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Kobus (Bovidae, Artiodactyla) from Late Miocene of Mohal Pati and Hasnot, Jhelum, Punjab, Pakistan

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Abstract

Kobus represents an extant genus of the family Bovidae that is also found in fossilized form. The genus is also known from the Siwaliks, and its remains are relatively rare compared to other bovid taxa, especially in the Late Miocene. This study is focused on the collection of fossils of the genus *Kobus* from the Mohal Pati and Hasnot area of the district Jhelum, Punjab, Pakistan. The remains include a mandibular fragment, and isolated upper and lower dentition, and a morphometric study of these remains indicates that they belong to the extinct species, *Kobus porrecticornis*, found from the Siwaliks, particularly from the Late Miocene. The description of these remains adds more knowledge to the morphological features of this species, which will be helpful to a better understanding of the Siwalik bovids in general and the relationship of this species with extant species in particular.

Keywords: Bovidae*, Kobus,* Mohal Pati, Hasnot, Siwaliks

1. Introduction

The Siwalik Group, which is known for its preservation of remains of mammals from 18 Ma to 0.6 Ma, has its best exposure in the Potwar Plateau of Pakistan (Flynn et al., 2024; Pilbeam, 2025) and has attracted researchers from around the globe who were interested in the study of fossils of these mammalian taxa (Pilbeam, 2025). One of the mammalian orders, Artiodactyla, attained the highest diversity among the other large mammals (Khan et al., 2010, 2013), and at least seven families (Bovidae, Giraffidae, Tragulidae, Cervidae, Suidae, Hippopotamidae, Anthracotheriidae) are known from the Siwaliks of Pakistan. The four families (Bovidae, Giraffidae, Tragulidae, Cervidae) constitute the suborder Ruminantia, which is the most diverse suborder (Khan et al., 2010). The family Bovidae is best known among the other ruminants, but some of the taxa of this family are poorly represented in terms of the number of fossils (Pilgrim, 1939; Akhtar, 1992). The least well-represented taxa include the genus *Elachistoceras*, *Kobus*, *Palaeohypsodontus*, *Nisidorcas*, and *Protragelaphus* (Gentry et al., 2014, 2025). The genus *Kobus* first appeared in the upper Miocene deposits representing the Dhok Pathan Formation belonging to the Middle Siwalik Subgroup of the Siwalik Group (Pilgrim, 1939; Khan et al., 2010; Gentry et al., 2014, 2025) and is still living in Africa, hence an extant genus of the bovids. Among fossils, the genus is monospecific with *Kobus porrecticornis* (8.1-7.7 Ma), although Gentry *et al*. (2025) have reported the presence of two more species in the form of *Kobus* sp. 1 and *Kobus* sp. 2 from the same deposits but with a different time

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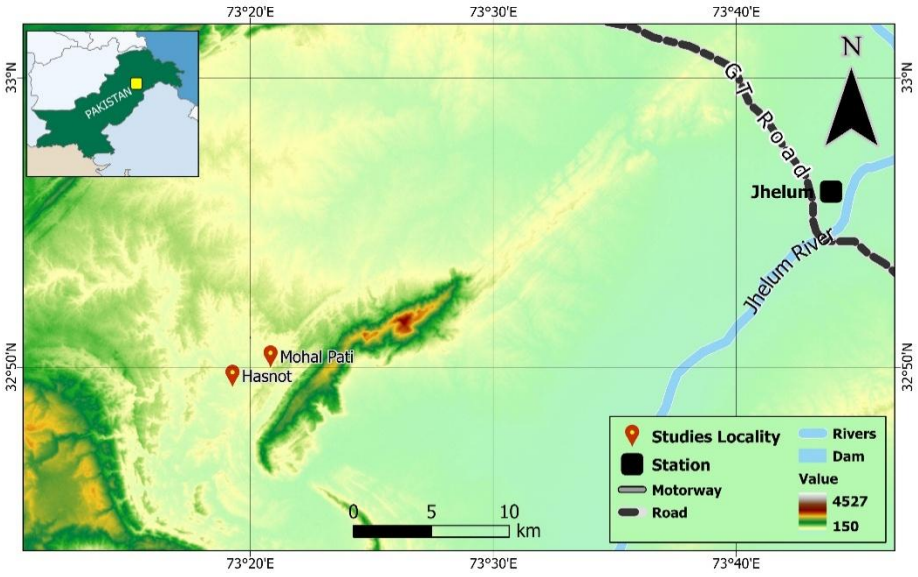

Figure 1. The geographic position of the Mohal Pati and Hasnot in the district Jhelum, Punjab, Pakistan.

frame. However, the morphology of the other two species is yet unknown, and most of the specimens are predominantly known for *Kobus porrecticornis*.

In this study, we describe the remains of the extinct species of the genus *Kobus* known predominantly from the Siwaliks of the Indian subcontinent. The specimens are valuable as they show the morphological variations present in the dental element of the Siwalik species, particularly p4s. The specimens have been collected from some localities, Mohal Pati and Hasnot villages, and the geographic and geological settings of these areas are given below.

Geographic & geological settings

The villages Mohal Pati and Hasnot are in the district Jhelum of the Punjab province of Pakistan. The village Hasnot, which lies about 70 km west of Jhelum city, is famous for its palaeontological collections made from the mid-1800s by various foreign researchers and has been reported in many pre-independence and post-independence palaeontological works (e.g., Pilgrim, 1913, 1937, 1939; Colbert, 1935; Sarwar, 1977; Akhtar, 1992; Khan et al., 2009; Khan & Flynn, 2017; Khan et al., 2020). The village Mohal Pati is located 3 km northeast of Hasnot. Both these villages have well-exposed Dhok Pathan outcrops in their vicinity. The outcrops/deposits present around these villages show dark to light colored sandstone and pale-yellow clay/siltstone that alternate with each other in cyclic deposition with a minute quantity of conglomerates that alternate (Barry et al., 2002; Zaheer & Khan, 2024). The age of these deposits ranges from 8 to 6.4 Ma (Fig. 1).

2. Materials and Methods

The material includes six specimens comprising upper and lower teeth. The material was collected through the surface collection, i.e., the collection areas or outcrops were surveyed/explored, and the material exposed on the surface was collected. The material was brought to the lab for preparation while completely wrapped in cotton. The material was prepared using fine needles. Each specimen was cataloged after preparation. The dental terminology follows Gentry *et*

Table 1 The nature of the material described in this study is within the collection area.

Catalog No.	Nature/Position	Locality
PUPC 23/355	A partially broken right upper third molar (rM3)	Mohal Pati
PUPC 23/361	An isolated right lower fourth premolar (rp4)	Hasnot
PUPC 24/158	An isolated left lower fourth premolar (lp4)	Mohal Pati
PUPC 24/157	A small left mandibular fragment having a fourth premolar (p4) and roots of the first molar (m1)	Mohal Pati
PUPC 24/159	Partially broken conjoined right lower fourth premolar and first molar (rp4-m1)	Mohal Pati
PUPC 24/183	An isolated left upper third molar (lM3)	Mohal Pati

al. (1999). The measurements were occlusal length and width, and were taken in millimeters with the use of digital Vernier calipers. Canon 6D was used for photography, and plates were prepared in Adobe Photoshop CC. The material

described is kept in the Palaeontology Laboratory, which is under the ownership of the University of the Punjab, Lahore, Pakistan. *Abbreviation:* est., estimated; L, Langebaanweg collection; PUPC, Punjab University Palaeontological Collection.

3. Systematic Palaeontology

Order Artiodactyla Owen, 1848
Family Bovidae Gray, 1821
Subfamily Antilopinae Gray, 1821
Tribe Reduncini Blaine, 1914 *sensu* Simpson, 1945
Genus *Kobus* Smith, 1840

***Kobus porrecticornis* Pilgrim, 1939**

Type specimen: GSI-B 229, frontlet with the horn cores (Pilgrim, 1939).
Type locality: Tatrot, Jhelum district, Punjab, Pakistan (Pilgrim, 1939).
Diagnosis: As given in Pilgrim (1939).
Stratigraphic range: Upper Miocene deposits of the Dhok Pathan (Gentry et al., 2014, 2025) and from the lower Pliocene deposits of the Tatrot Formations representing the Middle and Upper Siwalik Subgroup (Khan & Akhtar, 2014; Iqbal et al., 2015; Zaheer & Khan, 2024).

Studied material: Table 1 represents the nature of the material described in this study, with the collection area. PUPC 24/183, an isolated left upper third molar (lM3) (Mohal Pati); PUPC 23/355, partially broken right upper third molar (rM3) (Mohal Pati); PUPC 23/361, an isolated right lower fourth premolar (rp4) (Hasnot); PUPC 24/158, an isolated left lower fourth premolar (lp4) (Mohal Pati); PUPC 24/157, A small left mandibular fragment having fourth premolar (p4) and roots of the first molar (m1) (Mohal Pati); PUPC 24/159, partially broken conjoined right lower fourth premolar and first molar (rp4-m1) (Mohal Pati).

4. Results

PUPC 24/183 represents an isolated third left upper molar (LM3). The molar shows an early stage of wear (Fig. 2.1). The tooth is mesodont. The enamel is preserved only on the base of the protocone and hypocone; the rest is lost

due to weathering. The preprotocrista is longer than the postprotocrista, which is slightly anteriorly directed at its apex. The prehypocrista is slanting and also longer than the posthypocrista. Both the anterior and posterior fossettes are large and prominent, where the anterior one is C-like in appearance, is wider than the posterior, and possesses a small spur anteriorly. The posterior fossette is narrow anteriorly and wider posteriorly. The parastyle is almost broken, half of its length, though it is well developed and thick. The mesostyle is the thickest and lingually flared. The metastyle is prominent but weakly developed. The paraconous rib is prominent and larger than the metaconous rib, which is weak and more prominent at its base. The median valley is deep but narrow.

PUPC 23/355 is an upper third molar that shows signs of early wear and most of the protocone and apical part of the paracone are lost due to partial breakage (rM3) (Fig. 2.2). Due to this breakage, only a small part of the postprotocrista is preserved while some part of the pre- and postparacrista are lost from the apical portion. The hypocone and the metacone are fully preserved. The prehypocrista is longer than the posthypocrista, and overall, the lingual side of the hypocone is crescentic shaped, i.e., round. Metacone is also well preserved and slightly lingually oriented. Most of the anterior fossette is lost because of breakage. On the other hand, the completely preserved posterior fossette shows moderate broadness with a small spur almost in the center. Both the styles and ribs are large, prominent, flanked, and broad.

PUPC 23/361 is a lower fourth premolar (p4) that shows early wear (Fig. 2.3). The tooth is without any breakage and exceptionally preserved. It is pentacuspidate, trilobed, with three prominent valleys and a large groove. The anterior lobe has a large paraconid with its prominent parastylid. The postparacristid is in contact with the protoconid, which is the largest and highest cusp and has prominent pre- and postcristids. The metaconid is long, lingually projected, its cristid is bent anteriorly, and it is in contact with the paraconid. The contact between the metaconid and paraconid results in the closure of the anterior valley, which is the largest and broadest, and gives this premolar a semi-molarized appearance. The hypoconid and entoconid form the third lobe. The hypoconid is a small but

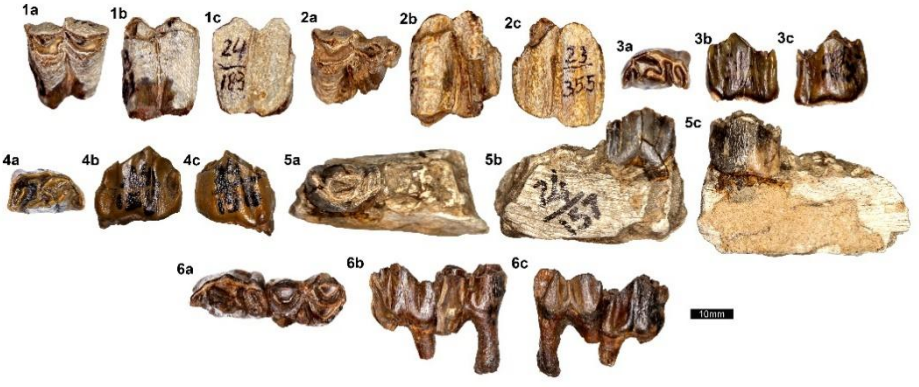

Figure 2. *Kobus porrecticornis*. **1.** PUPC 24/183, an isolated left upper third molar (lM3); **2.** PUPC 23/355, partially broken right upper third molar (rM3); **3.** PUPC 23/361, an isolated right lower fourth premolar (rp4); **4.** PUPC 24/158, an isolated left lower fourth premolar (lp4); **5.** PUPC 24/157, A small left mandibular fragment having a fourth premolar (p4) and roots of the first molar (m1); **6.** PUPC 24/159, partially broken conjoined right lower fourth premolar and first molar (rp4-m1). Views: a) occlusal, b) lingual, c) labial. The scale bar is equal to 10 mm.

Table 2. Measurements of the described teeth of *Kobus porrecticornis* in comparison with previously reported material.

Taxa	Catalog No.	Position	Length	Width	References
Kobus porrecticornis	PUPC 24/183*	Left M3	18.90	19.00	This study
	PUPC 23/355*	Right M3	20.20	17.20**	
	PUPC 23/361*	Right p4	16.70	10.30	
	PUPC 24/157*	Left p4	15.70	10.80	
	PUPC 24/158*	Left p4	17.50	10.30	
	PUPC 24/159*	Right p4	16.80	10.30	
		Right m1	16.30	10.70	
	PUPC 14/186	Left p4	13.50	8.00	Iqbal et al., 2015
		Left m1	18.20	11.00	
	PUPC 83/837	Left m1	16.50	10.80	Khan et al., 2014
Kobus subdolus	L15605	Left p4	12.00	8.00 est.	Gentry, 1980
		Left m1	15.00 est.	10.00 est.	
	L32850	Right p4	10.40	-	
	L46067	Right p4	11.40	-	
Reduncini gen. et sp. indet.	PUPC 68/60	Left p4	15.20	10.20	Siddiq et al., 2020

*Studied material. ** preserved measurements.

prominent cusp, while the entoconid is long and oriented lingually, and the entostylid is long, present perpendicular to the entoconid and also oriented lingually. The median valley is present between the metaconid and entoconid and is moderately broad and fully open lingually. The posterior valley is present between the entoconid and the entostylid.It is narrow and partially open apically. A large and deep groove is present between the protoconid and hypoconid. Enamel shows moderate rugosity.

PUPC 24/158 represents the second isolated lower fourth premolar (p4) in this study. The premolar shows the signs of the middle stage and slight breaking that resulted in the missing of a small part of the paraconid, parastylid, metaconid,

entoconid, and entostylid (Fig. 2.4). Both the paraconid and metaconid are oriented towards each other, and contact between them results in complete closure of the anterior valley. The metaconid is prominent and directed towards the entoconid but does not contact it. Hence, the median fossette is open. Due to the presence of a contact between the entoconid and entostylid, the posterior fossette has become completely closed. The morphology of other characteristics is like the PUPC 23/361.

A single mandibular fragment (PUPC 24/157) has a lower fourth premolar (p4) which is completely preserved, while only the roots of the m1 are preserved (Fig. 2.5). The mandibular body (corpus) shows the pattern of extreme weathering, presence of siltstone in which it was preserved, and woody texture. Despite the weathering, the corpus remains robust and thick, and its depth and width increase from anterior to posterior. The preserved mandibular length is 46.3 mm. The lower fourth premolar shows moderate wear. The parastylid, paraconid, protoconid, and entostylid are cracked and have been fixed using glue. The anterior valley is fully closed due to the fusion of the paraconid and the metaconid, and both the protoconid and the fused paraconid and metaconid make a globular or round appearance of this part of the tooth. Except for the above-mentioned and narrow and slim entoconid and entostylid, the other features of the tooth are morphologically like PUPC 23/361. The preserved roots of m1 show that the molar was bilobed, and the roots of the posterior lobe are visible at the point of breakage of the mandible.

PUPC 24/159 represents two teeth that are conjoined and sequentially representing a lower fourth premolar (p4) and lower first molar (m1), (Fig. 2.6). Except for the partial breakage of parastylid and metaconid, reduced paraconid, narrowing of the anterior valley, and the preservation of posterior roots, the p4 is like PUPC 23/361 in its morphology. The first lower molar (m1) shows extreme wear and partial breakage of the protoconid and the entoconid. Due to the extreme wear, both fossettes have become extremely narrow and crescentic in shape. A large and thick ectostylid is present in the median valley. The metastylid is prominent but moderately thick, while the mesostylid is extremely thick and large and round in appearance. The ribs are weakly developed. The anterior roots are partial, while the posterior roots are almost completely preserved.

4.1 Comparison

The described material includes three lower fourth premolars, and these are helpful in the identification of the studied specimens as reduncine (Table 2). The p4s of the reduncine have a partially or completely closed anterior valley, which results from the contact or fusion of the paraconid and metaconid (Gentry, 1980). In reduncine p4s, there is a tendency of the paraconid and metaconid to grow towards each other resulting either in contact or fusion of both these cusps and this situation is already known in the p4s of African extinct species *Kobus subdolus* from early Pliocene deposits of Langebaanweg, South Africa particularly in the mandible (L15605) described and illustrated by Gentry (1980, fig. 24); in one of the specimen (PUPC 14/186), from Pliocene deposits, of the Siwalik species, *Kobus porrecticornis* which was described and illustrated by Iqbal *et al*. (2015, fig. 2.1) and in one specimen (PUPC 68/60) from the Pleistocene deposits of the Siwaliks which was described as Reduncini gen. et sp. indet. by Siddiq *et al*. (2020, fig. 2F). Further, confirmation of reduncine affinity of the p4 specimens came from the work of Gentry (1980) who reported the occurrence of such closure of the anterior valley in 15 out of 31 p4s of *Redunca*

arundinum and also found in ontogenetically older *Kobus ellipsiprymnus*.

Other than above mentioned character, the fossil specimens show multiple dental traits common with primitive reduncines. The p4 has a strongly projected hypoconid and the presence of a groove between the hypoconid and protoconid, which is narrow and deep. in addition, as shown by the described material, teeth are mesodont or moderately hypsodont, with the presence of small but strong goat folds in the molars as well as a strong and developed median basal pillar in the median/transverse valleys. According to Gentry (1978, 1980), these features are noted in the taxa *Kobus subdolus*, *Kobus porrecticornis*, and *Kobus* aff. *porrecticornis*. The studied lower molar, PUPC 24/159, also shows the reduncine features, which include and are crowned by well-developed ribs, pinched labial cusps, a weak goat fold, and a small ectostylid (Fig. 2.6). These are reduncine features differentiating them from the Alcephalini, which possess rounded ribs and cusps, a prominent goat fold, and an enlarged ectostylid. Since *Kobus* constituted the majority of reduncine fauna in the Late Miocene (Gentry et al., 2014), we use *Kobus* for our attribution and identification as the species, *K. porrecticornis*.

5. Discussion

The subfamily Antilopinae is known from the Middle Miocene deposits of the Siwalik Group, and its first representatives come from the Kamlial Formation (Lower Siwalik Subgroup) in the form of Antilopinae unnamed genus and sp. (Gentry et al., 2025). The subfamily is today represented by many genera. However, the tribe Reduncini is known by a single genus, *Kobus,* which is also an extant genus that is now found in Africa with six species of antilopes of varying body size. The fossils of this genus are also known from the Late Miocene of Asia and Africa (Gentry, 1970; Gentry, 1997). It belongs to the tribe Reduncini of the family Bovidae (Pilgrim, 1939; Gentry, 1998; Gentry et al., 2025) and its fossils have been recovered from the Siwalik Group of Pakistan and India (Pilgrim, 1939; Khan et al., 2014; Iqbal et al., 2015; Zaheer & Khan, 2024; Gentry et al., 2025). The Siwalik species of genus *Kobus* is *K. porrecticornis,* which was originally described by Lydekker (1878) under the name of *Antilop porrecticornis* and again by the same author (Lydekker, 1886) under the name of *Gazella porrecticornis*. Pilgrim (1939) included the species under a new genus, *Dorcadoxa*. Later, Gentry (1970) placed the species in the genus *Kobus,* and Thomas (1980) and Gentry (1978, 1980) followed this suggestion, and this suggestion is still in use. According to the study of Thomas (1980), *K. porrecticornis* first appeared in the Dhok Pathan Formation in the type zone of this formation at the base of the Kundvali unit between sandstones 6 and 7, i.e., from the loc. 97. It is reported from the Baard's Quarry lower assemblage at Langebaanweg, Lukeino, and Mpesida in Africa as a reduncine species, which is the same or a similar species to the Siwaliks. The age of the Baard's Quarry lower assemblage, as reported by Hendey (1978), is about 2.0 Ma, i.e., the Pliocene, indicating that the Langebaanweg 'E' Quarry assemblage, despite the occurrence of the ancient *Kobus*, is older than Baard's Quarry lower assemblage as noted by Gentry (1980). According to Gentry (1997), it was previously observed by him (1980) that the horn cores collected from Baard's Quarry have smaller supraorbital pits as compared to the other localities, and in the Lukeino specimens, Thomas (1980) noted the presence of internal sinuses near the supraorbital pit. While discussing the relationship of *Kobus porrecticornis*,

Pilgrim (1913) followed the suggestions of Lydekker (1886) and placed it in the tribe Antilopini and suggested a close relationship of the *Aepyceros* based on the characters of the horn core and the maxilla. However, the reduncine affinity of *Kobus porrecticornis* was suggested much later by Gentry (1970).

Among the described material, the lower fourth premolars, i.e., p4s, are considered diagnostic in the family Bovidae. The described p4s are diagnostic enough in our case as shown in the study of Gentry (1980), which reported the closure of the anterior valley in the reduncine p4, and its occurrence ratio is nearly 50 percent in one species and more than 50 percent in other species. Other material described in this study also shows morphological features that are typical for the genus *Kobus,* which is known from the upper Miocene to lower Pliocene deposits, as shown in the comparison section of the described material. For about a hundred years, only one species of the genus was known the Siwalik, *Kobus porrecticornis*. But in recent studies by Gentry *et al*. (2014, 2025) have reported the presence of two more species from the Siwaliks without any description and illustration and these include: *Kobus* sp. 1 which is a slightly older species whose range is 9.3-7.9 Ma and a younger species of the genus, *Kobus* sp. 2 which is also known from Late Miocene with an age of 7.3-5.9 Ma. They further suggested that *K. porrecticornis* is restricted to the Miocene and its range is 8.1-7.7 Ma. Such an age limitation of *K. porrecticornis* in the upper Miocene deposits Siwaliks, does not correspond to the previous works done by Khan *et al*. (2008, 2014), and Iqbal *et al*. (2015) reporting *K. porrecticornis* from the much younger deposits in the Tatrot Formation (3.5-3.3 Ma).

6. Conclusions

In this study, we described the remains of the Siwalik reduncine species, *Kobus porrecticornis,* from the Late Miocene localities present in the surroundings of Mohal Pati and Hasnot villages. The material described includes the upper and lower dentition, which also includes the lower fourth premolars (p4s). The p4 is considered diagnostic in the ruminants, and in our case study, it we well applied. The description of this material shows the morphological variation in the M3s and p4s and hence adds further knowledge to the morphology of this species, which will result in a better understanding of this species.

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