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Dental morphometrics and taxonomic reassessment of Late Miocene boselaphines (Tragoportax, Selenoportax, Pachyportax) from the Bhandar Bone Bed (Dhok Pathan Formation), Pakistan

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ABSTRACT

Background: The Siwalik Group of the Himalayan foreland basin preserves a rich record of Late Miocene mammalian evolution, with the Dhok Pathan Formation yielding abundant boselaphine bovids. Deciduous premolars, particularly DP3, are rarely documented in these taxa, limiting understanding of juvenile morphology and taxonomic variability. Objective: To describe and diagnose a rare isolated left DP3 from the Bhandar Bone Bed (Dhok Pathan Formation) and compare it metrically and morphologically to published material for taxonomic assignment. Methods: The specimen was surface-collected, mechanically and chemically cleaned, catalogued as USKT-PC 100923, measured using a digital Vernier caliper, and photographed in standardized views. Qualitative description focused on preservation, enamel texture, cusp development, styles, ribs, median valley, fossettes, and cingulum. Quantitative comparison used length, width, and published DP3 measurements. Results: USKT-PC 100923 is an unworn left DP3 (length 18.60 mm, width 12.00 mm) with shiny smooth enamel, prominent cusps, well-developed labial styles and ribs, deep fossettes, shallow median valley, and anterior cingulum. Metrics fall within the range of published Tragoportax DP3 specimens. Conclusion: The specimen is assigned to Tragoportax punjabicus (Pilgrim, 1910), representing a rare documentation of deciduous dentition that enhances morphological data for Siwalik boselaphines.

Keywords
Boselaphini, deciduous premolar, Dhok Pathan Formation, Late Miocene, Siwaliks, Tragoportax punjabicus

INTRODUCTION

The Siwalik Group along the Himalayan foothills represents one of the most continuous and fossiliferous Neogene terrestrial sequences in southern Asia, documenting significant mammalian diversification during the Miocene (1,2). The Middle Siwaliks, encompassing the Nagri and Dhok Pathan formations, correspond to the Late Miocene interval and are characterised by thick sandstone and mudstone deposits formed in fluvial environments (3). The Dhok Pathan Formation, in particular, has yielded extensive vertebrate assemblages, including dominant artiodactyls such as bovids (4,5). Among Bovidae, the tribe Boselaphini is prominently represented in the Dhok Pathan Formation by medium- to large-sized genera, reflecting adaptations to mosaic woodland-grassland habitats with seasonal humidity (6,7). Bovids from this formation exhibit considerable morphological overlap in permanent dentition, complicating genus-level distinctions, especially between large forms like Selenoportax and Pachyportax (8). Deciduous teeth, however, remain poorly documented in Siwalik boselaphines, despite their potential to reveal ontogenetic variation and refine taxonomic diagnoses (9). The Bhandar Bone Bed in Jhelum District, Punjab, Pakistan, is a Dhok Pathan locality that has produced isolated bovid remains, but deciduous premolars are exceptionally rare there. The present study addresses this gap by describing a rare isolated left DP3 from the Bhandar Bone Bed and comparing it to published material. This specimen provides new insight into juvenile dental morphology of Dhok Pathan boselaphines and contributes to ongoing reassessment of taxonomic variability in the tribe. The objective is to describe and diagnose this rare DP3, assign it taxonomically through morphological and metric comparison, and evaluate its significance for Siwalik bovid systematics.

Materials and Methods

Specimens were collected through surface prospecting at the Bhandar Bone Bed, a locality within the Dhok Pathan Formation of the Middle Siwaliks in Jhelum District, Punjab, Pakistan. The Dhok Pathan Formation consists of alternating sandstones, clays, and shales deposited in fluvial settings during the Late Miocene (3,10). The studied specimen, an isolated left DP3, was recovered alongside other bovid teeth and catalogued as USKT-PC 100923 following institutional protocol combining collection year and serial number. Mechanical preparation involved brushes and needles, supplemented by acid treatment for matrix removal; broken fragments were consolidated using adhesive to preserve enamel integrity. The specimen is housed in the Department of Zoology, University of Sialkot, Pakistan. High-resolution photographs were taken using a DSLR camera in occlusal, lingual, and labial views with scale reference. Linear measurements (length and width in millimetres) were obtained using a digital Vernier caliper. Dental terminology follows standard descriptions for boselaphine premolars, emphasising cusp (protocone, paracone, metacone,

hypocone) prominence, labial structures (parastyle, mesostyle, metastyle, ribs), median valley depth, fossette size, and cingulum development (11). Comparative data derive exclusively from published measurements of Tragoportax DP3 specimens. Qualitative assessment focused on enamel texture, wear stage, and structural preservation; quantitative comparison involved direct range overlap and proportional ratios. Statistical inference was not applied due to limited sample size.

Systematic Palaeontology

Order Artiodactyla Owen, 1848 Suborder Ruminantia Scopoli, 1777 Family Bovidae Gray, 1821 Subfamily Bovinae Gill, 1872 Tribe Boselaphini Knottnerus-Meyer, 1907 Genus Tragoportax Pilgrim, 1937

Tragoportax punjabicus (Pilgrim, 1910)

Holotype. AMNH 19467, skull without hinder end of the occiput (11).

Type locality. Middle Siwaliks, Dhok Pathan, Punjab, Pakistan (12,13).

Stratigraphic range. Middle Siwaliks (14,15).

Diagnosis. A Tragoportax with moderately long, curved horn-cores with a large antero-posterior diameter, faintly twisted, slight torsion, cross-section triangular to subtriangular, well marked posterolateral and flattened sides. The postcornual fronto-parietal surface is a flat or slightly concave well defined depressed area, usually bordered laterally by well marked temporal ridges and caudally by a step leading to a slightly raised plateau.

Table 1. Measurements of USKT-PC 100923 (left DP3) in millimetres.

Specimen	Position	Length (mm)	Width (mm)	W/L ratio	Wear stage
USKT-PC 100923	lDP3	18.60	12.00	0.645	Unworn

Comparative measurements are summarised in Table 2, incorporating published DP3 data for *Tragoportax*. The length of USKT-PC 100923 falls within the observed range (16.74–19.26 mm), and width overlaps substantially (12.00–14.60 mm). Metric congruence supports morphological similarities in cusp and style development.

Table 2. Comparative measurements of DP3 in millimetres (comparative data from Bibi and Güleç, 2008 (9)).

Taxon	Catalogue no.	Position	Length (mm)	Width (mm)
Tragoportax punjabicus	USKT-PC 100923	lDP3	18.60	12.00
Tragoportax* cf. *amalthea	58 HAY09/007	lDP3	19.26	13 (e)
Tragoportax* cf. *amalthea	58-HAY19/114	rDP3	18.54	14.60
Tragoportax* cf. *amalthea	58-HAY19/209	lDP3	16.74	13.92

A species slightly smaller than Tragoportax browni, with relatively short upper premolar series; P2 rather longer than P3; upper molars with small entostyle; moderately developed styles and ribs; central cavities connect at mid wear and enamel moderately rugose (11,13,16).

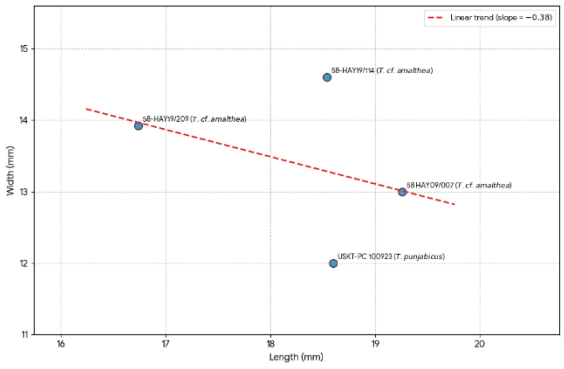

Figure 1 Figure X. Scatter plot illustrating the relationship between mesiodistal length and buccolingual width (in mm) of the upper deciduous premolar (DP3) in Late Miocene Tragoportax specimens from the Siwalik deposits. Individual points represent measured specimens of T. punjabicus and T. cf. amalthea, annotated by specimen number. The dashed regression line indicates a weak negative association between length and width (slope = −0.38), suggesting minor proportional variation in DP3 crown dimensions among the examined taxa.

USKT-PC 100923 is a well-preserved isolated left DP3 lacking breakage. The tooth is unworn, with no dentine exposure. Enamel is shiny and slightly smooth. Lingual and labial sides are prominent and well preserved, with the anterior side larger than the posterior. A shelf-like cingulum

is visible anteriorly. All cusps (protocone, hypocone, paracone, metacone) are prominent, clearly defined, well developed, and preserved, though cusp tips are slightly damaged. Labially, pillar-like structures including parastyle, paracone rib, mesostyle, metacone rib, and metastyle are highly prominent and developed. The median valley is shallow. Anterior and posterior fossettes are large and deep.

Differential diagnosis. The smaller size and weaker structure of the tooth distinguish it from large boselaphines such as Selenoportax and Pachyportax. Numerous boselaphine genera with varying body sizes have been identified from the Dhok Pathan Formation, including large forms Selenoportax and Pachyportax, and relatively small boselaphines Helicoportax, Elachistoceras, and Eotragus. Medium-sized boselaphines Tragoportax and Miotragocerus are known from the Siwaliks (17). The teeth are selenodont and tiny in size, allowing instantaneous differentiation from those of Selenoportax and Pachyportax due to lesser shape and fragile basal pillar (18). The morphometric data for USKT-PC 100923 are presented in Table 1. The tooth measures 18.60 mm in length and 12.00 mm in width, yielding a width/length ratio of 0.645. It exhibits no wear, consistent with an unworn stage.

DISCUSSION

The assignment of USKT-PC 100923 to Tragoportax punjabicus is robustly supported by its morphological and metric attributes, which align closely with published specimens of the species while distinguishing it from contemporaneous large boselaphines such as Selenoportax and Pachyportax (8,22). The unworn condition, smooth shiny enamel, prominent cusps, highly developed labial styles and ribs, deep fossettes, shallow median valley, and anterior shelf-like cingulum are characteristic of medium-sized boselaphine premolars, contrasting with the more robust and hypsodont dentition typical of larger genera in the Dhok Pathan Formation (17,18). Metric congruence, with length (18.60 mm) and width (12.00 mm) falling within the reported range for Tragoportax DP3 (16.74–19.26 mm length; 12.00–14.60 mm width), further corroborates this placement (9). This specimen thus extends the documented morphological variability in T. punjabicus, a species previously recognised primarily from permanent dentition and cranial elements in the Middle Siwaliks (11,13,23). The rarity of deciduous premolars in Siwalik boselaphines underscores the significance of this finding; such elements are infrequently preserved or reported, likely due to taphonomic biases favouring adult remains and the fragility of juvenile teeth (24). Comparative analyses with Eurasian Late Miocene Tragoportax (e.g., T. cf. amalthea from Sivas, Turkey) reveal consistent premolar proportions and structural features, supporting biogeographic affinities between Siwalik and Greco-Iranian provinces during the Turolian equivalent (9,25). However, the smaller dimensions and delicate basal structures here reinforce differentiation from larger taxa, aligning with earlier observations of size-based segregation among Dhok Pathan boselaphines (17). Theoretically, the documentation of juvenile dentition offers insights into ontogenetic trajectories within Boselaphini, potentially reflecting adaptations to mosaic habitats where medium-sized forms like Tragoportax exploited mixed feeding strategies amid increasing seasonality (8,26). Palaeoecologically, the predominance of boselaphines in the Bhandar Bone Bed assemblage indicates subtropical conditions with moist woodlands and occasional standing water bodies, consistent with fluvial deposition in the Dhok Pathan Formation (19,20,21). This humid mosaic likely facilitated the coexistence of medium- and large-sized grazers-browser intermediates, mirroring broader Late Miocene trends in southern Asia toward expanded grasslands (1,27). Strengths of this study include precise morphometric comparison with established datasets and the addition of a scarce ontogenetic stage to the Siwalik record, enhancing taxonomic resolution. Nevertheless, limitations are inherent in the isolated nature of the specimen and small sample size, precluding assessment of intraspecific variation, sexual dimorphism, or associated postcrania; methodological reliance on surface collection may introduce recovery biases, and generalizability is constrained to the Dhok Pathan Formation without broader stratigraphic sampling (10). Future investigations should prioritise targeted prospecting for deciduous elements across Siwalik localities, coupled with integrated cranio-dental and isotopic analyses to elucidate dietary shifts and dispersal patterns in Boselaphini. Such efforts would advance understanding of bovid diversification during the critical Late Miocene transition in southern Asia.

CONCLUSION

The DP3 crown measurements of Late Miocene Tragoportax specimens demonstrate limited and inconsistent dimensional variation, with no strong proportional relationship between mesiodistal length and buccolingual width. The regression trend indicates a weak negative association (slope = −0.38), suggesting that slightly longer DP3s are not necessarily wider, and in some cases may be marginally narrower. Overall, the observed pattern supports the interpretation that DP3 morphology in these specimens is relatively stable, and that differences among T. punjabicus and T. cf. amalthea fall within a narrow range of intraspecific or closely related interspecific variation.

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