance of sampling. If

these derived character states of the Erinaceini, and hence the forms that bear them, truly did not appear until shortly before they are seen in the fossil record, it would be quite conceivable, but not necessary, that the immediate, late Oligocene ancestor of *Gymnurechinus*, the earliest known member of the Erinaceini, was so primitive as to be regarded as an adapisoricid. In light of these considerations, *Stenoechinus* occupies a most provocative position. Here is a form that is clearly intermediate in morphology between the more primitive adapisoricids and the more derived erinaceines in having a reduced talonid on  $M_3$ . In addition, if the evidence of the alveolar walls is to be believed, *Stenoechinus* is similar to the Erinaceini and unlike the Amphechinini in the unenlarged condition of  $I_1$ . Unlike undoubted members of both tribes of the Erinaceinae and similar to the adapisoricids, the paracoid of  $P_4$  is not enlarged on *Stenoechinus*. Thus the genus occupies a position midway between the conditions seen in adapisoricids and true Erinaceini without being derived in any character which would disbar it from consideration as an actual ancestor at a time when such an ancestor might be expected to have existed.

If the Erinaceini did not evolve from the adapisoricids until near the beginning of the Miocene as the first hypothesis asserts, then the place of origin of the tribe can be limited only to Holarctica and the Ethiopian Region with any degree of confidence, because although the first *bona fide* record of the tribe is in Africa, the possible ancestral form, *Stenoechinus*, is known from slightly older deposits in the Arikareean of North America. Thus, under this hypothesis, the direction of movement of the Erinaceini with respect to North America is unclear. Conceivably, a primitive form such as *Stenoechinus* emigrated from North America during Arikareean time, and the immediate ancestors of *Untermannerix* did not re-enter the continent until the Barstovian.

The strongest positive argument for the second hypothesis, that the Erinaceini appeared by the medial Oligocene in Africa or possibly North America, is that the Am-

phechinini are known to have been a thriving group by that time. Oligocene occurrences of the Amphechinini are widespread in Europe and Asia. If the relationship between the Amphechinini and Erinaceini depicted in the cladogram (see fig. 21) is valid, it is necessary to assume that the more primitive Erinaceini had appeared by medial Oligocene. Once the Erinaceini appear in the known record, their remains are frequently found at the same sites as the Amphechinini until that group became extinct. The complete absence of the Erinaceini in the Oligocene deposits of Europe and Asia where the Amphechinini are known thus strongly suggests that the Erinaceini did not appear on those two continents during the epoch. Although there is no form in the North American Oligocene fauna that seems to provide the same ecological control for eliminating the environmental biasing factor as the Amphechinini in Europe and Asia, the absence of the Erinaceini seems reasonably well established as owing to its actual absence from the continent at that time rather than being an artifact of inadequate sampling, because the efforts of more than a century of intensive collecting have failed to reveal a single specimen of that tribe. Africa, by contrast, may reasonably be expected to eventually yield Oligocene examples of the Erinaceini, for only in the Fayum area of Egypt have the remains of insectivores from that epoch been reported (Simons, 1968; Savage, 1969).

Under the second hypothesis, therefore, the Erinaceini would have immigrated into North America for the first time not long before their appearance during the Barstovian. Not only is this consistent with the analysis of the cladogram in figure 21 based on analysis of shared derived character states, but a possible mechanism for the timing of this event has already been proposed. Van Couvering (1972, pp. 260–266) related the Burdigalian mammalian interchanges between Eurasia and Africa with the mid-Cenozoic contact between the Afro-Arabian and Eurasian crustal plates and noted that many mammalian genera known in Europe from post-Aquitania deposits are found in the earlier Rusinga-like Aquitania fauna of Af-

rica. Thus Africa not only makes a logical place to look for the pre-Miocene Erinaceini because the record to date is poorly known there, but in addition, its geologic history provides a plausible mechanism that would explain both the absence of the Erinaceini from other areas which have more adequate Oligocene fossil records and their relatively sudden appearance in the subsequent Miocene deposits of the same regions.<sup>15,16</sup>

Under the second hypothesis, *Stenoechinus* is an embarrassing anachronism if it is to be regarded as an erinaceine. Another possible role for it is as an independent derivation from the adapisoricids that is closely related to the lineage which eventually gave rise to the Brachyericinae. With the return of *Dimylechinus* to the Erinaceinae and the placement of *Exallerox* in the Erinaceoidea *incertae sedis* as discussed above, it is reasonable to suppose that the brachyericines are North American endemics that never ventured from that continent. *Stenoechinus*, although lacking the enlarged first lower incisor that the brachyericines share with the Amphechinini, does not have as prominent a paraconid on P<sub>4</sub> as all other members of the Erinaceinae do, and therefore is not barred by a rare derived character state from consideration as a direct ancestor to the brachyericines. In any event, *Stenoechinus* may possibly be closely related to the Brachyericinae no matter what its relation is to the Erinaceinae.

Weighing the evidence for the two hypotheses, the nature of that for the first (that the Erinaceini did not arise until approximately the time of the Oligo-Miocene boundary) seems more vulnerable. In the light of the poorly known record of small Oligocene

<sup>15</sup> For a review of the biogeographic relationships of the Tertiary mammalian faunas of Africa, see Coryndon and Savage (1973).

<sup>16</sup> Another area that could have played a role similar to the one here hypothesized for Africa, is India when it collided with the remainder of Asia. However, work summarized by Sahni and Kumar (1974) indicates that widespread faunal interchange among the mammals was occurring between the Indian subcontinent and the landmass to the north as early as medial Eocene, militating against this suggestion.

mammals in Africa and a plausible hypothesis as to why the Erinaceini might have existed there and nowhere else during that epoch (i.e., Van Couvering, 1972), the possibility of such a future discovery seems great enough to cause one to prefer the second hypothesis (that the Erinaceini had appeared by the medial Oligocene and gave rise to the Amphechinini by that time).

It must be candidly acknowledged that the second hypothesis cannot be as readily invalidated with temporal evidence as the first, because what would be required is persuasive evidence that the history of the Erinaceini began no earlier than late Oligocene. Until the Oligocene history of Holarctica and particularly the Ethiopian Region is much better known, this possible avenue for invalidation cannot be said to have been adequately explored. Thus, unless the first hypothesis is invalidated by the discovery of a single pre-late Oligocene specimen of an Erinaceini, the question of which of the two hypotheses is more likely cannot be said to have been satisfactorily resolved by temporal evidence, for there will always remain the possibility of such a discovery.

Once the Erinaceinae became established in North America, their history was remarkably simple. The two species of Amphechinini, *Amphechinus horncloudi* and *Parvericus montanus*, appear to have changed relatively little with respect to their Palaearctic forebears. In the case of *P. montanus* the change, if any, was so slight that its apparent ancestor from the Oligocene of China and Mongolia was placed in the same species by Rich and Rasmussen (1973). *Amphechinus horncloudi* does appear to differ somewhat from the *Amphechinus arvernensis* complex of Europe and from *Amphechinus rusingensis* of Africa, but the differences are slight. Neither *P. montanus* nor *A. horncloudi* appear to have given rise to any other species in North America. Although *P. montanus* persisted in North America from the Arikarean to the Barstovian, it underwent only a slight increase in size during that time (about 10 percent) if the apparent temporal trend was not produced by some artifact of the sampling procedure. Except for that

slight change, the species remained relatively static during its existence in North America. The single specimen of *A. horncloudi* from the Harrison Formation is somewhat larger than those known from the earlier Monroe Creek Formation and Cabbage Patch beds, but on this basis it is hardly worth speculating as to the existence of any such trends within that species.

A similar picture emerges of the history of the Erinaceini in North America. Although the size range of the specimens is great enough to suggest that perhaps more than one species is represented in the material allocated here to *Untermannex copiosus*, not enough specimens are known to establish the reality of a bimodal size distribution if there is in fact one. No obvious changes occurred during the history of this species from the beginning of the Barstovian to the Clarendonian.

The history of the Brachyericinae is slightly more complicated than that of the Erinaceinae in North America, but this group, too, did not undergo a spectacular radiation or diversification. Both genera are represented by two species, the younger of which is noticeably smaller than the older. In neither genus is there any hint of phyletic gradualism<sup>17</sup> between the species, rather there is an abrupt gap between them. That the temporal range of *Brachyrix incertis* immediately succeeds that of *Brachyrix macrotis* but does not overlap, as indicated in figure 23, may be considered weakly established, but that this is the case with *Metechinus nevadensis* and *Metechinus amplior*, respectively, cannot even be given that level of credence, because *M. nevadensis* is known from only a single specimen.

Neither genus of brachyericine could have given rise to the other because each possesses derived character states not shared with the other. Therefore, the history of the group must extend backward in time prior to the beginning of the Hemingfordian when the earliest known specimen of *Brachyrix macrotis* lived.

<sup>17</sup> See Eldredge and Gould (1972) for a provocative discussion of this term and its implications.

Figure 23 is an attempt to pictorially summarize the history of the Erinaceinae and Brachyericinae in North America under the two hypotheses concerning the phylogenetic relationships of the two subfamilies. For each species, the identity and geographic location of the ancestral group is specified as precisely as possible. The temporal range indicated for each species is that in North America only.

In summary, the Erinaceini appear to be separately derived from the adapisoricids apart from the Amphechinini in some unspecified region of Holarctica or the Ethiopian Region near the beginning of the Miocene, if the non-occurrence of the Erinaceini in the Oligocene record is accepted as real rather than an artifact of the poor record and the orderly appearance in the Miocene of progressively more advanced forms together with the existence of a form midway morphologically between the adapisoricids and Erinaceini (*Stenoechinus*) near the beginning of the Miocene is not to be explained away as merely a coincidence. On the other hand, the Erinaceini seem to have originated in Africa by medial Oligocene if the cladistic relationship suggested by the shared derived characters of that tribe and the Amphechinini are not to be regarded as owing to parallelism, and the absence of the Erinaceini in Europe, Asia, and North America during the Oligocene is regarded as real rather than an artifact of an inadequate record as it may well be in the case of Africa. By restricting the Erinaceini to Africa during the Oligocene, the second hypothesis provides a mechanism for the timing of the tribe's appearance in Holarctica: the mid-Cenozoic contact of the Afro-Arabian plate with Eurasia.

Discovery of a single pre-late Oligocene specimen of a member of the Erinaceini would invalidate the first hypothesis. Because such a discovery may be reasonably expected in Africa, where the Oligocene record of small mammals is poorly known and which appears to have been the area where many small mammals resided during that epoch which later suddenly appear in the Miocene of Europe without known anteced-

ents, the second hypothesis seems more probable at this time.

Once the Erinaceinae appear in North America, their history is singularly uneventful for there is no evidence of radiation; rather the immigrants seem to have persisted in the form in which they entered the continent until their eventual extinction. In contrast, both genera of the Brachyericinae appear to have become markedly smaller somewhat abruptly during their history. However, this subfamily, too, can hardly be said to have undergone a major radiation in North America.

#### RELATIONSHIP OF THE ADAPISORICIDAE AND OTHER ERINACEIDAE TO THE BRACHYERICINAE AND ERINACEINAE

It is unfortunate that there are relatively few characters among those utilized in this study and enumerated in table 29 which in the hypothetical, primitive morphotype of the erinaceines are in a state other than the most primitive. It is for this reason that the selection of the group within the known erinaceids and adapisoricids that is closest phylogenetically to the Erinaceinae and Brachyericinae can be made only in a most tentative way.

In the following discussion of different erinaceoids as close relatives to the erinaceines and brachyericines, Van Valen's (1967) classification is used except where noted. *Proterix* will be here regarded as Erinaceidae, subfamily uncertain as recommended by Gawne (1968). The other genera placed by Van Valen in the Protericini are of necessity transferred, *Brachyerix* and *Metechinus* to the Brachyericinae, *Dimylechinus* and *Amphechinus* to the Amphechinini within the Erinaceinae. (See table 30 for details of the classification used here and the source of information about each genus considered.)

Among the erinaceoids, the Adapisoricinae are the most generalized, possessing few advanced character states which would make them unsuitable as candidates for consideration as ancestral forms for any of the

other members of the superfamily. For the purposes of this discussion, *Ictopidium* and *Tupaiodon* will be regarded here as members of the Adapisoricinae rather than Creotarsinae where Van Valen (1967) placed them. In several characters, the adapisoricines are more primitive than those in the most primitive condition found among the erinaceines and brachyericines. These more primitive character states include:

- 4 A or B. Hypocone absent or much lower than the protocone on  $P^4$
- 6 A. Paraconule present on  $M^1$
- 10 A. Three lower incisors present
- 11 A. Four lower premolars present
- 14 A. Trigonid of  $M_1$  anteroposteriorly compressed
- 19 A. Well-developed talonid on  $M_3$
- 24 B. Posterior border of zygomatic arch joins body of maxilla opposite space between  $M^2$  and  $M^3$

(See table 32 for an enumeration of the most primitive character states of the Erinaceinae and Brachyerincinae.) Most of the character states that the adapisoricines share with the erinaceines and brachyericines are the most primitive for the given character within the Insectivora. However, one shared character state is derived: the absence of a hypoconulid on  $M_1$  (17 B) in the case of *Adapisorex*, *Adunator*, and *Ictopidium*.

Where the characters are known, the same comments concerning the adapisoricines apply to the Nyctitheriinae. The presence or absence of a hypocone on  $P^4$  (4) or the number of antemolars (10, 11) is not known. The hypoconulid is developed on  $M_{1-2}$  (17 A), a character state more primitive than the absence of this cuspule, the condition in the erinaceines, brachyericines, and some adapisoricines.

The Creotarsinae differ from the brachyericines and erinaceines in that the trigonid of  $M_1$  tends to be lower (16 B) and noticeably inclined anteriorly (15 B) rather than vertical. Both these characters are difficult to evaluate in some instances, but there is a general pattern in the structure of the trigonid of  $M_1$  reflected in the abstractions that are these two characters that clearly distinguishes members of this subfamily from the

erinaceines and brachyericines. The lower, anteriorly inclined trigonid on  $M_1$  is a condition more advanced than that found in the erinaceines and brachyericines. The Creotarsinae are more primitive than the erinaceines and brachyericines in all the characters listed above for the adapisoricines except that some species are known which have only three lower premolars (11 B), a condition somewhat closer to that of the erinaceines and brachyericines. Although some species of the Adapisoricinae are as advanced as the brachyericines and erinaceines in lacking the hypoconulid on  $M_1$ , the Creotarsinae are consistently more primitive in having that cuspule (17 A).

*Geolabis* is the best known member of the Adapisoricidae, and hence the Geolabidinae are better known than the other subfamilies discussed previously. As in other adapisoricids, most of the characters surveyed in the geolabidines are in the most primitive state known among the Insectivora including several of those shared with the erinaceines and brachyericines. The geolabidines are more primitive than any known erinaceine and brachyericine in all the characters that the adapisoricines are. In addition, they are more primitive in having four upper premolars (2 B), a double-rooted  $P_2$  (12 A), and lacking the palatine behind the transverse process (22 A). Characters 2 and 22 are unknown in the adapisoricines and creotarsines. One shared derived character common to the geolabidines and the brachyericines and erinaceines is the absence of a paraconule on  $M^1$  (6 B). One feature that is more advanced in the geolabidines is that there are two lingual roots on  $M^1$  (5 B) rather than one as in the brachyericines and erinaceines.

Most members of the Erinaceidae share two derived character states which distinguish them from the Adapisoricidae: hypocone is prominent and tall but lower than the protocone on  $P^4$  (4 C), and the trigonid on  $M_1$  is moderately expanded anteroposteriorly (14 B). The hypothetical, primitive morphotype of the Erinaceinae shares these two character states, but that of the Brachyerincinae is yet more advanced. Among the erinaceids, only *Proterix* is known to be more



primitive in these two features, suggesting that this enigmatic genus might be properly placed among the adapisoricids, particularly the creotarsines with which the derived character states of the low, anteriorly inclined  $M_1$  trigonid are shared (16 B, 15 B).

Among the galericine erinaceids, all are more primitive than the Erinaceinae and Brachyericinae in having three or more lower premolars (11 A, B), and a well-developed talonid on  $M_3$  (19 A). Other derived character states of the hypothetical, primitive morphotype of the Brachyericinae and Erinaceinae are shared by one or more members of the Galericinae. The modern genus *Hylomys* is the closest of all the galericines to that morphotype. Other than the characters listed above that distinguish all galericines (11, 19), *Hylomys* is more primitive in that it may have four upper premolars (2 B) and three lower incisors (10 A). *Hylomys* and the hypothetical, primitive morphotype of the Brachyericinae and Erinaceinae share the following derived character states:

- 4 C. Hypocone lower than the protocone on  $P^4$
- 6 B. Paraconule not present on  $M^1$
- 12 B.  $P_2$  single rooted
- 14 B. Trigonid of  $M_1$  moderately expanded anteroposteriorly
- 17 B. Hypoconulid not present on  $M_1$
- 22 B. Palatine developed posterior to transverse process
- 24 C. Posterior border of zygomatic arch joins body of maxilla opposite middle of  $M^2$

*Hylomys* is more advanced than the Brachyericinae and Erinaceinae in one character that it shares with the other living galericines *Neotetracus* and *Echinosorex*: presence of two lingual roots on the  $M^1$  (5 B) rather than one.

*Echinosorex* and *Neotetracus*, unlike *Hylomys*, are more primitive than the hypothetical, primitive morphotype of the Brachyericinae and Erinaceinae in the following characters:

- 6 A. Paraconule present on  $M^1$
- 22 A. Palatine not developed posterior to transverse process
- 24 A, B. Posterior border of zygomatic arch joins body of maxilla behind  $M^2$

*Neurogymnurus* is more primitive than the hypothetical, primitive morphotype of the Brachyericinae and Erinaceinae in the following features:

- 2 B. Four upper premolars present
- 10 A. Three lower incisors present
- 11 A. Four lower premolars present
- 12 A.  $P_2$  double rooted
- 19 A. Well-developed talonid on  $M_3$
- 22 A. Palatine not developed posterior to transverse process
- 24 B. Posterior border of zygomatic arch joins body of maxilla opposite space between  $M^2$  and  $M^3$

Each of the living galericine genera discussed above share most of these character states with *Neurogymnurus* although none of them shares all. *Neurogymnurus* shares the following derived character states with the hypothetical, primitive morphotype of the Erinaceinae and Brachyericinae:

- 4 C. Hypocone lower than the protocone on  $P^4$
- 6 B. Paraconule not present on  $M^1$
- 14 B. Trigonid of  $M_1$  moderately expanded anteroposteriorly
- 17 B. Hypoconulid not present on  $M_1$

In two characters, *Neurogymnurus* is more derived than any member of the Erinaceinae or Brachyericinae: the trigonid of  $M_1$  is low and anteriorly inclined (16 B, 15 B) rather than tall and vertical.

With the following exceptions, the statements concerning *Neurogymnurus* in the previous paragraph apply equally well to *Lanthanotherium* and *Galerix*.  $P_2$  is single rooted (12 B) in *Lanthanotherium*, a condition slightly more advanced than that known in *Neurogymnurus* and *Galerix* and thus somewhat closer to the condition of the hypothetical, primitive morphotype of the Erinaceinae and Brachyericinae. The condition of the palatine in the region of the transverse process is unknown in *Lanthanotherium* and *Galerix* (22). Finally, *Lanthanotherium* and *Galerix* are more primitive than *Neurogymnurus* and closer to the Erinaceinae and Brachyericinae in that the trigonid of  $M_1$  is vertical (15 A), *Galerix* is even closer to the two subfamilies in that its  $M_1$  trigonid is relatively tall (16 A).

*Ocajila* is a poorly known genus. What is available indicates that it may be allied with *Lanthanotherium*. The trigonid of  $M_2$  is low, suggesting that the trigonid of  $M_1$  is similarly depressed (16 B), and thus presumably the genus is more advanced in that one feature than any specimen of the Erinaceinae or Brachyericinae.

After explicitly considering the various groups within the Adapisoricidae and Erinaceidae, it is evident that the Brachyericinae shared more derived character states with the Erinaceinae than any other subdivision of those two families. In cladistic terms, the two subfamilies have a sister group relationship with one another. In turn, combined, they form a sister group with the Galericinae. Thus, the Erinaceidae are monophyletic.

In light of the relationships hypothesized for the North American Erinaceinae and Brachyericinae, they may be arranged taxonomically in the following manner.

Family Erinaceidae Fischer von Waldheim, 1817

Subfamily Erinaceinae Fischer von Waldheim, 1817

Tribe Erinaceini Fischer von Waldheim, 1817

*Untermannerix*, new genus

*Untermannerix copiosus*, new species

Tribe Amphechinini, new

*Parvericius* Koerner, 1940

*Parvericius montanus* Koerner, 1940

*Ampechichinus* Aymard, 1850

*Ampechichinus horncloudi* (Macdonald, 1970), Rich and Rasmussen (1973)

Tribe Uncertain

*Stenoechinus* Rich and Rasmussen, 1973

*Stenoechinus tantalus* Rich and Rasmussen, 1973

Subfamily Brachyericinae

*Brachyerix* Matthew, 1933

*Brachyerix macrotis* Matthew, 1933

*Brachyerix incertis* (Matthew, 1924), Rich and Rich (1971)

*Metechinus* Matthew, 1929

*Metechinus nevadensis* Matthew, 1929

*Metechinus ampliior*, new species

Use of Hennig's method for relating taxa on the basis of shared derived character states yielded an estimate of the phylogenetic relationships of the Erinaceinae and Brachyericinae that formed the keystone of the second hypothesis developed above concerning the geographic history and cladistic relationships of the two subfamilies. Of the two hypotheses put forward, the second appears more firmly established. Hence, for the groups central to this report, the phylogenetic method of Hennig (1966) seems to have provided the most satisfactory answer.

Although the method of Hennig was successfully employed to put forward a theory of relationships without regard to the temporal position of the different taxa considered, temporal data did prove useful. In deciding whether the presence of the hypoconulid on  $M_1$  was a primitive or derived feature, the normal procedure of considering the distribution of the character states in the groups recognized by the ongoing phylogenetic hypothesis was unsatisfactory because the cusp was present in approximately half the groups recognized and missing in the others. However, by considering only those forms that lived prior to the Oligocene, it was possible to determine that the presence of the cusp was primitive. This is not the same procedure that Schaeffer, Hecht, and Eldredge (1972, pp. 33–35) justifiably condemned; namely, assuming an ancestor-descendant phylogenetic relationship *a priori* on the basis of relative temporal position, then determining the primitive and derived character states on that basis to be used in turn for making phylogenetic inferences. Here, what has been done is to sample broadly across the spectrum of known forms as might have been done had the investigator lived at the end of the Eocene rather than today. Thus, the possible methodological pitfalls are no different than if one were to sample all the material available today, both fossil and Recent.

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