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New fossil record of *Hyaenictitherium pilgrimi* (Carnivora: Hyaenidae) from Dhok Pathan Formation of Hasnot, Pakistan

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Abstract New dental material—one maxilla bearing P3 and P4—of Early Pliocene hyaenid *Hyaenictitherium pilgrimi* from the Dhok Pathan Formation of Hasnot is described and discussed. The presence of this hyaenid from the Early Pliocene (Ruscinian equivalent) deposits at Hasnot is an important fossil record of this species from the Siwalik continental deposits of Pakistan. The purpose of the paper is to provide more information about the fossil record and its stratigraphic extension from Late Miocene to Early Pliocene from the Siwalik continental deposits.

Keywords Hyaenidae · Dental material · Early Pliocene · Fossil record · Stratigraphic extension

Abbreviations

UZ	Punjab University Paleontological Collection stored in Zoology Department, Lahore, Pakistan
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
PMU	University of Uppsala Museum of Evolution, Uppsala, Sweden
P3	Upper third premolar
P4	Upper fourth premolar
L	Maximal anteroposterior length
LmP4	P4 metastyle length
LpP4	P4 paracone length
W	Maximal transverse width
WaP4	Anterior P4 width at protocone and parastyle
WblP4	P4 width between paracone and metastyle

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Introduction

The Late Miocene middle-sized hyaenids are commonly known under the vernacular name ictitheres. This group of carnivore includes the genera of different size and different evolutionary trends (e.g. *Thalassictis* and *Hyaenictitherium*). However, the phylogenetic relationships between these genera are yet unclear (de Bonis et al. 2008). The genus *Hyaenictitherium* was erected by Kretzoi (1938) in his effort to sort out the confusion produced by earlier taxonomic schemes (Lydekker 1884; Pilgrim 1910, 1913, 1932; Zdansky 1924; Matthew 1929; Colbert 1935). The genus *Hyaenictitherium* has a wide geographic range in the Late Miocene, in Eurasia, it has been reported from China, Ukraine, Moldova, Pakistan, Iran, Turkey, Romania, Greece, Germany, Hungary and Spain (Werdelin and Solounias 1991; Werdelin et al. 1994; de Bonis 2005; Tseng and Wang 2007). In Europe, five Late Miocene species *Hyaenictitherium hyaenoides* (Zdansky 1924), *H. wongii* (Zdansky 1924), *H. intuberculatum* (Ozansoy, 1965), *H. parvum* (Khomenko, 1914) and *H. venator* (Semenov, 1989) have been described while from Africa, two Late Miocene species; *H. minimum* (de Bonis et al. 2005) and *Hyaenictitherium* cf. *H. parvum* (Werdelin 2003), have been reported, followed by *H. namaquensis* in the Early Pliocene of Libya, South Africa, and Kenya (Werdelin and Solounias 1991; Werdelin et al. 1994; Morales et al. 2005; Turner et al. 2008). The genus greatly expanded its geographic range in Eurasia between MN11 and MN13 (and

equivalent ages outside of Europe), reaching China to the east and the Indian subcontinent to the south during the Late Miocene. Overall, the available fossil record of *Hyaenictitherium* indicates that from Eurasia, this genus subsequently spread to northern Asia, southern Asia, and Africa as early as 7.0 Ma (Tseng and Wang 2007). Functional interpretation of the feeding apparatus of *Hyaenictitherium* suggests a greater emphasis on bone-eating relative to primitive taxa (*Hyaenotherium and Ictitherium*) (Ferretti 2007). The *Hyaenictitherium* is probably a paraphyletic and until now 10 species of this genus have been described (Werdelin and Solounias 1991). According to Werdelin and Solounias (1991), *H. indicum* represents a nomenclature problem; the holotype of *H. indicum* described by Pilgrim (1910) was never figured, and it is not numbered and not precisely located. Due to this reason and according to International Code of Zoological Nomenclature, Werdelin and Solounias (1991) proposed to restrict the name of *H. indicum* to the holotype material only. The materials other than the holotype (G.S.I. D53, D210, D211, D246, D.K.13, 403 and D.K.15, 790), subsequently assigned to *H. indicum* were transferred to *H. pilgrimi*, a new species erected by Werdelin and Solounias (1991). The holotype material for this new species *H. pilgrimi* is a right mandible (G.S.I. No. D53), figured by Lydekker (1884). From Europe, Asia and Africa, the different species of this genus so far described are *H. hyaenoides, H. indicum, H. pilgrimi, H. wongii, H. parvum, H. namaquensis, H. intuberculatum, H. venator, H. barbarum* and *H. minimum*. The goal of this study is to describe a new specimen of *H. pilgrimi* form the Siwalik continental deposits, which is dated from the Early Pliocene. This discovery is important because the earlier workers described this species from the Late Miocene of the Siwaliks.

Geological setting

The Hasnot village is situated at about 54 km west of the Jhelum city in the Potwar Plateau of northern Pakistan (see Fig. 1), surrounded by extensive Neogene freshwater sedimentary rocks. After the Dhok Pathan type locality in the Siwalik continental deposits, the Hasnot (Lat. 32°49′27.89N: Long. 73°07′52.68E) is another famous fossil-bearing site that has attracted a number of natural historians (Lydekker 1884; Pilgrim 1910, 1913, 1932; Matthew 1929; Colbert 1935; Pilbeam et al. 1977; De Vos et al. 1987; Barry and Flynn 1989; Behrensmeyer et al. 1995; Barry et al. 2002; Khan et al. 2009; Ghaffar et al. 2010) for its vertebrate assemblages. This fossil site represents lateral facies associations within the fine grained fossil-bearing floodplain deposits that are characteristic of fluvial depositional environments (Barry and Flynn 1989; Wills and Behrensmeyer 1995; Behrensmeyer et al. 1995; Barry et al. 2002). Lithostratigraphically, the fossil site belongs to the upper Dhok Pathan Formation (Middle Siwaliks), which is characterized by sandstones with alternate clays that are orange brown in color, scattered conglomerates in the lower part, and conglomerate with sandstone and clays in the upper part (Pilbeam et al. 1977; Cheema et al. 1977; Johnson et al. 1982; Barry et al. 1982). Although all five component formations (i.e. Kamlial, Chinji, Nagri, Dhok Pathan and Soan Formation) are well exposed in the area around Hasnot but the upper Dhok Pathan Formation has the most significant exposures in this area. The upper Dhok Pathan Formation is remarkable for its rich hipparionine assemblages and numerous artiodactyls as well as different carnivores. These assemblages suggest that the age of the study area is Latest Miocene–Early Pliocene (Colbert 1935; Barry et al. 2002; Khan et al. 2009; Ghaffar et al. 2010). The here described portion of right maxilla with P3-4 of *H. pilgrimi* has been collected from the Dhok Pathan Formation, near Hasnot village by the team of palaeontologists during the winter season of 1967. This is in the same vicinity where Pilgrim (1910) collected and described the material of *H. indicum*. The new fossil record of *H. pilgrimi* from Hasnot is important to correlate the stratigraphic correlations with the Chinese as well as with the European and African materials.

Materials and methods

The described specimen was collected from the area around Hasnot village (Dhok Pathan Formation), Punjab, Pakistan and is housed in the collections of the Abu Bakr Fossil Display and Research Centre, University of the Punjab, Lahore, Pakistan. The measurements were taken in millimeters with metric vernier calipers. The terminology of the tooth crown elements and manners of measurements follow Werdelin and Solounias (1991).

Systematic palaeontology

Order Carnivora Bowdich, 1821
Family Hyaenidae Gray, 1821.
Genus *Hyaenictitherium* Kretzoi, 1938
Type species *Hyaenictitherium hyaenoides* (Zdansky, 1924)
Hyaenictitherium pilgrimi, Werdelin and Solounias, 1991.

Synonymy

1884 *Hyaena sivalensis* Lydekker, p. 306, pls. 38:2; 39:2.
1910 *Palhyaena indica* sp. nov. Pilgrim, p. 64.

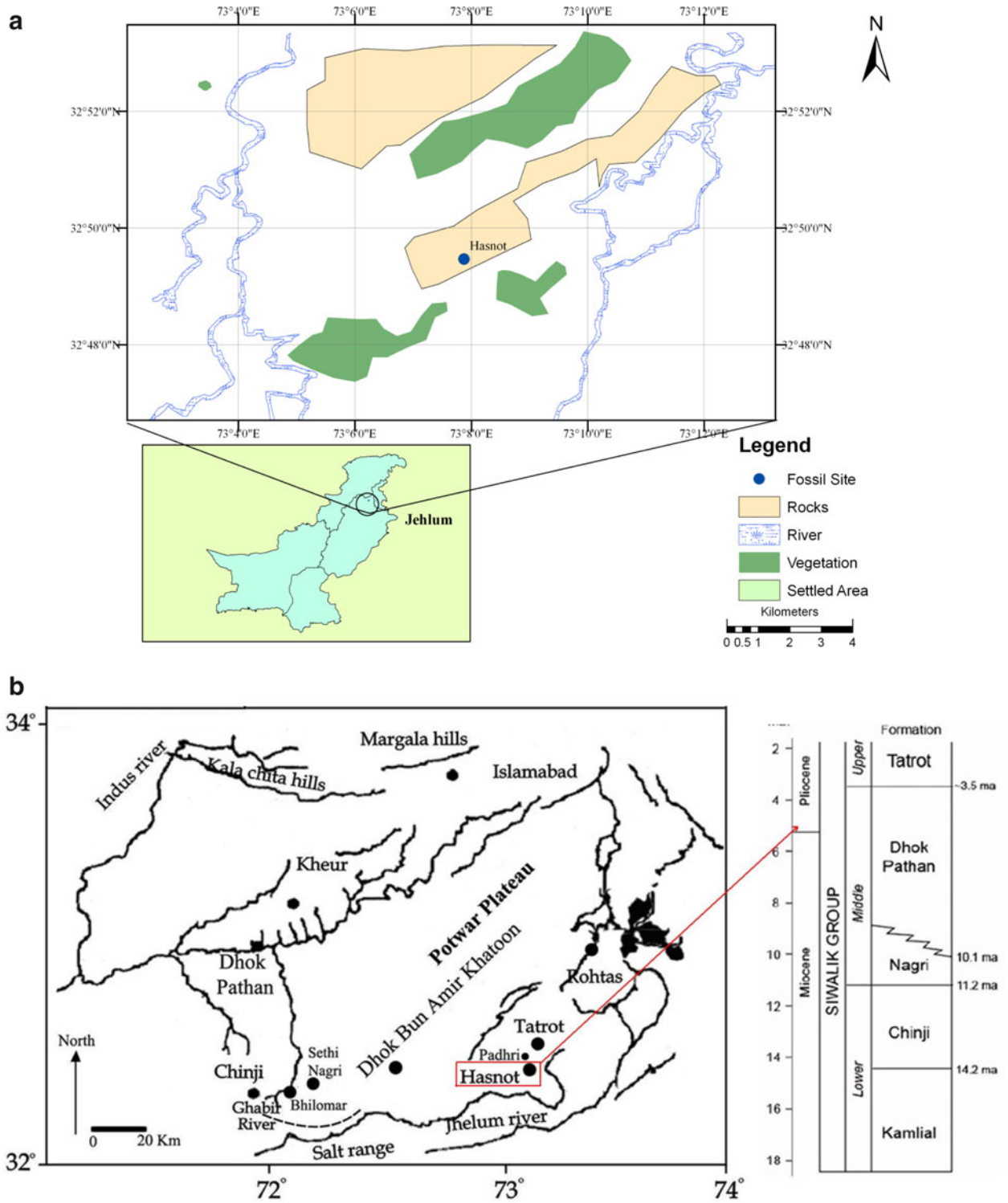

Fig. 1 **a** Map of Pakistan (*inset*) with an enlargement of study area (Hasnot) from Jehlum district, Punjab, Pakistan. **b** Map of Potwar Plateau (northern Pakistan) with fossil site and stratigraphic section of the major Siwalik formations (modified from Behrensmeyer and Barry 2005 and the boundary dates are from Barry et al. 2002)

1913 *Palhyaena* cf. *hipparionum* (Gervais), Pilgrim, pp. 282, 289.
1924 *Ictitherium hyaenoides* sp. nov. Zdansky, pp. 84–91.
1929 *Palhyaena indica* Matthew, p. 493.
1932 *Ictitherium indicum* (Pilgrim) Pilgrim, pp. 119–122, pls. 4:11–12; 5:8.
1935 *Ictitherium indicum* Colbert, pp. 107–108.

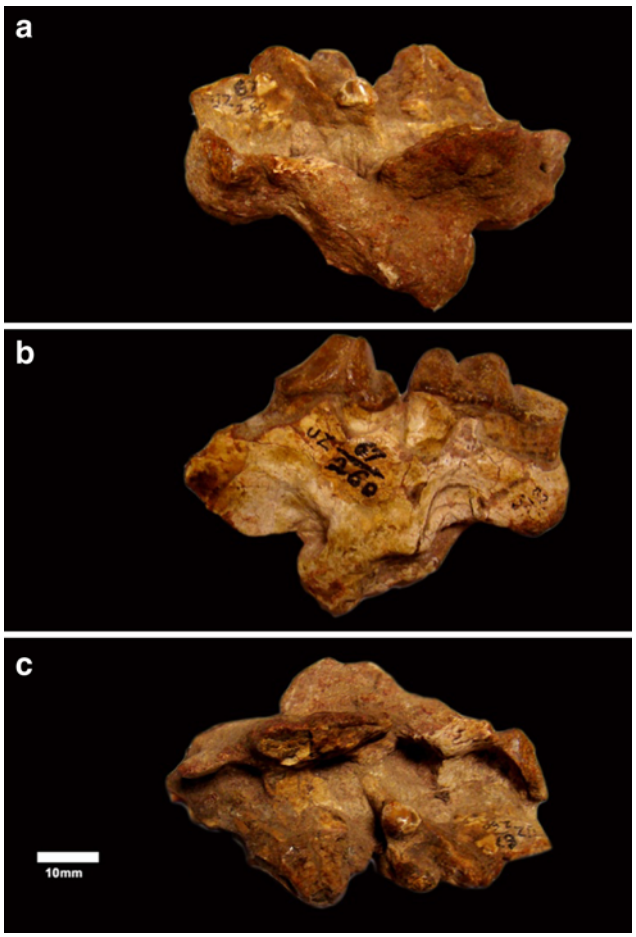

Fig. 2 UZ 67/260, right maxilla bearing P3 and P4 of *H. pilgrimi* from Hasnot, Middle Siwaliks, Pakistan; **a** Lingual view, **b** buccal view, **c** occlusal view. (*Scale bar* 10 mm)

1938 *Hyaenictitherium indicum* (Pilgrim) Kretzoi, p. 114.
1987 *Ictitherium indicum* (Pilgrim) De Vos, Leinders and Hussain, p. 361
1988 '*Ictitherium*' *indicum* Werdelin, pp. 255–256.
Hyaenictitherium pilgrimi (this paper).

Type Locality Hasnot, Dhok Pathan Formation, Jehlum District, Punjab Province, Pakistan.

Age Dhok Pathan Formation, Middle Siwaliks.

Stratigraphic extension Late Miocene–Early Pliocene.

Holotype G.S. I. No. D53, a right mandible with p4 and m1, from Hasnot, Dhok Pathan Formation, Jehlum District, Punjab Province, Pakistan.

Referred specimen UZ 67/260, right maxilla having P3 and P4 of *Hyaenictitherium pilgrimi*, from Hasnot, Middle Siwaliks, Pakistan.

Description (Fig. 2)

The only known material allocated to this species is an upper P3-4 on a piece of maxilla. The teeth are quite worn. The third premolar (P3) is a robust premolar with the main cusp dominating the tooth; an antero-lingual crest reaches the somewhat elevated basal cingulum, but without forming a separate cusp. The distal crest is short, and contacts a high cusp; the distal cingulum is wide and prolonged lingually. The base of the tooth is deep postero-lingually (Fig. 2; Table 1). The P4 is very sectorial carnassial, with a strong, low parastyle separated by a notch from the high paracone. The parastyle and protocone of P4 are subequal in size; a crest runs lingually from the apex of the parastyle to the apex of the protocone. The protocone does not form a real cusp, but extends the lingual wall of the cusp rootwards. A wear facet is located on the antero-lingual aspect of this rootward extension of enamel of the protocone. The metastyle is broken in its distal part and the protocone is projected mesiolingually. The paracone and metastyle blade are almost equal in length (12 mm).

Measurements for *H. pilgrimi* (G.S.I. No. D 246) are taken from Pilgrim (1932). Measurements for *H. hyaenoides* (IVPP V14737) are taken from Tseng and Wang (2007), while for *H. hyaenoides* (PMU M3852-3855) and *H. wongii* are taken from the data provided by Werdelin.

Discussion

The direct comparison of the studied material with the type specimen is not possible because the type material from the

Table 1 Comparative dental measurements (mm) of UZ 67/260 (*H. pilgrimi*) with other *Hyaenictitherium* species

Specimen # and species	P3		P4				
	LP3	WP3	LP4	WaP4	WbIP4	LpP4	LmP4
UZ 67/260 (*H. pilgrimi*)	21	11.2	31	17.6	9	12	12
G.S.I. D 246 (*H. pilgrimi*)	–	–	26.3	14.8	8.2	10.3	10.1
IVPP V14737 (*H. hyaenoides*)	19.9	11.5	28.4	15.3	9.5	11	11.2
PMU M3852-3855 (*H. hyaenoides*)	18	10.6	28.2	16	9.1	10.9	11.6
China (*H. wongii*)	16.6	9	25.5	13.9	8.5	9.3	9.9

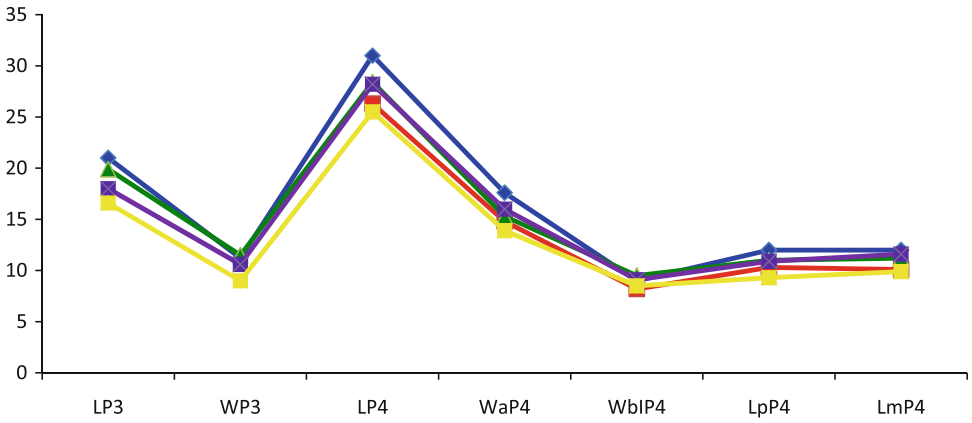

Fig. 3 Comparison of *H. pilgrimi* UZ 67/260 from Hasnot (*blue*), *H. pilgrimi* (G.S.I. No. D246) from Siwaliks (*red*), *H. hyaenoides* IVPP V14737 from Baogeda Ula (*green*), *H. hyaenoides* type specimen PMU M3852-3855 (*purple*) and a Chinese sample of *H. wongii* (*yellow*). The values mentioned in this figure are provided in Table 1

Siwaliks is known only from mandible (G.S. I. No. D53, a right mandible with p4 and m1). The only upper teeth presently known for *H. pilgrimi* are G.S. I. No. D246 (right P4) and D.K. 15,790 (left P4). Only the specimen numbered G.S. I. D246 has been figured by Pilgrim (1932). The measurements for D.K. 15,790 are not available. Therefore, only the P4 of the studied specimen can be compared with the specimen G.S. I. No. D246. The fourth premolar under study (UZ 67/260) has greater anteroposterior length and transverse width as compared to Siwalik specimen G.S. I. No. D246. Similarly, the third and fourth premolars of the studied specimen have greater anteroposterior length as compared to *H. hyaenoides* and *H. wongii*. While P3 of the studied specimen has lesser transverse width as compared to a Chinese specimen (IVPP V14737) both P3-4 have greater transverse width as compared to *H. hyaenoides* (PMU M 3852-38555) and *H. wongii*. Moreover, the specimen under study has greater tooth dimensions for paracone and metastyle blade as compared to other *Hyaenictitherium* specimens. Based on the ratio diagram of Werdelin (1988), the P4 dimensions of *H. pilgrimi* and *H. hyaenoides* appear to be more similar except the posteriorly placed protocone in *H. pilgrimi*. Similarly, overall dental morphology of studied specimen appears to be slightly more derived than that of *H. hyaenoides* and *H. wongii* and the specimens of *H. pilgrimi* are in general larger than *H. hyaenoides* and *H. wongii* (Fig. 3; Table 1). These morphological features of the specimen under study are consistent with the current understanding of the species; as the anterior part of parastyle in P4 is slightly broken and the protocone is situated more posteriorly as compared to the parastyle. This is also a diagnostic character of *H. pilgrimi*, whereas in *H. hyaenoides* the protocone and parastyle are in line with each other. On the basis of posteriorly placed protocone as compared to *H. hyaenoides*, the specimen under study is assigned to *H. pilgrimi*. Moreover, the specific diagnoses of *H. pilgrimi* are the hyaenid of relatively large size, with extremely sectorial dentition. Upper carnassial (P4) is with reduced protocone which extends substantially rootwards. In P4, the protocone and parastyle are subequal in size. In P3, the main cusp is completely dominating the tooth with a high posterior cusplet. All these characters are evident in the specimen under study (Pilgrim 1932; Howell and Petter 1980; Werdelin and Solounias 1991). According to Werdelin and Solounias (1991) the *Hyaenictitherium* is probably be paraphylectic and such taxa should nevertheless be instructive for revealing evolutionary trends during the transition to the hyaenid ecomorphological split (Tseng and Wang 2007).

Stratigraphic implications

The described specimen here from the Siwaliks was collected from the Early Pliocene, while the other fossils remain already assigned to this genus were collected and described from the Late Miocene, thus extending its stratigraphic range from Late Miocene to Early Pliocene. As indicated in the introduction, the genus greatly expanded its geographic range in Eurasia between MN11 and MN13. *Hyaenictitherium intuberculatum* from Turkey (de Bonis 2004) and *H. wongii* from Höwenegg, Germany (Bernor et al. 1980; Werdelin and Solounias 1991) are the earliest occurrences of the genus in Eurasia. Indeed, the period during the Late Miocene from MN11 to MN13 is marked by the presence of six species (*H. hyaenoides, H. wongii, H. parvum, H. intuberculatum, H. venator* and *Hyaenictitherium* sp.) of this genus. From the above discussion, it is clear that the *Hyaenictitherium* had a vast range of distribution from the Turolian onward. The available fossil record of *Hyaenictitherium* indicates that this genus dispersed from Europe to northern Asia, southern Asia and Africa (Qiu et al. 1979; Zhang et al. 2002; Tseng and Wang 2007). The species *H. pilgrimi* from the Siwaliks of Pakistan may be an offshoot of *H. hyaenoides* or *H. wongii*. This idea can be supported as the *H. indicum*

and *H. pilgrimi* from the Siwaliks are reported from the Latest Dhok Pathan Formation (10.1–3.5 Ma), substantially latter than in Eurasia. This is not unexpected as the Tibetan region falls broadly within the dispersal route from the western into the eastern hemisphere and during the Vallesian times, it was substantially lower than is the case now and would not have formed a barrier to the dispersal (Howell and Petter 1985). This assumption can be supported as the *H. hyaenoides* has been recently described from the Late Miocene of Inner Mongolia (Tseng and Wang 2007). After Pilgrim (1910, 1932 this is the first record of *H. pilgrimi* based on a new collection, whereas the previous publications were based on the fossil remains already collected and described by him (Howell and Petter 1980; Werdelin 1988; Werdelin and Solounias 1991). Although the exact stratigraphic level of these specimens from the Siwaliks (Pilgrim 1910, 1932) is not clear; however, the through investigations of the fossil sites mentioned in the literature (Pilgrim 1910, 1932; Howell and Petter 1980; Werdelin 1988; Werdelin and Solounias 1991; Zhang et al. 2002; Tseng and Wang 2007) indicate that these are from the Latest Miocene (Dhok Pathan Formation). The stratigraphic analyses of the fossil site clearly suggest that the specimen under study is from the younger stratigraphic range as the age of the fossil site is 5.5–4 Ma (Ruscinian; MN14). Werdelin and Solounias (1991) mentioned the Dhok Pathan age (Vallesian-Turolian; MN 9-12) for *H. pilgrimi,* but however the additional fauna particularly the Cervidae fossils collected from the study area (Hasnot) confirms the Ruscinian age (equivalent to MN14; Early Pliocene) of the fossil site because the earliest most fossil record of different species of tribe Cervini from the Siwaliks is not older than the Early Pliocene times (Barry et al. 2002; Khan et al. 2009; Ghaffar et al. 2010).

Conclusion

After Pilgrim (1910), this is the first record of *H. pilgrimi* based on a new fossil collection from the Siwaliks. The material described here is from the younger stratigraphic range (Early Pliocene), thus extending its stratigraphic range from Late Miocene to Early Pliocene. The new specimen supports an endemic evolution of the *Hyaenictitherium* in Asia, and thus implies an expansion before the Early Pliocene. Similarly, these species seem to follow a morphological trend of increasing size and robustness of teeth and this is consistent with the general hyaenid evolutionary trend. This trend of increasing size and robustness of teeth is also confirmed as the size of studied specimen is larger than that of the specimens already described from the Latest Miocene. Evidently, further work is required to confirm these biases; regarding the stratigraphy and palaeobiogeography of different *Hyaenictitherium* species and the specimen described here, if correctly attributed is important to precede further studies.

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