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Late Miocene Hyaenids from the Middle Siwaliks of Pakistan

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Abstract. – New dental material of the late Miocene hyaenids, *Percrocuta carnifex* and *Adcrocuta eximia latro,* from the Siwaliks of Pakistan were excavated and described. These fossils with sound arguments testify the validity of both the genera described by Kretzoi, and followed by others. Moreover, they also shed light on the biogeographic and stratigraphic evidences of these species and genera (*Percrocuta* and *Adcrocuta*) from the Siwalik continental deposits.

Key words: *Percrocuta carnifex, Adcrocuta eximia latro,* dental material, biogeographic and stratigraphic evidences..

INTRODUCTION

We recently (February, 2009) found a well exposed left mandibular ramus with p3-m1 of *Percrocuta carnifex* from the Nagri Formation, near village Nagri Sethi, Pakistan (Lat. 32° 44′ 51 N: Long. 72° 39′ 26 E). A portion of maxillae with P1-2 and P4 and mandibular ramus with p1-m1 of *A. eximia latro* was collected from Dhok Pathan Formation, from Dhok Pathan, Pakistan (Lat. 33° 08′ 10 N: Long. 72° 20′ 49 E) in 1998. The maxillary and mandibular fragments were excavated from the same place and might belong to single individual. Both of these Formations are considered as the middle member of the Siwalik group (Barry *et al.,* 2002; Ohja *et al.,* 2000, Pilbeam *et al*., 1977).

Roth and Wagner (1854) described *Hyaena eximia*, from Pikermi, Greece for the first time. This species was subsequently described from a number of other Eurasian localities of Turolian age (Solounias, 1981). Zdansky (1924) described *Hyaena variabilis*, closely related to *H. eximia*, from the deposits of late Miocene age from Shanxi, China. These two species (*H. eximia* and *H. variabilis*) were synonymized by Pilgrim (1931) as *Crocuta eximia*. *Crocuta eximia*, with two additional species (*C. variabilis* and *C. mordax*) was shifted to genus *Adcrocuta* by Kretzoi (1938). At the same time, Kretzoi created the genus *Percrocuta* for some other percrocutoid forms (hyaenids of relatively small size and with a reduced P^4 protocone). These taxonomic judgments by Kretzoi (1938) were largely ignored and several of these forms were subsequently referred to as various genera and most often to the genus *Crocuta*. In a major study of these forms Kurtén (1957) resurrected *Percrocuta* as a subgenus of *Crocuta* but considered *Percrocuta* and *Adcrocuta* synonymous. He also reattributed six species (*Hyaena variabilis, Crocuta mordex, C. gigantea, Percrocuta carnifex, P. grandis* and *Adcrocuta eximia*) previously assigned to *Hyaena* Brisson, *Crocuta* Kaup,

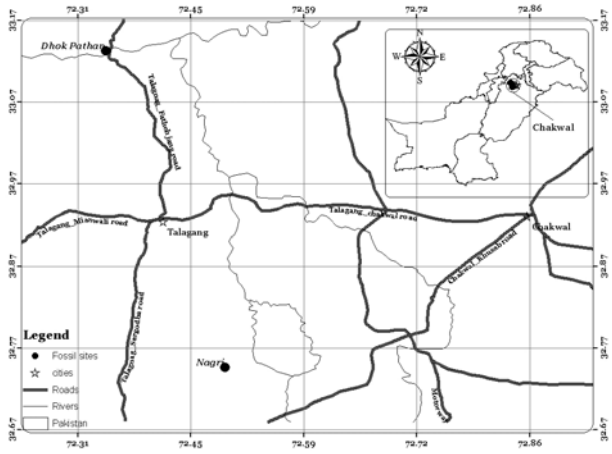

Fig. 1. Map of Pakistan (inset) with an enlargement of study areas (Nagri and Dhok Pathan) from Chakwal district.

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Percrocuta Kretzoi, and *Adcrocuta* Kretzoi, to *Percrocuta.* Similarly, he combined *H. variabilis* (Zdansky, 1924) and *C. mordax* (Pilgrim, 1932) as *C. gigantean latro* and further synonymized these forms with *H. eximia* having three subspecies as *C. eximia eximia*, *C. eximia variabilis* and *C. eximia latro*. In his review of Hyaenidae, Thenius (1966) separated *Percrocuta* from *Crocuta* at the generic level. Subsequently, Ficcarelli and Torre (1970) rehabilitated the genus *Adcrocuta* Kretzoi and formerly distinguished it from *Percrocuta*. Schmidt-Kittler (1976) and Chen and Schmidt-Kittler (1983) confirmed the distinctiveness of *Percrocuta* and *Adcrocuta* in the revision of Neogene hyaenids based on major differences in the deciduous dentition, among other factors. Moreover, Schmidt-Kittler subdivided the genus *Percrocuta* into two subgenera, *Percrocuta* and *Dinocrocuta*. Furthermore Schmidt-Kittler also recognized the genus *Allohyaena* as a distinct genus and is not closely related to *Percrocuta*. Lastly, Solounias (1981) synonymized *Percrocuta* and *Adcrocuta* with *Hyaenictis* Gaudry, whereas Kurtén (1982) considered *Percrocuta* and *Hyaenictis* as two distinct genera. Howell and Petter (1985) considered *Percrocuta*, *Adcrocuta* and *Allohyaena* as distinct genera. They also described the differences of these genera with *Hyaenictis*. Werdelin and Solounias (1990; 1991) placed *Adcrocuta* as a sister-group to recent *Crocuta crocuta.*

Kretzoi assigned four species to *Adcrocuta*, as *A. praecursor* (Kretzoi, 1938); *A. eximia* (Roth and Wagner, 1854); *A. variabilis* (Zdansky, 1924) and *A. mordax* (Pilgrim, 1932). Hendy (1974; 1978) added *A. australis* to this genus from Africa but Werdelin and Solounias (1990) and Qiu (1987) argued that the protocone in *A. australis* is less reduced as compare to *A. eximia* and the reduction of the protocone can characterize some *Chasmaporthetes*, which tend to unite *A. australis* with *Chasmaporthetes.* Bonis and Koufos (1981) also described a new subspecies *A. eximia leptoryncha* from Ravin de la Pluie in Macedonia. According to Howell and Petter (1985), *A. eximia* appeared in Europe as early as 11Ma and then in Asia. The particular attention should be given to their geologic age and their distribution in Neogene mammalian faunas. The fossil finds described here also support the idea of Howell and Petter (1985) that the radiation of "percrocutoid" would appear to have occurred in three phases, one was at the beginning of Astaracian, the genus *Percrocuta* appeared with several species of relatively small size; in Eurasia "percrocutoid" hyaenids did not persist after Middle Astarasian but persisted in sub-Himalayan Siwaliks. The second one was at the end of Astarasian, which apparently succeeded by the genus *Dinocrocuta*. The third radiation is *Adcrocuta* and the fossil finds described here from Dhok Pathan Formation, testify this radiation.

Abbreviations

CU-PUPC, Comsats University - Punjab University Paleontological Collection; AMNH, American Museum of Natural History; GUB, Benghazi, Garyounis University, Geology Department Museum; IHGP, Munich, Institute fur Palaontologie und Historische Geologie der Universitat Munchen; IVPP, Beijing, Institute of Vertebrate Paleontology and Paleoanthropology; IP, Tbilisi, Institute of paleobiology, Academy of Georgia, USSR; LGPT, Thessaloniki Laboratory of Geology and Paleontology, University of Thessaloniki; PIN, Moscou, Paleontological Institute, Academy of Sciences, USSR; PIUU, Uppsala, Paleontological Institute University of Uppsala; Ma, million years ago; A, *Adcrocuta*; C, *Crocuta*; P, *Percrocuta*; P1, first upper premolar; P2, second upper premolar; P4, fourth upper premolar; p1, first lower premolar; p2, second lower premolar; p3, third lower premolar; p4, fourth lower premolar; m1, first lower molar; L, largest length; W, width.

SYSTEMATIC PALAEONTOLOGY

Order Carnivora Bowdich, 1821
Family Percrocutidae Werdelin and Solounias, 1991
Genus *PERCROCUTA* Kretzoi, 1938
Percrocuta carnifex (Pilgrim, 1913)
(Figs. 2A-C)

Diagnosis

Percrocutids of relatively small size. Last molars (M2/m2) lost. The m1 lacking a metaconid or with a residual metaconid; tendency toward

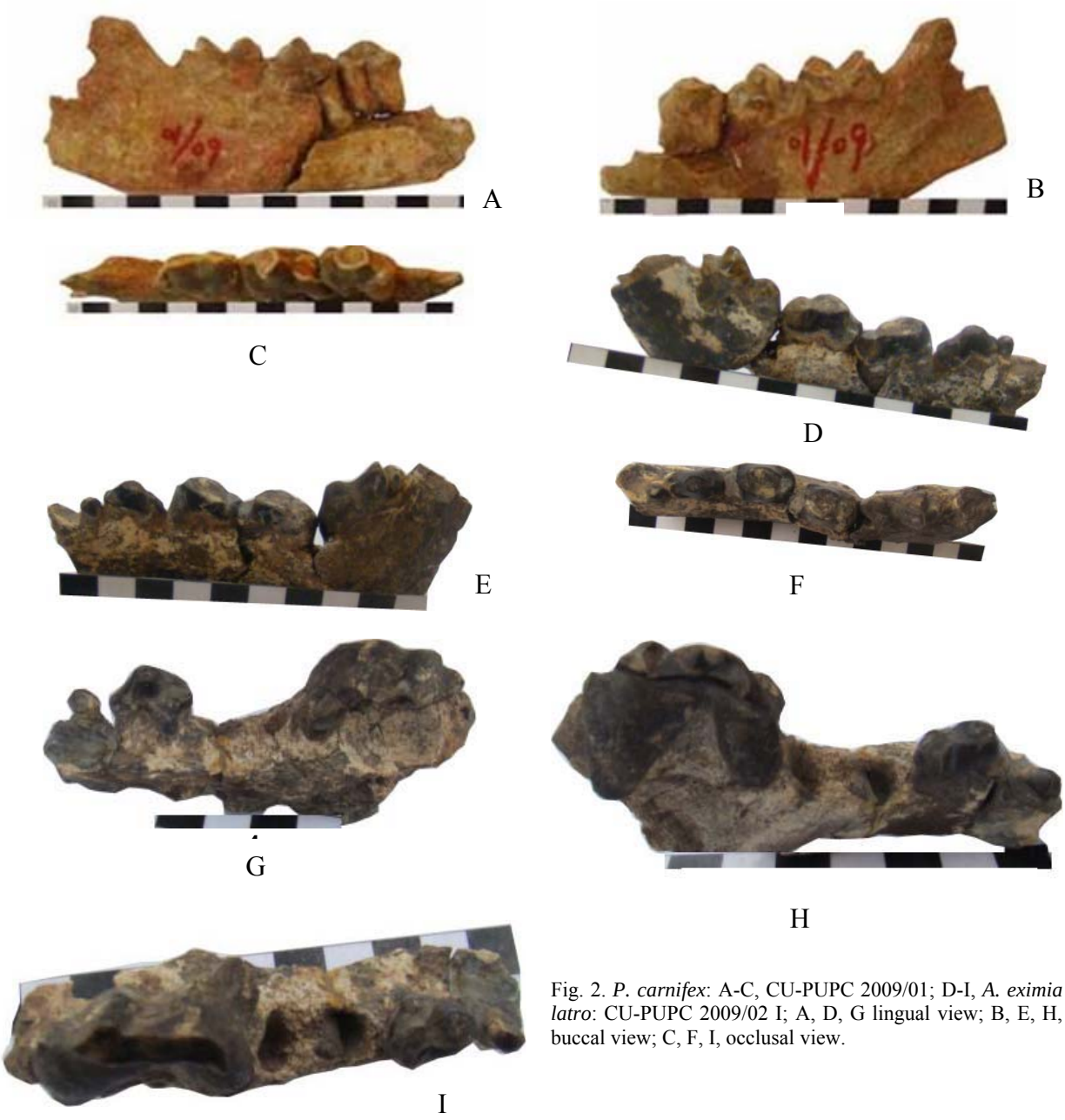

Fig. 2. *P. carnifex*: A-C, CU-PUPC 2009/01; D-I, *A. eximia latro*: CU-PUPC 2009/02 I; A, D, G lingual view; B, E, H, buccal view; C, F, I, occlusal view.

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 posterior to the anterior margin of the parastyle. Specialization of the dentition distinguished by hypertrophy of the anterior premolar; p2 and p3 are short (relative to p4 and m1) and broad with high robusticity indices (Howell and Petter, 1985).

Description

CU- PUPC 2009/01 is a left dentary fragment with p3-m1. The p3 has a small posterior accessory cusp and a very small cingulum anterolingually, while p4 has well developed anterior and posterior accessory cusps, the posterior one being larger and ending in a widened posterior cingulum. Third premolar (p3) is slightly smaller than p4 (Table I).

Table I.- Comparative dental measurements (mm) of *P. carnifex* with other *Percrocutid* species

Specimen # and species	p3		p4		m1	
	L	W	L	W	L	W
CU-PUPC 2009/1 (studied specimen)	20.5	11.5	22	12.2	25	12
GSI D-172 (*P. carnifex*)	16.7	-	19.8	12.2	21.6	11.1
AMNH 26602 (*P. tungurensis*)	19	16.5	24	15	32	14.5
IVPP-V. 4830 (*P.hebiensis*)	15.7	10.4	18.3	11	22	-
NMB 1962.870 (*P.miocenica*)	17	10.8	18.7	10.9	22.2	11
PIN 428.167 (*P.abessalomi*)	15.5	9.4	18	10.8	23	10.3

The m1 has a robust paraconid, compared to shorter protoconid and without metaconid. Similarly the paraconid is greater anteroposteriorly as compared to protoconid. The talonid basin is weakly developed but distinctive. The teeth show an advance stage of wear representing an older adult individual. The roots of p3 and anterior root of p4 are visible.

Family Hyaenidae Gray, 1821
Genus *ADCROCUTA* Kretzoi, 1938
Species *A. eximia latro* (Pilgrim, 1932)
(Fig. 2D-I)

Diagnosis

Hyaenid of moderate or large size. First premolar (P1/p1) present. Last molars (M2/m2) lost. The lower carnassial (m1) with a residual metaconid; tendency toward shortening of the talonid and elongation of the trigonid. P4 with a reduced protocone, situated more or less posterior to the anterior margin of the parastyle. Specialization of the dentition distinguished by hypertrophy of the anterior premolar; p2 and p3 are short (relative to p4 and m1) and broad with high robusticity indices. Lower carnassial (m1) is longer relatively to p4 in *Adcrocuta* than *Percrocuta* (Howell and Petter, 1985)

Description

CU-PUPC 2009/02 is a left maxillary portion with P1-2 and P4 and left dentary fragment with p1-m1. Maxillary P1 is a very small tooth with a rudimentary posterior cusp while in P2 the main cusp is high and the posterior accessory cusp is differentiated and there is also cingulum anterolingualy. P3 is missing but its alveoli indicate that it is a large tooth as compared to P2. P4 is a long upper carnassial tooth. Protocone in P4 is well developed and distinct conical cusp which projects anterolingually. The carnassial blade is missing while the roots on the buccal side are visible.

Lower teeth in this specimen are much worn except p1. The p2 crown has a suboval basal contour which is expanded posteriorly. In p3-4, the occlusal surface has been broken. Third premolar (p3) has a small posterior accessory cusp, while p4 has well developed anterior and posterior accessory cusps, the posterior one being larger and ending in a widened posterior cingulum. The p3 is slightly smaller than p4. The m1 is badly broken and the carnassial blade is missing but the talonid and rudimentary metaconid are preserved. The talonid is large, narrow posteriorly and with postero-buccal cingulum.

DISCUSSION AND ANALYSIS

The name *Percrocuta carnifex* is assigned to specimen CU-PUPC 2009/01. If we examine the specimen very carefully, it is clear that there is only space for a single tooth before p3 and after that there is a smooth surface just like diastema indicating that there is no p1, a special character is assigned to *Adcrocuta*. Secondly at the anterior tip of mandibular ramus there is a hollow mark indicating the presence of a canine tooth, while all other characters resemble with the type specimen, described by Pilgrim (1913, 1932) as *Hyaena carnifex* and *Crocuta carnifex* respectively. Subsequent authors used the Siwalik specimen as a reference for *Percrocuta carnifex* instead of *Crocuta carnifex*, described by Pilgrim (1932) but no significant material has been added from the Siwalik

Table II.- Comparative dental measurements of maxillary teeth and mandibular teeth with other *Adcrocuta* species from different countries.

Specimen # and species	P1		P2		P3		P4		M1	
	L	W	L	W	L	W	L	W	L	W
Maxillary teeth										
CU-PUPC 09/02 (Studied specimen)	7.5	5.5	18.0	11.9	(21.6)	(13.0)	34.4	19.0	-	-
Pikermi IHGP (*A.eximia eximia*)	7.6	7.0	15.7	11.4	20.8	14.6	35.1	17.2	-	-
China PIUU8 (*A.eximia variabilis*)	7.4	7.5	17.5	11.4	21.5	15.3	37.5	18.9	-	-
Russia PIN 2330 (*A.eximia praecursor*)	8.0	7.3	16.8	11.5	21.5	14.8	38.0	16.2	-	-
Greece LGPT RPL 14 (*A.eximia leptoryncha*)	7.3	7.0	17.7	12.9	22.8	15.6	38.5	18.2	-	-
Georgia IP B40 (*A. eximia miriani)*	-	-	15.0	10.6	21.6	14.5	34.0	17.3	-	-
Mandibular teeth										
CU-PUPC 09/02 (Studied specimen)	5.5	5.1	16	9	19.5	10.8	20.6	12.9	27	11.2
Pikermi IHGP (*A. eximia eximia*)	6.1	6.0	17.0	11.3	19.4	14.2	21.1	13.8	27.8	13.0
China PIUU8 (*A. eximia variabilis*)	5.1	5.5	15.4	10.7	19.4	13.6	21.8	13.7	27.5	12.9
Russia PIN 95 *(A. eximia praecursor*)	6.0	5.8	15.5	10.8	22.0	13.0	22.5	13.0	28.5	12.2
Greece LGPT RPL 15 (*A. eximia leptoryncha*)	-	-	13.0	9.3	18.0	12.0	22.3	11.3	28.2	11.9

(); measurements taken on roots

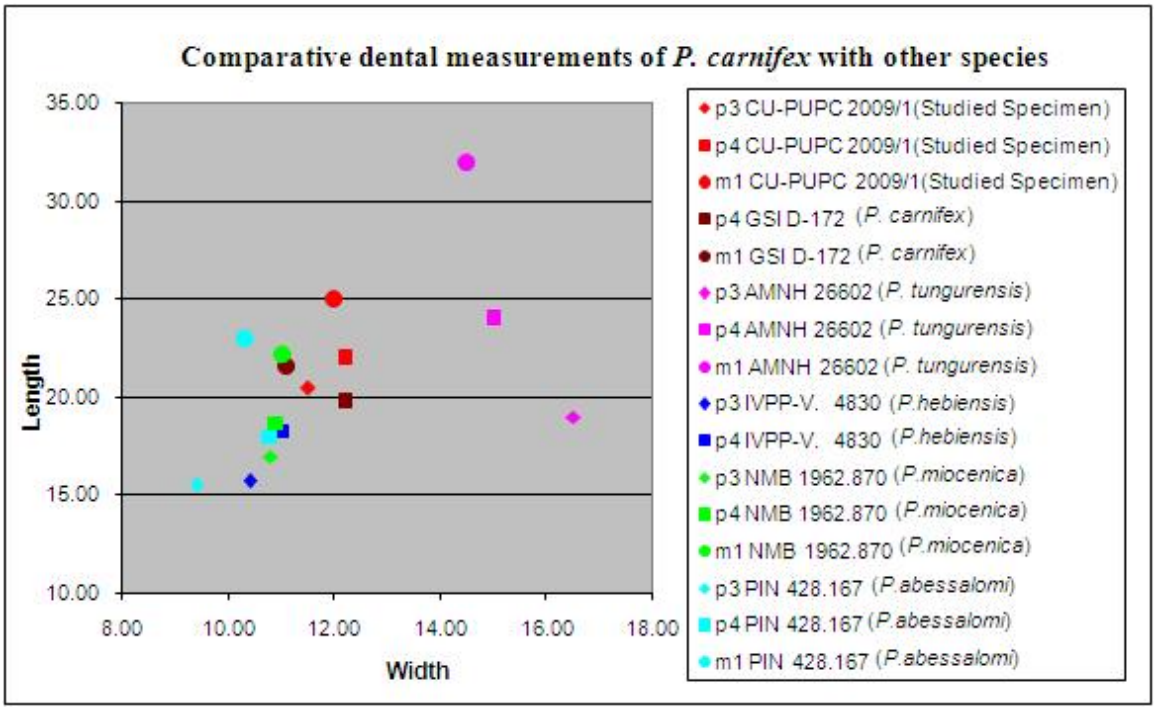

Fig. 3. Bivariate scatter diagram showing comparison of the studied specimen with the other percrocutid species.

continental deposits. The collection of fossil material of *Percrocuta carnifex* from the Nagri Formation (11.2-9Ma) extends its stratigraphic range from Chinji Formation (14.2-11.2Ma) – Nagri Formation (11.2-9Ma). The American Museum specimen (A.M. 19405) of *Percrocuta carnifex* comes from the base of the Chinji zone (Colbert, 1935); the specimens described by Pilgrim (1932) were found at the top of the Chinji beds while the specimen under study was collected from the Nagri Formation (early Late Miocene). Moreover Pilgrim also noted that, the ramus is rather deep just behind m1 and the lower border curves upward and the masseteric fossa extends forward to the posterior

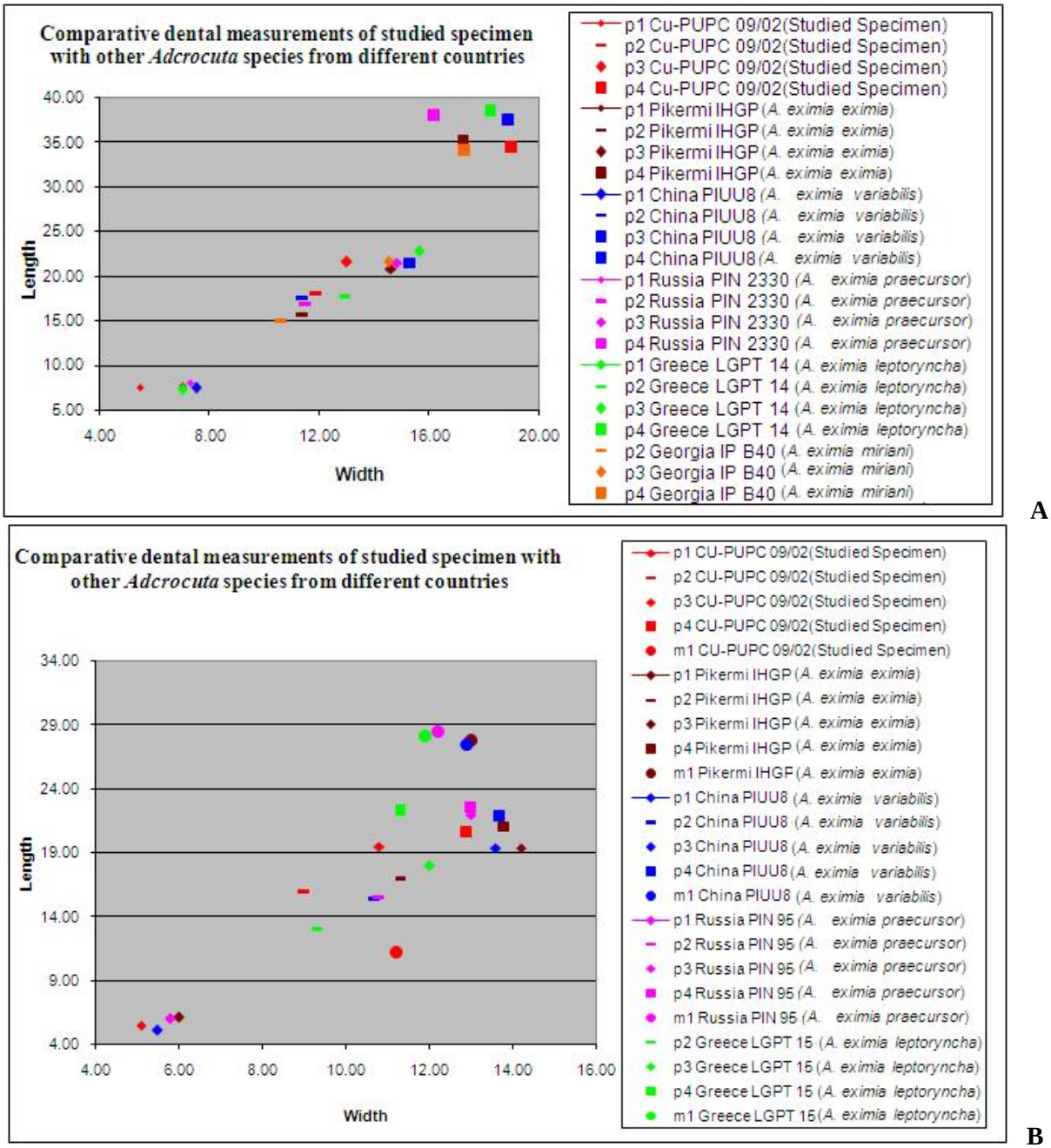

Fig. 4. Bivariate scatter diagram showing comparison maxillary teeth (A) and mandibular teeth (B) with the other *Adcrocuta* species.

border of m1. The specimen under study, exhibit the similar characters. The accessory cusps of p3 are weakly developed in the specimen under study, as in more-derived bone-cracking hyaenines, unlike chasmaporthetines with elongated and well-developed accessory cusps of the third premolar (Tseng and Chang, 2007, Antón, *et al.*, 2006).

The name *A. eximia latro* (Pilgrim, 1932), is assigned to the specimen CU-PUPC 2009/02, because it bears lower first premolar. Secondly, according to Ficcarelli and Torre (1970), the lower carnassial (m1) is longer relatively to p4 in type

species (*Adcrocuta eximia)* as compare to (*Percrocuta carnifex),* and the specimens under study have these characters, (Tables I, II). Similarly according to Schmidt-Kittler (1976), lower carnassial (m1) is less reduced in *Adcrocuta* than *Percrocuta.* Moreover m1 with less reduced talonid and sometime with metaconid in *Adcrocuta* but with a rudimentary talonid, unicuspid and without metaconid in *Percrocuta* are the characteristics of these genera. In *Percrocuta* m1 has a relatively reduced talonid with only one cusp (hypoconid) while in *Adcrocuta* talonid in m1 is large with a postero-buccal cingulum; the specimens under study exhibit these characters. In addition the mandibular ramii of the species under study cannot be compared because the mandibular ramus of *A. eximia latro* (CU-PUPC 2009/02) is badly deteriorated at the base. However, the ramus in *P. carnifex* (CU-PUPC 2009/01) is well preserved. It is rather deep just behind m1 and the lower border curves upward and this character was also noted by Pilgrim (1932) in GSI D-172 collected from the Chinji Formation. Similarly the depth of ramus in the studied specimen and AMNH specimen below the anterior border of m1 is 41mm and 40mm, respectively. The depth of ramus below p3 in both the specimens under study is 21mm and 29mm, respectively. Although the mandible of *A. eximia latro* is missing at the base even then it has greater depth (29mm) as compare to *P. carnifex* (21mm) that is well preserved. On the basis of above mentioned characters it is evident that the specimen assigned to *P. carnifex* is smaller in size as compare to *A. eximia latro*. CU-PUPC 2009/02 is different from *Hyaenictis* (*H. graeca*), because in *Hyaenictis graeca*, lower carnassial is long without any trace of metaconid, talonid is substantial, broad and irregularly square and not narrow posteriorly. However, the specimen under study has a rudimentary metaconid and a small talonid that is narrow posteriorly. Similarly narrow premolars of *H. graeca* and broad and robust premolars of *A.eximia* represent two different types of functionally distinct adaptations (Howell and Petter, 1985). From the Siwaliks, fossil remains of *P. carnifex* (*C. carnifex*; Pilgrim, 1932) were described from type section of Chinji Formation (Chakwal district) and Chinji Formation situated near Hasnot village (Jehlum district) but the specimen described here come from Nagri Formation of Nagri type locality (Chakwal district). Similarly the fossil material of *A. eximia latro* (*C. mordax*; Pilgrim, 1932) was described from the Dhok Pathan Formation near Hasnot village (Jehlum district) while the specimens described here were collected from the type section of Dhok Pathan Formation, Dhok Pathan (Chakwal district). In Eurasia the genus *Percrocuta* did not persisted after Middle Astarasian but persisted in the Siwalik continental deposits. The specimen of *P. carnifex,* under study from the Nagri Formation (early Late Miocene) confirms this idea. Similarly *Adcrocuta eximia* first appeared in Europe (11Ma) and then in Asia; the specimens of *A. eximia latro* described here from the Latest Dhok Pathan Formation (7-5Ma) also confirm these biases.

The percrocutids were referred for a long time to family Hyaenidae but Werdelin and Solounias (1991) distinguished them as a separate family Percrocutidae. However quite earlier Schmidt-Kittler (1976) and Chen and Schmidt-Kittler (1983) suggested the distinction of percrocutids from hyaenids, based on the deciduous dentition. The carnassial teeth of *A. eximia latro* show the hyaena like characters, since percrocutids have a different morphology of these teeth. On the basis of these characters, *P. carnifex* is placed in the family Percrocutidae while *A. eximia latro* is assigned the family Hyaenidae. Moreover the material of *P. carnifex* comes from the older stratigraphic range (Nagri Formation; lower Middle Siwalik) as compare to the fossils of *A. eximia latro*; that are from the younger stratigraphic range (Dhok Pathan Formation; upper Middle Siwalik). On the basis of carnassial tooth morphology, dentition size, structure and size of mandible and stratigraphic range of fossil finds, the *Percrocuta* material is referred to a separate family, Percrocutidae.

CONCLUSIONS

We report new materials of *P. carnifex* and *A.eximia latro* from the Late Miocene of the Siwalik continental deposits, which enhance our understanding of the late Miocene hyaenids. These findings provide a direct evidence of diversification and persistence of *Percrocuta* in the Siwaliks,

though it had become extinct around Astaracian in Eurasia. This study also proves the radiation of *Adcrocuta* in the Dhok Pathn Formation, upper Middle Siwaliks.

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