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A New Insectivore from the Oligocene of Mongolia and a New Subfamily of Hedgehogs[1]

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INTRODUCTION

A jaw of a previously undescribed genus of insectivores was collected in 1925 during the Third Asiatic Expedition to Mongolia, one year after the appearance of Matthew and Granger's (1924) descriptions of *Tupaiodon* and *Palaeoscaptor*. The only locality data recorded were that the jaw was found in the Hsanda Gol Formation near Tsagan Nor, but the dark staining of the jaw suggests the preservation of other fossils found in stratigraphic proximity to the lava flow dated 31.3–32.0 $\times$ 10^6 years (Evernden *et al.*, 1964, p. 193). This specimen appears to be the only one of its kind collected during the American expeditions, and, so far as we know, there are no additional specimens of the genus in the Russian and Polish collections made recently in the Mongolian Oligocene.

Attempts to determine the affinities of the new Mongolian genus led us to the conclusion that the new genus and three closely related genera should be accorded subfamily rank within the Erinaceidae. Meade (1941),

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Butler (1948), and Wilson (1960) were aware of the mutual similarities of two members of the subfamily, but Butler regarded them as specially related to *Neurogymnurus* and Wilson referred only to "the peculiar *Metechinus-Brachyerix* line which is confined to North America" without assigning a formal name. Van Valen (1967, pp. 262, 273) realized that *Brachyerix, Metechinus,* and *Dimylechinus* are closely interrelated and are not specially akin to *Neurogymnurus,* but he grouped the Brachyericinae with *Proterix* and several primitive erinaceines, allocating them all to Butler's tribe Protericini. Additional evidence now available makes a formal name desirable at subfamily rank for *Brachyerix, Metechinus, Dimylechinus,* and *Exallerix* (new genus).

We wish to thank Dr. Theodore Downs of the Los Angeles County Museum for the loan of the type specimen of *Metechinus fergusoni* Henshaw, 1942. Mr. John R. Woodyard of the University of California Department of Electrical Engineering kindly permitted the use of X-ray equipment for the X-ray skiagram of the jaw. The illustrations were made by Mr. Howard Hamman and Dr. F. S. Szalay. Drs. J. S. Mellett and L. Van Valen kindly read the manuscript and made numerous helpful suggestions.

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

ORDER INSECTIVORA ILLIGER, 1811[1]

SUPERFAMILY ERINACEOIDEA FISCHER VON WALDHEIM, 1817

FAMILY ERINACEIDAE FISCHER VON WALDHEIM, 1817

SUBFAMILY BRACHYERICINAE BUTLER, 1948, NEW RANK

Brachyericini BUTLER, 1948, p. 488.

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

INCLUDED GENERA: *Dimylechinus; Exallerix,* new genus; *Brachyerix;* and *Metechinus.*

KNOWN DISTRIBUTION: Middle Oligocene, Asia; late Aquitanian, Europe; Hemingfordian-Clarendonian, North America.

DIAGNOSIS: Short-faced erinaceids with greatly enlarged incisor,[2] I_1; M_3 lacking; P_4 double-rooted but reduced, with single-cusped trigonid in

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[1] Or Bowdich, 1821, and others. The matter is not clear (Van Valen, 1967, pp 269–270).

[2] Butler (1948, 1956) and others believed this tooth to be I_2 in all Erinaceinae, whereas Hürzeler (1944) preferred a noncommittal "A_5" (fifth tooth remaining anterior to M_1). Undescribed specimens of *Tupaiodon* (?including *Ictopidium* Zdansky, 1930) and *Palaeoscaptor* show that the tooth is probably I_1 as in the Echinosoricinae. The evidence will be given elsewhere.

all members except *Dimylechinus;* P^4 complex and with elongate metastylar blade in contrast to dimylids, situated beneath anterior end of orbit; molar trigonids open, elongate, with enhanced prevallid shear; teeth between I_1 and P_4 reduced to three or fewer procumbent, single-rooted teeth; anterior upper premolars reduced in number and size.

EXALLERIX[1] MCKENNA AND HOLTON, NEW GENUS

TYPE: *Exallerix hsandagolensis* McKenna and Holton, new species.

KNOWN DISTRIBUTION: Hsanda Gol Formation, middle Oligocene, Mongolia.

DIAGNOSIS: Dentition reduced. Anterior incisor enlarged. P_4 two-rooted, crown reduced to one main cusp; paraconid and metaconid lost. M_1 largest cheek tooth; paraconid large and elongated as a paralophid; paraconid valley (prefossid of Van Valen, 1966) extremely shallow; metaconid very close to protoconid, and with apex slightly farther forward than apex of protoconid. Jaw deep, with prominent, strong, rugose ridge extending from below P_4 to ventral edge of ramus, ending at anterior end of angular process.

Exallerix hsandagolensis McKenna and Holton, new species

Figures 1, 2

TYPE: A.M.N.H. No. 22083, right mandible lacking ascending ramus, angle, condyle, and part of symphyseal region.

HORIZON AND LOCALITY: Hsanda Gol Formation, middle Oligocene; found near Tsagan Nor, Mongolia.

DIAGNOSIS: Only known species of the genus. In size about 50 per cent larger than *Brachyeryx macrotis*[2] Matthew, 1933 (*in* Matthew and Mook, 1933).

DESCRIPTION

FORMULA: The dentition is reduced. The dental formula possibly is 2 1 2 ?2.

ANTERIOR INCISOR: The first tooth, broken near the tip, is an enlarged, laterally compressed incisor, I_1. On part of the labial side of the enamel toward the anterior of the tooth there is a fine embossed sculpturing formed by small circular knobs. Similar, although coarser, sculpturing

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[1] *Exallos,* Greek, meaning very different; plus *-erix,* Latin, meaning hedgehog, an ending in many erinaceid generic names.

[2] *"Talpa" incerta* Matthew, 1924, is a species of *Brachyerix* and may possibly have priority over *B. macrotis.*

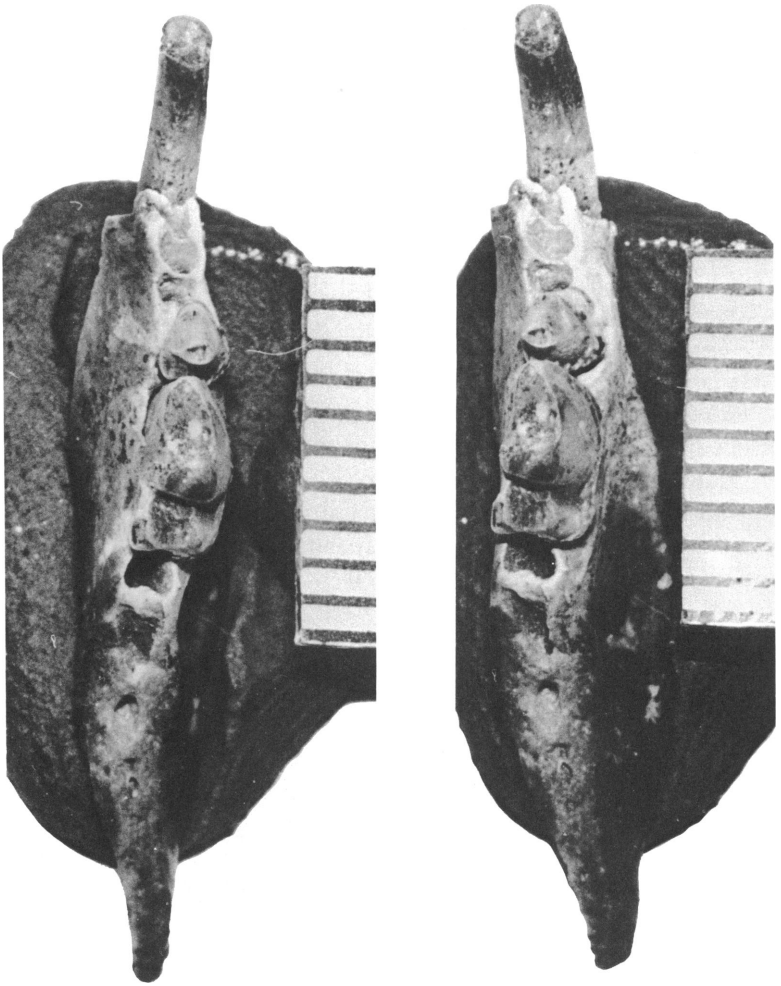

FIG. 1. *Exallerix hsandagolensis* McKenna and Holton, new genus and species. Type, A.M.N.H. No. 22083, fragmentary lower jaw with broken I_1, P_4, M_1 (see fig. 2 for the anterior root of M_2, now lost), from the middle Oligocene, Hsanda Gol Formation, Mongolia. Stereoscopic occlusal view. Scale in millimeters.

occurs along the base of the crown of P_4 and M_1. The bone of the symphysis on the lingual side of the jaw projects posteroventrally as a strong depressor muscle attachment ending below P_4. An X-ray photograph, from which the skiagram of figure 1 was made, shows that the posterior end of the incisor abuts against the anterior root of M_1.

ANTERIOR ALVEOLI: There are three alveoli between the incisor and P_4. They are interpreted as each holding a small, procumbent, single-rooted tooth. The first alveolus has the smallest opening, but it is deep. It presumably held I_2. The second alveolus is the largest, and deepest, descending ventrally almost to the incisor. This may have held the canine, the tiny I_3 having been absent. The third alveolus (for a premolar) has an opening nearly as large as the second, but it is extremely shallow. The wall between this alveolus and that of the anterior root of P_4 appears to be broken, but the alveoli may not have been completely separate.

P_4: P_4 has two roots. The crown is reduced to a single main cusp, the protoconid. A posterior cingulum indented by interdental wear occurs at the base of the crown and continues forward as a narrow lingual cingulum terminating at the anterior base of the crown. The base of the crown is higher in front than at the back of the tooth, and on the lingual side is nearly parallel with the ramus, but labially it dips sharply down, with the lowest part being near the front of the posterior root. Embossed sculpturing fills this V-shaped area, which appears slightly swollen or exoedaenodont. On the rest of the tooth the embossing is in the region where a cingulum occurs in many erinaceids; this is also true on the M_1. Toward the anterior of the labial side the embossing thins to a single row of heavy knobs.

The protoconid of P_4 is worn in two areas and lacks enamel in a third. At its apex the cusp has been worn at the same level and in the same curve as the occlusal wear on the paralophid of M_1, evidently as the result of attrition from the lingual half of the unknown P^4. Labially, a small wear facet near the apex continues forward the plane of prevallid wear of M_1. From its posterior slope, close to but not in contact with the paralophid of M_1, the enamel is absent, though not from wear. The posterior cingulum has been indented by interdental attrition against the base of the trigonid enamel of M_1, but above that point P_4 and M_1 are not in contact. The posterolingual corner of the protoconid thus lacks enamel from apex to root.

M_1: The trigonid is elongate and open as in *Dimylechinus* and *Metechinus,* with a more nearly anteroposterior orientation of the prevallid shear than is usual in erinaceids. The paraconid is worn and is therefore dorsally flattened. This wear extends along the top of the paralophid blade region and along the top of the lingual side of the trigonid where a paraconid valley (prefossid) occurs in most erinaceids. This lingual area is lower than the labial surface, but it has only a suggestion of a groove that might be a remnant of a lingually emerging valley in front of the metaconid. The protoconid and metaconid rise higher than the anterior region and

are rounded, subequal in size, and close together, being separated by a very shallow depression.

The talonid has two main cusps but lacks a hypoconulid. The entoconid is higher and sharper than the hypoconid and is nearly as high as the paraconid. A double row of embossed knobs occurs labially, along the base of the hypoconid enamel where it overhangs the mandible (exoedaenodonty). Posteriorly the knobs decrease in size and form a single row, which arches up to the posterior midline. This would correspond to Butler's posterobuccal ledge in some erinaceids. Besides the wear on the top of the paralophid, a large, triangular-shaped, prevallid shear surface occurs on the labial side of the paralophid, anterior to the protoconid. An additional area of intense breakage or wear curves down from the apex of the metaconid nearly to the base of the anterior half of the entoconid. That this is postmortem damage, possibly the result of rodent gnawing, is suggested by a groove on the mandible continuing the trend of the groove on M_1. Also, occlusion with the M^1 protocone does not appear to have been possible at this point. A very small, faint, postvallid shear surface for occlusion with the M^1 prevallum occurs on the posterior edge of the protoconid. Small areas of wear occur both on the labial and lingual sides of the metaconid. The entoconid is worn on the lingual side from contact with the posterior wall of the unknown M^1 protocone and has a sloping wear facet on its posterior wall. The hypoconid is worn slightly on top, the wear surface slanting posterolingually; a small shear surface occurs on the posterior side.

Posterior Alveoli: Behind M_1 there are several alveoli. The first two are for the roots of M_2. The jaw is broken diagonally through the posterior alveolus of M_2, and below this alveolus the canal leading to the mental foramen is exposed. Several small nutrient canals are also exposed along the posterior part of the broken surface.

At the time that figure 2 was prepared, the anterior root of M_2 was present. It has since been lost (fig. 1) and cannot be described further. From the size of the alveoli for its roots, it can be assumed that M_2 was a smaller tooth than M_1 but still well developed. There is no trace of an M_3. It is possible that an extremely small tooth with a very shallow root might have been present, but conclusive evidence is lacking, and M_3 was almost certainly lost as in *Dimylechinus, Metechinus,* and *Brachyerix.*

Mandible: The most distinguishing characteristic of *Exallerix* is the heavy jaw with massive muscle attachment areas. A rugose ridge starts below the P_4 and passes above the mental foramen down to the ventral edge of the ramus as far as the anterior end of the angular process. A broad concavity, probably formed by the body of the muscle attached to

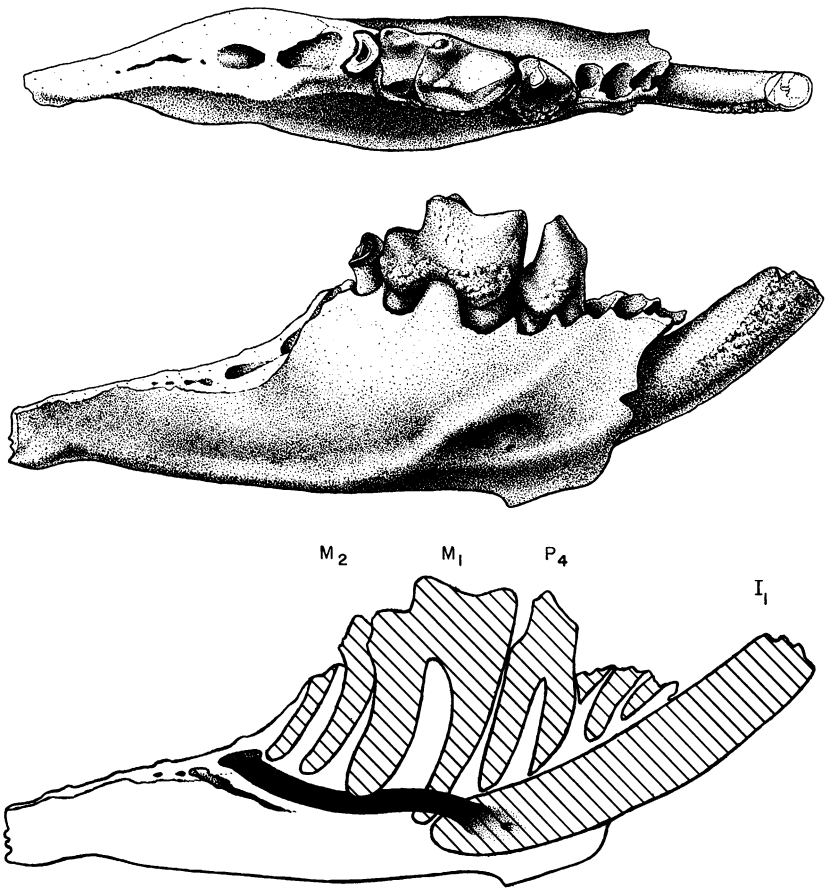

FIG. 2. *Exallerix hsandagolensis* McKenna and Holton, new genus and species. Type, A.M.N.H. No. 22083, fragmentary lower jaw with broken I_1, P_4, M_1, and anterior root of M_2 (now lost), from the middle Oligocene, Hsanda Gol Formation, Mongolia. *Above:* Occlusal view, with rear of jaw foreshortened because of parallax. *Center:* Buccal view. The roots of M_1 were not recognized to be dorsally displaced in their alveoli at the time the illustration was made; the tooth rested at a lower level in life. *Below:* X-ray skiagram, demonstrating extent of alveoli and canal to mental foramen. All approximately ×4.

the ridge, occurs dorsally on the labial side. The most probable muscle to attach to the ridge would seem to be a branch of the masseter muscle, even though the masseter does not appear to attach along the body of the ramus in any other erinaceid. On the ventral edge of the jaw anterior to the mental foramen is a rugose projection which probably was the

attachment of a depressor muscle. The body of the depressor muscle occupied a narrow concavity along the lingual side of the ventral "masseteric" ridge. A small ridge is also present along the ventral border of the mental foramen and meets the larger ridge at the posterior border of the foramen. The mental foramen opens below the anterior root of M_1. In all these mandibular features *Exallerix* is aberrant, differing widely from the more prosaic *Dimylechinus* and *Metechinus*. *Brachyerix* (F.:A.M. No. 74964, late Hemingfordian, Nebraska), however, shows a weak trace of a ridge in exactly the same position occupied by the laterally projecting "masseteric" ridge of the more exotic Mongolian genus.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF THE TYPE SPECIMEN OF *Exallerix hsandagolensis* McKENNA AND HOLTON, NEW GENUS AND SPECIES

I_1, maximum diameter at alveolus	2.4
Approximate combined anteroposterior length of three anterior alveoli between I_1 and P_4	3.0
P_4, anteroposterior diameter at base of crown on labial side	2.5
P_4, transverse width on posterior side	2.0
M_1, maximum anteroposterior diameter of crown	5.0
M_1, maximum transverse width across trigonid	2.6
M_1, maximum transverse width across talonid	2.5
Depth of jaw from anterior edge of M_1 alveolus to ventral edge at depressor muscle attachment, lingual side	7.2
Depth of jaw from edge of posterior alveolus of M_1 to ventral edge of jaw below, lingual side	5.9

AFFINITIES

Previously described insectivores from the Hsanda Gol Formation include *Tupaiodon morrisi, Tupaiodon minutus, Palaeoscaptor acridens,* and *Amphechinus? rectus.* In addition, an undescribed species of *Palaeoscaptor?* is represented by A.M.N.H. No. 22082, and still another undescribed erinaceid is present (A.M.N.H. No. 21647). Additional material of *Palaeoscaptor acridens* (A.M.N.H. No. 22080) has recently been prepared, which demonstrates that, in addition to its double-rooted M_3, *Palaeoscaptor* differs from *Amphechinus* (including *Palaeoerinaceus*[1]) in the number of teeth between I_1 and P_4: *Palaeoscaptor* appears to have five; *Amphechinus,* three. *Amphechinus? rectus* combines a double-rooted M_3 with three teeth between I_1 and P_4.

From deposits in North China of approximately the same age as the

[1] Incorrectly emended by Filhol and by Viret to *Palaerinaceus* and by Hürzeler to *Palerinaceus.*

Hsanda Gol Formation, Teilhard (1926) and Bohlin (1937, 1942) have described several additional *Amphechinus*- and *Palaeoscaptor*-like insectivores. Teilhard's *"Palaeoscaptor acridens"* from Saint-Jacques in Inner Mongolia would appear to be closely similar to *Amphechinus? rectus* by reason of size, double-rooted M_3, and the premolar count. The shape of the jaw may, however, be somewhat different. Bohlin (1937) described but did not name two species from the Shargaltein Valley of western Kansu which he referred with a query to *Palaeoscaptor.* They could represent *Amphechinus* with equal probability, and a similarity to *Amphechinus* (= *Palaeoerinaceus*) was noted by Bohlin. Five years later Bohlin (1942) described some insectivores from another Oligocene locality in Kansu, Taben-Buluk, and referred specimens to *"Palaeoerinaceus* cf. *rectus"* and to two new species, *Palaeoerinaceus kansuensis* and *P. minimus.* Bohlin regarded Matthew and Granger's (1924) genus *Palaeoscaptor* as synonymous with *Palaeoerinaceus,* and in this he was followed by Butler (1948) and Van Valen (1967). Bohlin's Taben-Buluk specimens appear to be referable to *Amphechinus* (= *Palaeorinaceus*) as he concluded, but his conclusion that *Palaeoscaptor* is synonymous with *Amphechinus* cannot now be accepted. *Palaeoscaptor acridens* is a more primitive erinaceine, with additional teeth between P_4 and I_1. It should retain generic rank.

The precise stratigraphic relations of all these Asiatic insectivores are not yet known. They do form a more or less graded morphologic sequence, *Tupaiodon-Palaeoscaptor-Amphechinus-Exallerix,* but that this represents temporal sequence is very unlikely.

Exallerix represents an extinct offshoot from the early Erinaceinae. The jaw and part of the dentition are all that are known of the animal, but enough peculiarities are present on the jaw alone to suggest that *Exallerix,* with *Metechinus, Brachyerix,* and *Dimylechinus,* deserves placement in a separate erinaceid subfamily. Convergent in some features with rodents, dimylids, apatemyids, and soricids, *Exallerix* has enlarged and elongated the lower incisor (I_1), shortened the jaw, reduced the teeth between I_1 and M_1 and behind M_1 in number, size, and complexity, and has apparently developed powerful masseter musculature inserted far forward on the lower jaw. The bite was powerful, slow, and obviously of the "nutcracker type" adapted to feeding on hard-shelled prey. The efficiency of P^4/M_1 shear was increased by opening the M_1 trigonid to produce a more anteroposterior and larger prevallid. The erinaceid subfamily Brachyericinae, comprising European *Dimylechinus,* American *Brachyerix* and *Metechinus,* and Asiatic *Exallerix,* evolved from *Palaeoscaptor*- and *Amphechinus*-like ancestors of the subfamily Erinaceinae.

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