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**Insectivora of the Miocene
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Jens Munthe* and Robert M. West

Department of Geology
Milwaukee Public Museum
Milwaukee, Wisconsin 53233

• Present address: Faculty of Natural Sciences and Mathematics, Stockton State College, Pomona, New Jersey 08240.

Abstract: Twenty-six specimens representing at least six taxa of Insectivora are present in a collection of approximately 1,000 small-mammal fossils from a site near the top of the Chinji Formation of the Neogene Siwalik Group. Two new species of Erinaceidae are described. *Galerix rutlandae* n. sp. most closely resembles *G. exilis*, from the Miocene of France. *Amphelchinus kreuzae* n. sp. shows relationships with several Miocene erinaceines known from Europe and Africa. Three lower premolars are very similar to those of the living *Echinosorex* of Southeast Asia. Also present are rare and fragmentary specimens which we refer to the Soricidae and Talpidae.

INTRODUCTION

Since 1976 a joint Howard University-Geological Survey of Pakistan project has studied fluvial sedimentary rocks of the Neogene Siwalik Group near Daud Khel, on the south bank of the Indus River at the western edge of Pakistan's Potwar Plateau. The stratigraphy of this area, and preliminary lists of the fossil vertebrates recovered from various levels have been published in earlier reports (Munthe *et al.*, 1979; Hussain *et al.*, 1979). The vertebrate assemblage from sites near the local top of the Chinji Formation as exposed northeast of Daud Khel has been designated the Daud Khel local fauna (Hussain *et al.*, 1977). A new species of the artiodactyl *Dorcatherium* from this fauna was described by West (1980), and analysis of some of the rodent material has been completed by Munthe (1980). This paper describes the Insectivora of the Daud Khel local fauna. The cricetid and murid rodents, the lower

vertebrates, and the biostratigraphic, biogeographic and paleoecologic implications of the Daud Khel local fauna are currently under study.

Only two Siwalik insectivore specimens have been described to date. A Pleistocene soricid from the Upper Siwaliks of northern India was recently described by Gupta and Badam (1977), and a fragmentary lower molar from Miocene Middle Siwaliks of northern India was designated the holotype of a new genus and species (*Siwalikosorex prasadi*) by Sahni and Khare (1976). We are uncertain as to the family assignment of this enigmatic specimen; it may represent an erinaceid. Excepting these two specimens, Siwalik fossil insectivores have been reported only in preliminary faunal lists. We reported soricids and erinaceids from Daud Khel (Hussain *et al.*, 1977, 1979), and Jacobs noted the presence of these families at several stratigraphic levels within the Siwaliks of the southern Potwar Plateau (in Pilbeam *et al.*, 1979).

There are few published records of fossil insectivores from southern Asia. Engesser listed soricids, *Desmanella* and other talpids, the echinosoricine *Galerix*, and erinaceines in Mio-Pliocene faunas of Turkey (Sickenberg *et al.*, 1975; Andrews and Tobien, 1977), but these have not yet been described. Similarly, the presence of soricids in Miocene faunas of eastern Afghanistan has been noted (Heintz *et al.*, 1978), but no specimens have yet been described or illustrated. The material described here comprises virtually the entire Neogene insectivore record from South Asia.

Most of the insectivore material recovered from Daud Khel is referable to the Erinaceidae (19 of 26 specimens). Both the hairy hedgehogs (Echinosoricinae), presently restricted to Southeast Asia and China, and the spiny or "true" hedgehogs (Erinaceinae), which are today more widely distributed in the Old World, are represented at Daud Khel. The remaining specimens are not determinable below the family level and would not be worthy of publication were they not most of the present South Asian fossil record of the Soricidae and Talpidae.

All fossils described below were recovered from Howard University-Geological Survey of Pakistan locality 18 at 32°55'45"N and 71°39'20"E, Mianwali District, Pakistan. Munthe *et al.* (1979) and Munthe (1980) discuss the stratigraphic and general geologic setting of this late Miocene site. The specimens are the property of the Government of Pakistan and are permanently housed in the National Museum of Natural History, Islamabad. Epoxy casts of type and figured specimens are at the Milwaukee Public Museum.

Acronyms used herein are: H-GSP = Howard University-Geological Survey of Pakistan, MPM = Milwaukee Public Museum, and FMNH = Field Museum of Natural History, Chicago.

SYSTEMATIC PALEONTOLOGY

Family Erinaceidae Bonaparte, 1838

Subfamily Echinisoricinae Cabrera, 1925

Genus *Galerix* Pomel, 1848*Galerix rutlandae* new species

(Figure 1, Table 1)

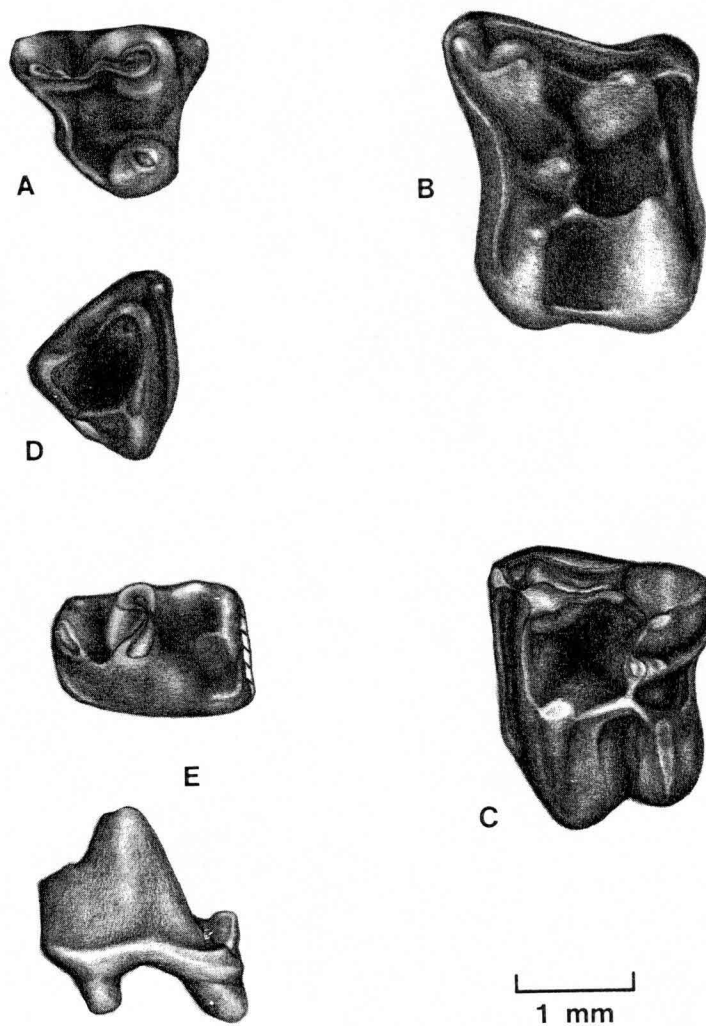


Figure 1. Teeth of *Galerix rutlandae* n. sp. A—Right P³, H-GSP 2368. B—Right M¹, H-GSP 2371, holotype. C—Left M², H-GSP 2372. D—Right M³, H-GSP 2373. E—Left P⁴, H-GSP 2374, occlusal and labial views.

Holotype: H-GSP 2371, right M¹, from H-GSP locality 18, upper Chinji Formation, late Miocene.

Paratypes: H-GSP 2368-2370, P³; 2372, M²; 2373, M³; 2374, P⁴; 2375, M³.

Etymology: Named in honor of Mrs. Nancy Rutland, Milwaukee Public Museum volunteer, who recovered many of the insectivore specimens from the Daud Khel concentrate.

Diagnosis: Smallest known species of *Galerix*; P³ lacking hypocone; M¹ and M² lacking distinct protoconule; upper teeth not greatly expanded transversely.

Description: Three P³s of *Galerix rutlandae* were recovered from locality 18 (Fig. 1A). They have three distinct and well-separated roots and a high and sharply conical paracone. A narrow crest extends posteriorly from the paracone to a less-distinct cusp, probably the metacone, at the posterolabial border. Although sharp, this crest did not function primarily in shearing; wear is confined to its ventral surface in all three specimens. On the lingual part of P³ is a well-developed protocone and a slight cingular swelling in the position of the hypocone. All three specimens have distinct posterolingual cingula, best-developed in H-GSP 2369.

No P⁴s referable to *G. rutlandae* have been recovered, but all three upper molars are represented in the Daud Khel collection. As is common in hedgehogs, the M¹ and M² (Fig. 1B, C) are very similar. The paracone and metacone are almost equal in size in M¹ and M², with the protocone being the largest cusp. Both teeth have prominent metaconules and very slight swellings along the paracone-protocone crest in the position of the protoconule. There are small and equally developed parastyles and metastyles on both M¹ and M². Sharp crests connect all the cusps, including a short ridge extending from the hypocone to the midpoint of the arcuate protocone-metaconule crest. The relatively great development of these crests around the protocone and metaconule gives these cusps a crescentic, nearly triangular appearance, whereas the other cusps are more conical. The cingula are more prominent on M¹; it lacks cingula only on the lingual faces of the protocone and hypocone, whereas M² completely lacks lingual cingula. The M¹ is larger than M² (Table 1); M¹ has the extreme posterior positioning of the metastyle and M² the posterior narrowing typical of echinosoricine upper molars. The root patterns of all the *G. rutlandae* upper molars are the same as those described for *Galerix* by Butler (1949, Figs. 12, 13).

The single *Galerix rutlandae* M³ (Fig. 1D) has equally developed paracone, metacone and protocone. There is no trace of a metaconule. These cusps are positioned in a nearly equilateral triangle and joined by low ridges. Only the paracone-protocone crest is nearly as high as the

cusps and shows significant wear. A prominent anterior cingulum extends from the small and otherwise isolated parastyle almost to the lingual margin of the tooth. There is a weak posterolingual cingulum behind the protocone, but no true hypocone.

A single moderately worn P_4 (Fig. 1E) is the only complete *G. rutlandae* lower tooth yet recovered. It has the well-developed trigonid and short talonid shelf typical of P_4 in other species of *Galerix*. The apex of the large protoconid is at the center of the tooth, flanked by a narrow, low paraconid and a large, conical metaconid. No distinct cusps are developed along the posterior margin of the tooth, which is somewhat damaged due to post-mortem abrasion, but an indistinct ridge extends toward the protoconid from the center of the posterior surface. Most of the P_4 occlusal wear is on the apices of the trigonid cusps, but there is also a faint wear facet on the labial surface of the paraconid-protoconid crest. Therefore, some shearing by the lingual surface of the P^3 blade over P_4 has taken place, although this wear does not appear on any of the *G. rutlandae* P^3 s.

A *Galerix rutlandae* M_3 trigonid, H-GSP 2375, shows heavy wear. The protoconid is positioned labial of the metaconid in this specimen, such that the metaconid-protoconid ridge is transversely straight while the paraconid-protoconid ridge is arcuate. There is a very faint antero-labial cingulum along the base of the latter ridge.

Discussion: The well-developed P^3 , the great width of M^1 , the very distinctive triangular M^3 lacking metaconule and hypocone, and the large P_4 with prominent metaconid are all diagnostic of *Galerix* alone among the Echinisoricinae. The protoconule is poorly developed in the M^1 and M^2 from Daud Khel, and while it is true that this cusp is frequently distinct in *Galerix*, this character is not stable enough to permit its use in separating *Galerix* from the other echinosoricines as suggested by Friant (1961).

The previously described Miocene European and African species of *Galerix* are very similar in size and are separated only on details of occlusal morphology. Of these occlusal features, perhaps the most significant is the presence of a well-developed hypocone on P^3 in some species (e.g., *G. socialis*, *G. moedlingensis*, *G. atticus*) while this cusp is lacking in others (e.g., *G. exilis*). The proportionately great width of the upper teeth in *Galerix moedlingensis* and *G. atticus* is also significantly different from the condition in other species, but the diagnostic characters separating some species, such as *G. sudrae* from *G. exilis* or *G. atticus* from *G. moedlingensis*, seem rather tenuous.

Opinions differ concerning the relationships among *Galerix* species and the proper nomenclature which should be used. Rümke (1976)

notes that some consider *Galerix exilis* to be a junior synonym of *G. socialis*, although the rather different P³s of these species makes this unlikely. Baudelot (1972) restricts *Galerix* to *G. africanus* and *G. sudreae* while placing the best-known species of the genus, *G. exilis*, in *Pseudogalerix* along with *P. stehlini* on the basis of priority. Engesser (1972) also considers *Pseudogalerix stehlini* very close to *Galerix exilis*, but uses the name *Galerix* for both. Because of the extensive use of the name *Galerix exilis* in the paleontologic literature, we follow Engesser here in regarding *G. exilis* as the proper name for this species.

In most respects, *Galerix rutlandae* resembles *G. exilis* most closely. The morphology of P³, the shapes of the upper molars, and the morphology of P⁴ are all virtually identical in these species. The low P⁴ paraconid illustrated by Engesser (1972, Fig. 4) for *G. exilis* is unlike that of *G. rutlandae*, but other *G. exilis* P⁴s which have been illustrated are identical to the *G. rutlandae* P⁴ (e.g., Baudelot, 1972, Pl. 9, Fig. 6; Bachmeyer and Wilson, 1970, Fig. 16). *Galerix rutlandae* differs from *G. exilis* primarily in its smaller size and lack of distinct protoconules on M¹ and M². The closest size comparison between *G. rutlandae* and previously described *Galerix* specimens is with P⁴ of *G. moedlingensis* and *G. atticus* (Rümke, 1976), but the upper teeth of these species are much wider than those of *G. rutlandae*.

The discovery of *Galerix* in the Siwaliks is not entirely unexpected. This genus is rather commonly recovered from Miocene deposits of Europe and Africa, and *Galerix* cf. *G. moedlingensis* has been reported from the Miocene of Turkey by Engesser (in Sickenberg *et al.*, 1975). *Galerix rutlandae* is of particular interest, however, as the easternmost record of the genus, especially since living echinosoricines are entirely restricted to eastern Asia.

cf. *Echinosorex* sp.
(Figure 2, Table 1)

A P₂, H-GSP 2376, and two P₃s, H-GSP 2377 and 2378, in the Daud Khel collection are very similar to these teeth in the living species of *Echinosorex*. The single-rooted P₂ (Fig. 2A) has small but distinct cusps positioned anterolingual and posterior to the conical central cusp. The central cusp is well-worn and the anterolingual cusp slightly worn. The P₃s (Fig. 2B) are much larger than the P₂. There is no cusp anterior to the large central cusp, but the posterior margin of the tooth is wide and there is a prominent posterolingual cusp. This is better-developed on H-GSP 2377 than on 2378. No cingula are present on either P₂ or P₃, except that which extends along the posterior margin of P₃ from the posterolingual cusp.

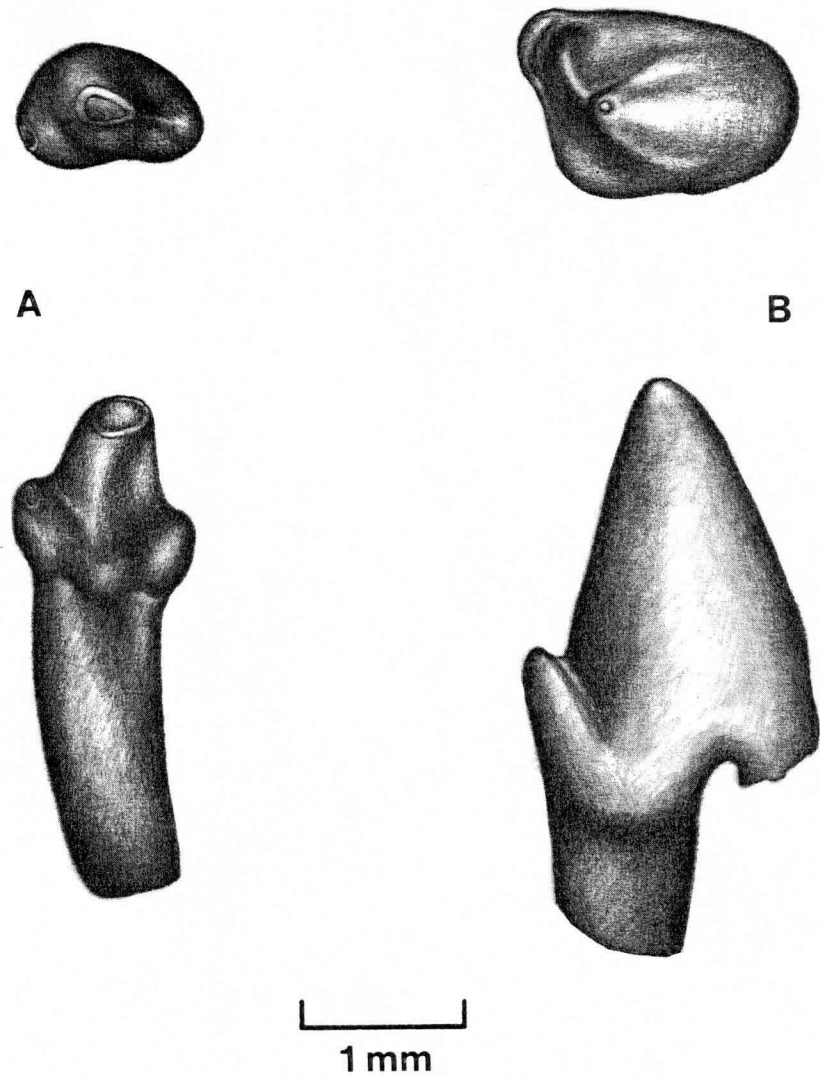


Figure 2. Teeth of cf. *Echinorex*. A—Right P₂, H-GSP 2376, occlusal and lingual views. B—Right P₃, H-GSP 2377, occlusal and labial views.

These teeth do not resemble any of the anterior teeth of known Miocene insectivores or small carnivores. They are, however, nearly identical with the P₂ and P₃ of living *Echinorex birmanicus* (e.g., FMNH 82614, mature male, from Burma). The Daud Khel teeth are only half the size of the *E. birmanicus* teeth, but their sizes relative to one another are the same as in *E. birmanicus* and they are markedly similar

in occlusal morphology. The only significant difference is the somewhat better development of the accessory cusps in the Daud Khel premolars.

Echinosorex (= *Gymnura* of early authors), the largest of the living hairy hedgehogs, is not known from Neogene fossils. It is considered to be rather distantly related to the other echinosoricines, in part because of its well-developed antemolar dentition. Phylogenetic hypotheses frequently suggest an independent derivation of *Echinosorex* extending back to the Miocene or Oligocene (Viret, 1938; Bulter, 1949). Neither *Lanthanotherium*, with its premolar reduction, nor *Galerix* appear to be likely ancestors for *Echinosorex*. The P₂ and P₃ from Daud Khel may represent an animal which would be a logical structural ancestor, but the materials are at present too fragmentary to draw such a conclusion.

Subfamily Erinaceinae Gill, 1872
Genus *Amphechinus* Aymard, 1849
***Amphechinus kreuzae* new species**
(Figure 3, Table 1)

Holotype: H-GSP 2380, left M¹, from H-GSP locality 18, upper Chinji Formation, Miocene.

Paratypes: H-GSP 2379, P³; 2381, I₂; 2382, M₃.

Etymology: Named in honor of Mrs. May Kreuz, Milwaukee Public Museum volunteer, who recovered many of the insectivore specimens from the Daud Khel concentrate.

Diagnosis: M¹ with isolated metaconule and hypocone; I₂ curved and morphologically complex; M₃ lacking talonid; cingula well-developed on cheek teeth.

Description: The P³ (Fig. 3A) is broken anterolabially, but would have been triangular in shape with the high, conical paracone near the center of the occlusal surface. There is a distinct protocone at the lingual apex, but its height is much reduced by wear. The ridge joining the paracone and the posterolabial margin is also heavily worn. Cingula are well-developed on the labial and posterolingual borders of the tooth, and an anterolingual cingulum is interrupted by breakage immediately anterior to the paracone.

The holotype M¹ (Fig. 3B) is almost square. The tooth has strong cingula extending almost entirely around the occlusal surface, interrupted only along the lingual faces of the protocone and hypocone. The metacone, protocone and hypocone are crescentic in shape at this wear stage, while the paracone and metaconule are conical. The metastyle is prominent and well-separated from the metacone. Both the metaconule and hypocone are isolated from the remaining cusps, as ridges connect-

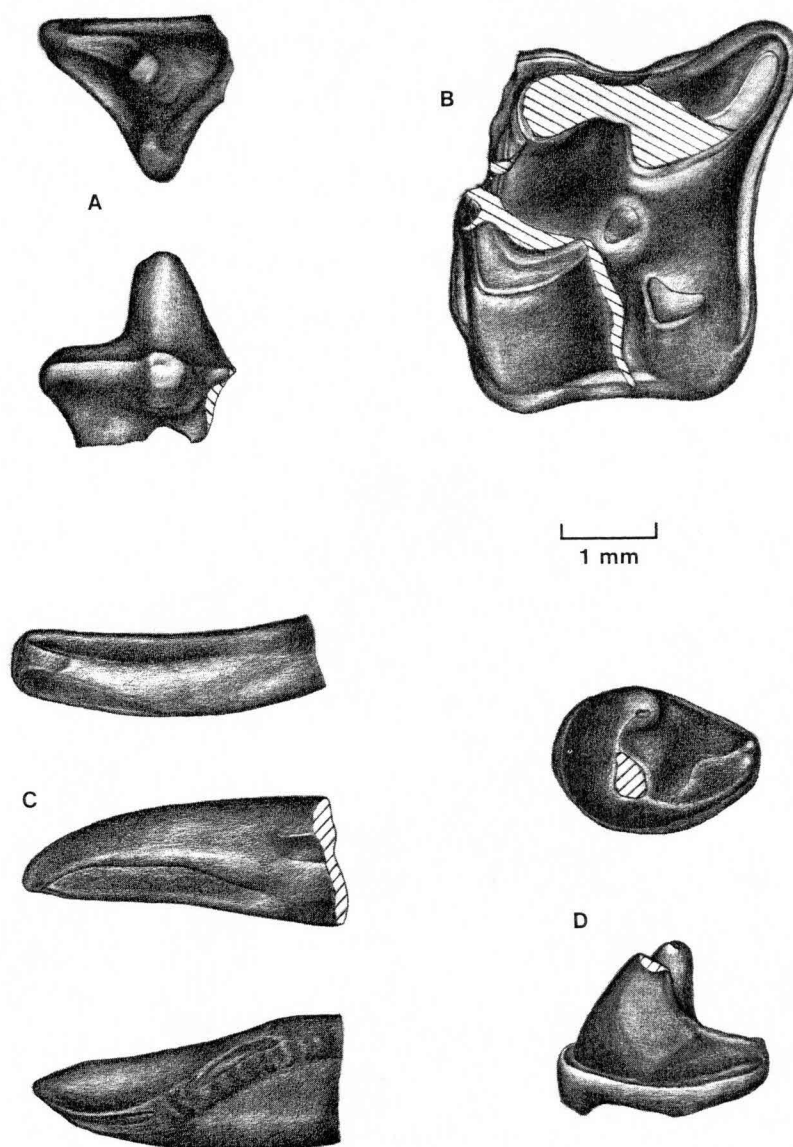


Figure 3. Teeth of *Amphechinus kreuzae* n. sp. A—Right P³, H-GSP 2379, occlusal and lingual views. B—Left M¹, H-GSP 2380, holotype. C—Right I₂, H-GSP 2381, dorsal, labial and lingual views. D—Right M₃, H-GSP 2382, occlusal and labial views.

ing the cusps are poorly developed. The parastyle is unknown; this part of the tooth is missing due to breakage in the *A. kreuzae* holotype.

The anterior part of a lightly worn right I_2 (Fig. 3C) is referred to *Amphechinus kreuzae*. The tooth is transversely curved and approximately oval in cross-section at the point where it is broken. There is a prominent interdental wear facet on the lingual surface, resulting from wear against the left I_2 . Striations on this wear surface suggest a scissor-like motion of the lower incisors. The dorsal surface is unusual for *Amphechinus* in having grooves both lingual and labial to a central ridge. The labial groove is particularly deep and long. The small and shallow wear facet at the anterior tip of the incisor suggests that wear against I^2 was only beginning; this I_2 probably represents a young individual.

The *A. kreuzae* M_3 (Fig. 3D) has a well-developed trigonid, but no trace of a talonid. The protoconid is broken, but it was approximately the same height as the metaconid and both are conical cusps. A well-worn, arcuate crest extends from the protoconid to the low paraconid. The tooth is entirely surrounded by a prominent cingulum.

Discussion: The erinaceine teeth from Daud Khel clearly seem to represent *Amphechinus*. The closely related *Gymnurechinus*, known only from the Miocene of Africa (Butler, 1956, 1969), is difficult to compare with the Daud Khel material as some of the characters separating it from *Amphechinus* can not be determined on the Daud Khel specimens. The Daud Khel I_2 is rather small for *Amphechinus*, and this tooth is supposed to be relatively small in *Gymnurechinus* also, but the root is missing in the Daud Khel specimen and the crown is missing in the African specimens so they can not be adequately compared. *Gymnurechinus* M_3 generally has at least a rudimentary talonid. The living erinaceines are mostly larger than the Daud Khel animal, and their P^3 s are much more reduced.

There are many nominal species of *Amphechinus*, ranging from early Oligocene to middle Miocene in age. Some species are larger or smaller than *A. kreuzae*, but at least *A. horncloudi* (Rich and Rasmussen, 1973) and *A. edwardsi* (see Viret, 1938) are in the size range of *A. kreuzae*. The Daud Khel erinaceine resembles these species, and others described by Baudelot (1972) and Gibert (1975) in certain respects, but is not similar enough to warrant assignment to any previously described species. *Amphechinus edwardsi* lacks a distinct metaconule and has a crest joining the hypocone to the metacone-protocone crest on M^1 . This is also true of *A. horncloudi*, which has a less triangular P^3 than *A. kreuzae*. *Amphechinus rusingensis* most closely resembles *A. kreuzae* in the morphology of M^1 . The M^1 cusps, particularly the hypocone, are almost as isolated as in *A. kreuzae*, but *A. rusingensis* was a significantly smaller animal. No previously described *Amphechinus* species shows

the same combination of isolated metaconule and hypocone on M^1 , complex I_2 , and very strong cingula on the cheek teeth which is present in *A. kreuzae*.

Although *Amphelichinus kreuzae* appears to be closely related to other African and European Miocene species of the genus, its unusual I_2 may indicate a specialization which sets *A. kreuzae* apart as a distinctive South Asian variant. The unusual anterior wear, the morphological complexity of the dorsal surface, and the evident mobility of the lower incisors relative to one another suggest a functional specialization different from anything seen elsewhere in the Erinaceinae.

Amphelichinus is rather well-known from the Oligocene of central Asia (Matthew and Granger, 1924; Bohlin, 1942; Sulimski, 1970). However, the fragmentary nature of the Daud Khel material makes comparison with Oligocene species referred to *Amphelichinus* difficult. Although it is reasonable to conclude that *A. kreuzae* is descended from Asian Oligocene species, it is impossible to trace this lineage at present.

Family Soricidae Gray, 1821

Soricidae indet.

(Figure 4, Table 1)

Two specimens, H-GSP 2383 and 2384, represent shrews. Both consist of M_2 - M_3 , and in size and occlusal morphology they appear to be referable to a single species. Neither is pigmented. H-GSP 2383, right M_2 - M_3 (Fig. 4), is the least worn.

The trigonid and talonid of M_2 are equally developed. The protoconid is very high and sharp and the entoconid is isolated. The M_3 trigonid is well-developed, but the talonid consists of only a single conical cusp. The lingual cingula are prominent on both M_2 and M_3 , and are expanded into wide shelves on the anterolabial side of the trigonid.

Unfortunately, M_2 and M_3 are not particularly distinctive teeth in the shrew dentition and no other soricid teeth have been recovered from Daud Khel. We are not able to determine the subfamily or genus assignment of the Daud Khel soricid. In fact, none of the Siwalik material previously identified as soricid is, in our opinion, determinable below the family level. This is true of specimens identified as *Siwalikosorex* n. gen. by Sahni and Khare (1976) and *Sorex* by Gupta and Badam (1977). Analysis of the relationships of Siwalik soricids must await the recovery of better material.

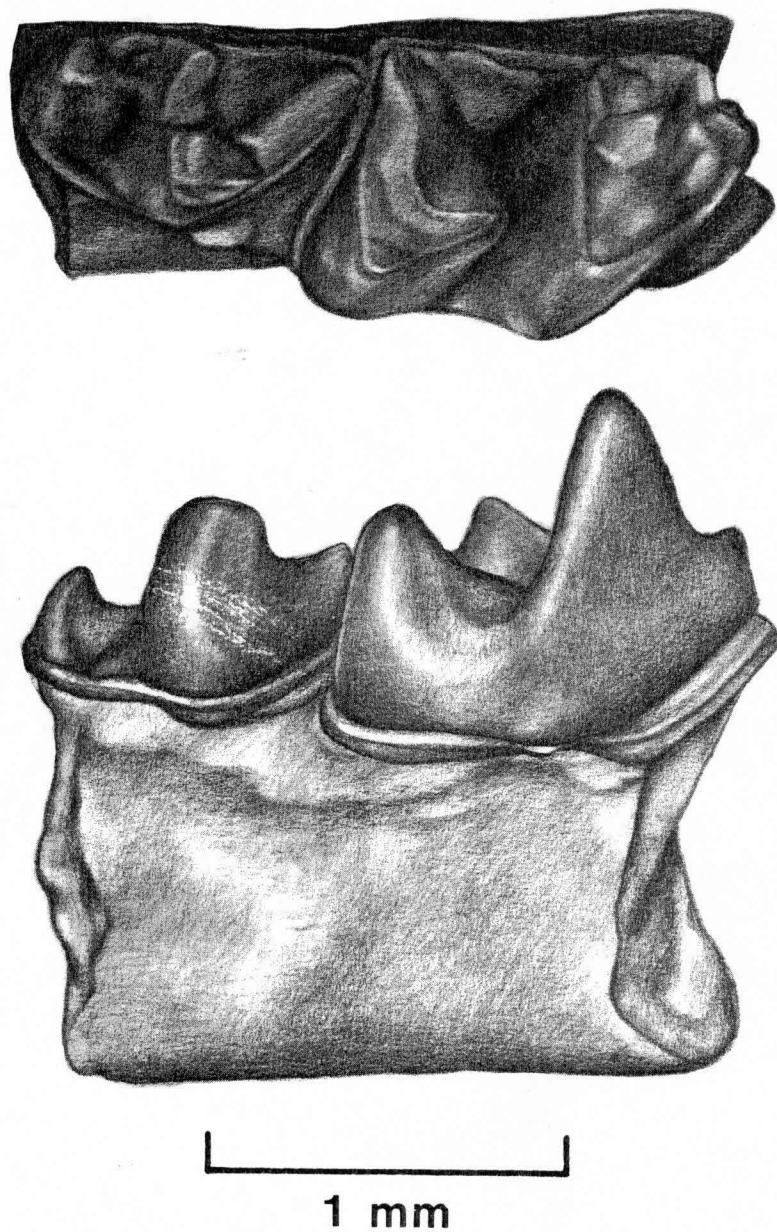


Figure 4. Mandible fragment with M₂-M₃ of Soricidae indet., H-GSP 2383, occlusal and labial views.

Family Talpidae Gray, 1825
Talpidae indet.
(Figure 5)

A single upper molar fragment, H-GSP 2385 (Fig. 5) is the only talpid specimen yet recovered from Daud Khel. This fragment is the paracone and parastyle of a talpid right M², but assignment of this specimen below the family level is not possible. H-GSP 2385 is the first record of the Talpidae from the Neogene of South Asia.

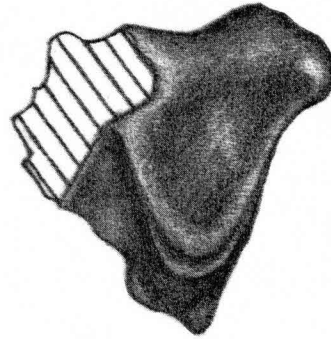


Figure 5. Paracone and parastyle of right M² of Talpidae indet., H-GSP 2385.

Table 1. Measurements of insectivore teeth from the Daud Khel local fauna (in millimeters).

H-GSP Number	Tooth	Length	Width
<i>Galerix rutlandae</i>			
2368	P ³	1.68	1.40
2369	P ³	1.72	1.28
2370	P ³	1.68	— —
2371 (holotype)	M ¹	2.20	2.68
2372	M ²	1.96	2.36
2373	M ³	1.40	1.28
2374	P ₄	1.68	1.24
2375	M ₃	— —	1.32
cf. <i>Echinosorex</i>			
2376	P ₂	1.04	.72
2377	P ₃	1.64	1.08
2378	P ₃	1.60	1.00
<i>Amphechinus kreuzae</i>			
2379	P ³	2.40 est.	1.72
2380 (holotype)	M ¹	3.80 est.	3.88
2381	I ₂	— —	.92
2382	M ₃	2.16	1.48
Soricidae indet.			
2383	M ₂	1.24	.76
2383	M ₃	.92	.52
2384	M ₂	1.08	.68
2384	M ₃	.92	.48

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Much of the matrix from H-GSP locality 18 was concentrated by Mr. J. J. M. Leinders (Instituut voor Aardwetenschappen, Utrecht) and the specimens described here were recovered from the concentrate by Mrs. Nancy Rutland and Mrs. May Kreuz (Milwaukee Public Museum). The figures were drawn by Ms. Susan D. Speerbrecher (Milwaukee Public Museum). Ms. Barbara Becher (Field Museum of Natural History, Chicago) made Recent insectivore comparative material available for study.

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