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**SAYYED GHYOUR ABBAS, MUHAMMAD ADEEB BABAR, MUHAMMAD AKBAR KHAN, BADAR UN NISA, MUHAMMAD KHALIL NAWAZ, & MUHAMMAD AKHTAR (2021). New proboscidean material from the Siwalik Group of Pakistan with remarks on some species.**

**Cover:** Partial upper molar of cf. *Paratetralophodon hasnotensis*, an extremely rare proboscidean species from the Siwalik Group. Specimen PUPC 15/249 in occlusal view.

**Citation:** Abbas, S.G., M.A. Babar, M.A. Khan, B.U. Nisa, M.K. Nawaz and M. Akhtar. 2021. New proboscidean material from the Siwalik Group of Pakistan with remarks on some species. *PaleoBios*, 38. ucmp\_paleobios\_54113. doi: <https://doi.org/10.5070/P938054113>.

# New proboscidean material from the Siwalik Group of Pakistan with remarks on some species

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Over the years a diverse assemblage of proboscidean remains has been recovered from the Lower to Upper Siwalik Subgroups of Pakistan and India. This article reports newly discovered dental material of tri- and tetralophodont proboscideans that includes cf. *Paratetralophodon hasnotensis* and *Choerolophodon* sp., and a Gomphotherium gen. et sp. indet., recently collected from late middle to late Miocene localities of the Pakistani Siwalik Group, with a brief history of these species. The partial premolar of cf. *Pa. hasnotensis* is described for the first time from the Siwalik Group, recovered from the Dhok Pathan Formation, and the specimens reported herein are the latest to be described after a 38-year gap from previously described material for this species. A preliminary survey of the literature and previously described material of Siwalik species suggests a revision of Siwalik Group proboscideans is much needed.

**Keywords:** proboscideans, Gomphotherium, *Paratetralophodon*, *Choerolophodon*, Siwaliks, paleontology

## INTRODUCTION

Proboscideans from the Siwalik Group represent a poorly studied assemblage of phylogenetically related mammals. The last review of this magnificent group was conducted 38 years ago by Tassy (1983). Proboscideans previously reported from the Siwaliks of Pakistan and India include a diverse assemblage of gomphotherium, choerolophodont, mammutid, amebelodont, and stegodont taxa (Falconer and Cautley 1846, Lydekker 1880, 1884, 1885, Pilgrim 1913, Osborn 1926, 1929, 1936, 1942, Sarwar 1977, Tassy 1983, Abbas et al. 2018). In the Siwaliks of the Indian subcontinent, gomphotheres are represented by three monospecific genera, *Gomphotherium* Burmeister (1837) [*G. browni* (Osborn, 1929)], *Paratetralophodon* Tassy (1983) [*Pa. hasnotensis* (Osborn, 1929)] and *Anancus* Aymard (1855) [*A. sivalensis* (Cautley, 1836)]; choerolophodonts by *Choerolophodon corrugatus* (Pilgrim, 1913); mammutids by the single species, *Zygodon metachinjiensis* (Osborn, 1929);

amebelodonts by two genera with a single species each, *Protanancus chinjiensis* (Pilgrim, 1913) and an undetermined species of *Konobelodon* Lambert (1990) (originally referred to *Mastodon grandincisivus* Schlesinger (1917), and later it was described as *Konobelodon* sp. in Abbas 2018); and stegodonts by the single genus *Stegolophodon* Schlesinger (1917) that most likely includes three species: *St. latidens* (Clift, 1828), *St. stegodontoides* (Pilgrim, 1913) and possibly, *St. cautleyi* (Lydekker, 1886). With the exception of genus *Anancus*, all of these taxa have been recovered from middle and late Miocene localities of the Siwalik Group (Figs. 1, 2). Although diverse, they are generally disassociated and fragmentary in nature, but the remains of these proboscidean species are rare.

Here we provide additional descriptions of isolated and fragmentary proboscidean remains collected from five localities of northern Punjab, Pakistan dating from the late middle to late Miocene and corresponding to the Lower (Chinji Formation) and Middle (Dhok Pathan Formation) Siwalik Subgroups. In addition, we review the published proboscidean genera and species from this

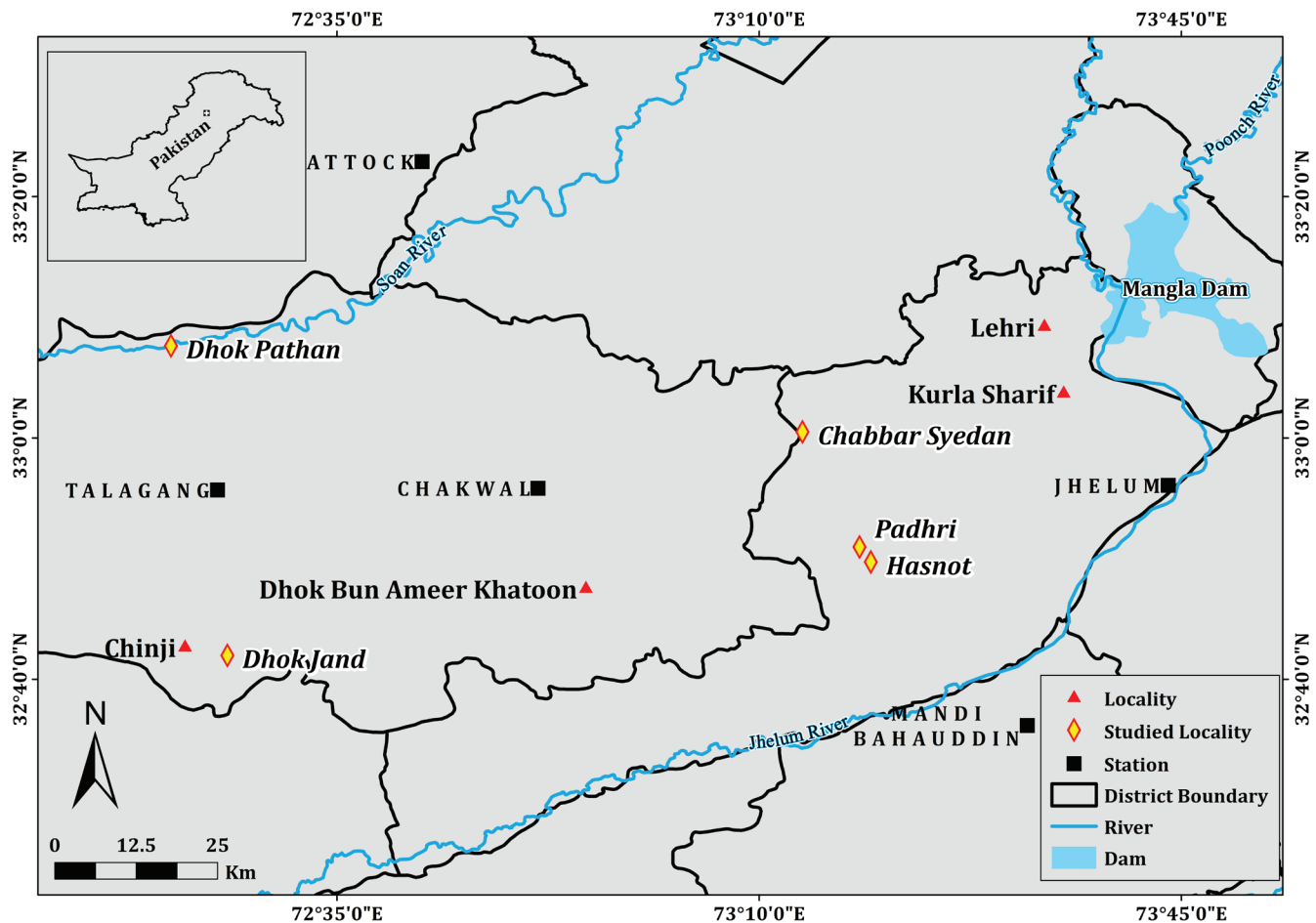
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**Citation:** Abbas, S.G., M.A. Babar, M.A. Khan, B.U. Nisa, M.K. Nawaz and M. Akhtar. 2021. New proboscidean material from the Siwalik Group of Pakistan with remarks on some species. *PaleoBios*, 38. ucmp\_paleobios\_54113.

**DOI:** <https://doi.org/10.5070/P938054113>

**Permalink:** <https://escholarship.org/uc/item/1877k1mz>

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**Figure 1.** Map showing the geographic position of the Padhri, Hasnot, Chabbar Syedan, and Dhok Jand localities (yellow diamonds) yielding the proboscidean remains described in this study from the district of Jhelum and Chakwal, Punjab, Pakistan, with respect to other localities known for mammalian remains (red triangles).

region highlighting: 1) problems concerning the status of these species; and 2) morphological variations present in the previously described material.

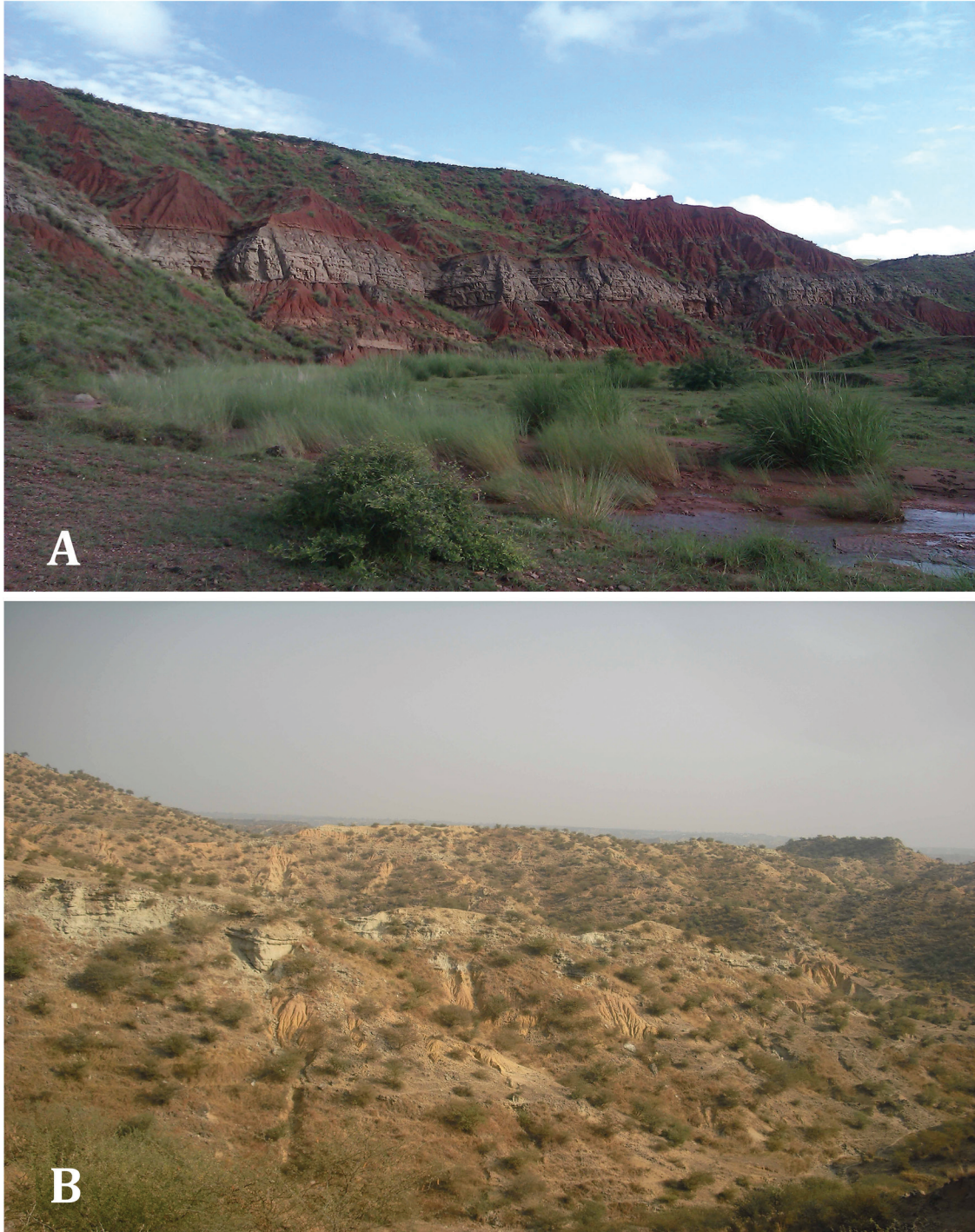
#### MATERIALS AND METHODS

The proboscidean fossil remains described here have been collected from areas surrounding the following Pakistani settlements: Dhok Jand and Chabbar Syedan (middle Miocene, Chinji Formation, Lower Siwalik Subgroup), and Padhri, Hasnot and Dhok Pathan (late Miocene, Dhok Pathan Formation, Middle Siwalik Subgroup) (Fig. 1).

**Dhok Jand**—Dhok Jand is a small village (Lat.  $32^{\circ} 42' 08.0''\text{N}$ ; Long.  $72^{\circ} 26' 05.8''\text{E}$  and altitude 592.76 m) located about 6.0 km southeast of the Chinji village, Chakwal, Punjab, Pakistan. Chinji Formation outcrops are well-exposed in the area surrounding Dhok Jand show lithology characteristic of this formation: bright

red clays and subsidiary brown gray sandstones (Dehm 1963, Badgley et al. 1998). PUPC 17/120, PUPC 17/121 and PUPC 15/232 have been collected from an unnumbered site near locality 641 of Badgley et al. (1998: figs. 2, 3). We estimate the age of this locality to be  $\sim 13.7$  Ma.

**Chabbar Syedan**—Chabbar Syedan is a small village (Lat.  $33^{\circ} 00' 34.9''\text{N}$ ; Long.  $73^{\circ} 13' 33.9''\text{E}$  and altitude 488.95 m) located about 17 km west-southwest of Sohawa at the western base of the Bakrala Ridge, Jhelum, Punjab, Pakistan. The outcrops are predominantly red claystones placed on subordinate hard gray sandstone with thin interbeds of siliceous nodules and conglomerates. Most fossils are found in hard, coarse-grained, siliceous sandstone (grit). The outcrops belong to the Chinji Formation (Sarwar 1977, 1990, Aftab et al. 2015, Abbas et al. 2016, Abbas 2018, Nawaz et al. 2019) with an age range of  $\sim 14$ – $11.4$  Ma based on ungulate faunal contents. PUPC 15/07 has been collected from Chinji



**Figure 2.** Lithology and typical exposure of the Chinji (**A**) and Dhok Pathan (**B**) Formations. In **A**, brick red colored clay and light gray sandstone characterize the Chinji Formation, while in **B**, pale yellow clay and dull, brown colored sandstone characterize the Dhok Pathan Formation.

Formation (late middle Miocene) outcrops of this site.

**Dhok Pathan**—The area around the Dhok Pathan Rest House (Lat. 33° 07' 34.0"N: Long. 72° 21' 14.5"E and altitude 327.05 m), near the Dhok Pathan village, has been assigned as the type section of the Dhok Pathan

Formation of the Middle Siwalik Subgroup ([Pilgrim 1913](#)). The Dhok Pathan village is situated near the Soan River about 75 km from Rawalpindi on Rawalpindi-Talagang Road. Here, extensive Neogene freshwater sedimentary rocks are present which are highly fossiliferous.

The average thickness of the sequence around this area is about 497 m (Barry et al. 2002). The Dhok Pathan type locality is characterized by less compacted gray sandstone with alternate pink to orange shales and clays and minor layers of interbedded conglomerates. Barry et al. (2002) have placed the outcrops in the middle C4Ar.2n–4n.3n, which shows that the age range of the Dhok Pathan Formation stratotype is ~9.5–7.5 Ma. PUPC 15/232 has been collected from the Kundwali locality of the Dhok Pathan Formation stratotype.

**Padhri**—Padhri is a small village situated about 67 km in the west-southwest of the city of Jhelum. Outcrops of the upper Dhok Pathan Formation are well-known and exposed in the vicinity of Padhri and has yielded a diverse mammalian fauna (Khan 2007). The specimens, PUPC 14/12 and PUPC 15/219, have been collected from the Thandi Kor site (Lat. 32° 84' 92.5"N; Long. 73° 30' 54"E and altitude 374.56 m) falling in the administrative boundaries of Padhri situated west of the Barnum Brown locality 113 (Colbert 1935: fig. 22). The estimated age of the locality is 7.0 Ma based on ungulate faunal elements (Khan 2007).

**Hasnot**—Hasnot village (Lat. 32° 50' 44.7"N; Long. 73° 17' 50.1"E and altitude 363.74 m) is situated about 70 km west-southwest of the city of Jhelum. Currently, the Bhuna kas (a stream), which is located west of Hasnot, is surrounded by many highly fossiliferous localities. It has well-exposed upper Dhok Pathan Formation of the Middle Siwalik Subgroup similar to Padhri. Lithostratigraphically, the sediments are characterized by sandstones with alternate clays and scattered conglomerates in the lower part and conglomerates with sandstones and clays in the upper part. The clays are orange brown in color and the Dhok Pathan Formation deposits ranges from 7.0 to 5.3 Ma in age (Pilbeam et al. 1977, Barry et al. 1982, Johnson et al. 1982, Barry 1987). PUPC 15/249 has been collected from this site.

Dental terminology and measurement protocols follow Tassy (2013, 2014) and measurements have been taken from occlusal surfaces in millimeters (mm) with the help of digital Vernier caliper.

**Abbreviations**—AMNH, American Museum of Natural History, New York; BP, Ban Pu exhibition center; BSM, Bayerische Staatssammlung für Palaontologie und historische Geologie, Munich; GSP, Geological Survey of Pakistan; PUPC, Punjab University Palaeontological Collection; TF, Thai–French expedition; UZ, Palaeontological collection in the Zoology Department, University of the Panjab, Lahore, Pakistan; Y-GSP, Yale Geological Survey of Pakistan expedition; B, Barnum Brown locality; dp/p,

deciduous upper/lower premolar; **M/m**, upper molar/lower molar; **L**, length; **W1, 2, 3...**, width of the first, second, third loph/lophid and so on; **DVD**, dorsoventral diameter; **DT**, transverse diameter.

#### SYSTEMATIC PALEONTOLOGY

ANIMALIA LINNAEUS, 1758

CHORDATA HAECKEL, 1874

MAMMALIA LINNAEUS, 1758

UNGULATA LINNAEUS, 1766

PAENUNGULATA SIMPSON, 1945

PROBOSCIDEA ILLIGER, 1811

GOMPHOTHERIIDAE HAY, 1922

CF. *PARATETRALOPHODON HASNOTENSIS* (OSBORN, 1929)

FIG. 3A–C

**Lectotype**—AMNH 19838, left M1–M2 (Osborn 1929: pp. 2, 3, fig. 3).

**Lectotype locality**—B103 (about 6.5 km to the north of Dhok Pathan).

**Diagnosis**—Tetralophodont bunodont elephantoid, skull with a straightened basicranium; high maxilla in the infraorbital process of the maxilla; orbits located directly above the anterior edge of the tooth series; premaxillary slightly divergent in front; regression of antorbital foramen upper; almost straight and slightly ventrally curved upper tusks; open angle of tooth eruption; crown of molars convex; functional development of M3 after wear of four lophs of M2; molars large and proportionally high; deposition of cement is significant; presence of posttrite central conules, more or less developed (Tassy 1983).

**Referred specimens**—PUPC 14/12, left p4 (Padhri); PUPC 15/219, partial left m?1 (Padhri); PUPC 15/249, partial right M3 (Hasnot).

**Description**—PUPC 14/12 is a partially broken semi-rectangular fourth premolar that is moderately worn, cracked and bilophodont but due to the presence of the thick posterior cingulid, it tends to be trilophodont. Anterior cingulid is small. In the first lophid, much of the dentine is missing and the pretrite cusp (protoconid) shows a small posterior pretrite central conule which is in contact with the median tubercle present in the first valley (Fig. 3A). The posttrite cusp (metaconid) of the first lophid is simple. In the second lophid, dentine and some part of the posterior wall of pretrite cusp (hypoconid) is broken and shows the trefoil structure. A small anterior pretrite central conule is in contact with the median tubercle present in the first valley. The posterior pretrite central conule is partially broken and confluent with the posterior cingulid. The posttrite cusp (entoconid) of this lophid is better preserved and has a



**Figure 3.** Siwalik proboscidean remains. **A–C.** cf. *Paratetralophodon hasnotensis*. **A.** Left lower fourth premolar (lp4?), PUPC 14/12, in occlusal view. **B.** Left lower first molar (lm?1), PUPC 15/219, in occlusal view. **C.** Right upper third molar (rM3), PUPC 15/249, in occlusal view. **D–I.** *Gomphotheres* gen. et sp. indet. **D.** Fragment of the left tusk, PUPC 17/120, in lateral (**D**) and cross-sectional (**E**) views. **F.** Tip fragment of a tusk, PUPC 17/121, in lateral view (**F**) and cross-sectional (**G**) views. **H.** Left upper first molar (lM1), PUPC 15/232, in occlusal view. **I.** Distal fragment of ?left molar, PUPC 15/07, in occlusal view. **J.** *Choerolophodon* sp. Deciduous left? lower fourth premolar (?ldp4), PUPC 15/232, in occlusal view. Scale bar=3 cm.

mesoconelet. The posterior cingulid is divided into two tubercles. Enamel is thick and heavy. Labial roots are partially preserved.

In PUPC 15/219, the last lophid and posterior cingulid are completely preserved, while the pretrite cusp of the penultimate lophid and valley are partially preserved (Fig. 3B). The penultimate valley has small tubercles at its base. The pretrite main cusp of the last lophid shows the trefoil structure, with the presence of anterior and posterior central conules, whereas the posttrite cusp has the mesoconelet only. The posterior cingulid is massive and can be distinguished into pretrite and posttrite half. The pretrite half has three tubercles arranged in a trefoil manner, while the posttrite half has two tubercles. The roots are preserved and the tooth enamel is thick.

In PUPC 15/249, the third, fourth and fifth loph and posterior cingulum are completely preserved, while the posterior wall of the second loph is only partially preserved. The pretrite cups of the third loph are better preserved and both the pretrite and posttrite half show clear trefoil structure. The pretrite trefoil is evident in the fourth loph and the posttrite cusp is divided into three portions (tubercles), anterior posttrite and central conule. The fifth loph has six tubercles and is least worn. The posterior cingulid is small but prominent and has six small tubercles. Cement deposition is abundant. A thick cingulid covers the base of the tooth lingually and the enamel is extremely thick (Fig. 3C).

**Remarks**—Among the specimens studied, the topography or constriction of the p4 (PUPC 14/12) is quite similar to the p4s of *Stegolophodon* sp. described by Buffetaut et al. (1988: fig. 1E, J) from Thailand, especially to BP01a (left P4), which was later included in the comprehensive study of the Thailand proboscideans by Thasod (2007: fig. 3.29E). However, both p4 specimens, PUPC 14/12 and BP01a, differ from each other in the construction of pretrite lophids by the presence of partially preserved trefoil structure in PUPC 14/12 and the breakage of this specimen hinders more detailed comparison. PUPC 14/12 also bears some morphological resemblance to the two p4s (HTA-41 and HTA-32) described by Sankhyan and Chavasseau (2018: fig. 4.3, 4.4). Sankhyan and Chavasseau (2018) assigned these as aff. *Stegolophodon* but also mentioned that, “The specimens regrouped under the name aff. *Stegolophodon* do not necessarily represent a single taxon.” Hence, they were not sure about their assignment. Therefore, PUPC 14/12 cannot be attributed to *Stegolophodon* with certainty on the basis of this resemblance. Furthermore, both p4s described by Sankhyan and Chavasseau (2018)

are distinct from PUPC 14/12 in the construction of the posterior cingulid and pretrite trefoil. The known p4 of the Siwalik trilophodont gomphotherid species *Gomphotherium browni* (Tassy 1983: plate vi, fig. 2) is clearly bilophodont and differs from PUPC 14/12 in its topography/construction of the posterior cingulid, which is very small in the previously reported specimen (BSM 3475 in Tassy 1983). However, in the development of the posterior cingulid (distal talonid), and judging from its recovery from the Dhok Pathan Formation PUPC 14/12, could represent *Paratetralophodon*. Also, PUPC 14/12 bears more resemblance with the p4 of *Paratetralophodon* sp. described and figured by Wang et al. (2017: fig. 7c) in general morphology and development of the posterior cingulid. However, the p4 of *Paratetralophodon* figured in Wang et al. (2017) has small mesoconelets on the second lophid unlike PUPC 14/12 is clear indication of distinction between the Siwalik and Chinese species. The p4 (PUPC 14/12), although partially broken, is clearly different from the both p4s (TF 6278 and TF 6279) described by Chavasseau et al. (2009; fig. 5H, I) in the development of pretrite trefoil and posterior cingulid, which are well-developed in PUPC 14/12. In both p4s attributed to *Stegolophodon* by Chavasseau et al. (2009), the pretrite trefoil is missing and posterior cingulid is very weak. On the other hand, the partial molar of PUPC 15/219 has pretrite trefoil in the last lophid, a character that excludes its association with *Stegolophodon*, which does not have this structure after the second or third lophid. Moreover, the pretrite half of the posterior cingulid is arranged in the trefoil manner. There is the possibility that PUPC 15/219 represents the distal fragment of an intermediate molar of *Paratetralophodon* judging from the mediobasal compression of lophids as well as its recovery from the Dhok Pathan Formation. The secondary trefoil is not developed in PUPC 15/219 but the posttrite central conule in distal lophid is frequently poorly developed in *Paratetralophodon*, and posterior central conule is frequently represented by subtle swelling on the distal and mesial flank of the posttrite half lophid, as can be seen PUPC 15/219 (Fig. 3B).

The large tooth size of PUPC 15/249 indicates that the specimen is tetralophodont and similar to the Middle Siwalik tetralophodonts (Tassy 1983). There are three tetralophodont species in the Middle Siwalik Subgroup *Pa. hasnotensis*, *Konobelodon* sp. and *St. stegodontoides* (Tassy 1983, Abbas 2018). Characters like the partial convexity of the occlusal surface, continuation of the pretrite trefoil to the fourth loph, presence of posttrite central conules that form a posttrite trefoil, lack of anancoidy, thick

enamel, abundant cement deposition and lack of extreme chevroning associate it with *Pa. hasnotensis*. However, it is slightly different from *Pa. hasnotensis* in that it does not have a complete and clear median sulcus, the fifth loph lacks pretrite central conules, but the latter conules are present in the lectotype of *Pa. hasnotensis* (AMNH 19838) chosen by Tassy (1983) as well as in the M3 of the skull (GSP 15032) described by Tassy (1983). In addition, the occlusal surface of the M3 is slightly less convex. It is worth noting that PUPC 15/249 is easily differentiated from *Stegolophodon* based on the trefoil structure in the fourth loph in both pretrite and posttrite halves, and from another Middle Siwalik tetralophodont, *Konobelodon* sp., in lacking extreme chevroning and the presence of trefoil structure in the fourth loph in both pretrite and posttrite halves (Schlesinger 1917: pl. 15; 1922: pl. 5, figs. 1, 2). PUPC 15/249 shows some resemblance to the M1 of *Tetralophodon longirostris* (Kaup, 1832) described and figured by Gasparik (2005: plate 1, fig. 5) and the M2 of *Konobelodon* sp. (*Mastodon grandincisivus* described and figured by Schlesinger 1917: plate 15, fig. 1). However, PUPC 15/249 clearly differs from both of these in having posttrite trefoil and according to Tassy (1983) this character has been observed in the M2 of GSP 15032 and the M3 of AMNH 19738. Although PUPC 15/249 shows a mixture of characters, it most closely resembles *Paratetralophodon*, comparing favorably to *Pa. hasnotensis*.

The strong development of the secondary trefoil present in PUPC 15/249 is also seen in *Paratetralophodon* but it is far weaker than that of PUPC 15/249. Among Siwalik proboscideans, *Anancus osborni* (Sarwar, 1977) specimens, UZ 67/256 and UZ 69/636, described by Sarwar (1977) is comparable to this specimen in showing strong development of the secondary trefoil. However, as noted by Tassy (1983), the generic placement of *A. osborni* is not appropriate because of the lack of anancoidy in this species. Therefore, the affinity of PUPC 15/249 remains unclear. There is also the possibility that PUPC 15/249 represents an unknown amebelodont (Hauro Saegusa personal communication, 2020).

#### GOMPHOTHERE GEN. ET SP. INDET.

##### FIG. 3D–I

**Referred specimens**—PUPC 17/120, a fragment of the left tusk (Dhok Jand); PUPC 17/121, apical fragment of tusk (Dhok Jand); PUPC 15/232, left M1 (Dhok Jand); PUPC 15/07, distal fragment of ?left molar (Chabbar Syedan).

**Description**—PUPC 17/120 represents the posterior fragment of an extremely weathered tusk cracked by

calcium carbonate with the outer layers partially missing (Fig. 3D, E). The tusk gradually bends downwards i.e., towards the ventral side. A small patch of enamel band is preserved at its lateral side. The Schreger line and angles are acute. Dentine is concentric and a thick layer of cement is present between the layers. The cross section of the tusk at the base is subcircular and it becomes gradually oval towards the tip (Fig. 3E). Its preserved length is 173.08 mm, DVD is 49.61 mm and DT is 55.18 mm. PUPC 17/121 is an apical fragment of a tusk (Fig. 3F, G). It is also extremely weathered and with calcium carbonate. The cross section is regularly oval (Fig. 3G). Its preserved length is 62.62 mm.

PUPC 15/232 is a trilophodont, bunodont, partially broken, cracked in the center and extremely worn molar (Fig. 3H). Due to extreme wear, the valleys are not visible in the center, confluent at the lingual side and partially preserved at the labial side. The preserved portion of anterior cingulum is thick and heavy. The enamel is thick and the roots are preserved, the posterior united into one.

PUPC 15/07 represents a partially preserved premolar in which penultimate lophid and posterior cingulid are completely and third lophid is partially preserved. The preserved portion is completely unworn and has an abundant quantity of cement (Fig. 3I).

**Remarks**—The subcircular to oval cross section, the downwards curvature of the tusk, presence of non-twisted enamel band at lateral side of the tusk, bunodont main cusps and the heavy enamel in the molar closely associate this specimen with the family Gomphotheriidae, thus excluding both the Amebelodontidae and Stegodontidae (Fig. 3D–G). PUPC 15/232, an upper molar, lacks a tetralophodont grade, therefore excluding these from stegodontids, konobelodonts and tetralophodont gomphotheres. The presence of the non-twisted lateral enamel band on the upper tusks and trilophodonty are characters typically found in the gomphotheres (Tassy 1983, 1985, 2013, 2014). *Gomphotherium browni* is the only trilophodont species of *Gomphotherium* reported from the Siwaliks. The upper tusk of this species is characterized by a ventral concavity, straightness in ventral/dorsal view, subcircular to oval cross-section and non-twisted lateral enamel band (Tassy 1983). This species differs from the contemporaneous amebelodont species, *Protanancus chinjiensis* (Pilgrim, 1913), in its less massive build, weak lateral curvature, non-twisted enamel band, and piriform cross section of tusks. The upper tusk, PUPC 17/120, also shows the following similar pattern of characteristics: tusk is rectilinear and regularly concave downward, and the non-twisted enamel band is situated

on the lateral face but the groove is missing owing to breakage (Fig. 3D). The described M1 (PUPC 15/232) is trilophodont and within the size range of *G. browni* (Table 1), but differs from other trilophodont species, e.g., *Pr. chinjiensis*, in its wear pattern because the loph borders in the *Protanancus* are more slanting due to prominent chevroning. Although the above-mentioned characters indicate the affinity of the referred specimens to *G. browni*, the fragmentary nature of the material is here referred only to Gomphothere gen. et sp. indet.

CHOEROLOPHODONTIDAE GHEERBRANT & TASSY, 2009

CHOEROLOPHODON SCHLESINGER, 1917

CHOEROLOPHODON SP.

FIG. 3I

**Referred specimen**—PUPC 15/252, an isolated partially broken? left dp4 (Dhok Pathan).

**Description and remarks**—PUPC 15/252 is an extremely worn dp4 that is partially broken. Much of the anterior cingulid and anterior lophid are missing (Fig. 3J). The dentine is well-exposed and only enamel of the lophid borders is preserved. The preserved enamel is extremely choerodont and ptychodont. Cement is also present.

Extreme ptychodonty and choerolophodonty suggest PUPC 15/252 is assignable to *Choerolophodon* (Tassy 1983, 1985, Sanders and Miller 2002, Abbas et al. 2018). On the other hand, the extreme wear also makes it

difficult to attribute the specimen to the dominant Middle Siwalik choerolophodont species, *Choerolophodon corrugatus* with certainty because this species is closely related to the European species, *C. pentelici* (Gaudry and Lartet, 1856), not the African species *C. kisumuenensis* (MacInnes, 1942). Both these European and African species differ in the choerodonty, ptychodonty, and cement deposition. Hence, the specimen is here referred to *Choerolophodon* sp.

DISCUSSION

Middle to late Miocene proboscideans from the Siwalik Group include *Gomphotherium browni*, *Choerolophodon corrugatus*, *Zygalophodon metachinjiensis*, *Konobelodon* sp., *Protanancus chinjiensis*, *Paratetralophodon hasnotensis*, *Stegolophodon latidens* and *St. stegodontoides* (Osborn 1926, 1929, 1936, 1942, Tassy 1983, Abbas 2018, Abbas et al. 2018). *Gomphotherium browni*, *C. corrugatus*, *Z. metachinjiensis* and *Pr. chinjiensis* share trilophodont grade, while *Konobelodon* sp., *Pa. hasnotensis*, *St. latidens* and *St. stegodontoides* share tetralophodont grade (Tobien 1972, 1976, Tassy 1983, Abbas 2018, Abbas et al. 2018). *Zygalophodon metachinjiensis* and *G. browni* are the rarest Siwalik taxa (Tassy 1983), while the others are recovered frequently.

Among the species described here, the remains of Gomphothere gen. et sp. indet. closely resembles the Lower Siwalik species, *G. browni*. Tassy (1983) noted that no

**Table 1.** Comparative measurements (in mm) of cheek teeth of cf. *Paratetralophodon hasnotensis*, *Choerolophodon* sp. and Gomphothere gen. et sp. indet. Abbreviations: L=tooth length; W=loph/lophid width; lp=left lower premolar; lm=left lower molar; rM=right upper molar; lM=left upper molar; rM=right upper molar; rdp=right lower deciduous premolar; \*=studied specimens; \*\*=measurements of preserved segment; - =missing data

Taxon	Reference	Specimen number	Element	L	W1	W2	W3	W4	W5	W6
cf. <i>Paratetralophodon hasnotensis</i>		PUPC 14/12*	lp4	54.71	36.32	46.82	46.49	-	-	-
		PUPC 15/219*	lm?1	54.99**	62.93	50.23	-	-	-	-
		PUPC 15/249*	rM3	117.87**	-	-	81.62	73.93	56.12	28.41
<i>Paratetralophodon hasnotensis</i>	Tassy (1983)	GSP 15032	lM3	210.00	92.80	95.50	86.00	-	-	-
		GSP 15032	rM3	211.50	92.30	95.1	-	80.50	69.60	-
<i>Choerolophodon</i> sp.		PUPC 15/252*	?ldp4	67.40	45.50	33.2	25.50**	-	-	-
<i>Choerolophodon corrugatus</i>	Tassy (1983)	GSP 11362	rdp4	71.90	32.00	37.70	40.00	-	-	-
		AM 19638d	rdp4	79.20	35.10	40.10	43.00**	54.30**	-	-
Gomphothere gen. et sp. Indet.		PUPC 15/232*	lM1	96.06	66.08	69.65	71.92	-	-	-
		PUPC 15/07*	lm?	63.84**	61.84	55.44	40.82	-	-	-

new remains of *G. browni* had been discovered during the Y-GSP expeditions from 1973 to 1982 and so his descriptions were of previously collected unpublished specimens in the Yale Peabody Museum, American Museum of Natural History, and the Bayerische Staatssammlung für Palaontologie und historische Geologie. *Gomphotherium browni* presents a combination of primitive and derived characters. The upper tusk and the construction of the loph reflect primitive characters, whereas the brevistre symphysis of the mandible, the posterior cingulum in m2, the pronounced brachydonty and the enamel thickening are derived characters. *Gomphotherium browni* appears to occupy a primitive position among the trilophodont bunodont mastodons (Tassy 1983). The holotype (AMNH 19417) is characterized by bunodonty, rounded main cusps, heavy enamel and comparatively low crown. Among these, the primitive characters include the heavy enamel and low crown (Tassy 1983, Shoshani and Tassy 1996, Sanders et al. 2004) and these characters differentiate *G. browni* from other representatives of this genus.

Chavasseau et al. (2009) more recently described specimens of *G. browni* from Thailand that included the following elements: four upper and two lower tusks, an upper premolar, four upper molars, and a mandible fragment with alveoli of m2 and well-preserved m3. Based on their morphology, the four upper molars belong to two different species: one belongs to a primitive species, the others are assignable to a more advanced group like *G. browni*. However, one should notice that these four molars attributed to *G. browni* by Chavasseau et al. (2009) are smaller than those of known respective specimens of *G. browni* and are more in the size range of *G. cooperi* (Osborn, 1932)/*G. annectens* (Matsumoto, 1925).

*Paratetralophodon hasnotensis* was first described by Osborn (1929) as *Serridentinus hasnotensis* based on dental remains from different sites of the Hasnot and Dhok Pathan regions. This species is based on three cotypes (no holotype was designated) AMNH 19948, AMNH 19738 and AMNH 19838. Later, AMNH 19838 was transferred to *Tetralophodon falconeri* (Lydekker, 1877) by Osborn in 1936. Tassy (1983) in revisiting the Siwalik proboscideans (gomphotherids, choerolophodonts, amebelodonts, mammutids, and stegodontids) stated that the other dental fragments referred to *Se. hasnotensis* were recognizable as *Pa. hasnotensis* and chose the AMNH 19838 (M1-M2) as the lectotype. However, he referred a trilophodont very worn m2 (AMNH 19747) to Mammutidae? indet., which was previously referred to *Se. hasnotensis*. He also referred a juvenile skull (AMNH 19686) from the

Dhok Pathan Formation to *Pa. hasnotensis*, which was previously assigned to *T. punjabiensis* (Lydekker, 1886) by Osborn (1936). Tobien (1972) referred AMNH 19448 and AMNH 19738, two of the three cotypes of *Se. hasnotensis*, to *Tetralophodon* without any specific assignment, and by doing so he brought these remains closer to *T. punjabiensis* (Lydekker, 1886). Lastly, the subspecies *T. punjabiensis progressus* was erected by Sarwar (1977) based on a left m3 (UZ 69/752) from the Tatrot Formation (Upper Siwalik Subgroup) and a new species, *Anancus osborni* Sarwar (1977), are now considered by Tassy (1983) to belong to *Pa. hasnotensis*. However, based on its size, the M3 of AMNH 19686 is within the upper limit of the range of variation of the M3 of *T. longirostris* in both length and width (Tassy 1983).

Wang et al. (2017) reported *Paratetralophodon* sp. from the late Miocene Shuijiazui locality, Lantian region, and ?*Pa. exoletus* (Hopwood, 1935) from Sangjialianggou of Jijiagou, Baode region, China. According to them, “the Lantian specimens are distinguished from *Pa. hasnotensis* in lacking posterior pretrite central conule of the third loph of the intermediate cheek teeth.” Our specimen does show a rudimentary posterior pretrite central conule in the fourth loph. Siwalik *Paratetralophodon* is the least studied and somewhat controversial taxon. Tassy (1983) described a skull of *Pa. hasnotensis* with some isolated dental remains, including the lectotype assigned by him and the two skulls, AMNH 19686 and GSP 15032. He assumed that they were all *Pa. hasnotensis* since no two species have similar tetralophodont M2s. However, he did note some differences among these specimens and the possibility that the material may represent two species. There are two tetralophodont species in the Middle Siwaliks, *Pa. hasnotensis* (Tassy 1983) and *Konobelodon* sp. (Abbas 2018). Both are known mainly from the Dhok Pathan Formation (late Miocene) of the Middle Siwalik Subgroup. *Paratetralophodon hasnotensis* is well known from the two skulls and isolated molars, while *Konobelodon* sp. is currently based on the lower tusks with the dentinal tubules in the dentine (Tassy 1983, Abbas 2018). The lower tusks of *Pa. hasnotensis* are not known. The molars of these two taxa as compared here are not that different. It is probable that both these species represent the same species once the lower tusks of *Pa. hasnotensis* are known.

*Choerolophodon corrugatus*, family Choerolophodontidae, is a dominant Middle Siwalik proboscidean species. This species has an extensive list of synonymies (see Tassy 1983, Abbas et al. 2018). Originally, the species was named *Mastodon pandionis* by Lydekker (1884),

later synonymized with *T. corrugatus* by Pilgrim (1913), then referred to *M. (Choerolophodon) corrugatus* by Schlesinger (1917), and most recently ascribed to *C. corrugatus* by Tassy (1983). Although this species is close to the European species *C. pentelici*, some dental remains present in the Dr. Abu Bakr Fossil Display and Research Center, Department of Zoology, University of the Punjab, Lahore and described by Tassy (1983), show morphology of *C. kisumuensis* (personal observations), which is somewhat more advanced. There is every likelihood that more than one species is present and Siwalik choerolophodonts need a revision.

Study of the published literature, formally described specimens and the wealth of proboscidean remains in the Dr. Abu Bakr Fossil Display and Research Centre at Punjab University, indicate that the Siwalik proboscideans were diverse with at least ten species presently known that range from middle Miocene to early Pliocene. We have noted considerable morphological variations in the Siwalik proboscidean dental material belonging to gomphotherids, amebelodonts, mammutids, and choerolophodonts, described elsewhere and housed in the Dr. Abu Bakr Fossil Display and Research Centre, Department of Zoology, University of the Punjab, Lahore, Pakistan. These variations are beyond those observed in the species denoting that previously allocated material to a single species belong to more than one species, as it has been discussed in the above paragraphs. There is every likelihood that the Siwalik gomphotherids, choerolophodonts, amebelodonts, mammutids, and stegodontids represent more species that may include some of the European, Southeast Asian, African and American taxa suggesting the systematic study and revision of the Siwalik proboscideans is warranted at this time.

#### CONCLUSIONS

The diversity of Siwalik proboscideans is great and represented by the tri- and tetralophodont grades. The trilophodont grade is found in the middle Miocene (Lower Siwalik Subgroup), while the tetralophodont grade extends into the early Pliocene (Upper Siwalik Subgroup). Remains of cf. *Paratetralophodon hasnotensis* are rare and have been described in this article after a gap of nearly 40 years. The Gomphotheres gen. et sp. indet. may represent a new species but the samples found to date are fragmentary. More work is needed in revising the Siwalik proboscideans.

#### ACKNOWLEDGEMENTS

We are greatly thankful to Dr. Shi-Qi Wang and Dr.

Hauro Saegusa for their comments on the material and improvements to the manuscript. The authors are also grateful to hosts and guides for their help with the field work. We are also thankful to the editors of the journal for the corrections kindly made by them and the anonymous reviewers whose comments greatly improved the manuscript.

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