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Comments on *Percrocuta carnifex* (Carnivora, Percrocutidae) based on new fossil material from the Nagri Formation (Middle Siwaliks) of Hasnot, Pakistan

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ABSTRACT

New dentary material of *Percrocuta carnifex* (PILGRIM, 1913) from the Nagri Formation of Hasnot, Pakistan, is described. Specimens of this species from the Siwalik continental deposits described by previous authors are discussed in detail. In addition to the taxonomic description of the new material, the occurrence and stratigraphic position of this species within the Siwalik Hills are re-evaluated. Except for the holotype, the specimens assigned to this species are very fragmentary. The newly discovered material, a right mandibular ramus containing teeth, is the best preserved specimen found to date. The comparative analysis, based on tooth morphology and dimensions of previously reported specimens and of the specimen studied here, suggests that this species is restricted to the Chinji and Nagri formations. Finally, the dental morphological features of the studied specimen and those of other species of *Percrocuta* are compared, and then the phylogenetic relationship between these species is discussed. The described specimen is thus important for the taxonomic, stratigraphic and phylogenetic knowledge of *P. carnifex* from the Siwaliks.

KEYWORDS | ***Percrocuta carnifex*. Carnivora. Percrocutidae. Miocene. Middle Siwaliks.**

INTRODUCTION

The Hasnot area, Pakistan, is famous for its fossil assemblages of very diverse mammalian fauna from the well exposed Chinji, Nagri, Dhok Pathan and Soan formations (Fig. 1), but the carnivores from the Siwalik Hills remain very poorly documented (Ghaffar and Akhtar, 2012; Ghaffar *et al.*, 2011; Ghaffar, 2005; Pilgrim, 1932; Lydekker, 1884). The most important Middle Siwalik carnivore localities after the type localities of Nagri and Dhok Pathan formations are the localities from the Hasnot area (Wang *et al.*, 2013; Ghaffar and Akhtar, 2012; Khan

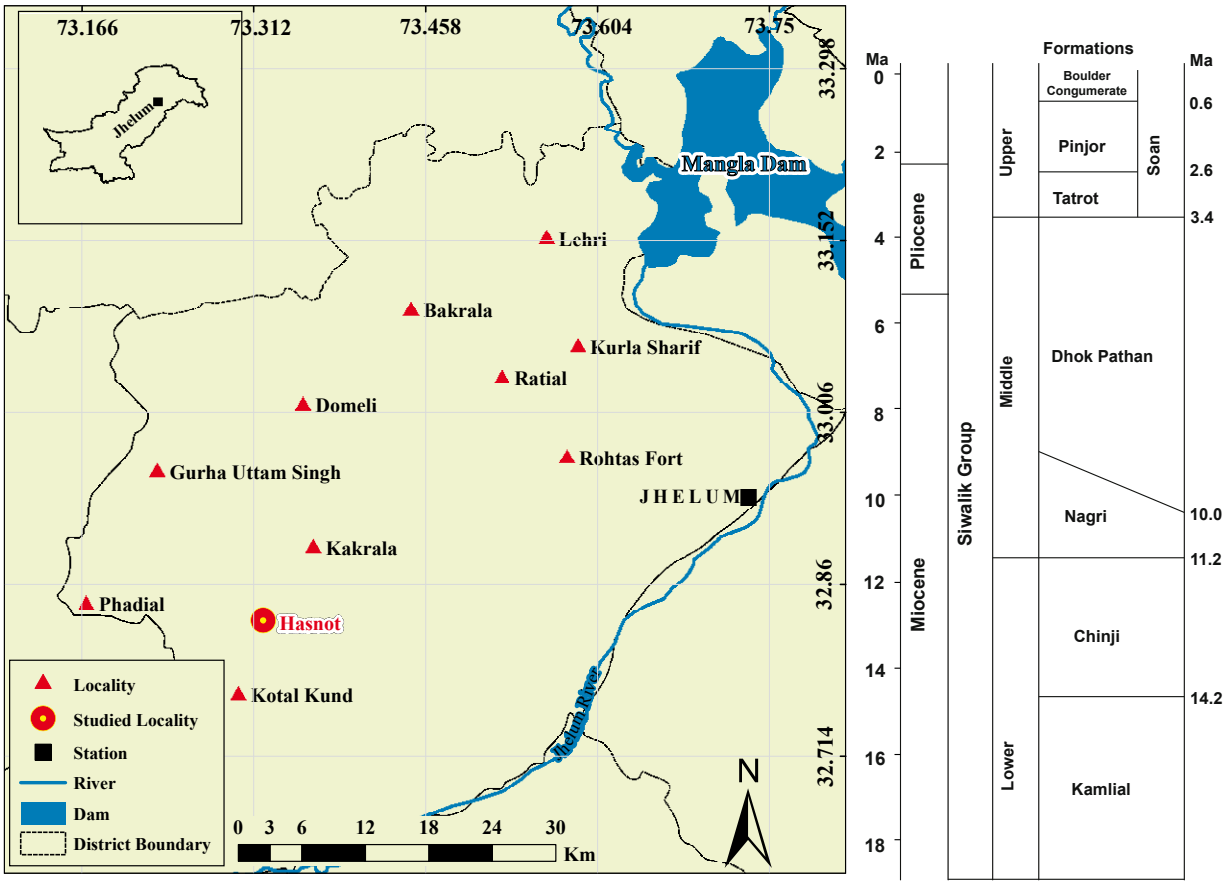

FIGURE 1. Location of the study area in the vicinity of Hasnot, in the Jhelum district, Punjab, Pakistan, with map of Pakistan (inset) and the general stratigraphic framework for the Miocene and Pliocene in the Siwaliks.

et al., 2009; Khan, 2007; Ghaffar, 2005; Barry *et al.*, 2002, 1982; Behrensmeyer *et al.*, 1995; Wills and Behrensmeyer, 1995; Barry and Flynn, 1989; Johnson *et al.*, 1982; Cheema *et al.*, 1977).

Different species of percrocutoid hyaenids, of late Middle Miocene (Chinji Formation) to Late Miocene (the Nagri and Dhok Pathan formations) age, have been reported from the Siwaliks of Pakistan (Ghaffar *et al.*, 2011; Morales and Pickford, 2006; Ghaffar, 2005; Howell and Petter, 1985; Kurtén, 1957; Colbert, 1935; Matthew, 1929; Pilgrim, 1932, 1931, 1913; Lydekker, 1884). The described species were ascribed to either the *Hyaena* or *Crocuta* genera of Hyaenidae. Kretzoi (1938) erected the genus *Percrocuta* for some percrocutoid forms of the family Hyaenidae [hyaenids of relatively small size and with a reduced protocone in the upper carnassial (P4)], but he was largely ignored, and several of these forms were subsequently ascribed to various genera, usually to *Crocuta*. In a major study of these forms, Kurtén (1957) reinstated the subgenus *Percrocuta*. Posteriorly, Schmidt-Kittler (1976) and Guanfang and Schmidt-Kittler (1983) suggested the distinction of percrocutids from the hyaenids based on the deciduous dentition. Werdelin and Solounias (1991) removed them from the family Hyaenidae, and placed them in the separate family Percrocutidae, which includes the genera *Percrocuta* and *Dinocrocuta* (Morales and Pickford, 2006; Werdelin and Kurtén, 1999; Howell and Petter, 1985). According to Kurtén (1957), *Percrocuta* comprises the dominant hyenas of the Pliocene. Taxonomic characteristics of species of this group from Asia, Europe and Africa have been described in detail (Kurtén 1957; Guanfang and Schmidt-Kittler, 1983; Howell and Petter, 1985). The main aim of this paper is to present the taxonomic study of a new specimen described here and to comment on the stratigraphy of the specimens from the Siwalik continental deposits described by earlier authors (Ghaffar *et al.*, 2011; Pilgrim, 1932).

GEOLOGICAL SETTING

The specimen PUPC 2016/16A, was collected in the fossiliferous site of the Hasnot village (32.82855°; 73.31510°), located about 54km west of the Jhelum city in the Potwar Plateau of northern Pakistan (Fig. 1). In this

area, extensive Neogene continental sedimentary rocks are well exposed. The region of Hasnot exposes the most complete sequence of the Siwalik Group (Kamlial, Chinji, Nagri, Dhok Pathan and Soan formations) and has yielded diverse fossil assemblage, mostly in the Dhok Pathan Formation. Fossil sites around Hasnot village are located in fine-grained fossil bearing floodplain deposits characteristic of a fluvial depositional environment (Barry *et al*., 2002, 1982; Barry and Flynn, 1989). The Chinji and Dhok Pathan formations are mud dominated whereas the Nagri and Soan formations are sand dominated (Wang *et al*., 2013; Willis and Behrensmeyer, 1995; Behrensmeyer *et al*., 1995). In the study area, the Nagri Formation consists of sandstone with subordinate clay and conglomerate intercalations. The sandstone is greenish grey, medium to coarse grained, moderately to poorly cemented, and cross-bedded, while the clay is sandy, reddish grey and pale orange; the proportion of the different deposits varies from section to section. The conglomerate beds vary in thickness and composition. The conglomerate beds in this area consists of pebbles of igneous rocks and Eocene limestone, similar to the conglomerates from the type section of the Nagri Formation. This formation has yielded fairly rich assemblages of vertebrate remains *i.e*. *Trilophodon*, *Pentalophodon*, *Dinotherium*, *Stegolophodon*, *Tetraconodon*, *Gaindatherium browni*, *Aceratherium lydekkeri*, *Chilotherium intermedium*, *Macrotherium salinum*, *Giraffokeryx punjabiensis*, *Dorcabune nagrii*, *Dorcatherium minus*, *Hemimeryx*, *Listriodon pentapotamiae*, *Palaeochoerus perimensis*, *Meganteron*, *Amphicyon palaeindicus*, *Lycyaena*, *Orycteropus browni*, *Crocuta carnifex* and *Eotragus* spp. (Shah, 2009; Khan, 2007; Ghaffar, 2005; Barry *et al*., 2002; Pilbeam *et al*., 1977; Colbert, 1935; Pilgrim, 1932, 1913, 1910; Matthew, 1929; Lydekker, 1884).

MATERIAL

The specimen described in this paper (PUPC 2016/16A) belongs to the Abu-Bakr Fossil Display and Research Centre, University of the Punjab (Lahore, Pakistan) and was collected by research associate, Mr. Muhammad Akhtar, of the Zoology Department during the winter season of 1984. The stratigraphic information of the fossil site, found with the specimen, revealed that it was collected from the Nagri Formation of Hasnot area. This locality lies across the Bunnah River, 2km SE of Hasnot village. For the comparative analysis, we used the material from the Siwaliks (PUPC 2009/1) described by Ghaffar *et al*. (2011), and the measurements of the specimens reported by Pilgrim (1932) and Howell and Petter (1985), which were based on the photographs/plates included in the respective papers. The lower dentition (GSI D 169–172; AMNH 19405 and CU-PUPC 2009/1) and two maxillary fragments (GSI D 168 and 173) described by Pilgrim (1932) were considered but not included in Table 1, as the material under study belongs only to the lower dentition.

Abbreviations. Organizations: AMNH: American Museum of Natural History New York; BMNH: British Museum of Natural History, London; CU-PUPC: COMSATS University-Punjab University Paleontological Collection; GSI: Geological Survey of India, Calcutta; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MNHN: Museum National d'Histoire Naturelle, Institute de paléontologie, Paris; NMB: National Museum, Belgrade; PIN: Paleontological Institute, Academy of Sciences, Moscow, USSR; PUPC: Punjab University Paleontological Collection.

Palaeontology. L: length; Ma: million years ago; d2: second lower deciduous molar; d3: third lower deciduous molar; d4: fourth lower deciduous molar; m1: first lower molar; m2: second lower molar; M2: second upper molar; mm: millimeters; p1: first lower premolar; p2: second lower premolar; p3: third lower premolar; p4: fourth lower premolar; P3: third upper premolar; P4: fourth upper premolar; W: width.

Previously described specimens from the Siwaliks with comments on the stratigraphy

To this date, the following specimens of Percrocut carnifex (Pilgrim, 1913) had been described (Ghaffar *et al*., 2011; Colbert, 1935; Pilgrim, 1932, 1913) from the Siwalik continental deposits:

i) GSI D 164; right m1, collected from Dhok Pathan Formation, Hasnot (Jhelum district).

ii) GSI D 168; left P4, collected from the Chinji Formation, Chinji.

iii) GSI D 169; a left mandibular ramus with the base of canine broken and p2-3, collected from the Chinji Formation, Chinji.

iv) GSI D 170; a left mandibular ramus with alveolus of canine and (p2-3, collected from the Chinji Formation, Chinji.

v) GSI D 171; a left mandibular ramus with p3-4, collected from the Chinji Formation, Chinji.

vi) GSI D 172 (holotype); a right mandibular ramus with d2-4, canine, p2-4 and molar (m1), collected from the Chinji Formation, Chinji.

vii) GSI D 173; right maxilla with canine and P2-3 collected from the Chinji Formation, Chinji.

viii) AMNH 19405; a left mandibular ramus with p4 and m1, collected from the Chinji Formation, Chinji (four miles northeast of Chinji Rest House).

ix) CU-PUPC 2009/01; left mandibular ramus with p3 and m1 collected from the Nagri Formation, near the village of Nagri Sethi.

Among the material described by Pilgrim 1932, only the specimen GSI D 164 is said to come from the Dhok Pathan Formation of Hasnot, but there is not an exact record of the fossil site. Moreover, the smaller length of the tooth of this specimen compared with the specimen described here suggests that this specimen is not as young as the Dhok Pathan Formation. Although the exact stratigraphic position of the rest of the listed specimens is not known, the lithological characteristics and stratigraphic context of their sites suggest that none of the specimens come from the Dhok Pathan Formation, then this species was probably restricted to the Chinji and Nagri formations.

The type specimen of *P. carnifex*, GSI D 172, and GSI D 173, were collected by Pilgrim (1932, 1913) from the top of the Chinji Formation south of the Nagri village. The specimens GSI D 168, 169, 170, and 171 were also collected by Pilgrim (1932, 1913) from the Chinji Formation. The type locality of this species is situated east of Chinji and south of the Nagri village. Colbert (1935) described a specimen (AMNH 19405) assigned to this species from the lower Chinji beds, four miles northeast of the Chijni Rest House. More recently, Ghaffar *et al.* (2011) described another specimen (CU-PUPC 2009/01) from the type section of the Nagri Formation. Among the material described by Pilgrim 1932, only specimen GSI D 164 is believed to come from the Dhok Pathan Formation of Hasnot, without an exact record of the location of the fossil site, as it had been collected by some native person of this vicinity.

According to the stratigraphic context and morphometric analysis of the already described specimens (Howell and Petter, 1985; Kurtén, 1957), we believe that all these were collected from the Chinji-Nagri formations, as the specimen described in this study came from Nagri Formation, near Hasnot village. Similarly, the small tooth length of the specimen GSI D 164 as compared to the specimen described here confirms that this specimen is not as young geologically as the Dhok Pathan Formation.

SYSTEMATIC PALAEONTOLOGY

Order: Carnivora Bowdich, 1821
Family: Percrocutidae Werdelin and Solounias, 1991
GENUS ***Percrocuta*** Kretzoi, 1938

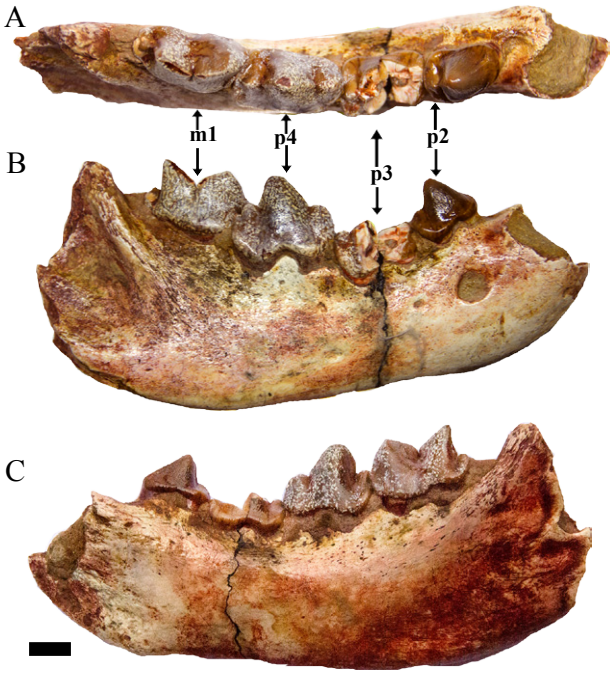

FIGURE 2. *Percrocuta carnifex* (PUPC 2016/16A), right mandibular ramus with p2, p4, m1 and broken basal portion of p3; A) occlusal view B) buccal view C) lingual view. Scale bar=10mm.

Type species: *Percrocuta carnifex* (Pilgrim, 1913)

Holotype. GSI D 172, right mandibular ramus of a juvenile individual from Chinji Formation with d2-4, canine and p2-m1.

Diagnosis. Percrocutid of relatively small size. Last molars (M2/m2) lost. The m1 is lacking a metaconid or presents a residual–metaconid; tendency toward shortening of the talonid and elongation of the trigonid. P3 with or without an internal root; P4 with a reduced protocone, situated more or less posteriorly to the anterior margin of the parastyle. Specialization of the dentition distinguished by hypertrophy of the anterior premolars; p2 and p3 are short (relative to p4 and m1) and broad with high robusticity indices (Howell and Petter, 1985).

Species: *Percrocuta carnifex* (Pilgrim, 1913)

Material. PUPC 2016/16A is a fragmentary right mandible including p2 and m1 with the crown of p3 broken (Fig. 2).

Description. The preserved length of the mandibular ramus is 132.0mm, whereas the maximum breadth of this ramus is 19.0mm. The depth of the ramus below p2 and m1 is 36.0mm and 44.0mm, respectively. It presents an excellent state of preservation and the teeth are at medium

TABLE 1. Dental measurements of *Percrocuta carnifex*, in millimeters. Data from Pilgrim (1932)[1], Colbert (1935)[2], Ghaffar *et al.*, (2011)[3], Howell and Petter (1985)[4] and Kurtén (1957)[5]

Specimens	P2		P3		P4		m1	
	L	W	L	W	L	W	L	W
PUPC 2016/16A (This study)	16.5	10	19.5	13	24	14	24	10.5
GSI D 172 (Type specimen)[1]	12	-	16.7	-	19.8	12.2	21.6	11.1
P. abessalomi (PIN 428.167)[4]	13	8	15.5	9.4	18	10.8	23	10.3
P. carnifex (GSI D 164)[1]	-	-	-	-	-	-	22.5	11.7
P. carnifex (GSI D 169)[1]	13.8	-	18.4	13.1	-	-	-	-
P. carnifex (GSI D 170)[1]	12.8	10.3	16.7	13.2	-	-	-	-
P. carnifex (GSI D 171)[1]	-	-	16.1	11.8	20.7	11.5	-	-
P. carnifex (AMNH 19405)[2]	-	-	-	-	21	11.5	22	11
P. carnifex (CU-PUPC 2009/01)[3]	-	-	20.5	11.5	22	12.2	25	12
P. gigantean (IVPP 13789)[4]	30.4	20.7	32	21	36.1	20.7	-	-
P. grandis (GSI D 162 and 231)[5]	20.4	14.3	-	-	29.5	17.3	30	-
P. hobeiensis (IVPP-V 4830)[4]	13.2	9.9	15.7	10.4	18.3	11	22	-
P. miocenica (NMB 1962.870)[4]	12.9	10	17	10.8	18.7	10.9	22.2	11
P. tobieni (BMNH 1469)[4]	12.7	7.7	15	9.9	17.4	10	19.8	9.1
P. tungurensis (AMNH 26602)[4]	18.5	14	19	16.5	24	15	32	14.5
Percrocuta sp. (MNHN unnumbered)[4]	-	-	18.3	12.1	-	-	21.2	9.3

wear. The main cusp of p2 is high with a rudimentary posterior cusp. The p3 is missing but its base is preserved, which gives the rough estimates about the tooth structure and size: its antero-posterior and transverse dimensions indicate the hypertrophy of this tooth (Table 1). Similarly, the main cusp of p4 is high, with well-developed anterior and posterior cusps of equal size. For m1, the paraconid is somewhat broader than the protoconid, which, however, is somehow taller and narrower than the former. A small cingulum is also present at the antero-buccal side of paraconid. A very small talonid is much reduced as compared to the trigonid. Both p4 and m1 show a finely wrinkled enamel. One prominent mental foramien is present below the midpoint of p2 about halfway down the depth of the jaw.

DISCUSSION

The mandibular ramus described here is missing its anterior region including the canine, but canine alveolus indicates a large canine was present. Similarly, the mandibular ramus is very smooth anterior to p2, giving the impression of a diastema and of the absence of p1, a characteristic also noted by Pilgrim (1932) in the type specimen of *P. carnifex*. The p2, with a prominent main cusp and a rudimentary posterior accessory cusp, is similar to the p2 of the type specimen as well as to GSI D 170. The slight difference noted for the p2 here described is that in the type specimen as well as in GSI D 170, it is straight whereas in the specimen described here it is tilted backward. The upper crown of p3 is missing, but the basal outline including the anterior and posterior accessory cusps is preserved, indicating that it is a larger tooth than p2 and equal in size to p4. Also, its anterior and posterior accessory cusps are very similar to the type material and other specimens (*i.e.* GSI D 169, 170), but the anterior and posterior accessory cusps are more prominent if compared to specimen CU-PUPC 2009/1. In p4, the anterior and posterior cusps are prominent and similar to type material, GSI D 171, AMNH 19405 and CU-PUPC 2009/1. The posterior portion of the p4 (posterior cusp) here described

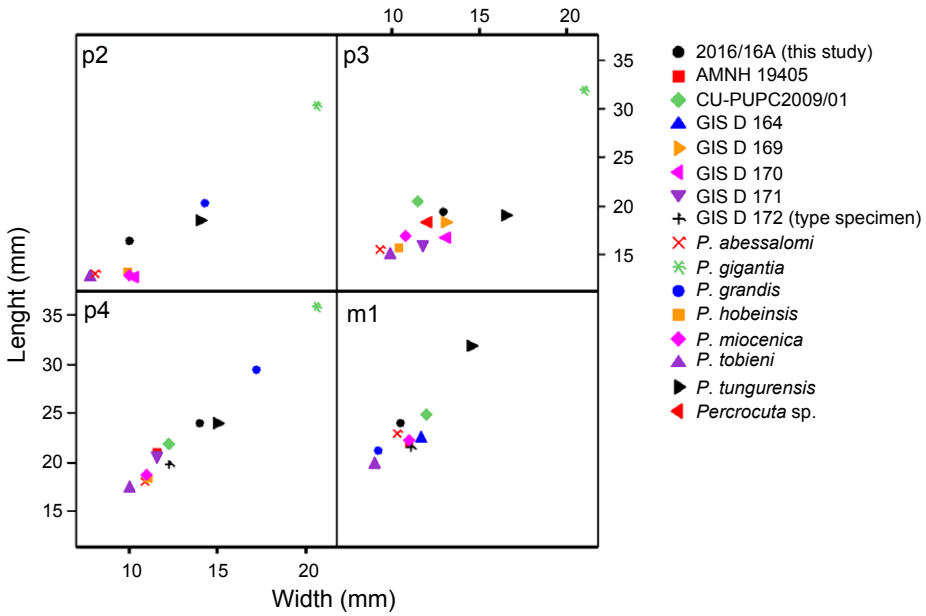

FIGURE 3. Scattered plot showing dental measurements of studied material and other specimens of *Percrocuta carnifex* from the Siwaliks, and other species of *Percrocuta* from Eurasia.

is overlapping with the anterior portion (paraconid) of m1 and this overlapping is also evident in AMNH 19405 but not observed in type material and GSI D 171. In the m1 described here, the paraconid, protoconid and unicuspid talonid are well preserved and similar to those in the type specimen and other specimens, such as GSI D 164, AMNH 19405 and CU-PUPC 2009/1. Moreover, in the m1 here described, the paraconid is broader than the protoconid whereas the protoconid is taller than the paraconid. The paraconid is broader as compared to the protoconid in all the specimens but in the type material, as well as in CU-PUPC 2009/1, these conids are almost equal in height. A protoconid taller than the paraconid, very similar to the situation seen in the m1 here described, can be observed in specimens GSI D 164 and AMNH 19405. In the type material and in GSI D 169, 171, the main cusps in p3-4 are tapering anteriorly, whereas they appear to be somehow blunt in the p3-4 of the specimen here described, of CU-PUPC 2009/1 and AMNH 19405, a difference that is due to the different stage of wear in these specimens. The above mentioned characteristics in comparison with the type material (GSI D 172) as well as all other specimens described from the Siwaliks allow us to assign this specimen to *P. carnifex*.

Morphometric analysis

According to the measurements (Table 1), the p2 described here is longer than the p2 in specimens GSI D 169, 170, 172, but narrower than GSI D 170. Similarly, the p3 here described is longer than the p3 in GSI D 169, 170, 171, 172, and shorter than CU-PUPC 2009/01, but is wider than GSI D 171, CU-PUPC 2009/01, and narrower than GSI D 169, 170. Moreover, the p4 described here is longer and wider than the p4 in GSI D 164, 172, AMNH 19405, CU-PUPC 2009/01. The length of m1 described here is bigger than the m1 in GSI D 164, 172, AMNH 19405, and smaller than CU-PUPC 2009/01, but narrower than GSI D 164, 172, AMNH 19405, CU-PUPC 2009/01 (Fig. 3). Similarly, the p2 described here is longer than the p2 in *Percrocuta abessalomi* (Gabunia, 1973), *Percrocuta tobieni*, *Percrocuta hobeiensis* and *Percrocuta miocenica* (Ciric, 1960), shorter than in *Percrocuta tungurensis* (Colbert, 1939), *Percrocuta grandis* (Kurtén, 1957), *Percrocuta gigantea* (Schlosser, 1903) and *Percrocuta* sp. from Al Jadidah, wider than in *P. abessalomi*, *P. tobieni*, *P. hobeiensis*, and equal to the ones of *P. miocenica*, and narrower than in *P. tungurensis*, *P. gigantea* and *P. grandis*. The p3 described here is longer than the p3 in *P. abessalomi*, *P. tobieni*, *P. hobeiensis*, *P. miocenica*, *P. tungurensis*, shorter than in *P. gigantea*, while broader than in *P. abessalomi*, *P. tobieni*, *P. hobeiensis*, *P. miocenica* and *Percrocuta* sp. from Al Jadidah, and narrower than *P. tungurensis* and *P. gigantea*. The p4 described here is longer than the p4 in *P. abessalomi*, *P. tobieni*, *P. hobeiensis*, *P. miocenica*, equal to the ones seen in *P. tungurensis*, and shorter than in *P. gigantea* and in *P. grandis*, while being wider than in *P. abessalomi*, *P. tobieni*, *P. hobeiensis*, *P. miocenica*, and narrower than in *P. tungurensis*, *P. gigantea* and *P. grandis*. The m1 described in this paper is longer than the m1 in *P. abessalomi*, *P. tobieni*, *P. hobeiensis*, *P.*

miocenica and *Percrocuta* sp. from Al Jadidah, while being shorter than in *P. tungurensis* and *P. grandis*, and wider than in *P. abessalomi*, *P. tobieni*, and *Percrocuta* sp. from Al Jadidah, and narrower than in *P. miocenica* and *P. tungurensis* (Fig. 3).

Morales and Pickford (2006) argued that percrocutids from the Late Miocene are larger than Middle Miocene species. Similarly, a gradual increase in size was observed in Eurasia from the small species *P. abessalomi*, *P. tungurensis*, *P. miocenica* to large species in the Late Miocene, such as *P. gigantea* and *P. grandis*. This gradual increase in size is also evident within the single species as the specimens recovered from Chinji Formation (GSI D 169, 170, 171, 172, AMNH 19405) have smaller lengths than those from the Nagri Formation (CU-PUPC 2009/01 and the specimen described here). Similarly, on the basis of tooth size, *P. carnifex* is smaller than *P. grandis*. On the basis of above statement, we can argue that specimen GSI D 164 may also belong to either the Chinji Formation or Nagri Formation rather than the Dhok Pathan Formation and more probably to the Chinji Formation, because the length and width of m1 fits well with the specimens described from this formation. If these observations are correct, they also indicate that no fossil material of *P. carnifex* has been recovered from the Dhok Pathan Formation yet.

Historical review and Stratigraphic analysis

After Pilgrim (1932), hyaenids of the Middle Siwaliks were critically studied by Kurtén (1957), by opting *Percrocuta* as a subgenus of *Crocuta*. On the basis of size differences and protocone structure in the upper premolar (P4), he recognized 5-6 species of percrocutids from the Siwalik Hills of the Indian subcontinent. Moreover, he argued that the metastyle blade of P4 in *Percrocuta* is longer than in *Hyaena* but shorter than in *Crocuta*. In *P. carnifex*, the trigonid of m1 is somewhat long, with a short talonid. As a result, unicuspid talonids can only be seen in this species as compared to other species of this genus. He also noted that this species appeared during the Early Pliocene, but more recently, Barry *et al*. (2002) established that the Chinji Formation belongs to late Middle Miocene (14.2–11.2Ma) and the Nagri Formation to the Late Miocene (11.2–9.5Ma).

Percrocutids appeared in the upper Middle Miocene, or Astaracian, in Eurasia and persisted for at least 3 million years (Howell and Petter, 1985), while in the Siwalik continental deposits they persisted longer than in Eurasia, as one species *P. grandis* (Kurtén, 1957) is described from the Dhok Pathan Formation. Moreover, during the Vallesian, *Adcrocuta*, *Adcrocuta eximia* (Pilgrim, 1932) was widely spread and it limited the expansion of percrocutids in Eurasia. From the Siwalik continental deposits, fossils of *A. eximia* were recovered from the Dhok Pathan Formation, and it possibly limited the distribution of percrocutids as the latter are mostly recovered and described from thr Chinji and Nagri formations. On the other hand, no fossil record of *A. eximia* is known to date from the Chinji or Nagri formations of the Siwaliks.

As mentioned earlier, a detailed description of different species of *Percrocuta* was made by Kurtén (1957) and Howell and Petter (1985). This genus appeared at the base of the Astaracian land mammal age, but the root of this group is still unclear, that is, the ancestors of *P. abessalomi*, *P. tobieni* and *P. miocenica* are unknown (Howell and Petter, 1985). However, these African species are considered more primitive than the Eurasian and Siwalik species. Some features are more specialized in *P. miocenica* than in *P. abessalomi* found in southeast Europe, Anatolia and eastern China, moreover, *P. miocenica* had a vast distribution with limited duration, being restricted to an earlier Astaracian age (MN zone 6), while *P. carnifex*, had a limited distribution and a duration longer than *P. miocenica*. A number of specimens of *P. carnifex* from the Chinji and Nagri formations of Siwaliks have been described. Howell and Petter (1985) suggested a close relationship between *Percrocuta* sp. from Al Jadidah and *P. carnifex* from Siwaliks by faunal exchange between the northern part of the Indian subcontinent and western Asia during the Late Astaracian. In western Asia, *P. carnifex* may have replaced *P. miocenica* and, according to Howell and Petter (1985), *P. tungurensis* was restricted to Mongolia, but it is known from Çandir, Turkey (Mayda *et al*., 2015; Schmidt-Kittler, 1976). Thenius (1966) and Soria (1980) argued that *P. tungurensis* derived from *P. carnifex*, and the stratigraphic analysis of the Tung Gur Formation of Mongolia and of the Chinji Formation supports this idea.

Phylogenetic relationships

Although p3 is not present in the specimen described here, its base is preserved and can be compared with *Percrocuta* sp. from the Hofuf Formation, Al Jadidah, Saudi Arabia (Middle Astaracian). This comparison shows that the basal outline of p3 is similar in both species. On the basis of material described here (*i.e*. lower dentition) and material from the Siwaliks described by previous authors, it is impossible to draw any conclusion regarding the ancestry of *P. carnifex*, but we can draw the following conclusions:

i) the hypertrophy of p3 in *Percrocuta* sp. from Al Jadidah, and in *P. carnifex* (based on the measurements of its base) from Siwaliks suggests a relationship between these two species, but *Percrocuta* sp. has an older stratigraphic range.

ii) the hypertrophy of p3 and small size of m1 in the material described here show that *P. carnifex* is closer to

P. tobieni and *P. miocenica* than to *P. abessalomi* and *P. tobieni*, although the morphological differences with *P. abessalomi* are slight (Howell and Petter, 1985). Similarly, the presence of a median internal root in P3 in *Percrocuta* sp. from Al Jadidah, places this species in the lineage of either *P. miocenica* or *P. carnifex* or in a common lineage for these two species. It is worth noticing here that *P. miocenica* is older than *Percrocuta* sp. and younger than *P. carnifex*. The median internal root of P3 is absent in *P. abessalomi* a difference between this species and *P. carnifex*. Due to that *P. miocenica* and *P. hebeiensis*, have very similar mandibular material, these two species can be tentatively synonymized, but more material is needed to confirm it, particularly upper dentitions of *P. hebeiensis*. In general *P. abessalomi* show more primitive characters than the other species, it has an older stratigraphic range and a smaller size. These characters suggest that it is a primitive species; however, they do not denote any relation to other percrocutid species, particularly to *P. carnifex*. On the other hand, *P. carnifex* shares some characters with *P. miocenica* and *P. tobieni*. The relationship between all mentioned species is obscure. Moreover, the Al Jadidah specimen has some common characters with *P. carnifex*, *P. tobieni* and *P. miocenica*.

iii) Kurtén (1957) noticed the similarities in the tooth morphology of *P. carnifex*, *P. grandis* and *P. gigantea* but the size of the teeth in the two latter species was greater than in *P. carnifex*. Moreover, *P. grandis* is intermediate between the *P. carnifex* and *P. gigantea*. The material of *P. grandis* was recovered from the Nagri and Dhok Pathan formations. The larger dimension of *P. grandis* compared to *P. carnifex* may explain its occurrence in the Dhok Pathan Formation. According to Kurtén (1957) *P. grandis* and *Adcrocuta eximia* show a parallel history as both species are recovered from the Nagri and Dhok Pathan formations. Moreover, Kurtén (1957) suggested that *P. grandis* and *P. gigantea* differ from each other mainly in size, and that they could be synonymized if new material of these two species were found.

Soria (1980) synonymized *P. abessalomi*, *P. miocenica* and *P. tobieni* with *P. carnifex*. She suggested a new name for all these species, *P. pilgrimi*, and proposed two subspecies *P. carnifex abessalomi* (*i.e.* to stand for *P. abessalomi* and *P. tobieni*) and *P. carnifex carnifex* (*i.e.* to stand for *P. miocenica* and *P. carnifex*). This distinction was based on the robustness indices of p2 and p3, which are lower in *P. carnifex abessalomi* when compared to *P. carnifex carnifex*. According to Soria, the former subspecies is more primitive, and the latter derived from it, but the proposition of Soria was not followed, as it did not include the robustness indices of p4 and m1. In our opinion, synonymizing different species can only be justified if there is a direct relationship between them, and to synonymize the above mentioned species, more studies on their linkage have to be done.

CONCLUSION

Dentary material of *Percrocuta carnifex* from the Nagri Formation of Siwaliks, Pakistan, is described. The morphology and morphometric analysis of all specimens from Siwaliks suggests that, until now, there is no record of this species from the Dhok Pathan Formation or from any equivalents of this formation in the Siwalik Hills or outside the region. This species is probably restricted to the Chinji and Nagri formations. The dental morphological similarities between species from Asia, Africa and Europe, suggest that there was a certain amount of gene flow through the Eurasia and Africa continents. The discovery of new species of older stratigraphic range (Kamlial Formation) might resolve the issue of the ancestry of *P. carnifex* or provide phylogenetic links between the species of this genus from different continents.

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