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Brachyerix, a Miocene Hedgehog from Western North America, with a Description of the Tympanic Regions of *Paraechinus* and *Podogymnura*

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ABSTRACT

Although living hedgehogs have long been regarded the archetypes of the primitive placental mammal, they have nonetheless had a complex Cenozoic history that is reflected in the recognition of three extinct and two living erinaceid subfamilies. Members of one extinct subfamily, the Brachyericinae, underwent a remarkable shortening of the skull and a reduction in the number of teeth during the Oligocene, Miocene, and early Pliocene. This trend culminated in the two North American genera, *Brachyerix* and *Metechinus*, in which only three teeth were retained anterior to P₄. *Dimylechinus*, a European form from the early Miocene, and *Exallerix* from the medial Oligocene of Asia both retained at least four teeth anterior to P₄. None of the four genera had an M₃.

Brachyerix and *Metechinus* occur from the Great Plains to the Pacific coast of North America. *Brachyerix* is temporally restricted to the Miocene; *Metechinus* occurs in late Miocene and early Pliocene sediments. Although both genera are known from several localities, they are never found together, which may reflect an ecological separation of these two forms during temporal overlap. Both are known only from cranial osteology.

During the past 40 years, the differences between these two North American genera have not been well defined, and only now with the availability of several specimens of each can the generic boundaries be adequately reviewed. Two species of *Brachyerix* are recognized in the present paper. *Brachyerix macrotis*,

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restricted to the early and medial Miocene, is the larger of the two and differs from *B. incertis*, new combination (late Miocene), in having a stronger lingual cingulum on P^3 and in entirely lacking a P^3 protocone. *Metechinus marslandensis* can now be synonymized with *B. macrotis*, whereas *Talpa incerta* and *Metechinus fergusoni* are both junior synonyms of *B. incertis*. Only *Metechinus nevadensis* still requires generic separation owing to its unique basicranium, small auditory bullae, nature of the sagittal crest, and relatively anteroposteriorly compressed M_1 trigonid.

Dimylechinus bernoullii is an adequate structural ancestor for *Brachyerix macrotis* and its descendents. However, as both *Dimylechinus* and *Exallerix* are known only from single specimens, their relationship to the North American brachyericines as well as to one another is not well understood and will not be until further specimens are found.

An appendix describing the ear regions of two living hedgehog genera, *Paraechinus* and *Podogymnura*, is included to supplement Butler's (1948) paper on the erinaceid ear region. *Paraechinus* is the only living erinaceid that has bony tubes covering part of the blood vessels contained in the tympanic cavity, a condition developed to the extreme in the Miocene *Brachyerix*.

INTRODUCTION

Living hedgehogs or members of the family Erinaceidae have long been regarded as the archetypes of the primitive placental mammal, virtually unmodified holdovers from the Mesozoic Era little affected by the passage of the past seventy million years. Although it is true that these small, vaguely ratlike animals have not changed as obviously from the form of the primitive Cretaceous insectivores as have horses and whales, they have had a complex Cenozoic history of their own that is reflected in the recognition of three extinct erinaceid subfamilies and two living ones.

One of these subfamilies, the Brachyericinae, underwent a remarkable shortening of the skull and reduction in the number of teeth. Four genera, all described during the past 50 years, have been assigned to this extinct subfamily. *Dimylechinus* and *Exallerix*, the two Old World medial Tertiary genera referred to this group, are each known only from fragmentary single specimens and consequently their relationship to each other and to the better known North American genera is obscure. However, the two North American genera, *Brachyerix* and *Metechinus*, are each known from a number of localities scattered widely over the western United States from the Great Plains to the Pacific Coast. At present, the skull and jaws of these two genera are known rather completely, but unfortunately, aside from a few questionably associated bones, there are no known post-cranial elements.

The first brachyericine specimen found was so fragmentary that its

erinaceid affinities were unrecognized. *Talpa incerta* Matthew, 1924, from the early Barstovian (early late Miocene) Lower Snake Creek beds of Sioux County, Nebraska, was based on a mandible fragment (AMNH 18891) with only M_2 preserved. In his discussion of the specimen, Matthew queried the familial as well as the generic assignment.

In 1929, Matthew described a much more complete brachyericine specimen and recognized its erinaceid affinities together with the unusually shortened and broadened skull that set it apart from all previously known members of that family. This partial skull and the incomplete lower jaws associated with it (UCMP 29600) from a site in the Esmeralda Formation of late Miocene or early Pliocene age near Tonopah, Nevada, was made the type of *Metechinus nevadensis* Matthew, 1929.

Four years later, Matthew named another new brachyericine genus and species on the basis of a skull from the Miocene Deep River Beds near Fort Logan, Montana. This species, *Brachyerix macrotis* Matthew (Matthew and Mook, 1933), was based on a skull, AMNH 21335. Only Meade (1941, pp. 45–46) has compared *Metechinus nevadensis* with *Brachyerix macrotis*. Unfortunately, the nature of the material of these two species then known did not permit him to recognize the striking differences in the proportions and structure of their basicranial and auditory regions.

Since 1933, two more species of brachyericines have been named from North America: *Metechinus marslandensis* Meade, 1941, and *Metechinus fergusonii* Henshaw, 1942. Subsequent discoveries have broadened our knowledge of the previously described species, however, and these two species now appear to be junior synonyms: *M. marslandensis* is placed here in *Brachyerix macrotis* and *M. fergusonii* in *Brachyerix incertis*, new combination. Several additional specimens, consisting of isolated teeth and one jaw, that have been referred to *M. marslandensis* by Reed (1960) and Love (1961) are assigned in the present paper to *B. macrotis*.

Two isolated upper molars identified by Galbreath (1953) as *Brachyerix* spp. cannot now be assigned to this genus. One is referable to *Metechinus nevadensis* and the other may not be an insectivore. An isolated lower molar identified by Wilson (1960) as an M_2 of *Metechinus* sp. cf. *M. marslandensis* appears to be an *Amphechinus* M_1 .

In addition to the specimens mentioned above, a number of other specimens that have added considerable detailed knowledge concerning the skull and jaws of *Brachyerix* and its close relative, *Metechinus*, have become available in recent years. Therefore a more extensive description of *Brachyerix* and comparison of it with *Metechinus* is now warranted.

TABLE 1
ORIGINAL DESIGNATIONS OF THE SPECIMENS OF *Brachytherix*

Name	Authority	Original Material	General Area	Rock Unit	Stratigraphic Position		Temporal Unit	Local Fauna
					in Rock Unit			
<i>Talpa incerta</i> Matthew, 1924	Matthew, 1924	Mandible with last molar and alveolus of M ₁ , AMNH 18891	Nebraska	Lower Snake Creek beds	Not given		<i>Merychippus</i> <i>paniensis</i> zone	Not named
<i>Brachytherix macrotis</i> Matthew, 1933	Matthew and Mook, 1933	Skull, AMNH 21335	Montana	Deep River beds	Upper of the two zones recognized by Scott (1893) and Douglass (1899)	Early part of late Miocene		Not named
<i>Metachinus marilandensis</i> Meade, 1941	Meade, 1941	Incomplete left man- dible with M ₁ and M ₂ , FMNH P26399	Nebraska	Marsland Formation	Not given	Early Miocene		Not named
<i>Metachinus fergusoni</i> Henshaw, 1942	Henshaw, 1942	Partial left maxilla and partial left mandible, LACM (CIT) 2817 and 2818	Nevada	Esmeralda Formation	Beneath the dendritic tufa layer, not far above the local base of the Esmeralda sediments	Late Miocene		Not named
<i>Metachinus marilandensis</i> Meade, 1941	Reed, 1960	Isolated teeth	Wyoming	Not given	Not given	Medial Miocene		Not named
<i>Metachinus marilandensis</i> Meade, 1941	Love, 1961	Right mandible, CM 14959	Wyoming	Split Rock Formation	Upper porous sandstone sequence (Love, 1961)	Medial Miocene		Split Rock

TABLE 1—Continued

Name	Authority	Original Material	General Area	Rock Unit	Stratigraphic Position in Rock Unit	Temporal Unit	Local Fauna
<i>Brachytherix inermis</i> (Matthew, 1924)	This paper	Fragmentary skull, F:AM 74954	California	Barstow Formation	Approximately 1000 feet below the Skyline Tuff	Barstovian	Not named
<i>Brachytherix macrolis</i> Matthew, 1933	This paper	Skull and mandible, UCMP 86137	Wyoming	Split Rock Formation	Upper porous sandstone sequence (Love, 1970)	Hemingfordian	Split Rock
<i>Brachytherix macrolis</i> Matthew, 1933	This paper	Crushed skull, F:AM 74965	Nebraska	Unnamed channel deposits	Not given	Medial Hem- ingfordian	Not named
<i>Brachytherix macrolis</i> Matthew, 1933	This paper	Left mandible with M ₁ and M ₂ , F:AM 74964	Nebraska	Unnamed channel deposits	Not given	Medial Hem- ingfordian	Not named
<i>Brachytherix macrolis</i> Matthew, 1933	This paper	Left mandible with M ₂ , F:AM 76693	Nebraska	Sheep Creek Formation	Near base of Sheep Creek Formation	Hemingfordian	Not named
<i>Brachytherix macrolis</i> Matthew, 1933	This paper	Right edentulous man- dible with alveoli for M ₁ and M ₂ , F:AM 76695	Nebraska	Harrison or Marland Formation	Not given	Arikarean or Hemingfordian	Not named
<i>Brachytherix macrolis</i> Matthew, 1933	This paper	Left mandible with M ₁ and M ₂ , USGS (PSB.D) Fossil Verte- brate Specimen D719A	Colorado	Troublesome Formation	Lower part of the Troublesome Forma- tion	Hemingfordian	Not named

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For the loan of material we thank Mr. J. Howard Hutchinson of the University of California, Museum of Paleontology, Berkeley, who found an associated skull and mandible of *Brachyerix macrotis* after the first draft of this paper had been written. This discovery has permitted the removal of many annoying qualifying remarks. Others who provided pertinent specimens include Dr. Donald E. Savage of the University of California, Department of Paleontology, Berkeley; Dr. Theodore Downs of the Los Angeles County Museum, Los Angeles; Dr. Craig C. Black formerly of the Carnegie Museum, Pittsburgh, and now of the Museum of Natural History, University of Kansas, Lawrence; Dr. Peter Robinson of the University of Colorado Museum, Boulder; Dr. William D. Turnbull of the Field Museum of Natural History, Chicago; and Dr. G. Edward Lewis of the United States Geological Survey, Paleontology and Stratigraphy Branch, Denver.

Mrs. Mary Lee Vickers typed the manuscript.

The following abbreviations are used with catalogue numbers:

ACM, Amherst College Museum, Amherst

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History

AMNH(M), Department of Mammalogy, the American Museum of Natural History

CM, Carnegie Museum

F:AM, Frick Collection, the American Museum of Natural History

FMNH, Field Museum of Natural History

KU, Museum of Natural History, the University of Kansas

LACM(CIT), California Institute of Technology collection in the Los Angeles County Museum

ROM, Royal Ontario Museum, Toronto, Canada

UCM, University of Colorado Museum

UCMP, University of California Museum of Paleontology, Berkeley

USGS(PSB,D), United States Geological Survey, Paleontology and Stratigraphy
Branch, Denver

UW, Department of Geology, the University of Wyoming, Laramie

ABBREVIATIONS FOR 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

FOR. R, foramen rotundum

FR, frontal

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
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
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
TVR, tube for Vidian ramus of promontory artery
VF, Vidian foramen
VR, Vidian ramus of promontory artery

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

ORDER INSECTIVORA ILLIGER, 1811

SUPERFAMILY ERINACEOIDEA FISCHER VON WALDHEIM, 1817

FAMILY ERINACEIDAE FISCHER VON WALDHEIM, 1817

SUBFAMILY BRACHYERICINAE BUTLER, 1948

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 (medial-late Miocene), western North America.

DIAGNOSIS: Distinguished from *Metechinus* by smaller size; nearly parallel lateral margins of basicranium (in ventral view), not converging pos-

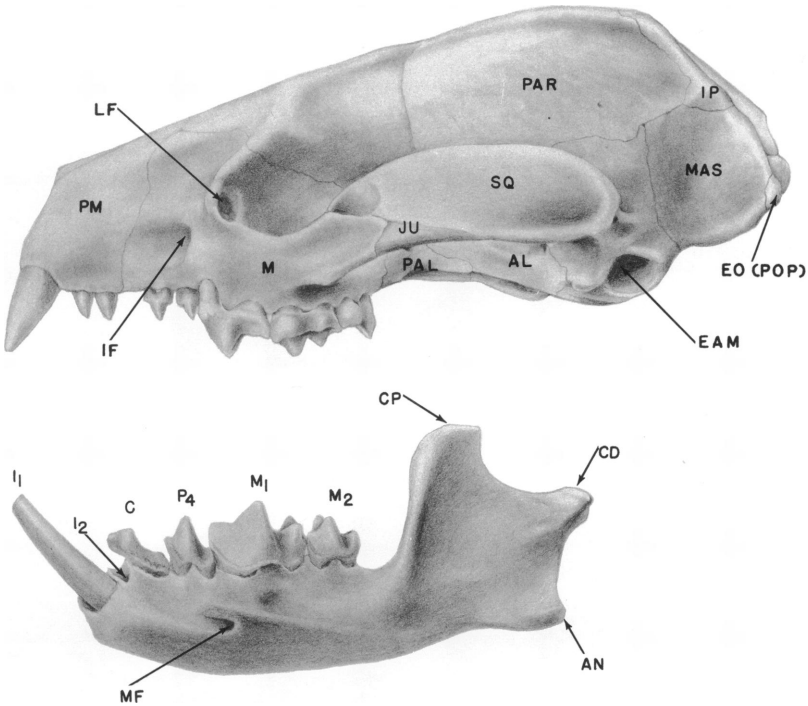


FIG. 1. *Brachyerix macrotis*, restoration of skull and mandible in lateral view based on AMNH 21335, F:AM 74965, UCMP 86137, and two specimens of *Metechinus nevadensis*, UCMP 29600 (type specimen), and F:AM 76696. Identifications of I₁, I₂, and P₂ are uncertain; see pp. 19–26 of text for discussion. Approximately $\times 3$.

teriorly at large angle; larger, more inflated auditory bullae closer to one another; temporal crests joining sagittal crest at frontal-parietal suture, not immediately posterior to nasal-frontal suture; flange separating posterior and lateral concave 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; and trigonid of M₁ more expanded anteroposteriorly.

Distinguished from *Metechinus* and *Dimylechinus* by internally inflected,

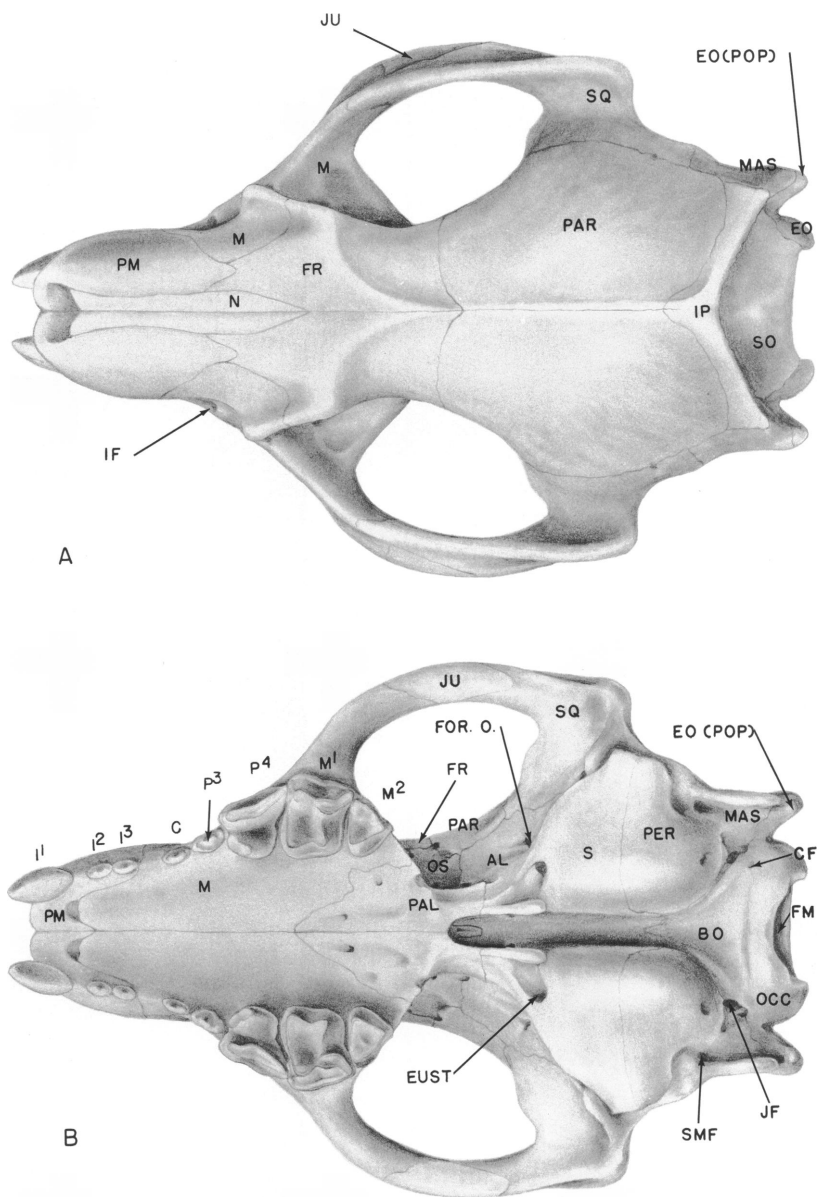


FIG. 2. *Brachyerix macrotis*, restoration of skull based on same specimens as used for figure 1. A. Dorsal view. B. Ventral view. Identification of P^2 is uncertain; see p. 19 of text for discussion. Approximately $\times 3$.

non-mediolaterally flattened angle on jaw that does not project posteriorly.

Distinguished from *Dimylechinus* by more posterior position of mental foramen beneath anterior root of M_1 , not beneath P_4 ; absence of P^2 ; rotation of M_2 midline to form angle of about 22 degrees with long axis of jaw, not lying subparallel; less anteroposterior constriction of lingual half of P^4 relative to buccal half; shortening of M^1 metastyle; presence of M^1 cingulum on buccal margin only, not on all four sides; posterior and buccal sides of M^1 straight or slightly excavated, not deeply concave; lack of hypocone on M^2 .

Distinguished from *Dimylechinus* and *Exallerix* by presence of three, not four, lower teeth anterior to P_4 .

Distinguished from *Exallerix* by smaller size; presence of P_4 paraconid; and absence of knobs on ventrobuccal surface of P_4 and M_1 .

SYNOPTIC DESCRIPTION: Erinaceids with short faces; palate thick, lacking any fenestration, and extending a short distance behind transverse crest; zygomatic arch deep over most of length, anterior face concave, and concave areas of lateral and posterior faces separated by flange; infra-orbital foramen above center of P^3 ; anterior end of orbit above anterior end of P^4 ; maxillary base of zygomatic arch above M^1 ; optic foramen near center of orbitosphenoid and anterodorsal to suboptic foramen; auditory bullae extremely large, inflated, and completely ossified; vessels and some nerves in tympanic cavity enclosed in bony tubes; basisphenoid pit absent; tympanic wing of alisphenoid extending lateral to postglenoid foramen; strong supraorbital crests and postorbital processes; strong temporal crests joining strong sagittal crest at frontal-parietal suture; mastoid process expanded posteriorly, forming strong lambdoid crests; paroccipital process contacting mastoid process; supraoccipital not emarginated along midline by foramen magnum; dental formula $I_2^{3?} C_1^1 P_1^2 M_2^2$; P^4 hypocone taller, its base broader than that of protocone; M^1 metacone and hypocone closer to tooth midline than paracone and protocone; and M_1 prevallid expanded anteriorly with hypoconid and protoconid equidistant from midline.

Brachyerix macrotis Matthew, 1933

Brachyerix macrotis MATTHEW, 1933, in Matthew and Mook, 1933, p. 2, figure 1, "*Brachyerix montanus*," *lapsus calami* by Matthew.
Metechinus marslandensis MEADE, 1941, p. 43.

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



FIG. 3. *Brachyerix macrotis*, type, AMNH 21335. Lateral view of skull. From the Deep River Beds east of the Smith River and 7 miles southeast of Fort Logan, Montana. $\times 3$.

the zygomae, anterior part of the nasals, and the anteropalatal region of the maxillae. (See figs. 3 and 4.)

TYPE LOCALITY AND STRATIGRAPHIC POSITION: Collected from the Deep River Beds east of the Smith River and seven miles southeast of Fort Logan, Montana.

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 and M_2 . From the "Marsland Formation"^[1], about seven miles northwest of Marsland, Nebraska" (Meade, 1941, p. 43). (See fig. 5.) In the original description (Meade, 1941, pp. 43-44) *M. marslandensis* was recognized to be smaller than *M. nevadensis*. At the time, no lower jaws had been found in association with

¹ See discussion on stratigraphy, p. 45.

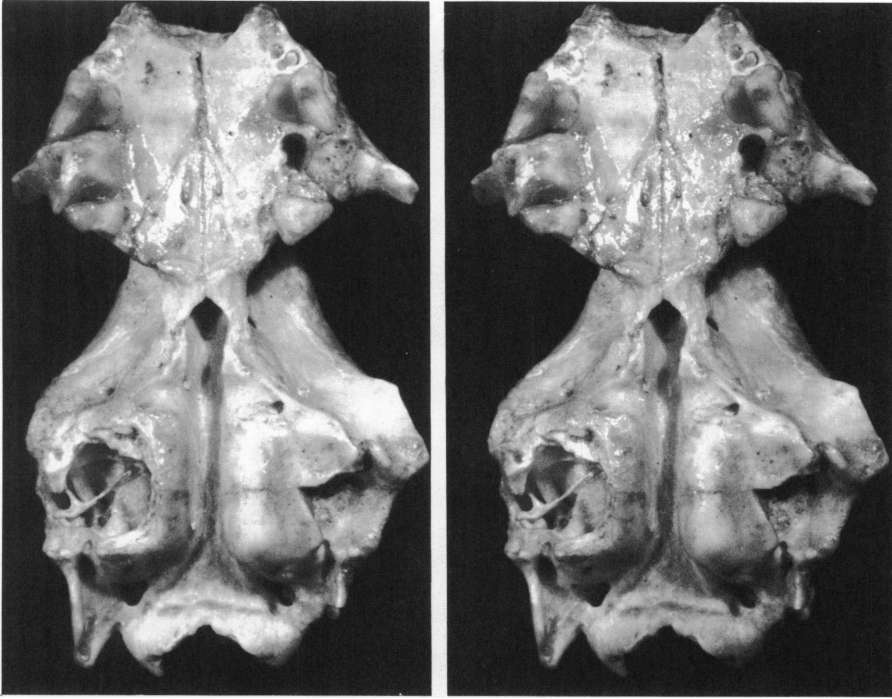


FIG. 4. *Brachyerix macrotis*, type, AMNH 21335. Ventral view of skull. $\times 3$.

a skull of *Brachyerix macrotis*. Subsequently, a skull of *B. macrotis* (UCMP 86137) with associated mandibles was discovered in the Hemingfordian part of the Split Rock Formation near Muddy Gap, Wyoming, and it is now clear that *M. marslandensis* should be synonymized with *B. macrotis*. As Reed (1960, p. 5) pointed out and we have confirmed by independent measurement, the length of M_1 is 3.8 mm. on FMNH P26399, which is only 0.3 mm. greater than the length of M_1 on UCMP 86137. A second feature of M_1 which links *M. marslandensis* to *B. macrotis* is the relatively elongate trigonid of that tooth. *M. nevadensis*, in contrast, has a more anteroposteriorly compressed M_1 trigonid.

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 . Found at UCMP locality V-69190, SW. $\frac{1}{4}$, NW. $\frac{1}{4}$, sect. 36, T. 29 N., R. 90 W., upper porous sandstone sequence of the Split Rock Formation of Love (1961, p. 14; 1970, p. 77), Fremont

County, Wyoming. (See figs. 6–11.)

“ . . . A.C.M. Nos. 10459–10460, 10462–10482, 11325, 11315–11321, 11427–11430; R.O.M. Nos. 2078, 2079; U.W. Nos. 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



FIG. 5. *Brachyerix macrotis*, FMNH P26399 (type of *Metechinus marslandensis*), left mandible. A. Occlusal view. B. Lateral view. From the “Marsland Formation [see discussion on stratigraphy, p. 45], about seven miles northwest of Marsland, Nebraska” (Meade, 1941, p. 43). $\times 3$.

and M_{1-2} ” (Reed, 1960, p. 5). Reed originally referred these specimens to *Metechinus marslandensis*, from the Split Rock Formation, NW. $\frac{1}{4}$, sect. 36, T. 29 N., R. 90 W., Fremont County, Wyoming.

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 . From the Split Rock Formation, NW. $\frac{1}{4}$, sect. 36, T. 29 N., R. 90 W., Fremont County, Wyoming. (See fig. 12.)

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. Found at Foley Quarry, NW. $\frac{1}{4}$, SW. $\frac{1}{4}$, sect. 15, T. 28 N., R. 49 W., Box Butte County, Nebraska in an unnamed channel deposit between the Box Butte Formation and rocks containing fossils characteristic of

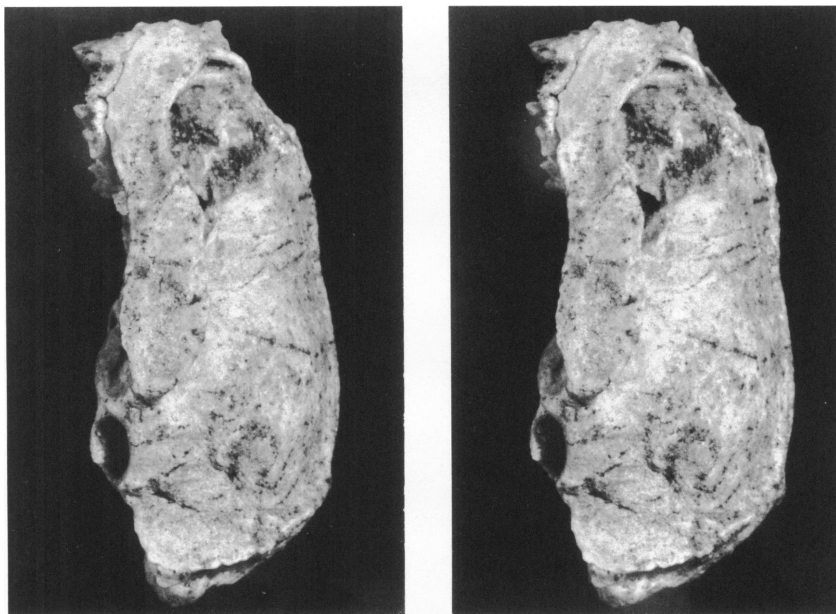


FIG. 6. *Brachyerix macrotis*, UCMP 86137. Lateral view of skull. From the Split Rock Formation, SW. $\frac{1}{4}$, NW. $\frac{1}{4}$, sect. 36, T. 29 N., R. 90 W., Fremont County, Wyoming. $\times 3$.

the Runningwater Formation (Cook, 1965). (See fig. 13.)

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 incisor; mandible broken posteriorly at mandibular foramen, anteriorly immediately in front of I_2 . Discovered in an unnamed channel deposit between the Box Butte Formation and rocks containing fossils characteristic of the Runningwater Formation exposed along Sand Canyon in NW. $\frac{1}{4}$, SW. $\frac{1}{4}$, sect. 29, T. 30 N., R. 47 W., Box Butte County, Nebraska.

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. Found at Greenside Quarry, NW. $\frac{1}{4}$, sect. 3, T. 25 N., R. 44 W., Sheep Creek Formation, Sioux County, Nebraska.

F:AM 76695, right 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 . Found in either the Harrison or Marsland Formation 5 to 7 miles northeast of Agate, Sioux County, Nebraska.



FIG. 7. *Brachyotus macrotis*, UCMMP 86137. Dorsal view of skull. $\times 3$.



FIG. 8. *Brachyerix macrotis*, UCMP 86137. Ventral view of skull. $\times 3$.

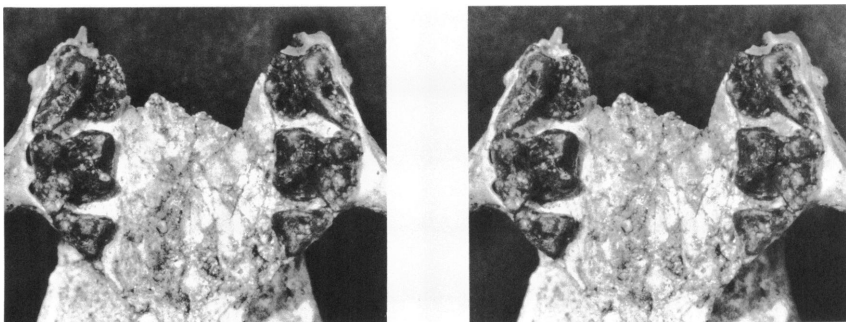


FIG. 9. *Brachyerix macrotis*, UCMP 86137. Ventral view of palate. $\times 4$.

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 . Found at USGS(PSB,D) Fossil Vertebrate Locality D719 (Barger Gulch, West) $5\frac{1}{2}$ miles east-southeast of Kremmling, Colorado, SW. $\frac{1}{4}$, SE. $\frac{1}{4}$, sect. 24, T. 1 N., R. 80 W. in the lower part of the Troublesome Formation.



FIG. 10. *Brachyerix macrotis*, UCMP 86137, right mandible. A. Medial view. B. Posterior view; note presence of inflected angle. $\times 3$.

DENTAL FORMULA: *Metechinus nevadensis* has the following dental formula for the upper dentition: $I^3 C^1 P^2 M^2$. *Brachyerix macrotis* has the same canine premolar and molar formula for the upper dentition. An additional premolar in *B. macrotis* is impossible, for the maxilla is complete along the tooth row on two specimens. Because the upper incisor dental formula of

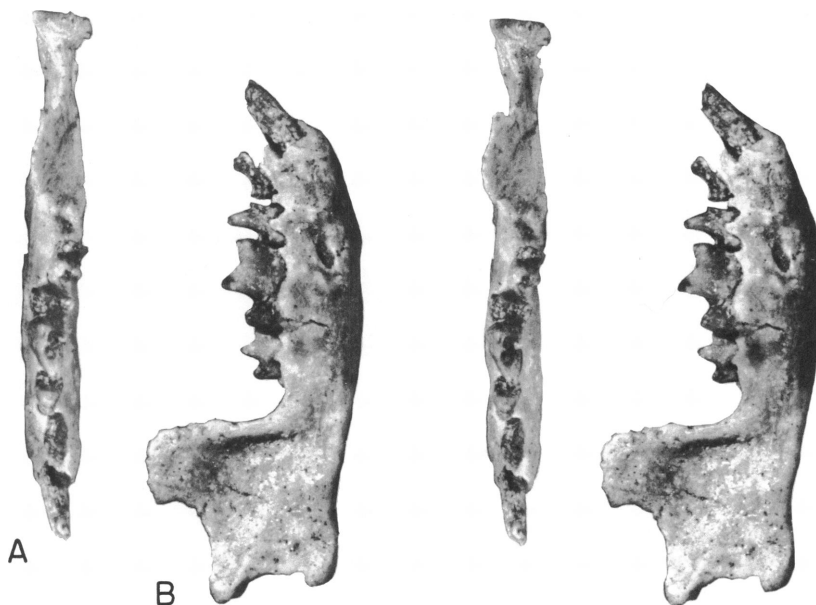


FIG. 11. *Brachyerix macrotis*, UCMP 86137, right mandible. A. Occlusal view. B. Lateral view. $\times 3$.

M. nevadensis is unreduced from that of the most primitive early Tertiary insectivores, it seems probable that a closely related species such as *B. macrotis* would have the same unreduced formula. The upper premolars and molars are assumed to be the following: P^3 , P^4 , M^1 , and M^2 . A triple-rooted condition is not found on any erinaceid tooth anterior to P^3 . Hence, the triple-rooted premolar here identified as the P^3 on *Brachyerix macrotis* cannot be homologous with any of the more anterior teeth.

Six teeth are known to have been present in the mandible. For the purposes of description, they shall be referred to here as the following: I_1 , I_2 , C_1 , P_4 , M_1 , and M_2 . Homologies of the three most posterior teeth are not in doubt.

TABLE 2
SKULL MEASUREMENTS (IN MILLIMETERS) OF *Brachyerix*

	<i>B. incertis</i> F:AM 74954	<i>B. incertis</i> LACM (CIT) 2817	<i>B. macrotis</i> AMNH 21335	<i>B. macrotis</i> F:AM 74965	<i>B. macrotis</i> UCMP 86137
Width across zygomatic arches	—	—	—	20.3 ^a	20.5
Width of palate including M ¹	9.9 ^b	—	14.1	11.4	11.4
Width of post-orbital constriction	—	—	7.7	6.2 ^a	8.3
Width between orbits ^c	—	—	9.5	8.3 ^a	9.7
Width of muzzle at infraorbital foramen	—	—	7.8	6.2 ^a	—
Width of braincase (at level of top of zygomatic arch)	—	—	15.3	12.0 ^a	16.3
Distance from anterior rim of orbit to infra-orbital foramen	—	—	2.0	1.9	—
Minimum width between jugular foramen and eustacean tube					
Left	6.8	—	8.0	—	7.5
Right	—	—	7.9	—	7.5
Length upper cheek teeth, P ⁴ –M ²					
Left	—	—	8.0	—	7.2
Right	—	—	—	—	7.2
C ¹ , anteroposterior diameter, left	—	—	—	1.3	—
C ¹ , transverse diameter, left	—	—	—	0.8	—
P ³ , anteroposterior diameter, left	1.3	—	—	1.4	—
P ³ , transverse diameter, left	0.8	—	—	0.8	—
P ⁴ , anteroposterior diameter					
Left	2.5	2.5	3.2	—	3.2
Right	—	—	3.3	3.2	3.0

TABLE 2—*Continued*

	<i>B. incertis</i> F:AM 74954	<i>B. incertis</i> LACM (CIT) 2817	<i>B. macrotis</i> AMNH 21335	<i>B. macrotis</i> F:AM 74965	<i>B. macrotis</i> UCMP 86137
P ⁴ , transverse diameter					
Left	1.6	1.8	2.2	—	2.3
Right	—	—	2.6	1.9	2.2
M ¹ , anteroposterior diameter					
Left	—	—	—	2.8	2.8
Right	—	—	3.1	2.9	2.8
M ¹ , transverse diameter					
Left	—	—	—	3.2	3.1
Right	—	—	3.9	3.3	3.1
M ² , anteroposterior diameter					
Left	—	—	2.3	1.7	1.6
Right	—	—	—	—	1.5
M ² , transverse diameter					
Left	—	—	2.7	2.4	2.1
Right	—	—	2.6	—	2.2

^a Measurement suspect because of distortion.

^b Position of M¹ estimated.

^c 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.

Clearly, the most anterior lower tooth is an enlarged incisor and probably I₁ (McKenna and Holton, 1967, p. 2, footnote 2). The tooth immediately behind could be either I₂ or I₃. For consistency and because no strong, contrary evidence exists, we have tentatively followed McKenna and Holton by referring to this second tooth as I₂ (see McKenna and Holton, 1967, p. 3).

Good evidence is available that the tooth here called a C₁ is in fact the lower canine. If the prevallid of M₁ of UCMP 86137 (mandible of *B. macrotis*) is placed in contact with the postvallum of P⁴ of F:AM 74965 (skull of *B. macrotis*), C₁ occludes with the anterior side of C¹. Hence, C₁ occluded with the posterior side of I³ if that tooth were present as it probably was. This is an impossible relationship if the tooth here called C₁ were any other tooth, for the lower canine normally occludes between these two upper teeth (C¹ and I³) among erinaceids.

TABLE 3
MANDIBLE MEASUREMENTS (IN MILLIMETERS) OF *Brachyotix*

<i>B. incertis</i> AMNH 18891	<i>B. incertis</i> LACM (CIT) 2818	<i>B. macrotis</i> FMNH P26399	<i>B. macrotis</i> F:AM 76693	<i>B. macrotis</i> F:AM 74964	<i>B. macrotis</i> CM 14959	<i>B. macrotis</i> UCMP 86137, Left	<i>B. macrotis</i> UCMP 86137, Right	<i>B. macrotis</i> USGS (PSB,D) Fossil Vertebrate Specimen No. D719A
Mandible depth below anterior part of P ₃	—	—	3.0	3.0*	3.1*	3.2	—	—
Mandible depth below M ₁ anterior root	2.3	2.7	2.8	3.7	4.0	3.2	3.2	4.6
Mandible depth below M ₂ posterior root	2.6	2.2	3.2	3.7	3.4	3.4	3.5	4.1
M ₁₋₂ length	—	5.0	—	5.5	5.8	6.0	6.0	6.2
C ₁ anteroposterior diameter	—	—	—	—	2.4	—	2.1	—
C ₁ transverse diameter	—	—	—	—	1.2	—	1.1	—
P ₄ anteroposterior diameter	—	—	—	—	1.7	1.9	1.8	—
P ₄ transverse diameter	—	—	—	—	1.4	1.3	1.3	—
M ₁ anteroposterior diameter	—	3.1	3.8	3.4	3.4	3.6	3.7	3.7
M ₁ trigonid length	—	2.0	2.2	2.0	2.1	2.1	2.3	2.3
M ₁ trigonid width	—	1.5	2.0	1.9	1.7	1.7	1.8	1.8
M ₁ talonid width	—	1.6	—	1.9	2.0	1.8	1.9	1.9
M ₂ anteroposterior diameter	1.9	2.0	2.3	2.4	2.3	2.4	2.3	2.5
M ₂ trigonid length	1.1	1.2	1.3	1.5	1.2	1.4	1.3	1.6
M ₂ trigonid width	1.0	1.2	1.3	1.5	1.4	1.3	1.4	1.4
M ₂ talonid width	0.9	1.0	1.2	1.2	1.3	1.2	1.2	1.2

* Minimum measurement owing to breakage.

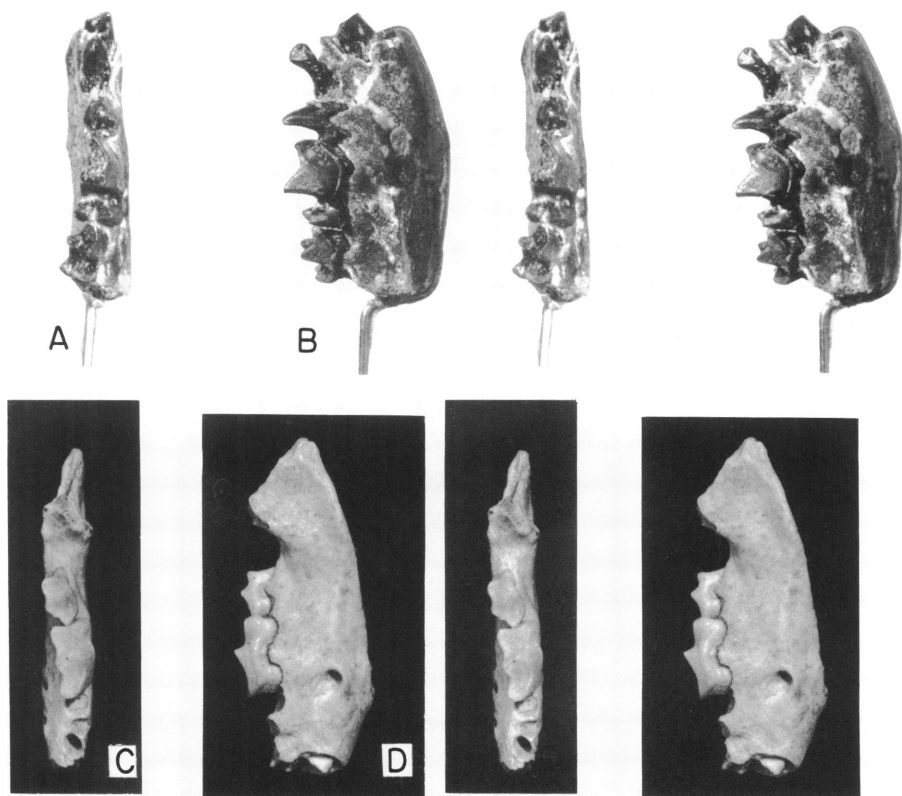


FIG. 12. *Brachyrix macrotis*. A, B. CM 14959, right mandible. From the Split Rock Formation, NW. $\frac{1}{4}$, sect. 36, T. 29 N., R. 90 W., Fremont County, Wyoming. A. Occlusal view. B. Lateral view. C, D. F:AM 74964, left mandible. From an unnamed channel deposit between the Box Butte Formation and rocks containing fossils characteristic of the Runningwater Formation exposed along Sand Canyon, NW. $\frac{1}{4}$, SW. $\frac{1}{4}$, sect. 29, T. 30 N., R. 47 W., Box Butte County, Nebraska. C. Occlusal view. D. Lateral view. $\times 3$.

The relatively large size of C_1 on *Brachyrix macrotis* indicates to us that the homologous tooth of *Exallerix hsandagolensis* was in the alveolus identified in the original description of the latter species as the site of the lower canine and not in the smaller alveolus immediately posterior and directly in front of P_4 (McKenna and Holton, 1967, p. 3). For the same reasons, the alveolus for P_4 , not A_2 , of *Dimylechinus bernoullii* (Hürzeler, 1944) appears to be the site of the C_1 homologue of *B. macrotis*. Although *B. macrotis* does not have a homologue of the smaller tooth behind C_1 such

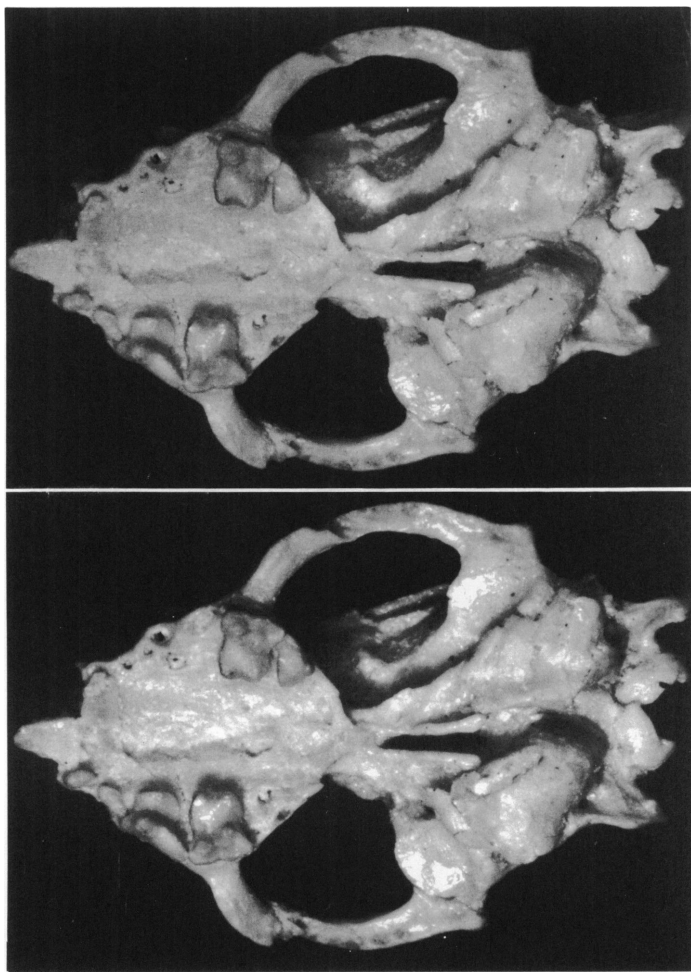


FIG. 13. *Brachyotris macrotis*, F:AM 74965. Ventral view of skull. From Foley Quarry, NW. $\frac{1}{4}$, SW. $\frac{1}{4}$, sect. 15, T. 28 N., R. 49 W., Box Butte County, Nebraska in an unnamed channel deposit between the Box Butte Formation and rocks containing fossils characteristic of the Runningwater Formation (Cook, 1965). $\times 3$.

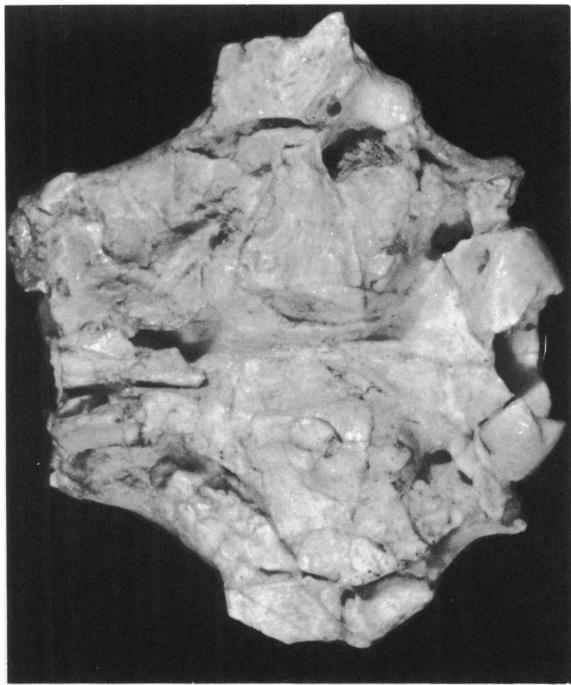
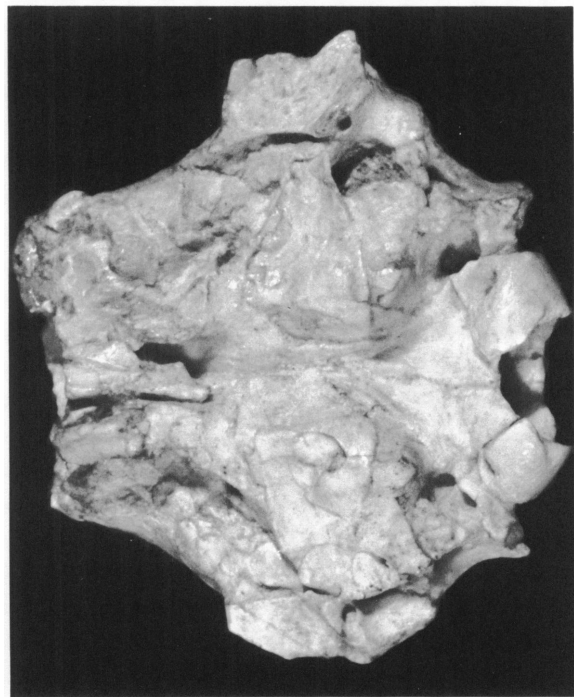


FIG. 14. *Metechinus nevadensis*, F:AM 74923. Ventral view of basicranium. From the Pojoaque Member of Tesuque Formation, near Santa Cruz, New Mexico. X3.

as is found in *D. bernoullii* and *E. hsandagolensis*, the occlusal relations between the upper and lower jaws of *B. macrotis* make it clear that a tooth had been lost from that position, for no lower tooth occludes between C^1 and P^3 , the site where a P_3 would be expected to occlude if present.

In summary, the dental formula for *B. macrotis* appears to be $I_2^{3?} C_1^1 P_1^2 M_2^2$.

UPPER DENTITION: C^1 : Both this tooth and the succeeding P^3 are mediolaterally compressed to such an extent that all the major structures on an individual tooth are arranged along a single anteroposterior axis. All the larger cusps are bladelike in form. The base of the paracone is about half as long as the tooth. The anterior and posterior sides of the paracone are concave dorsally. A wear facet parallel to the frontal plane truncates the apex of the cusp. Occupying the anterior third of the tooth is a prominent paracrista, and on the posterior sixth of the tooth is an equally strong, but shorter, metacrista. No modern hedgehog has as strong a paracrista on any tooth anterior to P^3 . As in most hedgehogs, this tooth is double rooted.

P^3 : Occupying the central third of the tooth is the base of the paracone. Both anterior and posterior edges of the paracone are straight. On both specimens of P^3 , the paracone apex has been truncated by a wear facet parallel to the frontal plane, but the unworn apical height was probably no more than two-thirds the crown length. In the skull F:AM 74965 a second wear facet is present on the posterior slope of P^3 paracone. The metastyle is smaller and lower than the paracone, and the two are linked by a metacrista. One cuspule is developed lingual to the metastyle and another is anterobuccal. Smaller than the metastyle, the parastyle is not joined by a crista to the paracone. Extending from the parastyle to the anterior side of paracone base is a well-developed lingual cingulum with no indication of a protocone. On the buccal side of the tooth between the parastyle and the base of the paracone is a weak cingulum. As in other brachyericines, P^3 is triple rooted, a condition found only in *Echinosorex* among modern erinaceids. The two stronger roots are above the parastyle and metastyle respectively, whereas the third, weaker root is between them, above the paracone.

P^4 : This tooth is several times larger than preceding P^3 . The height of the paracone, the tallest cusp on the tooth, is slightly more than half the length of the tooth. Beginning at the apex of the paracone, a wear surface extends along the posterior side of the cusp, onto the metacrista, terminating in the metastylar region. 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 larger and taller cusp

than the protocone and is posterolingual to it. 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. On worn teeth, a wear surface extends along the anterolingual edge of the tooth from the area of the hypocone across the protoconal area to the proximity of the paracone from which the wear surface is separated by a shallow notch. The anterior third of this surface slopes posterolingually and the posterior two-thirds lies parallel to the frontal plane. No parastyle is present, and the metacrista terminates posteriorly without a distinct metastyle. A weak cingulum is present along the buccal side of the tooth and, expanding slightly, extends around the anterior side of the base of the paracone to form a pre-cingulum. Developed above the protocone, paracone, and metacrista respectively, all three roots of the tooth are subequal in strength.

M¹: Largest tooth in the skull, M¹ is slightly broader and somewhat shorter anteroposteriorly than P⁴. The height of the paracone, the tallest of the four principle cusps, is half the length of the tooth. A nearly planar wear surface sloping anterobuccally is developed on the paracone apex. The paracone is anterobuccal to the metacone and their bases are confluent. In contrast, on M¹ 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 gently sloping posterior one. Crossing from the anterior to the posterior side of the cusp is a continuous wear surface that extends onto the metacrista, terminating at its posterior end. Strongest development of the wear surface occurs on the posterior slope of the metacone. In that area the width of the wear surface can be half the greatest width of the cusp. Third tallest and most lingual cusp on the tooth, the protocone is lingual and slightly anterior to the paracone. Its base projects 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 M² on some modern hedgehogs but never M¹. On the buccal side of the protocone is a wear surface that is continuous over a large part of the trigon basin. This wear surface extends onto the hypocone and in advanced stages of wear includes the lingual sides of the paracone and metacone bases as well. No trace of a metaconule is present. Linking the anterobuccal corner of the protocone and the anterolingual corner of the paracone are the well-developed preproto-crista and preprotoconule crista which grade imperceptibly into each other, for no paraconule is present. In anterior view this loph has a

broad inverted V-shaped profile. The postprotocrista is directed postero-buccally 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 to the metacone. 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. Between the posterior tip of the metacrista and the parastyle is a well-developed ectocingulum. Many modern hedgehogs duplicate this arrangement of the parastyle, metacrista, ectocingulum, and precingulum.

M²: No other cusps than those of the trigon are present on this tooth. Posterolingual to the paracone, the 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 metacone. Highest of the crests, the preprotocrista forms a continuous wall between the protocone and paracone. Linking the paracone and metacone is a centrocrista with a broad, inverted V-shaped profile in labial view. A prominent ectocingulum is present buccal to the paracone. Anterior to the paracone is a short precingulum.

LOWER DENTITION: I₁: On the single specimen where this tooth is preserved (right mandible, UCMP 86137), the tip is broken off. Assuming a constant rate of convergence of the dorsal and ventral margins of the tooth, the restored length above the alveolus is 6.4 mm., the preserved length 2.4 mm. The tooth is laterally compressed and imperfectly elliptical in cross section because the medial side is flattened. Below I₂, the dorsoventral axis is one and one-half times the length of the mediolateral axis. At this same point, the length of the dorsoventral axis is half the depth of the jaw. In a pattern typical of gliriform teeth, I₁ curves from an orientation parallel to the ventral margin of the mandible at its posterior extreme to an anterodorsal direction below I₂. The roots of I₂ and C₁ extend downward lateral to the I₁ root.

I₂: This single-rooted tooth is known only from its alveolus. The outline of the alveolus is nearly circular, with a diameter of 0.7 mm. on all three specimens where preserved. The alveolar depth is about one and one-half times the diameter.

C₁: Extending anteriorly from the root, the crown overlaps I₂. 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. A broad, bilobate ridge forms the posterior border of the tooth. Two weak crests extend from the protoconid to either end of this ridge. Eight cuspules are developed on the lingual side between the posterior end of the protoconid and the anterior edge of the bilobate ridge. Incisors, canines, and premolars all assume the general form of this tooth in modern hedgehogs where the teeth are crowded together.

Elliptical in outline, the alveolus for this single-rooted tooth has a major axis anterolaterally directed and 1.0 mm. in length and a minor axis 0.7 mm. long. Depth of the alveolus is 1.9 mm., about two-thirds the total depth of the mandible at this point. All alveolar dimensions given here were measured on C_1 in F:AM 74964.

P_4 : This tooth is shorter, broader, and taller than C_1 . Most prominent of the cusps is the protoconid; its height is 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. Of the other two trigonid cusps, only the paraconid is distinct and is a weakly developed cuspule at the anterior end of the labial cingulum, which is developed along the prevallid. There is a bulge in the base of the protoconid at the posterolingual corner but no sign of a separate metaconid. Greatest tooth breadth occurs at the anterior end of the short talonid. A crest with a few cuspules on it is developed along the posterior border.

On both the anterior and posterior sides of the partition between the alveoli for this double-rooted tooth are dorsoventrally oriented crests characteristic of erinaceids. The outline of the posterior alveolus on F:AM 74964 is rectangular with the mediolateral width 1.0 mm. and the anteroposterior length 0.7 mm. On the same specimen, the anterior alveolus has a trapezoidal outline. The maximum anteroposterior dimension of the anterior alveolus is 0.7 mm. and mediolateral is 0.8 mm. On F:AM 76693, C_1 alveolus is anterolingual to the anterior alveolus of P_4 rather than directly anterior. Possibly in response to this crowding, P_4 anterior alveolus of the latter specimen as compared with F:AM 74964 is smaller relative to the posterior one. Both length and width of the anterior alveolus are 0.5 mm. Again, possibly due to crowding, the posterior alveolus is more anteroposteriorly compressed in F:AM 76693. Anteroposteriorly, the alveolus is 0.5 mm. long and mediolaterally 1.1 mm. wide.

M_1 : The length of the trigonid is two-thirds the length of the tooth. The width of the trigonid is three-fourths its length. As in other brachyericines, 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 equal to, or 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 labial cingulum extends from a point buccal to the paraconid to another point buccal to the hypoconid.

Between the alveoli of the double-rooted M_1 is a much thicker partition than that between the alveoli for P_4 . The dorsoventral crest on this partition is stronger and broader than that on the P_4 partition. Both alveoli are roughly rectangular in outline. Dimensions of the anterior alveolus of F:AM 76693 are 1.0 mm. mediolaterally and 0.9 mm. anteroposteriorly. Dimensions of the posterior alveolus are 1.3 mm. mediolaterally and 1.1 mm. anteroposteriorly.

M_2 : This tooth is only about two-thirds as long and wide as M_1 . The trigonid length is three-fifths to two-thirds the total length of the tooth. The prevallid is not as expanded anteriorly as on M_1 , the width of the trigonid being equal to the length. 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 slightly narrower than the trigonid. Tallest of the talonid cusps, the entoconid is only slightly lower than the paraconid. Both the hypoconid and entoconid 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 is restricted to the central two-thirds of the prevallid.

This tooth is double rooted as are P_4 and M_1 . Unlike these two anterior teeth, the midline is not subparallel to the long axis of the mandible but forms an angle of 21–24 degrees in the occlusal plane, and the talonid is posterolingual to the trigonid.

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 very gently curved and rises to a maximum height over the glenoid region.

The preserved posterior parts of the nasals indicate that they were long and narrow as is typical of erinaceids. As the premaxilla has been broken off all specimens, its position can only be inferred. Breakage may have commonly occurred at the maxilla-premaxilla suture, for in two of the three specimens where this region is preserved, the pattern of breakage is the same. Breakage on the third specimen occurs posterior to that of the two with a similar breakage pattern. Among modern hedgehogs, the premaxilla fits into a groove, the lateral and medial walls of which are formed by the maxilla and ethmoid respectively. Such a groove may be seen in the two specimens mentioned above that have the similar breakage pattern. Assuming that the preserved anterior border of the maxilla is the actual border with the premaxilla, the suture between the two bones begins just anterior to the C^1 and extends dorsally, passing within 1.2 mm. of the infraorbital foramen and then up to the vicinity of the nasals. At this point, the suture turns posteriorly and terminates at the common juncture between the frontal, premaxilla, and maxilla. The frontal-premaxilla suture is less than 1 mm. long. The nasal-premaxilla suture extends anteriorly for the preserved length of the former bone. 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 (= Echinossoricinae).

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. Muscles of the snout originated in excavations on the anterior face of the zygomatic arch as in smaller species of the Galericinae.

PALATE: Owing to breakage, the anterior extent of the maxilla on the palate cannot be determined with complete confidence. However, at the anterior end of the preserved palatal process of the maxilla of F:AM

74965 is a small, shallow notch, which may represent the posterior border of the palatine fissure. Also, the shape of the anterior palatal region of the maxilla in *Metechinus nevadensis* is similar to that of the fragment preserved here. If the palatal region of the maxilla of F:AM 74965 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 14.3 mm. The palate extends for a short distance behind the transverse crest, as in members of the modern Erinaceinae.

Posterior palatine foramina are developed as notches in the transverse crest medial to the palatine-maxilla suture. The position of the posterior palatine foramina is duplicated in the galericines, but development as notches rather than as holes is found only in some erinaceine genera.

Extending posteriorly to a small foramen, a slight groove is developed on each 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. 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 *Brachyerix macrotis* 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 *B. macrotis* 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 (FIG. 15): Most of the anteromedial wall of the orbit is formed by the maxilla. The frontal, orbitosphenoid, and alisphenoid form most of the posteromedial wall of the orbit with small contributions from the palatine and parietal. All modern hedgehogs have this condition.

As in modern erinaceines, the orbitonasal foramen is near the anterior end of the palatine wall and close to the sphenorbital foramen. The suboptic foramen is near the posteroventral corner of the orbitosphenoid and slightly posterodorsal to the orbitonasal foramen. As in *Echinosorex*, the optic foramen is near the center of the orbitosphenoid and antero-dorsal to the suboptic foramen. However, the orbitosphenoid is not so anteroposteriorly expanded; therefore the optic foramen is not displaced

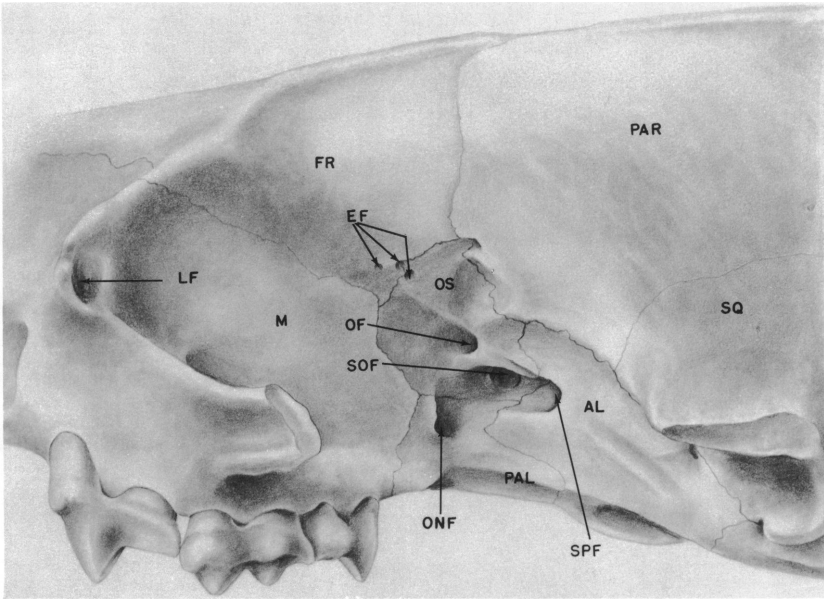


FIG. 15. *Brachyrix macrotis*, restoration of left orbitotemporal region of skull in lateral view based on AMNH 21335. $\times 5.5$.

so far anteriorly as in that genus. In other living hedgehogs, the optic foramen is closer to the alisphenoid and palatine sutures and in erinaceines is not exposed to lateral view owing to the forward expansion of the alisphenoid over the foramen. The ethmoid foramina lie near the orbitosphenoid-frontal suture as in the modern erinaceids. As in *Hylomys* and *Neotetracus*, the sphenorbital foramen is immediately posterior to the suboptic foramen. A crest that merges with the dorsal edge of the sphenorbital foramen extends anterodorsally, passing above the optic foramen. This crest forms the ventral boundary of a pit between the optic and ethmoid foramina. Similar depressions are present in various modern genera.

Extending posteriorly from the sphenorbital foramen, a groove passes above the external pterygoid process of the alisphenoid and below the foramen ovale before terminating at the anterolateral corner of the auditory bulla. It represents the pathway of the maxillary branch of the external carotid artery. No signs of openings for the alisphenoid canal are present although this structure is commonly found in modern hedgehogs above the carotid artery groove. 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: The alisphenoid and basisphenoid cannot be distinguished in this area and parts of the tympanic region on the three specimens available, so in cases of doubt the collective term sphenoid has been used in the present report. Both the palatine and sphenoid bones form internal and external pterygoid processes as in all modern erinaceids. The external pterygoid process passes posteriorly into the crest on the tympanic wing of the sphenoid. The tympanic wing extends lateral to the postglenoid foramen as in erinaceines, not galericines (*contra* Butler 1948, p. 456). The pterygoid is not present as a distinct ossification and is fused to the alisphenoid region of the sphenoid 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 processes in living hedgehogs. However, the poor preservation of all specimens in this area prevents a definite conclusion in this matter.

B. macrotis lacks the deep groove in the base of the skull that is terminated posteriorly by the basisphenoid pit which is the hallmark of the erinaceines. The sphenoid is not perforated.

As in the erinaceines, the condylar foramen is a single opening 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 anteroposteriorly and separated from the external auditory meatus by a double-walled partition. Part or all of this partition is formed by the mastoid but the periotic may contribute to the structure. Situated adjacent to the posterior end of the auditory bulla, the jugular foramen is anteroposteriorly elongated. The stylomastoid and jugular foramina are separated by a partition formed by the mastoid, which is breached by a groove. On one of the two specimens where this region is preserved, the groove is enclosed for part of its length to form a canal. In *Metechinus*, this partition extends farther ventrally from the main body of the skull to form a higher wall, and a canal is always present. This groove was occupied presumably 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). Extending antero-medially from the jugular foramen is a ledge-like process, which persists along the margin of the bulla to its posteromedial corner. A broad depression in this ledge passes into the jugular foramen and possibly

contained a large artery, vein, or nerve.

TYMPANIC REGION (FIGS. 16, 17): Bullae are longer than broad, closely approximated, and flask-shaped. The vertical, medial part is single walled, but the ventral, horizontal part is distinctly double walled with a layer of cancellous bone separating two layers of compact bone. Processes of the sphenoid, periotic, and tympanic bones form the bullae. AMNH 21355 shows the periotic-sphenoid suture in part, but as in all the adult hedgehogs we have examined, the alisphenoid-basisphenoid

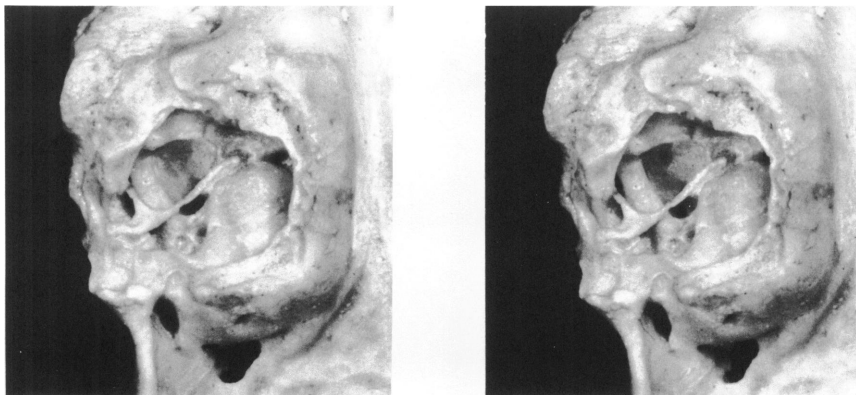


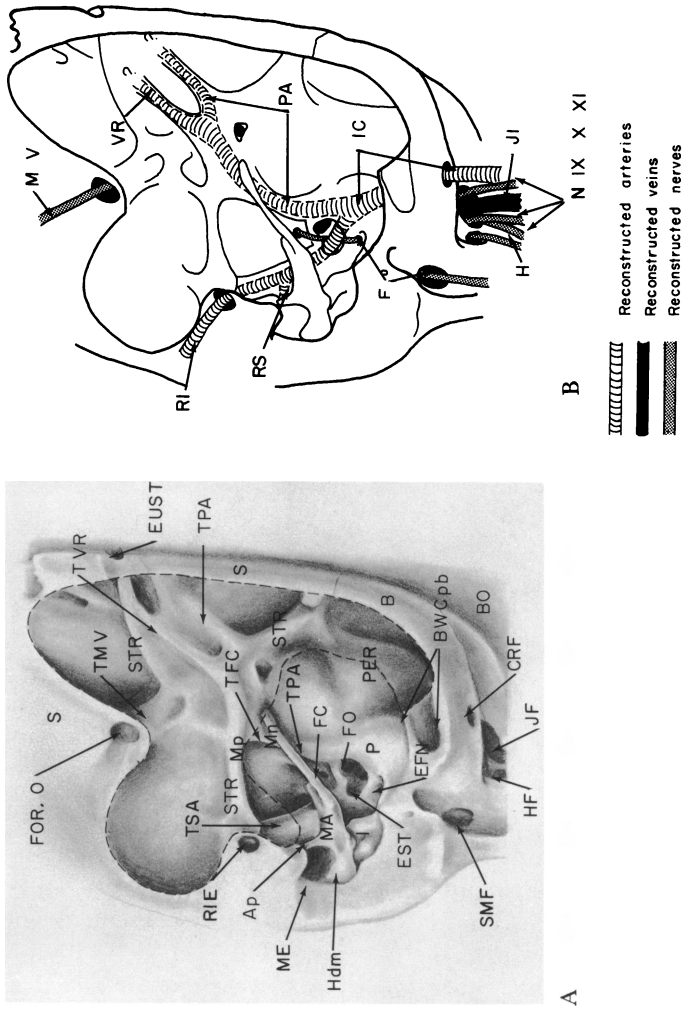
FIG. 16. *Brachyrix macrotis*, type, AMNH 21335. Ventral view of right tympanic region. $\times 5$.

suture is completely fused. The periotic, plus tympanic perhaps, forms about one-half the bulla. No separate tympanic is recognized due, perhaps, to post-mortem loss or more probably fusion with the other bullar bones. A ridge that runs from the postglenoid process to the small mastoid forms the upper edge of the tympanic cavity.

The eustachian canal enters the tympanic cavity at the anteromedial corner of the bulla, incising the sphenoid somewhat lateral to the midline of the skull. The canal is bridged ventrally at its medial end by the internal pterygoid process.

The structure of the tympanic roof is known from only one specimen, AMNH 21335, and is very unlike that in any of the modern erinaceids, except *Paraechinus*. No sutures are visible in the roof. Blood vessels and nerves were enclosed in bony tubes, but not all cylinders in the auditory capsule are hollow. The solid columns probably served only as structural supports for the bulla.

The internal carotid artery entered the tympanic cavity at the rear



through a foramen in the periotic. Immediately after entering, the vessel bifurcated into two branches, the stapedia and promontory branches of the internal carotid. The stapedia branch passed through a short tube, out a foramen, through the stapes, and into another tube, which it followed anteriorly. The superior ramus of the stapedia branched off the inferior ramus into a short vertical tube that leads into the brain cavity. The inferior ramus continued forward to exit from the tympanic cavity through a foramen in the tympanic wing of the sphenoid. Enclosed in a tube, the promontory artery continued forward across the promontorium and still enclosed in tubes bifurcated into (1) a large medial branch that entered the braincase at the base of a septum (or strut) near the midline of the skull and (2) a smaller lateral branch, the Vidian ramus. The lateral branch continued anteriorly almost twice as far as the medial before exiting from the tympanic cavity at the base of a medial strut that lies lateral to an expansion of the tympanic cavity into the braincase. Presumably, the palatine branch of nerve VII was included in this lateral tube and together with the promontory artery exited into the Vidian canal anteriorly.

The facial branch of nerve VII left the braincase in a small tube anterior to the fenestra ovale and entered the tympanic cavity through a foramen at the posteromedial base of the stapedia tube. The nerve entered the stapedia tube ventrally following it for part of its length and then exited the tympanic cavity through the stylomastoid foramen.

As in *Paraechinus*, 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. A distinct fenestra rotundum is not visible. In many of the living hedgehogs it is situated on the posterior face of the promontorium, and because of post-depositional cementation in the only *Brachyerix macrotis* skull (AMNH 21335) with this region prepared, the area is not exposed for examination.

Some cylinders and ridges in the tympanic cavity seem to have carried no nerves or vessels. These include one large transverse cylinder that extends from the anterior end of the stapedia tube to the promontory tube, and four major struts that occur near the midline of the skull. One lies medial to the promontorium and is distinctly grooved.¹ Two more lie medial to the tube that carried nerve V, and a fourth lies near

¹ A groove is present on a similar strut in some specimens of *Paraechinus*. It is present on the right, but not on the left, strut in AMNH(M) 166942. No structure is known to pass across the strut, and thus the notch may be developed in response to stresses applied to the strut (G. T. MacIntyre, 1968, personal commun.).

the midline of the skull further anterior.

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 malleus (known in two specimens, AMNH 21335 and UCMF 86137) is more slender than that in any of the modern erinaceids.¹ Unlike the anteroposteriorly flattened, shorter element in the living erinaceid genera, the manubrium (see Doran, 1879, and Henson, 1961, for ear ossicle terminology) is long, slender, and cylindrical. Short, robust, and somewhat anteroposteriorly flattened, the muscular process lies dorsal to the head. The head is flat and not expanded into the bulbous structure characteristic of modern forms, most extremely enlarged in *Neotetracus*. Forming a 90-degree angle with the long axis of the manubrium, the anterior process is slender and laterally flattened. It is much broader at its base near the head than along the rest of its length. In modern forms the anterior process is much more laterally flattened and deeper. In comparison with modern forms, the neck is very short, and the orbicular apophysis is more robust. The lamina is not present.

Incus and malleus are preserved in articulation in AMNH 21335. The incus has been obscured by post-depositional cementation to the posterior part of the tympanic cavity. Only that part which articulates with the malleus is readily observable. The medial and lateral edges of the articulation are more bulbous than those of the modern erinaceids, but the shape of the articular surface is concave as in the living forms.

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 smallest and most posterior foramen is probably the cochlear aqueduct. It is directly anterior to the hypoglossal canal in the exoccipital. A second foramen lies dorsal and lateral to the first and probably represents 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.

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 rather than in those that are nearer in size to *Brachyerix macrotis*. Both

¹ *Aethechinus*, *Hylomys*, and *Podogymnura* were not examined.

crests are strongly developed and meet where the sagittal plane intersects 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 *Metechinus nevadensis*.

The interparietal bone is expanded laterally and forms the dorsal part of the occipital crest as in recent erinaceines. Unlike that in any recent hedgehog, the crest is expanded anteriorly between the parietal and mastoid at its ventral extreme. Quite unlike any modern hedgehog, the mastoid has expanded posteriorly to form strong lambdoid crests in a manner similar to that in *Metechinus*. 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 in 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. The lateral surface of this bar is concave. Separating this concave surface from the groove on the posterior side of the first bar is a posterior projection of the second bar.

The posterior face of the skull is relatively flat and slopes postero-ventrally, departing further from the vertical than in modern erinaceids. Markedly prominent over its entire length, the suture between the exoccipital and supraoccipital bones passes immediately dorsal to the occipital condyles. 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 in erinaceines, there is no emargination of the supraoccipital along the midline by the foramen magnum.

MANDIBLE: The mental foramen lies below the anterior root of M_1 . A wide groove extends anterodorsally from the mental foramen beneath P_4 and widens still further dorsally beneath C_1 to form a shallow basin. Beneath the posterior root of P_4 the jaw is deepest. It slowly becomes shallower posteriorly and rapidly shallower anteriorly. One specimen (CM 14959) has a deep pit posterodorsal to the mental foramen and beneath the center of M_1 . This pit is shallow in three specimens and totally absent in two. A ridge extends posteriorly from a point between this pit and the mental foramen to a point on the ventral margin of the jaw below the anterior part of the masseteric fossa. The angle, rather than extending posteriorly well beyond the adjacent margin of the jaw as in modern erinaceids, protrudes only slightly in that direction and is

slightly more inflected than the angle of any modern erinaceid.

Extending forward from beneath the anterior end of M_1 , the unfused symphysis occupies the ventral two-thirds of the mandibular medial surface. The dorsal border of the symphysis is straight and nearly parallel to the ventral border, diverging somewhat anteriorly. An elongate groove that may have been the area of insertion for the geniohyoideus muscle extends almost the entire anteroposterior length of the symphysis, adjacent to its ventral margin.

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. Until abruptly terminated by the horizontal, nearly straight dorsal edge, the anterior border of the ascending ramus extends vertically with no indication of curving posteriorly with height. 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 the anterior edge of the ascending ramus posterodorsally to the mandibular condyle becoming weaker posteriorly. Immediately ventral to this ridge is the mandibular foramen, which is level with the tooth row and lies nearly midway anteroposteriorly between the borders 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 knife-edge thinness immediately above the angle. A ridge extending anteroventrally from the condyle forms the posteroventral border of the masseteric fossa. Above the condyle, the posterior border of the ascending ramus is as thin as a knife-edge. The posterior border curves anterodorsally from the condyle and meets the dorsal edge of the ascending ramus at a sharp angle.

REMARKS: Previously, all North American brachyericine jaw fragments were referred to *Metechinus* because *Brachyerix macrotis* was known only from a skull. Discovery of UCMP 86137, a skull of *B. macrotis* with associated mandibles from the Hemingfordian part of the Split Rock Formation, has shown that this species is a senior synonym of *Metechinus marslandensis*, a name which was previously applied only to lower dentitions.

***Brachyerix incertis* (Matthew, 1924), new combination**

Talpa incerta MATTHEW, 1924, p. 74.

Metechinus fergusoni HENSHAW, 1942, p. 101.

TYPE: AMNH 18891, right mandible with M_2 ; alveoli for M_1 and enlarged incisor; and missing posterior and dorsal parts of ascending

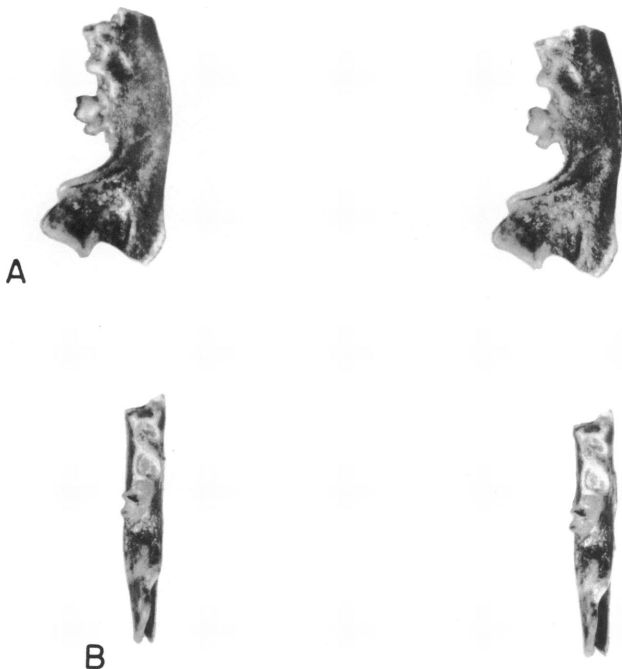


FIG. 18. *Brachyerix incertis*, type, AMNH 18891, right mandible. A. Lateral view. B. Occlusal view. From the Lower Snake Creek beds, Thomson's Quarry B of 1921, Sioux County, Nebraska. $\times 3$.

ramus, angle, and horizontal ramus anterior to M_1 . (See fig. 18.)

TYPE LOCALITY AND STRATIGRAPHIC POSITION: Lower Snake Creek beds, Thomson's Quarry B of 1921 (= Matthew's quarry '21,¹ Matthew, 1924), Sioux County, Nebraska.

DIAGNOSIS: Smaller species of genus; weak lingual cingulum on P^3 extending from parastyle to small protocone on posterior side of paracone.

REFERRED MATERIAL: LACM(CIT) 2817, type of *Metechinus fergusoni* Henshaw, 1942. Fragment of left maxillary with P^4 and parts of two alveoli belonging to M^1 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^3 ? . . ." LACM (CIT) 2818, [possibly from the same individual as the type of *Metechinus fergusoni* Henshaw, 1942, LACM (CIT) 2817 (Henshaw, 1942, p. 101)], left lower jaw with two anterior alveoli, P_4 - M_2 , and lower posterior region of the ramus.

¹ M. F. Skinner, 1969, personal communication.

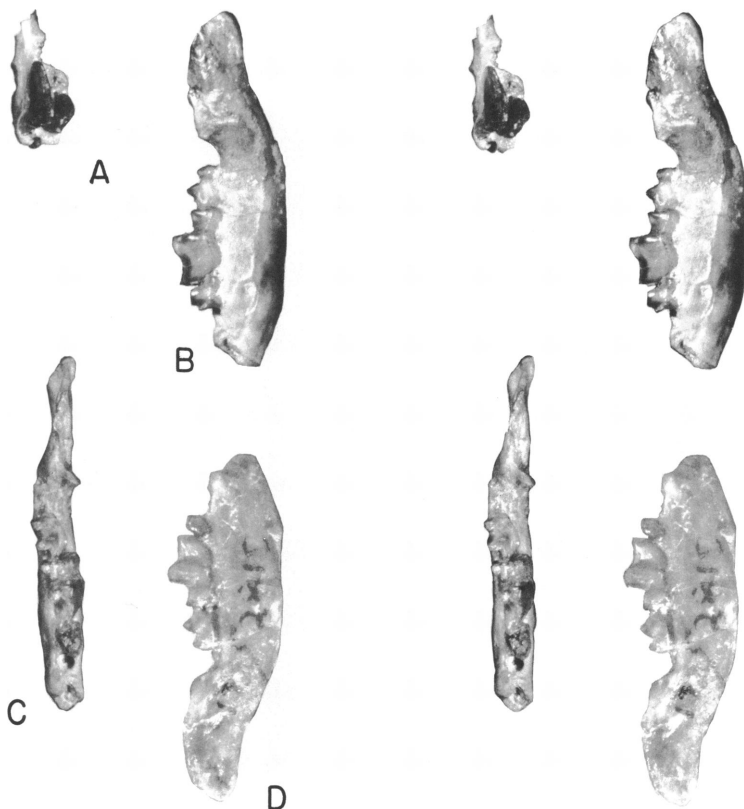


FIG. 19. *Brachyerix incertis*. A. LACM(CIT) 2817 (type of *Metechinus fergusoni*), left P⁴ in maxillary fragment, occlusal view. B–D. LACM(CIT) 2818 (found in association with LACM[CIT] 2817), left mandible. B. Lateral view. C. Occlusal view. D. Medial view. From the Esmeralda Formation, “. . . on the western flank of the San Antonio Mountains approximately 9 miles north of Tonopah, Nevada. The area where the fossiliferous strata are exposed is located at a point 3.67 miles N. 39° W. of Mineral Monument 206, U.S.G.S. topographic map of the Tonopah Quadrangle, Nevada, edition of 1908, reprinted 1922. . . .” (Henshaw, 1942, p. 82). $\times 3$.

As originally described, a third anterior alveolus was preserved (Henshaw, 1942, p. 101). The specimens were discovered at LACM (CIT) location 172 in the Esmeralda Formation. “The locality lies on the western flank of the San Antonio Mountains approximately 9 miles north of Tonopah, Nevada. The area where the fossiliferous strata are exposed is located at a point 3.67 miles N. 39° W. of Mineral Monument 206, U.S.G.S.

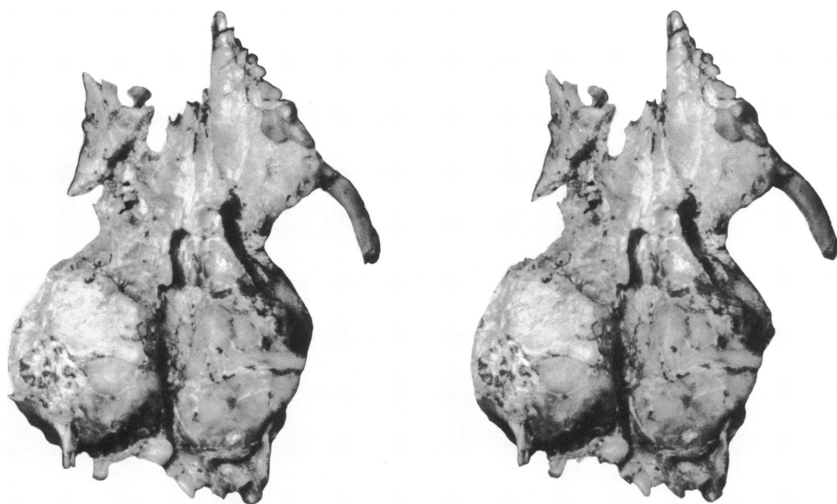


FIG. 20. *Brachyerix incertis*, F:AM 74954. Ventral view of skull. From Steepside Quarry, Barstow Formation, sect. 23, T. 11 N., R. 46 E., San Bernardino County, California. $\times 3$.

topographic map of the Tonopah Quadrangle, Nevada, edition of 1908, reprinted 1922. . . ." (Henshaw, 1942, p. 82). (See fig. 19.)

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^3-4 , posterior root of left C^1 , and alveoli of left M^1-2 . Found at Steepside Quarry in the Barstow Formation approximately 1000 ft. below the Skyline Tuff in sect. 23, T. 11 N., R. 46 E., San Bernardino County, California. (See fig. 20.)

DESCRIPTION: Same as for *B. macrotis* in all parts preserved except the few features mentioned in the diagnosis.

REMARKS: The type specimen of *Talpa incerta* (AMNH 18891) from the Barstovian Lower Snake Creek beds of Nebraska and the lower jaw from the Barstovian part of the Esmeralda Formation of Nevada referred to *Metechinus fergusoni* [LACM (CIT) 2818] are approximately the same in form and size of the mandible and M_2 . Presumably belonging to the same individual as the Nevada mandible, the type specimen of *M. fergusoni* [LACM (CIT) 2817], a maxilla fragment, is quite similar in both size and form of P^4 to the partial skull (F:AM 74954) from the Barstovian Barstow Formation of southern California. This partial skull

from California quite clearly has closer affinities with *Brachyerix macrotis* than with *Metechinus nevadensis*. Although markedly smaller than either genotypic species, the Barstow form is nearer to *B. macrotis* in size. Much more indicative of its closer relationship with *B. macrotis* is the presence of enlarged, closely approximated auditory bullae and the outline of the basicranium. In ventral view, the lateral margins converge posteriorly at a small angle, not at a large angle as in *M. nevadensis* (compare figs. 4, 8, 14, and 20). Because *T. incerta* is a brachyericine and not a talpid, it is removed from the genus *Talpa* and placed in *Brachyerix* as *Brachyerix incertis* (new combination). *Metechinus fergusoni*, proposed 17 years after *T. incerta*, is a junior synonym of *B. incertis*.

SPECIMENS INCORRECTLY REFERRED TO *Brachyerix*: Galbreath identified two teeth from two different sites in what he termed the Miocene Pawnee Creek Formation of northeastern Colorado as *Brachyerix* spp. (Galbreath, 1953, p. 92). An M^1 in a maxilla fragment, KU 9175, is referred to *Metechinus nevadensis* because the size and outline of this tooth are closer to M^1 of *M. nevadensis* than to M^1 of *Brachyerix macrotis*. M^1 of *M. nevadensis* has less concave borders and is more quadrate-shaped than M^1 of *B. macrotis* (*contra* Galbreath, 1953, p. 92). The second tooth, KU 9358, is a fragment of a molar that cannot be identified as an insectivore with certainty (*vide* Wilson, 1960, p. 21). It certainly is not brachyericine, for the paracone is no closer to the labial border of the tooth than the metacone, the metastyle is not pronounced, and the cusps are too low.

Wilson (1960, p. 21) tentatively identified KU 9988, an isolated lower molar from the Martin Canyon local fauna of northeastern Colorado, as M_2 of *Metechinus* sp. cf. *M. marslandensis*. However, this specimen appears to be M_1 of *Ampehechinus*.¹ As in M_1 of *Ampehechinus* and unlike M_2 of brachyericines, the cusps are slender, the paraconid is nearly the same height as the metaconid, and the trigonid is narrower than the talonid. Unlike M_1 of brachyericines and similar to M_1 of *Ampehechinus*, the trigonid is not anteroposteriorly elongated.

STRATIGRAPHY

Specimens of *Brachyerix* range in age from late Arikareean or Hemingfordian to late Barstovian and possibly later. Stratigraphic and temporal occurrences of these specimens accepted in the present paper are summarized in table 4 (pp. 46–47), and original designations are contained in table 1 (pp. 4–5).

¹ Van Valen (1967, p. 273) recognized the presence of *Ampehechinus* in the medial and late Miocene of North America.

Six specimens are known from western Nebraska. Grayson E. Meade collected the type of *Metechinus marslandensis* (FMNH P26399) 7 miles northwest of Marsland, Nebraska in deposits he identified as the Marsland Formation.¹ The restricted Marsland Formation (= Upper Harrison of Peterson, 1906), the Runningwater 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.

Two specimens, F:AM 74964 and 74965 (both *B. macrotis*) were collected by Ted Galusha in Box Butte County, Nebraska from unnamed local channel deposits that incise rocks containing a fauna most similar to that in the Runningwater Formation (Cook, 1965) and are overlain by the Box Butte Member of Cady (1940).² A fourth specimen of *B. macrotis*, F:AM 76693, was collected from Greenside Quarry, Sioux County, Nebraska, in the lower part of the Sheep Creek Formation. Another specimen of *B. macrotis*, F:AM 76695, was collected 5 to 7 miles northeast of Agate, Nebraska, where only the Marsland Formation (= Upper Harrison) and the Harrison Formation are known to crop out (Galusha, 1970, personal commun.). A right mandible, AMNH 18891, of *B. incertis* came from Thomson's Quarry B of 1921 in Sinclair Draw, Sioux County (see p. 41), which produced a part of the Lower Snake Creek fauna (Matthew, 1924).

In Fremont County, east central Wyoming, a right mandible, CM 14959, as well as several isolated teeth of *B. macrotis* (Reed, 1960), was found in association with mammals characteristic of the Split Rock local fauna in the upper porous sandstone sequence of the Split Rock Formation, considered to be of Hemingfordian age, medial Miocene (Love, 1961, p. 24). These specimens all came from or near locality 11V (Love,

¹Meade, in a letter to Malcolm C. McKenna dated June, 1967, stated that in 1941 when he published on *M. marslandensis* (referred to *B. macrotis* in this paper), he regarded the Marsland Formation "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."

²Cady (1940, p. 664) proposed the Box Butte as a member of the Sheep Creek Formation but in a later report (Cady and Scherer, 1946, p. 35) reserved the right to consider the Box Butte as a member of the Ogallala Formation. Cady even noted that the Box Butte might be a separate formation (Cady, 1940, p. 666), which is the opinion held by Galusha (personal commun., 1969) at present. In the present paper the Box Butte sediments will be considered a unit separate from and stratigraphically below the Sheep Creek Formation and stratigraphically above the Runningwater Formation, following the order proposed by McKenna (1965, p. 5).

TABLE 4
OCCURRENCES OF *Brachymeris*

	Arikarean	Hemingfordian	Barstovian	Clarendonian
Nebraska				
Species	<i>B. macrotis</i>	<i>B. macrotis</i>	<i>B. macrotis</i>	<i>B. incertis</i>
Locality	5-7 miles NE of Agate	7 miles NW of Marsland	Greenside Quarry	Thomson's Quarry B 1921
Formation	?Marsland (= Upper Harrison) or Harrison	?Marsland, Runningwater, or Sheep Creek	Unnamed local channel deposits	Lower Snake Creek beds
Wyoming				
Species			<i>B. macrotis</i>	
Locality			Loc. 11 V (Love, 1961), UCMP loc. V-69190	
Formation			Split Rock	
Colorado				
Species		<i>B. macrotis</i>		
Locality		Barger Gulch West		
Formation		Troublesome		

TABLE 4—Continued

Arikarean	Hemingfordian	Barstovian	Clarendonian
Montana Species Locality Formation	<div>←</div> <div><i>B. macrotis</i> 7 miles SW of Ft. Logan Deep River Beds</div> <div>→</div>		
Nevada Species Locality Formation			<i>B. incertis</i> CIT loc. 172 Esmeralda
California Species Locality Formation		<i>B. incertis</i> Steepside Quarry Barstow	

1970). From UCMP location V-69190, which is at or near Love's locality 11V, an almost complete skull together with associated mandibles of *B. macrotis* (UCMP 86137) was collected in the upper porous sandstone sequence of the Split Rock Formation.

One locality in north-central Colorado, Barger Gulch West, in the lower part of the Troublesome Formation (see Izett, ms) has produced a left mandible containing M_{1-2} [USGS (PSB,D) Fossil Vertebrate Specimen D719A] of *B. macrotis*. The presence of *Merycochoerus matthewi*, *M. proprius*, and *Mesogaulus* cf. *M. paniensis* in localities at or near the same stratigraphic level as Barger Gulch West suggests a late early Miocene age if a twofold division of the Miocene is used (Lewis, 1969) or a late Arikareean to Hemingfordian Age if a threefold division is employed.

In southern California, Steepside Quarry, which lies approximately 1000 feet below the Skyline Tuff in the Barstow Formation, has yielded a crushed skull of *B. incertis* (F:AM 74954). The fauna recovered from this quarry is similar to that in the Lower Snake Creek beds of Sioux County, Nebraska (Galusha and Tedford, 1969, personal commun.).

The fauna associated with a *B. incertis* maxilla [LACM (CIT) 2817] and ramus [LACM (CIT) 2818] from the sediments correlated with the Esmeralda Formation (Henshaw, 1942, p. 89) in the San Antonio Mountains near Tonopah has a disputed age. Henshaw 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 *?Aepycamelus stocki*¹ 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. Thus, because the Tonopah fauna is similar to that in parts of the Valentine Formation and more advanced than that in the Lower Snake Creek beds of western Nebraska, the Tonopah brachyericine specimens are the latest known occurrence of the genus *Brachyerix*.

¹ Macdonald (1956, pp. 198–199) substituted the name *Aepycamelus* for *Alticamelus* Matthew, which he considered a *nomen vanum*.

A skull of *B. macrotis*, AMNH 21335, was collected from the Deep River Beds 7 miles southeast of Fort Logan, Montana. It was reportedly found within a few hundred yards of the following specimens [most reported by Mook (Matthew and Mook, 1933)]: *Mookomys altifluminis* (AMNH 21360), *Merychippus* (AMNH 21330), *Merychys* (AMNH 21310), *?Cyclopidius* (AMNH 21306), *Brachycrus lateceps* (AMNH 21321 and 21322), *Promerycochoerus* (AMNH 21338), *Dromomeryx* (AMNH 21329), *Subdromomeryx antilopinus* (AMNH 21311), *Cranioceras kinseyi* (AMNH 21317), and *Alticamelus* (AMNH 21337) (see footnote, p. 48). *Mookomys* actually was collected from another locality.¹ The remainder of the assemblage is from at least three stratigraphic levels. *Cyclopidius* and *Promerycochoerus* are restricted to the Arikareean elsewhere. *Subdromomeryx* is known from Hemingfordian sediments, whereas *Brachycrus* occurs in both Hemingfordian and Barstovian rocks. *Dromomeryx* is restricted to the Barstovian; *Cranioceras* is known only from the Valentine Formation of late Miocene or early Pliocene age. Thus the age of the Deep River *Brachyerix* could range from Arikareean to Barstovian or possibly younger. However, because the *Brachyerix* is *B. macrotis*, we contend that the sediments which produced it are probably of Hemingfordian Age.

DISCUSSION AND COMPARISON

The supposed absence of a P⁴ hypocone in *Brachyerix* was previously thought to separate this genus from *Metechinus*. This cusp, however, is present in both *Brachyerix* species. More important differences between the two genera are to be found in the morphology and proportions of the basicranium together with the pronounced size differential. Figures 4, 8, 14, and 20 illustrate the differences in the outline and proportions of the basicranium. To point out the relative size differences between the species of the two genera simultaneously with their respective geologic ranges, the logarithm of the length of M₁, the most abundant element, is plotted with respect to time in figure 21.

At present, some (perhaps unknown) species of *Brachyerix* is the most probable ancestor for *Metechinus* on stratigraphic, geographic, and morphological grounds. *Brachyerix macrotis* first appears in the Hemingfordian (medial Miocene) of the Great Plains of the United States, and *M. nevadensis* makes its first appearance in this same area in the early Barstovian (late Miocene). Except for the basicranial and auditory regions, *M. nevadensis* is little more than an enlarged form of *B. macrotis*.

¹ Seven miles south of Fort Logan, Montana.

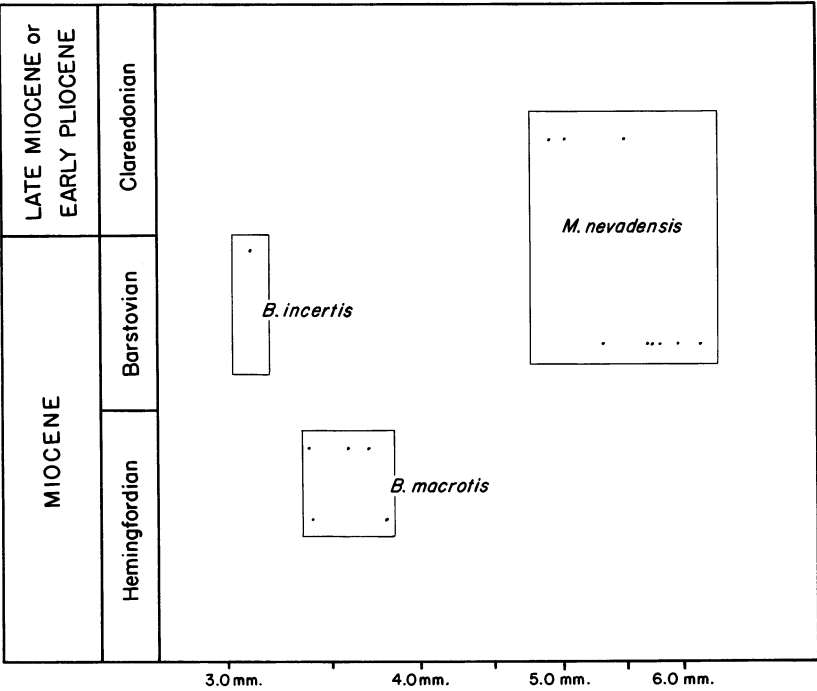


FIG. 21. Logarithmic plot of M₁ length in mm. of *Brachyerix* and *Metechinus* species. Each point represents the length of one tooth. Vertical length of enclosing figure indicates known geologic range of species. Those specimens of *Brachyerix* used for this figure are listed in table 3. The following specimens of *Metechinus* were used for this figure: UCMP 29600 (two teeth of one individual), type of *M. nevadensis*, from the Fish Lake beds, Nevada, UCMP location 2804; F:AM 74925, from the Santa Fe Group, New Mexico; and F:AM 76697-76700 (six specimens), Observation Quarry, NW. $\frac{1}{4}$, SE. $\frac{1}{4}$, sect. 4, T. 31 N., R. 47 W., Dawes County, Nebraska.

However, no specimen exists that is intermediate between the radically different conditions found in the basicranial and auditory regions of these two genera.

If *Brachyerix* were the direct ancestor to *Metechinus*, it would be reassuring to see a trend within the former genus toward an increase in size. Quite the contrary, however, is the case in the one lineage clearly derived from *B. macrotis*. Through its known history beginning in the Hemingfordian, this lineage became steadily smaller and eventually terminated in the diminutive Barstovian form *B. incertis*. It is not impossible that this example of the violation of Cope's Rule of the per-

sistent evolutionary trend toward size increase within a phyletic lineage is merely half an example of ecological displacement, one lineage becoming slowly smaller and conservatively retaining the ancestral basicranial condition and the other rapidly evolving into a larger form, *Metechinus*, with a radically modified basicranial region. If this is the case, the intermediates between the two lineages should be expected from late Hemingfordian deposits in North America. That the habitats of the members of the two lineages might have been different is indirectly supported by the fact that although the stratigraphic and geographic ranges extensively overlap, there is not a single occurrence of both *Brachyerix* and *Metechinus* from the same locality.

If *Metechinus* did in fact arise from *Brachyerix*, two morphological trends were reversed. In those erinaceids where the back of the jaw is known except *Metechinus* and *Brachyerix*, there is a deep indentation in the posterior margin of the mandible between the coronoid process above and the angle below so that the angle appears to project posteriorly away from the body of the mandible. In contrast, this indentation in the posterior margin of the mandible is absent in *Brachyerix* so that the angle does not appear to project posteriorly to any significant degree. In *Metechinus*, the excavation is present but not so pronounced as in other erinaceids excluding *Brachyerix*.

The trigonid of M_1 of *Brachyerix* is more anteroposteriorly expanded than that of *Metechinus*. If the relatively short trigonid present on M_1 of most non-brachyericine erinaceids is the ancestral condition for the brachyericines, a reversal of this trend is necessary to derive *Metechinus* from *Brachyerix*.

More remote from *Brachyerix* in both time and space, the two other brachyericine genera, *Dimylechinus* and *Exallerix*, are much less completely known.

Dimylechinus bernoullii Hürzeler, 1944, from the late or possibly medial Aquitanian (early Miocene) of Allier, France, differs from *Brachyerix* primarily in dental features and the character of the mandibular angle, although the remainder of the mandible and the muzzle of *D. bernoullii* are similar. Similar relationships between the positions of the zygomatic arch, anterior end of the orbit, and anterior opening of the infraorbital foramen relative to the positions of the teeth reflect the same shortening of the skull in *D. bernoullii* as is found in *Brachyerix*. Another feature common to both taxa that reflects the shortening in skull length is the reduced molar formula M_2^2 . *Brachyerix macrotis* and *D. bernoullii* are about the same size.

Dimylechinus bernoullii seems to have shortened its skull and yet has a

mandibular angle that projects posteriorly well beyond the adjacent posterior margin of the mandible. This suggests that the reduction in length of the skull of *Brachyerix* may not be functionally related to the shortened angle in that genus.

Dimylechinus bernoullii is the most likely ancestor to *B. macrotis* among the known erinaceids. No anatomical feature of either species prevents a direct relationship between the two species. Certainly the presence of an additional tooth in the maxilla and another in the mandible plus the presence of a hypocone on M^2 are features that might be expected in a *B. macrotis* ancestor that had not yet specialized to the degree found in that species. Supporting this contention is the fact that the lower tooth probably lost by the descendants of *D. bernoullii*, P_3 [= A_2 of Hürzeler's (1944) terminology], was already much smaller than the surrounding teeth. On *B. macrotis* there is no lower tooth occluding against the posterior surface of C^1 and the anterior surface of P^3 . Thus, there is a gap in the lower tooth row of *B. macrotis* just where the reduced P_3 was present in *D. bernoullii*. The relative geological ages of the two species are in concert with this relationship. The only serious obstacle is the necessity of an intercontinental migration from Europe to North America during the first third of the Miocene, but this was a time of considerable interchange between the two areas.

Exallerix hsandagolensis McKenna and Holton, 1967, from the medial Oligocene Hsanda Gol Formation of Mongolia, is known only on the basis of a right mandible fragment with I_1 , P_4 , and M_1 preserved. Because of the nature of the specimen, little can be said in way of comparison with *Brachyerix* except that both possess the elongated M_1 prevallid and the reduced lower molar formula that are the hallmarks of the brachyericines. *Exallerix hsandagolensis* is 50 per cent larger than *B. macrotis*, the larger *Brachyerix* species.

CONCLUSIONS

Two valid species of *Brachyerix* can be recognized at present in North American deposits. *Brachyerix macrotis* is the larger species and existed during the Hemingfordian (medial Miocene). *Brachyerix incertis*, the smaller species, evolved from *B. macrotis* with little change except for decrease in size. *Brachyerix incertis* lived during Barstovian (late Miocene) time. *Metechinus nevadensis* may be a more radically altered descendant of *B. macrotis* that increased, rather than decreased in size and persisted from the Barstovian to the Clarendonian (late Miocene or early Pliocene).

Dimylechinus bernoullii from the Aquitanian (early Miocene) of Europe is a perfectly adequate structural ancestor for *B. macrotis* and its descen-

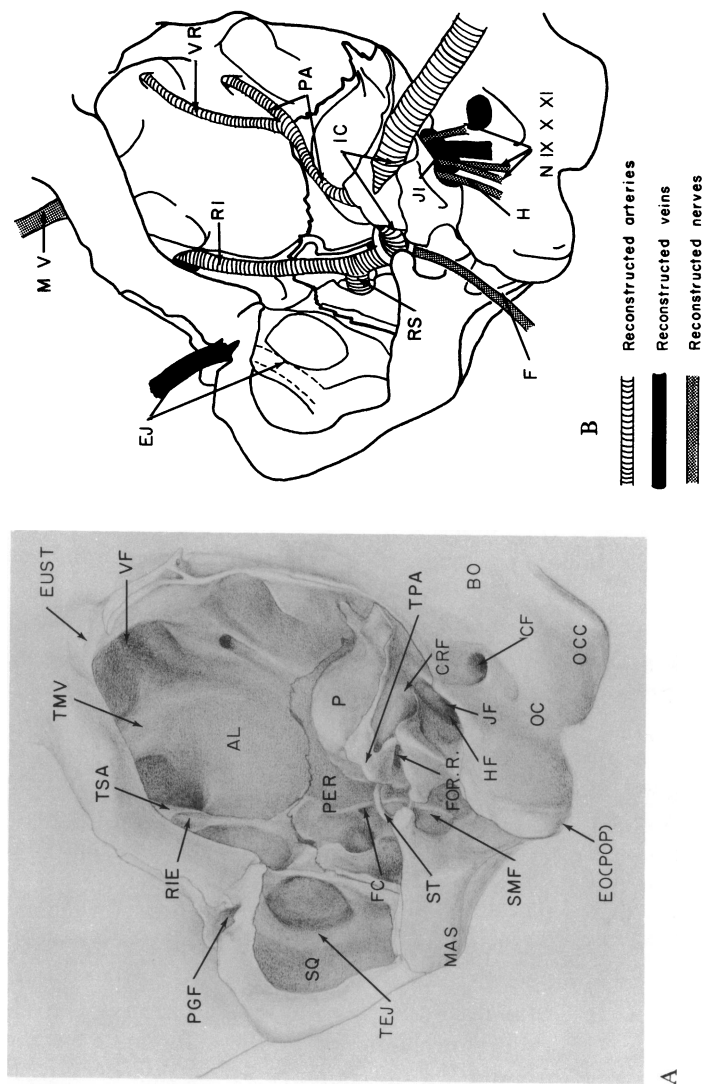


FIG. 22. *Paraechinus aethiopicus*, AMNH(M) 70098. Ventral view of right (reversed left) tympanic region (A) with arteries, veins, and nerves in position (B). $\times 5$.

dants. The necessity of intercontinental migration during the early Miocene is the only objection against this relationship.

Talpa incerta is a distinct species in the genus *Brachyerix* and this is recognized by the new combination *Brachyerix incertis*. Furthermore, *Metechinus marslandensis* is a junior synonym of *B. macrotis*, and *Metechinus fergusoni* is a junior synonym of *B. incertis*.

APPENDIX

DESCRIPTION OF THE TYMPANIC REGIONS OF *Paraechinus* AND *Podogymnura*

Figure 22

The tympanic regions of both *Paraechinus* and *Podogymnura* are described here because of the inadequacy of previous descriptions. *Paraechinus* has many similarities in the tympanic region to *Brachyerix* and is the only modern hedgehog that has blood vessels and nerves enclosed in bony tubes. The ear region of *Podogymnura*, no doubt due to its rarity in collections, has never been described.

Paraechinus.¹ The bullae are longer than wide and diverge from one another posteriorly. They are formed by processes of the sphenoid, periotic, and tympanic. The periotic is reduced from the condition seen in *Hylomys* and *Neotetracus* but similar to that in all Erinaceinae, *Podogymnura*, and *Echinosorex*. The tympanic roof is formed by the sphenoid, periotic, and squamosal. No postglenoid or mastoid processes are present; instead, a smooth crest defines the upper edge of the tympanic opening and is terminated anteriorly by the glenoid fossa, posteriorly by the stylomastoid foramen.

A broad, shallow excavation between the stapedia and the internal carotid arteries marks the origin of the tensor tympani muscle.

The internal carotid artery enters the bulla from behind through a foramen in the periotic and continues anteriorly in a bony tube, which extends onto the promontorium. Still enclosed in tubes, the artery bifurcates into a promontory branch and a stapedia branch. Both are enveloped in tubes for a short distance anterior to the bifurcation of the carotid. After leaving the tube, the promontory artery follows a well-developed groove on the promontorium and dorsal roof of the tympanic cavity until it enters the cranium through the carotid foramen in the sphenoid. The promontory artery then gives off a small lateral branch that follows a shallow groove forward to re-enter the cranium in the

¹ Description is based on three skulls: *Paraechinus aethiopicus* [AMNH (M) 31249 and 70098] and *Paraechinus* sp. [AMNH (M) 166942], some of which contained dried blood vessels within the auditory region.

Vidian canal of the sphenoid. We were unable to observe the path of the palatine branch of nerve VII. If it is similar, however, to that in those erinaceids reported on by Butler (1948), the nerve enters the tympanic cavity at the periotic-sphenoid suture, lies parallel to the Vidian ramus of the promontory artery, and exits into the Vidian canal. Slightly anterior to its origin from the internal carotid artery, the stapedia artery exits from a tube, follows a deep groove in the promontorium, passes through the stapes, and enters another deep groove in the periotic. The artery then gives off the ramus superior laterally, which passes through a foramen in the anterior end of the periotic. In one specimen [AMNH (M) 166942] the vessel enters a tube appressed against the anterior wall of the tympanic cavity slightly lateral to the promontorium. The ramus inferior continues forward, enters another bony tube, and passes out of the tympanic cavity through a foramen in the sphenoid. It then enters a shallow groove¹ ventral to the foramen ovale in the lateral wall of the orbit. Bony tubing around the anterior end of the inferior ramus is also present in *Atelerix albiventris*.

The facial canal carrying the hyomandibular branch of nerve VII is as Butler (1948, p. 456) describes it for all Erinaceidae. It opens into the tympanic cavity slightly anterior to the fenestra ovale and leads to the stylomastoid foramen.

The tympanic cavity is expanded anteriorly, posteriorly, laterally, and dorsally more than in any other modern hedgehog. Anteriorly the cavity extends far above the palatines, posteriorly into the periotic, and laterally far beyond the stapedia artery. The mandibular branch of nerve V is enclosed in a bony tube that passes through the anterior expansion of the tympanic cavity; the external jugular vein is enclosed in another tube appressed against the anterior wall of the lateral expansion. Some cylinders and ridges in the tympanic cavity carry no nerves or vessels and presumably serve as bullar supports.

The anterior process of the malleus is as long as the manubrium. The incus fits into a deep, rather narrow excavation in the periotic, lateral to the stapes.

Podogymnura:² The bulla is formed by at least the processes of the sphenoid and periotic. The tympanic is not preserved in the specimens we were able to examine. The roof of the tympanic cavity is formed by the sphenoid, periotic, and squamosal. The dorsal edge of the tympanic

¹ In AMNH (M) 166942 this is a covered canal.

² Description is based on two skulls of *Podogymnura truei* [AMNH (M) 61434 and 164482]. No ear ossicles or tympanic were preserved on either specimen.

opening is bordered by a low ridge that runs between the glenoid fossa and the low mastoid process. A low shelf extends medially beyond the ridge. No postglenoid process is present.

A deep triangular excavation at the base of the promontorium marks the origin of the tensor tympani muscle.

The roof of the tympanic cavity is like that in most other Erinaceidae, much as in *Erinaceus*. Grooves for the internal carotid, the stapedia, and the promontory arteries incise the promontorium. The stapedia groove is the largest of these three. The ramus superior is given off far posterior to the postglenoid foramen, directly lateral to the anterior opening of the facial canal into the tympanic cavity, as in *Neotetracus*. In all other erinaceids in which the region is known the opening for the facial canal is further posterior. The ramus inferior of the stapedia artery continues anteriorly in a well-defined groove in the tympanic roof and exits from the tympanic cavity through a notch in the sphenoid. The promontory artery follows the same path as it does in other modern erinaceids, with the palatine branch of nerve VII following a distinct groove in the sphenoid and exiting into the Vidian canal.

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