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New Discovery of *Hipparion theobaldi* Skull from the Late Miocene of Padhri, District Jhelum, Punjab, Pakistan and Associated Mammalian Fossil Assemblage

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Abstract: A fossil-bearing locality near Padhri village, Dhok Pathan, 55 km away from the tehsil Dina, Jhelum District, in the Potwar Plateau, Middle Siwaliks, Punjab, northern Pakistan, is significantly rich in mammalian fossils. This site has provided an abundant mammalian fossil fauna of Late Miocene age from the Dhok Pathan Formation (Fm.). The recovered material belongs to four families: Equidae (horses), Rhinocerotidae (rhinos), Bovidae (cows), and Suidae (pigs). We discovered a new skull of hipparionine *Hipparion theobaldi* from this locality along with 22 specimens from the associated assemblage of fossil mammals. The recovered material includes seven other species: the aceratheriine *Chilotherium intermedium*, boselaphines *Tragoportax punjabicus*, *Selenoportax vexillarius*, *Pachyportax latidens*, the antelope *Gazella lydekkeri* and suinine *Propotamochoerus hysudricus.* The specimens are isolated teeth, fragments of maxilla, mandibles and horn cores. The Dhok Pathan Fm. is generally composed of claystone, siltstone and sandstone beds and, based on the mammalian fauna, the Padhri fossil locality is dated as Late Miocene. Thi99s formation was deposited in a subtropical paleoenvironment and the predominance of fossil bovids indicates extremely moist conditions with small but frequent standing water bodies.

Key words: vertebrate paleontology, mammals, fossil horses, Dhok Pathan Formation, Siwaliks, Punjab

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1 Introduction

The Padhri fossil site (Fig. 1) in the Middle Siwaliks (Pilgrim, 1937, 1939; Barry et al., 2002; Draz et al., 2020b), which is located NW of Hasnot, 55 km away from tehsil Dina, in Jehlum district, Punjab, Pakistan (Bhatti et al., 2012; Draz et al., 2020b). The site has been well known for its Late Miocene mammalian fossil assemblage for more than 100 years and belongs geologically to the upper part of Dhok Pathan Formation (Fm.) (Colbert, 1935; Pilgrim, 1937; Barry et al., 1982, 2002; Willis and Behrensmeyer, 1994). The Dhok Pathan Fm. is characterized by light-colored sandstone with unweathered igneous rocks. The fossil mammals found here the indicate strong relationships with the Eurasian and African Late Miocene (Pickford, 1988; Bibi et al., 2009; Draz et al., 2020a, b) and the taxa give evidence of a dominant woodland to savannah during the deposition of the sediments, which reveals that the studied locality had a better humid and vegetated environment (Rossner, 2005, 2006; Khan, 2008). Paleoenvironmental interpretations of this formation provide an important record regarding Late Miocene environmental conditions (Abbas et al., 2018; Draz et al., 2020a, b). The paleosols include light ash-colored sandstone and orange-to-red claystone with horizons of conglomerates with small boulders that were deposited in a fluvial system (Draz et al., 2020b). This fluvial system made a complicated thick section of bogs, water bodies, forest and mounds of vegetation including herbs and shrubs (Khan et al., 2015). The length and width of the Dhok Pathan Fm. fossiliferous deposits vary at different places (Barry et al., 2002).

The Padhri surrounds are typified by their scattered vertebrate bones and teeth. Complete skeletons have not yet been discovered. There are four possible main types of fossil met with here: (1) fossils found in a very intense form/pattern over a small area; (2) fossils in scattered form; (3) fossils collected as general collections; (4) fossils lying embedded in some sort of crevice. Mostly, collection from Padhri includes solitary teeth, mandibles and partial skulls. Bovids (Artiodactyla) constitute quantitatively the dominant group (Draz et al., 2020b) with equids such as *Sivalhippus perimensis.*

A skull of a *Hipparion* taxon and other mammalian dental remains have been recovered from the outcrops at Padhri. In spite of the fact that the genus *Hipparion* was

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relatively diversified through the Late Miocene, it is not well documented in any of the particular sites in the Middle Siwaliks. The age of the studied locality on the basis of the discovered fauna is 7.0 to 5.0 Mya, which is similar chronologically with the Late Turolian of Europe (Barry et al., 2002; Bhatti et al., 2012).

In this paper, we document for the first time a well-preserved *Hipparion theobaldi* skull along with other mammalian dental remains from Padhri. We also aim to review the taxonomy and diversity of the mammalian fauna including the new specimen in the Dhok Pathan Fm., Middle Siwaliks, Punjab, Pakistan (Fig. 1). This study also considers the diversification of fossil mammals during the Late Miocene.

2 Material and Methods

2.1 Collection of fossils

Several field surveys were conducted to find fossils from Padhri in the Jhelum district, Punjab, N Pakistan (Lat. 31°5'0"N: Long. 72°41'0"E). The outcrops in the surroundings of Padhri were inspected comprehensively and the new *Hipparion* skull and associated fossil assemblage of mammals were collected for research during 2017–2019. Surface collection was the chief procedure for the collection of preferred specimens. Specimens unearthed were generally in good condition except for some that were found on erosional surfaces. However, in some places vigilant excavation was also done with the assistance of geological hammers, chisels, penknives, fine needles and brushes. To avoid damage, cotton bits and tissues were used to enfold the specimens during transportation from Padhri to the Palaeontology Laboratory, Department of Zoology, Government College University, Faisalabad, Pakistan, the institution where specimens are housed (GCUF).

2.2 Cleaning the residue particles and cataloging the fossil

To prepare the fossils for clear observations and taxonomic study, specimens were prudently washed to eliminate dust and sand particles to allow for morphological analysis. Attached sedimentary elements, e.g. clay and sand, were detached using different needles and brushes. The broken portions of the skull and other collected specimens were amalgamated by using 'Fixings', 'Elfy' and 'Magic Stone', etc. To evade ambiguity, minor morphological characters were attentively examined with the help of a magnifying glass. A catalogue/Collection number, PC-GCUF 08/18 was allocated to the specimens, which specifies the serial number (numerator) and year of collection (denominator).

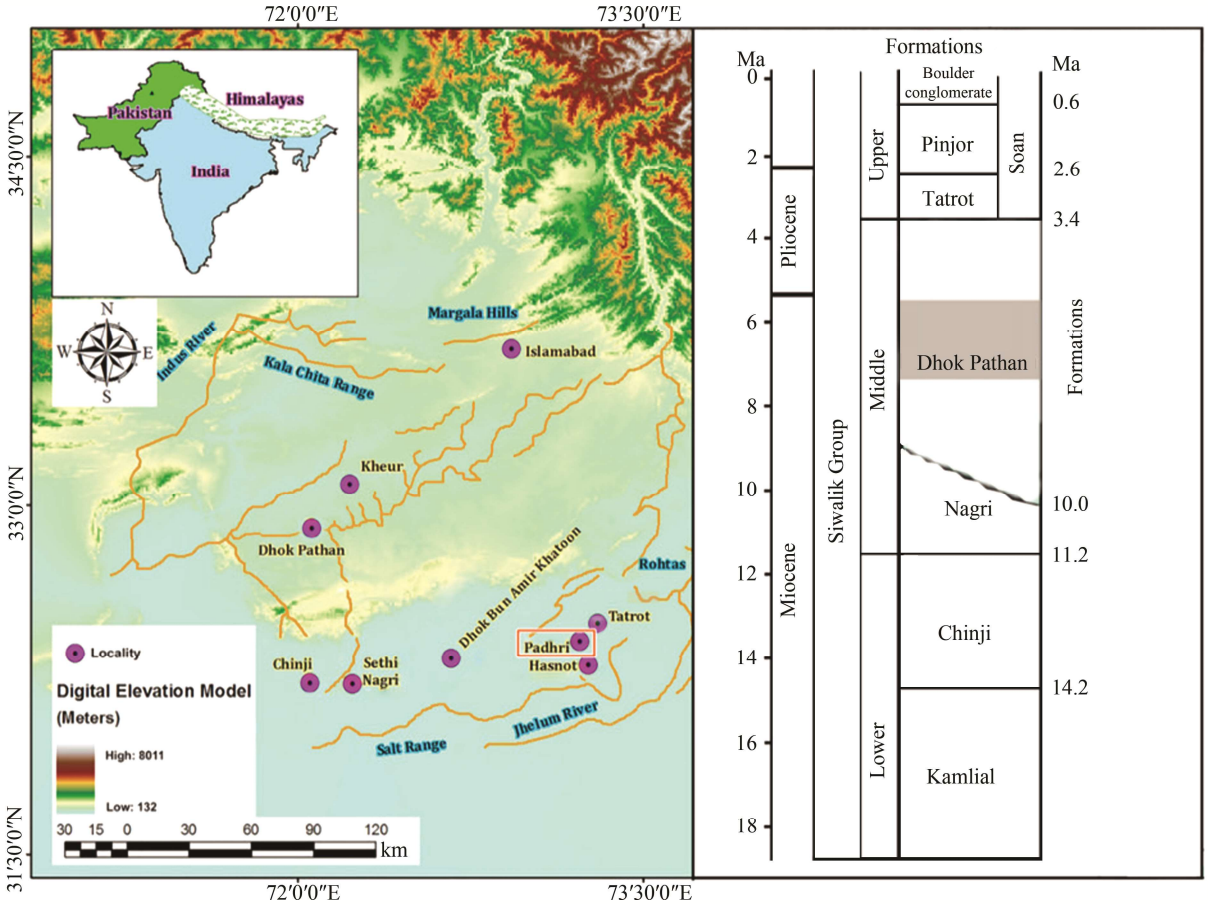

Fig. 1. Location map of the Potwar Plateau in northern Pakistan showing the studied locality Padhri village, Dhok Pathan in Jhelum district, northern Pakistan and the stratigraphic column showing the position of the Dhok Pathan Formation (data taken from Johnson et al., 1982; Barry et al., 2002; Dennell et al., 2008; Nanda, 2008; Draz et al., 2020b).

2.3 Measurements of the fossils

A digital Vernier Caliper was used to measure specimens and the scale is in millimetres (mm). The width and length of the studied specimens were measured at the maximum level of teeth.

2.4 Classification schemes

The new skull is identified as *Hipparion theobaldai* Colbert, 1935. There are two recent sets of classification schemes for *Hipparion.* A multi-genera system was applied by Bernor et al. (2014, 2018); Bernor and Sun (2015) and a single-genus system applied by Qiu et al. (1987) and Deng et al. (2012). In both the single-genus and multi-genera systems, *Hipparion theobaldi* has been referred to the genus *Sivalhippus*. The authors have applied the single-genus system in the current study.

2.5 Systematics and terminology

Tooth terminology and systematics follow the nomenclature of Eisenmann et al. (1988), Qiu et al. (1987) and Deng et al. (2012) for Equidae; Heissig (1972) for Rhinoceritade; Gentry and Hooker (1988), Janis (1988), Gentry (1994), and Barmann and Rossner (2011) for Bovidae; and Pickford (1988) for Suidae.

2.6 Comparison of studied specimens

The studied specimens were compared with other mammalian specimens in the Palaeontology Collection Government College University, Faisalabad (PC-GCUF), the Punjab University Palaeontology Collection, Lahore (PUPC), the Geological Survey of Pakistan, Islamabad (GSP), the Pakistan Museum of Natural History, Islamabad (PMNH), Geological Survey of India, New Delhi (GSI), the Natural History Museum, London (NHM, formerly BMNH), and the American Museum of Natural History, New York (AMNH).

2.7 Photography of specimens

A Canon EOS 1100 D (digital camera) was used to take photographs of the studied specimens. Figures were prepared utilizing PC software (Adobe Photoshop, Corel Draw and MS Paint).

2.8 Depository of the fossil specimens

The studied specimens are placed in the Paleontology Collection, Paleontology Laboratory, Department of Zoology, Government College University Faisalabad, Pakistan (PC-GCUF).

3 Systematic Paleontology

3.1 Order Perissodactyla Owen, 1848
Suborder Hippomorpha Wood, 1937
Family Equidae Gray, 1821
Subfamily Equinae Steinmann & Doderlein, 1890
Tribe Hipparionini Quinn, 1955
Genus *Hipparion* de Christol, 1832
Hipparion theobaldi (Lydekker, 1877)
Figs. 2a–e

Diagnosis (modified after Bernor and Hussain 1985; Bernor et al., 2010; Wolf et al., 2013): Large hipparionine horses with preorbital fossettes varying from being dorsoventrally high on the face and showing varying rim morphology. Cheek teeth vary from being relatively low-crowned to very high-crowned, ranging from 60 mm to >80 mm in maximum crown height; in middle adulthood, worn maxillary cheek teeth are complexly ornamented, with plicaballins, protocones ovate and flattened lingually.

Remarks: The Siwalik *Hipparion* has taxonomically phylogenetic similarities to the common Turolian species in Europe, Africa, as well as China (MacFadden and Bakr, 1979; MacFadden and Woodburne, 1982; Hussain and Bernor, 1984; Bernor and Hussain 1985; MacFadden and Woodburne, 2010; Sun, 2013; Wolf et al., 2013; Bernor and Sun, 2015). Khan et al. (2011a, 2014a) recognized that *Hipparion* is a clade in Indo-Pakistan encompassing five species, *H. theobaldi, H. anwari, H. nagriensis, H. perimensis,* and *H. antelopinum* with *H. turkanensis* in Libya and Kenya and *H. macrodon* in Uganda. Chinese taxa *H. platyodus* and *H. ptychodus* have been referred to the *Hipparion* group (MacFadden and Bakr, 1979; MacFadden and Woodburne, 1982; Bernor et al. 1990; Wolf et al., 2013).

Studied material: PC-GCUF 179/19, Skull; PC-GCUF 193/19, right P2; PC-GCUF 194/19, left P2; PC-GCUF 72/18, left M2; PC-GCUF 74/18 left m1 (Collected from Padhri, District Jhelum, Punjab, Pakistan).

Description: PC-GCUF 179/19 is a well-preserved skull of an adult individual with a complete series of upper dentition (Fig. 2). The generic and specific characters are well preserved: the snout is elongated and slender in shape; the buccinator fossa is present but poorly preserved

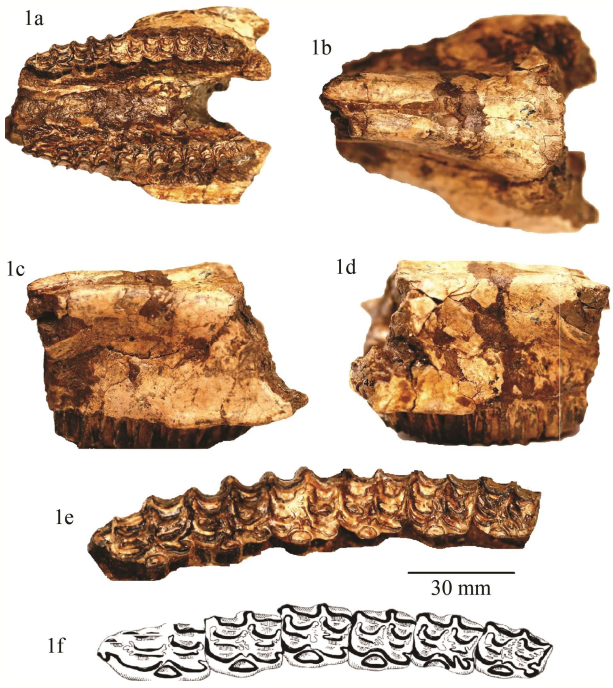

Fig. 2. *Hipparion theobaldi*; 1–PC–GCUF 179/19, views of partial skull: a–l ventral palatal; b–dorsal; c–right lateral; d–left lateral; e–right tooth series in occlusal view; f–pencil sketch of occlusal view of right tooth series M3–P2. Scale bar = 30 mm.

on the anterior side of P2; the premaxillary–maxillary structure extends posteriorly above P2; the infraorbital foramen lies below P3 and is anteroventral to the preorbital facial fossa, which is partially present near to the nasal and maxillary bones. The preorbital facial fossa, which is the principal diagnostic character of *Hipparion*, is weak, anteroposteriorly oriented with an egg-shaped outline.

Sagittal sutures are moderately visible (Fig. 1b) but difficult to distinguish. The partially broken lacrimal is almost triangular and lies posteroventral to the preorbital fossa. The anterior (maxillary) portion of the malar crest is moderately developed and the posterior portion is broken. On the dorsal occipital region, there are bilaterally symmetrical parietal crests that converge posteriorly. The posterior section of the occipital is not preserved and an endocast of the brain in sediment is exposed (Fig. 1b). The facial crest appears anteriorly at the boundary between P4 and M1.

Tuberosity in the maxillary is moderately present. The anterior palatine foramen is positioned near the middle of the protocone of the M2. The position of the suture between the lacrimal and posterior palatine foramen specifies that the orbit must have been very close to the preorbital facial fossa. The dorsal fringe of the preorbital facial fossa is distinct, but the further fringes of the fossa are slightly indefinite. The length of dental series extending from P2 to M3 is 157 mm. The P2 occlusal outline is triangular in shape due to the extended anterostyle. The middle grooves and ridged main cusps are present on the skull, which indicates that the animal was still young at the time of death. The elevation of the cusps and grooves is greater in the molars than in the premolars. The protocone is rounded and slightly convex from the buccal side in the premolars but flattened lingually in M1 and M2, while elongated in M3. A few small wrinkles are present on the lingual side of dental series. The paracone and metacone are almost straight in P2 while partially convex in shape on P3 and P4; both these cones are convex distinctly in M1, M2 and M3. Their buccal walls are flat in P2 but that of the paracone is convex and deflected posteriorly. The parastyle and mesostyle are well developed on the cheek teeth and protrude buccally. A middle groove is present on the parastyle of the premolar series but this groove is absent in the molar series. The mesostyle is broad and bifurcated in P2, P3 and M1, M2. There are four plications present on the anterior border of M2; the lingual plication is robust and directed posteriorly. Only one pli-protoconule is present in P2 and M3, whereas there are two in P4–M2, three in P3, which are all robust, long and anterobuccal in direction. Four to five plications are visible on the anterior margin of the postfossette, which are slightly slender and distributed evenly. No plication is present on the posterior border of the postfossette in M1 and M3. The hypoconal groove is moderately incised and narrow in P2, but broad and profoundly incised in P3–M2. The M3 has an open posterior border with the postfossette. The hypocone has weak constrictions in P2 and M3.

PC-GCUF 193/19 is a second right upper premolar, which is in the middle stage of wear (Fig. 3.1). It is almost triangular in shape with a moderately developed extended anterostyle. A pillar-like mesostyl is present and is similar to the parastyle in shape being narrow at the apex and broad at the base. The metastyle is straight and partially visible. The protocone is elongated and compressed. The

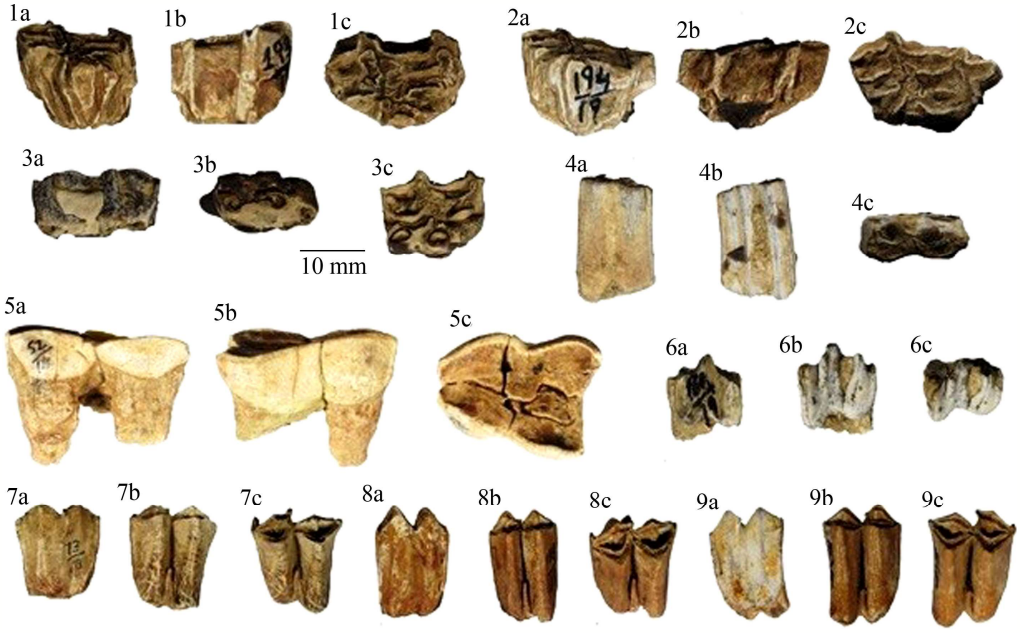

Fig. 3. Teeth of Padhri specimens: 1–4, *Hipparion theobaldi*: 1–PC-GCUF 193/19, right P2; 2–PC-GCUF 194/19, left P2; 3–PC-GCUF 72/18, left M2; 4–PC-GCUF 74/18, left m1; 5–*Chilotherium intermedium*: PC-GCUF 52/18, right P3; 6–9, *Tragoportax punjabicus*: 6–PC-GCUF 189/19, right p4; 7–PC-GCUF 73/18, left m1; 8–PC-GCUF 186/19, left m2; 9–PC-GCUF 187/19, right m2.

Views: a–lingual, b–buccal, c–occlusal. Scale bar = 10 mm.

paracone and metacone are similar in shape but the length of the paracone is greater anteroposteriorly. The hypocone is elongate and narrow and partially covered with sediment. The enamel folding is present on the pre-fossette and the post-fossette, both of which are plicated. The protoloph and metaloph are crescentic. The metaloph is partially separated from the hypocone.

PC-GCUF 194/19 is a well-preserved left second upper premolar in the middle stage of wear (Fig. 3.2). The protocone is ovate, flat lingually and rounded buccally. The paracone and metacone are clearly visible and almost equal in dimensions. The prefossette and postfossette are moderately preserved with plications. The prefosette is denser and more plicated than the postfossette and larger in length than the postfossette. The plicaballin is bifid. The styles are moderately developed. The parastyle is pointed, elongated and poorly developed. The mesostyle is prominent whereas the metastyle is thin. The hypoglyph is broad and less incised. The pli-protoconule is well-developed.

PC-GCUF 72/18 is an excellently preserved left second upper molar (Fig. 3.3). It is almost square with a well-developed elongate anterostyle and in an early stage of wear. The protocone is isolated, elongate and a compressed pillar-shape. The paracone and metacone are clearly visible and almost equal in dimensions. The hypocone is tapered, extended and covered with a dense coating of sediment. The prefossette and postfossette are moderately preserved with plications with the prefosette denser and more plicated than the postfossette. The mesostyle is prominent, pillar-like and parallel to the parastyle, broad at the base, becoming narrow at the apex. The metastyle is fairly well developed and straight in direction.

PC-GCUF 74/18 is a moderately preserved, elongate, left first lower molar in an early stage of wear (Fig. 3.4). This tooth is narrow in the crown and strongly hypsodont with thick and rugose enamel, enclosed with sediment, which is more apparent on the lingual side than on the buccal side. The hypoconid is forwardly directed and protoconid is directed posteriorly. The major conids are finely preserved. The protoconid and hypoconid are present on the buccal side and the metaconid and entoconid are present on the lingual side. The posterior part of the tooth is slightly higher than the anterior sideand the metaconid and entoconid are higher than the protoconid and hypoconid. The protoconid is circular and smaller than the hypoconid. The parastylid is poorly preserved. The hypoconulid is on the posterior side of the tooth and attached with the enamel of the hypoconid. The mesostylid is situated between the metaconid and entoconid and is similar in shape to the metaconid but opposite in direction; it is closed and coincides with the entoconid. The metaconid is elevated among all conids.

Comparison: Many researchers have distinguished a considerable difference in size in the dental and metapodial dimensions between *Hipparion* and *Cremohipparion* (e.g. Wolf et al., 2013). The studied genus *Hipparion* has a compacted and compressed protocone, which is strongly lingually flattened. The walls of the fossettes are thin in *Cremohipparion* and thick in *Hipparion* (Wolf et al., 2013). *Hipparion nagriensis* is restricted to the Nagri Fm. and is of intermediate size compared to two other species. *Hipparion theobaldi* is present in the Dhok Pathan (Middle Siwaliks) and Tatrot (Upper Siwaliks) formations and is identified by its large size and comparatively vigorous/robust metapodials. *Hipparion antilopinum* is contemporaneous with *Hipparion theobaldi* but of small size with gracile metapodials. The difference between *Hipparion theobaldi* and *Hipparion antilopinum* is primarily the size. *Hipparion theobaldi* is separated from *Hipparion antelopinum* on the basis of several characters such as: the greater size of molars, more oblong and less square teeth, compressed protocone, prominent preorbital facial fossa with strong anterior rim, deep pocket posteriorly, composite plications and plicaballin in upper dentition, deep ectoflexids in both lower premolars and molars, and metapodials robust. *Hipparion antelopinum* is a moderately sized species distinguished by small and very hypsodont teeth, oval protocone and complex enamel plications in the upper molars, well-developed pre-orbital fossa, tiny snout and slender metapodials (Hussain, 1971). Despite the massive enlargement in size of *Hipparion theobaldi*, it retains a basal cranial morphology with a dorsoventrally extensive pre-orbital facial fossa throughout its occurrence (Eisenmann et al., 1988; Khan et al., 2011a, 2014a).

Hipparion theobaldi and *Hipparion anwari* are large hipparionine horses; *H. anwari* has very high-crowned cheek teeth with a height of 85 mm in the molars, and a rectangular surface in early wear, the P2 is elongated on the occlusal side while the molars have complex plications on the mesial border of the pre-fossettes. The distal border of the post-fossettes in *H. anwari* is very complex in late wear; protocones are lingually flattened, buccally rounded with a deeply incised hypoglyph and massive post-cranial elements (MacFadden and Woodburne, 1982; Bernor and Hussain, 1985). *H. theobaldi* has a dorsoventrally high pre-orbital fossa synchronized with a facial maxillary crest, a continuous peripheral border with an anterior rim; the fossa is deeply pocketed posteriorly, long and anterior-ventrally oriented and medially deep; the P2 anterior styles are elongate, with maximum cheek tooth crown height of 67 mm and maxillary cheek teeth have large occlusal surfaces and pre-and post-fossettes; the protocones are distinctly flattened lingually and rounded buccally (Hussain and Bernor, 1984).

Hipparion nagriensis is a medium sized horse. The pre-orbital fossettes have a low dorsoventral height on the face, close to the facial maxillary crest, a continuous marginal border, anterior rim and deeply pocketed. The maxillary cheek teeth crown has 60–65 mm in height, complexly ornamented with distal border of the pre-fossettes and the mesial border of the post-fossettes; trifid plicaballins are present: protocones are oval, flattened lingually and rounded buccally. The hypoglyphs are broad and moderately deeply incised (MacFadden and Woodburne, 1982). *Hipparion antelopinum* are medium-sized and *Hipparion perimensis* are large horses; its pre-orbital fossa is 40–59 mm with the dorsoventral height being to the facial maxillary crest; the fossa peripheral

Table 1 Measurements (in mm) comparing cheek teeth of studied Padhri cranium of Hipparion theobaldi (PC-GCUF 179/19) with published cranial specimen PUZ 69/371

Position	rM3	rM2	rM1	rP4	rP2	rP2	lM3	lM2	lM1	lP4	lP3	lP2
						PUZ 69/371						
Length	26.2	23.9	23.1	27.3	27.8	35.1	26.5	23.4	23.4	26.1	27.7	34.4
Width	22.1	26.0	27.0	29.1	29.0	29.0	22.2	24.8	26.5	29.6	29.5	26.8
						PC-GCUF 179/19*						
Length	22.6	24.2	26.5	31.6	34.5	37.6	23.2	24.4	25.8	27.4	28.7	35.3
Width	19.5	23.5	24.4	24.6	27.7	26.5	21.2	22.6	24.5	25.6	26.9	26.5

*Studied specimens. Referred data is taken from MacFadden and Bakr (1980); Bruce and Michael (1982); Wolf et al. (2013).

border and anterior rim vary from strong to weak, the P2 anterior style is elongate in middle wear, and crown height of unworn permanent cheek teeth is 70 mm; the protocones are flattened lingually and rounded buccally and the hypoglyphs are moderately to deeply incised (MacFadden and Woodburne, 1982; Hussain and Bernor, 1984; Wolf et al., 2013).

Morphometrically and on the basis of comparative measurements with craniums (PUZ 69/371 and AMNH 98728) described by MacFadden and Bakr (1979) and MacFadden and Woodburne (1982), the studied specimens show much similarity with the type and already described specimens of *H. theobaldi* (Colbert, 1935; Table 1; Supp. Table 1). It is evident from the characters described above, and based on the configuration of the preorbital facial fossa, that the Padhri skull can be assigned to the genus *Hipparion* and to the large species *H. theobaldi* because of its large molars, complex fossette enhancement, deep incisure of hypoglyphs and compressed protocones with a flattened lingual side and buccally rounded.

3.2 Family Rhinocerotidae Owen, 1848
Subfamily Rhinocerotinae Owen, 1848
Tribe Aceratheriini Hay, 1902
Genus *Subchilotherium* Heissig, 1975
Subchilotherium intermedium Lydekker, 1884
Fig. 3.5

Studied material: PC-GCUF 52/18, right P3 (Collected from Padhri, District Jhelum, Punjab, Pakistan).

Description: PC-GCUF 52/18 is a moderately preserved right upper third molar (Fig. 3.5). Moderate rugosity is present on both the lingual and buccal sides. A posterior partial cingulum is present on the anterior side of the tooth, which is continuous on the lingual face of the protocone and the hypocone. The protocone is slightly constricted. The parastyle fold is moderately prominent, the antecrochet and crochet are short and thick. The protoloph is higher than the metaloph, both being at equivalent levels and both vertical to the ectoloph. The parastyle and paracone rib are partially damaged. The flange of the hypocone is poorly developed.

Comparison: The specimen is comparable to ones identified as *Chilotherium intermedium* by Matthew (1929) and Colbert (1935) from the Middle Siwaliks of Pakistan and *Chilotherium wimani* from the late Miocene of fugu, Shaanxi (Deng, 2001). *Chilotherium wimani* occupies a unique niche within the genus *chilotherium*. It has very few separated parietal crests, a strongly concave cranial dorsal profile, well-developed supraorbital tubercles, and a high occipital surface, indicating that ch. wimani is the most primitive of the known *Chilotherium* species. Characters such as the broad and flat ectoloph with a parastyle in the upper molar, to some extent oblique protoloph and metaloph, the metaloph larger than the protoloph, the internal cingulum partially present and a moderate constriction of the protocone that is less constricted off from the protoloph are all diagnostic features of *Chilotherium intermedium* (Heissig, 1972). The studied specimen encompasses all the abovementioned characters and is comparable with that of the published fossil remains. The studied material is significantly different on the basis of morphology from the large-bodied rhino *Brachypotherium fatehjangense* (Pilgrim, 1910). Heissig (1972) indicated that the M2 in *B. fatehjangense* is different from *Chilotherium intermedium* in having brachydont teeth, an evenly and wide flat concave ectoloph surface behind the paracone rib and the crista and the lingual cingulum are absent in the upper molar of *B. fatehjangense* (Khan et al., 2008). In the upper molars of another species, *Chilotherium anderssoni*, the lingual cingulum is weak and discontinuous, whereas in the studied specimen, it is well developed and continuous. The crista can be absent in *Chilotherium anderssoni* and the antecrochet is large enough to fill the whole median valley (Khan et al., 2008, 2011). The described Padhri specimen also shows similarities in size with PUPC 08/01, PUPC 07/93 (Supp. Table 1).

3.3 Order Artiodactyla Owen, 1848
Suborder Ruminantia Scopoli, 1777
Infraorder Pecora Linnaeus, 1758
Family Bovidae Gray, 1821
Subfamily Bovinae Gray 1821
Tribe Boselaphini Knottnerus-Meyer, 1907
Genus *Tragoportax* Pilgrim, 1937
Tragoportax punjabicus Pilgrim, 1910
Figs. 3.6–3.9; 4.1–4.2

Studied Material: PC-GCUF 189/19, right p4; PC-GCUF 73/18, left m1; PC-GCUF 186/19, left m2; PC-GCUF 187/19, right m2; PC-GCUF 19/18, partial right horn core; PC-GCUF 188/19, basal part of left horn core (Collected from Padhri, District Jhelum, Punjab, Pakistan).

Description: PC-GCUF 189/19 is a right fourth lower premolar (Fig. 3.6). It is moderately preserved and in the middle stage of wear. The p4 has a strong paraconid, metaconid and entoconid; however, the hypoconid is poorly preserved. The metaconid is T shaped and directed backward. The entoconid of the premolar is stronger than the metaconid. The enamel is shiny on the lingual side and

rugose on the buccal side. The anterior valley is open. The lingual surface appears flat and the buccal surface has two vertical grooves. The entostylid is fused with the entoconid. The parastylid is separated from the paraconid. PC-GCUF 73/18 is a left first lower molar (Fig. 3.7). It is well preserved and at an early stage of wear. All the principal conids, protoconid, metaconid, hypoconid and entoconid, are well preserved. The lingual conids are higher than the buccal ones. The entostylid is moderately developed whereas the metastylid is strongly developed. The moderately developed ectostylid is present in the transverse valley on the buccal side. The fossettes are narrow and deep. The tooth has wrinkled enamel with a transverse flange anteriorly. The buccal side is more rugose compared to the lingual side. A median basal pillar is present in the central valley. The cingulid is partially developed on the metaconid. PC-GCUF 186/19 is a left second lower molar (Fig. 3.8), well preserved and in an early stage of wear; it is narrowly crowned and hypsodont. All the principal conids are present in good condition. A partial cingulid is present on the anterior portion of the buccal side. A small ectostylid is situated in the transverse basin between the protoconid and the hypoconid. The entoconid is slightly more vertical than the other conids. The metaconid is T-shaped. The mesostylid and metastylid are more prominent than the entostylid. The central cavities are deep and narrow without any groove. The enamel is rugose and shiny. PC-GCUF 187/19 is a well-preserved right second lower molar in an early stage of wear (Fig. 3.9). It is hypsodont with an elevated crown. The protoconid is tall with inclined preprotocristids. The hypoconid is pointed between the pre-posthypocristids. The entoconid is crescent-shaped but small as compared to the metaconid. The ectostylid is broken at its tip. The metastylid is well developed. The fossettes are fairly narrow and hollow. Rugosity is more on the lingual side than the buccal side.

PC-GCUF 188/19 is the basal part of a left horn-core, partially broken at the apex (Fig. 4.1). The anterior keel is moderately developed at the base. The lateral side of the horn core is flat while the internal side is slightly convex. Longitudinal furrows are present on both the anterior and posterior surfaces. The cross section is an equilateral triangle at the base, which is broad and becomes compressed laterally towards the apex. The total preserved height is 71 mm, length 36 mm, and width is 21 mm. PC-GCUF 189/18 is a partial right horn-core, fairly long and laterally compressed with a broken upper part and an almost complete basal part (Fig. 4.2), and a total preserved height of 107 mm, length 38.6 mm, and width of 29.1 mm. The horn-core is slightly curved backwards, faintly twisted with weak torsion. The internal face is slightly convex and

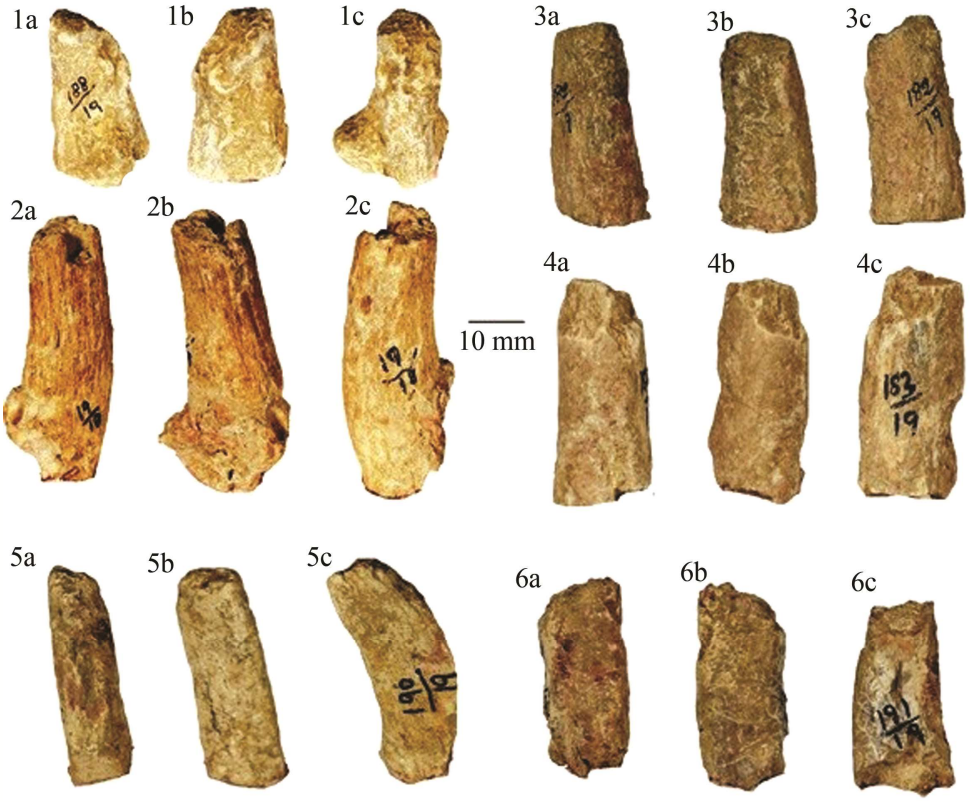

Fig. 4. Horn cores of Padhri specimens: *Tragoportax punjabicus:* 1–PC-GCUF 188/19, basal part of left horn core; 2–PC-GCUF 189/18, partial right horn core; *Pachyportax latidens;* 3–PC-GCUF 182/19, fragment of right horn core; 4–PC-GCUF PC-GCUF 183/19, fragment of left horn core; *Gazella lydekkeri:* 5–PC-GCUF 190/19, fragment of left horn core; 6–PC-GCUF 191/19, fragment of right horn core.
Views: a–anterior, b–posterior, c–medial.

the lateral face is flat. There is a partial antero-internal keel and a rounded postero-external keel. The basal cross-section is triangular in shape. The medio-lateral compression decreases from the base to the top. Weak irregular longitudinal grooves are present all along the surface.

Comparison: The studied materials can be referred to an herbivorous mammalian group. The crescentically shaped conids of selenodont nature indicate that the specimens can be referred the order Artiodactyla (Romer, 1974). The compressed outer conids favor insertion in the family Bovidae. The selenodont teeth are relatively small and with divergent stylids. They can be distinguished from teeth of *Selenoportax* and *Pachyportax* by their smaller size and the poor basal pillar (Gaudry, 1865; Arambourg and Piveteau, 1929; Pilgrim, 1937). Based on the detailed morphology, we conclude that generally the studied specimens belong to a boselaphine, a group identified by the crown neck and divergent styles (Pilgrim, 1939; Arambourg, 1947; Gentry, 1978; Bibi, 2007) with the metaconid of the p4 backwardly directed and an entoconid relatively stronger than the metaconid and an open anterior basin in the p4.

The genus *Tragoportax* has characters between *Miotragocerus* and *Selenoportax*. A T-shaped metaconid of the p4 is a representative character of *Tragoportax* (Spassov and Geraads, 2004; Kostopoulos, 2005; Bibi and Gulec, 2008). The horn-cores of *Tragoportax* are related to *Miotragocerus* in cross-section, with a scalene triangle, having a sharp postero-external keel, which can be differentiated from the isosceles triangle of *Selenoportax*, in having a rounded postero-external keel. The horn-cores of European *Tragoportax* taxa are tend to be less twisted and longer than those of the Lower Siwalik *Tragoportax* (Pilgrim, 1939; Kostopoulos, 2005, 2009; Khan et al., 2010; Asim et al., 2020). They also differ from other Siwalik bovids with respect to torsion in the horn cores. A slight torsion is found in *Tragoportax* whereas the small boselaphines *Eotragus* and *Sivaceros* and the non-boselaphine genus *Gazella* have no torsion (Thomas, 1984; Made and Hussain, 1993; Asim et al., 2020). The Padhri specimens are different from *Miotragocerus* in their larger size, partially more condensed premolars and more extravagant metaconids in p4 (Spassov and Geraads, 2004).

Tragoportax is represented by two species in the Siwaliks: *T. punjabicus* and *T. salmontanus* (Pilgrim, 1937, 1939). *T. punjabicus* is large species (Khan et al., 2010) whereas *T. salmontanus* is a comparatively small species (Pilgrim, 1937, 1939; Asim et al., 2020; Draz et al., 2020b). *Tragoportax punjabicus* is restricted to the Late Miocene of the Siwalik Group (Dhok Pathan Fm.) (Pilgrim, 1939; Akhtar, 1992; Khan et al., 2010; Asim et al., 2020). There is a single report of this genus from the Middle Miocene Chinji Fm. (Khan et al., 2013); however, all the other specimens are found in the Siwalik Late Miocene (Asim et al., 2020). The specimens differ from *T. salmantonus* in their large size (Asim et al., 2020). The dental proportions of the Padhri specimens support that they belong to *Tragoportax punjabicus* (Pilgrim, 1937, 1939). This species is also present in the Miocene of Eurasia (Bibi and Gulec, 2008; Kostopoulos, 2005). Comparative measurements of the studied specimens are provided in Supp. Table 1.

Genus *Selenoportax* Pilgrim, 1937

***Selenoportax vexillarius* Pilgrim, 1937**

Fig. 5.1–5.2

Studied material: PC-GCUF 181/19, left P3; PC-GCUF 180/19, right m2 (Collected from Padhri, District Jhelum, Punjab, Pakistan).

Description: PC-GCUF 181/19 is a well-preserved left third upper premolar, triangular in shape, narrow crowned and at an early stage of wear (Fig. 5.1). All the principal cones are well developed: the metacone is slightly more upward than the protocone; the paracone is more prominent than the hypocone. A partial cingulum is present on the posterior side. The median rib, separated from the parastyle, is prominent. The metasyle is thin and strongly developed. In the center of the premolar there is a deep fossette, which is almost V shaped. More rugosity is present on the lingual side as compared to the buccal side.

PC-GCUF 180/19 is a poorly preserved right second lower molar at a late stage of wear (Fig. 5.2). The protoconid is well developed while the hypoconid is partially broken; the entoconid is wedge-shaped with two cristids; the metaconid is slightly higher than the protoconid. Cement is partially present between the protoconid and the hypconid. The parastylid is moderately developed while the mesostylid and the entostylid are strongly developed. The anterior median rib is more prominent than the posterior median rib. The metastylid and entostylid are moderately developed. The enamel is thick and rugose and more wrinkled on the buccal side than the lingual side.

Comparison: According to the morphology, the studied specimens belong to a large boselaphine. The crescentic pattern of the crown reveals that the specimens belong to the genus *Selenoportax* (Khan et al., 2007). *Selenoportax* is a large boselaphine that is found continuously from the Lower to the Upper Siwaliks and more abundant in the Dhok Pathan Fm. A few fossils of *Selenoportax* have also been discovered from other parts of the Siwaliks (Lydekker, 1876; Thomas, 1984; Gentry, 1999; Barry et al., 2002). *Selenoportax* taxa have prominent entostyle/ entostylid, strong ribs and divergent styles/stylids (Pilgrim 1937, 1939). There is also a difference in the crown neck between *Selenoportax* and *Pachyportax*, which is high in the former but low in the latter (Khan et al., 2007, 2009). These genera are only present in the Middle Siwaliks of Pakistan (Baker and Akhtar, 1985; Akhtar, 1992, 1996; Samiullah et al., 2015; Draz et al., 2020a, b). *Selenoportax* and *Pachyportax* can be differentiated on the basis of their size and shape; but these two characters are not enough to differentiate them because they can vary in the members of the same species (Bibi, 2007). There are two named species, *Selenoportax vexillarius* and *Selenoportax lydekkeri* (Pilgrim 1937, 1939; Akhtar, 1992). The morphology and measurements of the Padhri specimens most resemble *Selenoportax vexillarius*, which have moderate-to-large size with strong median ribs, high-crowned and divergent styles/stylids. The comparative

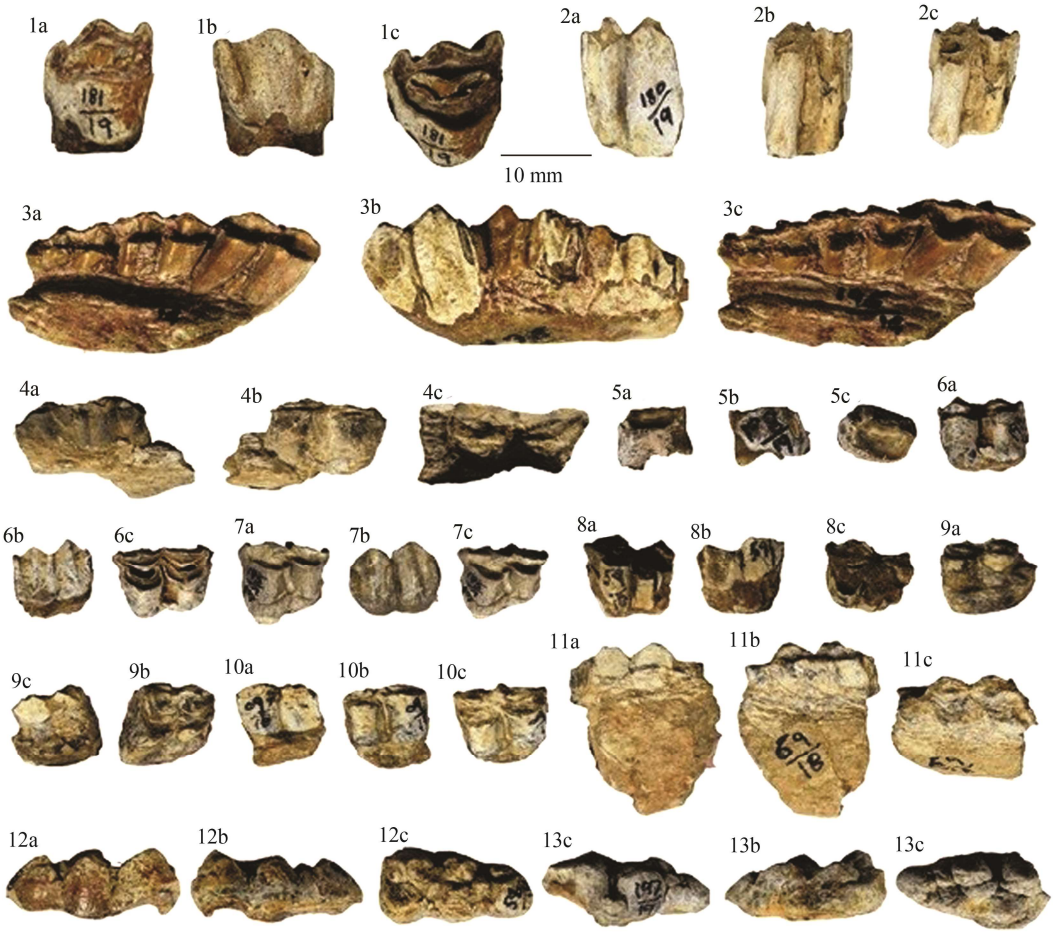

Fig. 5. Teeth of Padhri specimens: *Selenoportax vexillarius*: 1–PC-GCUF 181/19, left P3; 2–PC-GCUF 180/19, m2; *Pachyportax latidens:* 3–PC-GCUF 196/19, left maxilla with P3-M2; 4–PC-GUCF 184/19, left m2; *Gazella lydekkeri:* 5–PC-GCUF 198/19, left P4; 6–PC–GCUF 192/19, left M1; 7–PC-GCUF 185/19, left M1; 8–PC-GCUF 59/18, left M3; 9–PC-GCUF 66/18, right M3. 10–PC-GCUF 09/18, left m2; 11–PC-GCUF 69/18, left m3; *Propotamochoerus hysudricus*: 12–PC-GCUF 58/18, right M3; 13–PC-GCUF 197/19, right M3.
Views: a–lingual, b–buccal, c–occlusal. Scale bar is equal to 10 mm.

measurements of the studied specimens are provided in Supp. Table 1 and they indicate that these Padhri specimens are hypsodont and narrow crowned. There is a small size difference in the studied specimens, which might be due to intraspecific variation.

Genus *Pachyportax* Pilgrim, 1937
***Pachyportax latidens* Pilgrim, 1937**
Figs. 4.3–4.4; 5.3–5.4

Studied material: PC-GCUF 196/19, left maxilla with P3-M2; PC-GUCF 184/19, left m2; PC-GCUF 183/19, a part of horn core; PC-GCUF 182/19; a part of horn core (Collected from Padhri, District Jhelum, Punjab, Pakistan).

Description: PC-GCUF 182/19 is a moderately preserved pedicel-shaped horn-core (Fig. 4.3). The dorsal surface of the orbit is partially preserved. The horn-core inclination is not greatly divergent and the cross-section is almost round. The lateral side is slightly compressed; the medial surface is almost round. Numerous longitudinal furrows are present over all the surface. The third angle forms a semicircle on the inner side of the keel axis. The height of the fragment is 61.6 mm and width and length are 21.2 mm and 29.2 mm, respectively. PC-GCUF 183/19 is also a moderately preserved horn-core (Fig. 4.4). The dorsal orbital rim and the surface of the orbit are poorly preserved. The inclination is low in side view and not too divergent with the lateral portion somewhat convex. The medial surface is fairly rounded and the horn core is extremely thick at the base. Numerous longitudinal furrows are present on the surface of the horn. There is no keel and the specimen is sufficiently curved to form a semicircle on both anterior and posterior sides. The height of the fragment is 76.6 mm; width and length are 26.6 mm and 23.3 mm, respectively.

PC-GCUF 196/19 is a poorly preserved left maxilla with P3-M2 (Fig. 5.3) in an early stage of wear. P3 is hypsodont with faintly rugose enamel. The paracone is prominent vertically and higher than the hypocone but it

does not fuse with the other adjacent cones. The protocone and hypocone are present on the lingual side. A strongly developed parastyle is present near to the median rib. The entostyle is transversely extended. The fossette is present. The paracone and matacone of p4 are not fused and form an anterior wide valley, which is open lingually. The protocone is partially preserved; the hypocone is more prominent and inflated than all other cones. The buccal furrow is deep. The posterior valley is narrow and placed obliquely. The styles are present on the buccal side; the mesostyle is strongly developed compared to the other two. The cones are well differentiated, prominent and well developed in M1: the protocone is lower than the metacone; the hypocone is elongated; the paracone is partially fused. The parastyle is well developed; the metastyle is promiment. The buccal cones are higher than lingual cones. A prominent entostyle is present in the median valley. The anterior and posterior fossettes are well developed. The preprotocrista is slightly larger than the postprotocrista. The enamel is rugose on both the lingual and buccal sides. In M2 the hypocone is more prominent than all other cones. The entostyle is present between the protocone and the hypocone and is broad at the base and narrow to the summit of the crown. The median valleys are deep. The mesostyle is strongly developed and higher than the parastyle. The paracone rib is strong while the metacone rib is weak. The anterior fossette is broader than the posterior one. The posthypocrista is faintly pinched inward.

PC-GUCF 184/19 is a left second lower molar (Fig. 5.4). This specimen is excellently preserved and at early stage of wear. The crown is high and moderately narrow with thick and partially wrinkled enamel. Rugosity is prominent on the outer surface of the protoconid and the hypoconid. The protoconid is V-shaped and slightly lower than the hypoconid which is also V-shaped but less worn and broader antero-posteriorly. The metaconid is prominent but it is faintly worn and shorter than the entoconid, which is well developed. The anterior transverse flange is present. The metastylid is moderately developed.

Comparison: Pilgrim (1937) described *Pachyportax* and identified three species; *Pachyportax latidens, P. nagri* and *P. giganteus*. *Pachyportax* taxa have strong ribs and styles and the teeth are very hypsodont. The crown neck is not constricted like *Selenoportax.*

Pachyportax specimens are abundant in the Dhok Pathan Fm. (Abbas et al., 2018; Lydekker, 1876; Pilgrim 1937; Khan, 2008; Khan et al., 2009), with two species present in the Padhri locality: the large *P. latidens* and small *P. nagrii* (Abass et al., 2018; Pilgrim, 1937; Khan et al., 2009). Our specimens are placed in *P. latidens* because of the large size. Its presence in the Middle Siwaliks indicates a Late Miocene age (Pilgrim, 1937; Khan et al., 2009; Mahmood et al., 2019; Draz et al., 2020a, b). The studied specimens agree with *P. latidens* also in their selonodonty, and smaller size and week entostyle compared to *Selenopotax* (Gaudry, 1865; Arambourg and Piveteau, 1929; Pilgrim, 1937). The dental morphology of this genus *Pachyportax* has not been revised because there has been no discovery of a complete skull. The size of the teeth is variable but this is too insignificant from a taxonomic point of view. The comparative measurements of the Padhri studied specimens are provided in Supp. Table 1.

3.4 Subfamily Antilopinae Gray, 1821
Tribe Antilopini Gray, 1821
Genus *Gazella* Blainville, 1816
Gazella lydekkeri Pilgrim, 1937
Fig. 5.5–5.11

Studied material: Upper dentition PC-GCUF 198/19, left P4; PC-GCUF 192/19, left M1; PC-GCUF 185/19, left M1; PC-GCUF 59/18, left M3; PC-GCUF 66/18, right M3; lower dentition PC-GCUF 09/18, left m2; PC-GCUF 69/18, left m3; horn cores PC-GCUF 190/19, fragment of horn core; PC-GCUF 191/19, fragment of horn core (Collected from Padhri, District Jhelum, Punjab, Pakistan).

Description

Horn cores: PC-GCUF 190/19 is relatively a short and robust horn core that is weakly divergent with slight medio-lateral compression, moderately inclined against the parietal, and curving smoothly backward (Fig. 4.4). Partial deep longitudinal grooves are present along all the surface. The lateral face is semi circuler. The height is 72.1 mm, width 13.3 mm and length is 26.7 mm. The curve of the relatively short horn core PC-GCUF 191/19 is gently upwards and slightly backward in position (Fig. 4.6) and is slightly divergent and tapers towards the tip. It is untwisted and slightly more convex on the inner side than on the outer. The base is partially broken. There is no keel. Longitudinal furrows are present on the surface. The preserved height is 61.5 mm, length is 23.5 mm and width is 18.8 mm.

Upper dentition: PC-GCUF 198/19 is a well-preserved left fourth upper premolar (Fig. 5.5), almost triangular in shape and selenodont, and at a middle stage of wear. The enamel is moderately thick and shiny. The lingual side is more rugose than the buccal side. The central fossette is broad and relatively shallow. A partially developed mesostyle is present. The preparacrista is smaller and less curved compared to the postparacrista. PC-GCUF 192/19 is a left first upper molar, quadrate in shape (Fig. 5.6). Its lingual side is more rugose than the buccal side. The enamel is moderately thick and not so shiny. The major cones are well developed and narrow: the protocone and hypocone are slightly lower than the paracone and metacone. The posthypocrista is slightly larger than the prehypocrista. The fossettes are deep, narrow and crescentic in shape. The paraconal rib is moderately strong at the base. PC-GCUF 185/19 is a broad and low-crowned left first upper molar (Fig. 5.7). The enamel is shiny on both lingual and buccal sides. A strongly developed mesostyle is present. The protocone is prominent and lingually directed. The paracone is partially broken. The metacone and hypocone are equal in height and the metaconal rib is weak. The preprotocrista is slightly larger than the postprotocrista. Both the pre- and posthypocristae are nearly equal in length. The fossettes are broad and less deep. PC-GCUF 59/18 is a moderately preserved left third

upper molar (Fig. 5.8), quadrate in shape in an early stage of wear. The enamel is wrinkled and uniformly thick. All the four cones are inclined towards the median longitudinal axis of the molar. The base of the protocone is partially broken and less sharp than others. Rugosity is present around the hypocone. A partial cingulum, weak anteriorly, is present at the base of the hypocone on the posterior side of the tooth. A median basal pillar is absent. The protocone and hypocone are well developed. The paracone and metacone are moderately developed and the paracone is pointed with a strong parastyle. A d/Deep and narrow fossettes are/is present filled with cement. The metacone is less sharp than the protocone. A metastyle is also present. PC-GCUF 66/18 is a right third upper molar (Fig. 5.9). with moderate labial styles and a lingual cingulum. The protocone and hypocone are prominent but compressed laterally. The paracone and metacone are also well developed. Thick cingular shelves are present extending mesiolingually and distolingually. The postparacrista and premetacrista are connected on the crown in a low position. The fossettes are broad and less deep than others.

Lower dentition: PC-GCUF 09/18 is a left second lower molar (Fig. 5.10). The protoconid and hypoconid are prominent and compressed laterally and the paraconid and metaconid are also well developed. The postparacristid and premetacristid slope downwards. A weak mesostylid is present on the lingual side. A small and robust ectostylid is present in the transverse valley. The fossettes are broad but less deep than others. The posthypocristid terminates at the midline of the crown at the distal cingulid. PC-GCUF 69/18 is a moderately preserved left lower third molar (Fig. 5.11) in a late stage of wear. The enamel is wrinkled on the lingual and buccal sides. All the principal conids are well preserved; however, the lingual conids are higher than the buccal ones. The premetacristid is larger than the postmetacristid. The anterior fossettes is narrow while the posterior one is partially filled with sediment. The talonid is well preserved, present posteriorly.

Comparison: The small ectostylids, slightly prominent anterior rib and a goat fold in the lower molars are distinguishing characters that confirm that the Padhri specimen belongs to the genus *Gazella*. Pilgrim (1937, 1939) discovered two species of *Gazella* from the Dhok Pathan Fm. of the Middle Siwaliks: *G. lydekkeri* and *G. superba*, with the former larger than the latter (Khan et al., 2015). Recently, a few more fossil remains of *G. superba* were recovered from the Dhok Pathan Fm. (Khan et al., 2015). The teeth under study are different from other contemporaneous large bovids, such as *Tragoportax punjabicus*, *Pachyportax latidens* and *Miotragocerus gluten*, because of their weak stylid, rudimentary ectostylid and strong goat folds. Therefore, the presence of such diagnostic characters supports the assignment of the Padhri specimen to *G. lydekkeri* (Pilgrim, 1937). In our sample, the presence of sharp median ribs and styles with lack of median basal pillars in the upper molars and the presence of sharp median ribs and styles with median basal pillars in the lower molars, and comparable measurements (Supp. Table 1) confirms the similarity with the holotype (AMNH 19663) and already described specimens of *G. lydekkeri* (Pilgrim, 1937, 1939; Akhtar, 1992; Khan, 2008; Khan et al., 2009; Saeed et al., 2018). The morphometric characters of the teeth indicate that the differences between the specimens do not exceed the limits of variability.

3.5 Infraorder Suina Gray, 1821
Superfamily Suoidea Gray, 1821
Family Suidae Gray, 1821
Subfamily Suinae Zittel, in Zittel et al., 1891–1893
Genus *Propotamochoerus* Pilgrim, 1926
Propotamochoerus hysudricus Stehlin, 1899
Figs. 5.12–5.13

Studied material: PC-GCUF 58/18, right upper third molar rM3; PC-GCUF 197/19, right upper third molar rM3 (collected from Padhri, District Jhelum, Punjab, Pakistan).

Description: PC-GCUF 58/18 is a moderately preserved, partially broken right third upper molar (Fig. 5.12) in a middle stage of wear. This molar is bunodont with the typical suid layout of two main cones arranged in a loph. Rugosity is moderate on both the lingual and buccal sides. The enamel is fairly thick and wrinkled. The protocone and metacone are broken but both the hypocone and paracone are completely preserved. The posterior accessory cusps are prominent, supported by a bifurcated cingulum. The talon appears complex owing to the bifurcated cingulum. The buccal surface has moderate flare while the lingual flare is minimal. PC-GCUF 197/19 is a right upper third molar (Fig. 5.13) with very thick enamel and a partially broken base. The protocone and paracone are well developed with the former slightly higher than the latter. The metacone and hypocone are almost equal in height. The anterior, median and posterior accessory cusps are well developed. Both anterior and posterior furrows are deep. The median valley is broad and moderately deep.

Comparison: A number of species of the family Suidae are present in the Dhok Pathan Fm., such as *Conohyus indicus, Hippopotamodon sivalense, Lophochoerus nagrii, Propotamochoerus hysudricus* and *Tetraconodon magnus*. *Propotamochoerus hysudricus* is the only species representing the genus *Propotamochoerus* in the Siwaliks. *Propotamochoerus hysudricus* is thought to have originated from *Hyotherium pilgrimi*, a species in the Middle Miocene Chinji Fm. (Pickford, 1988; Bonis and Bouvrain, 1996; Sarwar et al., 2016; Aslam et al. 2021). However, *Propotamochoerus hysudricus* varies from *Hyotherium pilgrimi* in the saggital cusplets in P4, large size, modification in shape of the anterior zygomata and sharpening of the snout section (Sarwar et al., 2016). In the Middle Siwaliks, *P. hysudricus* is present in the Nagri Fm. and Late Miocene deposits of Dhok Pathan Fm. The Padhri specimens are included in *P. hysudricus* due to moderate enamel thickness in molars, shallow furchen and simple talon/talonid in lower and upper molars (Pickford, 1988; Batool et al. 2015; Sarwar et al., 2016; Dar et al., 2019; Draz et al., 2020b). Comparative measurements of the studied specimens are provided in Supp. Table 1.

4 Discussion

4.1 General Discussion

Mammalian fossils are abundant in the Miocene sediments of the Siwaliks (Colbert, 1935; Akhtar, 1996; Barry et al., 2002; Farooq et al., 2008; Khan, 2008; Ghaffar et al., 2010; Khan et al., 2011; Bhatti et al., 2012; Samiullah et al., 2015; Abbas et al., 2018; Akhtar et al., 2019; Dar et al., 2019; Guzmán-Sandoval and Rössner, 2019; Asim et al., 2020; Khan and Asim, 2020; Draz et al., 2020a, b). The studied localities around Padhri are situated in district Jhelum within the dominant Dhok Pathan Fm. (Khan, 2008a; Babar et al., 2013), which has a very rich mammalian fossil record, especially of artiodactyls (Zaheer et al., 2017; Saeed et al., 2018; Babar et al., 2018; Abbas et al., 2018; Dar et al., 2019; Draz et al., 2020a, b). The age of the upper Dhok Pathan Fm. at the studied locality is Late Miocene (Pilbeam et al., 1977; Barry et al., 2002; Khan et al., 2009a). The mammals from the Dhok Pathan Fm. are documented by excellently rich material, which has enhanced knowledge of the odontological morphometric characters of the Bovidae, Tragulidae, Suidae, Equidae and Rhinocerotidae (Ghaffar et al., 2010; Khan et al., 2011; Bhatti et al., 2012; Samiullah et al., 2015; Abbas et al., 2018; Akhtar et al., 2019; Dar et al., 2019; Guzmán-Sandoval and Rössner, 2019; Asim et al., 2020; Khan and Asim, 2020; Draz et al., 2020a, b; Samiullah et al., 2020). The Padhri sites also provide a complete picture of the faunal composition of Late Miocene mammals in the Siwaliks (Matthew, 1929; Colbert, 1935; Pilgrim, 1939). The order Artiodactyla is the richest element in the Dhok Pathan Fm. (Pilgrim, 1939; Pickford, 1988; Bhatti, 2005; Farooq et al., 2008; Bibi, 2007; Bibi et al., 2009; Akhtar et al., 2019; Draz et al., 2020a), with most taxa also recognized from other contemporaneous Siwalik sediments (Akhtar, 1992; Khan et al., 2009a). Also present at Padhri are Perissodactyla, Carnivora and Proboscedia (Pilbeam et al., 1977; Barry et al., 2002; Khan, 2007; Khan et al., 2009a; Khan et al., 2012).

Hipparion is an important marker for faunal correlation in the Late Miocene. *Hipparion theobaldi* has been identified from Padhri locality with other associated fauna. The genus *Hipparion* was reported by de Christol (1832) and Leidy (1847). They stated that this genus evolved from *Merychippus* during the Miocene. This genus *Hipparion* first appeared in IndoPakistan and then later in China and Africa in the Late Miocene (Berner and Hussain, 1985; Wolf et al., 2013). The rhinocerotid fauna of Pakistan is well diversified and is present across three distinct biostratigraphic zones ranging from Early Miocene to the Recent (Khan et al., 2008, 2011). The sites include the Manchar Fm. in the Sindh, the Bugti hills in Baluchistan, and the Siwalik hills in northern Pakistan (Foster-Cooper, 1934; Qiu and Xie, 1997). The Tibet Plateau on both sides of the Himalayas played an important role in the distribution and dispersal of rhinocerotids between Asia and the Indian subcontinent throughout the Oligocene (Antoine et al., 2003).

The mammalian fossil record of Padhri shows that the boselaphine bovids were highly diversified in the Late (Miocene (Kostopoulos, 2005; Khan, 2008a; Khan et al., 2010; Abbas et al., 2018, Draz et al., 2020a, b). Boselaphine fossils are abundant in Africa, Eurasia and the Siwaliks (Savage and Russell, 1983; Pickford, 1988; Nakaya, 1994; Khan et al., 2008; Bibi et al., 2009) *Tragoportax, Selenoportax* and *Pachyportax* are the dominant Late Miocene Siwalik boselaphines. However, *Selenoportax* remains have also been discovered from the Upper Siwalik (Akhtar, 1992; Khan et al., 2011) and the Miocene Shihuiba Fm. in China, which is 11.1–8.0 Mya in age (Qiu and Qiu, 1995; Steininger, 1999). The genus *Pachyportax* is present in the Nagri and Dhok Pathan formations of the Siwaliks (Mahmood et al., 2019; Draz et al., 2020a); the Baynunah Fm. in United Arab Emirates; Mpesida Beds in Kenya, Africa; and Marageh and Tagar in Afghanistan (Hill et al., 1985; Nakaya, 1994; Sen et al., 1997).

Gazella has survived into the Neogene in Africa, Asia, Europe, and Algeria (Arambourg, 1947; Gentry, 1970). The first occurrences of *Gazella* have been reported from the Neogene of Europe, Africa and Asia (Gentry, 1999; Kostopoulos, 2009). This genus was well developed during the Late Miocene to Early Pliocene and is reported from numerous localities in South Africa, China and Spain (Chen, 1997: Khan, 2008; Khan et al., 2012). Gentry (1999) and Kostopoulos (2009) noted that this genus became recessive in Asia during the Pliocene due to the cold environmental conditions while remaining dominant in Africa and the Middle East. Biogeographically, the Siwalik gazelles resemble the Eurasian and African Late Miocene fauna, which shows geographical development, transformation of gazelles and extinction of boselaphines during the Late Miocene to Early Pliocene (Bibi and Gulec, 2008). *Gazella lydekkeri* is morphologically similar with Eurasian Species *G. capricornis* (Bibi and Gulec, 2008). Fossils of this genus are present in East and North Africa, central and SW Europe, East Asia, Sub-Paratethys and the Siwaliks during the Late Miocene (Gentry, 1966, 1970, 1978, 1980; Savage and Russell, 1983; Gentry, 1994).

Padhri is one of the richest Late Miocene regions for fossil mammals in the Siwaliks in terms of suid species: *Hippopotamodon sivalense, Tetraconodon magnus, Conohyus indicus* and *Propotamochoerus hysudricus* (Falconer, 1868; Lydekker, 1883; Colbert, 1935; Pickford, 1988; Made, 1999; Batool et al. 2015; Dar et al., 2019). All the above mentioned species of suids were present in the Siwaliks with other artiodactyls such as *Selenoportax, Pachyportax, Tragoportax, Bramatherium* and *Dorcatherium*. The family Suidae was extensively distributed in Eurasia and Africa (Mors et al., 2019; Dar et al., 2019). The Siwalik species of suids like *Conohyus, Propotamochoerus, Sivachoerus* and *Sus* are abundant on the Indian subcontinent, but they might have migrated from Europe, Africa and other parts of the world (Matthew, 1929; Colbert, 1935; Pickford, 1988; Made, 1999). Overall, the Padhri Late Miocene sediments have a similar fauna to that of Turolian Land Mammal age, as described in North Africa, West Asia and Europe (Khan, 2008a; Babar et al., 2013). The species range throughout the Late Miocene and are also present across Eurasia from

China to Spain, and to the far south of South Africa (Pilgrim, 1939; Moya-Sola, 1983; Thomas, 1984; Bibi, 2007; Bibi and Gulec, 2008).

4.2 Paleoclimate

The recovered specimens of *Selenoportax, Pachyportax*, *Gazella*, and *Hipparion* clearly indicate that the studied locality belongs to the Late Miocene. The presence of Hipparion and larger metapodials in *Selenoportax vexillarius* are an indication of open to drier habitats in the surroundings of Padhri (Scott, 1985). The interpreted climatic conditions suggest that condensed rain forests were present during the Late Miocene (Barry et al., 2002). *Selenoportax vexillarius* and *Pachyportax latidens* lived in woodland environments (Khan et al., 2010). Drier and more open habitats can be implied for the larger bovids. Gazelles are variegated feeders that need vast land for grazing (Batool et al. 2015). The suids and hipparionines are also noted to live in relatively more arid and open environments (Khan et al., 2009). The rhinocerotids and hipparionine fauna indicate an evergreen woodland environment, similar to today's mixed monsoon forest and grassland glades of the Indian subcontinent (Colbert, 1935; Mathew, 1929; Pilgrim, 1937, 1939; Khan et al., 2010; Akhtar et al., 2020).

5 Conclusions

The studied locality Padhri, Dhok Pathan Formation, Middle Siwaliks, Punjab, Pakistan has revealed a significant number of fossils of Late Miocene age. The morphological characters and systematics of the described specimens have been discussed in detail here to elucidate the taxonomy. The fossil specimens of *Hipparion theobaldi* (a new skull), *Chilotherium intermedium*, *Tragoportax punjabicus, Salenoportax vexillarius, Pachyportax latidens, Gazella lydekkeri,* and *Propotamochoerus hysudricus* were excavated and are described. We have also reviewed the diversity of the Padhri mammalian fossils. Artiodactyls predominate in the Middle Siwaliks mammalian fauna during the Late Miocene. The studied fossils show that the family Bovidae includes the most copious taxa. On the basis of paleoenvironmental data from the mammals of the Padhri, Dhok Pathan Fm., we conclude that, during the Late Miocene, the climate at the studied locality was highly moist and well vegetated, with small but numerous open standing water bodies with dense rain forest that provided thick shelter. Paleobiogeographically, the studied taxa indicate a prevalence of woodland to savannah territory during the deposition of the Dhok Pathan Fm.

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