

SUIDAE FOSSILS FROM LATE MIOCENE DEPOSITS OF HASNOT AND PADHRI, JHELM, PUNJAB, PAKISTAN

HASSAN RAZA 

State Key Laboratory of Biogeology and Environmental Geology, School of Earth and Planetary Sciences, China University of Geosciences, Wuhan 430074, Hubei, PR China.

razahpu@gmail.com

SAYYED GHYOUR ABBAS 

Department of Zoology, University of Sialkot, 1-KM Main Daska Road, Sialkot, Pakistan. Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China.

ghyour.kazmi@gmail.com

MUHAMMAD AKBAR KHAN , AMINA TUFAIL 

Dr. Abu Bakr Fossil Display and Research Centre, Institute of Zoology, University of the Punjab, P.O. Box No. 54590. Lahore, Pakistan.

akbar.zool@pu.edu.pk, aminabatoool@gmail.com

KIRAN AFTAB , RAZIA IQBAL 

Department of Zoology, University of Gujrat, Hafiz Hayat Campus, 50700, Gujrat, Pakistan.

dr.kiran@uog.edu.pk (Corresponding author), razia.iqbal@uog.edu.pk

MUHAMMAD ADEEB BABAR 

Department of Zoology, University of Okara, Okara, Pakistan.

babar.zool@uo.edu.pk

KHALID MAHMOOD 

Department of Zoology, Faculty of Biological Sciences, Quaid-i-Azam University Islamabad, 45320, Pakistan.

mkhalid@qau.edu.pk

MUHAMMAD ASIM 

Department of Zoology, University of Narowal, Narowal, Pakistan.

m.asim@uon.edu.pk

ABSTRACT – New suid fossils comprising upper and lower dentition were recovered from the Dhok Pathan Formation (upper Miocene outcrops of Hasnot and Padhri) of the Siwalik Group in the Potwar Plateau of Pakistan. Most of the recovered material shows morphometric similarities with the Eurasian genera, *Propotamochoerus* and *Hippopotamodon*, and is allocated to *Propotamochoerus hysudricus*, *Hippopotamodon sivalense*, *H. major*, while a partial lower incisor is described as *Tetraconodon magnus* and some broken specimens are described as Suidae indet. These specimens add further data to the anatomical characteristics of these species, especially representing the first ever description of the upper third molar of *H. major* from the Siwaliks and incisor of *Tetraconodon magnus*.

Keywords: *Propotamochoerus*, *Hippopotamodon*, *Tetraconodon*, Siwaliks, Dhok Pathan Formation.

INTRODUCTION

The suids comprise a group of mammals that includes hogs, boars and pigs (Gongora *et al.*, 2011). Like the other mammals, the Neogene can be designated as the evolutionary period for Suidae, and such diversification is also seen in the middle and

later parts of the Siwalik Group of Indian subcontinent (Van der Made, 1996, 1998; Orliac *et al.*, 2010a, b; Batool *et al.*, 2015; Chavasseau, 2025). Various suid species have been reported from the Dhok Pathan Formation of the Middle Siwalik Subgroup (Pilbeam *et al.*, 1977; Barry *et al.*, 1980, 2002; Pickford, 1988; Batool *et al.*, 2015; Aslam *et al.*, 2021; Babar *et al.*, 2024a, b).



However, *Hippopotamodon* and *Propotamochoerus*, members of subfamily Suinae, are frequently found from the Middle Siwalik Subgroup (Pickford, 1988; Babar *et al.*, 2024a; Chavasseau, 2025) while a third large genus, *Tetraconodon*, a member of subfamily Tetraconodontinae, is rare (Babar *et al.*, 2021). With the disappearance of *Listriodon* and *Conohyus* during the late Miocene, *Propotamochoerus hysudricus* and *Hippopotamodon sivalense* became dominant suids with an abundant fossil record and a wide distribution across the Indian subcontinent (Pickford, 1988; Batool *et al.*, 2015; Aslam *et al.*, 2021; Van der Made *et al.*, 2022; Sankhyan & Chavasseau, 2024; Babar *et al.*, 2024a). The genus *Propotamochoerus* is found from the late Miocene to the early Pliocene of Eurasia, and in the Siwaliks, it is monospecific and ranges from the Nagri Formation (early late Miocene to the late Miocene) to the top of Dhok Pathan Formation (Chavasseau, 2025) and this age is comparable to the European species *Korynochoerus palaeochoerus*.

The genus *Hippopotamodon* is diverse in the Siwaliks (10.4 to 6.4 Ma), representing at least three species such as *H. sivalense*, *H. major*, and *H. antiquus* in the Siwaliks but it was considered monospecific by Pickford (1988) with *Hippopotamodon sivalense* Lydekker (1877) for a long time and he accommodated all the specimens in this single species by stating that a pattern of increasing size is shown in the *Hippopotamodon sivalense* specimens through time, those from the Nagri Formation being smaller than those from the Dhok Pathan Formation. Later, Pickford (2015) recognized four species from the Siwaliks: *Hippopotamodon sivalense*, *H. major*, *H. antiquus* and

H. pilgrimi. Among these, the validity of *H. pilgrimi* is doubtful. Nevertheless, *H. sivalense* is predominantly found in the upper portion of the Nagri Formation and throughout the Dhok Pathan Formation, also observed in younger strata within the Hasnot area. Notably, 78% of the *H. sivalense* specimens in the GSP collection were found in localities that also produce hominoid fossils (Pickford, 1988).

The genus *Tetraconodon* is a large sized suid, having extremely large sized and inflated P/p3–4, and it is currently known by five species, *T. minor*, *T. magnus*, *T. irramedius*, *T. irramagnus*, and *T. malensis* which were recovered from the Miocene deposits of Pakistan, India and Thailand (Pickford, 1988; Thaug-Htike *et al.*, 2005, 2007; Khan *et al.*, 2013; Babar *et al.*, 2021). All these species are poorly documented and based on isolated teeth and fragmentary dentognathic specimens, based on which *T. minor* is the smallest and *T. magnus* is considered as the largest species of the genus (*ibid.*).

The present study is focused on recently collected suid specimens from the Hasnot and Padhri areas of district Jhelum, Pakistan. The specimens have been subjected to morphometric analysis, compared with the previously collected specimens of suid genera and species from the Siwaliks of the Indian subcontinent, and they provide more anatomical and metric information, which will be helpful in ongoing reassessment of the Siwalik suids, leading to get a better picture of diversity of this group in extinct groups. A brief geographic and geological account of Hasnot and Padhri are given below from where the described specimens were collected (Figure 1).

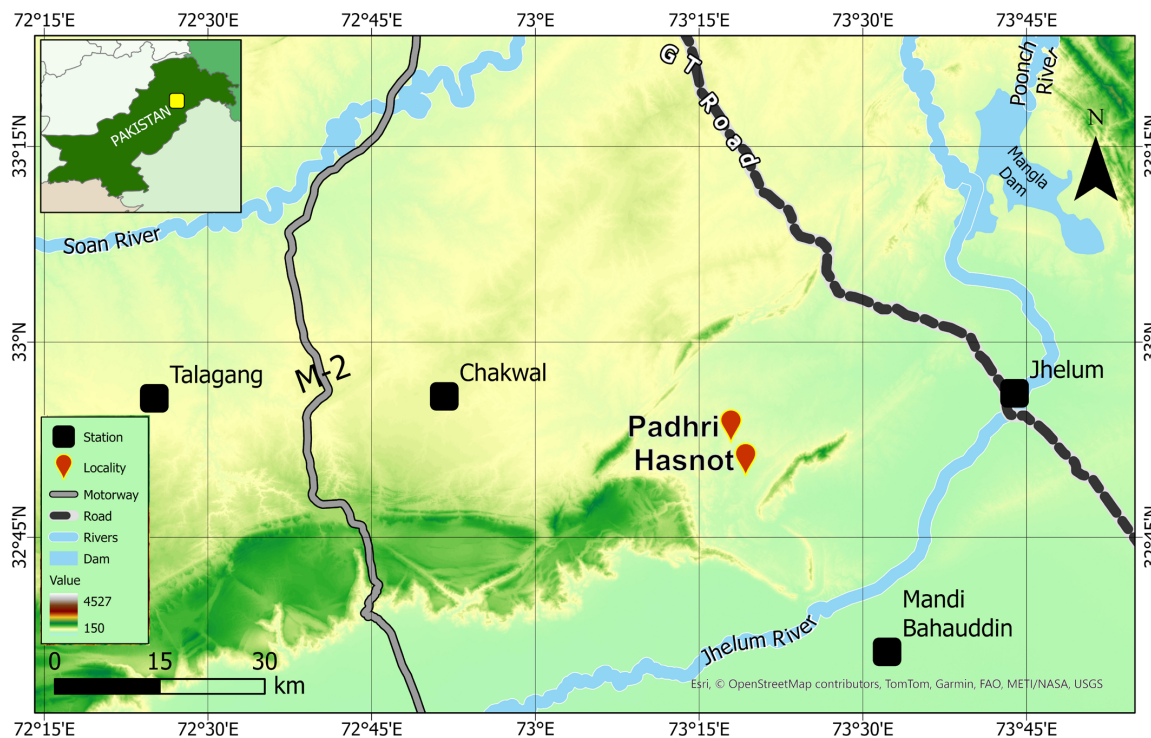


Figure 1. Map showing the location of Hasnot and Padhri in the district Jhelum, Punjab, Pakistan.

The Hasnot village (Lat. 32° 49'N; Long. 73° 18'E) lies around 70 kilometers west of Jhelum city while Padhri village lies about 3 kilometers north of Hasnot (Figure 1). The fossiliferous outcrops, whose width and length vary at different places in these areas, consist of alternating light pink to pale yellow colored claystone, light to dark grey sandstones and with horizons of small size conglomerates deposited by the fluvial system representing the Dhok Pathan Formation of the Middle Siwalik (Colbert, 1935; Vokes, 1936; Barry *et al.*, 2002; Khan *et al.*, 2024). These sites have been known for more than 150 years for the upper Miocene deposits containing mammalian fauna and belong to the middle and upper Dhok Pathan Formation (8–6.4 Ma; Barry *et al.*, 2002).

MATERIAL AND METHODS

The material studied includes ten specimens comprising incisors, premolar, upper and lower molars, and a mandibular fragment (Table 1). The surface collection method was used to collect fossils and most of these are surface finds. The collected specimens were prepared in the Paleontology Lab and displayed in the Dr. Abu Bakr Fossil Display and Research Centre, Institute of Zoology, University of the Punjab, Lahore, Pakistan. The measurements and nomenclature mainly follow Thaug-Htike *et al.* (2005). The measurements have been taken with the digital Vernier calipers and are given in millimeters (mm). Photography has been done with Canon 6D camera and figures have been prepared using Adobe Photoshop CC.

Intuition abbreviations: CCECL, Centre de Conservation et Eludes des Collections; DT, Dinopolis Teruel, Spain; GSI-B & K, Geological Survey of India, India; GSP, Geological Survey of Pakistan, Pakistan; MNCN BAT, Museo Nacional de Ciencias Naturales, Madrid, Spain, collection from Batallones; MNHN, Museum National d'Histoire Naturelle, Paris, France Lyon, France (previously MGL); NHMB, Natural History Museum, Basel, Switzerland; NHMUK, Natural History Museum, London, England; PUPC, Punjab University Paleontological Collection; SMNK Ma1 & Gips, Staatliches Museum für Naturkunde, Karlsruhe, Germany.

Anatomical abbreviations: I, upper incisor; i, lower incisor; M, upper molar; m, lower molar; p, lower premolar; l, left; r, right; L, length; W, width.

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen, 1848

Suborder SUOIDEA Gray, 1821

Family SUIDAE Gray, 1821

Tribe DICORYPHOCHOERINI Schmidt-Kittler, 1971

Propotamochoerus Pilgrim, 1925

Propotamochoerus hysudricus (Stehlin, 1899–1900)
(Figure 2A–C, D–F)

Holotype (Lectotype). GSI-B 30, right mandibular ramus in worn condition having p3–m3 (Pilgrim, 1926).

Type locality. Potwar Plateau, Pakistan (Lydekker, 1884).

Revised diagnosis. (based on Pilgrim, 1926; Pickford, 1988; Van der Made *et al.*, 1999): Suinae of moderate size; orbits open over talon of M3; zygomatic arches leave face at midline of M1; no diastemata in upper or lower cheek tooth rows; upper incisors have moderate enamel divisions and lower incisors are simple; canines fairly short having a thick cementum; stout and elongated premolars that increase in dimensions regularly from front to rear, bicuspid p4; molars are thin enameled, upper molars have moderately complex enamel division with shallow to deep grooves, lower molars are simpler than upper; M3/m3 large and with simple third lobe.

Stratigraphic range. Chinji to Tatrot formations of the Siwaliks (Pickford, 1988; Raza *et al.*, 2023; Sankhyan & Chavasseau, 2024; Babar *et al.*, 2024a).

New material. PUPC 14/85, rm1 (Hasnot); PUPC 21/74, left mandibular fragment with basal crown of p4, complete m1 and partially broken m2 (Hasnot).

Table 1. List of the collected specimens with their locality.

Catalog No.	Description	Locality
PUPC 14/85	Isolated right upper first molar (rM1).	Hasnot
PUPC 21/74	Left mandibular fragment with basal crown of p4, complete m1 and partially broken m2.	Hasnot
PUPC 21/75	Posterior lobe of left lower molar.	Hasnot
PUPC 21/77	Posterior lobe of right lower molar.	Hasnot
PUPC 17/37	Isolated upper left first incisor (lI1)	Hasnot
PUPC 17/38	Isolated left lower first incisor (li1)	Hasnot
PUPC 17/35	Isolated right upper first incisor (rI1)	Hasnot
PUPC 17/39	Isolated left lower first incisor (li1)	Hasnot
PUPC 17/45	Isolated right upper third molar (rM3)	Padhri
PUPC 21/76	posterior lobe of right upper molar	Hasnot

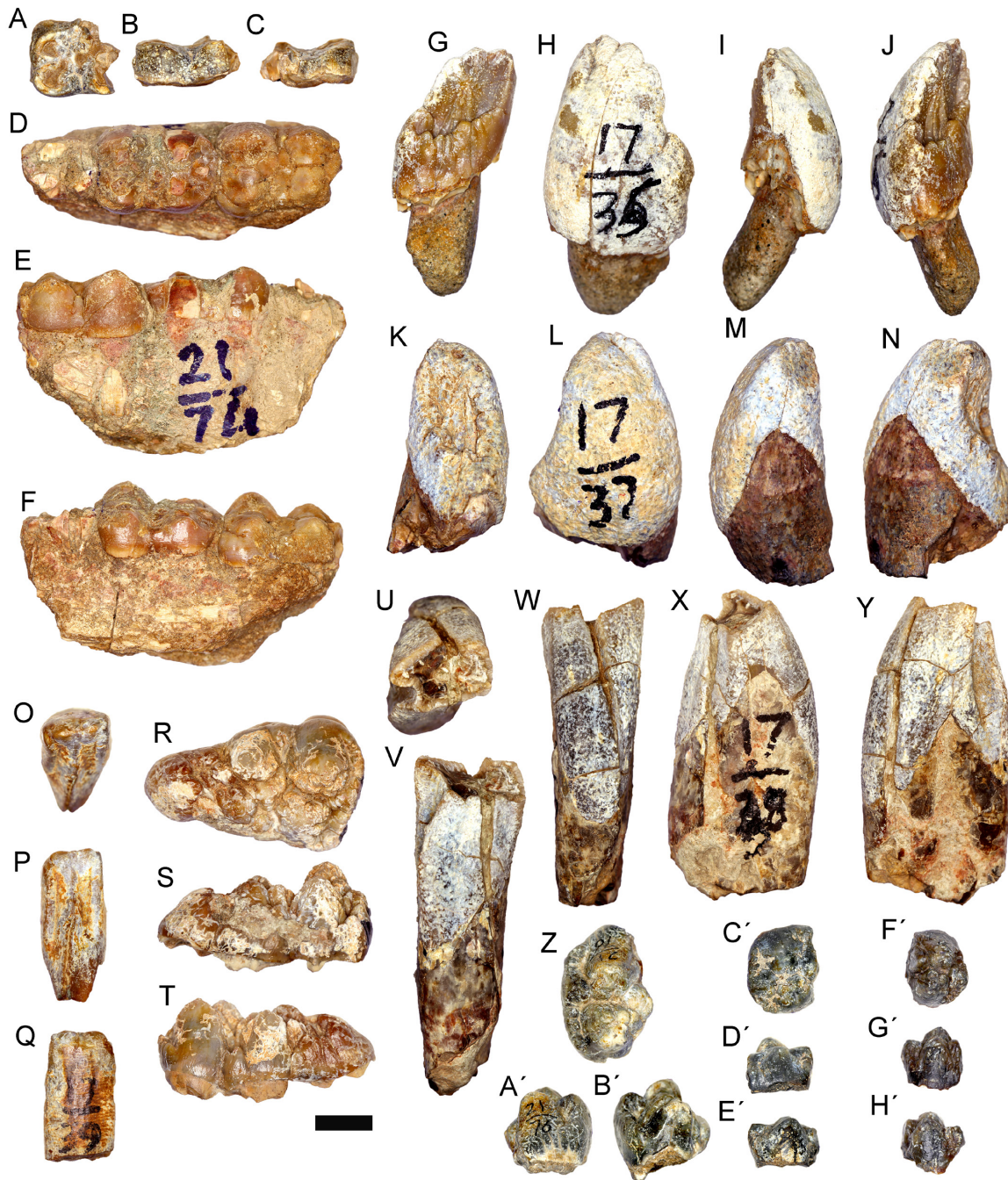


Figure 2. *Propotamochoerus hysudricus*. A–C, PUPC 14/85, m1; D–F, PUPC 21/74, left mandibular fragment with basal crown of p4, complete m1 and partially broken m2; *Hippopotamodon sivalense*. G–J, PUPC 17/35, right I1; K–N, PUPC 17/37, left I1; O–Q, PUPC 17/39, left i1; *H. major*. R–T, PUPC 17/45, right M3. *Tetraconodon magnus*. U–Y, PUPC 17/38, li1. Suidae indet. Z–B', PUPC 21/76, posterior lobe of left upper molar; C'–E', PUPC 21/75, posterior lobe of left upper molar; F'–H', PUPC 21/77, posterior lobe of lower right molar. A, D, O, R, U, Z, C', F', occlusal; B, E, G, K, H, L, P, S, V, A', D', G', lingual; C, F, Q, T, W, B', E', H', labial; I, M, X, anterior and J, N, Y, posterior views. Scale bar = 10 mm.

Description. PUPC 14/85 is an isolated fragmentary lower molar in the middle stages of wear (Figure 2A–C). The identification of this specimen as lower molar is based on the slope of the cusp, and the symmetric outline. The crown is low with a weakly developed

anterior cingulid. The protoconid and metaconid are well preserved, and the hypoconid and entoconid are partially preserved. The hypopreconulid is low and the protopreconulid is highly worn. The median valley is wide which is closed by metaectoconulid labially.

PUPC 21/74 is a left mandibular fragment preserving the basal crown of p4 and well preserved m1 and posteriorly broken m2 (Figure 2D–F). The corpus is not well preserved, heavily weathered, but shows better preservation labially than lingually. It is also broken ventrally and cracked under the protoconid of m1 at the labial side. Due to the breakage of the corpus at the lingual side, the roots are partially exposed. The roots and basal crown of the p4 are preserved. The crown is only represented by small fragments of dentine. The m1 is well preserved with thick enamel. A weakly developed anterior cingulid is present transversely. There are four cusps, the protoconid is low and well-preserved and is the most worn. A prominent protopreconulid is in connection with an anterior cingulid. The metaconid is the highest cusp and has a large metapostconulid. The hypopreconulid is large and lies close to this cusp. Both the hypoconid and entoconid are much lower than the protoconid and metaconid. A large hypopostconulid is in connection with the moderately developed and thick posterior cingulid. The median valley is broader lingually and with a weakly developed ectoconulid. The m2 is less worn and relatively more preserved. It is broken posterotransversely resulting in the loss of some parts of hypopostconulid and the partial loss of the posterior cingulid. The anterior cingulid is wider labially and weaker and narrower lingually. The protoconid is slightly more anterior than the highest metaconid. The grooves are few but not very deep. The rest of the morphology is like m1.

Comparisons. The morphology of the molars indicates that these samples belong to Suidae as they clearly differs from the Listriodontinae and Sanitheriinae in having less selenodont/lophodont, more bunodont and bulbous cusps; differs from the Palaeochoeridae in more complicated furrows in addition to the previously mentioned characters; differs from Hyotheriinae, in having more developed metapostconulid and hypopostconulid; and presence of relatively elongated lobes favors their inclusions in Suinae (Pickford, 1988; Van der Made, 1996; Tsubamoto & Taru, 2022). The bunodonty of these teeth differentiate them from *Hippohyus* and *Sivahyus* having hypsodont, more narrow molars with flattened cusps, and more choerodont cheek teeth. The specimens described are clearly smaller than *Hippopotamodon* and *Sivachoerus* which also have larger grooves, and relatively more hypsodont (Pickford, 1988; Van der Made *et al.*, 1999; Sein *et al.*, 2009; Babar *et al.*, 2024a). In addition to the size and hypsodonty, the labial cusps are slightly lower than the lingual cusps but have no difference in height, as in *Hippopotamodon* molar cusps. The lingual flare (inward spreading of the tooth toward the tongue) is minimal, but the buccal flare (outward spreading of the tooth toward the cheek) is moderate in these molars (Pickford, 1988). Further, the medium size, weakly to moderately deep furrows, protoconid becoming tall relative to the hypoconid, poorly developed lateral cingulids and relatively simple talonids/expansion of talonids are indicative of the genus *Propotamochoerus* and Siwalik species, *Propotamochoerus hysudricus* (Sankhyan & Chavasseau, 2024). Hence, based on this morphometric analysis (Figure 2A–B, 3A–B, Table 2), these specimens are described as *Propotamochoerus hysudricus*.

Hippopotamodon Lydekker, 1877

Hippopotamodon sivalense Lydekker, 1877

(Figure 2 G–Q)

Holotype. GSI-B 7, left maxilla with fragment of P4, broken M1 and M2 (Pilgrim, 1926).

Type locality. Hasnot, Padhri, Potwar Plateau, Pakistan (Pilgrim, 1926).

Diagnosis. A gigantic species of *Hippopotamodon* in which the upper molar row exceeds 110 mm in length. Length of m3 ranges between 54.5 and 66 mm, M3 length between 44.8 and 62 mm (Pickford, 2015).

Stratigraphic range. Middle Siwaliks (Pilgrim, 1926; Colbert, 1935; Pickford, 1988; Khan *et al.*, 2010; Batool *et al.*, 2015).

New material. PUPC 17/35, right I1 (Hasnot); PUPC 17/37, left I1 (Hasnot); PUPC 17/39, left i1 (Hasnot).

Description. PUPC 17/35 is an isolated upper incisor in which the crown is well preserved, spatula-shaped, with thick enamel and completely unworn (Figure 2G–J). It has a large paracone labially and a well-preserved small protocone which is in contact with a large cingulum covering the whole length lingually. The parapreconule and parapostconule are large and well preserved. The prestyle, basal fossa, preanticleline, presyncline, postcrista and endosyncline, can be observed occlusally. A small very low-lying entocone is also present, that is in contact with the lingual cingulum. The prefossa of the tooth also has two large ridges near the basal fossa, dividing into three grooves. No root is preserved; however, the sand that had filled the pulp cavity is still intact and continues to the basal crown. This indicates that the pulp cavity is large.

PUPC 17/37 is an isolated well-preserved upper incisor (Figure 2K–N). It is in the early stage of wear and slightly different from PUPC 17/35 in its morphology, in that the cingulum is smaller and much weaker, the protocone is small, prefossa has three ridges, and a large and thick enamel fold is present anterolabially. The distinction between parapostcrista and entocone is visible. A small portion of the root is also preserved.

PUPC 17/39 is an isolated lower incisor, which is well preserved and has thick enamel as observed from the point of breakage (Figure 2O–Q). The preconulid, postcristid, prefossid and endofossid are well preserved. The worn prestylid and endocristid can be observed occlusally. The preanticlelinid and presynclinid are located at the base of the crown. The worn endosynclinid is also present.

Comparisons. The specific features of described upper incisors (PUPC 17/35, PUPC 17/37), such as large size, recurved-shaped and raised lingual and labial borders with a central fossa surrounding it, the beaded occlusal surface, and bifurcation near the anterior edge, indicate that these belong to the genus *Hippopotamodon* (Colbert, 1935; Pickford, 1988, 2015). There are at least three species of the genus *Hippopotamodon* in the Siwaliks where *H. sivalense* and *H. major* are predominant (Van der Made & Hussain, 1989; Pickford, 2015). The first upper

Table 2. The measurement (in mm) of the studied teeth of *Propotamochoerus hysudricus* and *Hippopotamodon major* and *H. sivalense*. *studied specimen. **measurements as preserved. Referred data are taken from Colbert (1935), Pickford (1988, 2016), Khan *et al.* (2010), Batool *et al.* (2015) and Aslam *et al.* (2021).

Taxa	Number	Nature	L	W
<i>Propotamochoerus hysudricus</i>	PUPC 14/85*	m1	16.80**	14.65
		p4	12.00**	10.00
	PUPC 21/74*	m1	20.87	14.94
		m2	20.08**	16.19
			21.5 est.	
	GSP 10998	m1	17.60	13.00
	GSP 2807	m1	16.00	12.00
	GSP 457	m1	16.80	11.50
	GSP 6226	m1	16.70	12.00
	GSP 7384	m1	17.50	12.40
	GSP 5112	m1	18.40	11.70
	GSP 12732	m1	18.00	12.00
	GSP 4088	m1	18.80	12.30
	PUPC 16/103	m1	16.40	12.50
	PUPC 97/40	m1	16.80	12.70
	PUPC 97/40	m2	22.00	16.00
	PUPC 97/41	m2	20.90	16.80
	PUPC 16/103	m2	21.00	15.30
	PUPC 95/15	m2	23.40	16.00
<i>Hippopotamodon sivalense</i>	PUPC 17/37*	I1	23.76	18.23
	PUPC 17/35*	I1	23.86	17.75
	GSI-K 14/394	I1	23.00	18.00
	GSI-K 13/328	I1	25.00	15.00
	GSI-K 15/3660	I1	22.00	17.00
	PUPC 17/39*	i1	12.37	18.37
	GSP 122	i1	13.00	20.00
	GSP 192	i1	11.00	20.00
	GSI-B 539	i1	13.70	21.00
	GSI-K 13/9	i1	11.00	19.00
	MNCN Bat 10'08 G4.53	I1	20.20	11.20
	MNCN BAT 10'10 F4-14 + G4-51	I1	21.50	12.20
	MNCN BAT 10'10, F3-42	I1	20.00	11.90
	MNCN BAT-10-09 G2-83	i1	10.40	14.90
MNCN BAT 10'12 F2-65	i1	10.20	13.70	
<i>Hippopotamodon major</i>	MNHN LUB 657	i1	9.70	16.00
			10.00	15.90
	PUPC 17/45*	M3	37.91	23.28
	NHMUK M 9144 (B)	M3	37.60	26.00
	CCECL AA 10	M3	39.30	26.70
	MNHN SLO 913	M3	40.60	26.00
	MNHN SLO 1075	M3	41.00	26.00
	DT RO 2992	M3	41.40	26.50
			43.60	28.40
	MNCN Bat 10'14-E3-46	M3	44.50	28.30
	NHMB ML 41	M3	46.70	30.00
<i>Hippopotamodon sivalense</i>	GSP 3789	M3	53.20	31.80
	GSI-B 15	M3	65.00	37.00
	GSI-B 19	M3	57.00	41.50
	GSI-B 9	M3	55.00	38.50

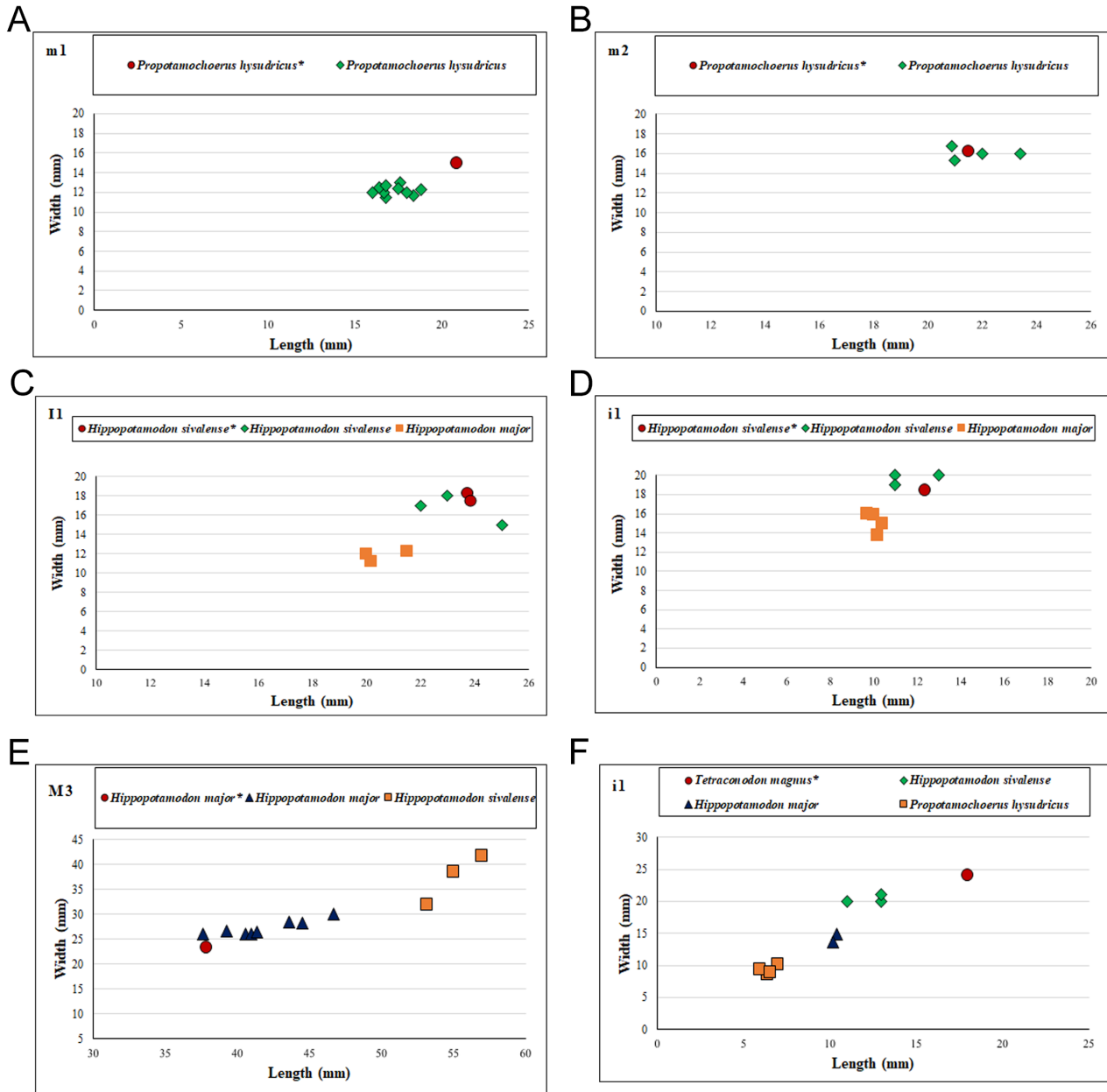


Figure 3. Comparative bivariate plots of described specimens based on Table 2 and Table 3. **A**, first molars in species of *Propotamochoerus hysudricus*; **B**, m2 of *P. hysudricus*; **C**, I1 of *Hippopotamodon sivalense*; **D**, i1 of *H. sivalense*; **E**, M3 of *H. major*; compared to dimensions of other taxa **F**, i1 of *Tetraconodon magnus* and other taxa. *studied specimen.

incisors of *H. major* are smaller in size (Figure 3C, Table 2), slightly linguo-labially compressed and elongate as compared to *H. sivalense*. The lower incisor (PUPC 17/39) is much larger than the lower incisor of *Propotamochoerus* (Table 3) and its length and width is larger than that of *H. major* (Figure 3D, Table 2). Overall, the morphometric characteristics of the studied specimens are similar to *H. sivalense*, documented from the Middle Siwaliks (Pickford, 1988); hence, these specimens are assigned to *H. sivalense*.

Hippopotamodon major (Gervais, 1850) (Figure 2R–T)

Holotype. Upper left third molar from Cucuron, figured by Gervais, 1850, pl. 12. Figure 2.

Type locality. Cucuron, Vaucluse (= Luberon) France (Gervais, 1850).

Diagnosis. Large species of suine in which the length of m3 ranges between 38.1 and 57.4 mm, and M3 between 34.5 and 49.5 mm (Pickford, 2015).

Table 3. Comparative measurements (mm) of PUPC 17/38 with the incisors of *Hippopotamodon sivalense* and *Propotamochoerus hysudricus*. Comparative data taken from Pickford (1988).

Taxa	Number	Nature	L	W
<i>Tetraconodon magnus</i>	PUPC 17/38	il	17.38** 18 est.	23.97
	GSP 122	il	13.00	20.00
<i>Hippopotamodon sivalense</i>	GSP19	il	11.00	20.00
	GSI-B 539	il	13.70	21.00
<i>Hippopotamodon major</i>	MNCN BAT-10-09 G2-83	il	10.4	14.9
	MNCN BAT 10'12 F2-65	il	10.2	13.7
	GSP 4028	il	7.0	10.1
<i>Propotamochoerus hysudricus</i>	GSP 6821	il	6.4	8.6
	GSP 7091	il	6.0	9.3
	GSP 6126	il	6.6	8.8

New material. PUPC 17/45, right M3 (Padhri) (Figure 3E, Table 2).

Description. PUPC 17/45 is an isolated M3 with a well-preserved crown and thin enamel as judged from the root crown junction (Figure 2R–T). The anterior cingulum is large and thick and is divided into small conules, covering the tooth anterotransversely. The protocone is lower than the paracone, the protopreconule is attached to the cingulum anteriorly and with the protocone posteriorly. The paracone is the highest cusp. Both the protocone and paracone have deep grooves and are separated from each other by the sulcus. The hypocone and metacone are low-lying and much smaller than the protocone and paracone. Also, the hypocone is slightly posteriorly positioned and slightly higher than the metacone. A hypopreconule is present anterior to the metacone and hypocone. The pentacone is well preserved and the pentapreconule is located anterior to this. The anterior valley is blocked in the center by the hypopreconule while it is blocked lingually by a small and weak hypopreconule, and labially by a large and metapreconule. The posterior valley is blocked by a large hypopostconule lingually and small pentapreconule labially.

Comparison. The molar of *Hippopotamodon* displays relatively thin enamel and grooves are dominant, while *Propotamochoerus* consists of moderately thick enamel, without large cingula and shallow grooves. The specific morphological characters of M3, such as large size, relatively thin enamel with different cusps height, labial cups being higher than the lingual ones, presence of a large cusp in the talon that lies lingually of the axis of the tooth indicate that it belongs to the genus *Hippopotamodon* (Pickford, 1988). The tooth is much smaller than the reported M3 of *H. sivalense* and falls in the range of *H. major* (Figure 3E, Table 2), hence described as *H. major*. Both these species are mainly differentiated based on the size of upper and lower third molars as given by Pickford (2015): *H. major* is a large species of suine in which the length of m3 ranges between 38.1 and 57.4 mm, and M3 between 34.5 and 49.5 mm while *H. sivalense*

is the largest species of the genus with m3 ranging in length between 48.3 and 62 mm, and M3 from 44 to 54.6 mm.

Subfamily TETRACONODONTINAE Lydekker, 1876

Tetraconodon Falconer, 1868

Tetraconodon magnus Falconer, 1868
(Figure 2U–Y)

Holotype (neotype). GSI-B 71, a right mandible with p2–m3 (Colbert, 1935).

Type locality. Potwar Plateau, Punjab, Pakistan (Colbert, 1935; Pickford, 1988).

Diagnosis. A large species of *Tetraconodon* in which the upper molar series exceeds 95 mm in length, and in which p3–4 are together longer than 75 mm (Pickford, 1988); M1 length about 33 mm (Van der Made, 1999).

New material. PUPC 17/38, lower first incisor (Hasnot).

Description. PUPC 17/38 is an isolated lower incisor, which is partially broken and cracked, and has thick enamel (Figure 2U–Y). The preconulid, postcrisid, prefossilid, and endofossilid are well preserved. The broken prestylid, endocrisid, prefossilid and endofossilid can be observed occlusally. The preanticiplinid and presynclinid are located at the base of the crown. The broken endosynclinid is also present.

Comparisons. The specimen PUPC 17/38 is extremely large sized and well compressed from both sides. Such a compression indicates the presence of other teeth contacting it from both sides. The morphology of this specimen and such appression indicate that it is the first incisor. The morphology of the PUPC 17/38 is clearly different from the incisors of rhinocerotids, hippopotamids, and proboscideans, which are long tusklike, and curved with continuous growth; however, the size is in range of the large hipparionine species. Nevertheless, the presence of endocrisid that divides the tooth into distinct

prefossilid, and endofossilid indicates that it is a lower incisor of a suid not an hipparionine that lacks such structures. Such morphology with these structures is found in the lower incisors of *Propotamochoerus* and *Hippopotamodon* from the Siwaliks and around the world; however, the size of the studied incisor (PUPC 17/38) is clearly larger than the known incisors of these genera (Figure 3F, Table 3). Based on its large size (despite its apical breakage), PUPC 17/38 is allocated to the genus *Tetraconodon* and to the largest species of the genus *T. magnus*. This is the first ever description of the incisor of the genus *Tetraconodon*.

Suidae indet.
(Figure 2Z–H')

New material. PUPC 21/76, posterior lobe of left upper molar (Hasnot); PUPC 21/75, posterior lobe of left upper molar (Hasnot); PUPC 21/77, posterior lobe of right lower molar (Hasnot).

Description. PUPC 21/76 is an isolated second lobe of an upper molar (Figure 2Z–B'). It is in early stage of wear. The posterior cingulum is thick with a well-developed hypopostconule, which is in contact with the hypocone. The hypocone and metacone with moderately thick enamel (judged from the point of breakage) are preserved. The hypopreconule, which is also preserved, is large and wide. The grooves are large and deep. The preserved length is 16.83 mm and width is 23.39 mm.

PUPC 21/75 represents the posterior lobe of an upper molar; the hypocone and metacone are preserved with thick enamel (Figure 2C'–E'). The metacone is high and the hypocone is low; the posterior cingulum is also present. The hypopreconule and hypopostconule are present. The preserved length is 12.84 mm and width is 15.52 mm.

PUPC 21/77 represents the posterior lobe of a lower molar (Figure 2F'–H') in which the hypoconid and entoconid are preserved along with hypopostconulid. The grooves are less in number but slightly broader. The preserved length is 11.82 mm and width is 14.83 mm.

Comparison. The identification of the specimens described above as Suidae indet. is based on the bunodonty, round cusps, choerodonty (complex enamel divisions), presence of grooves and conulids, cingulum fused protopreconule and large cingulum/cingulid with a prominent conule/conulid. Among these, PUPC 21/76 is proportionally large (based on width) indicating that it can be upper molar of a large suid such as *Hippopotamodon* and *Sivachoerus*. However, the cusps in this tooth fragment are narrower than those found in *Sivachoerus*. Both PUPC 21/75 and PUPC 21/77 are small sized but larger (based on width) than *Sivahyus*, smaller than *Tetraconodon*, *Sivachoerus*, and *Hippopotamodon* and are in the size range of *Hippohyus*, and *Propotamochoerus* (Pickford, 1988). However, these are morphologically different from *Hippohyus* favoring their association with *Propotamochoerus*. Nevertheless,

the incompleteness of these specimens hinders even the generic level allocation, hence described as Suidae indet.

DISCUSSION

The Middle Siwalik suids show diversity in genera, including *Conohyus*, *Propotamochoerus*, *Sivachoerus*, *Hippohyus*, *Hippopotamodon*, *Lophochoerus*, *Sivahyus* and *Tetraconodon* as well as *Listriodon*, which is restricted to Nagri Formation (Pilgrim, 1926; Matthew, 1929; Colbert, 1935; Pickford, 1988; Khan *et al.*, 2013; Batool *et al.*, 2015; Dar *et al.*, 2019; Babar *et al.*, 2021, 2024a, b; Sankhyan & Chavasseau, 2024; Raza *et al.*, 2023). The genera such as *Propotamochoerus*, *Sivachoerus*, *Sus* and *Conohyus* originated in the Indian subcontinent and dispersed to Europe and Africa (Matthew, 1929; Colbert, 1935; Pickford, 1988; Van der Made, 1999). In Pakistan, the previous records indicate that *Propotamochoerus hysudricus* occurred in the Dhok Pathan and Nagri formations, coexisting with *Hippopotamodon sivalense* and other genera like *Lophochoerus*, *Hippohyus* and *Sivahyus*, ranging from 10.3 to 6.6 Ma (Pickford, 1988; Babar *et al.*, 2021, 2024a, b; Sankhyan & Chavasseau, 2024; Raza *et al.*, 2023; Chavasseau, 2025). The fossil record of suids from the late Miocene deposits of Hasnot document many species such as *Hippopotamodon sivalense*, *Propotamochoerus hysudricus*, *Tetraconodon magnus*, and some others (Pickford, 1988; Batool *et al.*, 2015).

Propotamochoerus species demonstrate the diversity from the upper Miocene to lower Pliocene deposits across the Eurasia (Pilgrim, 1926; Pearson, 1928; Colbert, 1935; Lydekker, 1884; Van der Made & Han, 1994; Fortelius *et al.*, 1996; Batool *et al.*, 2015; Hou *et al.*, 2019; Sankhyan & Chavasseau, 2024; Babar *et al.*, 2024a; Chavasseau, 2025). The genus *Propotamochoerus* probably arose from a hyotherine suid and dispersed to southwestern Asia and Europe (Pickford, 1988) but the origin of the genus is still under discussion (Lazaridis *et al.*, 2022). In the late Miocene of the eastern Mediterranean, suids comprised two main lineages: the dominant *Hippopotamodon*, and the less common *Propotamochoerus* whose taxonomy is not fully resolved due to the fragmentary nature of most specimens, primarily consisting of dental remains. The taxonomic status of *Propotamochoerus* in the late Miocene remains complex and debated. For example, *Propotamochoerus provincialis*, recorded in late Miocene to early Pliocene European faunas, has uncertain taxonomic status. Notably, the late Miocene *Propotamochoerus* from southeastern Europe, particularly the Turolian samples, has been subject to extensive debate regarding its classification, and recent research proposed a new species, *Propotamochoerus aegaeus*, based on well-preserved specimens from Kryopigi, Greece, and including various Turolian records from southeastern Europe (Lazaridis *et al.*, 2022).

Propotamochoerus hysudricus, a member of the subfamily Suinae and the type species of the genus, is known from the Potwar Plateau, Pakistan and well represented by complete crania, mandibles and postcranials and is the most common

suid in the Middle Siwalik Subgroup. It is a medium-sized species that belongs to the subfamily Suinae (Pilgrim, 1926; Colbert, 1935; Pickford, 1988; Batool *et al.*, 2015; Raza *et al.*, 2023; Babar *et al.*, 2024a; Sankhyan & Chavasseau, 2024), mostly recovered from the Hasnot, Padhri and Dhok Pathan outcrops in Pakistan (Barry *et al.*, 2002). In addition to Pakistan, *P. hysudricus* has been discovered in different regions of Asia that include China, United Arab Emirates, and Myanmar. In United Arab Emirates, it is known from the Late Miocene of Abu Dhabi (Bishop & Hill, 1999). *Propotamochoerus hysudricus* has been also recovered from Yunnan, China (Liu & Ji, 2004). *Propotamochoerus hysudricus* (Stehlin, 1899–1900), originally described from Late Miocene deposits in Pakistan, is considered a problematic taxon requiring revision (Van der Made *et al.*, 1999; Hou *et al.*, 2019). It is possible that there are two species of the genus *Propotamochoerus* present in the Siwaliks, a large and a small species, as indicated by the size in the dental material or it may be due to sexual dimorphism. However, it needs the reassessment of all the material of the species and more skull materials. Recent work on the Y-GSP collection by Chavasseau (2025) maintained the single species, *P. hysudricus*.

The genus *Hippopotamodon* represents the large Suinae of Eurasia. It is currently represented by four species as listed above. However, the validity of some species is still to come with more new material. Two Siwalik species without any doubt are: *H. major* and *H. sivalense* (Van der Made & Hussain, 1989; Pickford, 2015) and the possibility of third species, *H. antiquus* as proposed by Pickford (2015) cannot be ruled out. Both share similar characteristics but differ in the size of their incisors and canines; *H. sivalense* has larger incisors and canines than *H. major* (Pickford, 2015, 2016). The M3 (PUPC 17/45) described in this study is much smaller than most of the previously described specimens of *H. sivalense* from the Siwaliks and represents *H. major* and is the first description of M3 from the Siwalik Group. Similarly, both upper incisors (PUPC 17/35, PUPC 17/37) which are described in this study show some differences in morphology and probably represent two different species. PUPC 17/35 is more like upper first incisor (GSP 12508) described and figured by Pickford (1988) while PUPC 17/37 is slightly different. Both these specimens are valuable for ongoing research work on Siwalik suids to distinguish the morphology of both species because incisors are very rare in findings as well as the lower incisor (PUPC 17/39) described in this study.

The genus *Tetraconodon* and its diverse species are present across various geological epochs, it includes taxa such as *T. minor*, *T. magnus*, *T. irramedius*, *T. irramagnus* and *T. malensis* (Pickford, 1988; Thaug-Htike *et al.*, 2005, 2007; Khan *et al.*, 2013; Babar *et al.*, 2021). The species *Tetraconodon magnus* is a large sized suid, which is present in Pakistan, India, Thailand and Myanmar (Pilgrim, 1926; Pickford, 1988; Khan *et al.*, 2013; Babar *et al.*, 2021). Earlier research indicated that *T. magnus* was primarily associated with Upper Siwalik deposits based on limited fossil evidence (Pilgrim, 1926; Colbert, 1935), however, Pickford (1988) argued for its classification as a

Middle Siwalik form based on more comprehensive data. It contributes to the understanding of *Tetraconodon* but also to extending its stratigraphical range within the Siwalik deposits. The evolutionary history of *Tetraconodon* is based on the fossil record of *Tetraconodon* and other tetraconodontines from the Siwaliks of Indo-Pakistan (Pickford, 1988; Thaug-Htike *et al.*, 2005). *Tetraconodon* was probably derived from the oldest Asian tetraconodontine, *Conohyus sindienseis* (= *Retroporcus sindienseis*), from the Kamlial or lower Chinji (lower middle Miocene) of the Siwaliks of Pakistan, Nepal and India; this species was also recovered from the middle Miocene deposits of Thailand (Thaug-Htike *et al.*, 2005).

Described first lower incisor (PUPC 17/38), though partially broken resulting in loss of the apex, is nevertheless identifiable to generic level. The presence of endocristid that forms the prefossilid and postfossilid is found in many mammalian taxa, but it is most evident in the family Suidae. Such morphology is prominent in the lower incisors of the genus *Hippopotamodon* (Pickford, 1988, fig. 137, 2016, figs. 4, 5, 10, 11; Liu *et al.*, 2004, fig. 4). Hence, PUPC 17/38 can be safely associated with family Suidae. However, the size of PUPC 17/38 is much larger than the lower first incisor of *Hippopotamodon*. Further, the endocristid is slightly lying posteriorly, making the prefossilid large but shallower than the postfossilid, which is smaller and deeper, and one may think that this is a deformed incisor. However, such morphology is also found in the right lower incisor of *Hippopotamodon erymanthius* (SMNK Ma1 Gips 17, Pickford 2016, fig. 5) and lower first and second incisors of the same species (SMNK Ma1 Gips 6, Pickford, 2016, fig. 10) from Mahmutgazi, Denizli-Çal Basin, Turkey. But all the lower first incisors of the *Hippopotamodon* spp. tend to be smaller and straighter (Pickford, 2015, 2016) contrary to the PUPC 17/38 in which the crown is more bent lingually. Based on the size and morphological differences, it cannot be associated with the genus *Hippopotamodon* and can be allocated to the genus *Tetraconodon* (Table 2) facilitating its allocation to the largest species of this genus, *i.e.*, *T. magnus*.

CONCLUSIONS

Propotamochoerus hysudricus, *Hippopotamodon sivalense*, *H. major*, *Tetraconodon magnus* and Suidae indet. are reported from the Dhok Pathan Formation of the Middle Siwalik Subgroup, Pakistan. The material adds substantial information in the anatomical and morphological character, because the upper and lower incisors of *Hippopotamodon sivalense* are least described, and the M3 of *H. major* is described for the first time from the Siwalik Group while lower first incisor of the genus *Tetraconodon* represents first ever description for this genus in the paleontological world.

DATA AVAILABILITY STATEMENT

The data supporting this study's findings are available from the corresponding author upon reasonable request.

ACKNOWLEDGEMENTS

This manuscript is a part of the MPhil thesis of the first author Hassan Raza. The authors are grateful to the anonymous reviewers and the editors for their comments, revisions, and suggestions.

FUNDING

No funding was received for this study.

AUTHOR CONTRIBUTIONS

Hassan Raza: writing – original draft; investigation; methodology. Sayyed Ghayour Abbas: writing – review, editing; visualization; investigation. Muhammad Akbar Khan: writing – review; supervision; data curation. Kiran Aftab: writing – review; methodology; editing; conceptualization. Muhammad Adeb Babar: resources, formal analysis. Khalid Mahmood: project administration, conceptualization. Muhammad Asim: supervision; conceptualization. Razia Iqbal: visualization; conceptualization. Amina Tufail: writing – original draft; investigation; methodology. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

DECLARATION OF AI USE

We have not used AI-assisted technologies to create, review, or any part of this article.

ETHICS

This work did not require ethical approval, collecting licenses, or previous authorizations.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

REFERENCES

- Aslam, S.; Khan, A.M.; Ahmad, R.M.; Iqbal, A. & Waseem, M.T. 2021. Systematic study of the new remains of *Propotamochoerus hysudricus* (Suidae, Mammalia) from the Late Miocene-Early Pliocene of Middle Siwaliks (Pakistan). *Arabian Journal of Geosciences*, **14**:73. doi:10.1007/s12517-020-06300-y
- Babar, M.A.; Aftab, K.; Khan, M.A.; Abbas, S.G.; Asim, M. & Akhtar, M. 2021. *Tetraconodon* and *Sivachoerus* (Suidae) from Dhok Pathan and Hasnot area of Potwar Plateau, northern Pakistan. *Arabian Journal of Geosciences*, **14**:1–6. doi:10.1007/s12517-021-08684-x
- Babar, M.A.; Abbas, S.G.; Khan, M.; Mahmood, K.; Jaber, F.; Raza, H. & Akhtar, M. 2024a. *Propotamochoerus* (Suidae) from the Siwalik Dhok Pathan Formation of Pakistan. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen Band*, **311**:191–204. doi:10.1127/njgpa/2024/1190
- Babar, M.A.; Abbas, S.G.; Khan, M.A. & Akhtar, M. 2024b. *Lophochoerus nagrii* (Suidae) from the Siwaliks (Neogene) of Pakistan. *Annales de Paléontologie*, **110**:102666. doi:10.1016/j.annpal.2024.102666
- Barry, J.C.; Behrensmeyer, K.A. & Morgan, M. 1980. A geologic and biostratigraphic framework for Miocene sediments near Khaur Village, northern Pakistan. *Postilla*, **183**:1–19.
- Barry, J.C. *et al.* 2002. Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology*, **28**:1–71. doi:10.1666/0094-8373(2002)28[1:FAECIT]2.0.CO;2
- Batool, A.; Khan, M.A. & Qureshi, N.A. 2015. New fossils of Suidae (Mammalia, Artiodactyla) from the Hasnot Late Miocene, northern Pakistan. *Journal of Animal and Plant Sciences*, **25**:578–590.
- Bishop, L. & Hill, A. 1999. Fossil Suidae from the Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates. In: P. Whybrow & A. Hill (eds.) *Fossil Vertebrates of Arabia, with Emphasis on the Late Miocene Faunas, Geology, and Palaeoenvironments of the Emirate of Abu Dhabi*. United Arab Emirates, Yale University Press, p. 254–270.
- Chavasseau, O. 2025. Siwalik Suidae and Palaeochoeridae. In: C. Badgley; M.E. Morgan & D. Pilbeam (eds.) *At the Foot of the Himalayas: Paleontology and Ecosystem Dynamics of the Siwalik Record of Pakistan*. Johns Hopkins University Press, p. 295–312.
- Colbert, E.H. 1935. Siwalik mammals in the American Museum of Natural History. *Transactions of the American Philosophical Society*, **26**:1–401. doi:10.2307/1005467
- Dar, F.Y.; Aftab, K.; Babar, M.A.; Khan, M.A.; Abbas, S.G.; Shahid, R. & Asim, M. 2019. New fossils of Suidae (Mammalia) from Dhok Pathan Formation of Siwaliks, Punjab, Pakistan. *Journal of Animal and Plant Sciences*, **29**:1198–1203.
- Falconer, H. 1868. *Paleontological Memoirs and Notes of the Late Hugh Falconer: Fauna Antiqua Sivalensis*. London, Robert Hardwicke, 591 p.
- Fortelius, M.; Werdelin, L.; Andrews, P.; Bernor, R.L.; Gentry, A.; Humphrey, L.; Mittmann, H.W. & Viranta, S. 1996. Provinciality, Diversity, Turnover and Palaeoecology in Land Mammal Faunas of the Later Miocene of Western Eurasia. In: R.L. Bernor; V. Fahlbusch & H.W. Mittmann (eds.) *The Evolution of Western of Eurasian Neogene Mammal Faunas*. University of New York Columbia Press, p. 414–449.
- Gervais, P. 1850. Zoologie et Paléontologie Françaises (Animaux Vertébrés). In: P. Gervais (ed.) *Ou Nouvelles Recherches sur les Animaux Vivants et Fossiles de la France*. Arthus Bertrand, p. 1–271.
- Gongora, J. *et al.* 2011. Revisiting the species status of *Pecari maximus* van Roosmalen (Mammalia) from the Brazilian Amazon. *Bonn Zoological Bulletin*, **60**:95–101.
- Gray, J.E. 1821. On the natural arrangement of vertebrate animals. *London Medical Repository*, **15**:296–310.
- Hou, S.; Su, D.F.; Kelley, J.; Deng, T.; Jablonski, N.G.; Flynn, L.J.; Ji, X.; Cao, J. & Yang, X. 2019. New fossil suid specimens from the terminal Miocene hominoid locality of Shuitangba, Zhaotong, Yunnan Province, China. *Journal of Mammalian Evolution*, **26**:557–571. doi:10.1007/s10914-018-9431-3
- Khan, M.A.; Abbas, S.G.; Aftab, K.; Babar, M.A.; Ali, M.; Malik, M.F. & Zaman, R. 2024. New fossils of *Tragoportax* and *Gazella* from Padhri, Pakistan, and comments on these genera in the Siwaliks. *Historical Biology: An International Journal of Paleobiology*, **36**:1180–1187. doi:10.1080/08912963.2022.2117041
- Khan, M.A.; Akhtar, M. & Iqbal, M. 2010. The late Miocene artiodactyls in the Dhok Pathan type locality of the Dhok Pathan Formation, the Middle Siwaliks, Pakistan. *Pakistan Journal of Zoology*, **10**:1–90.
- Khan, M.A.; Iqbal, M.; Nayyer, A.Q.; Akhtar, M.; Shahzadi, M. & Mahmood, K. 2013. *Tetraconodon* (Mammalia: Artiodactyla: Suidae) From the Late Miocene Dhok Pathan Formation of Pakistan. *Pakistan Journal of Zoology*, **45**:975–980.

- Lazaridis, G.; Tsoukala, E. & Kostopoulos, D.S. 2022. Validation of a prematurely abolished new *Propotamochoerus* Pilgrim, 1925 species (Mammalia, Suidae) from SE Mediterranean. *Comptes Rendus Palevol*, **21**:531–549. doi:10.5852/cr-palevol2022v21a26
- Liu, J.H. & Ji, X.P. 2004. Discovery of *Propotamochoerus hysudricus* from Tanguanyao area in Yongren, Yunnan Province, China. In: ANNUAL MEETING OF THE CHINESE SOCIETY OF VERTEBRATE PALEONTOLOGY, 9, 2004. *Proceedings*, Beijing, China Ocean Press, p. 49–54.
- Liu, L.; Kostopoulos, D.S. & Fortelius, M. 2004. Late Miocene *Microstonyx* remains (Suidae, Mammalia) from Northern China. *Geobios*, **37**:49–64. doi:10.1016/j.geobios.2003.01.007
- Lydekker, R. 1876. Molar teeth and other remains of Mammalia from the India Tertiaries. *Palaeontologica Indica*, **10**:19–87.
- Lydekker, R. 1877. Notices of new and rare Mammals from the Siwaliks. *Records of the Geological Survey of India*, **10**:76–83.
- Lydekker, R. 1884. Indian Tertiary and post-Tertiary Vertebrata. Siwalik and Narbada bunodont Suina. *Memoirs of the Geological Survey of India*, **10**:35–104.
- Matthew, W.D. 1929. Critical observations upon Siwalik mammals (exclusive of Proboscidea). *Bulletin of the American Museum of Natural History*, **56**:437–560.
- Orliac, M.J.; Antoine, P.O. & Ducrocq, S. 2010a. Phylogenetic relationships of the family Suidae; new insights on the relationships among Suoidea. *Zoologica Scripta*, **39**:315–330. doi:10.1111/j.1463-6409.2010.00431.x
- Orliac, M.J.; Antoine, P.O.; Roohi, G. & Welcomme, J.L. 2010b. Suoidea (Mammalia, Cetartiodactyla) from the early Oligocene of the Bugti Hills, Balochistan, Pakistan. *Journal of Vertebrate Paleontology*, **30**:1300–1305. doi:10.1080/02724634.2010.483554
- Owen, R. 1848. Description of teeth and portions of jaw of two extinct anthracotherioid quadruped discovered in the Eocene deposits on the NW coast of the Isle of Wight. *Quarterly Journal of the Geological Society*, **4**:103–141. doi:10.1144/GSL.JGS.1848.004.01-02.21
- Pearson, H.G. 1928. Chinese fossil Suidae. *Palaeontologia Sinica Series C*, **5**:1–75.
- Pickford, M. 1988. Revision of the Miocene Suidae of the Indian subcontinent. Munchner Geowiss. *Neues Jahrbuch für Geologie und Paläontologie*, **12**:1–92.
- Pickford, M. 2015. Late Miocene Suidae from Eurasia: the *Hippopotamodon* and *Microstonyx* problem revisited. *Münchner Geowissenschaftliche Abhandlungen, A*, **42**:1–126.
- Pickford, M. 2016. *Hippopotamodon erymanthius* (Suidae, Mammalia), from Mahmutgazi, Denizli-Çal Basin, Turkey. *Fossil Imprint*, **72**:183–201. doi:10.14446/FI.2016.183
- Pilbeam, D.; Barry, J.; Meyer, G.E.; Shah, S.M.I.; Pickford, M.; Bishop, W.W.; Thomas, H. & Jacobs, L.L. 1977. Geology and palaeontology of Neogene strata of Pakistan. *Nature*, **270**:684–689. doi:10.1038/270684a0
- Pilgrim, G.E. 1925. Presidential address to the Geological Section of the 12th Indian Science Congress. In: INDIAN SCIENTIFIC CONGRESS, 12, 1925. *Proceedings*, p. 200–218.
- Pilgrim, G.E. 1926. The fossil Suidae of India. *Memoirs of the Geological Survey of India, Palaeontologia Indica. New Series*, **8**:1–105.
- Raza, T.; Yasin, R.; Samiullah, K.; Fazal, R.M.; Hussain, K.; Abbas, A. & Mehmood, M. 2023. New collection of fossil remains of pigs (Mammalia: Artiodactyla: Suidae) from the Siwaliks of Pakistan. *Historical Biology*, **35**:1855–1870. doi:10.1080/08912963.2022.2124372
- Sankhyan, A.R. & Chavasseau, O. 2024. New suoid remains (Mammalia, Artiodactyla) from the Late Miocene of Haritalyangar, India. *Vertebrata Palasiatica*, **62**:69–84.
- Schmidt-Kittler, N. 1971. Die obermiozäne Fossilagerstätte Sandelzhausen Suidae, Artiodactyla, Mammalia. *Mitteilungen der bayerischen Staatssammlung für Paläontologie und historische Geologie*, **11**:129–170.
- Sein, C.; Made, J.V.D. & Rossner, G.E. 2009. New material of *Propotamochoerus* (Suidae, Mammalia) from the Irrawaddy Formation, Myanma. *Neues Jahrbuch für Geologie und Paläontologie*, **251**:17–31. doi:10.1127/0077-7749/2009/0251-0017
- Stehlin, H.G. 1899–1900. Über die Geschichte des Suiden Gebisses. Zweiter Teil. *Abhandlungen der Schweizerischen Palaontologischen Gesellschaft*, **27**:337–527.
- Thaug-Htike, C.S.; Tsubamoto, T.; Takai, M.; Natori, M.; Egi, N. & Maung, M. 2005. A revision of *Tetraconodon* (Mammalia, Artiodactyla, Suidae) from the Miocene of Myanmar and description of a new species. *Paleontological Research*, **9**:243–253. doi:10.2517/prpsj.9.243
- Thaug-Htike, C.S.; Takai, M.; Egi, N.; Tsubamoto, T.; Zin, M.M.T. & Maung, M. 2007. New species of large *Tetraconodon* (Mammalia, Artiodactyla, Suidae) from the late Miocene of Myanmar. *Paleontological Research*, **11**:307–315. doi:10.2517/1342-8144(2007)11[307:NSOLTMJ]2.0.CO;2
- Tsubamoto, T. & Taru, H. 2022. A new fossil specimen of the Suidae (Mammalia, Artiodactyla) from the upper Miocene Oiso Formation and a brief review of Neogene suids from Japan. *The Journal of the Geological Society of Japan*, **128**:287–293. doi:10.5575/geosoc.2022.0027
- Van der Made, J. & Han, D. 1994. Suoidea from the upper Miocene hominoid locality of Lufeng, Yunnan province, China. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C*, **97**:27–82.
- Van der Made, J. & Hussain, S.T. 1989. *Microstonyx major* (Suidae, Artiodactyla) from Nagri. *Estudios Geológicos*, **45**:409–416. doi:10.3989/egol.89455-6512
- Van der Made, J. 1996. Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, **33**:3–254.
- Van der Made, J. 1998. *Aureliachoerus* from Oberdorf and other Aragonian pigs from Styria. *Ann Naturhist Mus Wien*, **99**:225–227.
- Van der Made, J. 1999. Biometric trends in the Tetraconodontinae, a subfamily of pigs. *Transactions of the Royal Society of Edinburgh. Earth Sciences*, **89**:199–225. doi:10.1017/S0263593300007136
- Van der Made, J.; Krakhmalnaya, T. & Kubiak, H. 1999. The pig *Propotamochoerus palaeochoerus* from the upper Miocene of Grytsiv, Ukraine. *Estudios Geológicos*, **55**:283–292. doi:10.3989/egol.99555-6168
- Van der Made, J.; Choudhary, D.; Singh, N.P.; Sharma, K.M.; Singh, N.A. & Patnaik, R. 2022. *Listriodon dukkar* sp. nov. (Suidae, Artiodactyla, Mammalia) from the late Miocene of Pasuda (Gujarat, India): the decline and extinction of the Listriodontinae. *Paläontologische Zeitschrift*, **96**:355–383. doi:10.1007/s12542-022-00606-w
- Vokes, H.F. 1936. Siwalik Unionidae from the collection of the second Yale North India Expedition. *Contribution from the Paleontological Laboratory, Peabody Museum, Yale University*, **8**:133–141.

Received: 29 June 2025. Accepted: 18 December 2025.

Associated editor: Carolina Saldanha Scherer
Editor-in-chief: Matias do Nascimento Ritter