

Description of *Sivalhippus* (Equidae: Perissodactyla) from the Late Miocene Siwalik Sub-Group of Pakistan

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Cover Page Footnote

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DESCRIPTION OF *SIVALHIPPIUS* (EQUIDAE: PERISSODACTYLA) FROM THE LATE MIOCENE SIWALIK SUB-GROUP OF PAKISTAN

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ABSTRACT

New fossil mandible as well as isolated upper and lower dentitions of the late Miocene Hipparionine species, have been discovered from a locality of Chakwal, Punjab, Pakistan. By using morphometric and morphologic analysis, we have deduced that these specimens belong to *Sivalhippus theobaldi*. The body size of this species was intermediate between *Sivalhippus perimensis* and *Hipparion antilopinum* while its hypsodonty indicates that this species was a grazer to a larger extent which existed in mosaic of woodland and grassland in the Latest Miocene. However, the comparison with the recent horse (*Equus caballus*) mandible indicates some differences in dental and jaw lengths. The recent horse tends to have bigger and longer molars (higher hypsodonty indices) which may be attributed to a response towards changing vegetation, started at the end of the Miocene (ca. 6-7 Ma) strengthening the hypothesis that adaptive physiologies are a response towards a changing climate.

Keywords: Perissodactyls, Dhok Pathan, formation, Middle Siwaliks.

INTRODUCTION

All three-toed horses, present in Mio-Pliocene have been categorized under a unanimous term: *Hipparion*. In this time span *Hipparion* horses were widespread across the Old as well as New World (Webb et al., 1969). Due to the ubiquitous nature of all these horses across the old world, particularly, they are often termed “Hipparionine Fauna” and it is more conventionally related to the Neogene time span. The description of the Neogene horses is chiefly based on their dental characteristics and also based on postcranial features, but to a lesser extent (MacFadden, 1984).

Hipparionines are widely spread in the Siwaliks of Pakistan (Figure 1), specifically and dominantly in the Middle Siwaliks of Pakistan (Hussain et al., 1971). Four distinct species of *Hipparion* were described by Wolf et al., (2013). These species are *Sivalhippus nagriensis*,

Sivalhippus theobaldi, *Sivalhippus perimensis* and *Hipparion antilopinum*.

The present study comprises of morphometric and morphological identification as well as description of the late Miocene *Hipparion* viz *Sivalhippus theobaldi*. The lower jaw of above-mentioned species was collected from Dhok Pathan Formation of Chakwal, Pakistan (Long 72 °14 E, Lat 33 °07N). Furthermore, we have also compared *S. theobaldi* with recent horse i.e. *Equus caballus* as an un-conventional attempt to see the differences among two horse species.

This is first study to compare the morphometrics of a fossil mandible of an extinct horse species (*Sivalhippus theobaldi*), which is a far relative of recent day horse, with the recent horse (*Equus caballus*) and attempts to comment on adaptive physiologies as a response to changing climate.

MATERIALS AND METHODS

The specimens were sampled from the Dhok Pathan type locality of the Middle Siwaliks of Pakistan. Samples

were thoroughly washed and cleaned in Ecology and Evolutionary Biology Laboratory. All the specimens described here are housed in the Institute of Zoology, University of the Punjab, Lahore, Pakistan.

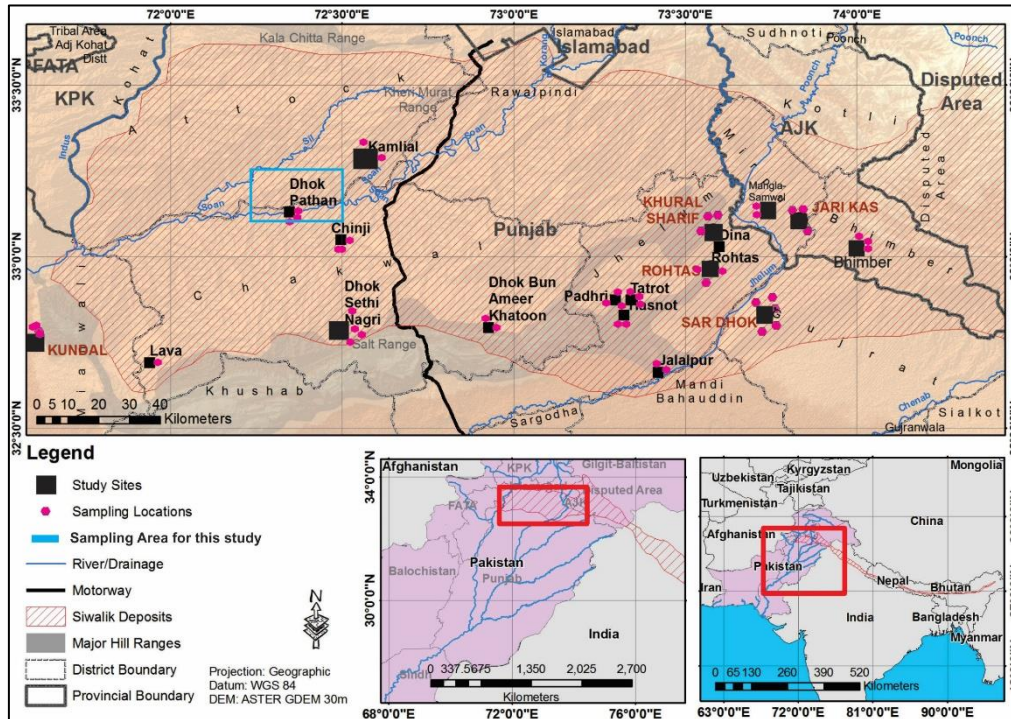


Figure 1: Map of the Siwalik sub-Group of Pakistan highlighting the studied area and other fossil-yielding localities from Barry et al., (2002).

Length and width are measured in millimeters (mm). Furthermore, the Width/Length ratio has also been taken into consideration. The specimen was cataloged as PUPC 09/15, where PUPC indicates Punjab University Palaeontological Collection, 09 is the number assigned to the sample and 15 is the year of collection. The dental terminology of the sample follows Wolf et al., (2013).

Abbreviations: L=Length, W=Width, mm=millimetre, P=Pre-molar, M=Molars.

Studied Material

PUPC 94/2000: A mandible of *S. theobaldi* having all the pre-molars and molars except the right fourth pre-molar (Figure 2). PUPC 06/15, An isolated left M^3 , PUPC 09/15, an isolated right P^2 , and

PUPC 07/15, an isolated left M^2 (Figure 3). An isolated right M^2 , PUPC 10/15, PUPC 08/15, an isolated left P^4 , and PUPC 11/15, an isolated left P^3 (Figure 4). Mandible of *Equus caballus* UDZ 515 (UDZ stands for university department of zoology while 515 is the sample number) (Figure 5).

RESULTS

Systematic Palaeontology:

- Order: Perissodactyla Owen (1848)
- Sub-order: Hippomorpha Wood (1937)
- Family: Equidae Gray (1837)
- Genus: *Sivalhippus* Lydekker (1877)
- Species: *Sivalhippus theobaldi* Lydekker (1882)

Holotype: GSI C153, Left Maxilla with DP 2-4.

Horizon: Middle Siwaliks

Diagnosis

A large size horse with pre-orbital facial fossa that is separated from orbit by a pre-orbital bone. Tridactyl feet. Cheek teeth completely ornamented with thick fossettes, plications, and bifid to trifid pre-caballins (Ghaffar, 2005).

Description

i. **General Description**

The described and discussed specimens comprise a mandible, pre-molars, and molars. Wolf teeth are not present in the mandible. The mandible is a well-preserved lower jaw having an intermediate stage of wear. It represents clear hypsodonty and teeth are highly extended and pillar-like in appearance. A layer of thin cement is present around the sample. The basal part of the mandible is reconstructed by the help of Plaster of Paris. Incisors and canines are absent.

ii. **Dental description**

a. **Pre-Molars**

PUPC 94/2000 is a well-preserved mandible *S. theobaldi*. Pre-Molars are molariform teeth. Protoconids and hypoconids are on the labial side while stylids are well preserved. In IP₂ mesostylid is slightly damaged. Protoconid is extended in the form of a perastylid. In IP₃, stylids are intact. Protoconid as well as hypoconid are broad. The rounded metaconid is somehow fused with the isthmus. IP₄ has a smaller entoconid as compared to other conids. The mesostylid is partially damaged. Entoflexid is longer in size as compared to metaflexid. The enamel on rP₂ is thick and rugose due to which dentine cannot be seen. A thin coating of cement is present on the buccal side. Circular mesostylid. rP₃ follows the same pattern as in rP₂. The upper pre molar (PUPC 09/15), represents some

striking features. It is a well-preserved tooth in an early stage of wear. It is highly elongated and represents a pillar-like appearance. Major cusps are highly developed and in a good preserving stage. The isolated protocone is somewhat rounded. It is covered by a moderately thick layer of cement. The paracone is deep and almost equal to the metacone in anteroposterior length. The lower pre-molars PUPC 8/15 and PUPC 11/15 are well preserved but slightly damaged. The metaconid is united with isthmus and almost rounded in general appearance. Both the pre molars are in the middle wearing stage.

b. **Molar**

All the molars either right or left are intact and represent an excellent preserving stage. The anteroposterior part of metaflexid represents complicated enamel in IM₁ while in IM₂ metastylid is a bit pointed and has a wavy outline. Protostylid and parastylid are pillar-like in general appearance. The rugosity of enamel is high and it is thick in IM₃. The crown is not much broader but narrower and represents extreme hypsodonty. Mesostylid is narrow. The depression on the lingual side is plihypoconid. Two prominent foldings, metaflexid and entoflexid are present. However, entoflexid is a little elongated and curved. Right M₂ (PUPC 10/15) represents the middle stage of wear, all the conids and stylids are well preserved. Protoconid is less broad than hypoconid. The Protoconid of rM₃ is also rounded and smaller as compared to the hypoconid. PUPC 06/15 and PUPC 07/15 are both isolated upper molars in which all the loph viz. ectoloph, metaloph and protoloph are prominent and in a good preserving stage. Complex enamel folding is represented in fossettes. Both pre and post-fossettes represent many plications of thickly deposited enamel. The cusps are highly developed and a thin

coating of cementation is all over the crown

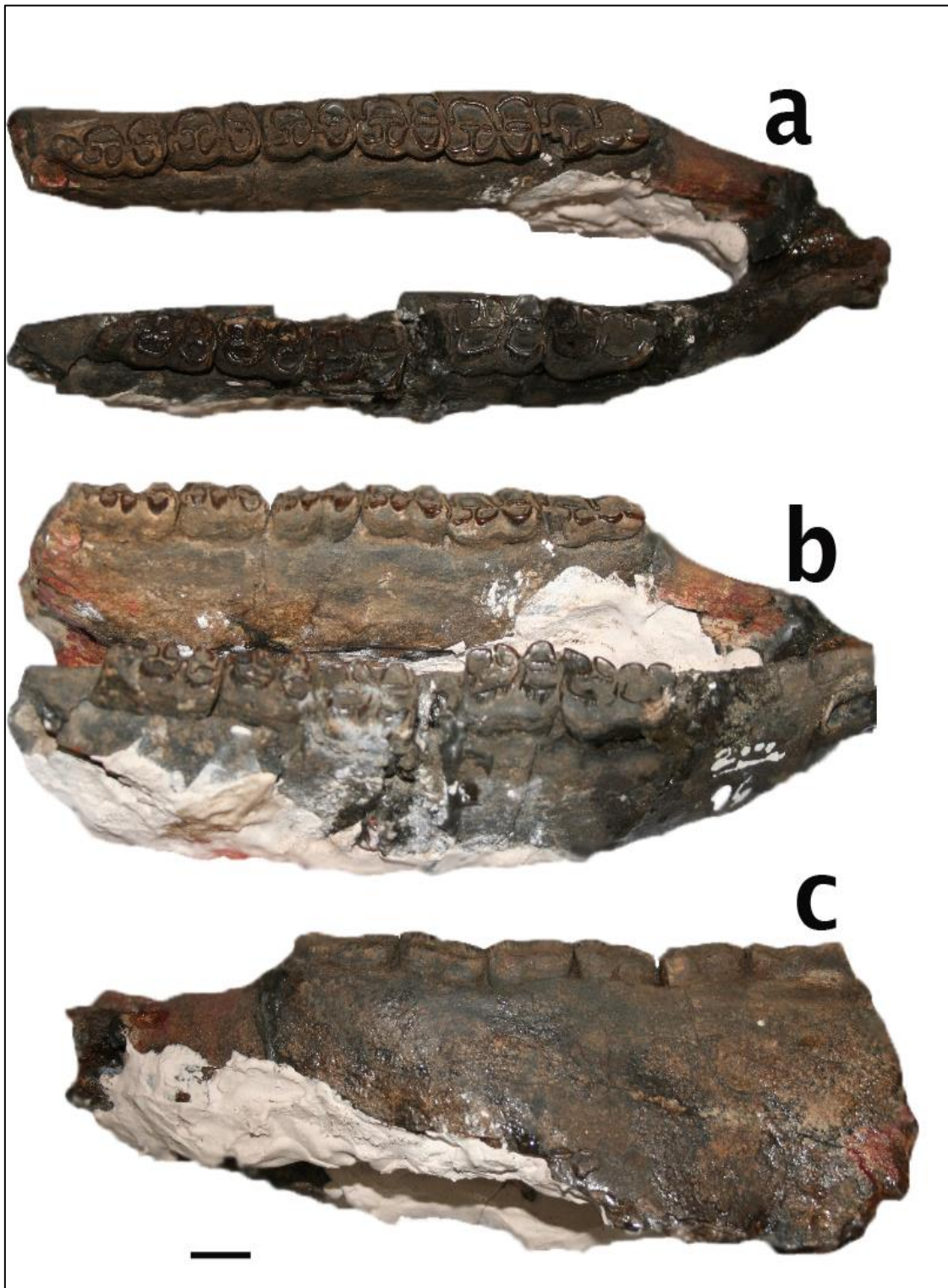


Figure 2: PUPC 94/2000, Mandible of *Sivalhippus theobaldi* representing (a) Occlusal view, (b) Lingual view, (c) Labial view. Scale bar is of 10mm.

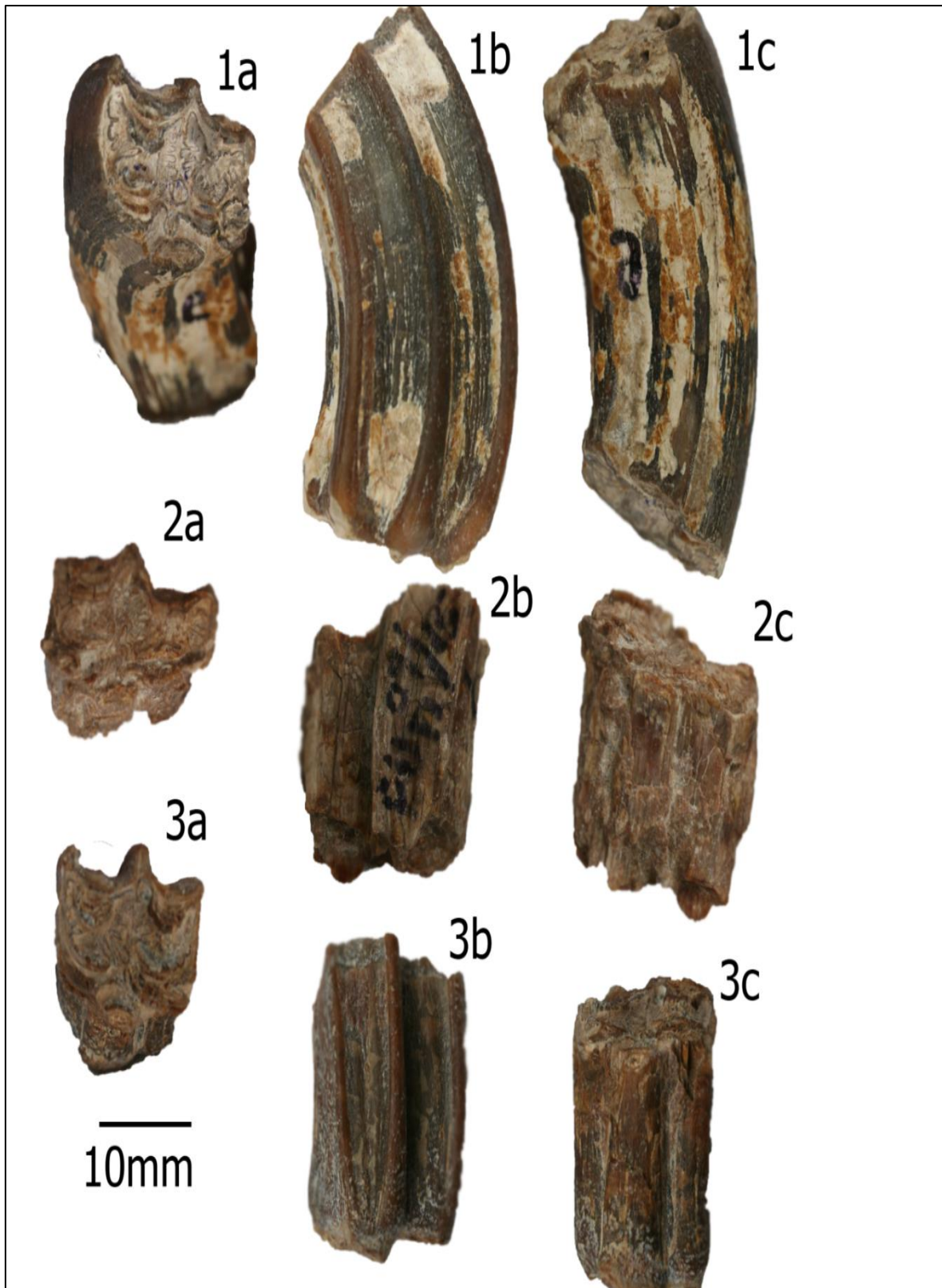


Figure 3: *Sivalhippus theobaldi*, 1. PUPC 06/15, left M³; 2. PUPC 09/15, right P²; 3. PUPC 07/15, left M² (a) occlusal view; (b) buccal view; (c) lingual view). The scale bar equals 10 mm.



Figure 4: *Sivalhippus theobaldi*, 1. PUPC 10/15, right M₂; 2. PUPC 08/15, left P₄; 3. PUPC 11/15, left P₃ (a) occlusal view; (b) buccal view; (c) lingual view). The scale bar equals 10 mm.

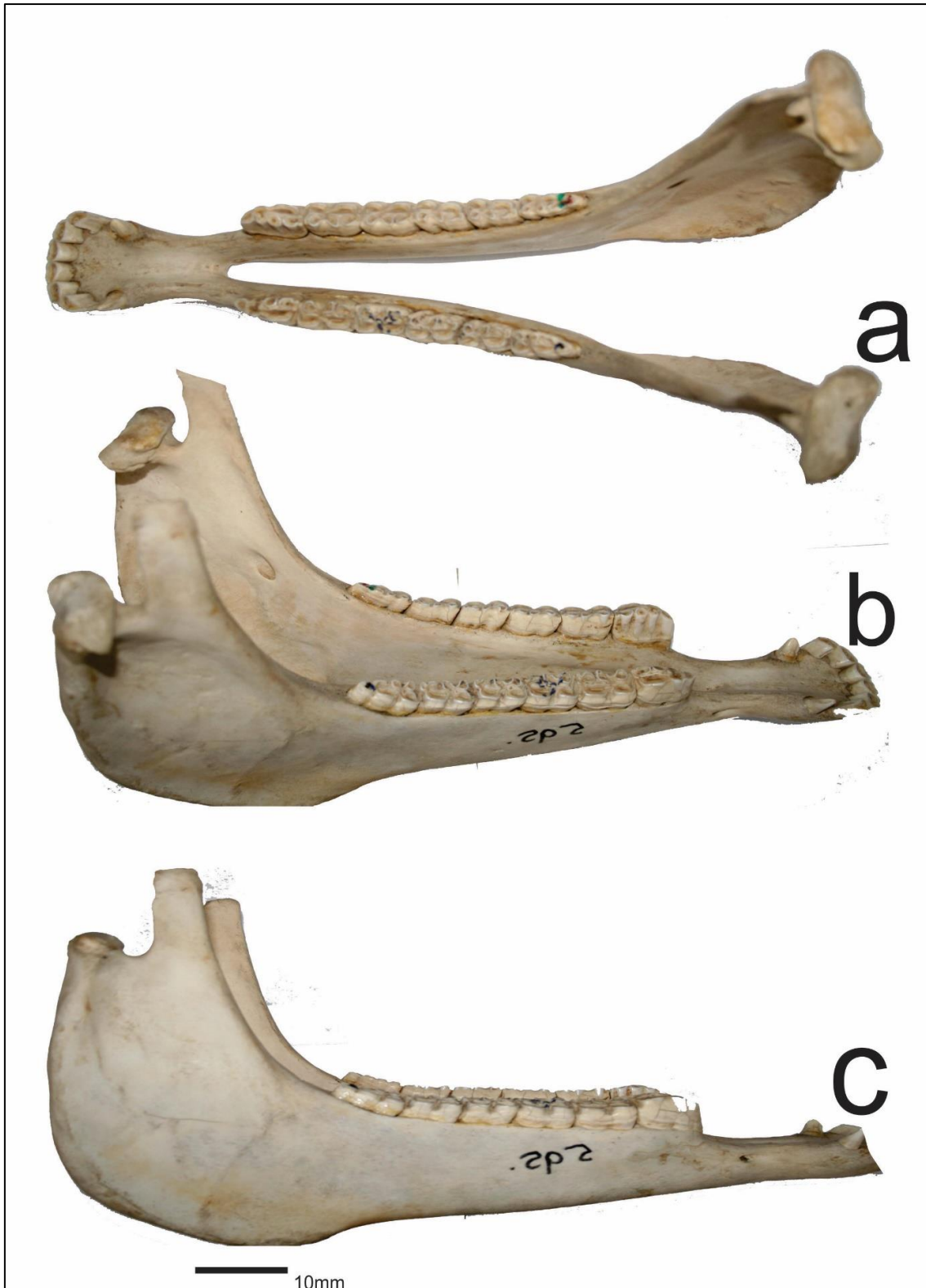


Figure 5: UDZ 515, Mandible of *Equus caballus* representing (a) Occlusal view, (b) Lingual view, (c) Labial view. The scale bar measures 10mm.

Table 1: The comparison of cheek teeth measurements of *Sivalhippus theobaldi* with its members as well as with other sister species in mm. The referred material is used from *Colbert (1935), #Ghaffar (2005), **Falconer and Cautley (1849), ##Bernor and Hussain (1985).

Taxa	Specimen Number	Position	Length (mm)	Width (mm)
<i>S. theobaldi</i> (Studied)	PUPC 10/15	rM ₂	25	14
	PUPC 08/15	IP ₄	24	19
	PUPC 11/15	IP ₃	26	13
	PUPC 06/15	IM ³	25	22
	PUPC 07/15	IM ²	24.5	22
	PUPC 09/15	rP ²	29.5	19
	PUPC 94/2000	IP ₂	29.2	14.2
		IP ₃	23.9	16.3
		IP ₄	24	16.2
		IM ₁	21.7	13.2
		IM ₂	22.5	12.4
		IM ₃	29.4	11.6
		rP ₂	28.9	13.1
		rP ₃	23.4	13.7
		rM ₁	24.8	14
		rM ₂	21.8	12.2
<i>S. theobaldi</i>	#PUPC 2000/94	P ₂	25	13
	#GCS 11/19	P ₂	25	14
	#GCS 11/20	M ₁	21.0	15.0
	#PUPC 07/167	P ₄	23	15.6
	##BMNH 2647	M ²	21.3	19.8
	#PUPC 83/498	P ₃	26.5	13
	#PUPC 07/174	M ₂	21.7	13.9
	*UPC 68/499	M ₂	26.0	14.0
	#PUPC 2000/94	P ₄	25.0	18.0
	*AMNH 29806	M ₂	25	15
	#PUPC 2000/99	M ₂	25.1	15
	<i>H. antilopinum</i>	#PUPC 13/78	M ₃	24.5
#PUPC 13/69		P ₃	27	16
#PUPC 2000/99		P ₄	22.5	16
##BMNH 2647		M ³	21.3	19.8
*BSM H-15		M ₁	20.9	12.8
*PC-GCUF 10/42		M ₃	24	11
*AMNH 198559		M ₂	25	14
#PUPC 2000/99		M ₂	22	15
#PUPC 13/76		P ₄	24.5	12.7
<i>S. perimense</i>	**GSI C349	P ²	33.2	27
	<i>Equus caballus</i> (Extant)	UDZ515	rM ₃	28.5
rM ₂		20.3	11.8	
rM ₁		21.8	13.5	
rP ₄		23.7	15.1	
rP ₃		23.5	15.2	
rP ₂		29.7	12.2	
IM ₃		28.9	11.3	
IM ₂		20.2	12.9	
IM ₁		21.8	13.5	
IP ₃		23.4	15.1	
IP ₄		22.7	14.1	
IP ₂		30.2	12.2	

Table 2: Mandibular measurements taken in millimeters (mm). Terminology followed by Pascika et al., (2011). Terminologies having * are introduced by the author.

No	Mandibular Character	<i>S. theobaldi</i> (mm)	<i>E. caballus</i> (mm)
1	IGChThL	161.6	162.0
1a	ILChThL	160.2	160.4
2	IMThL	76.7	74.6
3	IPmThL	79.7	85.7
4a	MHM3	66.3	74.6
4b	MHM1	55.8	60.15
4c	MHPA	44.5	40.6
5	Symphysis	31.1	33.8
6	*DRLM	60.2	67.1
7	*DRLP	36.2	39.4

DISCUSSION AND COMPARISON

The studied sample has been compared and discussed with reference to already published data of *S. theobaldi* and other Late Miocene *Hipparion* species as well as with the recent horse (Table 1). The comparative analysis of the sample reveals the resemblance with already published records. The morphologic and morphometric analysis of this mandible supports its addition in a broader group of the Late Miocene horses i.e. Hipparionines.

The body size of *S.theobaldi* is larger comparatively, while *H. antilopinum* and *H. nagriensis* were shorter in body height (Colbert et al., 1935). The molars are slightly more developed and are not much squariform as compared to *H. antilopinum*. *S. theobaldi* represents higher degrees of hypsodonty than *H. antilopinum* and *H. nagriensis*. The dentition of *S. theobaldi* has a complex dental pattern. The protoconid of the studied sample is compressed as described by Falconer and Cautely, (1849). The enamel border is simple and has less bifid to trifid plications but *H. antilopinum* and *H. nagriensis* has a complex pattern of plications in pre and post-fossettes. Two hypoglyphs are deeply incised in *S.theobaldi* while hypoglyphs in other species are not as deeply incised but moderate. The described samples represent all the basic characteristics of *S. theobaldi*.

Significant differences have been found between recent horses and extinct *S. theobaldi*. The IGChThL (Inferior greater cheek-teeth row length P₂-M₃) of the mandible is greater in recent horse along with ILChThL (Inferior lesser cheek-teeth row length, measured along the crowns P₂-M₃) which indicate a change in dietary pattern to somewhat harsh and drier feeding habit. Inferior molars row length (IMThL) is more in *S. theobaldi* than *E. caballus* as compared to the inferior premolars row length (IPmThL) which is lesser in *S. theobaldi*. A jaw expansion is also noted as MHM3 (Mandibular height caudal to M₃), MHM1 (Mandibular height rostral to M₁), MHPA (Mandibular height rostral to P₂), DRLM (distance between right and left molars) and DRLP (distance between right and left premolars) are greater in length in *E. caballus* while in *S. theobaldi* jaw is smaller (Table 2). The length of the symphysis in *S. theobaldi* is lesser than in the recent horse.

While the general comparison to recent horse species *E. caballus* (UDZ515) represents some differences in length and width, the pattern of plication and enamel structure. Recent horses are more divergent and represent a higher degree of hypsodonty as compared to *S. theobaldi* which may be attributed to the adaptive physiologies as a response to the changing climate which favored grazers (Khan et al., 2020).

The higher significance of the Siwalik hipparionines is due to the fact that they are useful tools for reconstructing Biochronology and Palaeozoogeography (MacFadden and Bakr, 1979). Due to their isolated dentition and cranial features, hipparions are widely explored and studied. Hipparionine limbs represent a higher degree of modifications regarding their niche from exclusively forest to mosaic environmental conditions (Sondaar, 1977).

The higher values of carbon and oxygen stable isotopes indicate that they favored wider and drier areas of vegetation pattern (Waseem et al., 2019). The earliest appearance of Hipparionine species was recorded at about ~9.5 Ma while *Equus* appeared around 2.48 Ma (Barry et al., 1982, 2002; Wolf et al., 2013). Other late Miocene fauna along with *Hipparion* includes *Selenoportax*, *Pachyportax*, many species of Rhino, etc. All these taxa exploited comparatively more arid and open habitats like today's mixed seasonal forest of the Siwaliks, Pakistan.

CONCLUSION

A preserved mandible of *Hipparion* has been unearthed from the Dhok Pathan Formation of the Middle Siwaliks, Pakistan. Morphologic and morphometric analysis indicates that the mandible belongs to *S. theobaldi*, which is a divergent species of three-toed horses. The described and discussed material enhances the evidential proofs of *Sivalhippus* presence in the Dhok Pathan Formation. The rich diversity of faunal elements is highly helpful in understanding and reconstructing the palaeoenvironmental clues as well as it explores the niche and habitat preferences of past animals which was once present in the Late Miocene of Pakistan. *S. theobaldi* is medium to large in body size while the enamel around the fossettes is simple (Colbert, 1935).

The presence of medium-sized antelopes alongside *Sivalhippus* in the Dhok Pathan Formation, indicate wooded, grassy savannahs and grasslands which were present during the late Miocene to the early Pliocene time span.

AUTHORS CONTRIBUTION

MTW and SZ collected the samples during the fieldwork. AI and MA processed the fossil samples and collected the recent horse sample as well. AMK overall supervised the study.

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CONFLICT OF INTEREST

The authors state no conflict of interest of any kind with any individual or organization.

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