Rev. bras. paleontol. 19(2):347-356, Maio/Agosto 2016

doi: 10.4072/rbp.2016.2.16

Nota científica/Scientific note

NEW MATERIAL OF *SIVAONYX BATHYGNATHUS* (LUTRINAE, MUSTELIDAE) FROM THE EARLY PLIOCENE OF SIWALIKS, PAKISTAN

ABDUL GHAFFAR
Meteorology Department, COMSATS Institute of Information technology (CIIT), Islamabad, 44000, Pakistan.
aghaffar@comsats.edu.pk

MUHAMMAD AKHTAR
Department of Zoology, Quaid-i-Azam Campus, University of the Punjab, Lahore, 54000, Pakistan.
drakhtarfdrc@hotmail.com

ABSTRACT – Seven species of *Sivaonyx* genus have been described so far from Eurasia and Africa. The type species of the genus is *Sivaonyx bathygnathus* (Lydekker), of which the holotype specimen is GSI D33. In this paper, new fragmentary material from the Dhok Pathan Formation (Middle Siwaliks) of Hasnot, Pakistan is described. Among the known late Miocene-Pliocene fossiliferrous localities, Hasnot is the only fossil bearing locality that preserves a significant fossil record of the genus *Sivaonyx*. Phylogenetic relationships and stratigraphic implications of the newly discovered material with already described specimens from the Siwaliks as well as with all known species of *Sivaonyx* from Africa and Asia are given. The new description of the specimen from the early Pliocene (5.3-3.5Ma) show a younger stratigraphic range than described earlier in the Siwalik continental deposits.

Key words: *Sivaonyx bathygnathus*, fossil material, Hasnot, Dhok Pathan Formation, phylogenetic relationships.

INTRODUCTION

The right mandible fragment with p4-m1 of *Sivaonyx bathygnathus* (Lydekker, 1884) was collected from the Dhok Pathan Formation, near Hasnot village by the team of palaeontologists during the winter season of 2003. This record is significant because Mio-Pliocene carnivores are poorly represented in the Siwalik continental deposits. The new fossil of *S. bathygnathus* from Hasnot is thus an important addition for taxonomic as well as stratigraphic correlations. Hasnot village (32°49'27.89N/73°07'52.68E) is situated in northern Pakistan, approximately 54 km west of Jhelum city (Figure 1). This area has yielded one of the most taxonomically diverse carnivore faunas of late Miocene-early Pliocene age. At least, 19 genera in eight families of carnivores are recognized from this area including large and small carnivores (Ghaffar, 2005). Worldwide the subfamily Lutrinae (family Mustelidae) is represented by nine genera and 13 species. In the Siwalik continental deposits, *Sivaonyx* is represented by two species; *S. bathygnathus* and *S. gandakasensis* Pickford, 2007 (Grohé *et al*., 2013). These bunodont otters successfully occupied the continental ecosystems of Europe, Asia, Africa and North America. Similarly, family Mustelidae is the most diverse family of carnivores with more than 60 extant species (Wilson & Reeder, 1993). Late Miocene otters from the Dhok Pathan Formation of the Siwaliks have been described by various authors (Lydekker, 1884; Pilgrim, 1931; Brown, 1926; Matthew, 1929; Colbert, 1935; Pickford, 2007). All the described specimens including the type specimen and the specimen under study were collected from the Hasnot area. Similarly on the basis of similarities to the type specimen (GSI D33) of *S. bathygnathus* from the Siwaliks, other species of this genus have been described from the Miocene-Pleistocene deposits of North America, Europe and Africa (Repenning, 1976; Alcalá, 1994; Hürzeler, 1987; Pilgrim, 1931; Villalta & Crusafont-Pairó, 1945; Willemsen, 1992, 1999; Hendey, 1974; Morales *et al*., 2005; Morales & Pickford, 2005a,b; Pickford, 2007; Petter *et al*., 1991; Stromer, 1931; Werdelin, 2003; Bonis *et al*., 2008; Peigné *et al*., 2008; Grohé *et al*., 2013).

All the Siwalik formations (*i.e.* Kamlial, Chinji, Nagri, Dhok Pathan and Soan Formation) are well exposed in the Hasnot area surrounded by extensive Neogene freshwater sedimentary rocks. Like the Dhok Pathan type locality, the Hasnot is another famous fossil-bearing site in the Siwalik continental deposits (Lydekker, 1884; Pilgrim, 1910, 1913, 1932; Matthew, 1929; Colbert, 1935; Pilbeam *et al*., 1977; De Vos *et al*., 1987; Barry & Flynn, 1989; Behrensmeyer *et al*., 1995; Barry *et al*., 2002; Khan *et al*., 2009; Ghaffar *et al*., 2010). This fossil region contains lateral facies associations within the fine-grained fossil-bearing floodplain deposits that are characteristic of fluvial depositional environments (Barry & Flynn, 1989; Wills & Behrensmeyer, 1995; Behrensmeyer *et al*., 1995; Barry *et al*., 2002). Based on the lithological characteristics, the study area 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). The fossil assemblages (*i.e.* hipparionines, artiodactyls and carnivores) collected from the study area

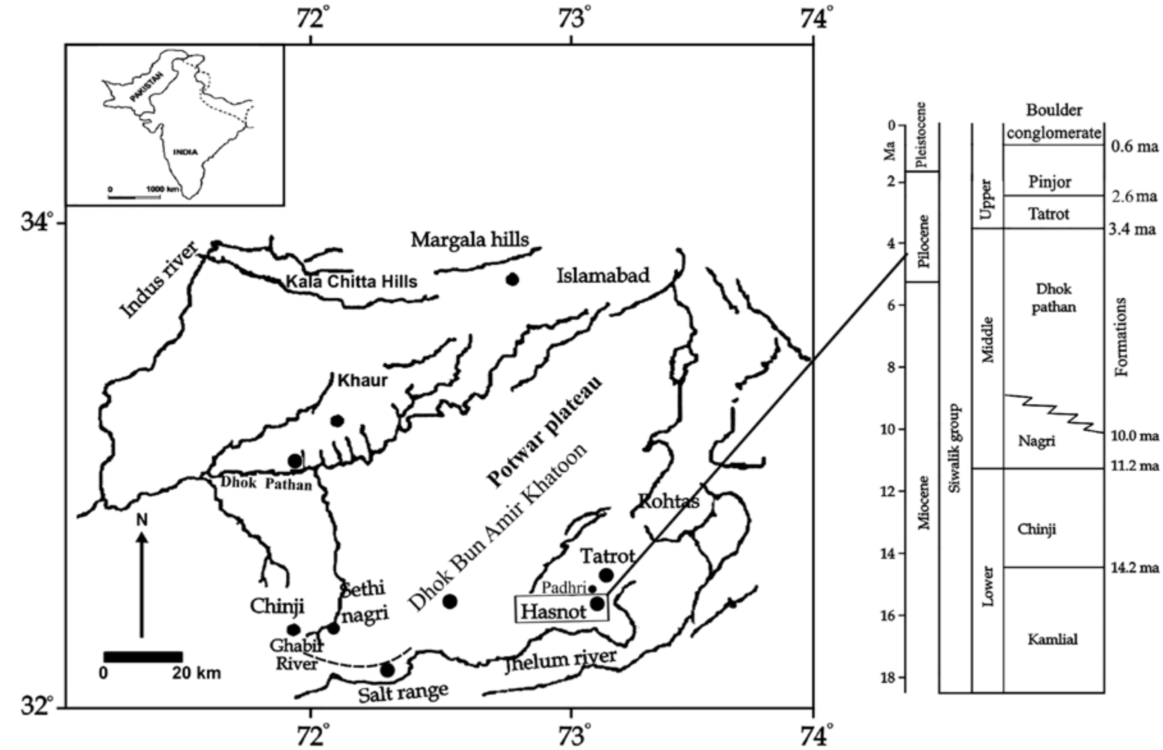

Figure 1. Map of Potwar Plateau (northern Pakistan) with fossil site and stratigraphic section of the major Siwalik formations (modified from Behrensmeyer & Barry, 2005; boundary dates are from Barry *et al*., 2002).

suggest that the age of the fossil site is latest Miocene-early Pliocene (Colbert, 1935; Barry *et al*., 2002; Khan *et al*., 2009; Ghaffar *et al*., 2010).

The aim of this paper is to describe the mustelid fauna from the Siwalik continental deposits. The taxonomy and even the diversity of these bunodont otters has been the subject of much debate based on the fragmentary nature of their fossil record. The fossil record of Siwalik mustelids is based on the fragmentary mandibles, maxillary portions and even isolated upper and lower teeth. Due to this fragmentary nature of the fossil record, assignment of different species to different genera are controversial; this is particularly the case with *Sivaonyx* and *Enhydriodon*. The recovery of new fossil material provides an opportunity to reassess the stratigraphic implications as well the taxonomic assignments of fossil otters from the Pliocene sediments of Hasnot, Pakistan.

MATERIAL 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. Measurements were taken in millimeters with metric vernier calipers. Comparisons were made with the different species of *Sivaonyx*, available from Asia, Africa and Europe (Table 1). The specimen is catalogued by giving a number that consists of the year of collection followed by a serial catalogue number (*e.g.* 2003 /15). Upper case letters stand for upper teeth and lower case letters stand for lower teeth. The morphological and metrical characters of the specimen are described and its systematic determination is discussed in detail.

Abbreviations: AMNH, American Museum of Natural History, New York, USA; **BAR**, fossils from Baringo District, Community Museums of Kenya; **BMNH**, British Museum of Natural History, London, United Kingdon; **BSPG**, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; **GSI**, Geological survey of India; **GSP-Y**, Yale University-Geological Survey of Pakistan; **IVPP V**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, Vertebrate collection; **KNM**, Kenya National Museum, Nairobi; **NK**, fossils from Nkondo, Uganda National Museum, Kampala; **PUPC**, Punjab University Palaeontological Collection; **SAM PQ-L**, Iziko South African Museum, Cape Town; **TM**, fossils from Toros-Menalla, Chad; **YPM**, Yale Peabody Museum, **S**, *Sivaonyx*, **p4**, fourth lower premolar, **m1**, first lower molar.

SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Family MUSTELIDAE Fischer, 1817
Subfamily LUTRINAE Bonaparte, 1838

Sivaonyx Pilgrim, 1931

Type species. *Sivaonyx bathygnathus* Lydekker, 1884.

Table 1. Lower dental measurements (in mm) of different *Sivaonyx* species. Measurements are taken from Pilgrim (1932), Colbert (1935) Qi (1983), Zong (1997), Werdelin (2003), Morales *et al*. (2005), Morales & Pickford (2005a,b), Pickford (2007), Peigné *et al*. (2008), Grohé *et al*. (2013).

Species & Specimen No.	Position	Length	Width
Sivaonyx bathygnathus (PUPC 2003/15) Studied material	p4	7.5	5.5
	m1	16	9.5
S. bathygnathus GSI D 33 (holotype)	m1	17.1	9.7
GSI D 156	m1	16	9.4
GSI D 250	m1	16.4	9.1
AM 19509	m1	16.5	9.5
IVPP V 6886.12	m1	15.9	9
S. cf. *bathygnathus* (YV 2517)	m1	14	8
S. gandakasensis GSP-Y 4225 (holotype)	m1	15	7.9
GSP-Y 11703	m1	13.9	7.9
GSI D 249	m1	14.4	8.6
BMNH M 13175	m1	15.4	9.1
S. gandakasensis BMNH G 4	m1	12.8	7.6
Sivaonyx cf. *gandakasensis* CM-03-A	m1	13.7	7.6
YPM 20206	m1	15.4	8.5
S. hessicus BMNH 27486 (holotype)	m1	15.9	8.6
S. beyi TM 171-01-033 (holotype)	m1	20.3	
TM 172-05-0019	m1	22.8	13.4
TM 355-02-0029	m1	20	11.6
TM 247-01-0059	m1	21.5	12.7
S. ekecaman KNM-KP 10034 (holotype)	m1	21.2	13.5
BAR 720’03	m1		12.8
BAR 567’05	m1	20.1	13
S. soriae KNM-LU 337 & 338 (holotype)	m1	17.6	10.5
BAR 1984’05	m1	17.5	10.6
S. hendeyi SAM PQ-L 5000 (holotype)	m1	21.3	13.1
S. kamuhangirei Unnumbered (holotype)	m1	26	15.9
NK 1988’89	m1		14.4
S. africanus BSPG 1930 XI 1 (holotype)	m1	22.2	

Other species. *Sivaonyx africanus* (Stromer, 1931), *Sivaonyx hendeyi* (Morales *et al*., 2005), *Sivaonyx ekecaman* (Werdelin, 2003), *Sivaonyx kamuhangirei* (Morales & Pickford, 2005a), *Sivaonyx hessicus* (Lydekker, 1890), *Sivaonyx beyi* (Peigné *et al*., 2008), *Sivaonyx gandakasensis* (Pickford, 2007) *Sivaonyx soriae* (Morales & Pickford, 2005b), *Sivaonyx senutae* (Morales & Pickford, 2005b).

Distribution. Middle-late Miocene of Asia (India, Pakistan, Thailand, China), late Miocene of Europe (Germany, Turkey). Late Miocene-early Pleistocene of Africa (Egypt, Chad, Ethiopia, Kenya, Uganda, South Africa).

Sivaonyx bathygnathus Lydekker, 1884
(Figure 2)

Studied material. PUPC 2003/15, fragmentary right mandible lacking the incisors and m2 and includes p4-m1 and the roots of p3.

Diagnosis. Lutrinae of large size; having a P4 of an approximately quadrate shape with a moderately trenchant paracone-metacone blade; paracone somewhat stoutly built; metacone very slightly elongate; parastyle well developed but low; with two internal cusps, protocone and hypocone, lower than the outer cusps, somewhat swollen and expanded so that the basin-shaped area is contracted; with a strong internal cingulum; mandible with a ramus deeper than the length of m1; canine large; p1 single rooted; p4 broad posteriorly, with a strong, outwardly situated posterior cusp and a broad cingulum, no anterior accessory cusp; m1 very

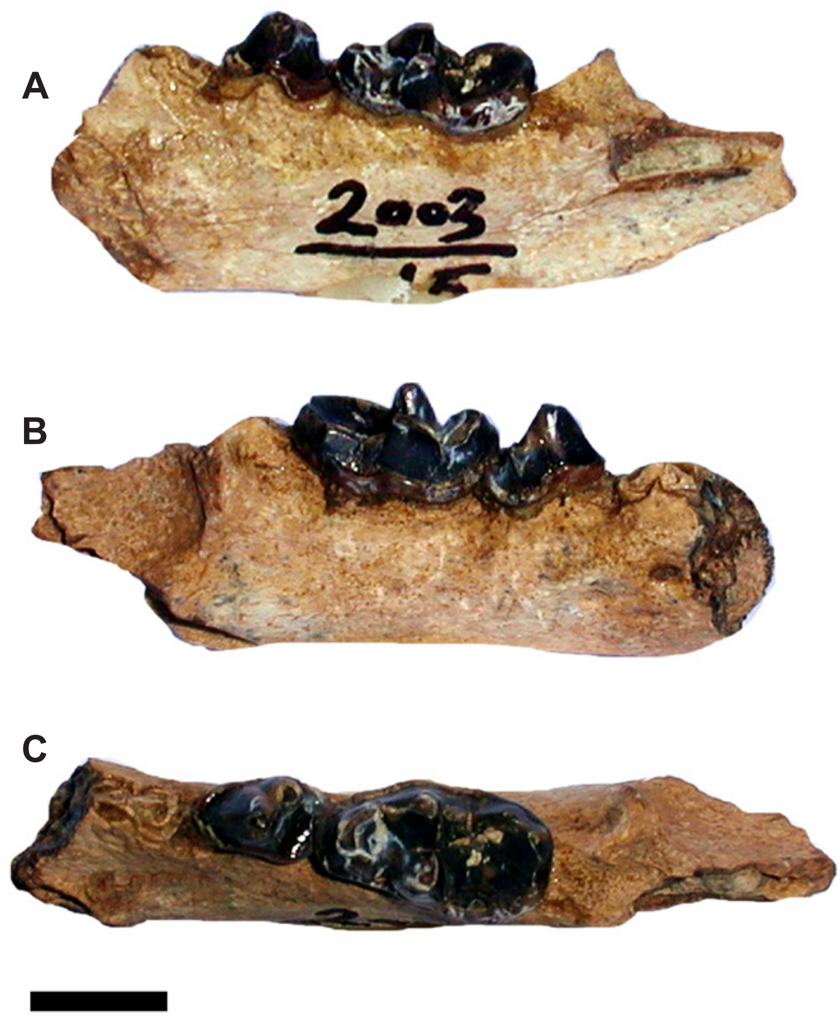

Figure 2. *Sivaonyx bathygnathus*, PUPC 2003/15. **A**, lingual; **B**, buccal and **C**, occlusal views. Scale bar = 10 mm.

broad; paraconid situated so as to be bisected by the median axis of the tooth; metaconid as high as paraconid; talonid broader than trigonid and approximately equal in length to it, basin-shaped, surrounded by a ring of cusps of which the entoconid is as well developed as the hypoconid; m2 small, oval (Pilgrim, 1932; Grohé *et al*., 2013).

Description. PUPC 2003/15 is a fragmentary right mandible lacking the incisors and m2 and includes p4-m1 and the roots of p3. The preserved length of the mandibular ramus is 58.2 mm. The maximum breadth of this ramus is 9.6 mm. The depth of the ramus below p3 and m1 is 21 mm and 17.7 mm, respectively. The preserved length of symphysis is 8.5 mm. It is in an excellent state of preservation and the teeth are at medium wear. In p4 the main cusp (protoconid) is high with sharp anterior edge and the anterior cusp is absent while the posterior cusp (post-protocind cusplet) is well developed and prominent, particularly on the outer side of the tooth. In m1, the metaconid and protoconid are almost equal in size but both are higher than the paraconid. Moreover, the metaconid is more lingual than the paraconid. The protoconid and the paraconid are separated by a well-marked carnassial notch while a deep V-shaped valley separates the paraconid from the metaconid. The metaconid is displaced distally with respect to the protoconid and is curved backwardly in lingual view. A small cuspule is also present at the distal base of the protoconid. The talonid exhibits a tall hypoconid crest but lower than the paraconid, a weaker and curved entoconid crest, and a narrow and shallow talonid basin. Both p4 and m1 show finely wrinkled enamel (Figure 2). The symphysis is deep and short. There are two mental foramina, one beneath p3 and the other one beneath p4. The anterior one is slightly larger than the posterior one. The hollow space left by the canine is also well preserved, it is circular in its general outline and its diameter is 6 mm.

DISCUSSION

This paper deals with the description of new material of *Sivaonyx bathygnathus* from the early Pliocene (Middle Siwaliks) of Hasnot. The holotype (GSI D 33) of this species (*Sivaonyx bathygnathus*) is a left mandible fragment with partial p4-m1, alveoli of canine (C) and p1-p3 illustrated by Lydekker (1884, pl. 27, fig. 3), and re-illustrated and figured by Pohle (1919, pl. 2, fig. 2) and Matthew (1929, fig. 8). Direct comparison of the morphological features of the studied material with the type specimen and with the additional materials described by Pilgrim (1932) and Colbert (1935) permits comparison with the lower carnassials from the Siwalik continental deposits. The type species *S. bathygnathus* has long been the only *Sivaonyx* species reported from Asia. This species was originally described from the late Miocene of the Siwalik Hills of Pakistan (Hasnot, Potwar Plateau; Lydekker, 1884; Pilgrim, 1931, 1932; Matthew, 1929, Colbert, 1935). Later on, the same species was reported in the late Miocene of Haritalyangar, India (Prasad, 1968, incorrect identification), Lufeng and possibly Yuanmou, Yunnan Province of China (Qi, 1979, 1983; Zong, 1997; Qi *et al*., 2006). The studied specimen was collected from the same vicinity (*i.e.* Hasnot; Dhok Pathan Formation; Middle Siwaliks) from where the Holotype specimen described by Lydekker (1884) was found. Although the origin and age of the type material is not precisely known, a literature review indicates that the described specimens of *S. bathygnathus* were collected from late Miocene-early Pliocene deposits and according to Pilgrim (1931) most possibly from the late Miocene sediments. The morphology of the studied specimen is similar to the type specimen as well as the additional specimens described by earlier workers (Lydekker, 1884; Pilgrim, 1931, 1932; Matthew, 1929; Colbert, 1935). The specimen under study differs from the holotype material (GSI D 33) as well as from GSI D 156 and AM 19509 by its smaller length and width dimensions of m1. According to Pickford (2007), *S. gandakasensis* is the oldest *Sivaonyx* species described from Kaulial, Nagri Formation, lower Middle Siwaliks of Pakistan. Moreover, the tooth dimensions of the studied material are greater than those of *S. gandakasensis* and *S. hessica* but are smaller than the other Eurasian and African species (see Table 1). Similarly, the studied specimen is different from *S. gandakasensis* as this species is recognized by the narrow and triangle-shaped trigonid, paraconid-protoconid blades forming a more opened angle, higher than the metaconid and a narrower talonid basin relative to the trigonid. In the studied specimen, the mandible ramus is deeper than the length of m1, p4 broad posteriorly, with a strong posterior cusp, situated outwardly, m1 broad, metaconid and paraconid are almost equal in height, talonid broader than the trigonid and approximately equal in length to it, talonid is basin-shaped, surrounded by a ring of cusps of which the entoconid is as well developed as the hypoconid. Pilgrim (1931) argued that there are strong morphological similarities of *Sivaonyx* species within the Europe and Subcontinent India. Later on Pickford (2007) agreed with Pilgrim's views and even suggested that the genus *Sivaonyx* occurred in Africa and Asia.

Affiliation of different species to *Sivaonyx* and *Enhydriodon* is still controversial due to fragmentary nature of fossil records of mustelids. The size difference between *Enhydriodon* and *Sivaonyx* is small and even the morphology of the lower carnassial (m1) is similar in both the genera. In general, bunodont teeth are referred to *Enhydriodon* while the sectorial dentition is referred to *Sivaonyx*, and the specimen under study show the sectorial dentition. In addition, in *Sivaonyx*, the cusplets encircles the entire tooth and usually found together to form two elongated cusps, as seen in the specimen under study, while in *Enhydriodon* cusplets around the margin of talonid tend to be discrete.

As stated above, apparently, the morphological differences in *Sivaonyx* and *Enhydriodon* are very small, but *Enhydriodon* has precedence over *Sivaonyx* and on this basis Werdelin & Lewis (2013) considered that the African fauna belonged to *Enhydriodon* rather than to *Sivaonyx*. The fossil record of family Mustelidae is much better in Asia compared to Africa. At present, the taxonomy of *Sivaonyx* and *Enhydriodon* is under revision and it is very difficult to assign different species either to *Sivaonyx* or to *Enhydriodon* because the overlapping diagnostic characteristics make it difficult to assign different species to these two genera. Based on the above observation, we here attribute the new Hasnot material to *Sivaonyx* rather than to *Enhydriodon* as this paper deals with the lower dentition and the type material of *Sivaonyx bathygnathus* is similar to the material described in this paper. In addition to the above-mentioned points, additional observations regarding the studied specimen are here considered.

Werdelin & Lewis (2013) included the African specimens in *Enhydriodon*, which they considered to be the senior synonmy over *Sivaonyx*, but the horizon mentioned for *Enhydriodon sivalensis* by Pilgrim (1931) is Upper Siwaliks while for *Enhydriodon falconeri* may be the Dhok Pathan age. Werdelin & Lewis (2013) also mentioned that the specimens collected from Koobi Fora, assigned to different species of *Enhydriodon* are larger, with morphology distinct from *Sivaonyx* species (*Sivaonyx beyi* and *Sivaonyx bathygnathus*). Based on stratigraphic and biochronological context, we can argue that among the bunodont otters, *Vishnuonyx chinjiensis* has an older stratigraphical range (Lower Siwaliks) than *Sivaonyx* [*S. bathygnathus* and *S. gandakaensis* (Middle Siwaliks)]. Similarly, *Sivaonyx* has an older stratigraphic range than *Enhydriodon* [*E. sivalensis* and *E. falconeri* (upper Middle Siwaliks-Upper Siwaliks). For the stratigraphic implications, we rely on Pilgrim Zone's (1913) and our own field observations based on the associated faunas from the Hasnot region which accord with these Zones (Pilgrim Zones). The Zones defined by Pilgrim (1913) are broad but provide a general sense to the sequences of events. However, the fauna from different Pilgrim Zones is mostly in agreement with our new collections and findings. At this stage, with a very limited material, we can only suggest that smaller specimens of two genera (*Sivaonyx* and *Enhydriodon*) from the older stratigraphic range can be assigned to *Sivaonyx* while the large specimens from the younger stratigraphic range can be assigned to *Enhydriodon*. This fits well with the African (Koobi Fora) materials because most of these species are described from strata which are equivalent in age to the Upper Siwaliks. The increase in size over time within the *Sivaonyx* lineage cannot be assessed because the studied specimen has smaller anteroposterior dimensions than the type specimen and other specimens of the same species collected from late Miocene sediments.

According to Pickford (2007), *Sivaonyx* (*S. bathygnathus* and *S. gandakasensis*) is intermediate between *Vishnuonyx* (*V. chinjiensis*) and *Enhydriodon* (*E. sivalensis* and *E. falconeri*). At the end of the Miocene, the molluscivorous lineage *Enhydriodon* evolved and then persisted until the end of the Pliocene. In Africa, *Sivaonyx* increased in body size and developed extremely bunodont dentition. According to Werdelin & Lewis (2013), this statement is consistent with the data available from Koobi Fora, Africa. At the generic level, the increase in size over time might be persistent within these three genera (*Vishnuonyx*, *Sivaonyx*, *Enhydriodon*) as argued by Morales & Pickford (2005a,b). The morphological modification can be justified as the specimens described from the younger stratigraphic range of Koobi Fora, Africa, may be more bunodont compared to the more sectorial dentition mentioned by Werdelin & Lewis (2013). Werdelin & Lewis (2013) also mentioned this blunt characteristic for the newly described species *E. ekecaman* (Early Pliocene age; 3.58-3.44 Ma). By summarizing the above statements, we can only comment that there is a morphological modification from sectorial dentition to bunodont dentition within these genera. *Sivaonyx gandakasensis* from Gandakas (Nagri Formation), Pakistan, is the oldest representative of the genus *Sivaonyx* from Siwalik continental deposits of Pakistan. Similarly, the fossil remains of this species from northern Thailand (12.4-12.2 Ma) are the oldest known remains of this genus from Asia (Grohé *et al*., 2013). Subsequently, *Sivaonyx beyi* from the Late Miocene of Toros-Menalla, Chad, is the oldest representative of this genus from Africa (Peigné *et al*., 2008).

The stratigraphic analyses of the fossil site indicate that the specimen under study is from the younger Dhok Pathan Formation (early Pliocene) as the additional fauna, particularly the Cervidae fossils collected from the area (Hasnot), confirms the Ruscinian age (equivalent to MN14; early Pliocene), because the earliest record of different species of tribe Cervini in the Siwaliks is not older than the early Pliocene (Barry *et al*., 2002; Khan *et al*., 2009; Ghaffar *et al*., 2010; Ghaffar & Akhtar, 2012). According to mitochondrial DNA analysis, the Muntiacinae-Cervinae split occurred at Miocene/Pliocene transition (Pitra *et al*., 2004) and this is in agreement with the early Pliocene fossil record of family Cervidae from the Siwaliks continental deposits.

The studied specimen is somewhat smaller than the type specimen. Although the stratigraphic range of the type specimen (D 33) is not clear, it may be assumed from the literature that it is from the Dhok Pathan Formation (late Miocene). From the area around Hasnot, the fossils occur in pockets and all the component formations, *i.e.* Kamilial, Chinji, Nagri, Dhok Pathan and Soan Formation, are well exposed in the vicinity of Hasnot area (Ghaffar, 2005; Khan *et al*., 2009). The exact fossil site from which the mandible was collected is 2.5 Km on the SW side of Hasnot village towards the Kotal Kund across the Bunnah river. The fossil site represents the upper Dhok Pathan Formation (early Pliocene). Cheema *et al*. (1977) described the Dhok Pathan Formation as being typically represented by monotonous cyclic alternations of sandstone and clay beds. Conglomerate in the form of lenses and a layer is an essential character of the upper part of Dhok Pathan Formation. The thickness of one sandstone-clay cycle varies from 6-60 m. The diversified rich mammalian fauna from the fossil site is also indicative of a Pliocene age (Shah, 2009). According to extensive field surveys from 1998-onward, particularly in the Dhok Pathan type locality as well as at Hasnot, we observed that the latest Miocene-Pliocene strata (Upper Dhok Pathan Formation; 6-3.5 Ma) are richer in faunal assemblages compared to late Miocene deposits (Early-Middle Dhok Pathan Formation; 10.1-6 Ma). Based on Cervidae fossil remains, we can argue that the different localities in the study area (around Hasnot village) belongs to Upper Dhok Pathan Formation (Pliocene) in addition to late Miocene sediments (Early-Middle Dhok Pathan Formation).

ACKNOWLEDGMENTS

The authors want to thank to L. Werdelin for the preliminary identification and kindly providing the literature regarding this paper. The first author is also grateful to R.M. Ibrahim and his team (COMSATS Library Information Services) for their efforts to provide the necessary literature for this study. Moreover, we would like to thank the reviewers for their corrections and constructive remarks to improve this manuscript. This research is supported by Higher Education Commission, Pakistan (grant No. 20-2234/R & D/11) to Abdul Ghaffar under National Research Program for Universities (NRPU) to study Pliocene Mammalian Fauna from the Siwaliks of Pakistan.

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Received in November, 2015; accepted in February, 2016.