

A Collection of Hipparionines from the Middle Siwaliks (Late Miocene) of Pakistan

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Key words

Dhok pathan formation, *Proboscideipparion*, *Plesiohipparion*, *Hippotherium*, Mohal Pati, Siwaliks

ABSTRACT

The present study is focused on the collection of three toed horses known as hipparionines from the Late Miocene of the Siwalik Group of Pakistan. The specimens have been collected from the Dhok Pathan stratotype in the district Talagang and Mohal Pati village of district Jhelum, Punjab, Pakistan. The morphological traits of the specimens indicate that one specimen belongs to the genus *Proboscideipparion* and others were categorized as *Hipparionini* indet. but shows the features of some other genera such as *Plesiohipparion*, *Hippotherium* etc.

INTRODUCTION

The Siwalik Group or Siwaliks that range from 18 Ma to 0.6 Ma has produced an abundant mammalian fauna that has attracted researchers from around the world for nearly 200 years (Flynn *et al.*, 2024). The ungulates are most frequent finds in this mammalian fauna and have been described extensively (Colbert, 1935; Khan *et al.*, 2010, 2012). Two orders of the ungulates are of special interest because of their abundance, Artiodactyla (even toed ungulates) and Perissodactyla (odd toed ungulates) where perissodactyls are represented by three families; Chalicotheriidae, Rhinocerotidae and Equidae (Colbert, 1935; Khan *et al.*, 2012; Hussain, 1971). The members of the family Equidae first appeared in the Late Miocene and

have been considered important not only in taxonomic but stratigraphical context (Hussain, 1971; Wolf *et al.*, 2013; Bernor *et al.*, 2025). In other words, their presence in certain deposits in the Siwaliks is considered age specific and these are useful for relative dating. Traditionally, these were represented by two genera *Hipparion* and *Equus*, and by five species *Hipparion theobaldi*, *Hipparion antelopinum*, *Hipparion nagriensis*, *Hipparion* sp. and *Equus sivalensis* (Hussain, 1971; Bernor and Hussain, 1985; Hussain *et al.*, 1992; Bernor *et al.* 2019). However, recent assessment of the Siwalik hipparionines from the late Miocene deposits by Wolf *et al.* (2013), resulted in the recognition of four genera *Cormohipparion*, *Sivalhippus*, *Hipparion*, and *Cremohipparion* and seven species *Cormohipparion* sp., *S. nagriensis*, *S. perimensis*, *S. theobaldi*, *S. anwari*, *Hipparion* sp. small and *Cremohipparion antelopinum*. Even more recently, the work of Jukar *et al.* (2018, 2019) has recognized two more genera, *Eurygnathohippus* and *Plesiohipparion* from the Indian subcontinent Siwalik, which resulted in further increase of equid diversity. Despite the extensive study of the equids, their taxonomy in the Siwaliks remains problematic and needs specific attention.

We are describing some hipprionine remains collected

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from the Dhok Pathan stratotype in the district Talagang and Mohal Pati village of district Jhelum, Punjab, Pakistan that will add further anatomical knowledge in this group to resolve the taxonomic issues of this group.

Mohal Pati is a small village located near the famous Bhandar Bone Bed of Pilgrim (1913) in district Jhelum, Punjab, Pakistan. It is located 1.5 km northeast of Bhandar, and 2.5 km northeast of palaeontologically famous Hasnot village (Fig. 1). According to Pilgrim (1913), the sediments at the Bhandar Bone Bed are considered as the upper Dhok Pathan Formation, and Johnson *et al.* (1982) has palaeomagnetically determined that the age of these sediments is 6 to 7 Ma, representing Chron 4 of magnetic polarity time scale of LaBrecque *et al.* (1977) that corresponds to C3r of geomagnetic polarity time scale of Ogg (2020). This age corresponds well with the upper Dhok Pathan Formation as well as the upper late Miocene. Lithologically, the sediments are characterized by pale yellow silt/claystone and dark to light colored sandstone with minute quantity of conglomerates, consistent with the Dhok Pathan Formation of the Middle Siwalik. However, some of the specimens came from nearby area, Andar Kas, whose deposits are dated to Nagri Formation about 9.2 to 10 Ma (Johnson *et al.*, 1982).

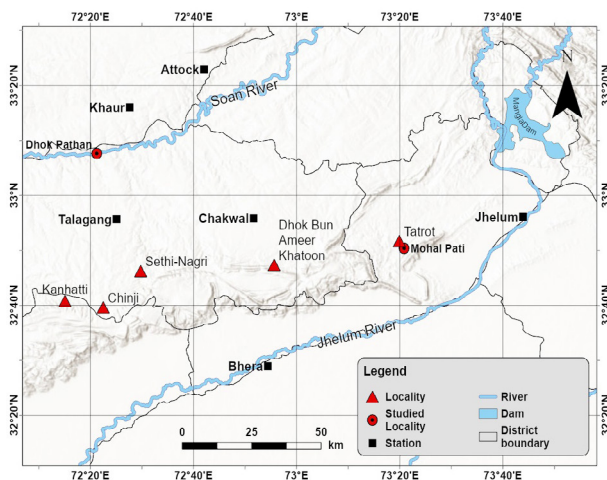


Fig. 1. Map showing the location of areas in Punjab, Pakistan from where new specimens have been collected.

Dhok Pathan village is located in Talagang district of Punjab, Pakistan at the bank of Soan River (Fig. 1). Pilgrim (1913) assigned the outcrops of near the Dhok Pathan Rest House as type locality of the Dhok Pathan Formation, and area from the Naragghi to Markhal village as the stratotype of the Dhok Pathan Formation. Lithologically, the sediments are characterized by pale yellow silt/claystone and dark to light colored sandstone

alternating with thin beds conglomerates. The specimens described in this study came from two localities, Kundrali and Dhendar as reported by Aftab *et al.* (2022). Kundrali locality corresponds well to Barnum Brown locality 38 (B38) and Dhendar roughly corresponds to B40-B41 as shown in fig. 18 of Colbert (1935). The age of these localities is between 7.9 to 7.6 Ma as determined by Barry *et al.* (1980) corresponding to C4n.2n to C4n.1n of geomagnetic polarity time scale of Ogg (2020).

MATERIALS AND METHODS

The material includes 13 specimens comprising isolated upper and lower cheek teeth. The collection area of each specimen is given in parentheses. The surface collection was the primary method for the collection of specimens as recommended by Behrensmeyer and Barry (2005). After collecting or excavating the samples, these were wrapped in cotton for transportation to the laboratory. In the lab., the specimens were prepared by washing and removing sediments (silt/clay/mud or sand) using very fine needle. The partially broken specimens, found broken or broken while preparing, were glued using GMSA glue. After preparation, the specimens were catalogued using numerator and denominator and PUPC as institutional abbreviation. For example, in PUPC 23/129, PUPC stands for Punjab University Palaeontological Collection, 23 as year of collection, and 129 as number of the specimen collected in this year. We followed Bernor *et al.* (2010, 2017) and Wolf *et al.* (2013) for taxonomy, and the terminology for the description of dental material is given in Figure 2. Measurement protocols follow Eisenman *et al.* (1988), and measurements were taken using digital Vernier caliper. Occlusal length and width were recorded in millimeters. The photos were taken using DSLR camera, Canon 6D, and photos were arranged in plates using Adobe Photoshop. The specimens are housed in Dr. Abu Bakr Fossil Display and Research Centre, Institute of Zoology, Quaid-e-Azam Campus, University of the Punjab, Lahore, Pakistan.

SYSTEMATIC PALAEONTOLOGY

Order Perissodactyla Owen, 1848

Suborder Hippomorpha Wood, 1937

Family Equidae Gray, 1821

Tribe Hipparionini Quinn, 1955

Genus *Proboscoidipparion* Sefve, 1927

cf. *Proboscoidipparion* sp.

(Fig. 3.1)

Referred material: PUPC 23/97, right p4 (Mohal Pati).

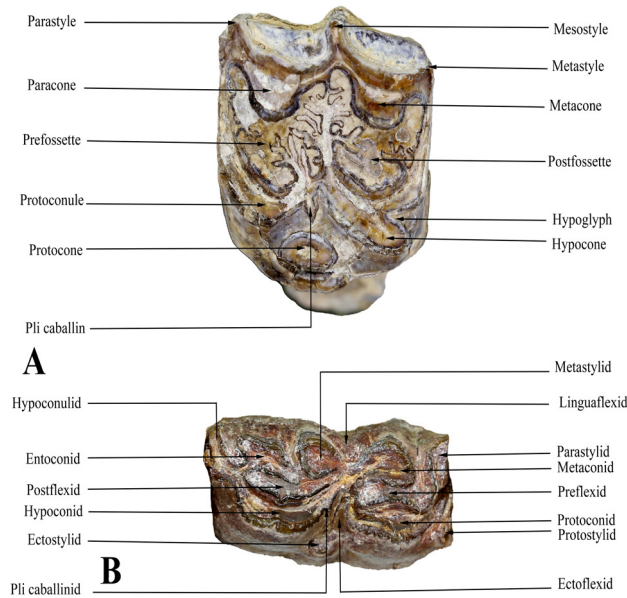


Fig. 2. Dental terminology being used in this study for the description of dental material. Topology of A, upper tooth, B, lower tooth.

Description

PUPC 23/97 is highly worn and partially broken p4 as judged by its dimensions (Fig. 3.1). Parastylid, protostylid, protoconid, and hypoconulid are partially broken. The metaconid is high lingually with slightly round anterior border, while metastylid is completely pointed and shows completely triangular morphology and both forming a houfenoid double knot. Both, the linguaflexid and ectoflexid are deep and U-shaped. The pre- and postflexid are compressed labiolingually, narrow and plicated. Its preserved length is 24 mm and width is 13.7 mm.

Comparative remarks

The described molar, PUPC 23/97, shows houfenoid double knot (metaconid and metastylid triangular in form and positioned more or less symmetrically), a character of *Eurygnathohippus*, *Plesiohipparion*, and *Proboscoidipparion* (Qiu *et al.*, 1987; Bernor and Lipscomb, 1991; Bernor and Sun, 2015). The specimen lacks the ectostylid that differentiates it from *Eurygnathohippus* and lacks the pli caballanid that isolates it from *Plesiohipparion* (Bernor and Sun, 2015), but associate the specimen to *Proboscoidipparion*. Further, the molar has round anterior and lingual border of the metaconid that confirms its affinity to *Proboscoidipparion* (as stated by Bernor and Sun, 2015) and such a morphology is found in *Proboscoidipparion pater* in late wear stage lower molar V 8172 described and figured by Bernor and Sun (2015, Fig. 3F3). PUPC 23/97

differs from *Sivalhippus* species in straighter posterior border of the metaconid and more houfenoid morphology. Based on these observations the specimen is described as cf. *Proboscoidipparion* sp. until more specimens are recovered from the area.

Hipparionini indet (Fig. 3.2-3.13)

Referred material

PUPC 23/113, right DP3 (Mohal Pati); PUPC 23/140, right M2 (Dhok Pathan); PUPC 23/114, right M2 (Mohal Pati); PUPC 23/136, right M2? (Dhok Pathan); PUPC 23/112, right M3 (Mohal Pati); PUPC 23/137, ?M? (Dhok Pathan); PUPC 23/111, partial upper molar (Mohal Pati); PUPC 23/115, partially broken left dp4 (Mohal Pati); PUPC 23/101, anterior portion of p2 (Mohal Pati); PUPC 23/99, left m1? (Mohal Pati); PUPC 23/100, right m1? (Mohal Pati); PUPC 23/134, left m3 (Dhok Pathan).

Description

PUPC 23/113 is a very small and partially broken deciduous upper premolar (Fig. 3.2). The meta- and hypocone are half, resulting in loss of metastyle and hypoglyph. It is completely unworn. The protocone is small and flat lingually, giving almost triangular appearance. Both the para- and mesostyle are equally developed and are thick. The fossettes are wide and deep. Its preserved length is 19.8 mm and width is 21.2 mm.

PUPC 23/140 is partially broken, slightly worn M2 (Fig. 3.3). The metacone is well preserved, rest of the cusps are partially broken. Only the lingual half of the protocone is preserved. The parastyle is partially preserved, the mesostyle is large and thick while the metastyle is weakly developed. The plications are weak due to early wear. Its preserved length is 22.4 mm, and preserved width is 19.4 mm.

PUPC 23/114 is a partially broken and highly worn M2 (Fig. 3.4). The paracone is completely broken and protocone is partially preserved. The protocone is elongate, compressed lingually and slightly round lingually. The posterior border of prefossette is slightly plicated while the anterior border of postfossette has only spur. Hypoglyph is deeply incised. Only metastyle is preserved. Its preserved length is 26.1 mm and width is 23.4 mm.

PUPC 23/136 is broken anteriorly, resulting in loss of most of the protoconule and paracone (Fig. 3.5). The enamel is also lost from most of the tooth. The metacone is elongated and narrows posteriorly. The fossettes are only sparsely plicated. The hypoglyph is very deep, isolating the hypocone. Its preserved length is 20.7 mm, and preserved width is 21 mm.



Fig. 3. cf. *Proboscidiapparion* sp. 1, PUPC 23/97, right p4. Hipparionini indet. 2, PUPC 23/113, right DP3; 3, PUPC 23/140, right M2; 4, PUPC 23/114, right M2; 5, PUPC 23/136, right M2?; 6, PUPC 23/112, right M3; 7, PUPC 23/137, ?M?; 8, PUPC 23/111, partial upper molar; 9, PUPC 23/115, partially broken left dp4; 10, PUPC 23/101, anterior portion of p2; 11, PUPC 23/99, left m1?; 12, PUPC 23/100, right m1; 13, PUPC 23/134, left m3.

Views: a. occlusal, b. lingual, c. labial. Scale bar equal to 10 mm.

PUPC 23/112 is a partially worn M3 (Fig. 3.6). The protocone is isolated, compressed lingually, and tends to be oval in shape. The fossettes are wide and deep. The parastyle is thick and strong while the mesostyle is moderately thick, and the metastyle is weakly developed. The hypoglyph is deeply incised, isolating the hypocone. Its preserved length is 30.7 mm and width is 21.5 mm.

PUPC 23/137 is partially preserved upper molar (Fig. 3.7). It preserves the para- and metacone with some portion of the pre- and postfossette. The opposing border of the pre- and postfossette are complexly plicated. Its preserved length is 21.6 mm, and preserved width is 12.7 mm.

PUPC 23/111 is a partially preserved upper molar (Fig. 3.8). The posterior border of the prefossette and anterior border of postfossette are sparsely plicated. The para- and mesostyle are thick. The preserved length is 23.5 mm and width is 14.5 mm.

PUPC 23/115 represents a small sized deciduous lower premolar in which anterior lobe is broken resulting in loss of protoconid and associated structures, and metaconid (Fig. 3.9). The hypoconid is extremely large and partly wavy. The metastylid is preserved which is triangular in shape and it is pointed lingually. The entoconid is large and flat. The hypoconulid is large, lingually pointed. Its preserved length is 18.8 mm and width is 12 mm.

PUPC 23/101 represents paraconid, protoconid and metaconid of p2 (Fig. 3.10). It is highly worn. The paraconid is triangular and metaconid is oval. Its preserved length is 15.7 mm and preserved width is 11.7 mm.

PUPC 23/99 is partially broken and moderately worn m1 (Fig. 3.11). The apex of metastylid is completely lost while the metaconid is partially preserved. A thick protostylid is present. The linguaflexid is deep and V shaped, as well as ectoflexid. The hypoconilid is partially preserved. Its preserved length is 22.2 mm, and preserved width is 12.4 mm.

PUPC 23/100 is broken anteriorly resulting in loss of most of the protoconid, metaconid and hypoconulid, and complete loss of proto- and parastylid (Fig. 3.12). Pli caballanid is prominent. Both the linguaflexid and ectoflexid are shallow. It is moderately worn. Its preserved length is 22.3 mm, and preserved width is 11.8 mm.

PUPC 23/134 is slightly broken and in early wear (Fig. 3.13). The protostylid is broken and reaches half of the height of the tooth. The parastylid is slightly broken and weak. The proto- and hypoconid are almost equal in length and have round borders. Both the metaconid and metastylid are oval in shape, linguaflexid is deep and V shaped. The hypoconid is small and rectangular in shape. The hypoconulid is large and made prominently third lobe and has a large stylid. Its length is 25.2 mm and width is

10.5 mm.

Comparative remarks

The material described here as Hipparionini indet. is heterogeneous in nature and it is composed of different species. Due to the breakage of the material, most of the material cannot be identified to a generic or specific level, and some of the material corresponds to a small species (Fig. 3.6, 7, 13), *Hipparion/ Cormohipparion* sp. small described by Wolf *et al.* (2013) and Bernor *et al.* (2025) but the nature of this species is uncertain as discussed by the same authors that more material is needed for the precise allocation of the material reported to this species. We are tentatively placing all such cheek teeth in the referred material (PUPC 23/112, PUPC 23/115 and PUPC 23/134) that may correspond to *Hipparion/ Cormohipparion* sp. small. to Hipparionini indet. until more material is recovered to fully resolve the nature of the *Hipparion/ Cormohipparion* sp. small. Among rest of the materials, PUPC 23/140 (Fig. 3.3) shows the confluence of the pre- and postfossette, a character of *Hippotherium* (Bernor *et al.*, 2017) but the plications are less complex, and protocone and hypoglyph are not preserved to show their morphology. PUPC 23/136 shows weak fossette plications, trifold pli caballin, deeply incised hypoglyph, and elongate protocone that makes a pli posteriorly (Fig. 3.5), characters that can associate with *Cormohipparion* but the specimen is broken and slightly deformed, also it is in early wear. PUPC 23/113 seems DP3 but maybe just erupted M1/M2. It is unworn and does not show occlusal morphology in detail, however, besides the isolated protocone, a pli caballin is also visible (Fig. 3.2). Its morphology in this state is close to *Baryhipparion tchikoicum* described and figured by Deng *et al.* (2016, Fig. 3). Similarly, PUPC 23/137 (Fig. 3.7) is slightly worn M3 that can be compared with *Baryhipparion tchikoicum*. PUPC 23/115 is an incomplete dp4 (Fig. 3.9) whose affinity can be made with *Hipparion/ Cormohipparion* sp. small or with *Baryhipparion*. Nevertheless, more material is needed to fully assess the presence of *Baryhipparion* in Siwaliks. PUPC 23/100 is partially broken (Fig. 3.12) that hinders its specific attribution; however, the preserved tooth morphology is similar to the specimens described above as *Eurygnathohippus* sp.

DISCUSSION

The Siwalik equids are extremely important in terms of biogeographic distribution, evolution and diversification of this group in Asia (Wolf *et al.*, 2013; Sankhyan *et al.*, 2023). The classification of the Siwalik equids remained

a matter of problem and debate since their first discovery and opinions have been changed from time to time and from one researcher to other (e.g., Falconer and Cautley, 1849; Lydekker, 1876; Colbert, 1935; Hussain, 1971; Bernor and Hussain, 1985; Wolf *et al.*, 2013; Sankhyan *et al.*, 2023; Bernor *et al.*, 2025). However, Wolf *et al.* (2013), after the detailed analysis of all the Siwalik material from the Late Miocene have proposed the presence of four genera *Cormohipparion*, *Sivalhippus*, *Hipparion*, and *Cremohipparion* and seven species *Cormohipparion* sp., *S. nagriensis*, *S. perimensis*, *S. theobaldi*, *S. anwari*, *Hipparion* sp. small and *Cremohipparion antelopinum*. Even more recently, the work of Jukar *et al.* (2018, 2019) has recognized two more genera, *Eurygnathohippus* and *Plesiohipparion* from the Indian subcontinent Siwalik, which resulted in further increase of equid diversity. Some years later, Sankhyan *et al.* (2023) identified the presence of the genus *Proboscoidipparion* from the Haritalyangar, adding another genus of hipparionine equids in the Siwaliks. *Proboscoidipparion* sp. is reported based on a lower molar in this study as well and from the Late Miocene. This genus is strictly Pliocene in its age range and predominantly known from China, as well as from the Turkey and England. This genus is recently reported from the Haritalyangar area (Sankhyan *et al.* 2023), but most of the specimens are from very latest Miocene deposits. Among the other specimens that could not be identified to either generic or specific level, Hipparionini indet., contain three specimens (PUPC 23/113, PUPC 23/137 and PUPC 23/115) that are potential candidates of yet another hipparionine genus, *Baryhipparion*, in the Siwaliks. However, more material is needed to confirm its occurrence in the Siwaliks. One of the specimens, PUPC 23/100 shows all the morphological features of *Cremohipparion* material described by Lydekker (1876) but such morphology is also found in the genus *Eurygnathohippus* described by Bernor *et al.* (2013, 2020). It is quite probable that the genus *Eurygnathohippus* predates all other records in the Siwaliks and is point of distribution to the other regions. However, more material is needed and ongoing taxonomic reassessment of the Siwalik hipparionines will answer to such questions related to taxonomy and biogeography of this group.

CONCLUSIONS

The present study focused on thirteen recently collected materials of the hipparionine remains resulted in the identification of the genus *Proboscoidipparion* in the Siwaliks of Pakistan based on a lower molar after its previous identification in the Siwaliks of India by

Sankhyan *et al.* (2023). The other materials is described as Hipparionini indet. awaiting new material. Some of the specimens in Hipparionini indet, are potential candidates of some other genera that have not been previously reported from the Siwaliks and new materials and/or reassessment of already collected material will reveal their exact taxonomic position.

DECLARATIONS

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Generative AI and AI-assisted technology statement

The authors declare that no generative AI and AI assisted technology was used in the creation of this manuscript.

Statement of conflict of interest

The authors have declared no conflict of interest.

REFERENCES

- Aftab, K., Khan, M.A., Babar, M.A., Abbas, S.G., Ghaffar, A., Akhtar, M., Iqbal, R. and Afsheen, S., 2022. New hipparionine fossils from the Dhok Pathan Formation of Punjab, Pakistan. *Hist. Biol.*, **34**: 1218-1227. <https://doi.org/10.1080/08912963.2021.1970152>
- Barry, J.C., Behrensmeyer, A.K. and Morgan, M., 1980. A geologic and biostratigraphic framework for Miocene sediments near Khaur Village, northern Pakistan. *Postilla*, **183**: 1–19.
- Behrensmeyer, A.K. and Barry, J., 2005. Biostratigraphic surveys in the Siwaliks of Pakistan. A method for standardized surface sampling of the vertebrate fossil record. *Palaeont. Elect.*, **8**: 1-24.
- Bernor, R.L. and Hussain, S.T., 1985. An assessment of the systematic, phylogenetic and biogeographic relationships of Siwalik Hipparionine horses. *J. Vert. Palaeontol.*, **5**: 32-87. <https://doi.org/10.1080/02724634.1985.10011845>
- Bernor, R.L. and Lipscomb, D., 1991. The systematic position of *Plesiohipparion* aff. *huangheense* (Equidae, Hipparionini) from Gülyazi, Turkey.

- Mitt. Bayer. Staatssam. Paläontol. Hist. Geol., **31**: 107-123.
- Bernor, R.L. and Sun, B., 2015. Morphology through ontogeny of Chinese Proboscideipparion and Plesiohipparion and observations on their Eurasian and African relatives. *Vert. PalAsia*, **53**: 73-92.
- Bernor, R.L., 2020. Sahabi *Eurygnathohippus feibeli*: Its systematic, stratigraphic, chronologic and biogeographic contexts. *Riv. Ital. Paleontol. Stratigrafia*, **126**: 561-581.
- Bernor, R.L., Armour-Chelu, M., Gilbert, H., Kaiser, T.M. and Schulz, E., 2010. Equidae, in *Cenozoic mammals of Africa*, (eds. L. Werdelin and W. L. Sanders), University of California Press, Berkeley, CA. pp. 685-721. <https://doi.org/10.1525/california/9780520257214.003.0035>
- Bernor, R.L., Cirilli, O., Jukar, A.M., Potts, R., Buskianidze, M. and Rook, L. 2019. Evolution of early *Equus* in Italy, Georgia, the Indian Subcontinent, East Africa, and the origins of African zebras. *Front. Ecol. Evol.*, **7**: 166. <https://doi.org/10.3389/fevo.2019.00166>
- Bernor, R.L., Gilbert, H., Semperebon, G.M., Simpson, S. and Semaw, S., 2013. *Eurygnathohippus woldegabrieli*, sp. nov. (Perissodactyla, Mammalia), from the middle Pliocene of Aramis, Ethiopia. *J. Vertebr. Paleontol.*, **33**: 1472-1485. <https://doi.org/10.1080/02724634.2013.829741>
- Bernor, R.L., Göhlich, U.B., Harzhauser, M. and Semperebon, G.M., 2017. The Pannonian *C. hipparions* from the Vienna basin. *Palaeogeog. Palaeoclimat. Palaeoecol.*, **476**: 28-41. <https://doi.org/10.1016/j.palaeo.2017.03.026>
- Bernor, R.L., Morgan, M.E. and Nelson, S., 2025. Siwalik bovidae. In: *At the foot of the Himalayas: Paleontology and ecosystem dynamics of the Siwalik record* (eds. C. Badgley, M.E. Morgan and D. Pilbeam). Johns Hopkins University Press. pp. 260-271.
- Bernor, R.L., Semperebon, G.M., Rivals, F., Avilla, L.S. and Scott, E., 2020. *Examining evolutionary trends in Equus and its close relatives from five continents*. Frontiers Media SA. pp. 1-243. <https://doi.org/10.3389/978-2-88963-555-9>
- Colbert, E.H. 1935. Siwalik mammals in the American Museum of Natural History. *Trans. Am. Phil. Soc. N.S.* **26**: 1-401. <https://doi.org/10.2307/1005467>
- Deng, T., Wang, H., Wang, X., Li, Q. and Tseng, Z.J., 2016. The late Miocene Hipparion (Equidae, Perissodactyla) fossils from Baogeda Ula, Inner Mongolia, China. *Hist. Biol.*, **28**(1-2): 53-68.
- Eisenmann, V., Alberdi, M.T., De Giuli, C. and Staesche, U., 1988. *Studying fossil horses*. EJ Brill, Leiden, The Netherlands. pp. 1-58.
- Falconer H. and Cautley P.T., 1849. *Fauna antique sivalensis, being the fossil zoology of the Siwalik Hills, in the north of India*. London. pp. 1-9.
- Flynn, L.J., Raza, S.M., Morgan, M.E., Barry, J.C. and Pilbeam, D., 2024. *The Potwar Siwaliks: An impressive Neogene record of terrestrial rocks and fossils*. <https://doi.org/10.1144/SP543-2022-251>
- Hussain, S.T., 1971. Revision of *Hipparion* (Equidae, Mammalia) from the Siwalik Hills of Pakistan and India. *Veslag Bayer Akad Swiss, N.S.*, **147**: 1-68.
- Hussain, S.T., Bergh, G.D., Steensma, K.J., Dee Visser, J.A., De Vos, J., Arif, M., Van Dam, J., Sondaar, P.Y., Malik, S.M. 1992. Biostratigraphy of the Plio-Pleistocene continental sediments (Upper Siwaliks) of the Mangla-Samwal Anticline, Azad Kashmir, Pakistan. *Proc. Kon. Ned. Akad. V. Wetenscl.*, **95**: 65-80.
- Johnson, N.M., Opdyke, N.D., Johnson, G.D., Lindsay, E.H. and Tahirkheli, R.A.K., 1982. Magnetic polarity, stratigraphy and ages of Siwalik group rocks of the Potwar Plateau, Pakistan. *Palaeogeog. Palaeoclimat. Palaeoecol.*, **37**: 17-42. [https://doi.org/10.1016/0031-0182\(82\)90056-6](https://doi.org/10.1016/0031-0182(82)90056-6)
- Jukar, A.M., Sun, B. and Bernor, R.L., 2018. The first occurrence of *Plesiohipparion huangheense* (Qiu, Huang and Guo, 1987) (Equidae, Hipparionini) from the late Pliocene of India. *Boll. Soc. Paleontol. Ital.*, **57**: 125-132.
- Jukar, A.M., Sun, B., Nanda, A.C. and Bernor, R.L., 2019. The first occurrence of *Eurygnathohippus* (Mammalia, Perissodactyla, Equidae) outside Africa and its biogeographic significance. *Boll. Soc. Paleontol. Ital.*, **58**: 171-179.
- Khan, M.A., Akhtar, M., Iliopoulos, G. and Hina. 2012. Tragulids (Artiodactyla, Ruminantia, Tragulidae) from the Middle Siwaliks of Hasnot (late Miocene), Pakistan. *Riv. Ital. Paleontol. Stratigr.* **118**: 325-341.
- 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 J. Zool.*, **10**: 1-190.
- LaBrecque, J.L., Kent, D.V. and Cande, S.C., 1977. Revised magnetic polarity time scale for Late Cretaceous and Cenozoic time. *Geology*, **5**: 330-335. [https://doi.org/10.1130/0091-7613\(1977\)5<330:RMPTSF>2.0.CO;2](https://doi.org/10.1130/0091-7613(1977)5<330:RMPTSF>2.0.CO;2)
- Lydekker, R., 1876. Molar teeth and other remains of

- Mammalia from the India Tertiaries. *Pal. Ind.* **10**: 19-87.
- Ogg, J.G., 2020. Geomagnetic polarity time scale. In: *Geologic time scale*. Elsevier. pp. 159-192. <https://doi.org/10.1016/B978-0-12-824360-2.00005-X>
- Pilgrim, G.E., 1913. Correlation of the Siwaliks with Mammal Horizons of Europe. *Rec. Geol. Sur. Ind.*, **43**: 264-326.
- Qiu, Z., Huang, W. and Guo, Z., 1987. The Chinese hipparionines fossils. (In Chinese, with an English summary). *Paleontol. Sin., N.S. C.*, **175**: 1-125.
- Sankhyan, A.R., Abbas, S.G., Khan, M.A., Babar, M.A. and Yasin, A., 2023. Diversity of hipparionines (Perissodactyla: Equidae) from the late Miocene–Pliocene Siwalik deposits at Haritalyangar, India. *Annales de Paléontologie. Elsevier Masson*, **109**: 102602. <https://doi.org/10.1016/j.annpal.2023.102602>
- Wolf, D., Bernor, R.L. and Hussain S.T. 2013. A systematic, biostratigraphic, and paleobiogeographic reevaluation of the Siwalik Hipparionine Horse assemblage from the Potwar Plateau, Northern Pakistan. *Palaeontogr. Abt. A*, **300**: 1–115. <https://doi.org/10.1127/pala/300/2013/1>