

THE LATE MIOCENE BOVIDS OF MOHAL PATI, JHELUM, PUNJAB, PAKISTAN

M. Zaheer* and M. A. Khan

Fossil Display & Research Centre, Institute of Zoology, University of the Punjab, Quid-e-Azam Campus, Lahore, Pakistan

*Corresponding author's e-mail: mariamzaheer2009@gmail.com

ABSTRACT

Six species of bovids are identified based on the new collection done from the Late Miocene deposits in the vicinity of Mohal Pati, Punjab, Pakistan. The described specimens are allocated to *Prostrepsiceros vinayaki*, *Tragoportax punjabicus*, Genus indet. aff. *Eotragus*, *Pachyportax* sp., *Kobus* sp., and Hypsodontinae indet. The stratigraphic range of *Prostrepsiceros vinayaki* is extended from the previously known age, that of the subfamily Hypsodontinae is extended to Dhok Pathan Formation; incisor of the genus *Kobus* is described for the first time from the Siwalik Group. Also, we have commented on the recently done work on the bovid taxonomy and highlighted some of the problems present in the bovid taxonomy.

Key words: Siwaliks, Mohal Pati, *Prostrepsiceros*, *Tragoportax*, *Eotragus*, Miocene.

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INTRODUCTION

Bovidae is diverse and occupied most areas of the world and almost all habitats. The family is also present in the Indian subcontinent, where it is known both in the extant and extinct forms. The family has more than 20 million years of history in the fossil record, and a diverse assemblage of bovids is known from the Siwalik Group of the Indian subcontinent (Pilgrim, 1937, 1939; Akhtar, 1992; Barry *et al.*, 1982; Khan *et al.*, 2009, 2010, 2012, 2023; Antoine *et al.*, 2013; Abbas *et al.*, 2018). In the Middle Siwalik Subgroup, bovids were predominant taxa among all the ungulates (Barry *et al.*, 2002; Khan *et al.*, 2009, 2010, 2012) and in the Dhok Pathan Formation of this Subgroup, some large sized bovids were also present along with small to medium sized bovids. The taxonomic status of bovids is in flux and a recent publication of Gentry *et al.* (2014) has proposed a classification scheme of the Siwalik bovids to raise this issue and they have also provided the stratigraphic distribution of the bovids including the Dhok Pathan Formation bovids. In their preliminary study of Siwalik bovids, they have reported *Selenoportax* aff. *vexillarius*, *Selenoportax falconeri*, *Selenoportax giganteus*, *?Pachyportax* sp., Gen. indet., aff. *Selenoportax?* sp., *Miotragocerus pilgrimi*, *Miotragocerus punjabicus*, *Tragoportax salmontanus*, *?(Sivaceros) vedicus*, *Gazella lydekkeri*, *Prostrepsiceros vinayaki*, *?Prostrepsiceros*, large sp., *Nisidorcas planicornis*, *?Protragelaphus* sp., Antilopinae large sp. indet., *?Antilopinae*, small sp., *Kobus* sp. 1, *Kobus porrecticornis*, and *Kobus* sp. 2 from

Dhok Pathan Formation only. Diversity of the bovids is evident from the above listed species.

The purpose of this study is to describe the bovid specimens from the Dhok Pathan Formation outcrops of the Hasnot area and comment on recent work on bovid taxonomy. The specimens have been collected from the Bhandar Bone Bed of Pilgrim (1913) in the vicinity of Mohal Pati, comprising a cluster of localities.

Geographic and geological settings: Bhandar Bone Bed of Pilgrim (1913) is located nearby the Bandar and Mohal Pati villages, Jhelum, Punjab, Pakistan (Fig. 1). Mohal Pati is located about 3 km northeast of paleontologically famous Hasnot village and round about 1 km in the northeast of Bhandar village. The area around the Mohal Pati village corresponds to Brown locality 24 (B24) and collection has been done between B135 and B8, shown in Colbert (1935, fig. 22, p. 46). With reference to Pilgrim (1913), the Bhandar Bone Bed is characterized by the upper Dhok Pathan Formation, and Johnson *et al.* (1982) have palaeomagnetically calculated the ages of these localities. The updated ages of these localities are given, after the calibration with Cande and Kent (1995) geomagnetic polarity time scale, are given by Barry *et al.* (2002) as following; 6.670 to 6.306 Ma for B8, B24, and B135 while 6.684-6.448 Ma for B6-7 localities. The time relates well with the upper Dhok Pathan Formation as well as the upper Late Miocene. Lithologically, pale yellow silt/claystone and dark to light colored sandstone with minute quantity of conglomerates, denoting to Dhok Pathan Formation of the Middle Siwaliks.

MATERIALS AND METHODS

Material: The material includes seventeen (17) specimens including mandibular fragments, and isolated or serially arranged upper and lower incisors, premolars, and molars.

Fossil preparation: These specimens were brought in the Dr. Muhammad Akbar Khan's Palaeontology Lab for preparation. The specimens were washed with water to remove dirt and sand, then prepared with fine needles, and broken parts were glued with GMSA glue.

Cataloging: The specimens were cataloged using year number as nominator, serial number of specimens in that year as denominator, and PUPC as institutional abbreviation, e.g., (PUPC 23/224).

Measurements and nomenclature: Two measurements, antero-posterior as length and labiolingual as width in occlusal view, were taken using digital Vernier caliper in millimeters in precision of 0.01 mm. The measurements are given in Table 1. Nomenclature follows slightly modified from Gentry *et al.* (1999) as given in Khan *et al.* (2015, fig. 2).

Photography: The photos of specimens were taken using Canon 6D and plates are made using Adobe Photoshop CC.

Systematic Palaeontology:

Family Bovidae Gray, 1821
Subfamily Gazellinae Gray, 1821
Tribe Antilopini Gray, 1821

Prostrepsiceros vinayaki Pilgrim, 1939

Holotype: GSI -B 799, the left horn core (Pilgrim, 1939).

Type locality: Nila, Attock, Punjab, Pakistan (Pilgrim, 1939).

Emended diagnosis (based on Bibi 2011): A bovid of medium to small size characterized by horn cores that arise from above the orbit with the moderate inclination and basal divergence, torsion that is anticlockwise in the right horn core and relatively helical, very strong mediolateral compression with an oval basal cross-section and flat antero-medial surface, a prominent anterior keel that originates anteromedially, and a posterior keel that is variable in expression. Shallow postcornual fossa is present, and the supraorbital foramina is small, pear-shaped, single, or multiple. The protocone is well-pinned and compressed antero-posteriorly, fossette narrow and crescentic in upper molar; corpus is thin, inward deflected and very deep under m3; p2 is small, paraconid devoid of parastylid, all the valleys are small and slit-like; hypsodont lower molars with narrow and crescentic fossette, weakly to

moderately developed ectostylids, moderately rugose enamel.

Stratigraphic range: Dhok Pathan Formation, Late Miocene (Pilgrim 1939; this study).

New material: PUPC 23/216, partially broken right M3?; PUPC 23/222, isolated right p2; PUPC 23/219, isolated partially broken left m1; PUPC 23/215, isolated partially broken left m2; PUPC 23/214, left mandibular fragment with partially broken m1-m3.

Description: PUPC 23/216 is a partially broken and moderately worn upper molar. It is mostly broken labially resulting in complete loss of metacone, and enamel of paracone is partially preserved at labial side (Fig. 2.1). Preprotocrista is slightly flat while postprotocrista is round. Prehypocrista is small and posthypocrista is large and flat (pinched) making hypocone almost rectangular. The anterior fossette is fully preserved and it is small and narrow. Enamel is slightly to moderately rugose. No style or rib is preserved while roots are partially preserved.

PUPC 23/222 represents a lower p2 with partially preserved lower second premolar with a small part of silt covered corpus (Fig. 2.2). The premolar is well-preserved and just slightly worn at protocone-metacone apex. Paraconid is small and devoid of parastylid, protoconid and metaconid are distinct, hypoconid and entoconid with entostylid are well-developed. All the valleys are small and slit-like. The labial groove is small. The enamel is slightly rugose.

PUPC 23/219 is a partially broken lower first molar. The apices of metaconid and entoconid are broken and tooth is highly worn (Fig. 2.3). A partially preserved and weak goat fold is present at praeprotocristid which is slightly compressed and longer than postprotocristid. The hypoconid is V shaped and both pre- and posthypocristid are equal in size. Due to heavy wear both anterior and posterior fossettes have become extremely small and narrow. The styles and ribs are very weakly developed but ectostylid is well-developed. Enamel is slightly rugose at labial side.

PUPC 23/215 is a partially broken and moderately worn lower second molar. The apex of entoconid is partially broken (Fig. 2.4). A large, prominent but weak goat fold is present at the praeprotocristid which is larger than postprotocristid. The hypoconid is triangular in shape but unlike the PUPC 23/219, the prehypocristid is slightly larger than posthypocristids. The fossettes are small and extremely narrow. The stylids which are divergent, and ribs are weak including a small ectostylid present in the median. The enamel is moderately rugose. A fragment of corpus at labial side, and roots are also preserved.

PUPC 23/214 represents is mandibular fragment with partially preserved first molar, and partially broken second and third molar. The corpus is slightly bent under

the junction between m1 and m2 at the lingual side resulting in inward deflection of molars (Fig. 2.5). The length of the mandibular fragment is 46.6 mm. m1 is slightly higher than m1 and m2, and enamel is almost completely lost in anterior lobe resulting in preservation of some part of dentine, while in posterior lobe hypoconid is completely preserved and entoconid is completely broken. m2 is most preserved, only apices of metaconid and entoconid are broken. The goat fold is well-developed and present on the preprotocristid. The cusps are oriented slightly posteriorly. Praeprotocristid and prehypocristid are longer than respective posteristids. Fossettes are very small and narrow. Styliids and ribs are extremely weak. Enamel is moderately rugose. m3 is partially broken in which hypocone is partially broken, apex of metaconid, entoconid, and hypoconulid are completely broken. The goat fold is well-developed and large. Rest of the morphology is similar to m2.

Comparison: The described material shows morphological features of Antilopini in very hypsodont, styles diverge strongly from the neck of the crown, the enamel bordering the fossettes of the molar teeth shows little or no tendency towards a complicated pattern of folding, and goat fold is less marked than in some caprine genera (Pilgrim, 1937, 1939; Gentry, 1966). The common Antilopini in Dhok Pathan Formation is *Gazella*. However, the studied specimens differ from *Gazella* in having relatively large size, more rugosity and presence of relatively large and thick ectostylid (basal pillar) (Fig. 2.1-5, Table 1). The other antilopine species is *Prostrepsiceros*, which is reported from the Dhok Pathan Formation based on the left horn core. No dental remains known to this species from the Siwalik, however, comparison with the right mandible (MNHN.F.TRQ412) with p4-m3 from Küçükçekmece West, Turkey, described and figured by Kostopoulos and Sen (2016, fig. 10, p. 290), indicates close resemblance between the described and Turkish specimen. This morphological similarities and size of the specimens (Table 1) allow us to designate new specimens to *Prostrepsiceros* and to the Siwalik species *P. vinayaki*.

Subfamily Bovinae Gray, 1821
Tribe Boselaphini Kottnerus-Meyer, 1907
Genus *Tragoportax* Pilgrim, 1937

***Tragoportax punjabicus* (Pilgrim, 1910)**

Holotype: GSI-B 486, a skull (Pilgrim, 1937).

Type locality: Dhok Pathan, Talagang, Punjab, Pakistan (Pilgrim, 1937).

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. The basioccipital has a longitudinal groove between the anterior and the posterior tuberosities, at the bottom of which often runs a weak sagittal crest. Occipital is high and basioccipital is short. Premolar series is short, upper molars hypsodont with divergent styles and prominent median ribs. P2 has a distally sloping parastyle with a short parastyle-mesostyle part and bilobed lingually. P3 has a lingually inflated hypocone. The p4 has a strong paraconid, metaconid and entoconid. The entoconid is fused with the endostylid. The anterior valley of p4 is open (Khan *et al.*, 2010).

Stratigraphic range: Chinji Formation, Middle Miocene (Khan *et al.*, 2013) and Nagri and Dhok Pathan formations, Late Miocene (Pilgrim, 1937, 1939; Akhtar, 1992; Khan *et al.*, 2010, 2012, 2014; Abbas *et al.*, 2018)

New material: PUPC 23/224, left M1; PUPC 23/225, right M2; PUPC 23/227, right M2; PUPC 23/226, left p2.

Description: PUPC 23/224 is a moderately worn upper first molar with small fragment of maxillary bone (Fig. 2.6). The roots of P4 are also partially preserved, while maxillary bone is present under the molar and on the labial side but roots are exposed. The M1 is well-preserved. The anterior lobe is more worn, smaller, and lower than the posterior. The protocone is extremely pinched/compressed antero-posteriorly and preprotocrista bears a well-developed cingulum transversely. The postprotocrista is small, reaching only two third of the prehypocrista. Anterior fossette is small, narrow, and wide posteriorly while posterior fossette is large, and wide anteriorly. Styles and ribs are well-developed, thick, and strong while a small entostyle is present in the median valley. The enamel is moderately rugose. PUPC 23/225 is a well-preserved and moderately worn upper second molar. It is morphologically like PUPC 23/224 except fossettes are larger and wider entostyle is large and thick, and posthypocrista is slightly pinched (Fig. 2.7).

PUPC 23/227 is a highly worn and partially broken upper second molar (Fig. 2.8). The protocone is partially broken resulting in loss of some part of postprotocrista. Due to the heavy wear and partial breakage, the morphology of the tooth has slightly deformed. The anterior lobe is smaller and slightly lower than the posterior. The protocone is positioned slightly anterior, oriented anteriorly, and a weak cingulum is present at the preprotocrista. The fossettes have become extremely narrow. The styles and ribs are prominent but weak probably due to wear. Prehypocrista is slating due to slight pinching, posthypocrista is also compressed and bears a weak cingulum. A small entostyle is present in

the median valley. Enamel is moderately rugose. The roots are also well-preserved.

PUPC 23/226 is unworn and well-preserved lower second premolar. It is birooted and posterior root is slightly preserved (Fig. 2.9). The paraconid is well-developed and large. The protoconid and metaconid are easily distinguishable. The hypoconid, entoconid and entostylid are also prominent. An apical slit near the metaconid represents the anterior valley, the median valley is also slit-like but much larger than the anterior valley while the posterior valley is largest and lying between the entoconid and entostylid. The enamel is shiny and moderately rugose.

Comparison: The described teeth (PUPC 23/225, PUPC 23/225, PUPC 23/227, PUPC 23/226) are clearly different from that of *Pachyportax* and *Selenoportax* by their smaller size, their more brachyodont character, and the weaker entostyles. The upper molars (PUPC 23/225, PUPC 23/225, PUPC 23/227) are much quadrate and hypsodont type, styles are prominent and divergent, the protocone is pinched/compressed antero-posteriorly while hypocone is compressed anteriorly, entostyles are weakly developed fossettes are moderately wide, and enamel is also moderately rugose (Fig. 2.6-9). These characters associate the these studied specimens with genus *Tragoptax* as such morphological features are known in the type skull of *T. browni* (synonym of *T. punjabicus*) described and figured by Pilgrim (1939 fig. 28 p. 787). The lower premolar, PUPC 23/226 also shows some features of genus *Tragoptax* like the moderately rugose enamel and small and open valleys (Fig. 2.9) in addition to size that is smaller than *Pachyportax* and *Selenoportax*. Based on the above-mentioned morphometric similarity of the new material with that of *T. punjabicus*, the specimens are described here as *T. punjabicus*.

Genus indet. aff. *Eotragus*

New material: PUPC 23/223, IM3; PUPC 23/221, right mandibular fragment with highly worn p4-m1; PUPC 23/220, right mandibular fragment with posterior lobe of m1, highly worn and partially broken m2-m3.

Description: PUPC 23/223 is an upper third molar with some part of maxillary bone which is partly covered with hard siltstone (Fig. 3.1). The tooth is moderately worn reaching its late stage. The molar morphology is well-preserved, except the apex of paracone is partially broken. The anterior lobe is wider than the posterior one. The protocone is V shaped because of the slight compression of preprotocrista. The postprotocrista meets the prehypocrista and does not reach postparacrista. The prehypocrista is small and posthypocrista is slightly compressed. The fossettes are extremely narrow but slightly wide posteriorly. The styles and ribs are well-developed. The enamel is moderately rugose.

PUPC 23/221 is a small mandibular fragment with the last premolar and first molar (Fig. 3.2). The corpus is fragile and cracked under the junction of p4 and m1. It gradually becomes wider posteriorly. The preserved mandibular length is 28.8 mm. Both teeth are highly worn, however p4 is less worn and better preserved. In p4, the paraconid and parastylid are easily distinguishable, the protoconid, metaconid, hypoconid and entostylid are distinguished structure; the entoconid is incipient. The anterior valley is large, deep, open at apex and close at base. Due to the wear, the median valley has become small in the form of an islet and the posterior valley has vanished. A large labial groove is present anterior to the hypoconid. The m1 is worn, and the preprotocristid and entoconid are broken. The fossettes, stylids, and ribs are not present, however, a prominent ectostylid is present in the median valley. The cusps are oriented posteriorly.

PUPC 23/220 represents a mandibular fragment with a partially broken and worn molar series. The corpus is thin and weathered. The preserved mandibular length is 33.1 mm. The dentine of cusps of the posterior lobe m1 are preserved (Fig. 3.3). The anterior lobe of m2 is also partially preserved where postprotocristid is partially preserved, and enamel is only preserved at the base of metaconid and metastylid, which is extremely divergent. Also, the apex of entoconid is broken. Only posterior fossette is preserved which have become extremely narrow. The m3 is partially broken as only the anterior portion of hypoconulid is preserved at labial side. The tooth is worn like m2, but it is more preserved. The fossettes are narrow and crescentic in shape. Stylids are extremely weak. A weak ectostylid is present in the median valley. The enamel is rugose.

Comparison: The specimens (PUPC 23/223, PUPC 23/221, PUPC 23/220) described here poses a lot of problems in the taxonomic attribution (except PUPC 23/223) due to the extreme wear and breakage, and the affinity of these specimens to *Eotragus* is based on the thin corpus, small size, rugose enamel and aligned lingual cusps in molars, in addition to the primitive nature (Fig. 3.1-3, Table 1). PUPC 23/223, an M3, is a well-preserved and displays features of typical bovid characteristics that are very close to "*Protoryx*" sp. described and figured by Kostopoulos *et al.* (2018, fig. 6, p. 188). However, such a late occurrence of *Protoryx* has not been suggested from the Siwalik and keeping this in mind along with general morphology and size of the specimens (Fig. 2, Table 1), they are affinitised to *Eotragus*.

Tribe Bovini Gray, 1821

Genus *Pachyportax* Pilgrim, 1937

Pachyportax sp.

New material: PUPC 23/228, partially broken rM2.

Description: PUPC 23/228 is a partially broken upper second molar. Only the partial part of prehypocrista is preserved. Both the preproto- and postprotocrista are pinched toward lingual side while round towards the labial side. Only the anterior fossette is preserved and it is wide. The styles and ribs are well-developed, thick and strong though metaconous rib and metastyle are slightly less developed. The median valley equipped with a small tubercle like entostyle. The enamel is rugose at the lingual side (Fig. 3.4).

Comparison: The described tooth PUPC 23/228 seems to be hypsodont despite wear, entostyle is prominent although broken, paracone and metacone are strongly convex even riblike internally, and the outline of the crown is quadrate (Fig. 3.4). These features associate it with the genus *Pachyportax*. It differs from *Selenoportax* in having a small size, less hypsodont, the base of the crown somewhat broader, and somewhat less rugose (Pilgrim, 1937, 1939). Also, PUPC 23/228 show morphological resemblance to M2 AMNH 29964 described Pilgrim (1939 fig. 51 p. 827). Based on these characters and resemblance, PUPC 23/228 is allocated to the genus *Pachyportax*, however, as the specimens is partially broken, hindering specific allocation, and referred here as *Pachyportax* sp.
Tribe Reduncini Gray, 1821

Kobus sp.

New Material: PUPC 23/230, right i2; PUPC 23/229, right mandibular fragment with m1.

Description: PUPC 23/230 represents a moderately worn lower incisor. It is spatula shaped with rectangular outline. The anterior apex of the incisor is round, and its wall is bulging out making the posterior side convex. The posterior side is concave because the apex of the incisor is long and pointed. The enamel is not present on the lingual side except near the root crown junction. The enamel is smooth (Fig. 3.5).

PUPC 23/229 is a small mandibular fragment with a lower first molar. The corpus is partially preserved but it is stout and thick (Fig. 3.6). The preserved mandibular length is 24.5 mm. The morphological features in m1 are well-preserved and it is only slightly worn. The labial cusps are oriented posteriorly, and apices of the cusps are sharp. A large goat fold is present at the preprotocristid. The preprotocristid is slightly pinched and longer than the postprotocristid. The fossettes are wide centrally and less deep. The metastylid is well-developed and thick but partially broken at the apex, the metaconous rib is well-developed and lying posteriorly. The mesostylid is complete and well-developed. The entostylid is also well-developed and thick while the entocounous rib is less developed. A moderately developed ectostylid is present in the median valley which is broken at the apex.

Comparison: The morphology of PUPC 23/230 (Fig. 3.5) matches well with the i2 of the extant bovid genus *Kobus* in having very pointed apex at the anterior side which is also concave, round posterior apex and convex posterior outline. The blade is also broad as compared to the reported incisors of the genus *Gazella* and is smaller than that of giraffids and palaeomerycids. The enamel is smooth to further distinguish it from the giraffids and palaeomerycids. PUPC 23/229 is characterized by better-developed ribs, more pinched labial cusps, relatively weak goat fold, and smaller ectostylid (Fig. 3.6) to associate it to the tribe Reduncini as compared to rounded ribs and cusps, tall and large ectostylid, and large goat fold that are found in Alcephalini. The predominant Late Miocene reduncine genus is *Kobus* (Gentry *et al.* 2014), hence, the specimens are allocated to the genus *Kobus* but more specimens are needed for the specific allocation.

Hypsodontinae indet.

New material: PUPC 23/217, right mandibular fragment with m3; PUPC 23/218, left m3.

Description: PUPC 23/217 is a mandibular fragment with hypsodont lower third molar. The corpus is thin and seems not much deep. The preserved mandibular length is 20.9 mm. It is at late stage of early wear and the apices of metaconid and entoconid are partially broken (Fig. 3.7). The first lobe is much larger than the second one which is larger than the third one, and the tooth becomes narrow posteriorly. A well-developed and thick goat fold is present at the praeprotocristid. The cusps are oriented posteriorly. The protoconid and hypoconid are V shaped and their precristids are long. The fossettes are narrow but long. Only the metastylid is well-developed. The hypoconulid is well-developed and has a small back fossette of m3. Posterior valley has a small tubercle at its base.

PUPC 23/218 represents a slightly worn and well-preserved lower third molar. It is hypsodont, cusps are crescentic, and enamel is rugose (Fig. 3.8). The molar is slightly convex lingually, concave labially and the anterior lobe is high. A large goat fold is present on the preprotoconid. The preprotocristid is pinched while the postprotocristid is round at the apex. On the other hand, pre- and posthypocristids are slightly pinched. The metastylid is slightly broken at the apex, the mesostylid is developed from the mid to apex, and the entostylid is weakly developed. The ribs are pronounced. The fossettes are moderately wide. The anterior valley has a large ectostylid that almost reach the apex and posterior valley is small and devoid of anything. The hypoconulid is also well-developed, becoming pointed posteriorly and having a small postfossette of m3.

Comparison: PUPC 23/217 and PUPC 23/218 are hypsodont, thin, styles are rather straight, and enamel is rugose. PUPC 23/217 is metrically and morphologically,

in terms of the presence of goat fold, weak stylids, and lack of ectostylid in the median valley, close to *Gazella* but the rugosity is more than previously reported in known Siwalik species of the genus *Gazella* and favours its allocation to *Kubanostragus* but being only specimen in the collection and lack of satisfactory record of this genus in the Siwalik do not permit such allocation. PUPC 23/217 is more like miniature *Selenoportax* in its general morphology that can be associated to genus *Helicoptax* as reported by Pilgrim (1937, 1939). However, as mentioned above, the tooth has a more developed goat

fold, more hypsodont, the presence of extremely developed ectostylid in the anterior valley, and extremely rugose enamel (Fig. 3.8) do not allow to associate this specimen to the genus *Helicoptax*, and the hypsodonty is in favour of subfamily Hypsodontinae rather than the tribe Bovini or Boselaphini. In the present state of knowledge of previously recorded genera from the Siwaliks and lack of more material, both these molars are here designated as Hypsodontinae indet. until more material is collected.

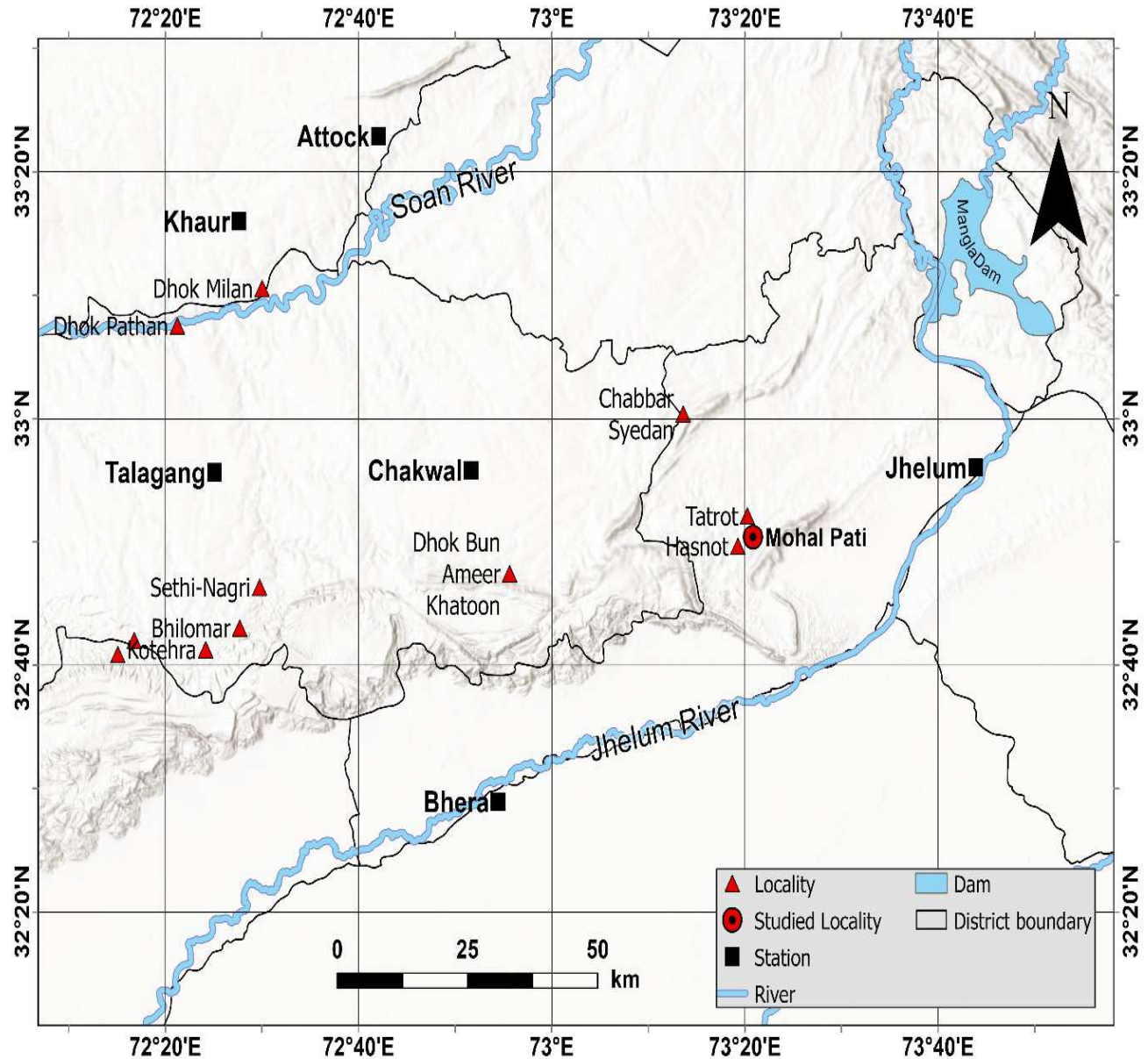


Fig. 1. Location of the Mohal Pati site in relation to Hasnot and Tatrot in the district Jhelum, Punjab, Pakistan.

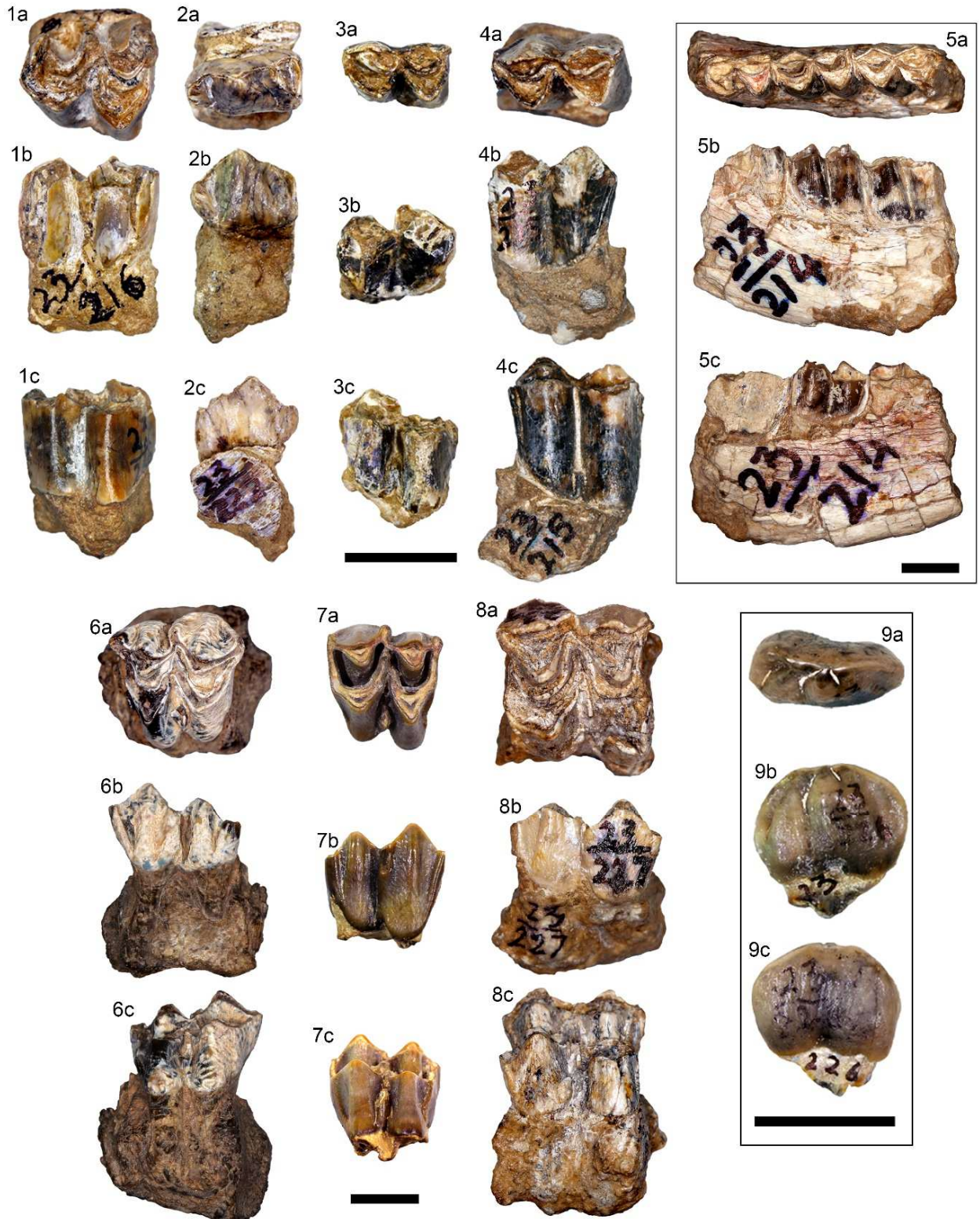


Fig. 2. *Prostrepsiceros vinayaki*. 1. PUPC 23/216, partially broken right M3?; 2. PUPC 23/222, isolated right p2; 3. PUPC 23/219, isolated partially broken left m1; 4. PUPC 23/215, isolated partially broken left m2; 5. PUPC 23/214, left mandibular fragment with partially broken m1-m3; *Tragoportax punjabicus*. 6. PUPC 23/224, left M1; 7. PUPC 23/225, right M2; 8. PUPC 23/227, right M2; 9. PUPC 23/226, left p2. Views. a) occlusal, b) lingual, c) labial. Scale bar equals to 10 mm.

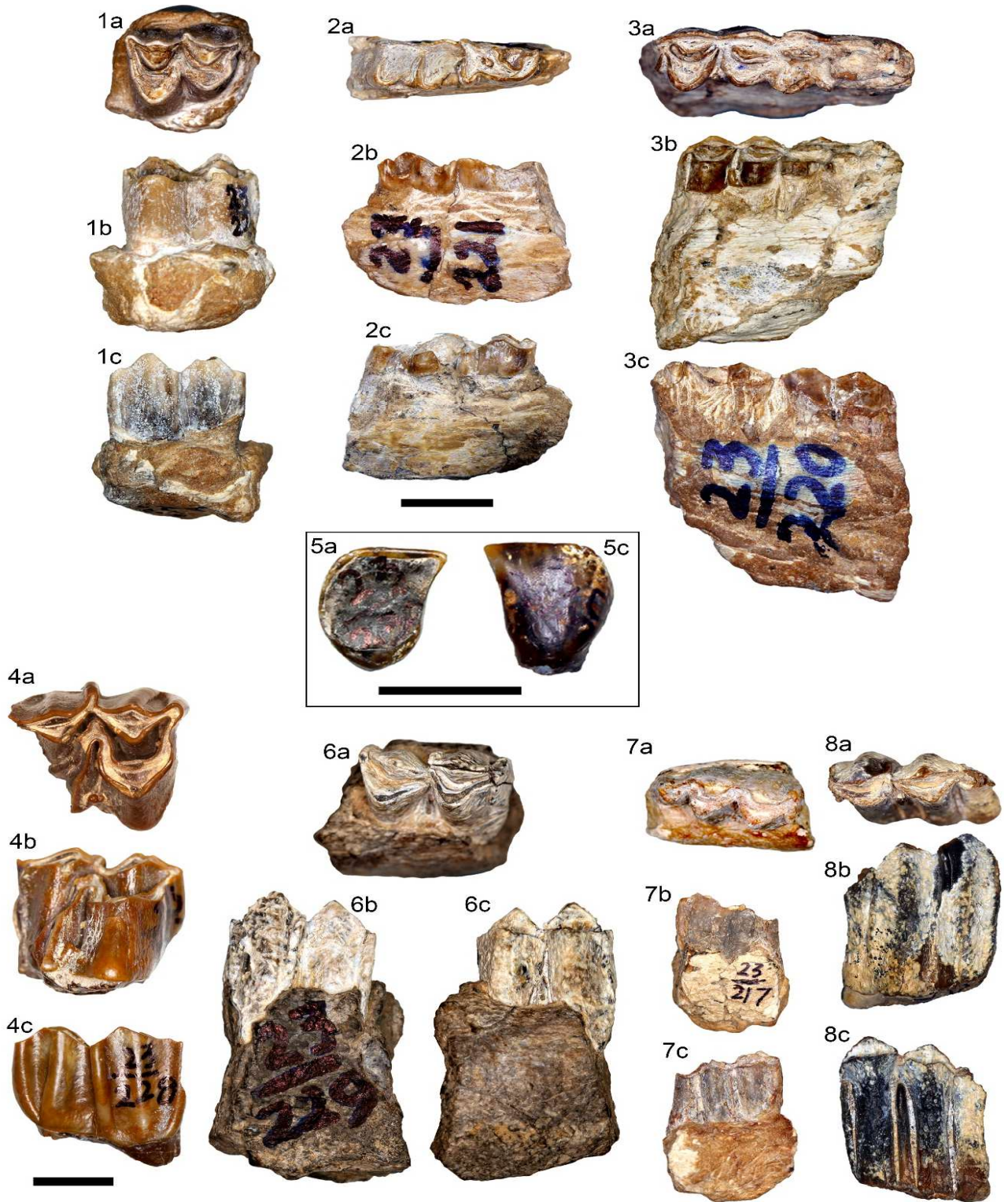


Fig. 3. Genus indet. aff. *Eotragus*. 1. PUPC 23/223, 1M3; 2. PUPC 23/221, right mandibular fragment with highly worn p4-m1; 3. PUPC 23/220, right mandibular fragment with posterior lobe of m1, highly worn and partially broken m2-m3; *Pachyportax* sp. 4. PUPC 23/228, partially broken rM2; *Kobus* sp. 5. PUPC 23/230, right i2; 6. PUPC 23/229, right mandibular fragment with m1; Hypsodontinae indet. 7. PUPC 23/217, right mandibular fragment with m3; 8. PUPC 23/218, left m3. Views. a) occlusal, b) lingual, c) labial. Scale bar equals to 10 mm.

Table 1. Comparative measurements of the specimens described in this.

Taxa	Catalog No.	Nature/Position	Length	Width	Reference	Comments
<i>Tragoptax punjabicus</i>	PUPC 23/224*	Left M1	18.2	18.8		
	PUPC 23/225*	Right M2	18.5	19.8		
	PUPC 23/227*	Right M2	19.8	21.7		
	PUPC 23/226*	Left p2	13	6.2		
<i>Tragoptax punjabicus</i>	AMNH 19662	M1	18	18	Pilgrim 1937	<i>T. browni</i> type skull
		M2	20	20		
<i>Prostrepsiceros vinayaki</i>	AMNH 29884	p2	15.5	11.5		
	GSI-B 486	M1	18	18		
		M2	20	20		
	GSI-B 820	p2	10.5	7		
	PUPC 23/216*	Right M3?	13	13**		
	PUPC 23/222*	Right p2	10.9	5.4		
	PUPC 23/219*	Left m1	12	7.5		
	PUPC 23/215*	left m2	13.2	8.7		
	PUPC 23/214*	Left m1	11.4 est.	8 est.		
		Left m2	13 8.6	8.3		
<i>Prostrepsiceros</i> sp.		Left m3	14.2**	8.6		
	TRQ412	Right m1	9.2	6.7		
		Right m2	11.2	8.4		
		Right m3	16.2	8.2		
		Right M2	21.1**	21.3		
		Left M2	19	23	Kostopoulos & Sen 2016	
<i>Pachyoptax</i> sp.	PUPC 23/228*	Left M2	14.4	13.8		
	PC-GCUF 11/139	Left M3	10	6.5	Abbas <i>et al.</i> 2018	
<i>P. cf. nagrii</i>	PUPC 23/223*	Right p4	11	7.4		
	PUPC 23/221*	Right m1	11.6	8.7		
Genus indet. aff. <i>Eotragus</i>	PUPC 23/220*	Right m2	14**	8.6		
		Right m3	10.4	11.58		
	GSP-Y 41459	rM3	13.1	11.5	Solounias <i>et al.</i> 1995	
	Sa 1033	Left M3	13.4	11.7	Van der Made 2012	
	Sa 1036	Left M3	11.8	11.5		
	Sa 1057	Right M3	15.7	14.6		
	Sa 1096	Left M3	14.1	15.5		
	Sa 10793b	Left M3	11.4	6.4		
	Sa 1035	right p4	12.4	7.7		
		Right m1	13.7	8.6		
<i>Eotragus noyei</i>		Right m2	19.3	8.6		
		Right m3				
<i>Eotragus clavatus</i>						

	Sa 1059	right p4	11.4	6.5
		Right m1	11.6	8.3
		Right m2	13.2	8.4
		Right m3	16.4	8.4
	Sa 1097	right p4	11.4	7.8
		Right m1	12.3	9.1
		Right m2	14	11.1
		Right m3	16.8	9.6
<i>Kobus</i> sp.	PUPC 23/230*	Right i2	8	6.3
	PUPC 23/229*	Right m1	17.6	10.6
Hypsodontinae indet.	PUPC 23/217*	Right m3	19	8.4
	PUPC 23/218*	Left m3	21.1	10.2
<i>Helicoportax</i> cf. <i>tragelaphoides</i>	GSI-B 821	Left m3	23	10.5
<i>H. praecox</i>	AMNH 29868	m3	22	9.5
<i>Miotragocerus</i> cf. <i>gluten</i>	AMNH 19426	m3	21	11
? <i>Miotragocerus</i> sp.	AMNH 29863	m3	23	10
	AMNH 19578	m3	23	10.5

Pilgrim 1937

DISCUSSION

The family Bovidae is diverse and abundant in the Siwaliks, and this has been reported in many previous studies (e.g., Pilgrim, 1937, 1939; Akhtar, 1992; Khan, 2007; Khan *et al.*, 2009, 2010, 2012, 2013; Gentry *et al.*, 2014; Babar, 2017; Abbas *et al.*, 2018; Asim *et al.*, 2020). The diversity of the Siwalik bovids is underestimated and a lot of genera and species were either considered *nomen dubium* or have been synonymized with other genera and species (see Solounias, 1981; Kostopoulos, 2005; Bibi, 2011; Abbas *et al.*, 2021) are now being considered valid, hence, the taxonomy of the Siwalik bovid is in flux and there is every likelihood the presence of new genera and species in the Siwaliks (Gentry *et al.*, 2014; Khan, *et al.*, 2021). Such an influx in the taxonomic analysis always creates problems for researchers, and extraordinary cautious steps are necessary when describing new, specifically isolated material.

The bovid material described in this study has been collected from the extension of Bhandar Bone Bed near the Mohal Pati village. This bone bed, from where the described specimens are collected, is dated between 6.684 to 6.306 million years in the previous studies (Johnson *et al.*, 1982; Barry *et al.*, 1982, 2002) and its fauna is typical of the upper Dhok Pathan Formation reported from the Hasnot area (see Khan *et al.*, 2009; Batool *et al.*, 2014, 2015, 2016). The new material has been attributed to *Prostrepsiceros vinayaki*, *Tragoptax punjabicus*, genus indet. aff. *Eotragus*, *Pachyoptax* sp., *Kobus* sp., and Hypsodontinae indet. This indicates that between 6 to 5 million years, a diverse assemblage of the bovids was present in this area.

The genus *Prostrepsiceros* is mainly known from the Late Miocene of Eurasia, perhaps Greco-Iranian Province (Gentry, 1971; Bouvain and Thomas, 1992; Kostopoulos, 2005, 2009; Bibi & Güleç, 2008; Bibi, 2011; Geraads *et al.*, 2011; Kostopoulos & Bernor, 2011; Kostopoulos & Sen, 2016; Spassov *et al.*, 2019) in addition to Africa (Bibi, 2011). It was reported from the Siwaliks as Gazellinae gen. indet. (aff. *Helicotragus*) *vinayaki* based on left horn core from the Dhok Pathan Formation of Nila by Pilgrim (1939), later ascribed as *Prostrepsiceros vinayaki*. Genus *Prostrepsiceros* has not been described by Khan *et al.* (2009) and Batool *et al.* (2016) from the Hasnot area. In his most comprehensive PhD work, Khan (2007) has not reported *Prostrepsiceros* from this area. This clearly indicates that the description of *Prostrepsiceros* from the upper Dhok Pathan Formation is a valuable addition to paleontology of the area. Further, it is interesting that Gentry *et al.* (2014) confined *Prostrepsiceros* in a very short period i.e., 8.3 to 7.9 Ma and it is not supported by our study, however, Bibi (2011) has reported *Prostrepsiceros* cf. *vinayaki*

from Asa Koma and Kuseralee Members of the Middle Awash, Ethiopia that ranges from ~5.7 and ~5.2 Ma. Hence, we are extending the known age range of *Prostrepsiceros vinayaki* and describing the dentition of this species from the Siwalik Group for the first time. Gentry *et al.* (2014) also reported the other antilopine species from the Siwalik that are closely related to *Prostrepsiceros* include ?*Prostrepsiceros* large sp. (8.1 Ma), *Nisidorcas planicornis* (9.0 Ma), ?*Gazella* sp. (13.2 to 12.0 Ma), and *Gazella lydekkeri* (10.1 to ?6.2 Ma).

The genus *Tragoptax* has been reported from the Siwaliks since the work of Pilgrim (1910) in the form of *Tragocerus punjabicus* that was later ascribed as *Tragoptax punjabicus* (Solounias, 1981). The type species of the genus is *T. salmontanus*, and there is no reconsideration for this species. However, other Siwalik species of the genus are under considerable debate since the work of Kretzoi (1941), and Khan *et al.* (2023) have recently reviewed the literature and concluded that only two species (*T. salmontanus* and *T. punjabicus*) are present in the Siwaliks. Nevertheless, suggested synonymy of *T. punjabicus* and *T. amalthea* by various researchers need to be resolved along with synonymy of Siwalik *Tragoptax* species with *Miotragocerus* suggested by Gentry (1974) and Gentry *et al.* (2014) also unresolved. Although, the material described here is not enough to comment on this issue, however, based on the material present in the Dr. Abu Bakr Fossil Display & Research Centre, University of the Punjab, Lahore, Pakistan and the material described by Khan *et al.* (2010, 2012), we do not believe that Siwalik *Tragoptax* species can be synonymized with the genus *Miotragocerus*.

Though, the material attributed to the genus indet. aff. *Eotragus* is fragmentary except the upper third molar but the general morphology and size of the specimens match well with the genus *Eotragus* rather than *Gazella* or any other genus. The genus *Eotragus* is also known in various countries of Afro-Eurasia (see Van der Made, 2012; Suraprasit *et al.*, 2015). From the Indian subcontinent, two species, *E. minus* and *E. noyei*, are known. *E. minus* is known from the Bugti area outside the Siwaliks (Ginsburg *et al.*, 2001) while *E. noyei* is known from the Siwalik and Bugti areas of Pakistan (Solounias *et al.*, 1995; Khan *et al.*, 2021). Besides these, Khan *et al.* (2008, 2009) described some specimens as *Eotragus* sp. from the Lower and Middle Siwaliks. The lower third molar (GCUF-PC 08/01) described by Khan *et al.* (2008) is similar in morphology to the lower third molar of *Eoceros cristatus* (= *Eotragus*) figured by Zittel (1925, fig. 290, p. 212) and lower third molars of *Eotragus clavatus* described and figured by (Van der Made 2012, fig. 96-101, p. 170), however, GCUF-PC 08/01 is more worn. On the other hand, the teeth in the mandibular fragment (PUPC 05/11) described and figured by Khan *et al.* (2009, fig. 5.10, p. 745) has more

compressed labial cusps that are posteriorly oriented as well as its size is small. Such compression of labial and posterior orientation cusps is also seen in the smallest Siwalik bovid species, *Elachistoceras khauristanensis* (Thomas, 1977, plate 15, fig. 4, 10-11). Such morphology along with small size of the teeth, indicates that PUPC 05/11 may not belong to *Eotragus* rather to *Elachistoceras*. The dental material described by Khan AM *et al.* (2021) as *E. noyei* is evidently smaller than the previously described *E. noyei* material and falls in the range of *Elachistoceras khauristanensis*. Also, the morphology of molars is quite like M1 (GSP 7047) described and figured by Thomas (1977, plate 15, fig. 6) in having compressed protocone, narrow fossettes, well-developed styles and paraconous rib, while lower dentition seems more hypsodont than *Eotragus*. We can say that the material described by Khan *et al.* (2021) as *E. noyei* is heterospecific.

The genus *Pachyportax* was ascribed by Pilgrim (1937) and he identified two species, *P. latidens* and *P. nagrii* from the Siwaliks. Later, he also erected a subspecies, *P. l. dhokpathanensis* based on the cranial material from the Dhok Pathan type locality that was later synonymized with *P. latidens* (Khan *et al.*, 2009, 2010, 2012). For a long time, only two species of this genus were recognized by the researchers, however, Gentry *et al.* (2014, table 2) proposed very different taxonomic scheme for the genus *Pachyportax* by recognizing a single species, *?Pachyportax* sp. at 7.2 Ma, and have not mentioned or discussed any other species from the Siwalik in the text. This contradicts all previous studies (Pilgrim, 1937, 1939; Akhtar, 1992; Bibi, 2007; Khan, 2007; Khan *et al.*, 2009, 2010, 2012; Babar, 2017; Abbas *et al.*, 2018). Also, they have not provided any reason to omit the other species or discussed the reason that led them to conclude that only one *Pachyportax* species is present in the Siwaliks.

Kobus is a genus, representing during the late Miocene to present-day (Gentry and Gentry, 1978). The fossil record of this genus is mainly present in Africa and Asia (Gentry and Gentry, 1978; Gentry, 1980; Khan *et al.*, 2014; Iqbal *et al.*, 2015; Bibi *et al.*, 2018). Two specimens have been described in this study, a lower second incisor (PUPC 23/230), and right mandibular fragment with m1 (PUPC 23/229). The incisor is described for the first time for the genus *Kobus* in the Siwaliks and it has been compared with the extinct species, *Kobus kob* (FMNH 27480 and MSU Museum 2721). The m1 is typical of the genus *Kobus* described from the Late Miocene to Early Pliocene deposits as done in the respective comparison section. In the Siwaliks, a single species, *Kobus porrecticornis*, was known. However, Gentry *et al.* (2014) has added two more species, *Kobus* sp. 1 from 9.3 to 7.9 Ma and *Kobus* sp.2 from 7.3 to 5.9 Ma, as well as they restricted *Kobus porrecticornis* from 8.1 to 7.7 Ma. The restriction of

Kobus porrecticornis to Late Miocene is contrary to studies of (Khan *et al.*, 2014; Iqbal *et al.*, 2015) in which this species is reported from the Tatrot Formation (3.5-3.3 Ma). The specimens described in this study may represent the *Kobus* sp.2 of Gentry *et al.* (2014) that range from 7.3 to 5.9 Ma but there is no described material to compare with the material reported in this study.

The status of subfamily Hypsodontinae is still controversial that is composed of *Kubanostragus*, *Hypsodontus*, *Palaeohypsodontus* and *Turcocerus*. Some authors do not accept its subfamily status rather prefer to place the above-mentioned genera in family or subfamily as *incerte sedis* or indet (Métais *et al.*, 2003; Barry *et al.*, 2005; Gentry *et al.*, 2014). According to Gentry *et al.* (2014), Hypsodontinae was present in the Siwalik at 14.0 Ma in the form of *Hypsodontus sokolovi* and second species, *Hypsodontus pronaticornis*, ranges from 13.8 to ~12.8 Ma. Before this study and Gentry *et al.* (2014), there was a single report of Hypsodontinae in the form of *Palaeohypsodontus zinensis* described by Khan *et al.* (2008) from the Kamli Formation. However, Gentry *et al.* (2014) has reported that *P. zinensis* ranges from 25.0 to 18.5 Ma and from Suleman Range. This indicates the presence of *P. zinensis* well within the Kamli Formation. These specimens, PUPC 23/217 and PUPC 23/218, are extending the range of the subfamily to Dhok Pathan Formation.

Conclusions: The present study described the bovid remains collected from the Late Miocene deposits of the Mohal Pati near the village Bhandar and Hasnot in Jhelum, Punjab, Pakistan. The taxonomic study resulted in the identification of possible six species that are *Prostrepsiceros vinayaki*, *Tragoportax punjabicus*, genus indet. aff. *Eotragus*, *Pachyportax* sp., *Kobus* sp., and Hypsodontinae indet. Among these, we are the extending the known age range of *Prostrepsiceros vinayaki* and describing the dentition of this species for the first time from the Siwalik Group; the incisor is described for the first time for the genus *Kobus* in the Siwaliks and extending the range of the subfamily Hypsodontinae to the Dhok Pathan Formation.

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