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Khalid MAHMOOD,
Michael MORLO,
Sayyed GHYOUR ABBAS,
Muhammad ADEEB BABAR &
Muhammad AKBAR KHAN

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The Lutrinae (Mustelidae, Carnivora, Mammalia) from the Upper Miocene to the Lower Pleistocene deposits of Pakistan

Khalid MAHMOOD
Dr. Abu Bakr Fossil Display & Research Centre, Department of Zoology, University of the Punjab, Quid-e-Azam Campus, Lahore 54590 (Pakistan)
and Department of Zoology, Govt. Islamia Graduate College Kasur, Punjab (Pakistan)
khalidkasuri1@gmail.com (corresponding author)

Michael MORLO
Forschungsinstitut Senckenberg, Abt. Messelforschung und Mammalogie, Senckenberganlage 25, 60325 Frankfurt (Germany)
michael.morlo@senckenberg.de

Sayyed Ghyour ABBAS
Department of Zoology, University of Sialkot, Sialkot, Punjab (Pakistan)
sayyed.ghyour@uskt.edu.pk/ghyour.kazmi@gmail.com

Muhammad Adeeb BABAR
Department of Zoology, University of Okara, Okara, Punjab (Pakistan)
babar.441@googlemail.com

Muhammad Akbar KHAN
Dr. Abu Bakr Fossil Display & Research Centre, Department of Zoology, University of the Punjab, Quid-e-Azam Campus, Lahore 54590 (Pakistan)
akbar.zool@pu.edu.pk

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ABSTRACT
Well-preserved new dental material of subfamily Lutrinae (Mustelidae, Carnivora) comprising of upper and lower premolars and molar were recovered from the Hasnot, Padhri, Bhimber areas of the Siwaliks of Pakistan. Three specimens are described in this study: an m1 collected from Pleistocene deposits of Bhimber is attributed to *Enhydriodon* cf. *falconeri*, an upper fourth premolar (P4) recovered from Hasnot (7 to 5.3 Ma) is so unique in having round borders/external walls, basal lingual cingulum is straight at mesial border, postparacrista short and having less buccal concavity, lack a cusplet between proto- and hypocone that it allowed us to create a species, *Sivaonyx sarwari* n. sp., and an isolated lower fourth premolar (p4) collected from Padhri (7-5.5 Ma) is described as *Sivaonyx bathygnathus*. Among these, *Enhydriodon falconeri* is reported for the first time from the Pleistocene deposits of the Siwaliks, while *Sivaonyx sarwari* n. sp. represents the smallest species of the genus. The present specimens add to the records of the rare mustelid species and also challenge the evolutionary time transgression of some Siwalik lutrine species proposed by previous studies.

KEY WORDS
Carnivora, Mustelidae, *Enhydriodon*, *Sivaonyx*, Siwaliks, otters, new species.

RÉSUMÉ
Les Lutrinae (Mustelidae, Carnivora, Mammalia) des dépôts du Miocène supérieur au Pléistocène inférieur du Pakistan.
Du nouveau matériel dentaire bien conservé de la sous-famille des Lutrinae (Mustelidae, Carnivora) comprenant des prémolaires supérieures et inférieures, ainsi que des molaires, a été découvert dans les régions de Hasnot, Padhri et Bhimber des Siwaliks du Pakistan. Trois spécimens sont décrits dans cette étude : une m1 collectée dans les dépôts pléistocènes de Bhimber est attribuée à *Enhydriodon* cf. *falconeri*, une quatrième prémolaire supérieure (P4) trouvée à Hasnot (7 à 5,3 Ma) est si unique – elle présente des bords/parois externes arrondis, un cingulum lingual basal droit au niveau du bord mésial, un postparacrista court et une concavité buccale moindre, une absence de mini-cuspide entre le proto- et l'hypocône – qu'elle nous a permis de créer une espèce nouvelle, *Sivaonyx sarwari* n. sp., et une quatrième prémolaire inférieure isolée (p4) collectée à Padhri (7-5,5 Ma) est décrite comme *Sivaonyx bathygnathus* (Lydekker, 1884). Parmi ces taxons, *Enhydriodon falconeri* est signalé pour la première fois dans les dépôts pléistocènes des Siwaliks, tandis que *Sivaonyx sarwari* n. sp. représente la plus petite espèce du genre. Les spécimens étudiés viennent s'ajouter aux rares enregistrements d'espèces de mustélidés et remettent également en question le rythme évolutif de certaines espèces de loutres des Siwaliks proposé par des études antérieures.

MOTS CLÉS
Carnivora,
Mustelidae,
Enhydriodon,
Sivaonyx,
Siwaliks,
loutres,
espèce nouvelle.

INTRODUCTION

The family Mustelidae is diverse with small (weasel) to medium (honey badger, sea otters) sized Carnivora. The family was more diverse in the past and many extinct species have been described from the Lower Miocene to Pleistocene deposits across the world. The family was also present in the Siwaliks (Indian subcontinent) from the Middle Miocene through the Middle Pleistocene with a lot of taxa (see Pilgrim 1932; Colbert 1933, 1935; Prasad 1970; Pickford 2007; Jasinski *et al.* 2023; Jiangzuo *et al.* 2021; Mahmood 2023; Mahmood *et al.* 2023). In the Siwaliks, it is represented by the subfamilies, Mellivorinae, Guloninae and Lutrinae (Pilgrim 1932; Colbert 1933, 1935; Pickford 2007; Jiangzuo *et al.* 2021). The Mellivorinae genera and species proposed by Pilgrim (1932) are: *Mellivora* Storr, 1780 (*Mellivora sivalensis* Pilgrim, 1932), *Eomellivora* Zdansky, 1924 (*Eomellivora*? *necrophila* Pilgrim, 1932, *Eomellivora* ? *tenebrarum* Pilgrim, 1932) and *Promellivora* Pilgrim 1932 (*Promellivora punjabiensis* Pilgrim, 1932). The Guloninae is represented by "*Martes*" Pinel, 1792 (although synonymy with *Cernictis* Hall, 1935 is under consideration), *Ibericti*s Ginsburg & Morales, 1992, *Plesiogulo* Zdansky, 1924, and *Circamustela* Petter, 1967 (Pilgrim 1932; Colbert 1933, 1935; Mahmood *et al.* 2023), while Lutrinae is represented by the genera *Amblonyx* Rafinesque, 1832 (tribe Aonychini) and *Vishnuonyx* Pilgrim, 1932, *Sivaonyx* Pilgrim, 1931, and *Enhydriodon* Falconer, 1868 (Pilgrim 1932; Colbert 1935; Pickford 2007; Raghavan *et al.* 2007; Jiangzuo *et al.* 2021; Mahmood *et al.* 2023). Among these, *Plesiogulo*, "*Martes*" and *Ibericti*s are monospecific in the Siwalik with *Plesiogulo* aff. *crassa* Teilhard, 1945, "*M.*" *lydekkeri* Colbert, 1933, and aff. *Ibericti*s sp., respectively (Colbert 1933, 1935; Mahmood *et al.* 2023), while no definite species of *Circamustela* is yet defined as it is based on some isolated remains (Sankhyan *et al.* in press). The genus *Vishnuonyx* is monospecific in that region with *V. chinjiensis* Pilgrim, 1932, while *Amblonyx* is represented by two species, *A. indicus* Raghavan, Pickford, Patnaik & Gayathri, 2007 and *A. barryi* Jiangzuo, Yu & Flynn, 2021 (Pickford 2007; Raghavan *et al.* 2007; Jiangzuo *et al.* 2021). The genus *Sivaonyx* also has two species in the Siwalik with the earlier and smaller *S. gandakasensis* Pickford, 2007 and the younger and larger *S. bathygnathus* Lydekker, 1884, and *Enhydriodon* with a smaller, *E. falconeri* Pilgrim, 1931, and a larger, *E. sivalensis* Falconer, 1868 (Pilgrim 1932; Pickford 2007; Ghaffar & Akhtar 2016; Jiangzuo *et al.* 2021).

Here we describe some newly unearthed remains of Lutrinae from the Middle Miocene to Upper Pleistocene deposits of the Siwaliks of northern Punjab from three different locations.

GEOLOGY

Hasnot

The Hasnot area includes upper Middle and Lower Siwaliks, but it mainly comprises the Middle Siwaliks Dhok Pathan Formation. The village is situated 70 km west of Jhelum city (32°50'44.7"N, 73°17'50.1"E, alt. 1193.38 ft; Fig. 1). This area is highly fossiliferous and deposited by a riverine and lake system of Neogene age. Lithostratigraphically, the sediments are characterized by sandstones with alternate clays and scattered conglomerates in the lower part and conglomerates with sandstones and clays in the upper part (Fig. 1). The clays are orange-brown in color and the time of deposition ranges from 7 to 5 Ma (Pilbeam *et al.* 1977; Barry *et al.* 1982; Johnson *et al.* 1982; Barry 1987). Barry *et al.* (1982) made excellent efforts on the Hasnot composite reference section depicted as Tatrot-Andar kas section. This section provides additional information about the vertebrate fossil localities of the Hasnot area. The Dhok Pathan Formation in the Hasnot area is 800-900 meter thick (Barry *et al.* 1982).

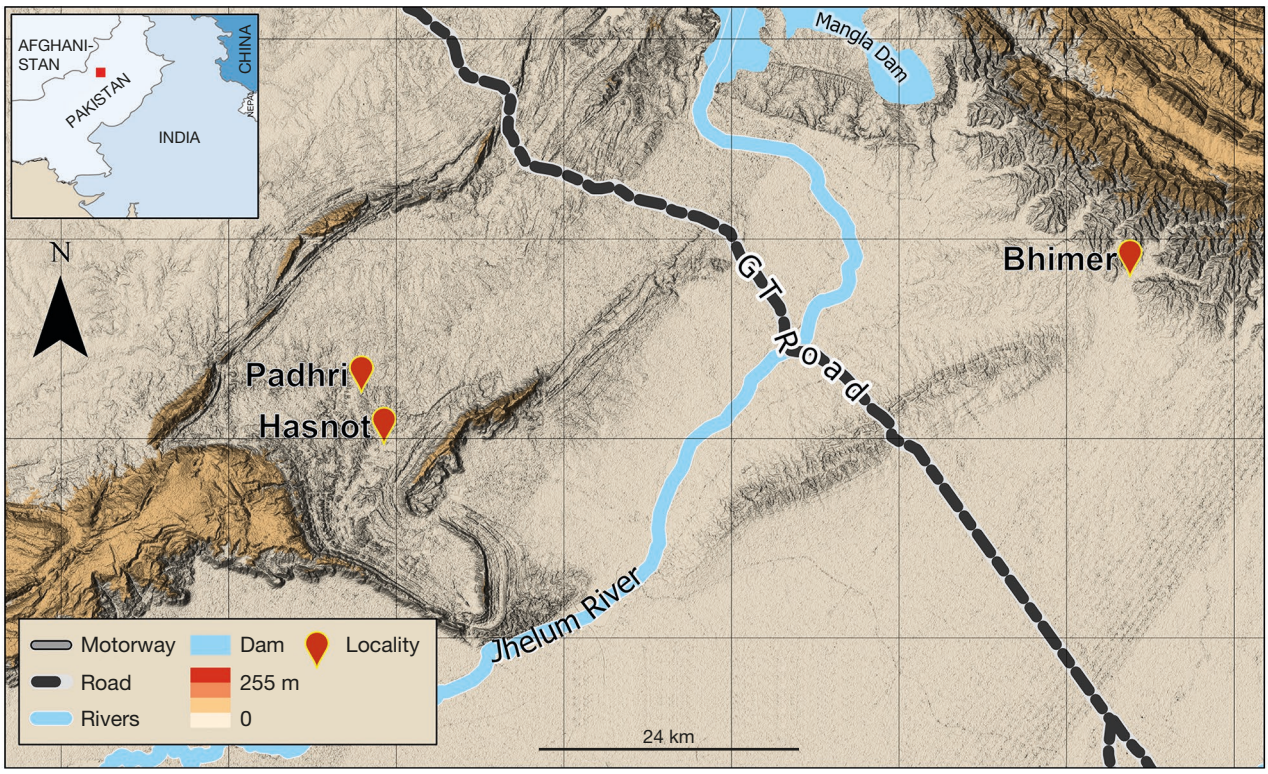

Fig. 1. — Map showing Hasnot, Padhri and Bhimber with the famous Siwalik sites in Potwar Plateau, Pakistan (inset studied outcrops).

Padhri

The locality of Padhri is located 67 km in the west of Jhelum city and it comprises the upper Dhok Pathan Formation of the middle Siwaliks of Northern Pakistan (Fig. 1). The area nearby the village is highly exposed and has yielded a diverse mammalian fauna, especially some Carnivora (Pilgrim 1932; Khan *et al.* 2023). The most productive fossil site named Chashma (32°52'24.1"N, 73°18'00.2"E, alt. 1272.23 ft) is placed in the southeast of the village (Barry *et al.* 1982, 2002). The estimated age of the outcrops in the vicinity of Padhri is 7-5.5 Ma (Khan 2007).

Bhimber

Bhimber, spelled as Bhimbur in Opdyke *et al.* (1979), is a city situated in the northeast of Pabbi Hills, southeast of Mirpur, and in the southwestern Azad Jammu & Kashmir, Pakistan (Fig. 1) (Opdyke *et al.* 1979). The new carnivoran material was recovered from the Lower Pleistocene Pinjor Formation (*c.* 2.4 Ma) in Bhimber. The fossiliferous site is above the height of 70 meters. The whole section of 350 m height is divided into four magnetic polarity zones based on three magnetic transitions. The doublet of bentonitized tufts previously identified in the Mangla-Samwal anticline straddle the N1/R1 transition, and on this basis, we correlate this magnetic transition to the Gauss/Matuyama boundary. The normally magnetized zone above the 200-m line would therefore be correlative with the Olduvai normal event of the Matuyama reversed magnetic epoch (Opdyke *et al.* 1979).

Table 1. — The material studied in this work with its locality and age.

Sr. No	Description	Locality and Age
PUPC 83/01	right mandibular fragment with m1 and root of m2	Bhimber: Early Pleistocene
PUPC 16/29	lp4	Padhri: Late Miocene
PUPC 17/64	lP4	Hasnot: Late Miocene

MATERIAL AND METHODS

The material comprises three specimens that include isolated upper and lower premolars and a molar (Table 1). It is housed in the Dr. Abu Bakr Fossil Display and Research Centre, University of the Punjab, Lahore, Pakistan. The slightly modified crown terminology and measurement manners follow that of Grohé *et al.* (2022). The upper-case letter represents upper dentition (e.g., P) and lower-case letter represents lower dentition (e.g., m). The measurements were taken with digital Vernier caliper and expressed in millimeters (mm). The photographs were taken by a digital camera (Canon 6D) and the plate prepared in Adobe Photoshop CC.

Note

Wang *et al.* (2018) inferred that the tribe Enhydriodontini is a wastebasket for bunodont otters as proposed by Morales & Pickford (2005) and Pickford (2007), that is why we use inversion marks (“ ”) for these terms in our study.

ABBREVATIONS

PUPC	Punjab University Palaeontological Collection, University of the Punjab, Lahore, Pakistan;
BMNH/NHM	British Museum of Natural History / Natural History Museum, London (= NHMUK);
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, China;
IPSMG	specimen number of Ipswich Borough Council Museum, Ipswich, United Kingdom;
GSI	Geological Survey of India, Calcutta, India;
SAM-PQL	South African Museum, Department of Quaternary Palaeontology, South Africa;
DIK	Dikika, Ethiopia.

SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Family MUSTELIDAE Swainson, 1835
Subfamily LUTRINAE Bonaparte, 1838
Genus *Enhydriodon* Falconer, 1868

Enhydriodon cf. ***falconeri*** Pilgrim, 1931
(Fig. 2A1-A4)

HOLOTYPE. — BMNH/NHM 4847, an isolated left P4 figured by Matthew (1929: 472, text-fig. 11) and by Pilgrim (1931: pl. 2, figs 3, 3a).

TYPE LOCALITY. — Indeterminate/unknown locality in the Siwaliks Hills (Falconer 1868; Pilgrim 1931).

DIAGNOSIS. — Small species of *Enhydriodon* intermediate in dimensions between *Sivaonyx bathygnathus* and *Enhydriodon sivalensis*, with voluminous conical hypocone in P4 lacking ridge directed into central valley; two post-protocone cusps oriented linguodistally, the most lingual one not blocking the lingual outlet of the central valley. Parastyle large but low. "Lutrine crest" well developed and swollen, but not forming a separate cusp. Lingual opening of m1 trigonid narrow U-shaped (Pickford 2007).

STRATIGRAPHIC RANGE. — Unknown, probably Tatrot to Pinjor formations (Matthew 1929; Pilgrim 1932; Pickford 2007); Pinjor Formation (in this study).

REFERRED MATERIAL. — PUPC 83/01, right mandibular fragment with m1 and root of m2.

DESCRIPTION

The corpus is robust but not fully preserved (Fig. 2A1-A4). A deep mylohyoid line is present which subsequently joins the partially preserved pterygoid shelf at the lingual side while the preserved buccal side is bulged. Its preserved length is 40.1 mm. It bears an m1 and root of m2. The metaconid is partially broken in m1, rest of the tooth is well-preserved, and it is moderately worn. In m1, the paraconid is thick and eye-shaped as a result of moderate wear. It connects with the protoconid through a crest and forms a pronounced carnassial notch. The trigonid basin is small and lingually blocked by a portion of a long and strong mesial cingulid which covers the base of the tooth completely. The protoconid is thick and has the postprotocristid equipped with a well-developed cuspid. A large gap separates this cuspid from the buccal cusp of the talonid, i.e., the hypoconid and the closely attached hypoconulid. The entoconid is also well-developed. It connects with the meta- and hypoconulid through its crests and completely closes the distal and lingual side of the talonid basin. The talonid basin is much larger than the trigonid basin and partially open at its buccal side. There is a small diastema between m1 and m2. Only the alveolus with root of m2 is preserved. It was single-rooted and situated much higher than m1.

REMARKS

The wide paraconid and postprotocristid equipped with a well-developed cuspid, large talonid basin, more or less equally developed para-, proto-, and metaconid, and a large cingulid (Fig. 2A1-A4) associate the specimen with the genus *Enhydriodon*. There are two species of *Enhydriodon* known from the Siwaliks, *E. falconeri* and *E. sivalensis* (Pilgrim 1932; Verma & Gupta 1992; Willemsen 1992, 1999; Pickford 2007). *Enhydriodon falconeri* is known from the latest Pliocene Tatrot Formation, while *E. sivalensis* has been recorded from the Middle to Upper Pleistocene Pinjor Formation (Pickford 2007). The present specimen has been collected from Pleistocene outcrops of Bhimber, Azad Jammu Kashmir (AJK), that are equivalent to the Pinjor Formation. This further justifies its association with the genus *Enhydriodon* rather than *Sivaonyx*. However, the studied specimen is smaller than the known specimens of *E. sivalensis*, and morphologically PUPC 83/01 is extremely similar to GSI-D 161, described and figured by Pilgrim (1932) as *E.* cf. *falconeri* (see Fig. 2A4, A5) which is why we also attribute it to *E.* cf. *falconeri*. Nevertheless, it has been previously noted by Pilgrim (1932: 87) that "in respect of the structure of its ml, *Enhydriodon falconeri* closely resembles *Sivaonyx*. In fact, except by its larger size and the relatively slightly broader talonid it does not seem that the genera can be separated on the characters of m1 alone".

Genus *Sivaonyx* Pilgrim, 1931

TYPE SPECIES. — *Lutra bathygnatha* Lydekker, 1884 by original designation.

Sivaonyx sarwari n. sp.
(Fig. 2B1-B3)

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DERIVATION OF NAME. — After Dr Muhammad Sarwar, the second vertebrate palaeontologist of the Punjab University and who have done extensive field work during the 1963-1977 throughout Pakistan, that resulted in the identification and exploration of new localities and became a source of guidance for the field work for the future palaeontologists of Pakistan.

HOLOTYPE. — PUPC 17/64, lP4.

TYPE LOCALITY. — Hasnot, Jhelum, Punjab, Pakistan.

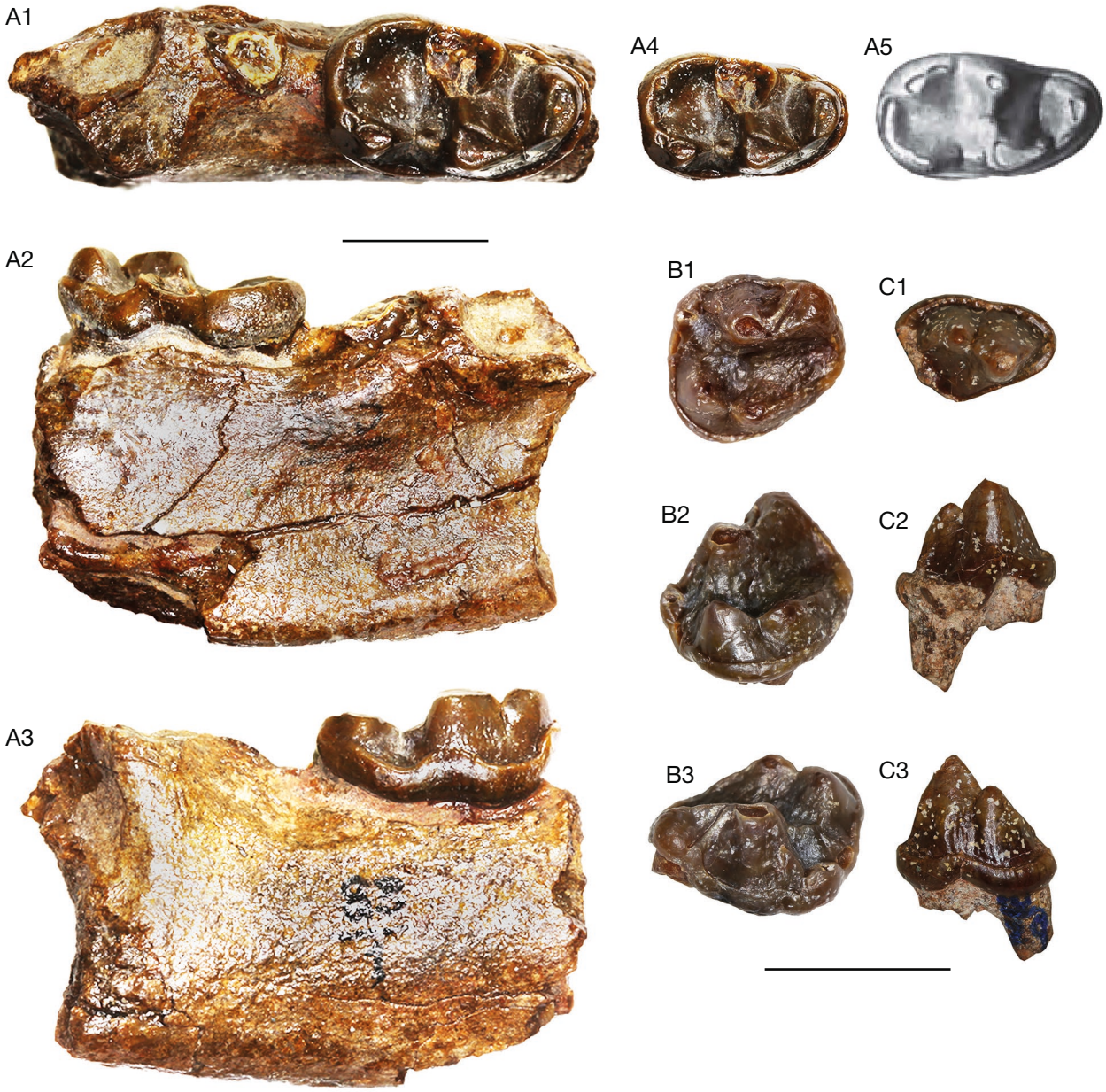

Fig. 2. — **A1-A5**, *Enhydriodon* cf. *falconeri*: **A4**, PUPC 83/01, right mandibular fragment with m1 and root of m2; **A5**, GSI-D 161 from Pilgrim 1932; **B1**-**B3**, *Sivaonyx sarwari* n. sp.; PUPC 17/64, lP4; **C1**-**C3**, *S. bathygnathus* (Lydekker, 1884), PUPC 16/29, lp4. **A1**, **A4**, **A5**, **B1**, **C1**, occlusal views; **A2**, **B2**, **C2**, lingual views; **A3**, **B3**, **C3**, buccal views. Scale bars: A1-A3, B, C, 10 mm; A4, A5, not to scale.

Diagnosis. — A small *Sivaonyx* species having P4 with round borders/external walls, basal lingual cingulum is straight at mesial border, postparacrista short and having less buccal concavity, lack a cusplet between proto- and hypocone, small mesial valley hence, less pinched mesial border, and very long posthypocrista, the crest that joins hypocone with metastyle/metacone.

Differential diagnosis. — Differs from all *Sivaonyx* species being small in size, having round outline, basal lingual cingulum is straight at mesial border, and small mesial valley hence, less pinched mesial border. It differs from *Sivaonyx bathygnathus* in having short postparacrista, less spaced proto- and hypocone, and having no cusplet between proto- and hypocone; from *Sivaonyx gandakasensis* in short postparacrista, long posthypocrista, and more buccal concavity of postparacrista; from *Sivaonyx hessicus* Lydekker, 1890 in having weak buccal concavity of postparacrista, no cusplet between proto- and hypocone, very long posthypocrista; from *Sivaonyx hendeyi* Morales, Pickford & Soria, 2005 in lacking notch between paracone and metastyle, having very long posthypocrista, and weak buccal cingulum; from *Sivaonyx ekecaman* Werdelin, 2003 in having longer pre- and postparacrista, slightly distally positioned protocone, lack of notch between paracone and metastyle, weak buccal concavity of postparacrista, no cusplet between proto- and hypocone, large median valley, and very long posthypocrista; and from *Sivaonyx soriae* in having slightly distal position of protocone, weak buccal concavity of postparacrista, no cusplet between proto- and hypocone, very long posthypocrista.

Stratigraphic range. — Dhok Pathan Formation of the Middle Siwaliks (Late Miocene).

DESCRIPTION

PUPC 17/64 is nearly rectangular with round outline, well-preserved and slightly worn (Fig. 2B1-B3). All the cusps are well-developed and prominent. The paracone is the highest, massive, with a rounded external wall and a prominent parastyle. The parastyle is low in height and it is separated from paracone by a small notch. Three crests originate from the paracone, mesial crest (preparacrista) connects the paracone to the parastyle, distal (postparacrista) to the metacone and the metacrista, and the third (lingual crest) connects to the protocone through crista obliqua. The metacrista is small and the metastyle/metacone is bulbous. The paracone is connected to the metacone. A prominent slanting cingulum is also present between the paracone and metacone and is connected to metastyle. The coupled protocone and hypocone are well-developed and distinct, separated by only a small notch. The protocone is slightly higher than the hypocone. The hypocrista is extremely long and becomes slightly round distally, rendering tooth round outline. The median fossette is large, oval in shape and separates trigon and talon. A thick cingulum fully covers the base of the tooth that has three roots (Fig. 2B1-B3).

COMPARISON

The presence of a protocone far from the paracone and a large cingulum that covers the base of the tooth in PUPC 17/64 differentiate it from *Paludolutra*, and presence of a less developed hypocone, a protocone far from the paracone, a more sectorial paracone-metastyle, and that it is longer than wide in addition to its small size differentiate it from *Enhydriodon*. *Vishnuonyx* and *Sivaonyx* are the other two "enhydriodontine" genera present in the Siwaliks. PUPC 17/64 differs from the P4 of all *Vishnuonyx* species in having round outline, robust parastyle, short metacrista, very long posthypocrista, and wider central basin in addition to incomplete lingual shelf. Even the space between the protocone and hypocone is smaller in PUPC 17/64 than in *Vishnuonyx* while the space between the parastyle and paracone is wider in *Vishnuonyx*. *Sivaonyx* is represented by two species, a small, *Sivaonyx gandakasensis* and a large, *S. bathygnathus* (Pickford 2007; Grohé *et al.* 2013; Ghaffar & Akhtar 2016). PUPC 17/64 is smaller than any known P4 of both of these species (Table 2). However, it shares more morphological similarity with the P4, GSI-D 157, of *Sivaonyx bathygnathus* first described and figured by Pilgrim (1932: pl. 2, fig. 16) and later figured by Pickford (2007: fig. 9A). These similarities include the large paracone with a round lingual wall, low but heavy parastyle, a large and bulbous metastyle/metacone, a large and wide median fossette, and a very long posthypocrista (Fig. 2B1-B3). Based on these similarities, we are allocating PUPC 17/64 to *Sivaonyx*. However, due to its minute size, its rounded outline, the short metacrista, small space between protocone and hypocone, the more developed cingulum, less pinched preprotocrista or anterotransverse wall of the tooth, we do not assign it to one of the known species but designate it as a new species, *Sivaonyx sarwari* n. sp. It differs from other *Sivaonyx* species as given in differential diagnosis.

Sivaonyx bathygnathus (Lydekker, 1884)

HOLOTYPE. — GSI D 33, left mandible with p4-m1 and alveoli of c1-p3 (Lydekker 1884).

TYPE LOCALITY. — Hasnot, Punjab, Pakistan (Lydekker 1884).

DIAGNOSIS. — Large species of the genus *Sivaonyx* with slightly sectorial aspect to P4 and m1, but showing a talonid basin broader than the trigonid (Pickford 2007).

STRATIGRAPHIC RANGE AND GEOGRAPHIC DISTRIBUTION. — This species well-known from the Late Miocene, Dhok Pathan Formation of Siwaliks (Pilgrim 1932; Pickford 2007) and Southern China (Zong 1997; Qi *et al.* 2006).

REFERRED MATERIAL. — PUPC 16/29, lp4.

DESCRIPTION

PUPC 16/29 is a left p4. The base of tooth is partially broken postero-lingually. It is monocuspid, slightly worn and subtriangular in shape. It has a thick and strong cingulum at the base labio-lingually. The protoconid is large, pyramidal, slightly compressed buccally and highest. The distal cuspid is small, slightly buccally positioned, and separated from the protoconid by a small notch. A wide basal platform is present in the front of the distal cuspid lingually. It is double-rooted, and the distal root is more preserved (Fig. 2C1-C3).

COMPARISON

The described p4, PUPC 16/29, is broad distally, with a strong, and a broad cingulid, no mesial accessory cusp, outwardly situated distal cusp; and these are the characters of p4 given in the diagnosis of *Sivaonyx bathygnathus* given by Pilgrim (1932). Further, while describing p4 (GSI-D 244), Pilgrim (1932) writes: "distal accessory cusp is almost as strong and probably little inferior in height to the main cusp and it lies well on the outside of the median axis" and the same morphology is described by Pickford (2007), i.e., presence of a distal accessory cusp, a cingulid that covers the base of whole tooth, and a broadly expanded distal platform. In this regard, morphology and dimensions of the specimen (Fig. 2C1-C3; Table 2) are close to *S. bathygnathus*, hence, we referred it to *Sivaonyx bathygnathus*.

DISCUSSION

The Siwalik mustelids are much more diverse than it is usually comprehended. A recent publication of Jiangzuo *et al.* (2021) has identified new genera and species that were not identified from the Siwalik previously. These belong to both Lutrinae as well as Guloninae and Mellivorinae. Jiangzuo *et al.* (2021) reported the gulonine *Iberictis* and *Plesiogulo* and the lutrine *Amblonyx* for the Siwaliks, while *Vishnuonyx*, *Sivaonyx* and *Enhydriodon* are well known from the Siwaliks. Before this, Guloninae was represented by only "*Martes*". The first description of *Amblonyx* was provided by Raghavan *et al.* (2007) with *A. indicus* while

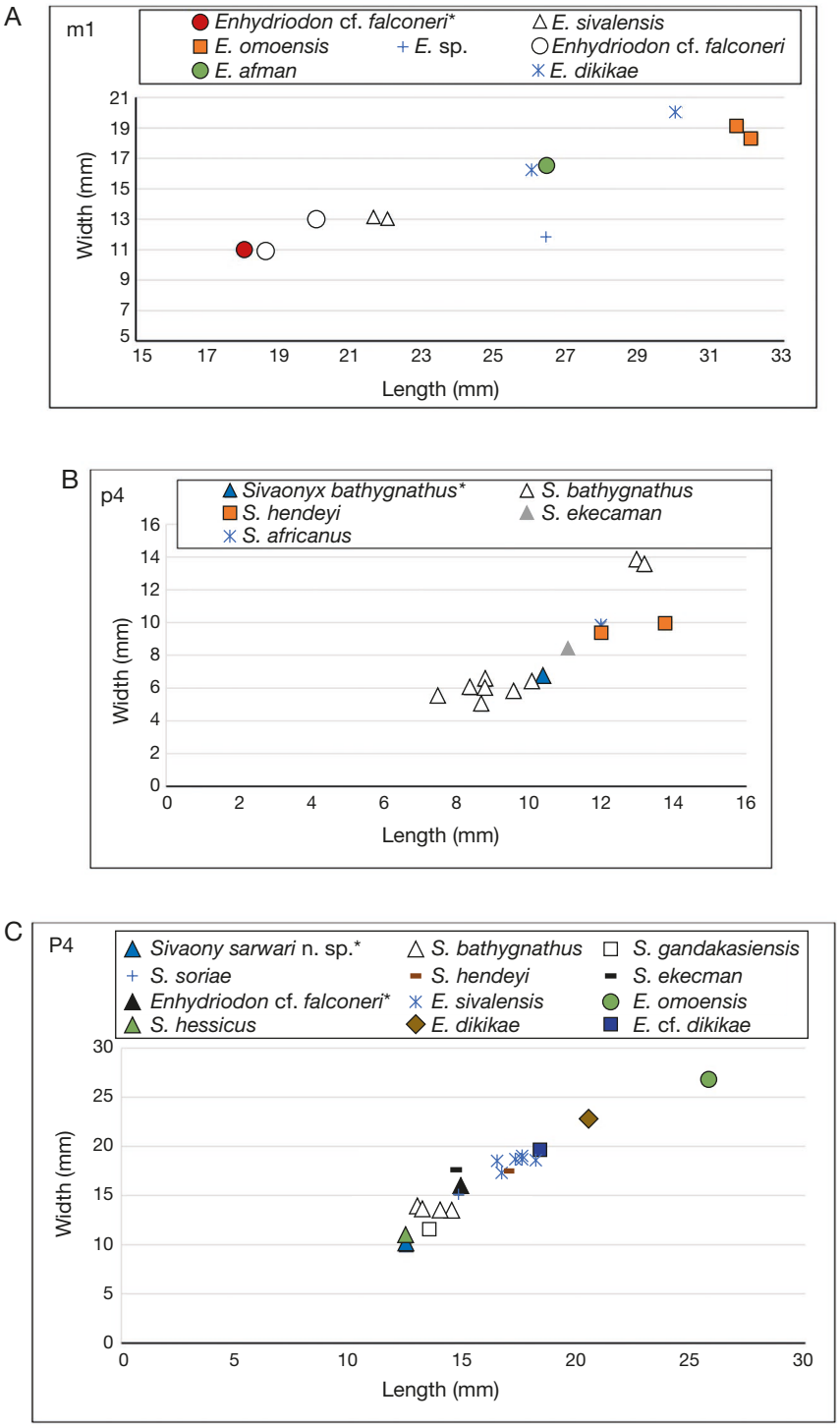

FIG. 3. — Comparative measurements of described taxa represented in scatter plots: **A**, *Enhydriodon* cf. *falconeri*; **B**, *Sivaonyx bathygnathus*; **C**, *Sivaonyx sarwari* n. sp.

Jiangzuo *et al.* (2021) described a second species, *A. barryi*. The presence of *Circamustela* is tentatively based on two m1s from Haritalyangar (Sankhyan *et al.* in press)

In the Mio-Pleistocene Siwalik the extinct "enhydriodontine" include three genera: *Enhydriodon*, *Sivaonyx* and *Vishnuonyx* (Pilgrim 1932; Pickford 2007; Grohé *et al.* 2013, 2020; Kargopoulos *et al.* 2021). *Vishnuonyx* from the Siwalik of Pakistan was thought to be the oldest genus and the least advanced because it has not a bunodont dentition in fact, and it was considered as a good candidate for an ancestral Enhydrini as suggested by Willemsen (1999) (new data do not support this, see below). It was described from the Chinji Formation (Pilgrim 1932), which can be dated at about 13.7-11.6 Ma (Pickford 2007). However, Grohé *et al.* (2020) reported a new species, *Vishnuonyx maemohensis*, from the middle Miocene (14.2-13.2 Ma)

of Mae Moh Basin, Thailand, which is the oldest species of the genus. Nevertheless, no *Vishnuonyx* remains have been found in the collection described in our study. The present study deals with the description of the remains of *Enhydriodon* and *Sivaonyx*. Both these genera more derived in their morphology toward a bunodont dentition.

The genus *Enhydriodon* had a wide geographical distribution and includes many species (see Table 2), especially in Africa. Two species are known from the Siwaliks, *E. falconeri*, and *E. sivalensis*. *Enhydriodon falconeri* is based on an isolated P4 whose exact provenance is unknown as it is mentioned "Siwalik Hills" by Pilgrim (1932). All *Enhydriodon* remains in the collection till the work of Pilgrim (1932) were collected from the Siwalik Hills, and from the neighbourhood of Hasnot. Later, one mandible NHM M 15397 was collected at Tatrot. It was described by Pickford (2007) and he also confirmed that all specimens described by Pilgrim came from the Tatrot Formation (Tatrot zone in Pickford 2007). In summary, all the specimens of *E. falconeri* are supposedly from Pliocene deposits, while PUPC 83/01 was collected from Pleistocene deposits. Hence, it is the first description of *E. falconeri* younger than Pliocene in age from the Siwaliks of Indian subcontinent, hence the idea of time transgressive evolution of *Enhydriodon* in the Siwaliks is not supported by this discovery.

The genus *Sivaonyx* is known by many species in Africa and Eurasia, with the higher diversity known from Africa (Pilgrim 1932; Morales & Pickford 2005; Morales *et al.* 2005; Pickford 2007; Haile-Selassie 2008; Grohé *et al.* 2013; Kargopoulos *et al.* 2021). Two Siwalik *Sivaonyx* species are known. *S. gandakasensis* is considered to be the older and smaller species. It is described from Kaulial, Nagri Formation (Upper Miocene), lower Middle Siwaliks of Pakistan (Pickford 2007) and in Haritalyangar (Grohé *et al.* 2013). This species is well known from the Siwaliks and has also been described from northern Thailand. While working on the Siwalik "Enhydriodontini", Pickford (2007) suggested that there is a sequence of evolution from *Vishnuonyx* via *Sivaonyx* to *Enhydriodon* and from the Lower to the Upper Siwaliks (Pickford 2007: fig. 23), and considered Siwalik as the epic center of this radiation. It is the fact that *Vishnuonyx* is oldest member of tribe "Enhydriodontini" but whether *Vishnuonyx* is the ancestor of this tribe, remains speculative based on the recent studies given below. The studies done by Grohé *et al.* (2013, 2020) have shown that Siwalik is the center of "Enhydriodontini" radiation is not supported by these studies. *Vishnuonyx maemohensis*, from the Middle Miocene (14.2 and 13.2 Ma) of Mae Moh Basin described and figured by Grohé *et al.* (2020), and *Sivaonyx gandakasensis*, described and figured by Grohé *et al.* (2013), is known from the Middle Miocene (12.4-12.2 Ma) deposits of Chiang Muan Thailand and from Pakistan because a mandibular fragment (BMNH G 4) that was previously described and figured by Pickford (2007) was referred to *S.* cf. *gandakasensis* by Grohé *et al.* (2013). Hence, Grohé *et al.* (2013) provides the evidence for the presence of *Sivaonyx* in same strata as that of *Vishnuonyx* in Thailand and thus contradict the hypothesis of Pickford (2007). Instead, the evolution of "enhydriodontines" in Asia obviously starts earlier than previously thought. Moreover, new hypotheses must also include the record of Miocene "enhydriodontines" from Europe and Africa, and the migratory routes and sequence of radiation needs yet to be determined. As, *Vishnuonyx* and *Sivaonyx* occur earlier than previously thought by Pickford (2007) because of the new remains described since then. Kargopoulos (*et al.* 2021) also described *Vishnuonyx* in Europe; *Sivaonyx gandakasensis* is probably the same form as *Sivaonyx* from Eppelsheim (see Grohé *et al.* 2013), so there were already exchanges between Asia and Europe (as well as Africa) early on in the Middle Miocene and early Late Miocene for *Visnuonyx* and in the Late Miocene for *Sivaonyx*.

The second species is *Sivaonyx bathygnathus*. Its holotype (GSI-D 33) is a left mandible fragment with partial p4-m1, alveoli of canine (c) and p1-p3 illustrated by Lydekker (1884: pl. 27, fig. 3), which was re-illustrated and figured by Pohle (1919: pl. 2, fig. 2) and Matthew (1929: fig. 8). This species was originally described from the Upper Miocene deposits of the Hasnot (Lydekker 1884; Pilgrim 1931, 1932; Matthew 1929; Colbert 1935; Pickford 2007). Later, the same species was reported in the Late Miocene of Lufeng (Qi 1983) and possibly Yuanmou, Yunnan Province of China (Zong 1997; Qi *et al.* 2006). 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 Upper Miocene-Lower Pliocene deposits and according to Pilgrim (1932) most possibly from Upper Miocene sediments. Ghaffar & Akhtar (2016) also recovered their sample of *Sivaonyx bathygnathus* from Hasnot outcrops. The p4 specimens described and figured by Lydekker (1884), or Pilgrim (1932) and even in Pickford (2007) are all partially broken. The p4 (PUPC 16/29) described in this study is important in that it is well-preserved and almost unworn. PUPC 16/29 also enlarges our knowledge of intraspecific morphological variability in p4 of *S. bathygnathus*, as all previously known specimens have a more buccally positioned distal accessory cuspid. The measurement corresponds well with the already known measurements (Fig. 3; Table 2).

A third species of the genus *Sivaonyx*, *S. sarwari* n. sp., is described here based on an isolated upper fourth premolar (P4). This premolar is smaller in dimensions than all of the known species of the genus (Fig. 3; Table 2) and show peculiarities in its morphology like round outline, basal lingual cingulum straight at mesial border, and small mesial valley hence, less pinched mesial border along with very long posthypocrista or distal border in general. PUPC 17/64 is so small that its dimensions are even smaller than smallest known *Sivaonyx* P4s, IVPP V 6886.3 and IVPP V 6886.4, from Lufeng, China. With respect to proportions, PUPC 17/64 dimensions correspond well even to lower p4s, IVPP V6886.8+13 and IVPP V6886.8, given

TABLE 2. — Comparative measurements of *Enhydriodon* cf. *falconeri*, *Sivaonyx sarwari* n. sp. and *Sivaonyx bathygnathus* (Lydekker, 1884) (in mm). Comparative data taken from Pilgrim (1932), Colbert (1935), Chow (1961), Qi (1983), Zong (1997), Werdelin (2003), Morales & Pickford (2005), Morales *et al.* (2005), Pickford (2007), Peigné *et al.* (2008), Geraads *et al.* (2011), Werdelin & Manthi (2012), Grohé *et al.* (2013, 2022), Werdelin & Lewis (2013), Peigné (2016), Koufos *et al.* (2018) and Valenciano & Govender (2020). *, studied specimens; **, measurements as preserved; **est.**, estimated measurements.

Taxa	SpecimenNo	Nature	Length	Width	RatioW/L
Enhydriodon cf. *falconeri*	PUPC 83/01*	rm1	18.0	11.0	0.69
	NHM M 15397	rm1	18.6	10.9	0.59
	Chow, 1961	lm1	20.0	13.0	0.65
E. sivalensis Falconer, 1868	IPSMG 1949.187	rm1	22.0**	13.0**	0.59
	GSI D 161	rm1	21.60	13.1	0.61
Enhydriodon omoensis Grohé, Uno & Boisserie, 2022	L 56-1	m1	32.1	18.3	0.57
	OMO 18-1972-99	m1	31.7**	19.1**	0.60
Enhydriodon dikikae Geraads, Alemseged, Bobe & Reed, 2011	DIK-56-9 (holotype)	m1	30.0**	20.0**	0.66
	DIK-24-15	m1	26.0	16.2	0.62
Enhydriodon afman Werdelin & Lewis, 2013	KNM-ER 3110 (holotype)	m1	26.4	16.5	0.63
Enhydriodon sp.	OMO 3/0 10084	m1	26.4**	11.8**	0.45
Sivaonyx sarwari n. sp.	PUPC 17/64*	lP4	12.50	10.00	0.80
Sivaonyx bathygnathus (Lydekker, 1884)	GSI K13.14	lP4	14.00 est.	13.40	0.96
	GSI D 157	lP4	14.50	13.4	0.92
	IVPP V 6886.3	rP4	13.0	13.8	1.06
	IVPP V 6886.4	lP4	13.2	13.5	1.02
S. gandakasensis Pickford, 2007	GSP 4616	rP4	13.5	11.5	0.85
Sivaonyx hessicus Lydekker, 1890	PV-9002	lP4	12.50	10.7	0.85
S. soriae Morales & Pickford, 2005	BAR 1720'00	P4	14.8	15.0	1.01
S. hendeyi Morales, Pickford & Soria, 2005	SAM-PQL 50000B (holotype)	P4	16.9	17.4	1.03
S. ekecaman (Werdelin, 2003)	KNM-KP 10034A (holotype)	P4	16.5	–	–
	BAR 566'05	P4	14.7	17.5	1.19
E. falconeri Pilgrim, 1932	NHM M 4847	lP4	14.9	15.8	1.06
E. sivalensis	GSI NRV 2/468	rP4	17.3	18.6	1.08
	NHM M 37153	rP4	16.7 est.	17.2	1.03
	NHM M 37154	rP4	17.6	18.9	1.07
	NHM M 37154	lP4	17.6	18.9	1.07
	NHM M 37155	lP4	18.2	18.5	1.01
	GSI RCS 777A cast	lP4	16.5	18.4	1.11
	GSI RCS 777A cast	rP4	17.6	18.6	1.05
E. omoensis	P 791-18 (holotype)	P4	25.8**	26.7**	1.03
E. dikikae Geraads, Alemseged, Bobe & Reed, 2011	DIK-56-9 (holotype)	P4	20.5	22.7	1.11
E. cf. *dikikae*	KNM-KP 49887	P4	18.4	19.5	1.06
Sivaonyx bathygnathus (Lydekker, 1884)	PUPC 16/29*	lp4	10.4	6.70	0.64
S. bathygnathus	PUPC 2003/15	p4	7.50	5.50	0.73
	GSI D 156	lp4	9.6	5.80	0.60
	GSI D 244	rp4	10.1	6.40	0.63
	IVPP V 6886.3	rp4	13.0	13.8	1.06
	IVPP V 6886.4	lp4	13.2	13.5	1.02
	IVPP V 6886.8+13	lp4	8.80	6.00	0.68
	IVPP V 6886.9	lp4	8.40	6.00	0.71
	IVPP V 6886.10	lp4	8.80	6.50	0.74
	PDYV 1585	lp4	8.70	5.00	0.57
S. hendeyi Morales, Pickford & Soria, 2005	SAM-PQL 50000A (holotype)	p4	12.0	9.40	0.78
	SAM-PQL-9138	p4	13.8	9.90	0.72
S. ekecaman	BAR 720'03	p4	11.1	8.40	0.76
S. africanus Stromer, 1931	BSPG 1930 XI 1 (holotype)	p4	12.0	9.80	0.82

by Qi (1983) and reused by Pickford (2007). Also, with respect to the position of protocone and hypocone, space between these cusps, and lack of any cusplet between protocone and hypocone, shortness of preparacrista and to some extent postparacrista, IVPP V6886.3 is almost similar to PUPC 17/64. It is probable that, based on similarity in size and morphology, Lufeng material also belongs to *Sivaonyx sarwari* n. sp.

CONCLUSIONS

In the present study we have described the newly collected material of the subfamily Lutrinae (Mustelidae) from the Pakistan Siwaliks. The material came from Upper Miocene to Lower Pleistocene deposits of Hasnot, Padhri, and Bhimber and three taxa *Enhydriodon* cf. *falconeri*, *Sivaonyx sarwari* n. sp., and *S. bathygnathus* were recognized. Among this material, m1 of *E. falconeri* has been described for the first time from the Pleistocene deposits of the Siwaliks and an isolated upper fourth premolar is designated as the holotype of *Sivaonyx sarwari* n. sp. due to its small size and unique morphology. Hence, we are extending the stratigraphic range of *E. falconeri* to the Pleistocene, and add a third species of *Sivaonyx* in the Siwaliks. We also think that the Lufeng (China) material belongs to this newly erected species.

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