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The first specimen of *Deinotherium indicum* (Mammalia, Proboscidea, Deinotheriidae) from the late Miocene of Kutch, India

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Abstract.—Deinotheriidae Bonaparte, 1845 is a family of browsing proboscideans that were widespread in the Old World during the Neogene. From Miocene deposits in the Indian subcontinent, deinotheres are known largely from dental remains. Both large and small species have been described from the region. Previously, only small deinothere species have been identified from Kutch in western India. In the fossiliferous Tapar beds in Kutch, dental remains have been referred to the small species *Deinotherium sindiense* Lydekker, 1880, but the specimens are too fragmentary to be systematically diagnostic. Here, we describe a large p4 of a deinothere from the Tapar beds and demonstrate that it is morphologically most similar to *Deinotherium indicum* Falconer, 1845, a large species of deinothere, thereby confirming the identity of deinotheres at Tapar. *Deinotherium indicum* from Tapar is larger than other deinotheres identified from Kutch and is the first occurrence of the species in the region. This new specimen helps constrain the age of the Tapar beds to the Tortonian and increases the biogeographic range of this species—hitherto only known from two localities on the subcontinent. This specimen also highlights the morphological diversity of South Asian deinothere p4s and allows us to reassess dental apomorphies used to delimit Indian deinothere species. Lastly, we argue that by the late Miocene, small deinotheres in Kutch were replaced by the large *Deinotherium indicum*.

Introduction

Deinotheriidae is a family of browsing graviportal proboscideans with brachydont, bilophodont cheek teeth (except for trilophodont deciduous fourth premolars and first molars), and downturned lower tusks (Harris, 1978; Sanders et al., 2010). Deinotheres originated in Africa in the late Oligocene (Sanders et al., 2004) and subsequently dispersed into Eurasia by the early Miocene (Tassy, 1989; Sanders et al., 2010; Antoine et al., 2013). Very little morphological change occurred during their evolutionary history except for an increase in body size (Gräf, 1957; Harris, 1973, 1976; Tobien, 1988; Huttunen, 2002b; Poulakakis et al., 2005; Pickford and Pourabrishami, 2013). Three genera are widely considered valid: the primitive and diminutive *Chilgatherium* Sanders, Kappelman, and Rasmussen, 2004, and the larger *Prodeinotherium* Éhik, 1930 and *Deinotherium* Kaup, 1829 (Sanders et al., 2010). *Deinotherium* is stratigraphically younger (and generally larger) than *Prodeinotherium* (Harris, 1978), with some species, e.g., *Deinotherium giganteum* Kaup, 1829, exceeding 10 tons in weight (Larramendi, 2016). There are thought to be three valid species of *Deinotherium*: *Deinotherium giganteum* from western and central Eurasia, *Deinotherium indicum* Falconer, 1845 from the Indian subcontinent, and *Deinotherium bozasi* Arambourg, 1934 from East Africa (Sahni and Tripathi, 1957; Harris, 1973; Huttunen, 2002b; but see Pickford and Pourabrishami, 2013, for an alternative taxonomic scheme). *Deinotherium bozasi*, the last known species, went extinct in the early Pleistocene (ca. 1 Ma).

South Asian deinotheres are known largely from isolated teeth in lower to upper Miocene deposits in the Siwalik Group of Indo-Pakistan, the Manchars of Sind in eastern Pakistan, the Gaj Series in the Bugti Hills of western Pakistan, the Dharmsala Group of northern India, Kutch and Perim (Piram) Island in western India, and in the Dang Valley in Nepal (Falconer, 1845, 1868; Lydekker, 1876, 1880; Pilgrim, 1912, 1917; Forster-Cooper, 1922; Palmer, 1924; Sahni and Tripathi, 1957; Dehm, 1963; Khan et al., 1971; Sahni and Mishra, 1975; West et al., 1978; Barry et al., 1982; Sahni and Gupta, 1982; Raza et al., 1984; Vasishat, 1985; Tiwari et al., 2006; Bhandari et al., 2010; Sankhyan and Sharma, 2014; Kapur et al., 2019). The taxonomic validity of the large species, *Deinotherium indicum* from the Tortonian of Perim Island in the Gulf of Cambay and Haritalyangar in the Siwalik Hills, is generally accepted. However, several species have been described from smaller teeth recovered from uncertain stratigraphic contexts in the Bugti Hills, Siwalik Hill, Potwar Plateau, and the Manchars: *Antoletherium* of Falconer, 1868, *Prodeinotherium pentapotamiae* Lydekker, 1876, *Deinotherium sindiense* Lydekker, 1880, *Deinotherium naricum* Pilgrim, 1908, and *Deinotherium orlovii*

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Sahni and Tripathi, 1957; the validity of these taxa is still debated (Lydekker, 1880; Gräf, 1957; Sahni and Tripathi, 1957; Harris, 1973; Huttunen, 2002b; Pickford and Pourabrishami, 2013; Bhandari et al., 2015).

We here report the first occurrence of *Deinotherium indicum* from the Tapar beds in Kutch, western India. Deinothere remains are rare in Kutch. Lydekker (1876) described two specimens collected by Mr. F. Fedden (Wynne, 1872) from the village of Sambera (Sambda)—an incomplete right M1 (GSI A3) and a right M2 (GSI A10), as *Prodeinotherium pentapotamiae* based on their small size. Lydekker (1885) also reported a third specimen of *P. pentapotamiae* from Kutch—an incomplete left M1 (GSI A4). Since these early discoveries, the only other deinothere specimens from Kutch are a proximal fragment of a humerus from Sambera (Sahni and Mishra, 1975) and dental remains referred to *Deinotherium sindiense* from Tapar (Bhandari et al., 2015) and Palasava (Kapur et al., 2019). This new find of *Deinotherium indicum* from Kutch expands the geographic distribution of this species, hitherto only known from two or three localities. This specimen also increases our understanding of the variation in dental morphology of South Asian deinotheres, thereby allowing for a reassessment of previously defined dental apomorphies associated with this group. It also clarifies the taxonomy of Neogene deinotheres from Kutch and helps constrain the age of the Tapar beds to the late Miocene.

Geological setting

Stratigraphic information.—The Neogene deposits from Kutch have been classified as the Khari Nadi, Chhasra, and Sandhan formations (Biswas, 1992; Catuneanu and Dave, 2017). The Khari Nadi and Chhasra formations (early Miocene) have been interpreted to be shallow-marine environments, whereas the Sandhan Formation (middle Miocene to Pliocene) is thought to represent a more terrestrial coastal setting (Catuneanu and Dave, 2017). The Tapar beds of the Kutch Basin in western India, known for their rich vertebrate fauna, consist of medium- to coarse-grained sandstones, siltstones, and mudstones with intermittent conglomerate beds (Fig. 1.3) and have been considered to form part of the Khari Nadi Formation in the past (Bhandari et al., 2010, 2015, 2018; Patnaik et al., 2014). However, this is problematic because the Tapar beds are lithologically different from the Khari Nadi Formation. Unlike the latter, the Tapar sequence has abundant coarse-grained sandstone beds ingrained with pebbly clasts, calcareous nodules, agate pebbles, mudclasts, and conglomerates. These beds bear the greatest similarity to the Sandhan Formation (Biswas, 1992; Catuneanu and Dave, 2017) and likely represent a fluvial regime. The specimen of *Deinotherium indicum* described herein was eroding from a layer of pseudoconglomerate sandwiched between layers of micaceous sandstone in the Tapar beds (Fig 1.3). The pseudoconglomerate consists of mud clasts and soil concretions derived from paleosol horizons and lacks the typical pebbles and cobbles of a true conglomerate. This pseudoconglomerate is equivalent to the fossiliferous conglomerate described by Bhandari et al. (2018).

Locality information.—Specimen PU KT-1 was found at Tapar, Kutch (23°15′12.28″N, 70°08′46.20″E), in the state of Gujarat, western India (Fig. 1.2).

Materials and methods

Specimen PU KT-1 is a right p4. It was collected in the Tapar beds by NPS, RP, KMS, NAS and YPS and cleaned with brushes. The specimen is now accessioned in the paleontological collections of the Department of Geology, Panjab University, Chandigarh. Measurements were taken using digital calipers.

Repositories and institutional abbreviations.—BGR/LBEG = Bundesanstalt für Geowissenschaften und Rohstoffe/ Landesamt für Bergbau Energie und Geologie Hannover, Hannover, Germany; GSI = Geological Survey of India, Kolkata, India; IMM = Nei Mongol Museum, Hohhot, China; NHMUK = The Natural History Museum, London, UK; PU = Panjab University, Chandigarh, India; SNSB-BSPG = Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany. Upper case letters P and M refer to upper premolars and molars, whereas lower case letters p and m refer to mandibular premolars and molars, respectively; numbers following these letters indicate tooth position.

Systematic paleontology

Proboscidea Illiger, 1811
Deinotheroidea Bonaparte, 1845
Deinotheriidae Bonaparte, 1845
Deinotheriinae Bonaparte, 1845
Deinotherium Kaup, 1829

Type species.—Deinotherium giganteum Kaup, 1829.

Other species.—Deinotherium indicum Falconer, 1845 and *Deinotherium bozasi* Arambourg, 1934.

Diagnosis.—Large deinotheres. Dental formulae as for the family; tendency for the development of subsidiary styles on P3 and P4, and for simplification of the postmetaloph ornamentation of M2 and M3 when compared to *Prodeinotherium*. The skull rostrum not parallel to the mandibular symphysis and nearly horizontally aligned; rostral trough and external nares wide; preorbital swelling sited anteriorly on the rostrum; skull roof short and narrow at the temporal fossae; occiput sloping gently posteriorly; occipital condyles elevated above the level of the external auditory meatus; paroccipital process very elongate. Postcranial skeleton with cursorial modifications to graviportal structure; scapular spine reduced with no acromion or metacromion; carpals and tarsals narrow with dolichopodous metapodials exhibiting functional tetradactyly. (Modified from Harris, 1973.)

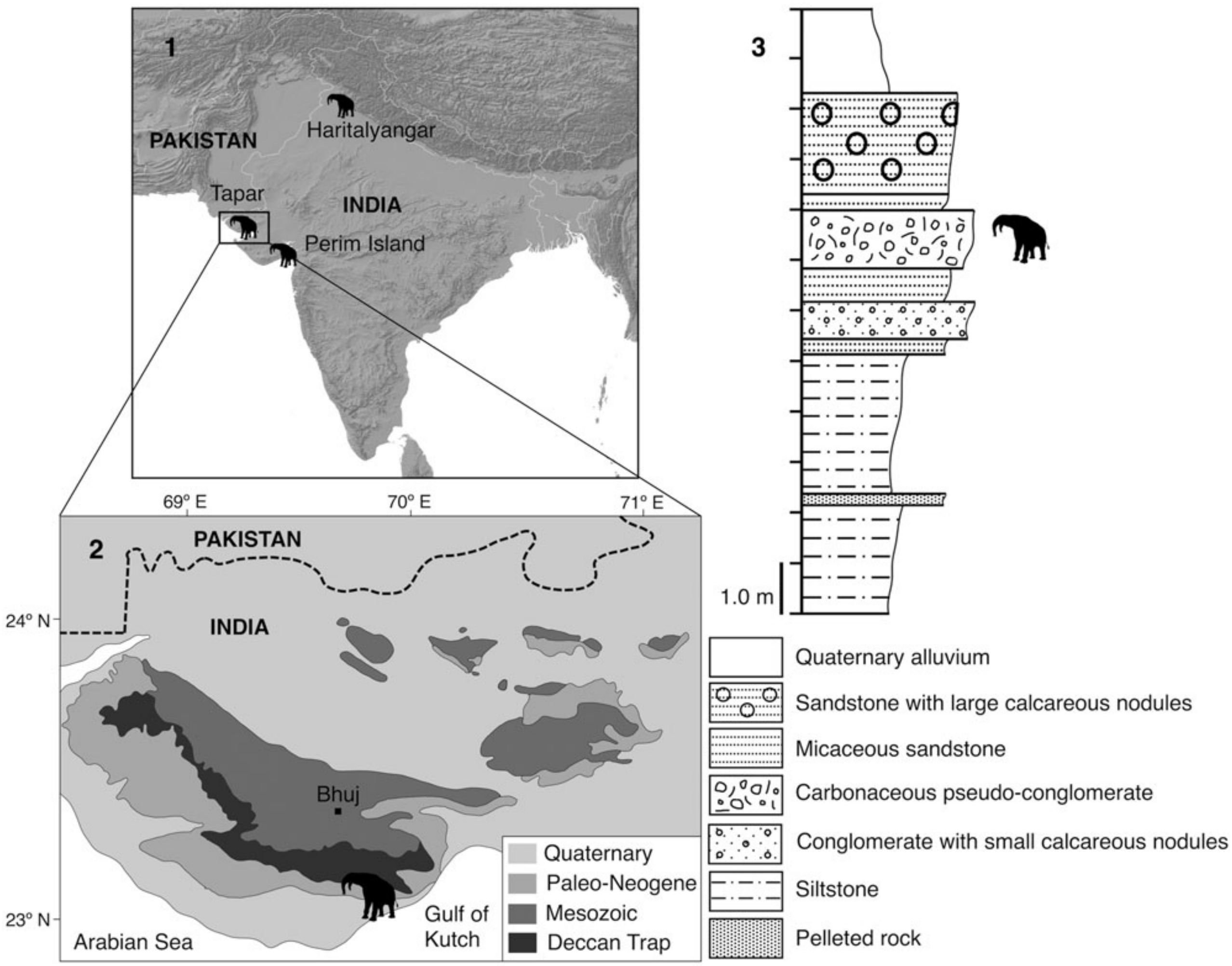

Figure 1. Geographic distribution of *Deinotherium indicum* in the Indian subcontinent: (**1**) locator map showing the three major localities where *D. indicum* was found; (**2**) geological map of Kutch; (**3**) stratigraphic column of the Tapar locality.

Deinotherium indicum Falconer, 1845
Figures 2, 3.1–3.4

1845 *Dinotherium indicum* Falconer, p. 360, pl. 14, figs. 1, 1a.
1868 *Dinotherium perimense* Falconer, p. 415.
1936 *Deinotherium indicum*; Osborn, p. 94 (emended spelling).

Holotype.—Hypolophid and posterior cingulum of a left m2 (NHMUK PV OR 14756) from a ferruginous conglomerate along the shoreline, Perim (Piram) Island, Gulf of Cambay, Gujrat, India (Falconer, 1845, pl. 14, figs. 1, 1a).

Diagnosis.—Very large deinothere with thick enamel on dentition. Mandible deep and wide, with a slightly convex labial surface, and a more circular cross section toward the posterior; m2 with transverse valley between the protolophid and metalophid and well-developed talonid; m3 bounded by tubercles on either side; m1 with tubercle on the buccal surface at the opening of the transverse valley. (Modified from Sahni and Tripathi, 1957.)

Occurrence.—Tortonian (late Miocene) of Perim Island in the Gulf of Cambay, Gujarat, India (21°37′N, 72°22′30″E), Haritalyangar in the state of Himachal Pradesh, India (31° 32′N, 76°38′E), and Tapar in Kutch, India (23°15′12.28″N, 70°08′46.20″E) (Fig. 1.1).

Description.—Specimen PU KT-1 is a slightly worn isolated right p4 from a large deinothere (Fig. 2). The tooth is subrectangular in occlusal view and bilophodont. The anteroposterior length is 76.0 mm, the transverse diameter of the metalophid is 55.0 mm, and that of the hypolophid is 61.0 mm. Maximum crown height is 51.0 mm. The posterior width is greater than the anterior. The enamel is weathered and cracked over the entire occlusal surface, but the four main cusps (protoconid, hypoconid, metaconid, and entoconid) are well defined. The metalophid and hypolophid are anteriorly concave with the latter being slightly longer and narrower than the former. These two lophids are connected by the post-protocristid, which descends into the transverse valley and joins the pre-hypocristid. The longitudinal ridge formed by the post-protocristid and pre-hypocristid is buccally positioned so that the transverse valley is wide and deep and

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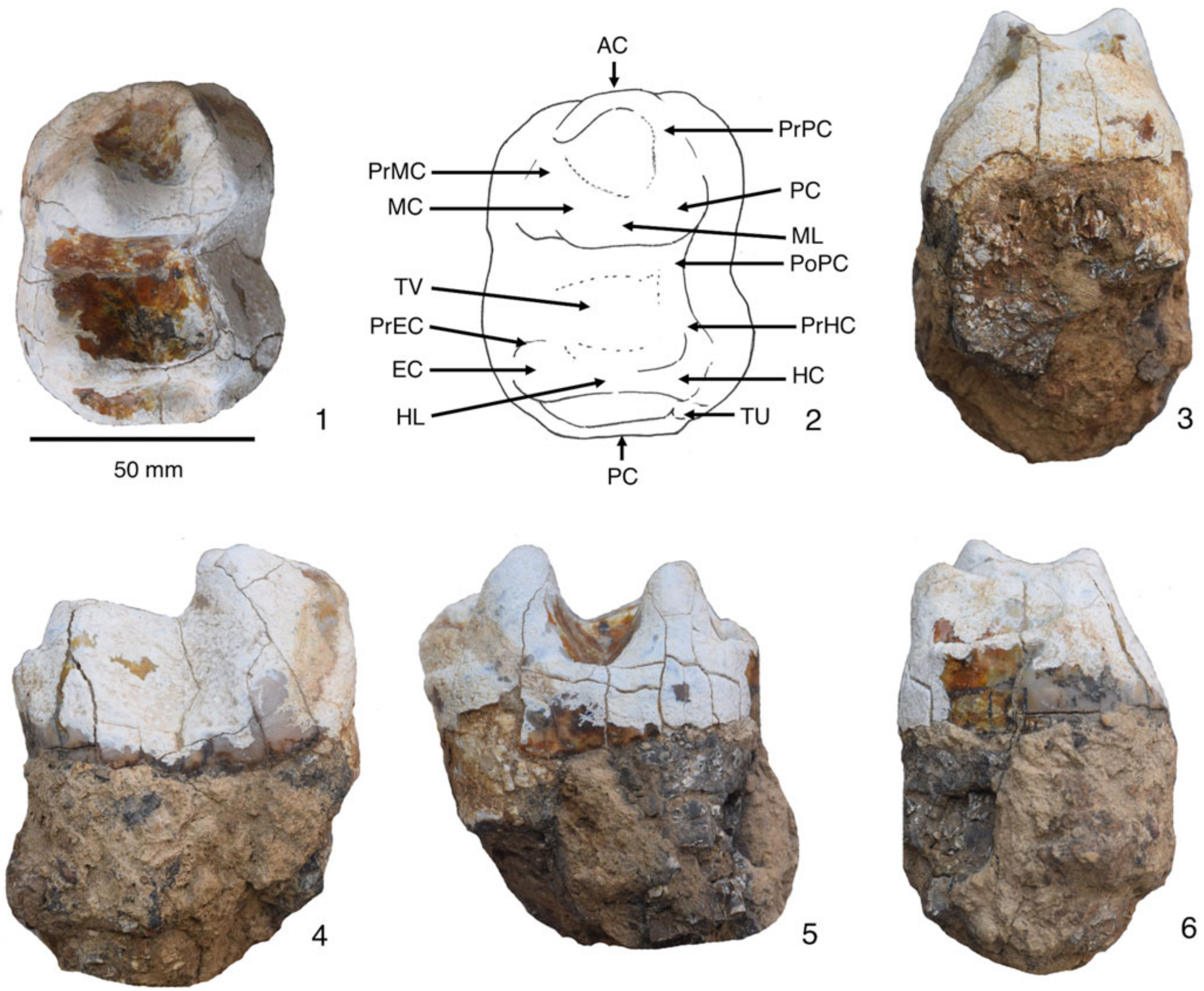

Figure 2. *Deinotherium indicum*, PU KT-1, right p4: (**1**) occlusal view; (**2**) line drawing of the occlusal view; (**3**) anterior view; (**4**) buccal view; (**5**) lingual view; (**6**) posterior view. AC = anterior cingulum; EC = entoconid; HC = hypoconid; HL = hypolophid; MC = metaconid; ML = metalophid; PC = protoconid; PoPC = post-protocristid; PrEC = pre-entocristid; PrHC = pre-hypocristid; PrMC = pre-metacristid; PrPC = pre-protocristid; TU = tubercle; TV = transverse valley.

covers most of the mesiolingual surface. The transverse valley is blocked completely on the buccal side and open on the lingual side. The pre-entocristid is low and descends toward the transverse valley. A very small tubercle is present on the posterobuccal surface. The cingulum is absent on both buccal and lingual sides, but a well-developed but weakly crenulated cingulum is present at the anterior edge. The posterior cingulum is also well developed, weakly crenulated, and fused with a post-hypocristid.

Remarks.—The present specimen is the largest deinothere tooth known from Kutch, much larger than the teeth described by Lydekker (1880) and Kapur et al. (2019) from this region. Complete and unworn lower dentition from South Asian deinotheres are rare. The hypodigm of *Deinotherium indicum* from Perim Island includes a mandibular fragment with p3–m3, but with broken crowns (NHMUK PV OR 14739a; Falconer, 1868, pl. 33, fig 5). The incomplete nature of the lower dentition from the Perim Island specimen prevents a morphological comparison to PU KT-1, but the p4s are very similar in size (Table 1). Sahni and Tripathi (1957) described three additional p4s referred to *Deinotherium indicum*. Two p4s (GSI A585, A586) from Haritalyangar are well worn and therefore unsuitable for a morphological comparison; they are however similar in size to PU KT-1 (Fig. 3.2, 3.3, Table 1). The third p4 (GSI A596) is from an unknown locality, but bears many morphological features in common with PU KT-1 including the longitudinal ridge being more buccally positioned resulting in a wide and deep transverse valley, and a well-developed anterior cingulum with a strong C-shaped extension (Fig. 3.1, 3.4). The main difference between these two specimens is in the placement of the tubercle. Sahni and Tripathi (1957) reported that the tubercle on GSI A596 is placed next to the longitudinal ridge on the buccal side (they erroneously listed this specimen as a left p4 when in fact it is a right p4). In contrast, the tubercle on PU KT-1 is located posterobucally near the posterior cingulum (Fig. 2).

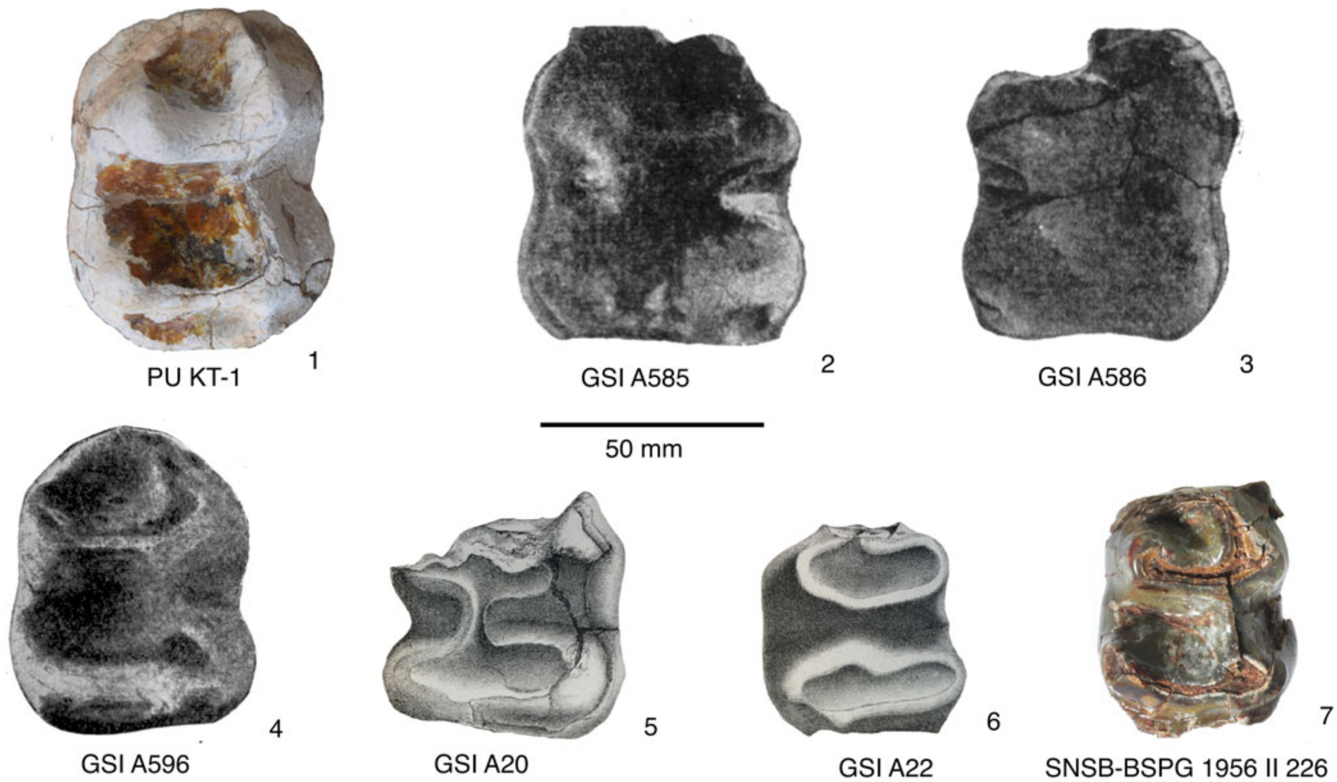

Figure 3. Deinothere p4s from the Indian subcontinent: (**1**) PU KT-1, *Deinotherium indicum*, right p4; (**2**) GSI A585, *Deinotherium indicum*, right p4; (**3**) GSI A586, *Deinotherium indicum*, left p4; (**4**) GSI A596, *Deinotherium indicum*, right p4; (**5**) GSI A20, *Antoletherium*, left p4; (**6**) GSI A22, *Prodeinotherium pentapotamiae*, left p4; (**7**) SNSB-BSPG 1956 II 226, *P. pentapotamiae*, right p4. Figures 3.2, 3.3, and 3.4 modified from Sahni and Tripathi (1957); Figures 3.5 and 3.6 modified from Lydekker (1880).

Three smaller p4s have also been reported from the Indian subcontinent (Fig. 3.5–3.7, Table 1). Two have been referred to *Prodeinotherium pentapotamiae* (SNSB-BSPG 1956 II 226 and GSI A22) and the third belongs to the specimen of *Antoletherium* (GSI A20). The specimen of *Antoletherium* is a left mandibular fragment with p4–m2 (Lydekker, 1880, pl. 29, figs. 2, 3). The anterobuccal surface of the p4 is damaged, therefore we cannot comment on the structure of the cingulum (Fig. 3.5). However, much like PU KT-1, the tooth is subrectangular with the hypolophid being longer than the metalophid. The longitudinal ridge, in contrast, although positioned somewhat buccally, bends mesially, in effect dividing the transverse valley into two halves. Sahni and Tripathi (1957) reported a tubercle on the buccal surface formed in the valley between the metalophid and hypolophid, but this structure is not clear in Lydekker's (1880, pl. 29, figs. 2, 3) illustration (Fig. 3.5). This tooth is also considerably smaller than PU KT-1 (Table 1). The morphology seen on the p4 of *Antoletherium* is reflected in the left p4 (GSI A22) referred to *P. pentapotamiae* by Lydekker (1880; Fig. 3.6) and a right p4 (SNSB-BSPG 1956 II 226) described by Dehm (1963) from Cheskewala, 14 km SW of Chinji Village (Fig. 3.7). On both of these teeth, the longitudinal ridge appears to bisect the transverse valley into two halves, in contrast to PU KT-1. The p4 of *Antoletherium* (GSI A20) and of *P. pentapotamiae* (GSI A22) each lack a posterior cingulum, and GSI A22 lacks any dental tubercles. Both of these teeth are also smaller than PU KT-1 (Table 1). SNSB-BSPG 1956 II 226 and GSI A22 both lack a strong anterior cingulum (Fig. 3.6, 3.7).

Table 1. A comparison of deinothere p4s from Asia. Lp4 = left p4; Rp4 = right p4; * = incomplete specimen; + = measurement was greater on the complete tooth. All measurements in mm.

Specimen Number	Species	Locality	Tooth	Length	Width
NHMUK PV OR 14739a*	*Deinotherium indicum*	Perim	Lp4	73.7	66
GSI A 585*	*Deinotherium indicum*	Haritalyangar	Rp4	70+	61
GSI A 586*	*Deinotherium indicum*	Haritalyangar	Lp4	70+	61
GSI A 596	*Deinotherium indicum*	Unknown	Rp4	68	55
PU KT-1	*Deinotherium indicum*	Tapar	Rp4	76	60
SNSB-BSPG 1956 II 226	*Prodeinotherium pentapotamiae*	Cheskewala	Rp4	56	45.8
GSI A22	*Prodeinotherium pentapotamiae*	Sind	Lp4	45.7	44.2
GSI A20	*Antoletherium*	Kushalgarh	Lp4	53.3	52.1
IMM-C-2005-0017	*Prodeinotherium sinense*	Bantu Village	Rp4	61.0	53.0
BGR/LBEG Hannover tt 88	*Prodeinotherium* cf. *P. pentapotamiae*	Ban Sop Kham	Rp4	54.0	48.0

Discussion

The first deinothere teeth from Tapar were reported by Bhandari et al. (2015) and referred to *Deinotherium sindiense* based on their small size. However, these remains are too fragmentary to be systematically diagnostic, therefore, until additional evidence is presented, we consider *Deinotherium indicum* to be the only species of deinothere from the Tapar Beds. Assessing Neogene deinothere taxonomy from isolated teeth is challenging because very little dental variation exists between the genera *Prodeinotherium* and *Deinotherium* and among their species (Gräf, 1957; Harris, 1973; Huttunen, 2002a). Based on its size, PU KT-1 is comparable to teeth referred to *Deinotherium indicum* from Perim Island, Haritalyangar, and an unknown locality (Table 1), *Deinotherium giganteum* p4s from Europe (Depéret, 1887; Gräf, 1957; Tobien, 1988; Gasparik, 1993; Huttunen, 2002a; Vergiev and Markov, 2010; Pickford and Pourabrishami, 2013), and *Deinotherium bozasi* p4s from Kenya (Harris, 1976). It is larger than p4s referred to *P. pentapotamiae* and *Antoletherium* from South Asia (Table 1), a p4 referred to *P.* cf. *P. pentapotamiae* from Thailand (Sickenberg, 1971), a p4 from Chinese *Prodeinotherium sinense* Qiu et al., 2007 (Table 1), p4s from *P. bavaricum* (von Meyer, 1833), and *P. hungaricum* Éhik, 1930 from Europe (Gräf, 1957; Gasparik, 1993; Huttunen, 2002a; Huttunen and Göhlich, 2002; Koufos et al., 2003; Pickford and Pourabrishami, 2013; Tóth and Hyžný, 2013), and *P. hobleyi* (Andrews, 1911) from East Africa (Harris, 1973). PU KT-1 is however smaller than the p4s referred to *Deinotherium proavum* Eichwald, 1835 from Europe, although it is morphologically similar (Pickford and Pourabrishami, 2013). Nonetheless, we choose not to synonymize similarly sized Old World deinotheres until more crainal and postcranial remains are recovered from India. Based on size and geographic provenance, we refer this tooth to *Deinotherium indicum*.

The presence of *Deinotherium indicum* at Tapar is helpful in refining the age of the locality. It has been suggested previously that the Tapar locality is early Miocene in age (Bhandari et al., 2010). However, similar-sized p4s referred to *Deinotherium indicum* have been recovered from Haritalyangar (Table 1), a locality that has been magnetostratigraphically dated to 10.1–8.6 Ma (Pillans et al., 2005), and thus we can infer a similar age range for Tapar. The faunal assemblage from Tapar includes Muridae gen. indet. sp. indet. of Illiger, 1811, an indeterminate 'insectivore,' ?Amphicyonidae sp. of Haeckel, 1866, *Sivapithecus* sp. of Pilgrim, 1910, *Gomphotherium* sp. of Burmeister, 1837, *Brachypotherium* sp. of Roger, 1904, a large rhinocerotid, hipparionine horses, *Kachchhchoerus salinus* (Pilgrim, 1926), *Sanitherium schlagintweiti* von Meyer, 1866, *Dorcatherium minus* Lydekker, 1876, *Giraffa priscilla* Matthew, 1929, cf. *Protragocerus* sp. of Depéret, 1887, and cf. *Gazella* sp. of de Blainville, 1816 (Bhandari et al., 2010, 2015, 2018). This fauna is similar to that found at Haritalyangar and other similarly aged faunas from the Dhok Pathan Formation on the Potwar Plateau in Pakistan (Barry et al., 1982; Pillans et al., 2005), further indicating a late Miocene (Tortonian) age for Tapar. This age assessment supports the correlation of the Tapar beds with the younger Samdhan Formation, rather than the older Khari Nadi Formation.

The morphology of this largely complete p4 helps resolve some of the problems surrounding the systematics of Indian deinotheres. Sahni and Tripathi (1957) argued that an apomorphy of *Deinotherium indicum* is the presence of a dental tubercle (homologous to a style) on the 'outer side' of p4, whereas *Prodeinotherium pentapotamiae* (their *Deinotherium pentapotamiae*) lacks this structure. We interpret the 'outer side' to mean the buccal surface, because the only p4 that they described with a tubercle is GSI A596, a right p4 with a tubercle on the buccal margin of the occlusal surface (Fig 3.4). This apomorphy has been problematic because it has been used to synonymize much smaller and older taxa, e.g., *Antoletherium* (a taxon formerly synonymized with *P. pentapotamiae*), with the larger *Deinotherium indicum* (see Sahni and Tripathi, 1957). We examined the validity of this apomorphy by comparing the known p4s from the Indian subcontinent, Europe, China, and Africa. PU KT-1 has a small tubercle, but is placed posterobucally, and not in the transverse valley unlike the similarly sized p4, GSI A596. The p4 of *P. pentapotamiae* (GSI A22) lacks tubercles (Fig. 3.6), but the similarly sized p4 of *P. sinense* has a buccal tubercle (Qiu et al., 2007, figs. 2, 3). Huttunen (2002a) also showed that in a sample of European deinothere teeth, styles or tubercles were present on both large and small p4s. Moreover, Harris (1973) stated that apart from the p3, the lower dentition of African *Prodeinotherium* and *Deinotherium* are identical except for size, and that the presence of mesostyles is diagnostic to the superior P3 and P4 of *Deinotherium*. Given the variation in the presence of tubercles or styles on the inferior dentition, particularly on the p4s of both large and small Asian deinotheres, and the lack of variation in deinothere inferior dentition from Europe and Africa, we reject the presence of tubercles as an apomorphy of *Deinotherium indicum* as stated by Sahni and Tripathi (1957). We agree with Harris (1973) and Huttunen (2002a) that the major differences between *Deinotherium* and *Prodeinotherium* inferior dentition lie primarily in size and not in morphology.

Based on our analysis of the morphological variation in deinothere p4s, we revise Sahni and Tripathi's (1957) taxonomy of *Deinotherium indicum* and exclude *Antoletherium* from the list of synonymized species. *Antoletherium* was described by Falconer (1868) based on a drawing of a mandibular fragment with p4–m2 discovered by Lieutenant Garnett at Kushalgarh near Attock in what is now Pakistan. The stratigraphic provenance of the Kushalgarh fossils is unknown (Theobald, 1881), but biostratigraphically, the fossils are inferred to correlate with the Lower to the lowermost Middle Siwaliks or middle Miocene (Flynn et al., 2013). Despite the small size of *Antoletherium*, Sahni and Tripathi (1957) used the presence of a buccal tubercle on the p4 (not seen in Lydekker's 1880 illustration) along with other tubercles on the m1 and m2 to synonymize it with *Deinotherium indicum*. However, because we do not regard tubercles on the p4 as a valid apomorphy, and the small *P. sinense* also has tubercles on m1–m3 (Qiu et al., 2007), the morphological criterion used by Sahni and Tripathi (1957) is too variable and cannot be used diagnostically for the large genus *Deinotherium*. The older stratigraphic context for *Antoletherium* provides additional evidence against its synonymy with *Deinotherium indicum*. A general trend in deinothere evolution is a temporal increase in size across successive taxa (Gräf, 1957; Harris, 1978; Tobien, 1988; Huttunen, 2002b; Poulakakis et al., 2005; Pickford and Pourabrishami, 2013), further indicating that the specimen of *Antoletherium* represents a distinct older and smaller taxon. Moreover, *Antoletherium* bears the greatest metric similarlty to the middle Miocene *P. pentapotamiae* (Table 1). Thus, we accept Lydekker's (1880) original synonymization of *Antoletherium* with the latter.

Previously, only small deinotheres (*Prodeinotherium pentapotamiae* and *Deinotherium sindiense*) have been documented from Kutch (Lydekker, 1880; Bhandari et al., 2015; Kapur et al., 2019). Small specimens of deinotheres referred to *Deinotherium sindiense* have been recovered from Palasava (Kapur et al., 2019) and Pasuda (Bhandari et al., 2015), and although direct dates are not available, the associated fauna suggest a middle Miocene (Langhian–Serravalian, ca. 15.9–11.6 Ma) age. Small deinothere remains from the undated locality of Sambera have been referred to *P. pentapotamiae* (GSI A10; Lydekker, 1876). *Prodeinotherium pentapotamiae* is commonly found in the middle Miocene Lower Siwaliks (Dehm, 1963; West et al., 1978), suggesting a similar middle Miocene age for Sambera as well. Determining whether multiple species of small deinotheres existed during the middle Miocene is beyond the scope of this study, but based on isolated dentition alone, *Deinotherium sindiense* and *P. pentapotamiae* are very similar to one another in size (Supplemental Table 1). However, we follow Bhandari et al. (2015) and reject the hypothesis proposed by Sahni and Tripathi (1957) that *Deinotherium sindiense* is synonymous with *Deinotherium indicum* considering its far smaller size (Supplemental Table 1) and the fragmentary nature of the holotype (Lydekker, 1880) precluding a detailed morphological comparison. The confirmed presence of *Deinotherium indicum* at Tapar shows that ecosystems in western India experienced a replacement of smaller deinotheres by larger species in the late Miocene, just as has been seen in the northern part of the Indian subcontinent (Sahni and Tripathi, 1957) and elsewhere in the world (Harris, 1983).

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Accessibility of supplemental data

A tabular list of specimens and measurements used for comparison is available in Supplemental Data 1. Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.dfn2z34wz.

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