Estudios Geológicos, 63 (2)
julio-diciembre 2007, 135-146
ISSN: 0367-0449

First fossil small-clawed otter, *Amblonyx*, with a note on some specimens of *Lutra*, from the Upper Siwaliks, India

Primer ejemplar fósil de tipo nutria Amblonyx*, con una nota sobre ejemplares de* Lutra *del Siwaliks Superior, India*

P. Raghavan[1], M. Pickford[2], R. Patnaik[3], P. Gayathri[4]

ABSTRACT

Otter-like mammals have been reported from the Indian sub-continent for more than a century and a half. Enhydriodontini are far more common and have a longer fossil record than either Lutrini or Aonychini. This paper describes and interprets two fossils from the Pleistocene of Panchkula and Pipalwala, India. The Panchkula specimen represents a large species of *Amblonyx* (Aonychini) whereas the Pipalwala specimen is likely to represent a large individual of *Lutra palaeindica* (Lutrini).

Key words: Otters, *Amblonyx*, *Lutra*, Pleistocene, India, Siwaliks, new species.

RESUMEN

Mamíferos de tipo nutria han sido señalados en el subcontinente Indio desde hace más de un siglo y medio. Los Enhydriodontini son de lejos los más comunes y tienen un mayor registro fósil que los Lutrini o los Aonychini. En este trabajo describimos e interpretamos dos fósiles procedentes del Pleistoceno de Panchkula y Pipalwala, India. El ejemplar de Panchkula representa una especie de talla grande de *Amblonyx* (Aonychini), mientras que el ejemplar de Pipalwala representa a un individuo de talla grade de *Lutra paleoindica* (Lutrini).

Palabras clave: Nutrias, *Amblonyx*, *Lutra*, Pleistoceno, India, Siwaliks, nueva especie.

Introduction

The recovery of lutrine otter fossils is a rare event in the Indian subcontinent in contrast to the remains of enhydriodont otters, which have been found on a more regular basis. More than a century passed between the discovery of the skull and mandible of *Lutra palaeindica* Falconer (1868) and the Pipalwala specimen (Verma *et al.*, 2003) which probably represents the same taxon. We here report the discovery of an aonychine otter in the Pinjor Formation of the Siwalik Group, the first of this tribe known from the subcontinent.

Geological context and faunal association

The Siwalik Group of freshwater molasse sediments (~6000 m) spanning the period ~18-0.5 Ma, developed in response to the rising Himalayas to the north (fig. 1) and sinking Foreland Basin to the south (Tandon, 1991) (fig. 1). The Siwalik Group is subdivided into the Lower, Middle and Upper Siwalik Subgroups based on faunal assemblages and lithofacies criteria (Pilgrim, 1913; Prakash *et al.*, 1980). The Upper Siwalik Subgroup is divided into Tatrot (~5.26 to ~2.5 Ma), Pinjor (~2.5 to ~1.7 Ma) and Boulder Conglomerate Formations (~1.7 to

[1] School of Archaeology and Anthropology, Australian National University, Canberra ACT 0200, Australia; E-mail: ramapithecus@usa.net.
[2] Martin Pickford, Collège de France, UMR 5143 du CNRS, Case postale 38, 8 rue Buffon, 75005 Paris, E-mail: pickford@mnhn.fr.
[3] CAS in Geology, Panjab University, Chandigarh-160014, India, E-mail: rajeevpatnaik@gmail.com.
[4] Department of Anthropology, Panjab University, Chandigarh-160014, India, E-mail: marshalwolf@yahoo.co.in.

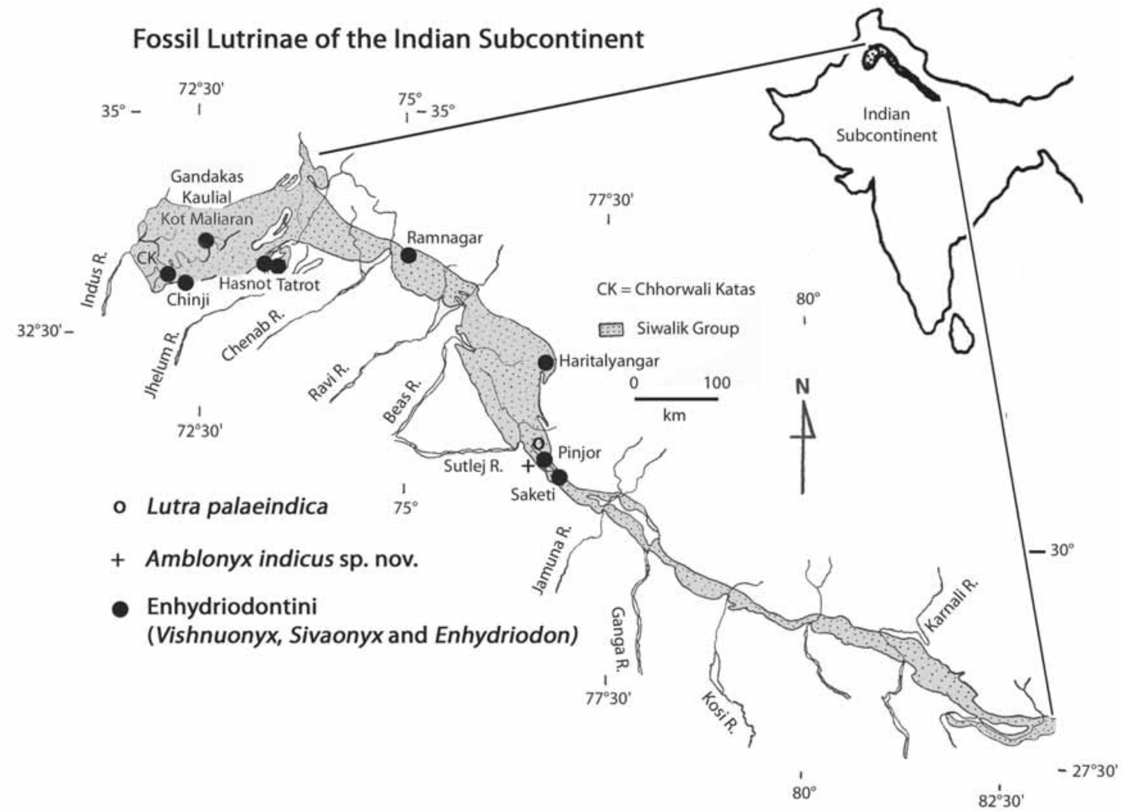

Fig. 1.—Map of the Indian subcontinent showing outcrops of the Siwalik Group to the south of the Himalayas and fossil otter occurrences, most of which are Enhydriodontini.

~0.5 Ma). The Pinjor and Boulder Conglomerate Formations are well exposed along the Ghaggar River Section which is located northeast of Chandigarh near the town of Panchkula (fig. 2). Tandon & Kumar (1985) reported a volcanic ash bed in the Ghaggar river section (fig. 2b), which was dated to around 2.14 ± 0.5 Ma on the basis of fission track dating (Mehta *et al*., 1988). Recently, Kumaravel *et al*., (2005) carried out a comprehensive palaeomagnetic stratigraphy of the Ghaggar River section spanning a thickness of ~ 1000 m aged between 2.7 Ma and 0.5 Ma (fig. 2b, c). The Upper Siwalik sequence in this section includes a small outcrop of the Tatrot Formation (slightly over 60 m thick) near Khetpurali, characterized by the presence of fine, medium and coarse-grained, grey sandstones and variegated mudstones deposited in low sinuosity streams, mainly of a trunk river system (Kumaravel *et al*., 2005). The Tatrot fauna of this area comprises *Stegodon bombifrons, Pentalophodon khetpuralensis*, *Hipparion antelopinum, Hexaprotodon sivalensis*, *Hipparion theobaldi,* and *Camelus sivalensis* (Sahni & Mitra, 1980; Nanda, 1978).

Pinjor is the only type locality of the Siwalik Group in India: the rest of the type localities are in Pakistan. In the Ghaggar River Section, the Pinjor Formation is about 380 m thick (basal part of section in fig. 2b), and consists of brown to greyish-brown, fine, medium and coarse-grained sandstones, multistorey sandstones, pebbly sandstone, pedogenic and non-pedogenic overbank facies deposited in high gradient, low sinuosity streams, mainly of piedmont drainage (Kumaravel *et al*., 2005). Pilgrim (1913) characterized the Pinjor zone by the first appearance of *Equus* and *Camelus*. Other taxa known from this region are *Dilatomys* sp., *Tatera pinjoricus, Mus linnaeusi, Stegodon insignis, Archidiskodon planifrons, Elephas hysudricus, Equus sivalensis, Leptobos* and *Bos* (Patnaik, 2003; Nanda, 1978). The overlying (~575 m thick) Boulder Conglomerate Formation is largely unfossiliferous and was deposited mainly in braided river channels and proximal alluvial fans (upper part of section in fig. 2b).

The otter horizon (A in fig. 2a) in the Ghaggar River section (~2.14 Ma) (figs. 1, 2) has yielded an associated fauna which includes murine rodents, *Elephas* sp., *Equus* sp., *Rhinoceros* sp., *Sus* sp., *Hexaprotodon* sp., *Camelus* sp., Bovinae indet., molluscs (*Lamellidens jammuensis*, *Parreysia tatrotensis*, *Parreysia* sp., *Melanoides tuberculata*, *Lymnaea brevicauda*), crabs (*Potamon* sp.) and fish (Cyprinidae, Siluridae, *Rita* sp., *Heterobranchus palaeindicus*) (Raghavan, 1990). The otter-yielding mudstone/siltstone intercalation is ~3 m thick and represents a pedogenically overprinted floodplain deposit. Pedogenesis has resulted in formation of calcareous nodules some of which are adhering to the fossil. The *Amblonyx* specimens came from one of these nodules. There are three other fossiliferous sites above this level along the Ghaggar River, which have yielded rodents such as *Mus linnaeusi* (fig. 2, G1) and *Tatera pinjoricus* (fig. 2, G2) (Patnaik *et al.*, 1996; Patnaik, 1997). 2 metres above level G1, large mammals such as antlered deer, *Capra* and unidentified bovine elements have been recovered (Raghavan, 1990). Locality G3 (fig. 2) is a richly fossiliferous deposit which has yielded fish (Cyprinidae, Siluridae, *Rita* sp., *Heterobranchus palaeindicus*), frogs (*Rana* sp.), mammals (*Nesokia panchkulaensis*, *Hystrix* cf. *H. leucurus*, *Chandisorex* sp.), ostracods (*Ilyocypris bradyi*, *Ilyocypris monstrica*, *Candona candida*, *Candonopsis* cf. *C. kingsleyi, Cypris decaryi*, *Cypris subglobossa*, *Zonocypris costata*, *Zonocypris mckenziei*, *Stenocypris* sp., *Megalocypris* sp.), molluscs (*Lamellidens jammuensis, Parreysia tatrotensis, Parreysia* sp., *Melanoides tuberculata*, *Lymnaea brevicauda*) crabs (*Potamon* sp.) and charophytes (*Tectochara* sp., *Tectochara* cf. *T. sahnii*, *Chara* cf. *C. contraria*, *Chara* cf. *C. surajpuriea*, *Chara* cf. *C. fragilis*, *Sphaerochara prolifera*) (Raghavan, 1990; Bhatia, 1996, 1999). Raghavan (1990) divided the assemblage into proximal or stream, stream bank and distal/ land communities.

Abbreviations

NHM: Natural History Museum, London.
SFP: Saketi Fossil Park, India.
PR: P. Raghavan.
CL: Catalogue.

Systematic description

Family Mustelidae Swainson, 1835
Subfamily Lutrinae Bonaparte, 1838
Tribe Aonychini Sokolov, 1973
Genus *Amblonyx* Rafinesque, 1832
Species *Amblonyx indicus* nov.

Diagnosis: Large species of *Amblonyx*, 50% larger (linear dimensions) than *Amblonyx cinereus*. Post-hypoconid crista in m/1 directed disto-buccally.

Holotype: Associated remains comprising PR-1-CL4- fragment of mandible with canine and premolar; PR-1-CL2: left M1/ in poor condition; PR-1-CL3: broken left lower jaw with p/4; PR-1-CL1: right mandible containing m/1 and posterior part of p/4, root of m/2; PR-1-CL5; distorted cervical vertebra; PR-1-CL6: broken vertebra.

Repository: Museum, Department of Anthropology, Panjab University, Chandigarh-160014, India.

Type locality: Panchkula, India (Pinjor Formation) (fig. 2a).

Age: Late Pliocene ca 2.14 Ma on the basis of stratigraphy, fission track dating and magnetostratigraphy (fig. 2b).

Description

The mandible (fig. 3) contains the right m/1 in light wear. In the trigonid, the metaconid is slightly behind the level of the protoconid. The crests joining the metaconid and the protoconid are separated by a notch in the midline of the tooth. The paraconid is far from the metaconid, leaving a V-shaped lingual opening in the trigonid basin. There is a deep notch between the paraconid and protoconid. The post-protoconid crest is low but sharp and is separated from the hypoconid by a narrow transverse incision. This crest, and the hypoconid behind it, are positioned some distance lingually of the buccal margin of the crown. Behind the hypoconid, there is a small cusp, now confluent with the hypoconid due to wear, which swings buccally at its distal extremity. The buccal cingulum is continuous from anterior to posterior and anteriorly it extends onto the lingual aspect of the paraconid. The talonid basin slopes bucco-lingually and is bordered postero-lingually by a low rim forming the lingual talonid cusp. Distally this cusp is separated from the posterior hypoconid crest by a shallow valley. The trigo-

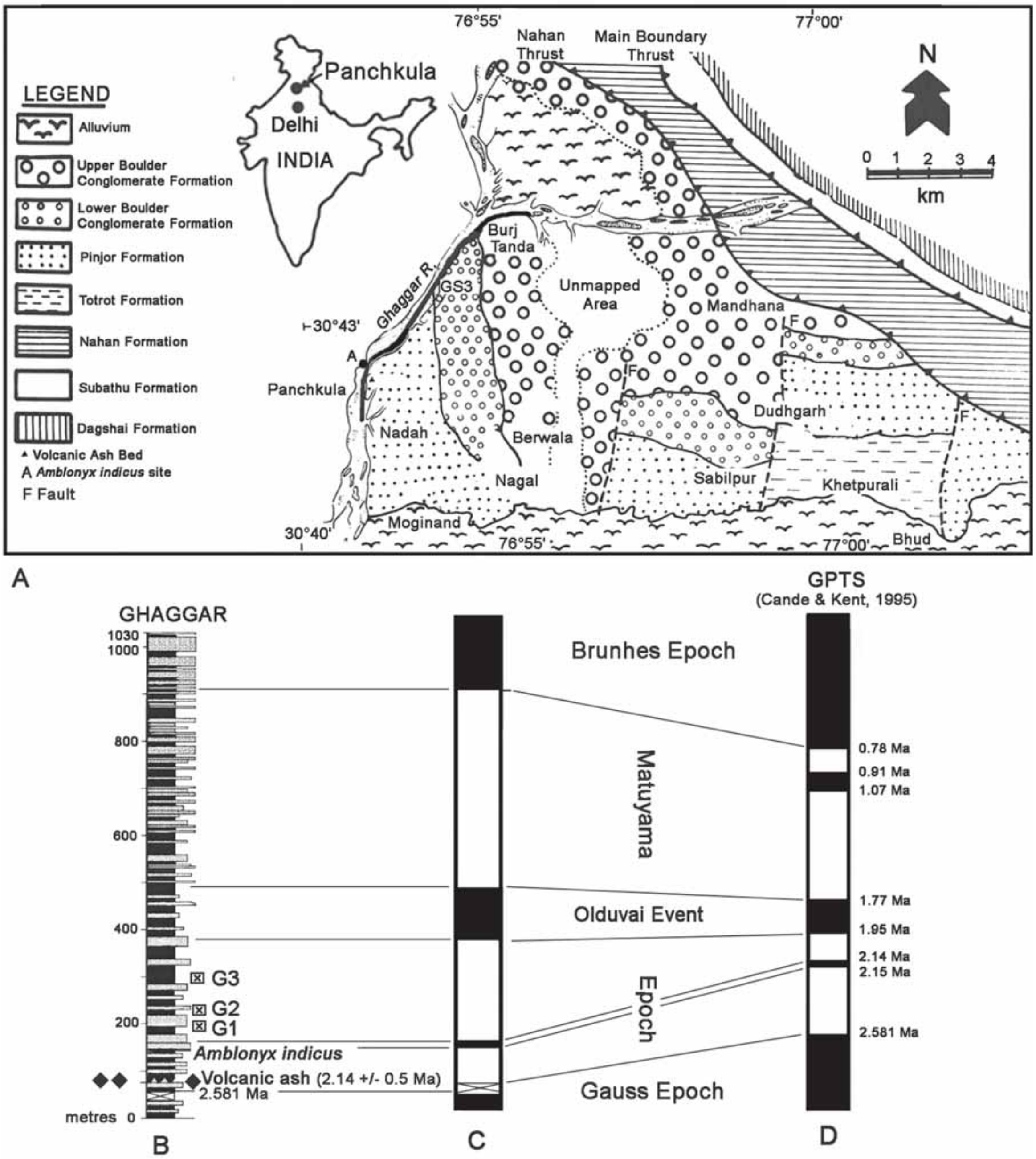

Fig. 2.—Geology, stratigraphy and magnetostratigraphy of the Panchkula area, Ghaggar River, India, showing the discovery locus of the Panchkula Otter, *Amblonyx indicus* sp. nov. A) Geological map modified from Kumar & Tandon, 1985). B-D) Lithostratigraphic column, magnetostratigraphy and correlation of Ghaggar River Section with the GPTS (modified from Kumaravel *et al.*, 2005). G1-G3 fossil sites.

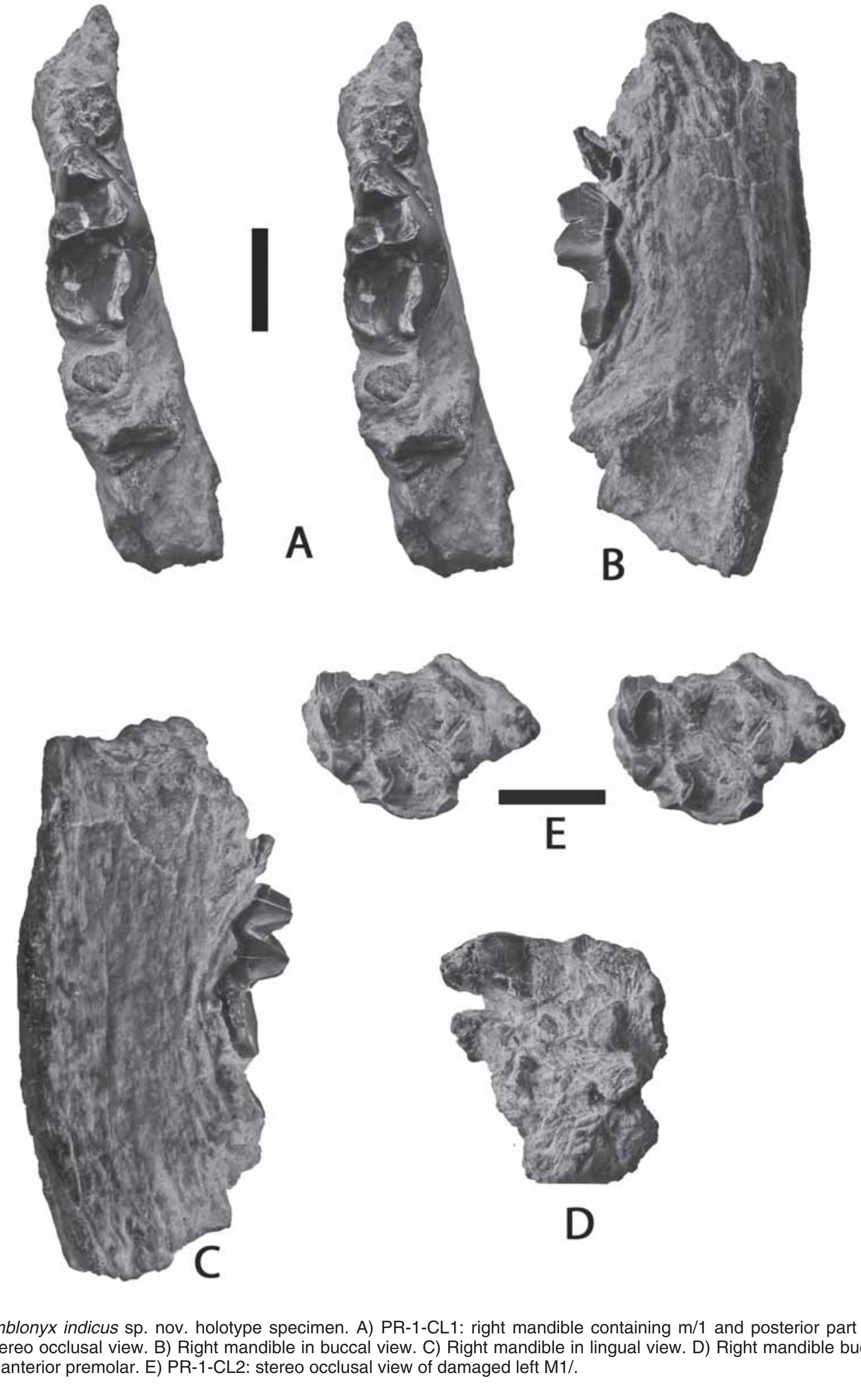

Fig. 3.—*Amblonyx indicus* sp. nov. holotype specimen. A) PR-1-CL1: right mandible containing m/1 and posterior part of p/4, root of m/2 in stereo occlusal view. B) Right mandible in buccal view. C) Right mandible in lingual view. D) Right mandible buccal view of canine and anterior premolar. E) PR-1-CL2: stereo occlusal view of damaged left M1/.

Table 1.—**Measurements (in mm) of the teeth of *Amblonyx indicus* sp. nov. from Panchkula, India (e = estimated measurement)**

Tooth	Length	Breadth
Right m/1	17.2	10
Right p/4	—	5.6[e]
Right p/1	5.6[e]	4.0e
Right lower canine	8.7[e]	6.9

nid is marginally narrower (9.2 mm) than the talonid (10.0 mm).

The remnant of p/4 in the right mandible shows a buccal cingulum, but the tooth is too poorly preserved to reveal details of the crown morphology although its breadth can be estimated (table 1). The m/2 is uniradiculate, and its crown would have been higher than the talonid of the m/1. The masseteric fossa is deep and extends as far forwards as the m/2.

The fragment containing the canine and a premolar are poorly preserved, but reveal that the anteriormost premolar lies behind the canine and not lingual to it. However, the jaw is poorly preserved in this part and difficult to interpret.

The overall shape of the crown of M1/ appears to have been losenge-shaped, but it is so poorly preserved that it is not possible to provide measurements or details of the morphology of the crown except that it shows a wedge- or dune-shaped protocone behind which is a broad hypocone (table 1).

Discussion

The specimen from Panchkula differs from *Lutra lutra* by the relatively broad talonid of its m/1 in which the post-protoconid crest and hypoconid are positioned some distance from the buccal cingulum, leaving a narrow shelf between these cusps and the buccal edge of the tooth. The post-hypoconid crest swings buccally at its distal extremity, which is unusual among otters (fig. 3) many of which have the crest swinging lingually. This morphology of the hypoconid complex is important to understand, since this part of the tooth occludes with the metacone-metastyle complex of the P4/, which consequently ought to be displaced more buccally in this species than it is in other otters. The buccal cingulum is also complete.

In all these features and in the details of crown shape and disposition of cusps, the m/1 in the Panchkula otter resembles those of the extant Asian small-clawed otter, *Amblonyx cinereus* and the Clawless otter of Africa, *Aonyx capensis*. Bivariate plots of the tooth and those of *Lutra lutra*, *Aonyx capensis* and *Amblonyx cinereus* show that the Panchkula fossil plots within the range of metric variation of *Aonyx capensis* (fig. 5) confirming the broad outline of the lower first molar relative to its length. The m/1 of *Lutra aonychoides* from Yushe, China, (Teilhard de Chardin & Leroy (1945) also falls within the range of metric variation of *Aonyx capensis* but it is a bigger specimen than the Panchkula example.

Because the Panchkula tooth is closer morphologically to those of *Amblonyx cinereus* than to those of *Aonyx capensis* we conclude that it belongs to this genus, but since it clearly represents a much larger animal, we create a new species for it, *Amblonyx indicus*. The Panchkula otter is smaller than the specimen of *Lutra aonychoides* from Yushe, China (Teilhard de Chardin & Leroy, 1945).

Lutra aonychoides from Yushe and Locality 49, China (Teilhard de Chardin & Leroy, 1945; Zdansky, 1924) is significantly larger (m/1 = 19 x 11.5 mm) than the Panchkula otter (m/1 = 17.2 x 9.9 mm), but the proportions of the talonid to trigonid in the m/1, and the detailed morphology of the cusps indicate that the two fossils are closely related. Neither of the specimens falls near the extrapolated regression line of *Lutra*, but close to the *Aonyx* – *Amblonyx* regression and it is considered likely that both these specimens belong to *Amblonyx* rather than to *Lutra*.

The fossil species *Lutrogale palaeoleptonyx* (Dubois, 1908) has a relatively broad m/1 (fig. 5) which is close in size to that of *Amblonyx indicus* described here. Von Koenigswald (1933, 1940) did not illustrate the m/1 from Sangiran, Java, so a suitable comparison cannot be made with the Indian specimen. Willemsen (1986) examined the question, and concluded that the Javan fossil belonged instead to a species close to *Lutrogale perspicillata*. Given that teeth of *Lutrogale perspicillata*, the extant Smooth-coated otter, tend to be narrower relative to length than those of *Lutra lutra* (fig. 5) (Pohle, 1919; Willemsen, 1980, 1986), then it is more likely that the Javan specimen belongs to *Amblonyx* or another Aonychini, rather than to *Lutrogale*, a Lutrini.

Other fossil otters that have a relatively broad talonid in the m/1 are *Tyrrhenolutra helbingi* (Hürzeler, 1987) from Italy, *Cyrnaonyx antiqua* (Helbing, 1935) from various sites in Europe, and *Limnonyx* species from Spain and other parts of Europe (Crusafont Pairo, 1950; Nordmann, 1858) (fig. 5).

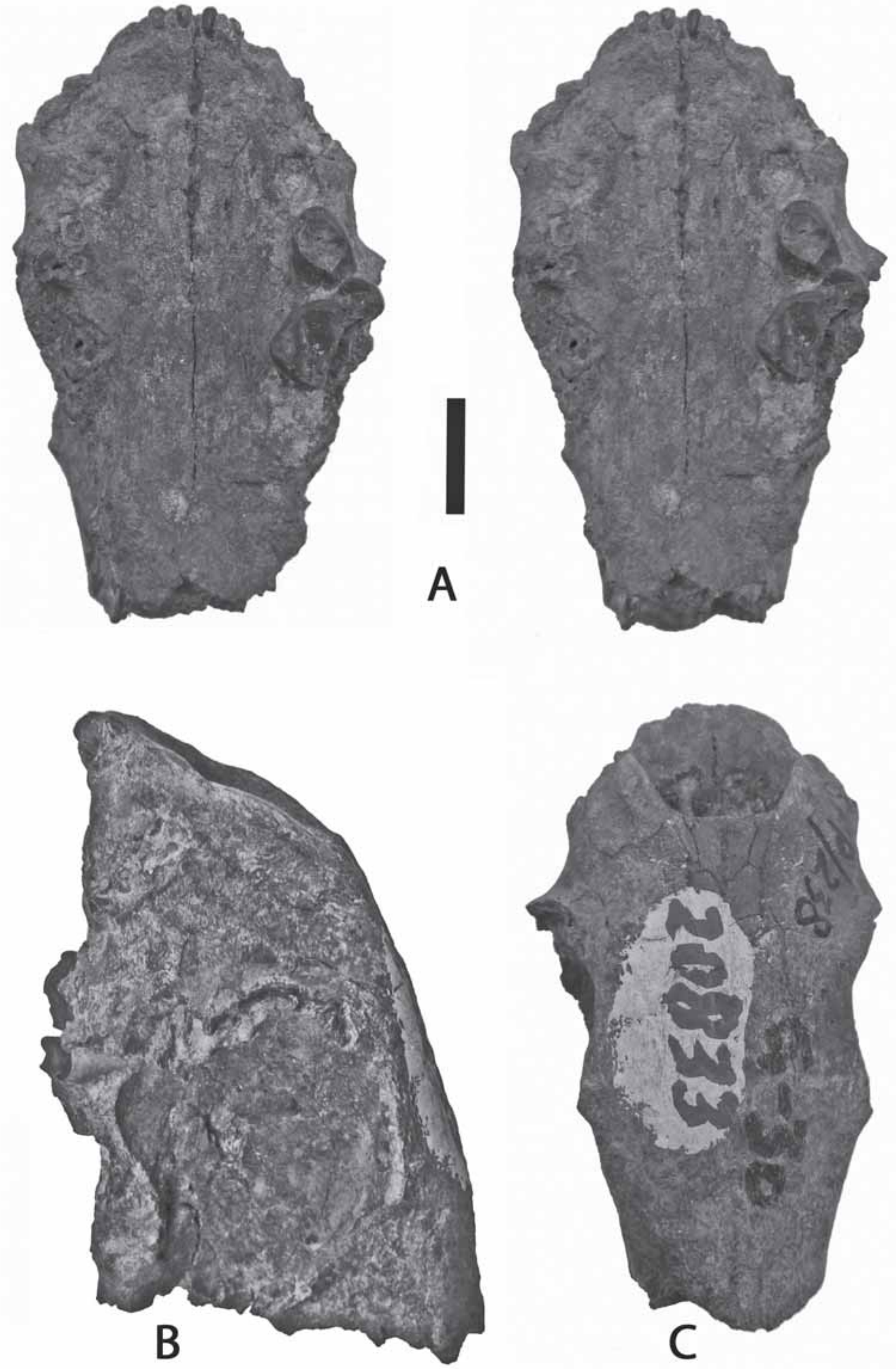

Fig. 4.—SFP 238, *Lutra palaeindica* snout from Pipalwala, India A) Stereo occlusal view. B) Left lateral view. C) Dorsal view.

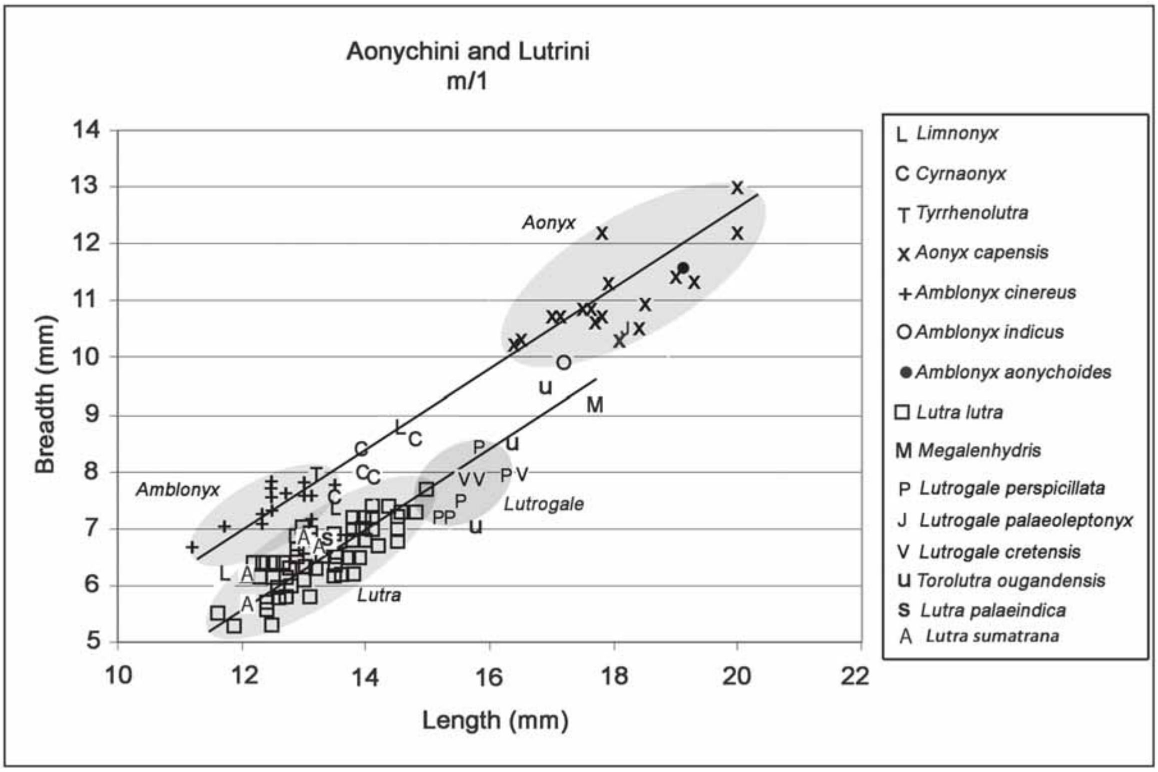

Fig. 5.—Aonychini and Lutrini m/1 length and breadth dimensions and comparisons with Asian and European Plio-Pleistocene otters (data for extant Lutrini and Aonychini from Pohle, 1919, and Willemsen, 1992).

None of them are as large as the Indian fossil, all plotting close to *Amblonyx cinereus*.

Megalenhydris barbaricina from Sardinia was interpreted by Willemsen & Malatesta (1987) to be an Aonychini, but the length-breadth proportions of the m/1 are close to those of *Lutra lutra* and widely divergent from the regression of the aonychine group (fig. 5) and in terms of m/1 proportions, it seems to be an enlarged version of *Lutra*.

Lutra bravardi has been approached to *Aonyx* by some authors (Kurten, 1968; Pohle, 1919) on account of the relatively broad P4/, but Willemsen (1992) considered that it fell comfortably within the range of morphometric variation of the genus *Lutra*. Direct comparisons cannot be made with *Amblonyx indicus* as the latter species shares no parts in common with *Lutra bravardi*, which is known only by upper teeth, and possibly a tibia.

The body weight of *Amblonyx indicus* would have been appreciably greater than that of *Amblonyx cinereus* which weighs about 3.2 kg (Larivière, 2003; Timmis, 1971), and judging from the dimensions of the m/1 it would have fallen near the lower limit of the range of body weight variation of *Aonyx capensis*, that is ca 11-12 kg (Larivière, 2001).

Tribe Lutrini Bonaparte, 1838
Genus *Lutra* Brünnich, 1772
Species *Lutra palaeindica* Falconer, 1868

Holotype: NHM M 37151, skull

Paratype: NHM M 37152, mandible

Referred material: SFP 238 (20833) Snout with broken left P3/ and P4/. Pipalwala, Pinjor Formation. R.L. Garg coll. (Verma *et al*., 2002, Pl. 13).

Description

The type specimens of *Lutra palaeindica* have been mentioned on many occasions, and all authors

Table 2.—**Measurements (in mm) of teeth attributed to *Lutra palaeindica***

Tooth	Length	Breadth
NHM M 37151 P4/	11.5	8.5
SFP 238 P3/	6.5	4.8
SFP 238 P4/	—	9.5
NHM M 37152 m/1	13.1	6.7

are agreed that they belong to the genus *Lutra* (Lydekker, 1884, 1885; Matthew, 1929; Pohle, 1919; Willemsen, 1992). Metrically the P4/ and m/1 plot out close to the centre of distribution of points of *Lutra lutra* (figs. 5, 6).

SFP 238 is the snout of a large otter (Verma *et al*., 2002) retaining damaged left P3/ and P4/, and the roots or partial to complete alveoli of the other teeth (fig. 4). The intermaxillary suture is not yet fused, despite the fact that the individual had the M1/ erupted at the time of death, judging by the sediment-filled alveolus behind the P4/ (fig. 4). There are differences in the lingual half of the P4/, from that of the holotype of *Lutra palaeindica*, the protocone being slightly more distally positioned relative to the anterior margin of the tooth. The parastyle is strongly developed, but the paracone and metacone are broken. Measurements are provided in table 2.

The P3/ in SFP 238 is a robust tooth, lacking the apex due to damage. It is narrower anteriorly than posteriorly, and is completely surrounded by a cingulum. The protocone has a prominent post-protocone crest and the tooth is positioned in the palate such that this crest is in line with the inner edge of the parastyle of the P4/. The same disposition seems to have occurred in the holotype in which the P3/ itself is missing, but in which the alveoli are well preserved.

The P1/ alveolus and that of the anterior root of the P2/ are located lingually to the canine alveolus as in the holotype of *L. palaeindica* (table 2).

Discussion

The Pipalwala otter snout SFP 238 (20833) was briefly described and illustrated by Verma *et al*., (2002). It is appreciably larger than the holotype of *Lutra palaeindica*, but its P4/ plots out close to the large end of the range of variation of *Lutra lutra* (fig. 5). Since the P4/ in the holotype of *Lutra palaeindica* plots close to the centre of the scatter of points of *Lutra lutra*, it is not improbable that the two Siwalik specimens belong to a single species. An alternative identification would be with the genus *Lutrogale* (fig. 6), but the specimen is too poorly preserved to provide satisfactory evidence for this suggestion.

Lutra palaeindica possesses a narrow m/1 characteristic of the piscivorous otter *Lutra lutra*. The other species of this tribe also possess narrow m/1s which therefore seems to be a constant feature of the tribe Lutrini, in contrast to the broader m/1s of Aonychini, which prey predominantly on shellfish (figs. 5, 6). Classified among the Lutrini are *Paralutra* from Europe (Roman & Viret, 1934), *Algarolutra* (Malatesta & Willemsen, 1989), *Sardolutra* (Willemsen, 1992), *Cyrnoluta* (Pereira & Salotti, 2000) and *Megalenhydris* (Willemsen, & Malatesta, 1987) from the Mediterranean, *Lutrogale* (Gray, 1865), *Lontra* (Gray, 1843), *Pteronura* (Gray, 1837), and *Satherium* (Gazin, 1934) from America, and *Lutra maculicollis* and *Torolutra* (Petter, Pickford & Howell, 1991) from Africa. Among these genera, the Indian fossils have been reported as being closest morphologically to *Lutra sumatrana*, the extant hairy-nosed otter of Southeast Asia (Lydekker, 1884; Pohle, 1919). We see no reason to oppose this view (figs. 5, 6) although it is not beyond the realms of possibility that the Pipalwala specimen belongs to *Lutrogale*.

On the basis of m/1 dimensions the body weight of *Lutra palaeindica* would have been similar to that of extant *Lutra lutra*, or about 5-10 kg (Yom-Tov *et al*., 2006).

At present, niche separation plays an important role in otter diversity in South-East Asia (Sivasothi & Nor, 1994) and the same seems to have been the case in the past. The Pleistocene deposits of the Siwalik Group have yielded remains of true otters encompassing two different dietary adaptations, a small piscivore (*Lutra palaeindica*) and a large shellfish predator (*Amblonyx indicus* sp. nov.). If we add to this the well known giant otter-like mammal, *Enhydriodon sivalensis,* the diversity of otters in these deposits is quite high. *Enhydriodon* probably preyed predominantly on bivalves rather than crabs. The Siwalik otters thus present an interesting case of niche separation among Pleistocene riverine otters of the Indian subcontinent.

The disproportionate representation of otter tribes in the Siwaliks Group remains to be explained: Enhydriodontini (several dozen specimens), Lutrini

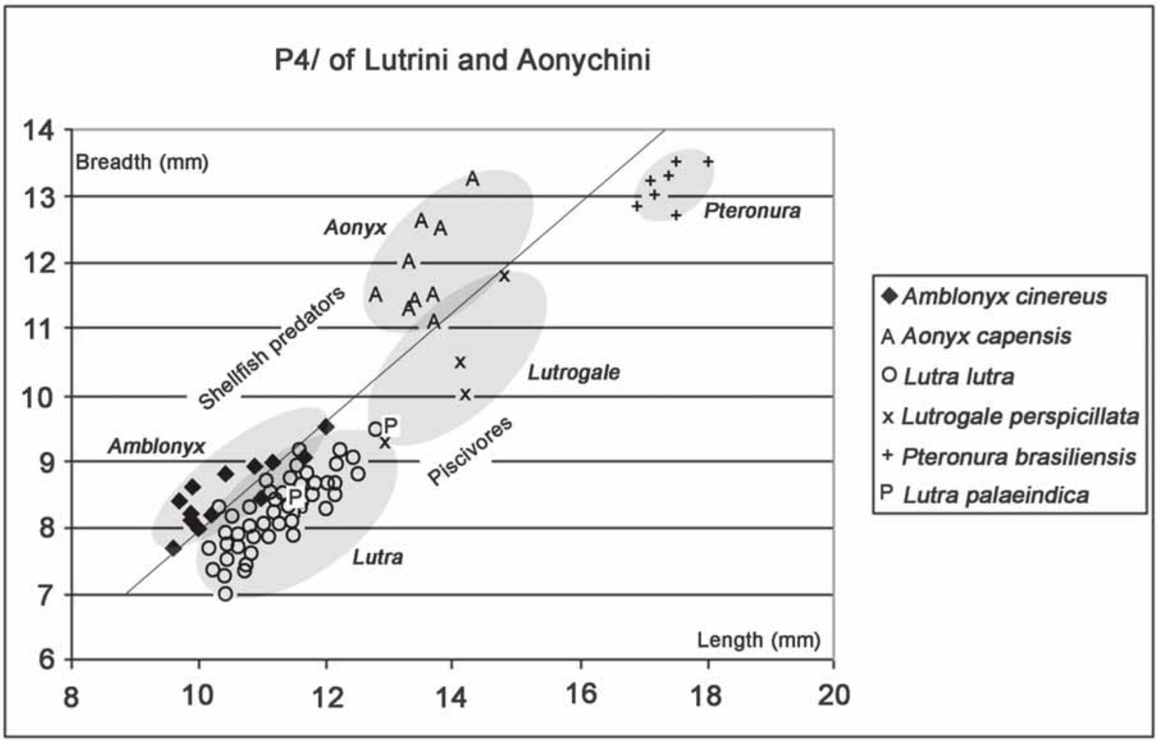

Fig. 6.—Aonychini and Lutrini P4/ length and breadth dimensions and comparisons with Indian Plio-Pleistocene otters attributed to *Lutra palaeindica* (data for extant Lutrini and Aonychini from Pohle, 1919, and Willemsen, 1992).

(three fossils) and Aonychini (one fossil). Fish and molluscs are present throughout the Siwalik sequence, so it is probably not a question of availability of prey categories. Otters spend much of their lives in or near water (rivers, swamps, ponds, lakes) so one would expect them to be better represented in the fossil record than they are. Perhaps the skeletal remains of Lutrini and Aonychini, being quite small otters, were subject to destruction by predators (crocodiles, large snakes, carnivores) whereas the more solidly constructed and large snouts of *Enhydriodon* had better chances of becoming fossilized, indicating the operation of a taphonomic filter. For the moment, the question remains unanswered.

The adaptations of the Indian fossil otters to different niches are reflected in the dental morphology and body size, the piscivore being small (ca 5-10 kg) with sectorial carnassials, the cancrivore being medium sized (ca 11-12 kg) with semi-bunodont carnassials whereas the molluscivore was large (ca 22-25 kg) with mastoidized carnassial cusps.

Conclusions

Lutrini and Aonychini are extremely rare in Indian fossil deposits and are confined to Plio-Pleistocene deposits, unlike the remains of Enhydriodontini which are reasonably well represented and span the period from Middle Miocene to Pleistocene. We here describe and interpret some fossils from the Pleistocene of India attributed to the otter tribes Aonychini and Lutrini. A large shellfish predator is identified as a new species of *Amblonyx*, *A. indicus*. The dimensions of the teeth indicate that this species was similar in body size (estimated at ca 11-12 kg) to the extant Cape clawless otter (*Aonyx capensis*) (ca 12-18 kg (Larivière, 2001)), from which it differs by the morphology of the talonid basin of the m/1, which, in contrast, approaches the Indian specimen to the genus *Amblonyx*.

Other large otters from the Plio-Pleistocene of Asia have been described, including *Lutra aonychoides* from China (Zdansky, 1924) and *Lutra palaeoleptonyx* from Java (Dubois, 1908; Von

Koenigswald, 1933, 1940). Both of these taxa possess broad m/1s and are likely to represent Aonychini rather than Lutrini, and were thus probably predominantly shellfish predators. *Lutra robusta* (Von Koenigswald, 1933) is based on a P4/ from Java, which Willemsen (1986) considered to belong to *Lutrogale palaeoleptonyx*. It cannot be compared with the Panchkula otter due to lack of parts in common.

Lutrini from the Pleistocene of India have been known for more than a century (Falconer, 1868) but their remains are rare. The new specimen from Pipalwala is larger than the type specimen of *Lutra palaeindica*, but probably belongs to this species. This is because the teeth of the type specimens plot near the centre of metric variation of *Lutra lutra*, while the Pipalwala specimen plots near the large end of the range of variation. The range of variation of the teeth of *Lutra sumatrana* is based on only four specimens, all of which fall into the lower half of the range of variation *Lutra lutra*. Unfortunately the teeth in the Pipalwala specimen are damaged, making it difficult to assess the meaning of the slight differences in morphology that can be made out between it and the holotype of *Lutra palaeindica* and there is a faint possibility that it belongs to *Lutrogale* rather than to *Lutra*.

ACKNOWLEDGEMENTS

Funding from the French CNRS (UMR 5143) is gratefully acknowledged. Thanks to Drs A. Mathur, and R. Loyal (University of Panjab, Chandigarh) and Dr V.P. Mishra (GSI Lucknow) for access to fossils in their care. Rajeev Patnaik would like to thank DST, New Delhi for the financial support.

References

Bhatia, S.B. (1996). The Ostracoda fauna and the Charophyte flora of the Siwalik Group: Palaeogeographic and Palaeoecologic implications. *Publ. Center Advan. Stud.*, 5: 99-106.

Bhatia, S.B. (1999). Revision of the Charophyte flora of the Siwalik Group (Neogene-Quaternary) of the Lesser Himalaya, India. *Australian J. Botany*, 47(49): 474.

Bonaparte, C.L. (1838). Synopsis Vertebratorum Systematis, *Nuovi Ann. Sci. Nat. Bologna*, 2: 105-133.

Brünnich, M.T. (1772). *Zoologiae fundamenta praelectionibus academicis accomodata*. Hafniae, Lipsiae.

Crusafont-Pairó, M. (1950). *Limnonyx*, un nuevo Lutrido del Mioceno español, *Notas Com. Ins. Geol. Miner. España*, 20: 3-14.

Dubois, E. (1908). Das geologischer Alter der Kendeng- oder Trinil-Fauna. *Tijd. Kon. Ned. Aar. Genoot.,* 25: 1235-1270.

Falconer, H. (1868). On *Enhydriodon (Amyxodon)* a fossil genus allied to *Lutra*, from the Tertiary strata of the Siwalik Hills. Vol. 1. *Palaeontological Memoirs and Notes,* Edited by R.I. Murchison, London.

Gazin, C.L. (1934). Upper Pliocene mustelids from the Snake River Basin of Idaho. *J. Mammalogy*, 15: 137-149.

Gray, J.E. (1837). Description of some new or little known Mammalia principally in the British Museum. *Mag. Nat. Hist*., 1: 577-587.

Gray, J.E. (1843). *List of the Specimens of Mammalia in the Collection of the British Museum*. London, British Museum (Natural History), 216 p.

Gray, J.E. (1865). Revision of the genera and species of Mustelidae contained in the British Museum. *Proc. Zool. Soc. London*, 1865: 100-154.

Helbing, H. (1935). *Cyrnaonyx antiqua* (Blainv.) ein Lutrine aus dem europäischen Pleistozän. *Eclog. Geol. Helv*. 28: 563-577.

Hürzeler, J. (1987). Die Lutrinen (Carnivora, Mammalia) aus dem "Grosseto-Lignit" der Toscana. *Schweitzer. Paläont. Abh.* 110: 28-48.

Kumaravel, V., Sangode, S.J., Rohtash K., & Siddaiah, S.N. (2005). Magnetic polarity stratigraphy of Plio-Pleistocene Pinjor Formation (type locality), Siwalik Group, NW Himalaya, India. *Current Sci. India*, 88: 1453-1461.

Kurten, B. (1968). *Pleistocene Mammals of Europe*. Wiedenfeld & Nicholson, London, 317 p.

Larivière, S. (2001). *Aonyx capensis*. *Mammalian Species Sheets, Amer. Soc. Mammalogists*, 671: 1-6.

Larivière, S. (2003). *Amblonyx cinereus*. *Mammalian Species Sheets, Amer. Soc. Mammalogists*, 720: 1-5.

Lydekker, R. (1884). Indian Tertiary and Post-Tertiary Vertebrata: Siwalik and Narbada Carnivora. *Mem. Geol. Surv. India, Palaeontologica Indica*, 2: 178-355.

Lydekker, R. (1885). *Catalogue of the Fossil Mammalia in the British Museum (Natural History)*. London, British Museum (Natural History) 268 p.

Malatesta, A., & Willemsen, G. (1989). *Algarolutra* g.n. established for a fossil otter of the Sardinia Island. *Geol. Romana*, 25: 285-286.

Matthew, W.D. (1929). Critical observations upon Siwalik Mammals. *Bull. Amer. Mus. Nat. Hist*. 56: 437-560.

Mehta, Y. P., Thakur, A. K., Nand, L., Shukla, B., & Tandon, S. K. (1993). Fission track age of zircon separates of tuffaceous mudstones of the Upper Siwalik subgroup of Jammu– Chandigarh sector of the Punjab sub-Himalaya. *Current Sci. India*, 64: 519-521.

Nanda, A. C. (1978). Fossil equids from the Upper Siwalik Subgroup of Ambala, Haryana. *Himalayan Geol.*, 8: 149-177.

Nordmann, A. Von (1858). Palaeontologie Südrusslands II. *Felis*, *Hyaena*, *Canis*, *Thalassictis*, *Mustela*, *Lutra*, *Spermophilus*, *Arvicola*, *Spalax*, *Castor*, *Lepus*, und *Equus*. H.C.Friis, Helsingford, 111-190.

Parkash, B., Sharma, R. P., & Roy, A. K. (1980). The Siwalik Group (molasse) sediments shed by collision of continental plates. *Sed. Geol.*, 25: 127-159.

Patnaik, R. (1997). New Murids and Gerbillids (Rodentia, Mammalia) from Pliocene Siwalik sediments of India. *Palaeovertebrata*, 26: 129-165.

Patnaik, R., Auffray, J-C, Jaeger, J.J., & Sahni, A. (1996). House mouse ancestor from Late Pliocene Siwalik sediments of India. *C. R. Acad. Sci. Paris*. 319: 431-434.

Patnaik, R. (2003). Reconstruction of Upper Siwalik palaeoecology and palaeoclimatology using microfossil palaeocommunities. *Palaeogeogr. Palaeoclimatol. Palaeoecol*., 197: 135-150.

Pereira, E., & Salotti, M. (2000). *Cyrnolutra castiglionis* une nouvelle forme de loutre (Mustelidae, Lutrinae), dans un dépôt du Pléistocène moyen, Castiglione 3CG (Oletta, Haute-Corse). *C. R. Acad. Sci. Paris, Sci. Terre*, 331: 45-52.

Petter, G., Pickford, M., & Howell, F.C. (1991). La loutre piscivore du Pliocène de Nyaburogo et de Nkondo (Ouganda, Afrique orientale): *Torolutra ougandensis* n.g., n.sp. (Mammalia, Carnivora). *C. R. Acad. Sci. Paris*, 312: 949-955.

Pilgrim, G. E. (1913). The correlation of the Siwaliks with the mammalian horizons of Europe. *Records Geol. Surv. India*, 43: 264-325.

Pohle, H. (1919). Die unterfamilie der Lutrinae. *Arch. Naturges. Berlin*, 85: 1-247.

Rafinesque, C.S. (1832). Description of a new otter, *Lutra concolor*, from Assam in Asia. *Atlantic J*., 1: 62.

Raghavan, P. (1990). New records of microfossil assemblages from the basal Pinjor Formation at Panchkula, Haryana (India). *Bull. Indian Geol. Assoc*., 23: 29-37.

Roman, F., & Viret, J. (1934). La faune de mammifères du Burdigalien de La Romieu (Gers). *Mém. Soc. Géol. France, Nouvelle Série*, 21: 2-3.

Sahni, A., & Mitra, H. C. (1980). Neogene palaeobiogeography of the Indian subcontinent with special reference to fossil vertebrates. *Palaeogeogr. Palaeoclimatol. Palaeoecol.,* 31: 39-62.

Sokolov, I.I. (1973). Napravleniya evolyutsii i estestvennaya klassifikatsiya podsemeistva vydrovykh (Evolutionary trends and the classification of the subfamily of otters). *Byull. Mosk. O Ispyt Prirody, Otd. Biol.,* 78: 45-52.

Sivasothi, N., & Nor, B. (1994). A review of otters (Carnivora: Mustelidae: Lutrinae) in Malaysia and Singapore. *Hydrobiologia*, 285: 151-170.

Swainson, W. (1835). A Treatise on the Geography and Classification of Animals. *The Cabinet Encyclopaedia*. London, Longman, Rees, Orme, Brown & Longman. 367 p.

Tandon, S. K. (1991). The Himalayan Foreland: Focus on Siwalik Basin. In: *Sedimentary Basins of India: Tectonic Context* (Tandon, S. K., Pant, C. C., & Casshyap, S. M., eds.), Gyanodaya Prakashan, Nainital, 177-201.

Tandon, S. K., & Kumar, R. (1984). Discovery of tuffaceous mudstones in the Pinjor Formation of Punjab sub-Himalaya, India. *Current Sci. India*, 53: 982-984.

Teilhard de Chardin, P., & Leroy, P. (1945). Les Mustelidés de Chine. *Publ. Inst. Géobiol. Pékin*, 12: 1-56.

Timmis, W.H. (1971). Observations on breeding the oriental short-clawed otter *Amblonyx cinerea* at Chester Zoo. *International Zoo Yearbook*, 11: 109-111.

Verma, B.C., Mishra, V.P., & Gupta, S.S. (2003). Pictorial Catalogue of Siwalik Vertebrate Fossils from Northwest India. *Geol. Survey India, Catalogue Series*, 5: 1-376.

Von Koenigswald, G. (1933). Beitrage zur Kenntnis der fossilen Wirbeltiere Javas. I. Teil. *Wet. Med. Dienst. Mijnb. Ned. Indie*, 23: 1-127.

Von Koenigswald, G. (1940). Neue *Pithecanthropus*-Funde 1936-1938. Ein Beitrag zur Kenntnis der Praehominiden. *Wet. Med. Dienst. Mijnb. Ned. Indie*, 28: 1-205.

Willemsen, G. (1980). Comparative study of the functional morphology of some Lutrinae, especially *Lutra lutra*, *Lutrogale perspicillata* and the Pleistocene *Isolalutra cretensis*. *Proc. Koninkl. Nederl. Akad. Wetensch*., 83: 289-325.

Willemsen, G. (1986). *Lutrogale palaeoleptonyx* (Dubois, 1908), a fossil otter from Java in the Dubois collection. *Proc. Koninkl. Nederl. Akad. Wetensch*., 89: 195-200.

Willemsen, G. (1992). A revision of the Pliocene and Quaternary Lutrinae from Europe. *Scripta Geol*. 101: 1-115.

Willemsen, G., & Malatesta, A. (1987). *Megalenhydris barbaricina* sp. nov., a new otter from Sardinia. *Proc. Koninkl. Ned. Akad. Wetensch*., 90: 83-92.

Yom-Tov, Y., Heggberget, T., Wiig, O, & Yom-Tov, S. (2006). Body size changes among otters, *Lutra lutra*, in Norway: the possible effects of food availability and global warming. *Oecologia*, 150: 155-160.

Zdansky, O. (1924). Jungtertiäre Carnivoren Chinas. *Palaeont. Sinica*, 2: 1-149.

Recibido el 15 de marzo de 2007
Aceptado el 12 de julio de 2007