



Fossil lagomorphs from the Potwar Plateau, northern Pakistan

Alisa J. Winkler, Lawrence J. Flynn, and Yukimitsu Tomida

ABSTRACT

Siwalik Group sediments on the Potwar Plateau have yielded approximately 20 cranial and postcranial remains of leporids from nine localities. The oldest dental remains (late Miocene, 7.4-6.5 Ma) are from the Hasnot area, Dhok Pathan Formation. These specimens are assigned to *Alilepus elongatus*, sp. nov. *Alilepus elongatus* is diagnosed in part by a p3 with the anterior end elongated, posteroexternal and postero-internal reentrants each extending approximately halfway across the tooth, thick enamel on posterior border of trigonid smooth to heavily crenulated in postero-internal reentrant, and thin enamel on anterior border of talonid lightly to heavily crenulated. The p4 to m2s may have an anteroexternal reentrant and crenulations on the anterior end of the talonid. Three teeth dating to the Pliocene (ca. 3.5 Ma) are assignable only to Leporidae. The youngest specimen from the Potwar Plateau is a single incomplete m1 or m2 from the Pabbi Hills, Soan Formation (early Pleistocene, ca. 1.7 Ma). Its incompleteness could allow referral to *Pliopentalagus* sp., *Pliosiwalagus* sp. or *Caprolagus* sp. All postcranial remains from the Potwar Plateau date from the late Miocene. They are not identified specifically, but are likely referable to *A. elongatus*. The paucity of lagomorphs recovered from the Siwalik Group, northern Pakistan, may reflect a predator bias, as thousands of other small mammals have been collected.

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INTRODUCTION

Over ten thousand fossil small mammal specimens represent the diverse Neogene-age microfaunas of northern Pakistan. The most productive

area yielding by far the majority of the fossils is the Potwar Plateau, a >20,000 km² region southwest of Islamabad, with a thick sequence of sedimentary deposits known as the Siwalik Group. The Siwaliks span early Miocene to early Pleistocene time (>18-

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<2 Ma), with rich, superposed fossil faunas throughout. In spite of an impressive set of fossil assemblages amassed over the course of 25 years, representation by fossil Lagomorpha (rabbits, hares, and pikas) remains poor. Throughout much of the sequence, lagomorphs appear to be absent, and where they occur, they are apparently rare. Flynn et al. (1997) recovered a single isolated molar of an ochotonid (pika) from the base of the Siwalik Group. Similarly, Wessels (2009) found limited evidence of an ochotonid in the Murree Formation at Sehwan, Sind Province.

Leporidae (rabbits and hares) have been known from the Indian Subcontinent for many years, but only from the Pliocene and younger deposits of northern India (Forsyth Major 1899; Patnaik 2001, 2002). As the record of leporids emerged in Pakistan, it was noted at the family level in a series of reports, for example, by Barry et al. (2002), who cited the family as ranging back to the late Miocene. We report here in greater detail the leporids from the Potwar Plateau, northern Pakistan, represented by approximately 20 cranial and postcranial specimens from nine localities, dating from the late Miocene to earliest Pleistocene.

Geologic Context

The most continuous and well-exposed Siwalik series is found in northern Pakistan and best researched in the Potwar Plateau. The Siwaliks are fluvial deposits, thick clastic wedges derived from the uplift of the ranges adjacent to the Tibetan Plateau during the Neogene. On the Potwar Plateau, the Siwaliks are found in a folded belt extending from the Salt Range in the south to the Margala Hills in the north, and from the Jhelum River in the east to the Indus River in the west. Siwalik deposits are significant because they are highly fossiliferous and represent relatively continuous and complete sedimentation. The thick sequence is divided into formations recognized on the basis of dominant lithology. At the base is the Kamli Formation that yielded the pika. The superposed Chinji Formation, including bright red mudstones and buff to bluish channel sands, has produced thousands of small mammals, but no lagomorphs. The subsequent Nagri Formation sandstones, dominantly bluish, also lack lagomorphs. It is the upper levels of the overlying Dhok Pathan Formation, mudstones related to mainly buff-colored channel sands, that produced the most and the oldest Leporidae. Thereafter, younger deposits (Soan Formation) have produced only one leporid tooth. These strata

have been dated using paleomagnetic techniques (see below).

The Potwar Plateau lagomorphs are from localities Y457, Y921, Y456, Y581, Y908, Y975, DP13, DP8, and DP24. The geologically oldest Siwalik leporids (ca. 7.4 Ma; Y457 and Y921) show the group to have entered the Siwalik record late in the Miocene. Barry et al. (2002) evaluated the density of fossil samples to estimate that the actual faunal introduction could have been as old as 7.8 Ma. All localities but DP8 and DP24 are near the village Hasnot. DP8 is younger, about 3.5 Ma, and from about 5 km north of Hasnot. The youngest locality that has produced lagomorphs in Pakistan is DP24 (ca. 1.7 Ma), which is in the Pabbi Hills to the east.

Barry et al. (2002) presented the Dhok Saira paleomagnetic log, the tool for dating deposits in the Hasnot area (Figure 1). This section near Hasnot correlates to chrons C4n.2n through C3An.2n of the geomagnetic polarity time scale. Interpolation assigns ages for localities resolvable at the scale of 10^5 years. Useful dates are thereby assigned to localities Y457, Y921, Y456, Y581, Y908, and DP13. Previous work assigned approximate ages for DP8 (late Gauss Chron, Opdyke et al. 1979) and for DP24 (overlying the Olduvai event, Keller et al. 1977). Y975 can be projected to about chron C3Bn in the Kotal Kund paleomagnetic section of Opdyke et al. (1979).

Based on these interpretations, Leporidae are present in the Potwar Plateau at sites dating from the late Miocene to early Pleistocene. From oldest to youngest, most of the specimens are late Miocene in age (between 7.4 and 6.5 Ma). Three teeth from DP8 are Pliocene in age (ca. 3.5 Ma), and one specimen from DP24 is early Pleistocene (ca. 1.7 Ma).

MATERIALS AND METHODS

Specimens described here were collected over the course of field campaigns from the years 1975 to early 1997. Most were found as a consequence of an intensive effort to document the microfauna from the Siwaliks that included screening large quantities of fossiliferous sediment to retrieve teeth and other fossils of small mammals. In the process, bulk samples of sediment yielding small bones were passed through screens to sort out fossil remains. This process sometimes yielded lagomorph teeth and bones. However, lagomorphs, being large (among small mammals), also were recovered by careful prospecting of fossil localities. Searches conducted on hands and

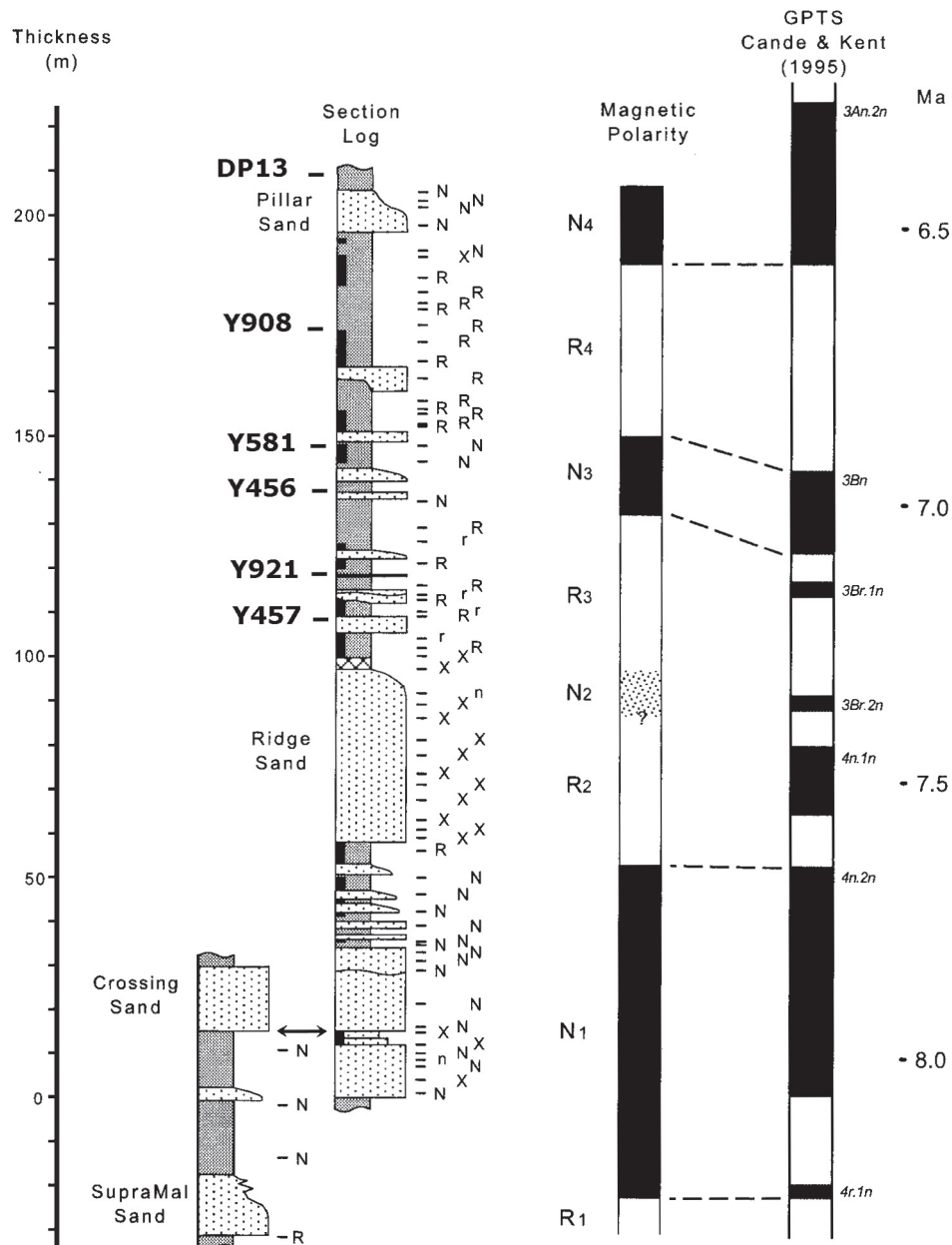


FIGURE 1. Dhok Saira paleomagnetic log (with leporid localities) based on a stratigraphic section southeast of Padhri, northern Pakistan. This log, which correlates to chrons C4n.2n through C3An.2n, is the basis for dating the deposits in the Hasnot area (after Barry et al. 2002; magnetostratigraphic time scale of Gradstein et al. 2004).

knees produced as many leporids as did screening. Nowhere were lagomorphs abundant. Some localities produced several fossils, but as will be seen below, separate elements quite conceivably represented single individuals in life. Thus, it appears that leporids truly are rarely encountered in Siwalik fossil localities.

Leporid tooth terminology for p3 (the most diagnostic tooth position recovered from the Siwa-

liks; no P2s, another diagnostic tooth position, were recovered) is illustrated in Figure 2. Measurements of the teeth were made using a reticule in a Wild M5 stereomicroscope. For measurement, teeth were held so that the occlusal surface was perpendicular to the table supporting the microscope. Illustrations of the occlusal surface of each tooth were made with the tooth in the same orientation used for measurement. Pencil drawings

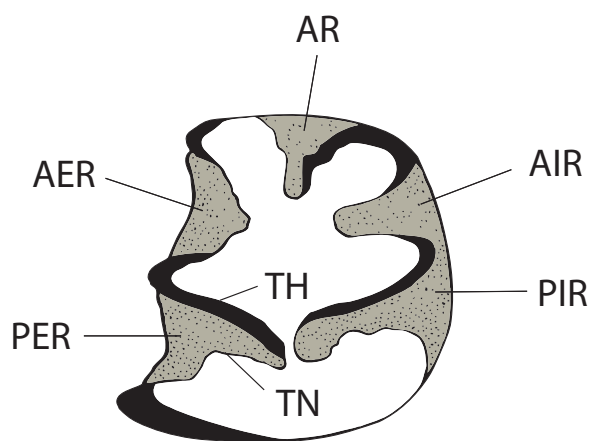


FIGURE 2. Tooth terminology for leporid p3s. **AER**, anteroexternal reentrant (= protoflexid); **AIR**, anterointernal reentrant (= paraflexid); **AR**, anterior reentrant (= anteroflexid); **PER**, posteroexternal reentrant (= hypoflexid); **PIR**, posterointernal reentrant (= mesoflexid); **TH**, thick enamel on posterior border of trigonid; **TN**, thin enamel on anterior border of talonid. Tooth terminology is modified from White (1991).

were made by YT using a camera lucida. Final illustrations were made by tracing these pencil drawings using Adobe Illustrator CS2.

Institutional Abbreviations. **BMNH**, Natural History Museum, London, England. **DP**, Dartmouth-Peshawar, localities and fossils found during a collaborative program between universities at Dartmouth and Peshawar, Lamont Geological Observatory, and the University of Arizona. **GSP**, Geological Survey of Pakistan, the repository for the material reported here. Casts will be made available at Southern Methodist University, National Science Museum, Tokyo, and Harvard University. **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China. **IMNH**, Idaho Museum of Natural History, Idaho State University, Pocatello, Idaho; **Y**, Yale, a prefix in the system of locality designations developed in the 1970s at Yale University.

Anatomical Abbreviations. p3, **AER**, anteroexternal reentrant (= protoflexid); **AIR**, anterointernal reentrant (= paraflexid); **AR**, anterior reentrant (= anteroflexid); **PER**, posteroexternal reentrant (= hypoflexid); **PIR**, posterointernal reentrant (= mesoflexid); **TH**, thick enamel on posterior border of trigonid; **TN**, thin enamel on anterior border of talonid. Tooth terminology is modified from White (1991).

SYSTEMATIC PALEONTOLOGY

Order LAGOMORPHA

Family LEPORIDAE

Subfamily LEPORINAE

Alilepus Dice, 1931

Alilepus elongatus, sp. nov.

Figures 3, 4; Table 1

Holotype. GSP 50951, right p3 from locality Y921, upper part of the Dhok Pathan Formation.

Referred Material. GSP 50953, left P3 or P4; GSP 34504, left p3; GSP 34505, right dp3; GSP 34506, left dp4; GSP 34508 and GSP 50952, likely m1s; GSP 52500, left p4-m2; GSP 39389, right mX. GSP 53241, right M1 or M2 is tentatively referred.

Occurrence. GSP 34504 - 34506, 34508 are from DP13. GSP 39389 and 50951 - 50953 are from Y921, "Bunny Hill" (these specimens are comparable in size and may represent the same individual); GSP 52500 is from Y456; and GSP 53241 is from Y975. All are from the upper part of the Dhok Pathan Formation, Siwalik Group, Potwar Plateau, Pakistan.

Age. Y921, 7.35 Ma; Y456, 7.2 Ma; Y975, 7.2 Ma; DP13, 6.5 Ma.

Etymology. Specific name "*elongatus*" is Latin for "prolonged," referring to the anteroposteriorly elongate trigonid on p3.

Diagnosis. Lower third premolar roughly triangular in shape with anterior end elongated; connection between trigonid and talonid slightly oblique and located slightly labial to the midline. PER, PIR, and AER all distinct (primitive); AIR may be distinct or weak; AR lacking (primitive). Both PER and PIR extend approximately halfway across the tooth, but PIR is slightly deeper. AER and AIR anteroposteriorly elongate. TH smooth in PER, smooth to heavily crenulated in PIR; TN lightly to heavily crenulated. Enamel in AER lightly crenulated; smooth to lightly crenulated in AIR.

Description. Measurements of *Alilepus elongatus* and comparative specimens are given in Table 1. *Alilepus elongatus* is comparable in size to other species of *Alilepus*, except it is larger (as are other species in the genus) than *A. wilsoni*, and dp4 width is considerably less than the range of *A. annectens*.

The P3 or P4 (GSP 50953; Figure 3.7) is incomplete: it is missing its external and much of its posterior portions. The internal reentrant (= hypostria) extends approximately two-thirds the way across the tooth and is heavily crenulated. The

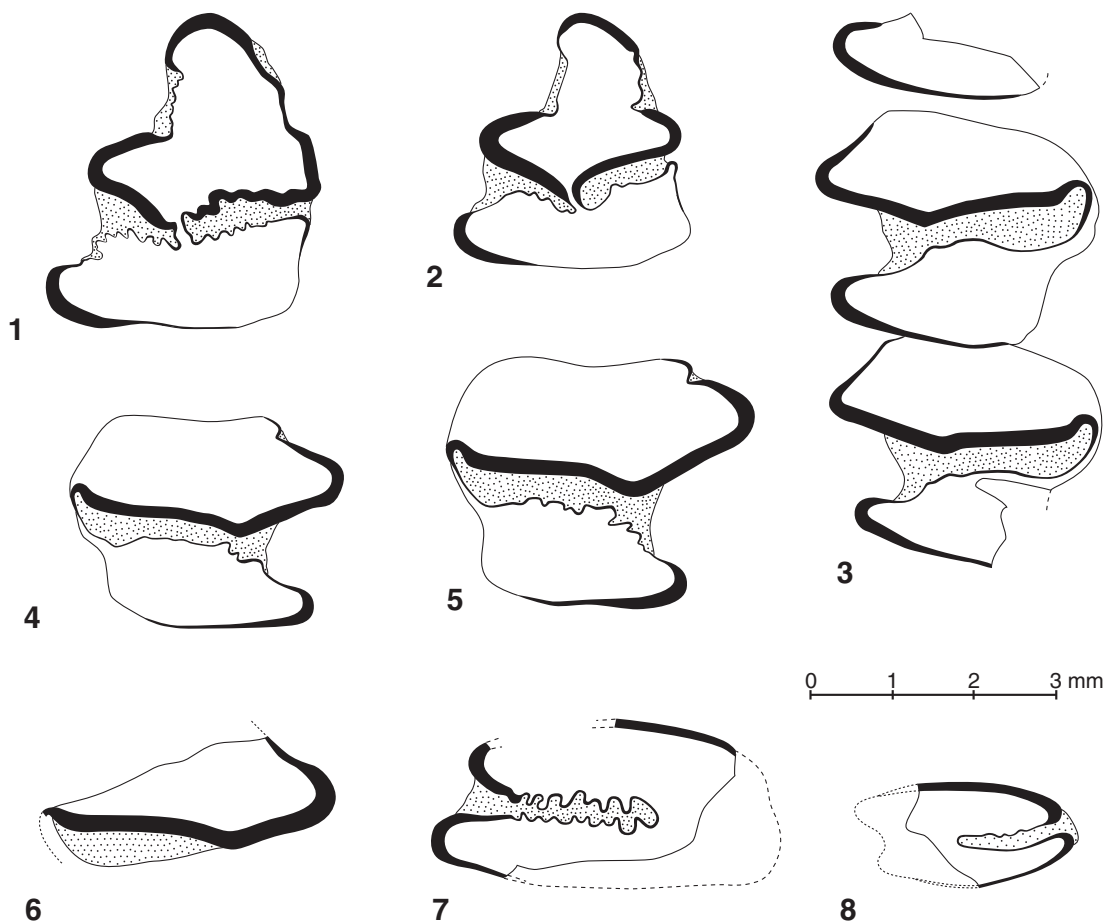


FIGURE 3. Camera lucida drawings of *Alilepus elongatus*, sp. nov. 1, GSP 50951, holotype, right p3 (reversed), from Y921. 2, GSP 34504, left p3, from DP13. 3, GSP 52500, left p4 (fragment), m1, m2, from Y456. 4, GSP 34508, right m1, from DP13. 5, GSP 50952, right m1, from Y921. 6, GSP 39389, right mX, from Y921. 7, GSP 50953, left P3 or P4, from Y921. 8, GSP 53241, right M1 or M2, from Y975.

talon is wider, and likely slightly shorter, than the trigon.

The M1 or M2 (GSP 53241, Figure 3.8) is likely from a sub-adult specimen because of its smaller size, possession of a relatively shallow internal reentrant with simple crenulations, and in side view, the size of the tooth increases toward its root. The internal reentrant of this specimen extends less than two-thirds the way across the tooth and is lightly crenulated. The talon is wider, and slightly shorter, than the trigon. GSP 53241 is only tentatively assigned to *A. elongatus* because the tooth is a sub-adult, from a relatively undiagnostic tooth position, and is the only lagomorph from locality Y975.

Like the adult p3, the dp3 (GSP 34505; Figure 4.1) is roughly triangular in outline and has four reentrants. Unlike the adult, the connection

between the trigonid and talonid is much less oblique, and is almost parallel to the long axis of the tooth. The width of the dentine within this connection is also wider in the juvenile tooth. The TH within the PER and PIR is smooth. The TN is gently crenulated in the PIR and smooth in the PER. Like the adult p3, an imaginary line between the external and internal extensions of the trigonid is slightly oblique. Unlike the adult, on the juvenile tooth the anterior extension of the trigonid is almost continuous longitudinally with the short connection between the trigonid and talonid. AER and AIR are distinct: there is some cement in AER, but almost none in AIR. Enamel in the AIR is smooth: enamel on the inside on the AER is chipped away.

The dp4 (GSP 34506; Figure 4.2) has a separate trigonid and talonid. On the trigonid there is a gentle anteroexternal reentrant and a distinct deep

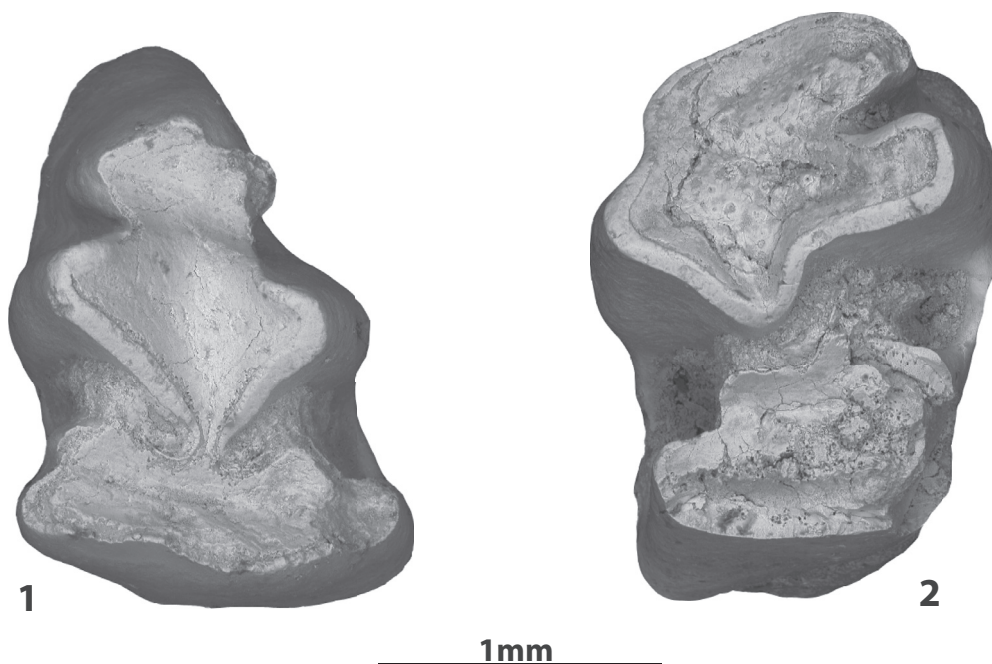


FIGURE 4. Scanning electron photomicrographs of juvenile lower premolars of *Alilepus elongatus*, sp. nov. 1, GSP 34505, right dp3. 2, GSP 34506, left dp4.

internal reentrant (not observed on any adult post-p3 teeth). There is a single, wide crenulation on the anterior end of the talonid. The trigonid is wider than the talonid.

The p3 (Figure 3.1, 3.2) is roughly triangular in occlusal outline. The trigonid is trefoil in shape with an elongated anterior end. A line drawn transversely through the external and internal extensions of the trigonid is slightly oblique, with the external side slightly inferior. There are four reentrants. The PER and PIR are deep, and each extends about halfway across the tooth, although the PIR on GSP 50951 is slightly deeper than the PER. These two reentrants are separated by the narrow, slightly oblique connection of (primarily) enamel between the trigonid and talonid. The PIR is almost closed off on its internal side. Within the PER and PIR, TN is lightly crenulated on GSP 34504 and heavily crenulated in GSP 50951. The TH is smooth within both the PER and PIR on GSP 34504. In GSP 50951 TH is smooth in the PER, but heavily crenulated in the PIR. The large AER is anteroposteriorly elongate, has cement extending continuously down the tooth, and forms almost a right angle with the long axis of the tooth. The AIR is distinctive on GSP 34504 (although not as large as the AER), is anteroposteriorly elongate, and forms almost a right angle with the long axis of the tooth. The AIR is weak on GSP 50951. The inside

borders of both the AER and the AIR on GSP 34504 are lightly crenulated. AR is lacking.

GSP 52500 (Figure 3.3) is an incomplete tooth row: the p4 is represented by only the external and posterior portions of the talonid, m1 is complete, and the m2 is complete except for the internal-posterior part of the talonid. GSP 34508 (Figure 3.4) and 50952 (Figure 3.5) are right m1s. These teeth have a wider trigonid than talonid. There is a distinct anteroexternal reentrant on the trigonid of GSP 34508 and 50952. This reentrant is lacking on the m1 and m2 of GSP 52500. GSP 39389 (Figure 3.6) includes only the posterior portion of the trigonid. The specimen does not appear to have an anteroexternal reentrant.

Discussion. The genus *Alilepus* was erected by Dice (1931) based on the type species “*Lepus*” *annectens* Schlosser, 1924, from the late Miocene localities of Ertemte and Olan Chorea, Inner Mongolia, China (Schlosser 1924). Dice’s (1929, p. 342) diagnosis (for *Allolagus*, but that name was pre-occupied, so changed to *Alilepus* in 1931) included a direct quote from Schlosser (1924) that the anterior lower premolar (p3) is formed “of two columns connected in the centre [sic] of the tooth by a bridge of dentine.”

White (1991) revised the genus based on study of *Alilepus* from the late Miocene to Pliocene of Eurasia and North America. White’s (1991, p.

TABLE 1. Measurements (in mm) of *Alilepus* from Pakistan, China, the United States, and Kenya. Abbreviations: L, length; N, number of specimens; OR, observed range; W, width; X, mean.

Tooth position	Taxon								
	<i>A. elongatus</i>	<i>A. annectens</i> ^a	<i>A. longisinuosus</i> ^b	<i>A. lijic</i>	<i>A. laskarewid</i>	<i>A. hibbardje</i>	<i>A. vaguse</i> ^e	<i>A. wilsoni</i> ^e	<i>Alilepus sp.f (Kenya)</i>
dp3 L									
N	1	14	—	—	—	—	—	—	—
X	—	2.09							
OR	1.72	1.60-2.50							
dp3 W trigonid									
N	—	14	—	—	—	—	—	—	—
X		1.45							
OR		1.20-1.85							
dp3 W talonid									
N	1	14							
X	—	1.66	—	—	—	—	—	—	—
OR	1.48	1.30-2.05							
dp4 L									
N	1	10	—	—	—	—	—	—	—
X	—	1.88							
OR	1.68	1.65-2.10							
dp4 W trigonid									
N	1	10	—	—	—	—	—	—	—
X	—	1.69							
OR	1.16	1.50-1.90							
dp4 W talonid									
X	—	1.45							
OR	1.10	1.30-1.70							
p3 L									
N	2	14	34	1	—	7	22	11	3
X	—	3.39	3.18	—		3.3	3.2	2.6	3.47
OR	3.16-3.96	3.20-3.75	2.80-3.45	2.98		3.0-3.4	2.4-3.8	2.4-2.7	3.33-3.75
p3 W									
N	2	—	—	—	—	7	22	11	—
X	—					3.0	3.0	2.3	
OR	2.88-3.24					2.6-3.3	2.1-3.7	2.0-2.4	
p3 W trigonid									
N	—	14	34	1	—	—	—	—	3
X		2.85	2.90	—					2.95
OR		2.50-3.20	2.40-3.45	2.30					2.67-3.25
p3 W talonid									
X	—	3.20	3.14	—	—	—	—	—	3.17
OR		2.90-3.60	2.80-3.60	2.80					3.00-3.50
m1 L									
N	3	—	31	1	—	—	—	—	—
X	2.79		2.78	—					
OR	2.56-3.00		2.20-3.30	2.70					

TABLE 1 (continued).

Tooth position	Taxon								
	<i>A. elongatus</i>	<i>A. annectens</i> ^a	<i>A. longisnuosus</i> ^b	<i>A. lii</i> ^c	<i>A. laskarewi</i> ^d	<i>A. hibbardje</i> ^e	<i>A. vaguse</i> ^e	<i>A. wilsonje</i> ^e	<i>Alilepus sp.</i> ^f (Kenya)
m1 W trigonid									
N	3	—	31	1	—	—	—	—	—
X	3.51	—	3.20	—	—	—	—	—	—
OR	3.40-3.64	—	2.40-3.80	2.90	—	—	—	—	—
m1 W talonid									
X	2.53	—	2.54	—	—	—	—	—	—
OR	2.48-2.60	—	2.00-2.90	2.30	—	—	—	—	—
m2 L									
N	1	—	21	—	—	—	—	—	—
X	—	—	2.78	—	—	—	—	—	—
OR	2.60	—	2.10-3.05	—	—	—	—	—	—
m2 W trigonid									
N	1	—	21	—	—	—	—	—	—
X	—	—	3.13	—	—	—	—	—	—
OR	3.28	—	2.30-3.60	—	—	—	—	—	—
m2 W talonid									
X	—	—	2.45	—	—	—	—	—	—
OR	2.44	—	1.80-2.90	—	—	—	—	—	—
p3-m3 L			alveolar L						
N	—	2	8	—	1	1	5	2	—
X	—	—	15.50	—	—	—	16.5	—	—
OR	—	12.7-14.2	12.00-17.10	—	17.8	18.0	15.4-17.3	11.7-12.2	—
			toothrow L						
N	—	—	6	—	—	—	—	—	—
X	—	—	13.80	—	—	—	—	—	—
OR	—	—	13.40-15.20	—	—	—	—	—	—

^aMeasurements of isolated teeth of *A. annectens* from Ertemte 2, from Qiu (1987). Length of p3-m3 from Locality 73, from Bohlin (1942).

^bMeasurements of *A. longisnuosus* from Qiu and Han (1986).

^cMeasurements of *A. lii* from Jin (2004).

^dMeasurements of *A. laskarewi* from Gureev and Konkova in Gureev (1964)

^eMeasurements of *A. hibbardje*, *A. vaguse*, and *A. wilsonje* from White (1991 table 3). White (1991) did not provide measurements of ?*A. browni*. Measurement of p3-m3 was alveolar length.

^fMeasurements of three *Alilepus* p3s from Kenya are from casts.

69) emended diagnosis was: “medium- to large-sized leporids with cranium and mandible fully modernized. P2 with deeply incised MAR and shallow EAR; p3 with PIR as deep or shallower than PER; PIR often pinched off to form an enamel lake; AIR shallower than PIR and usually missing; AR absent; TH smooth to slightly folded; AER shallow with smooth thin enamel.” White (1991) noted that the distribution of the genus was the Turolian (late

Miocene) to early Villafranchian (early Pliocene) of Eurasia and the late Clarendonian (late Miocene) to late Blancan (Pliocene) of North America.

We assign the Pakistani specimens to the genus *Alilepus* based on the presence of a bridge connecting the trigonid and talonid and separating distinct PER and PIR, which are of about equal depth. The AIR is shallower than the PIR, and an AR is lacking. Several characters of the Pakistani

specimens differ slightly from White's (1991) diagnosis: 1) the PIR of one of the two Pakistani p3s is slightly deeper than the PER; 2) the PIR is never pinched off to form an enamel lake, but there are only two Pakistani p3s; 3) the TH is smooth in both posterior reentrants on one Pakistani tooth, but on the other tooth it is smooth in the PER but well crenulated in the PIR, and 4) the AER has smooth to lightly crenulated thin enamel. The differences observed from White's (1991) diagnosis are not considered significant enough to warrant generic distinction.

We conservatively assign the Pakistani specimens to one morphologically variable species. The geologically older p3 from Y921 (holotype, GSP 50951) is about 22% longer and 13% wider, has a shallower AIR, and generally has more crenulated enamel in the reentrants compared to the p3 from DP13 (GSP 34504). The m1 from Y921 (GSP 50952) differs from the p4-m2 from Y456 (GSP 52500), and the m1 from DP13 (GSP 34508) in having more crenulated enamel on the anterior end of the talonid. An anteroexternal reentrant is present on the m1s from Y921 and DP13, but not on the specimen from Y456.

Comparisons with other species of *Alilepus* from Asia. Four generally accepted species of *Alilepus* are described from Asia: *A. annectens* Schlosser, 1924, *A. longisinuosus* Qiu and Han, 1986, *A. lii*, Jin, 2004, and *A. laskarewi* Khomenko, 1914. The type species is *A. annectens* ("*Lepus*" *annectens* of Schlosser 1924). Schlosser (1924) does not provide a formal diagnosis or detailed descriptions, so comparisons made here are with Qiu's (1987) more detailed descriptions (also lacking a diagnosis) based on additional collections from Ertemte and from Harr Obo. Qiu (1987) described the p3 of *A. annectens* as having a bridge connecting the trigonid and talonid, and possessing an AER, a PER, and a PIR (e.g., the AIR is lacking). The AER is wide and shallow, and the PER is narrow and deep, extending about half-way across the tooth. The PIR is more variably developed, but it never extends more than about one-third of the way across the tooth. Two out of about 14 p3s have an enamel lake instead of a PIR. Variable development leads to a variable bridge between the trigonid and talonid. Generally, toward the midline the PER and PIR both curve posteriorly. All folds persist to the base of the crown, and all are filled with cement. The dp3 of *A. annectens* is variable but similar in morphology to p3, except the PIR is deeper, and the bridge is narrower. The PIR may close off to form an enamel

lake. When lightly worn, there is a shallow groove in the position of the AIR: this is lost rapidly in more worn specimens.

The p3s of *A. elongatus* differ in having a distinct AIR and an AER, which is shallower, but more anteroposteriorly elongate than in *A. annectens*. The latter is likely related to the trigonid of *A. elongatus* being more anteroposteriorly elongate. Crenulations in the reentrants of *A. annectens* are minor or absent: there are moderate crenulations in three reentrants of GSP 34504, and strong crenulations in three reentrants of GSP 50951. Toward the midline, the PER and PIR do not curve posteriorly on GSP 50951. On GSP 34504 the PER is straight, and the PIR curves slightly posteriorly. On *A. annectens* the PER in particular curves strongly posteriorly. The dp3 of *A. elongatus* has a distinct AIR, versus its development only as a groove in lightly worn *A. annectens*. The p4-m2s of *A. elongatus* may have a distinct cement-filled anteroexternal reentrant; this reentrant is lacking in *A. annectens*.

Alilepus longisinuosus Qiu and Han, 1986, is described from 69 specimens of latest Miocene age from Lufeng, Yunnan, China. This species is characterized by a variably developed bridge connecting the trigonid and talonid: the bridge may be wide, narrow, weak, or absent. The PIR is consistently deep, although it varies, and may be equal in depth to the PER or somewhat longer or shorter. Crenulations on the enamel of p3 are weak to absent. A distinct anteroexternal reentrant on p4 to m2 is lacking. The dp3 lacks an AER. The dp4 lacks an anterior lobe on the trigonid and has only two roots.

The p3s of *A. elongatus* differ from those of *A. longisinuosus* with the former having a distinct narrow bridge between the trigonid and talonid, reentrants more crenulated, a distinct AIR, a more elongate trigonid, and a distinct anteroexternal reentrant on some p4 to m2s. The dp3 of *A. elongatus* has a distinct AER, and the dp4 has an anterior lobe on the trigonid.

Alilepus lii, Jin, 2004, is known from a single mandible with p3-m1 from Huainan, Anhui, China. It is estimated as being latest Miocene in age (Jin, 2004). This species is characterized by its relatively small size, shallow AIR, strong crenulations on the TN of the PIR and the PER, rather wide bridge linking trigonid and talonid, and PIR distinctly less deep than the PER. On the p4-m1 there are distinct crenulations on the anterior side of the talonid, and an anteroexternal reentrant is lacking.

The p3s of *A. elongatus* are similar to those of *A. lili* in general morphology, including having distinctive crenulations on the TN of the PER and the PIR. *Alilepus elongatus* has a better-developed AIR, somewhat more anteroposteriorly elongate trigonid, and a distinctly deeper PIR (resulting in a narrower bridge between the trigonid and talonid). The p4 and m1 of *A. lili* have distinct crenulations on the anterior side of the talonid, as do some specimens of *A. elongatus*. However, those specimens of *A. elongatus* with crenulations also have a distinct anteroexternal reentrant, a character lacking on *A. lili*. Among Asian species, *A. lili* is most similar to *A. elongatus*.

Alilepus laskarewi Khomenko, 1914, was originally assigned to *Lepus* by Khomenko in 1914. It is from near the village of Taraklia in what is now Romania, and may be of Miocene age (Dice 1931). The name of the species (and its author) is sometimes translated from Russian into English as *A. laskarevi* Chomenko, 1914. Based on Khomenko's illustration (Khomenko 1914, plate 1.20) of the enamel pattern of p3, Dice re-assigned the species to *Alilepus*. Dice noted that *A. laskarewi* differed from *A. annectens* in the former's longer p3, with the greater length being primarily in the area anterior to the main pair of reentrant angles (likely the PER and the PIR). Dice (1931) also mentioned the presence of an AER on p3, and seemed to imply this reentrant was lacking on *A. annectens* (but it is present).

The p3 of *A. laskarewi* includes an AER, a PER, and a PIR. The AR and AIR are lacking. The PER extends a little over halfway across the tooth and curves posteriorly near the median longitudinal plane. The PIR extends about one-third the way across the tooth and is straight. The bridge between the trigonid and talonid is wide. No crenulations are shown in Khomenko's illustration (Khomenko 1914, plate 1.20). Crenulations are absent or extremely gentle and an anteroexternal reentrant appears to be absent in the p4-m2s.

The p3s of *A. elongatus* differ from the p3 of *A. laskarewi* in that *A. elongatus* has an AIR, a deeper PIR (and thus a narrower bridge between the trigonid and talonid), and crenulations in the reentrants. In addition, the p4-m2s of *A. elongatus* have crenulations on the anterior end of the talonid and may have anteroexternal reentrants.

Comparisons with other species of *Alilepus* from North America. White (1991) recognized three species of *Alilepus* in North America: *A. hibbardi*, *A. vagus* Gazin, 1934, and *A. wilsoni*. He questionably assigned a fourth species, *?Alilepus*

browni (Hay 1921) to *Alilepus*. The temporal range of *Alilepus hibbardi*, *A. vagus*, and *A. wilsoni* is late Clarendonian (late Miocene) to late Blancan (late Pliocene). *?Alilepus browni* is from the early Irvingtonian (early Pleistocene).

Alilepus hibbardi White, 1991, is known from a complete skull and a total of five isolated teeth from Idaho, California, and Nevada. On p3, the PIR is generally shallow: it extends from about one-fourth to one-third the way across the tooth. On one tooth it is present as an enamel lake. The relative location of PIR is transverse or anterior to the PER. The PER extends about halfway across the tooth. There is a wide bridge between the trigonid and talonid. The AIR is lacking, although there is a slight indentation in the area of this reentrant on one tooth. The TH of the PER and the PIR may be smooth or lightly crenulated. Enamel of the AER is smooth. The p4-m2s of the holotype (IMNH 38695) have many light crenulations on the anterior end of the talonid and lack anteroexternal reentrants.

In comparison, *A. elongatus* has a deep PIR located transverse to the PER, a distinct AIR, and an anteroposteriorly elongated trigonid. GSP 50959 is more heavily crenulated than specimens of *A. hibbardi*, but the degree of crenulations on GSP 34504 may be comparable. The p4-m2 of *A. elongatus* and *A. hibbardi* both have crenulated reentrants, but *A. hibbardi* lacks an anteroexternal reentrant, which is sometimes present on *A. elongatus*.

Alilepus vagus Gazin, 1934, includes abundant remains from Nebraska, Idaho, and Washington (White 1991). Various authors have assigned the species to either *Alilepus* or *Pratilepus*. The three p3s illustrated by White (1991) have a PER extending at least halfway across the tooth and a PIR extending about one-third of the way across or forming an enamel lake. AIR is present or absent. White (1991) noted that dentally, *A. vagus* differed from *A. hibbardi* in the former having p3s with a deeper PER. Thus, differences between the p3 of *A. elongatus* and *A. vagus* are comparable to the differences between *A. elongatus* and *A. hibbardi*. Comparisons were not made between the p4-m2 of *A. elongatus* and *A. vagus*.

Alilepus wilsoni White, 1991, is known from two fragmentary mandibles and 10 isolated p3s from Arizona. It is diagnosed as differing from other species of *Alilepus* in its smaller size and having a p3 with the PER with the inner portion widened and deflected anteriorly. This taxon has also been considered an immature *Lepus* or *Hypolagus* (White 1991). Presence of an elongated PER and lack of

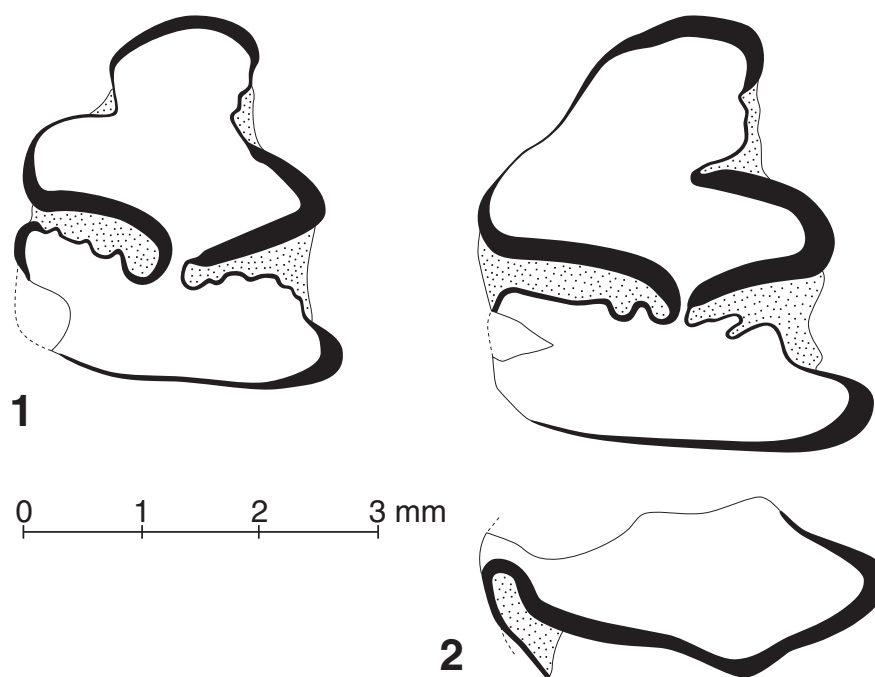


FIGURE 5. Camera lucida drawings of *Alilepus* sp. from the late Miocene of Kenya. Drawings were made from casts of the specimens. 1, KNM-TH 967/21219, right p3, from the Lukeino Formation, Tugen Hills, Kenya. 2, KNM-LT 22999, right p3-p4, from the Lower Nawata Formation, Lothagam, Kenya.

a PIR makes *Alilepus wilsoni* significantly different from *A. elongatus*.

White (1991) questionably assigned *Brachylagus browni* Hay, 1921, (*Hypolagus browni* Dice, 1929) from Arizona to ?*A. browni*. The holotype of ?*Alilepus browni* is a fragmentary cranium, which “has no features that can be used for identification” (White 1991, p. 74). There are four isolated p3s of immature individuals. White’s (1991) emended diagnosis of the species notes its small size and that the innermost part of the PER is not expanded and curved anteriorly as in *A. wilsoni*. Compared to the p3 of *A. elongatus*, the p3 of ?*A. browni* lacks a PIR or it may be present as an anteriorly located enamel lake, and AIR may be absent or present as a small indentation.

Voorhies and Timperley (1997) assigned six isolated p3s from the Stewart Quarry, late Barstovian (ca. 13 Ma) of Nebraska, to *Alilepus* sp. The specimens are assigned to *Alilepus*, versus *Hypolagus* or *Pronotolagus* (both found in the same sediments) because they have either an enamel lake or a PIR. We agree with Voorhies and Timperley (1997) that these specimens conform to the generic diagnosis of *Alilepus* (White 1991), albeit an *Alilepus* with very primitive morphology

(and certainly not comparable to the derived morphology of *A. elongatus*). Indeed, the Stewart Quarry specimens are quite similar in size and morphology to lithosympatric *H. fontinalis*. Voorhies and Timperley (1997) echoed White’s (1991) proposal that *Alilepus* originated in North America, and later dispersed to the Old World, but added that the origin of the genus was at least 12 million years ago.

Comparisons with *Alilepus* from Africa. A few p3s of *Alilepus* have been reported from Africa, but none have yet been described thoroughly. Cf. *Alilepus* was reported by Darwent (2007) from the late Miocene Lemudong’o Fauna, Kenya. Unfortunately, Darwent (2007) the material from Lemudong’o does not include any p3s. Haile-Selassie et al. (2004, figure 5) listed ?*Alilepus* in a composite faunal list from the late Miocene Adu-Asa and lower Sagantole formations, Middle Awash, Ethiopia. There was, however, no discussion of this taxon in the text, nor any illustrations. Wesselman et al. (2009) re-assigned the Adu-Asa material to *Serengetilagus*, and the Sagantole remains, including two p3s (dated at 4.85 Ma), to *Alilepus* sp. Photographs and brief descriptions were provided. The Ethiopian *Alilepus* appears distinct from

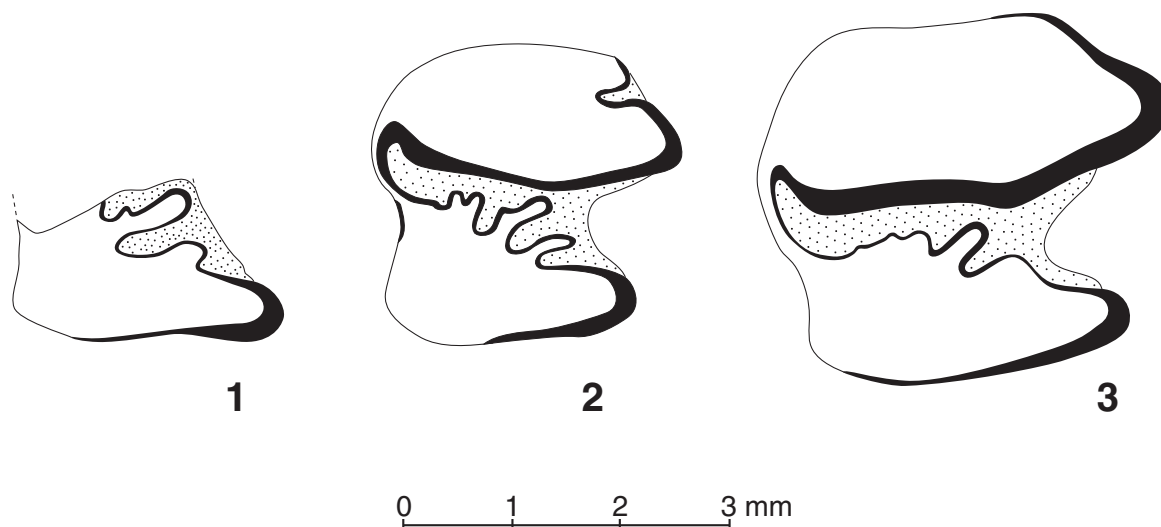


FIGURE 6. Camera lucida drawings of 1, *Pliopentalagus* sp., *Pliosiwalagus* sp. or *Caprolagus* sp., GSP 34829., talonid of right m1 or m2, from DP24. 2, *Pliopentalagus huainanensis*, IVPP V 10817.5, right m2, from the Laodong locality, Huainan, Anhui Province, China. 3, *Caprolagus hispidus*, BMNH 26.8.12.1, left p4 (reversed), Recent specimen from Nepal.

the Siwalik and Kenyan specimens in (the Ethiopian specimens) possessing a very deep AR; PIR may be less deep than on the Siwalik/Kenyan *Alilepus*, but this is difficult to tell with certainty from the photographs. The length and width measurements of one Ethiopian p3 are given - 3.00 x 2.87 mm: the length is slightly shorter than the Siwalik and Kenyan p3s, but such small sample sizes preclude meaningful comparisons. The Ethiopian *Alilepus* needs to be more thoroughly illustrated and described before accurate comparisons can be made.

Winkler (2002) noted that a “premolar” (p3; figure 5.1) from the Lukeino Formation, Kenya (bracketed by radioisotopic dates of 5.9-5.7 Ma), was likely conspecific with specimens from the Siwaliks (described here as *Alilepus*). In Winkler (2002) this p3 was reported as Family Leporidae, gen. and sp. nov. Cranial and postcranial remains of *Alilepus* were reported from Lothagam, Kenya, from the Lower Nawata Formation (Figure 5.2; Winkler 2003). Radioisotopic dating placed these specimens at 6.57-6.54 Ma (Winkler 2003).

Comparable morphology suggests the two Kenyan *Alilepus* p3s illustrated in Figure 5 belong to the same species. The difference in size is similar to that between the two adult p3s of *A. elongatus*, and within the range of variation seen in other species of *Alilepus*. Morphology of the Kenyan specimens is comparable to that of *A. elongatus*, including relative width of the PIR, a lightly crenulated AER, and a lightly crenulated TN: neither

Kenyan specimen has a crenulated TH. The major differences between the Kenyan and Pakistani specimens are that the Kenyan specimens have a less anteroposteriorly elongate trigonid, and the AIR may be absent. An incomplete p3 of a second specimen from the Lower Nawata Formation (KNM-LT 23179, Winkler 2003, figure 5.2B) also lacks an AIR and has a less elongate trigonid. Compared to the specimens illustrated in Figure 5, KNM-LT 23179 has a trigonid which narrows only slightly anteriorly, has a more anteriorly placed PIR, a wider bridge between the trigonid and talonid, and lacks crenulations in the reentrants. Differences between KNM-LT 22999 and KNM-LT 23179 are most likely due to morphological variation within a species, as both specimens are from the same general geographic area and are of comparable geologic age. Leporid p3 morphology is notably variable within a species, and the differences between *A. elongatus* and the Kenyan *Alilepus* may reflect morphological variability within a geographically widespread species. Because sample sizes are small, the Kenyan material is conservatively assigned as “near” *A. elongatus*. The Kenyan record is the likely result of dispersal of *A. elongatus* or a sister taxon from southern Asia to Africa during the late Miocene.

Pliopentalagus sp., *Pliosiwalagus* sp. or
Caprolagus sp.

Figure 6.1

Referred Material. GSP 34829, talonid of right m1 or m2.

Occurrence. DP24, Pabbi Hills microsite, Soan Formation.

Age. Ca. 1.7 Ma.

Description. The crenulation pattern on the anterior border of the talonid of GSP 34829 (Figure 6.1), with two very distinctive crenulations, is strikingly different from the pattern seen on all other p4, m1, or m2s from the Potwar Plateau. There is a long anterior crenulation (extending about one-third of the width of the talonid), which has a small spur along its length. Distal to this crenulation is a second shorter one: it is about one-third the length of the first. In side view, the tooth curves posteriorly toward the base of the crown, suggesting it may be an m2 rather than m1, and not a p4. Talonid width of GSP 34829 is 2.40 mm.

Discussion. GSP 34829 was compared with the talonids of p4 (for completeness), m1s, and m2s of other leporids having strong enamel crenulations. Among extant forms, this includes *Pentalagus* and *Caprolagus*. Among extinct taxa, it includes *Pliopentalagus* and *Pliosiwalagus*.

Pentalagus furnessi, the Amami rabbit, is currently known only from the Amami Islands, southwestern Japan. The only fossil record of *Pentalagus* is two isolated teeth from the latest Pleistocene, Tokunoshima, Japan (Tomida and Otsuka 1993). *Caprolagus hispidus*, the hispid hare, lives along the southeastern foothills of the Himalayas in India, Nepal, and possibly Bangladesh (where it may be extinct). The only fossil record of *Caprolagus* was reported by Forsyth Major (1899) from the ?Upper Siwaliks of India. Patnaik (2002) re-assigned this material to the genus *Pliosiwalagus* Patnaik, 2001.

Pentalagus has very large crenulations on the mesial borders of the talonids of p4, m1, and m2. Compared to the GSP 34829, the occlusal surface of *Pentalagus* is much more heavily and deeply crenulated with the deepest crenulations extending about 2/3 of the width of the talonid, and directed about 45 degrees to the anteroposterior axis of the tooth. Thus, we do not consider GSP 34829 to pertain to this genus.

The extant genus *Caprolagus* may have well-crenulated anterior borders on the talonids of p4, m1, and m2. The degree and development of crenulations is variable, but may be close to that seen in the Pakistani specimen. However, as seen Figure 6.3, and based on our study of other specimens, the crenulations are not as pronounced on *Caprolagus* as on GSP 34829. Thus, although we cannot rule out the possibility that GSP 34829

belongs to *Caprolagus*, we consider it less likely than assignment to *Pliopentalagus* or *Pliosiwalagus*.

Pliopentalagus includes material from Europe, China, and Afghanistan. *Pliopentalagus dietrichi* from Slovakia (Fejfar 1961; Daxner and Fejfar 1967) and *P. moldaviensis* from Moldavia (Gureev and Konkova in Gureev 1964) are both late Ruscinian in age. Chinese taxa include *P. huainanensis* (the oldest species of the genus, latest Miocene, MN 13; Jin 2004), *P. dajushanensis* (early Pliocene), and *P. anhuiensis* (late Pliocene) from Anhui Province (Tomida and Jin 2009; = spp. B and C, respectively, of Tomida and Jin 2002). *Pliopentalagus huainanensis*, *P. dajushanensis*, and *P. anhuiensis* represent a sympatrically evolving lineage showing gradual changes in several characters through time (Tomida and Jin 2009). The most recent species of *Pliopentalagus* is *P. progressivus* from Henan Province, dating to the latest Pliocene or earliest Pleistocene (Liu and Zheng 1997). *Pliopentalagus nihewanensis* was also described from China (Cai 1989), but Tomida and Jin (2005) have re-assigned this species to *Trischizolagus*.

Pliopentalagus sp. was described from the early Pliocene Pul-e Charkhi locality, Afghanistan (Sen and Erbajeva 1995). This material, as well as specimens assigned to *Serengetilagus* by Sen and Erbajeva (1995), was originally allocated to *Trischizolagus* cf. *maritsae* by Sen (1983). Averianov and Tesakov (1997) returned *Pliopentalagus* from Pul-e Charkhi to *Trischizolagus*.

GSP 34829 was compared with published descriptions and illustrations of all species of *Pliopentalagus*. The largest of the crenulations on GSP 34829 is significantly larger than any seen on the five illustrations of m1s (Daxner and Fejfar 1967) and 8 lower molariform teeth (Fejfar 1961) of *P. dietrichi*. No p4, m1, or m2s of *P. moldaviensis* Gureev and Konkova in Gureev, 1964, are available for comparison.

Three mandibles of *P. huainanensis* were described and illustrated by Jin (2004, figures 2, 4). The p4-m2 of this species was diagnosed as having a distinct anteroexternal reentrant (PET in terminology of Jin 2004). Unfortunately, the trigonid is lacking on GSP 34829. The pattern of enamel crenulations on GSP 34829 is close to, but does not exactly match, the range of variation seen in *P. huainanensis* (e.g., Figure 6.2). The p4-m2 of *P. dajushanensis* and *P. anhuiensis* have basically the same enamel pattern on the mesial border of the talonid as *P. huainanensis* (Tomida and Jin 2009). Thus, the results of comparisons of GPS

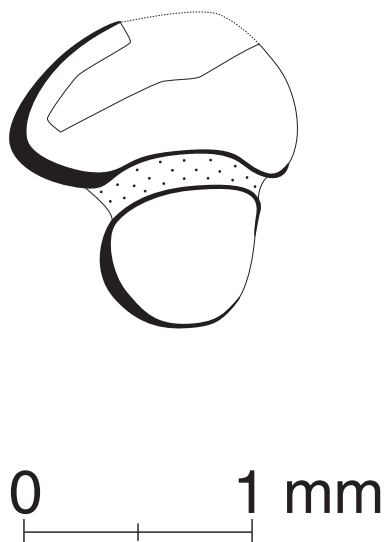


FIGURE 7. Leporidae, genus and species undetermined, GSP 34511, left m3, from DP8.

34829 with *P. dajushanensis* and *P. anhuiensis* are the same as that with *P. huainanensis*.

Pliopentalagus progressivus was described based only on one isolated p3 and one isolated p4 or m1 (Liu and Zheng 1997). It was distinguished by characters of the p3 and is the largest species of *Pliopentalagus*. It was considered the species of *Pliopentalagus* most similar to the extant taxon, *Pentalagus furnessi*. The p4 or m1 of *Pliopentalagus progressivus* was neither illustrated nor described, nor were its measurements given.

Patnaik (2001, 2002) described two species of *Pliosiwalagus* based on small samples of Pliocene age (one locality about 3.5-4.5 Ma and the other about 2.5 Ma) from Himachal Pradesh, northern India. The genus is diagnosed by characters of p3, but is characterized also by possessing strongly crenulated thin enamel on p3-m2 (Patnaik 2002). The crenulation pattern seen on the thin enamel of GSP 34829 is within the range of variation of the enamel pattern on the p4-m2s of the illustrated specimens of *Pliosiwalagus whitei* (Patnaik 2001, figure 11a, b), however, the Pakistani specimen is too incomplete for definitive assignment to this genus.

Leporidae, genus and species undetermined
Figure 7

Referred Material. GSP 34510, incomplete right trigonid of p4, m1, or m2; GSP 34828, incomplete left trigonid of p4, m1, or m2; GSP 34511, left m3; GSP 49889, left distal humerus; GSP 49887, right

acetabulum; GSP 50585, right distal tibia; GSP 50269, left astragalus; GSP 50954, left calcaneus; GSP 34503, left metatarsal; GSP 39403, left cuboid.

Occurrence. GSP 34510, 34511, 34828 are from DP8; GSP 39403, 34503, and 50954 are from Y457; GSP 50585 from Y581; GSP 49887, 49889, and 50269 are from Y908. Specimens from DP8 attributed to the local Tatrot Formation: all others are from the upper part of the Dhok Pathan Formation, Siwalik Group, Potwar Plateau, Pakistan.

Age. Y457, 7.4 Ma; Y581, 7.15 Ma, and Y908, 7.0 Ma; and DP8, ca. 3.5 Ma.

Discussion. Two small incomplete trigonids of p4, m1, or m2s (GSP 34510, 34828) are different in size and color and probably were not from the same individual. Both teeth lack an anteroexternal reentrant. However, the m3 (GSP 34511) is similar in size and color to GSP 34510, so these teeth possibly represent the same individual. The m3 (Figure 7) has a semi-circle shaped trigonid with the rounded portion anterior. The talonid is round and about half the size of the trigonid. The m3 measures 1.40 mm length, 1.24 mm trigonid width, and 0.66 mm talonid width. All of these dental remains (from locality DP8, ca. 3.5 Ma) are clearly Leporidae, but lack features diagnostic of *Alilepus*, and we hesitate to assign them at the generic level. Leporid post-cranial remains from the Hasnot area compare well with extant Leporidae of similar size and are likely referable to *Alilepus*.

DISCUSSION AND CONCLUSIONS

The nature of the Pakistani lagomorph record is surprising. Why is there only a single isolated ochotonid tooth at ca. 18 Ma, and an apparent lack of lagomorphs, from either family, between 18 and 7.4 Ma? Is the absence of Lagomorpha between 18 and 7.4 Ma real? We believe it is, as there are good samples of small mammals throughout the Siwaliks from the upper levels of the Kamli Formation through the Dhok Pathan Formation (Flynn et al. 1998). However, the pattern of occurrence of lagomorphs at the base of the Siwalik sequence and the top of the Dhok Pathan Formation and younger units suggests that taphonomic factors were at play at those times. At these Siwalik levels, lagomorphs are uncommon. The presence of only a single lagomorph tooth at the base of the Kamli Formation may reflect a predator bias in the early Miocene. The appearance of leporids, and more specifically, of leporines, only in the late Miocene is not unexpected, as this is the earliest appearance

of this group elsewhere in the world, e.g., in North America (but earlier in the late Miocene), Europe, Asia, and Africa (Patnaik 2002; Voorhies and Timperley 1997). Given the large number of fossil small mammals known from northern Pakistan, the paucity of leporines thereafter (latest Miocene and younger) is indeed surprising because leporines are often a common element in modern assemblages. As with the earlier records of lagomorphs, these more recent records may also record a predator bias: i.e., predators that captured few larger lagomorphs compared to other smaller prey items. From elsewhere on the Indian Subcontinent, lagomorphs are (poorly) known from only Pliocene and younger deposits (Forsyth Major 1899; Paknaik 2001, 2002). Further collecting in northern Pakistan is not expected to yield abundant additional specimens, but perhaps more diagnostic remains may be collected, especially from the younger units. This would add tremendously to our knowledge of the southern Asian record of this important group.

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