Revision of the Mio-Pliocene bunodont otter-like mammals of the Indian Subcontinent

Revision de los mamíferos bunodontos de tipo nutria del Mio-Plioceno del Subcontinente Indio

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ABSTRACT

A revision of the Enhydriodontini of the Indian Subcontinent is undertaken on the basis of previously described and recently collected bunodont otter-like fossils from the sub-Himalayan Siwalik Group. It is confirmed that, with the passage of geological time spanning the period 13 – 3 Ma, there occurred a progressive increase in body size, a reduction of the anterior part of the premolar row and an increase in degree of cheek tooth bunodonty and cusp mastoidization. Functional analysis of a snout with a partly preserved incisor battery of *Enhydriodon sivalensis*, reveals that it was probably a molluscivore, preying principally on bivalves, while other species of enhydriodonts were more likely to have been piscivores and cancrivores. One new species of *Sivaonyx* is described from the base of the Late Miocene of Pakistan. Bunodont otter-like mammals from Eurasia, Africa and North America are briefly discussed in light of the revision of the Indo-Pakistan ones. The origins and phylogenetic relationships of these mammals remains obscure. The major differences in dental anatomy indicate that these Old World otter-like mammals should not be classified in Enhydrini, but in a tribe of their own Enhydriodontini new tribe.

Key-words: Mio-Pliocene, otter-like mammals, Indian Subcontinent, biochronology, taxonomy, phylogeny, diet, Enhydriodontini

RESUMEN

La revisión de los Enhydriontinos del subcontinente Indio se aborda, tanto en base a los fósiles de nutrias bunodontas previamente descritos, como a los hallazgos recientemente realizados en el Grupo de los Siwaliks en el sub-Himalaya. Se confirma que durante el período de tiempo comprendido entre los 13 a 3 Ma hubo un progresivo incremento en la talla corporal, una reducción de la parte anterior de la serie premolar y un incremento en el grado de bunodoncia y mastoidización de las cúspides de los dientes. El análisis funcional de un hocico de *Enhydriodon sivalensis* con la batería de incisivos parcialmente conservados revela que esta especie fue parcialmente malacófaga, alimentándose principalmente de bivalvos, mientras que otras especies de enhydriontinos fueron más piscívoras y cancrívoras. En el trabajo también se describe una nueva especie de *Sivaonyx* procedente de la base del Mioceno Terminal de Paquistán. Los mamíferos bunodontos de tipo nutria de Eurasia, África y América del Norte son brevemente discutidos a la luz de la revisión realizada para las formas paquistaníes. El origen y relaciones filogenéticas de estos mamíferos permanecen oscuros. Las importantes diferencias en anatomía dental indican que estos mamíferos de tipo nutria del Viejo Mundo no deberían ser clasificados como Enhydrini, sino en una tribu propia, Enhydriodontini nueva tribu.

Palabras-clave: Mio-Plioceno, mamíferos de tipo nutria, Subcontinente Indio, biocronología, taxonomía, filogenia, dieta, Enhydriodontini

Introduction

The existence of extinct bunodont otter-like mammals has been known for a century and a half (Falconer, 1868; Hürzeler, 1987; Lydekker, 1884a, 1884b, 1885; Meneghini, 1863; Pilgrim, 1931, 1932; Willemsen, 1999). The taxonomy, and hence the diversity, of these creatures has been the subject of much debate, principally because of the fragmentary nature of their fossil record. Not one type spe-

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cimen among the dozen or so described taxa posses-ses associated upper and lower dentitions. In addi-tion, because the quantity of material is restricted, it has been difficult to determine the limits of variabi-lity within each species. As the sample has impro-ved, it has emerged that there has been an admixtu-re of unrelated fossils attributed to some species.

The recovery of new fossil remains from the Mio-Pliocene of the Indian subcontinent provides an opportunity to reassess this group of aquatic mammals.

Up to 2006, the following species of Mio-Plio-cene otter-like mammals with tendencies to deve-lop bunodont dentitions have been described or mentioned in the palaeontological literature (gene-ra and species are listed as originally identified and in the order that the remains were described : many of the generic attributions have subsequently been modified).

Indian Subcontinent

Enhydriodon sivalensis Falconer, 1868
Lutra bathygnatha Lydekker, 1884a
Enhydriodon falconeri Pilgrim, 1931
Vishnuonyx chinjiensis Pilgrim, 1932

Mainland Asia (China, Russia)

Enhydriodon cf *falconeri* Pilgrim, 1931 (Chow, 1961)
Sivaonyx bathygnathus (Lydekker, 1884a) (Qi, 1983)
Enhydriodon sp. Titov *et al*. (2006)

Europe

Enhydriodon campanii Meneghini, 1863
Lutra hessica Lydekker, 1890
Lutra reevei Newton, 1890
Enhydriodon latipes Pilgrim, 1931
Enhydriodon lluecai Villalta & Crusafont-Pairo, 1945
Sivaonyx lehmani Crusafont-Pairo & Golpe-Posse, 1962b
Paludolutra maremmana Hürzeler, 1987
Tyrrhenolutra helbingi Hürzeler, 1987 (its status with respect to Enhydriodontini is not clear ; it could be an Aonychini)

Africa

Lutra aff *capensis* Stromer, 1920
Lutra aff *hessica* Lydekker, 1890 (Stromer, 1920) (probably *Torolutra ougandensis*)
Enhydriodon africanus Stromer, 1931
Vishnuonyx chinjiensis Pilgrim, 1932 (Morales & Pickford, 2005b)
Enhydriodon ekecaman Werdelin, 2003a
Vishnuonyx angololensis Werdelin, 2003b
Enhydriodon aethiopicus Geraads *et al*., 2004 (a synonym of *Pseudocivetta ingens*)
Enhydriodon hendeyi Morales, Pickford & Soria, 2005
Sivaonyx soriae Morales & Pickford, 2005a
Sivaonyx senutae Morales & Pickford, 2005a
Sivaonyx kamuhangirei Morales & Pickford, 2005a

North America

Enhydriodon cf *lluecai* Repenning (1976) = *Enhy-dritherium terraenovae* Berta & Morgan, 1985
Enhydriodon sp. nov. Repenning (1976)

Ages of otter-like mammals from the Indian Subcontinent

All the bunodont otter-like mammals from the Indian Subcontinent came from the Siwalik sequen-ce in the foothills south of the Himalayas (figs. 1, 2). Most of the fossils have imprecise stratigraphic con-texts, but historically, approximate ages have been proposed on two bases. The first is biochronology, which itself is somewhat imprecise on account of the fact that many of the Siwalik fossil collections represent assemblages from areas encompassing various stratigraphic horizons. Biostratigraphic sche-mes were proposed for the Siwaliks by Pilgrim (1913) Colbert (1935) and others, based on the evo-lutionary stages of the faunal assemblages relative to each other, and over the years a consensus built up that there were several mammal «ages» or «zones» represented in the subcontinent. In ascending order these were named Kamlial, Chinji, Nagri, Dhok Pat-han, Tatrot and Pinjor zones (fig. 2). Research during the past three decades has resulted in better definition of the stratigraphy of these regions, and thus of the faunas that they yielded. In broad terms, the Kamlial and Chinji zones are late Middle Mioce-ne, approximately equivalent to MN 6 and MN 7/8
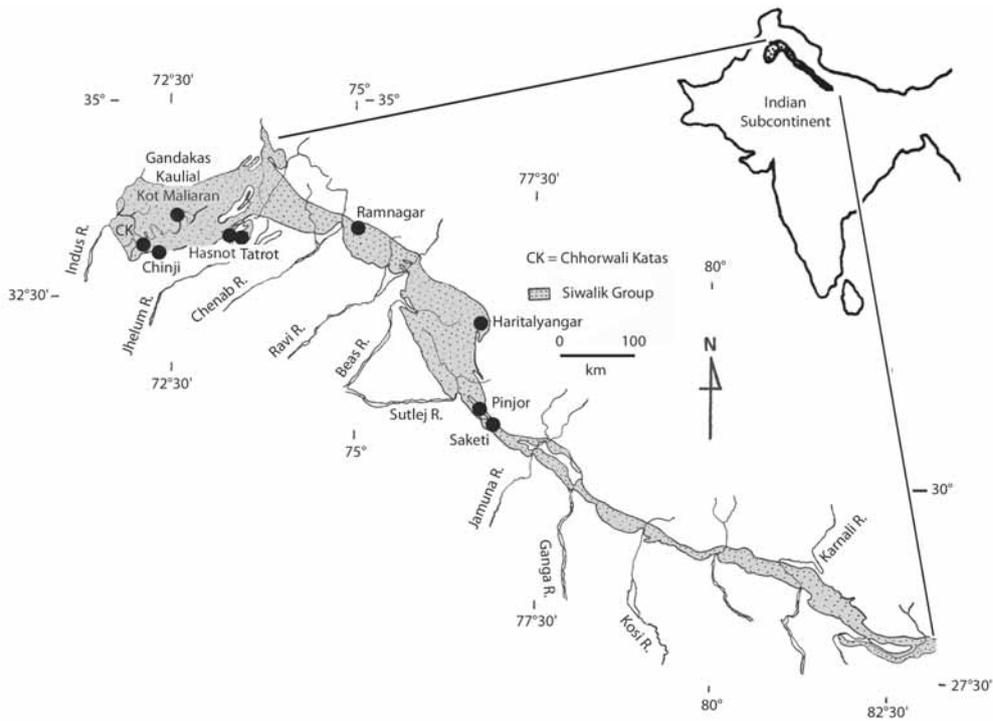
Fig. 1.—Distribution of Siwalik Group deposits and fossiliferous areas in the northwestern sector of the Indian subcontinent (modified from Sehgal & Nanda, 2002b).

Fig. 2.—Biochronology of Siwalik Group deposits that have yielded fossils of bunodont otter-like mammals (Haritalyangar is reported to have yielded *Sivaonyx*, but the basis is not clearly established).

in Europe, Nagri and Dhok Pathan are Late Miocene correlating approximately with MN 9-10 and MN 11-13 respectively, Tatrot is Latest Miocene about equivalent to MN 13 and Pinjor is Middle to Late Pliocene, equivalent to about MN 14-15. Although a great deal of doubt still exists about the precise discovery locus of many of the fossils, the zones defined by Pilgrim (1913, 1934) are sufficiently broad that, despite their drawbacks, they do provide a general sense of the sequence of events and, to some extent, the timing of events. Figure 2 provides a summary of the succession as it pertains to the lutrines discussed in this paper.

The second approach for determining the age of Siwalik fossils is stratigraphy which was generally neglected during the 19th and early parts of the 20th Century. In the past three decades advances have been made, particularly in areas such as the Siwalik Hills which have been mapped in detail (Verma & Gupta, 1992) and which are now demonstrated to span particular time periods, and these findings have been incorporated into figure 2. Thus, even though the timing of events in the lutrine succession is not very refined, the broad outlines of lutrine evolution in the subcontinent can be discerned.

The lutrines discussed in this paper are treated in ascending stratigraphic order. The Potwar succession, Pakistan, is subdivided into its classic units, Chinji, Nagri, Dhok Pathan and Tatrot zones (Barry *et al*., 1982, 1985; Pickford, 1988) and the Siwalik Hills is referred broadly to the Pinjor zone although some deposits equivalent to the Tatrot zone occur there (Nanda, 1981). For greater detail the reader is referred to the papers by Verma & Gupta (1992) for the Siwalik Hills, and by Johnson *et al*. (1983) and Pillans *et al*. (2005) for Haritalyangar. Other works consulted in the context of geochronology and biochronology of the Siwaliks are by Ranga Rao *et al*. (1988) Nanda (1981, 1994, 1997, 2002) Nanda & Sehgal (1993, 2005) and Sehgal & Nanda (2002a, 2002b).

Methods and data base

This revision is based on observation of original fossils whenever possible, and on casts where original material has been destroyed or misplaced. Only a few specimens, mainly those from Haritalyangar, could not be restudied. It is clear that some of the published literature is misleading, either in terms of morphology (line drawings, for example) or dimensions (eg plate captions reporting figures at natural size when they are up to 10% smaller or larger). In order to standardise the measurements, I have remeasured all the available Indo-Pakistani fossils, taking into account damage such as missing cingula or broken cusps in

teeth, something that was not always specified in the original descriptions. It is evident from the divergence in dimensions obtained for particular teeth that different authors have oriented specimens in different ways. A few fossils could not be remeasured, and for these I have employed the published values. In the accompanying tables of measurements, I have specified whether the measurements are mine or those of other authors.

Abbreviations

AM – American Museum of Natural History, New York
ENM – Ethiopian National Museum, Addis Ababa
IPSMG – Ipswich Museum, Ipswich
IVPP – Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing
GSI - Geological Survey of India, Calcutta
GSP – Geological Survey of Pakistan, Quetta
KNM – Kenya National Museum, Nairobi
MNHN – Muséum National d'Histoire Naturelle, Paris
NHM – Natural History Museum, London
UCMP – University of California Museum of Palaeontology
USNM – US National Museum of Natural History
WIHG –Wadia Institute of Himalyan Geology, Dehra Dun

Systematic descriptions

Family Mustelidae Swainson, 1835
Subfamily Lutrinae Bonaparte, 1838
Tribe Enhydriodontini nov.

Diagnosis : Lutrines in which the protocone of P4/ is well separated from the paracone by a wide valley; hypocone more or less enlarged and inflated and positioned on the lingual border of the talon. Mandibular ramus deeper than length of m/1. Lower p/4 bicuspid with the posterior cusplet inflated and shifted buccally.

Contained genera :
Enhydriodon Falconer, 1868
Sivaonyx Pilgrim, 1931
Vishnuonyx Pilgrim, 1932
Paludolutra Hürzeler & Engesser, 1976

Genus *Vishnuonyx* Pilgrim, 1932

Type species : Vishnuonyx chinjiensis Pilgrim, 1932

Table 1.—**Measurements (in mm) of the dentition of *Vishnuonyx chinjiensis,* from Pakistan**

Specimen	Tooth	Length	Breadth	Locality	Data source
GSI D 223	P4/	11.5	9.1	Chinji	Own data
GSI D 245	p/4	7.5	4.3	Chinji	Own data
GSI D 245	m/1	11.7	6.3*	Chinji	Pilgrim, 1932*
GSI D 245	m/2	5.0	3.3	Chinji	Pilgrim, 1932
WIHG FR 24/18	p/4	7.2	4.3	Ramnagar	Own data
NHM G 4	p/4	8.6	5.6	Chhorwali Katas	Own data
NHM G 4	m/1	13.0	7.4	Chhorwali Katas	Own data
NHM G 4	m/2	6.2	5.8	Chhorwali Katas	Own data

* Breadth of m/1 of D 245 has been estimated from the figure in Pilgrim (1932).

Species *Vishnuonyx chinjiensis* Pilgrim, 1932

Diagnosis : Talonid of m/1 much lower than trigonid; paraconid and protoconid separated by deep incision, and with well developed vertical shearing surface; talonid slightly wider than trigonid. P4/ with small parastyle, hypocone diminutive and positioned disto-lingually to the protocone, and producing slight swelling in the lingual margin of the tooth.

Synonymy :
v1932 - *Vishnuonyx chinjiensis* gen. et sp. nov., Pilgrim, pp. 60, 93-96, Pl. 2, fig. 17, Pl. 4, fig. 6.
v1993 - *Vishnuonyx chinjiensis* Pilgrim, Nanda & Sehgal, p. 118.

Holotype : GSI D 223, left P4/ (cast in NHM, M 13351) (fig. 3A).

Type locality : Chinji, Pakistan

Additional material :
GSI D 245, mandible with p/4-m/2 from Chinji, Pakistan (Pilgrim, 1932, p. 60, 94, Pl. 4, fig. 6) (fig. 3B).
NHM G 4 (NHM Gill collection) right mandible with p/4-m/2 from Chhorwali Katas, Pakistan (fig. 3C).
WIHG FR 24/18, left mandible fragment carrying p/4, from Ramnagar, India (Nanda & Seghal, 1993).

Localities and stratigraphic range : Chinji, Chhorwali Katas, Ramnagar, late Middle Miocene (Chinji Zone).

Description

Mandible

NHM G 4, a right mandible with p/4 to m/2 (fig. 3C) collected by W.D. Gill from Chhorwali Katas, Pakistan, is well preserved and the teeth are lightly worn. The mandible is 17 mm deep beneath the m/1. The symphysis extends distally to the level of the anterior root of p/3. There are three prominent mental foramina, one each beneath the p/2, p/3 and p/4. The masseteric fossa is deep and extends anteriorly as far as the level of the rear of m/2.

Dentition

The p/4 has a high principal cusp to which is applied a prominent disto-buccal cusplet about 2/3 the height of the main cusp. These two cusps are widely separated at their apices but fused at the base. The tooth is surrounded by a cingulum and distally there is a widish platform.

The m/1 has a trigonid that is appreciably higher than the talonid. The protoconid is the tallest cusp and the metaconid is higher than the paraconid. Between the protoconid and paraconid there is a deep incision, the buccal side of the cusps forming a strong vertical shearing surface oriented at an oblique angle (*ca* 40°) to the long axis of the tooth row. The anterior edge of the paraconid is almost vertical. The lingual opening of the trigonid valley is not obstructed by crests from the paraconid and metaconid, and in occlusal view this part of the tooth has a concave margin. Behind the protoconid there is a small but clearly defined post-protocone cusplet (posterior accessory cusplet) separated from the talonid by a valley. This cusplet is slightly internally positioned relative to the buccal margin of the tooth. There is a prominent buccal cingulum. The talonid slopes markedly downwards towards the trigonid. It is composed of two groups of cusps arranged round the periphery of the central basin, a lingual group and a buccal group which are separated from each other by a wide valley in the centre of the distal margin of the tooth.
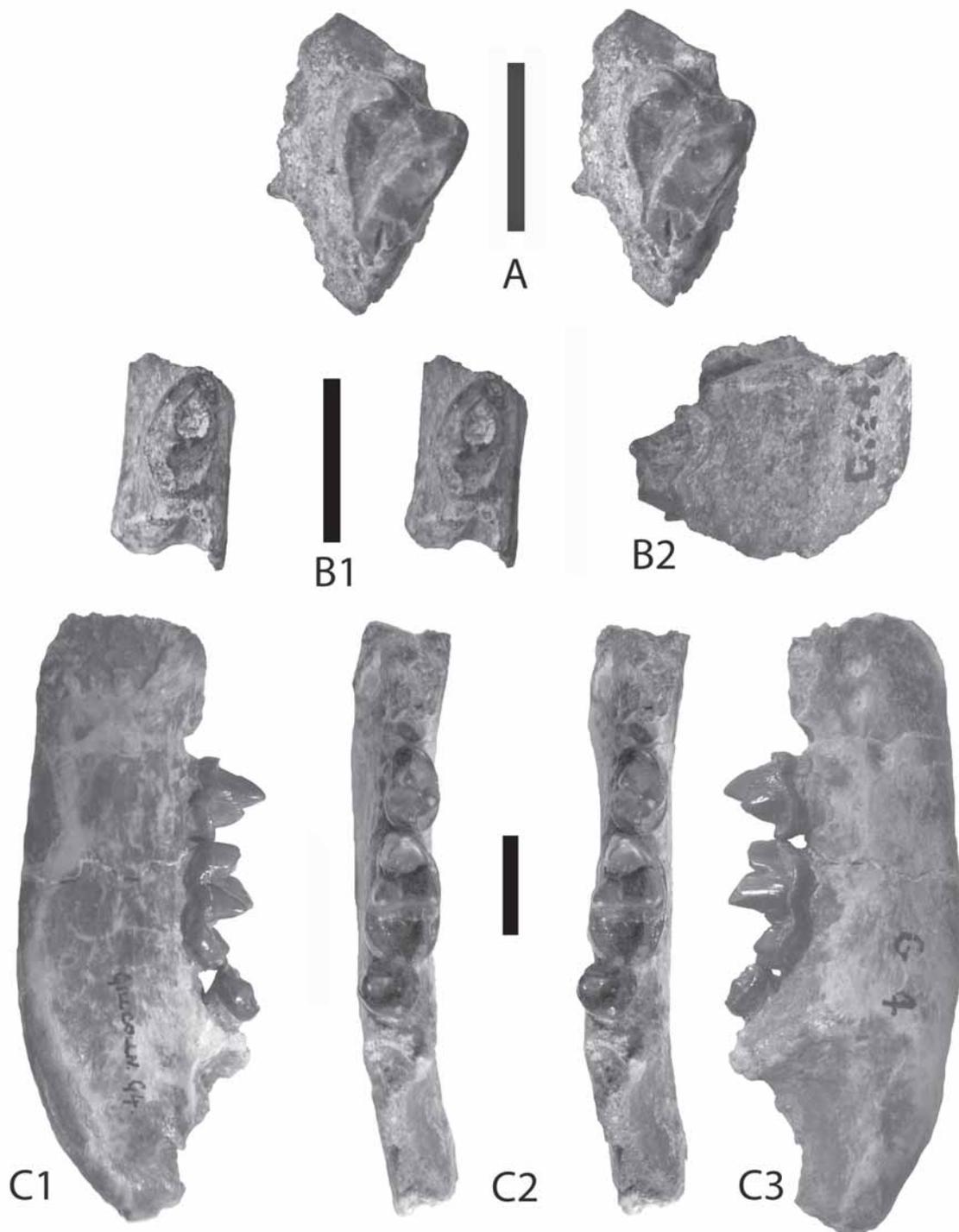
Fig. 3.—*Vishnuonyx chinjiensis*, A) GSI D 223, holotype maxilla fragment with left P4/ from Chinji, Pakistan (stereo occlusal view); B) GSI D 245, left mandible fragment with p/4 from Chinji, Pakistan (B1 - stereo occlusal and B2 - lingual views); C) NHM G 4, right mandible with p/4-m/2 from Chhorwali Katas, Pakistan (C1 - lingual, C2 - stereo occlusal and C3 - buccal views) (scale bars : 10 mm).

The m/2 is almost circular in occlusal outline, and is higher than the talonid basin of the m/1 and dips towards it. The tooth has a single root. Occlusally there are three cusps, a large lingual one which has an inwardly directed crest, and a smaller buccal one and a diminutive disto-buccal one. There are buccal and lingual cingula.

Measurements of the teeth are provided in table 1.

Discussion

Vishnuonyx chinjiensis was hitherto known from an isolated left P4/ (GSI D 223) (fig. 3A) and a mandible fragment with p/4-m/2 (GSI D 245) (Pilgrim, 1932). The m/1 in the mandible was lacking its trigonid but the length could be estimated. The new specimen collected by W.D. Gill from Chhorwali Katas, Pakistan, is more complete than the specimen available to Pilgrim, and its teeth are lightly worn. Pilgrim (1932, p. 95) already observed several similarities between the mandibles of *Vishnuonyx chinjiensis* and *Sivaonyx bathygnathus*, including the great depth of the jaw, the large masseteric fossa, the broad, basin-shaped talonid of m/1 and the presence of two cusplets in the p/4. Examination of the type specimen in Calcutta in 2007, revealed that the rear of the paratype jaw has broken off, so that only the part with the p/4 remains (fig. 3B). In the Wadia Institute of Himalayan Geology, there is a left mandible fragment containing the p/4 from Ramnagar (Nanda & Sehgal, 1993) which closely resembles the paratype from Chinji. The p/4 lacks the apex of the main cusp.

The dentition of *Vishnuonyx chinjiensis* is of the shearing type, and from this it can be deduced that the species probably did not crush shellfish, althhough, like the extant small-clawed otter, *Amblonyx cinereus*, it might have consumed them by leaving them in the sun for the heat to open them (Larivière, 2003; Timmis, 1971). An interesting point about *Vishnuonyx*, which allies it to the Enhydriodontini rather than to any other group of otters, is the large separation between the paracone and protocone of the P4/, the latter cusp being close to the lingual border of the crown, and not near the centre of the mesial border. Furthermore, although the hypocone is small, it is nevertheless clearly defined and is responsible for producing a swelling in the lingual margin of the tooth. Thus,

even though the occlusal outline of the tooth is almost triangular, the hypocone makes the lingual border convex rather than straight. This morphology announces the more quadrangular occlusal outline that typifies later Enhydriodontini such as *Sivaonyx* and *Enhydriodon*. However, the overall primitive nature of the dentition, such as the talonid of m/1 being lower than the trigonid cusps, indicates that *Vishnuonyx* is a primitive member of the tribe, and could represent the initial stages of engagement of a lutrine lineage on a trajectory that culminated in larger, bunodont forms such as *Sivaonyx* and *Enhydriodon*.

Pilgrim (1932) noted that the dental morphology of *Vishnuonyx* is intermediate between that of *Potamotherium* on the one hand, and of *Sivaonyx* and *Enhydriodon* on the other, but he excluded an ancestor-descendent relationship between *Potamotherium* and the later genera. Instead he aligned *Potamotherium* with *Lutra*, and envisaged a separate evolutionary group comprising *Vishnuonyx*, *Sivaonyx* and *Enhydriodon*. The fossil collected from Chhorwali Katas by Gill provides support for this view, reflected in the decision to include *Vishnuonyx* in the Enhydriodontini. It does not refute an eventual relationship to *Potamotherium* (Pohle, 1919), the morphology of which could represent the grundplan from which other otters may have evolved (Savage, 1957) although this has been the subject of debate (De Muizon, 1982).

Body weight of Vishnuonyx

Vishnuonyx was a small enhydriodontine (fig. 4) its upper and lower carnassials being close in dimensions to those of *Amblonyx cinereus*, the extant Asian small-clawed otter, which has a body weight about 3.2 kg (Larivière, 2003).

Genus *Sivaonyx* Pilgrim, 1931

Type species : Lutra bathygnatha Lydekker, 1884a (p. 193, Pl. 27, figs. 3-4).

Diagnosis : (modified from Pilgrim, 1931, 1932) : Large lutrine with approximately quadrate P4/ having a trenchant outer blade (ie, lacking the incison between the paracone and metacone). Lingual cusps of P4/ lower crowned than buccal cusps; strong to weak lingual cingulum. Four lower pre-

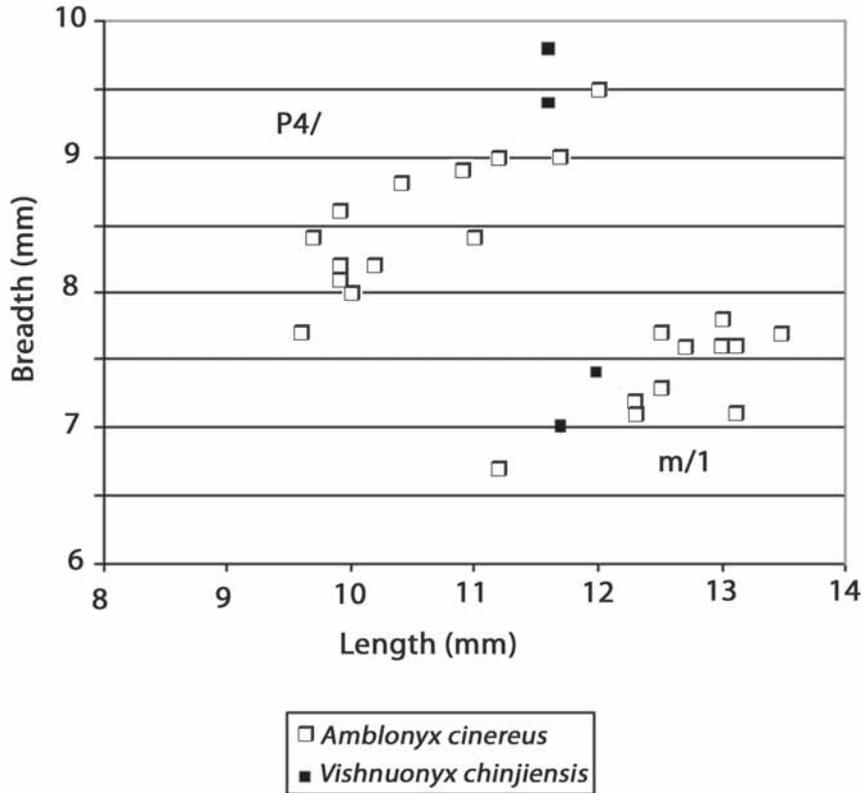## P4/ and m/1 of *Vishnuonyx chinjiensis* and *Amblonyx cinereus*

Fig. 4.—Metric comparison of P4/ and m/1 of the extant Asian short-clawed otter (*Amblonyx cinereus*) and *Vishnuonyx chinjiensis* (data for *Amblonyx* from Pohle, 1919).

molars present. Canine large, p/4 broad posteriorly and m/1 very broad. Metaconid of m/1 as high as paraconid, talonid broader than trigonid, equal to it in length, basin-shaped and bordered by a ring of cusplets of which the lingual talonid cusp (entoconid) is as well developed as the hypoconid; m/2 small; p/1 single rooted. Lower dental formula 3-1-4-2.

Species *Sivaonyx gandakasensis* sp. nov.

Diagnosis : Small species of the genus *Sivaonyx* with moderately bunodont aspect to P4/ and m/1.

Synonymy :
pv1932 - *Sivaonyx bathygnathus* (Lydekker), Pilgrim, pp. 60, 89 (GSI D 249 only).

Holotype : GSP 4225, right mandible with c, p/1-p/4, m/1, alveolus of m/2 (figs. 5C, 6A).

Type locality : Locality 182, Gandakas, Pakistan

Additional material

GSP 4616, right P4/ from loc. 182, Gandakas, Pakistan.
GSP 11703, left mandible with broken p/4-m/1, alveolus m/2, from loc. 317, Kot Maliaran, Pakistan.
GSP 11748, right mandible with talonid basin of m/1 preserved, from loc. 317, Kot Maliaran, Pakistan.
GSI D 249, mandible with m/1 from 6 km SSW of Kaulial, Pakistan (Pilgrim, 1932, p. 89, not Kamlial as reported in his paper) (fig. 5B).
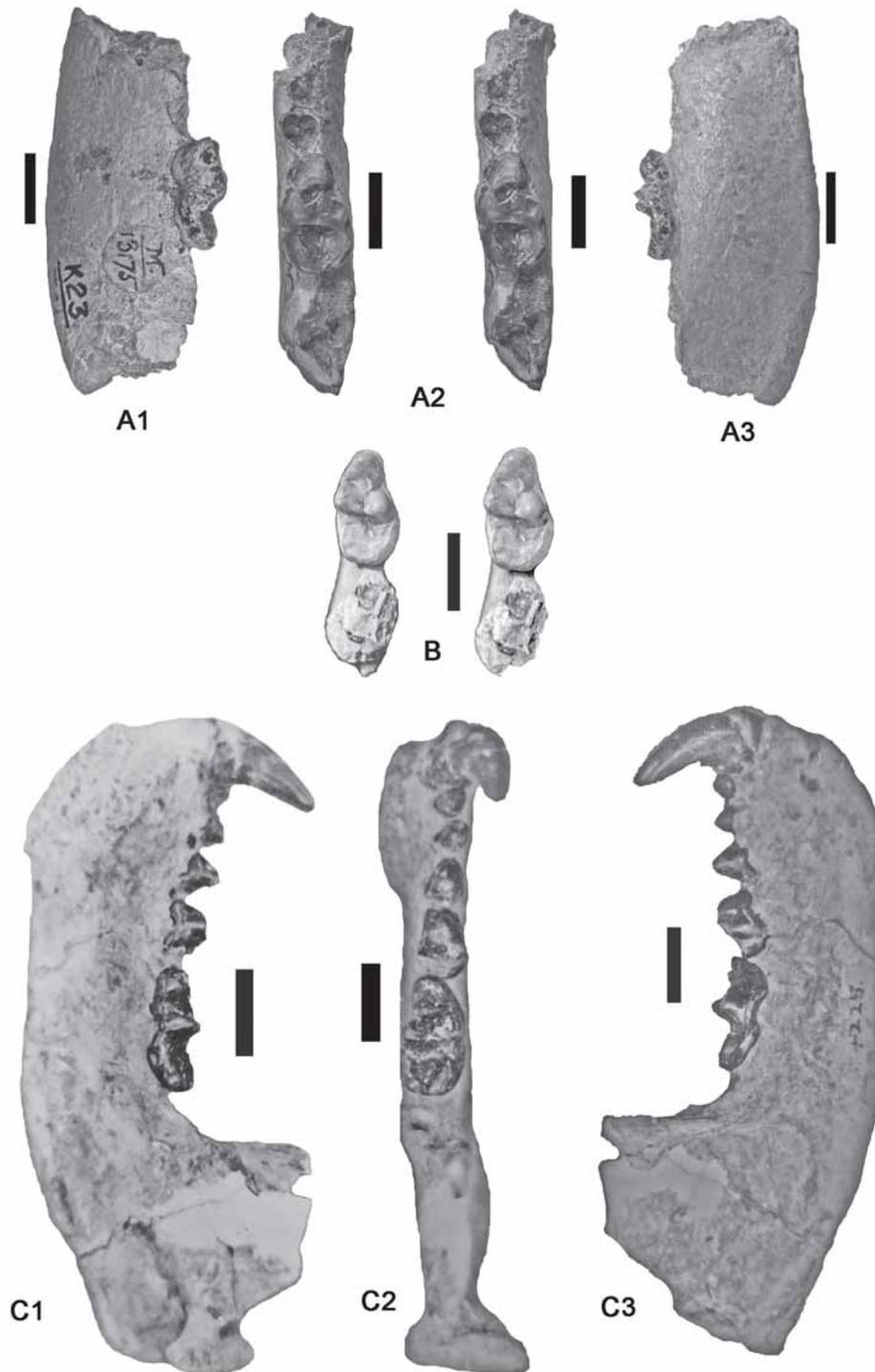NHM M 13175, mandible with m/1 from Kaulial, Pakistan (figs. 5A, 6B).

Fig. 5.—*Sivaonyx gandakasensis*, A) NHM M 13175, left mandible with m/1 from Kaulial, Pakistan (A1 - buccal, A2 - stereo occlusal and A3 - lingual views); B) GSI D 249, left mandible fragment with m/1 from 6 km SSW of Kaulial, Pakistan (stereo occlusal view), C) GSP 4225, holotype right mandible with c/1-m/1 from Gandakas, Pakistan (C1 - lingual, C2 - occlusal and C3 - buccal views) (scale bars : 10 mm).
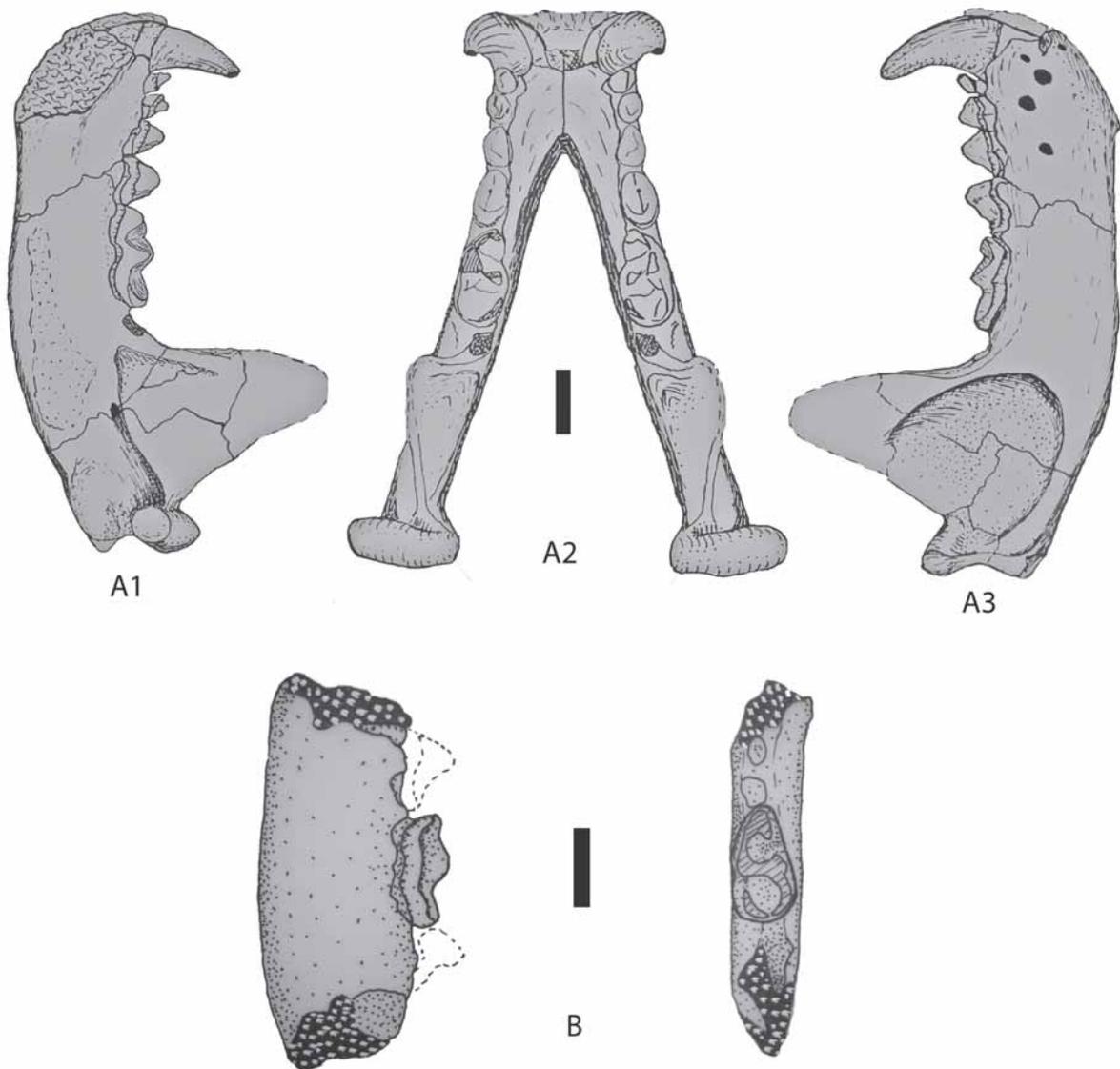
Fig. 6.—*Sivaonyx gandakasensis*, interpretive line drawings of A) GSP 4225, right mandible (A1 - lingual, A2 - occlusal view with mirror image and A3 - buccal views; B) NHM M 13175, left mandible (B1 – buccal and B2 – occlusal views) (scale bars : 10 mm).

Localities and stratigraphic range : Gandakas, Kot Maliaran, Kaulial, Late Miocene (upper Nagri Zone).

Description

Mandible

GSP 4225 is an almost complete mandible lacking the incisors and m/2, along with part of the ascending ramus (figs. 5C, 6A). The symphysis is unfused and extends back to the rear of p/3. The distal part of the symphysis has a slight depression for the geniohyoid muscle, but it is weak when compared with the mandible of *Torolutra ougandensis* from Lukeino, Kenya (Morales *et al.*, 2005b). There are five mental foramina, three large ones beneath the anterior premolars and two smaller ones beneath the canine. The mandibular foramen is situated in line with the tooth row, about 17.7 mm
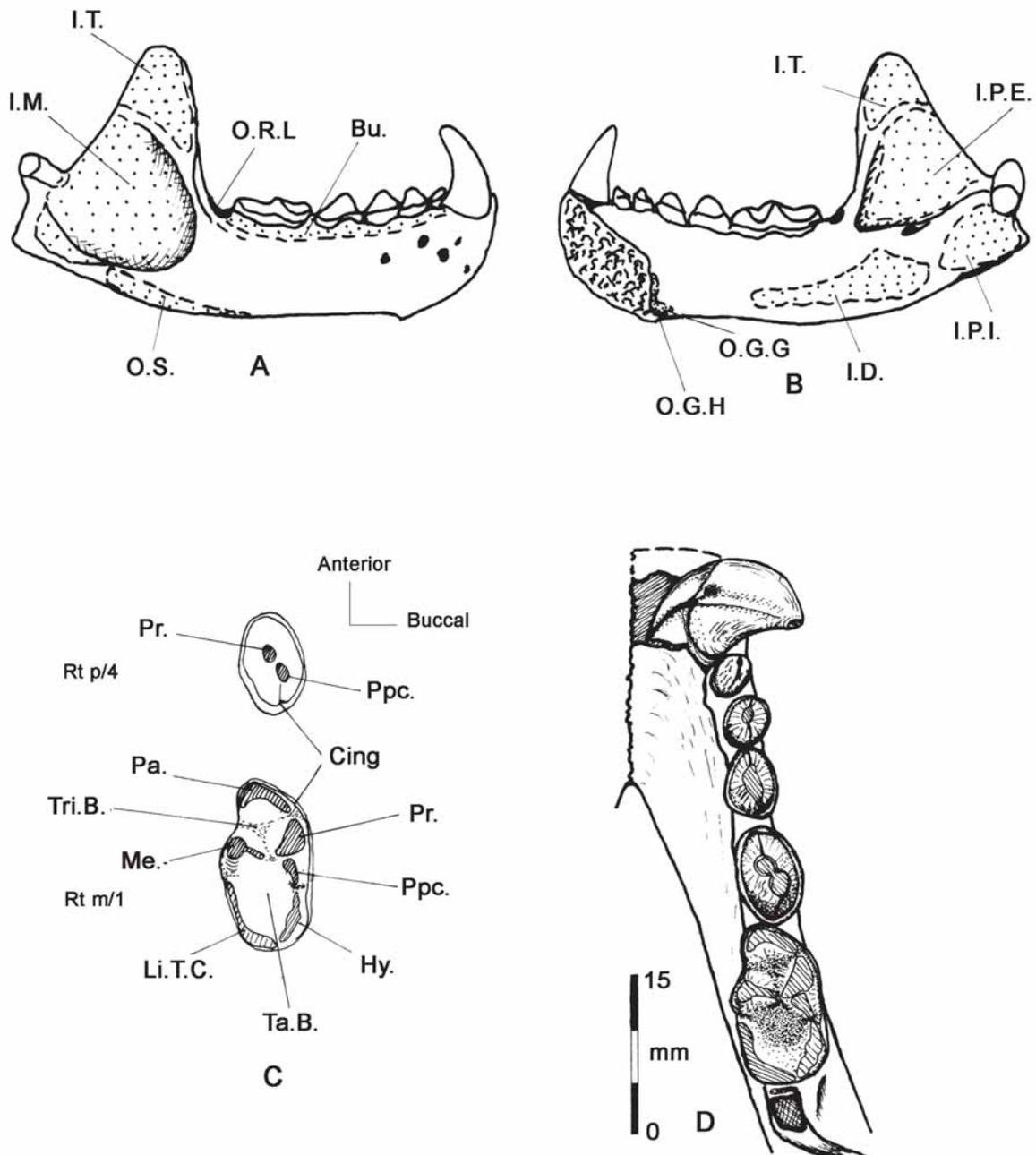
Fig. 7.—GSP 4225, *Sivaonyx gandakasensis*, sp. nov. A and B) interpretation of mandibular musculature, A) buccal view, B) lingual view (Bu – buccinator; I.D. – insertion of digastricus; I.M. – insertion of masseter; I.P.E. – insertion of external pterygoideus; I.P.I. – insertion of internal pterygoideus; I.T. – insertion of temporalis; O.G.G. – origin of genio-glossus; O.G.H. origin of genio-hyoideus; O.R.L. – origin of lower lip retractor; O.S. – origin of sterno-mandibularis). C) nomenclature of lower p/4 and m/1 (Cing. – cingulum; Hy – hypoconid; Li.T.C. – lingual talonid cusp; Me – metaconid; Pa – paraconid; Ppc. – post-protoconid cusplet; Pr – protoconid; Ta.B. – talonid basin; Tri.B. – trigonid basin), D) occlusal view of holotype right mandible.

behind the m/1. The area for insertion of the digastric muscle reaches forwards to the front end of m/1 and backwards to a point below and just behind the mandibular foramen (fig. 7B). The insertion of the internal pterygoideus lies below the mandibular condyle and extends forwards to a point 8 mm behind the mandibular foramen. The insertion of the external pterygoideus is in front of and mostly above the condyle, although its vental border sweeps gently downwards from the condyle towards the root of the m/2.

The coronoid portion of the ascending ramus is vertically oriented wheras in *Aonyx* it leans backwards at an angle of about 15° from vertical. The root of m/2 is situated at the base of the coronoid process, appreciably higher than the alveoli of the other teeth, and consequently, the surface of m/2 probably dipped towards the m/1 as in *Aonyx* and *Enhydriodon*. The insertion of the masseter muscle is in a large fossa in front of the condyle. It reaches anteriorly to the rear edge of m/2 and has a raised lower border at the rear. On the buccal side of the root of m/1 there is a sharply defined ridge leading ventrally to the gingival level. This probably represents the origin of the lower lip retractor.

The origin of the sterno-mandibularis lies along the ventral border of the jaw, starting beneath the middle of m/1 and extending backwards onto the buccal surface of the jaw about 25 mm to the rear where there is a slight inflexion in the border of the mandible (fig. 7A). The chin area is pitted with numerous nutritive foramina.

Measurements of the mandibles and dentitions are provided in table 2.

Lower dentition (figs. 7C, 7D)

The incisors are missing but the gap between the canines in which they would have fitted is about 8.8 mm.

The canine is a large pointed, curved, conical tooth which sweeps upwards and backwards and leans gently outwards. The enamel on the anterior surface is smooth while that on the rear is rugose, reflecting preferential anterior abrasion. On the mesial surface there is a longitudinal ridge bordered on both sides by a shallow furrow, the anterior one of which terminates in a fovea just above the cervix. A cingulum leads distally from this fovea. The root is oval in section with a longitudinal groove on the mesial surface. There is a small wear facet at the apex of the crown.

Table 2.—**Measurements (in mm) of the mandible and teeth of *Sivaonyx gandakasensis* (all specimens re-measured by author) (e = estimated measurement)**

Specimen	GSP 4225	GSP 11703	GSI D 249
Length of canine	7.4	—	—
Breadth of canine	6.5	—	—
Height of canine	15.8e	—	—
Length of p/1	3.6	—	—
Breadth of p/1	3.5	—	—
Length of p/2	5.3	—	—
Breadth of p/2	4.2	—	—
Length of p/3	7.0	—	—
Breadth of p/3	4.9	—	—
Length of p/4	8.7	8.7e	—
Breadth of p/4	6.3	6.0e	—
Length of m/1	15.0	13.9	14.4
Breadth of m/1	7.9	7.9	8.6
Length of m/2 alveolus	3.7	6.0e	—
Breadth of m/2 alveolus	2.7	3.5e	—
Length canine to m/1	45.3	—	—
Distance between canines	8.8e	—	—
Distance between m/1s	14.4e	—	—
Distance between internal ends of condyles	23.8	—	—
Distance from rear of condyle to front of canine	81.1	—	—
Width of condyle	16.5	—	—
Diameter of condyle	6.3	—	—
Distance from alveolar margin to posterior mental foramen	8.0	8.0e	—
Distance from alveolar margin to middle mental foramen	7.0	—	—
Distance from alveolar margin to anterior mental foramen	9.6	—	—
Distance from alveolar margin to foramina beneath canine	5.5, 11.0	—	—
Depth of mandible beneath p/3 including height of tooth	16.5e	—	—
Depth of mandible beneath m/1	15.5e	—	18.1
Length of symphysis	26e	—	—
Depth of symphysis	13.6	—	—
Thickness of mandible at m/1	8.8	8.7	9.1
Thickness of mandible at canines (2 x 10.6)	21.2	—	—
Distance from rear of condyle to front of coronoid process	29.9	—	—
Distance from front of condyle to anterior extremity of masseteric fossa	27.2	—	—
Length of tooth row including incisors and m/2	50e	—	—
Trigonid to m/1 length ratio	0.57	0.64	—

The first lower premolar lies immediately behind the canine. It is a single-rooted tooth and has a single mesially positioned cusp with a sharp ridge leading distally to a wide cingular platform. The tooth is completely surrounded by a cingulum, except
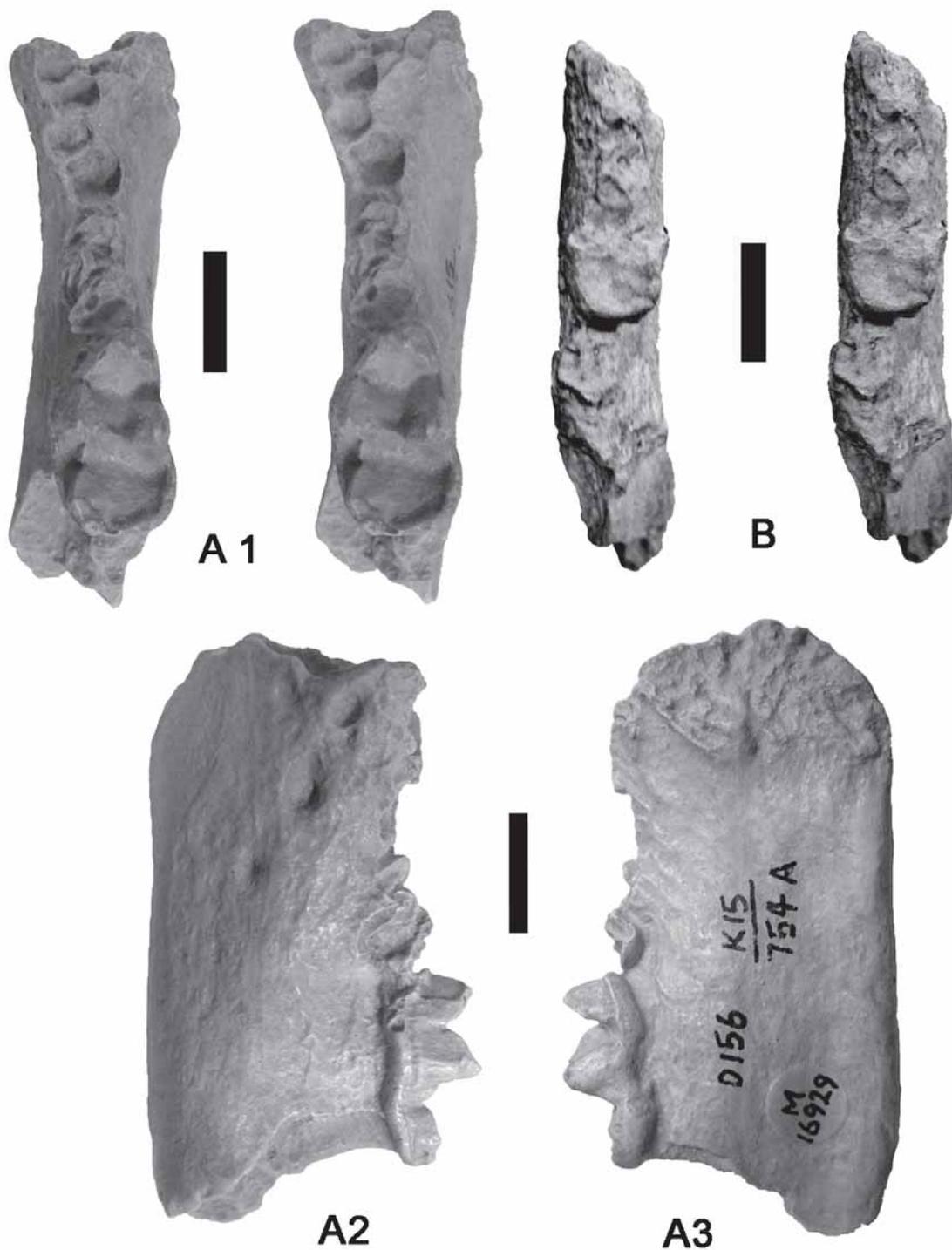
Fig. 8.—*Sivaonyx bathygnathus*, A) GSI D 156, left mandible with m/1 from Hasnot, Pakistan (A1 – stereo occlusal, A2 – buccal and A3 – lingual views of a cast in the NHM, London), B) GSI D 250, right mandible with part of m/1 from Hasnot, Pakistan (stereo occlusal view of cast in the NHM, London) (scale bars : 10 mm).

where it is worn away on the mesio-buccal corner. The enamel is wrinkled.

The second lower premolar is two-rooted and it is oriented obliquely in the jaw, such that its anterior end points mesio-buccally. The crown is an enlarged version of that of the p/1. The principal cusp is over the anterior root and possesses a distinct wear facet at its apex which extends onto the mesial surface of the tooth.

The third lower premolar is a larger version of p/2 but is oriented straighter in the jaw. The enamel is rugose except where it is worn away at the apex and on the distal part of the main cusp. It has a complete cingulum.

The p/4 also has two roots, but it is composed of two cusps and a broad expanded distal platform. It is oriented straight in the tooth row. The principal cusp has a closely applied accessory cusp on the bucco-distal corner. There is a shallow furrow on the buccal surface of the tooth where the two cusps join. There is an 8-shaped wear facet at the tips of the two cusps. A slight but sharp ridge extends from the posterior cusp to the distal part of the cingulum. A cingulum completely surrounds the crown.

The m/1 is the largest of the cheek teeth, and has a well developed trigonid and a large, basin-shaped talonid. Immediately behind the protoconid there is a low but distinct posterior accessory cusplet. A short gap separates this cusplet from a series of low cusps which surround the talonid basin. There are two main groups of talonid cusps, one situated round the bucco-distal corner, the other round its lingual edge. They are separated from each other by a narrow but deep valley, and with wear there appear two crescentic facets separated by a thin band of enamel. A gap separates the metaconid from the talonid cusps. In GSP 4225, wear is moderately advanced so that the original heights of the trigonid cusps cannot be estimated accurately. The metaconid is least worn, but has a distinct facet extending from its apex down the disto-buccal surface to the valley that separates it from the protoconid. The protoconid is worn almost flat, producing a triangular facet, and there is a slight vertical facet on its buccal surface. Evidently crushing was the major function of this tooth with the carnassial function reduced in importance. There is a valley separating the wear facets of the protoconid and paraconid. The latter cusp possesses a crescent-shaped wear facet with the two limbs of the crescent pointing distally. A small vertical buccal wear facet is also evident. A prominent gap separates the lingual corner of the paraconid

from the mesial corner of the metaconid, leaving the trigonid valley open lingually. A cingulum extends along the buccal surface of the tooth and round the anterior and lingual parts of the paraconid. There is a slight fold of enamel on the metaconid, possibly representing an extension of the cingular structure onto this cusp. The cingulum is lightly crenulated and slightly rugose where unabraded.

The second lower molar is missing, but it lay behind and above the m/1. The m/2 alveolus has an indication of a second small shallow one in front of it. Colbert (1935) recorded a specimen in which m/2 was double-rooted. The entire cheek tooth row from canine to m/2 is straight, and the jaw crosses under it from antero-lingual to postero-buccal.

GSP 11703, a left mandible fragment contains broken p/4 and m/1 and the alveolus of m/2. The posterior mental foramen is present beneath the anterior margin of p/4. The ventral border is preserved almost to the symphysis, where a corner of the geniohyoid fossa is preserved. The remains of the teeth are similar to those in GSP 4225. GSP 11748, from the same locality as GSP 11703 is a fragment of right mandible, possibly from the same individual as it.

Upper dentition

GSP 4616 is an upper right P4/ from loc. 182, Gandakas, the same locality as the mandible GSP 4225. The parastyle is low but distinct, separated from the paracone by a valley. The paracone is the highest cusp and is continuous with the metastyle, there being no sign of an incision between them, although there is a broad buccal concavity. The protocone is well separated from the paracone by a broad valley. There is a post-protocone crista which extends linguo-distally from the protocone, almost forming a distinct cusplet where it swells slightly distally. This crest is separated from a diminutive hypocone by a notch. The hypocone is slightly to the rear of the level of the paracone, and directly distal to the protocone. It has a bucco-lingually compressed aspect and this leaves a voluminous central basin between the buccal and lingual cusp groups. This imparts a quadrate outline to the front half of the tooth. The linguo-distal margin of the tooth is markedly oblique, running almost straight from the hypocone to the metastyle. There is a sharp cingulum round the protocone extending onto the hypocone.

The Gandakas P4/ (fig. 9C) differs from Pilgrim's material of *Sivaonyx bathygnathus* (GSI D
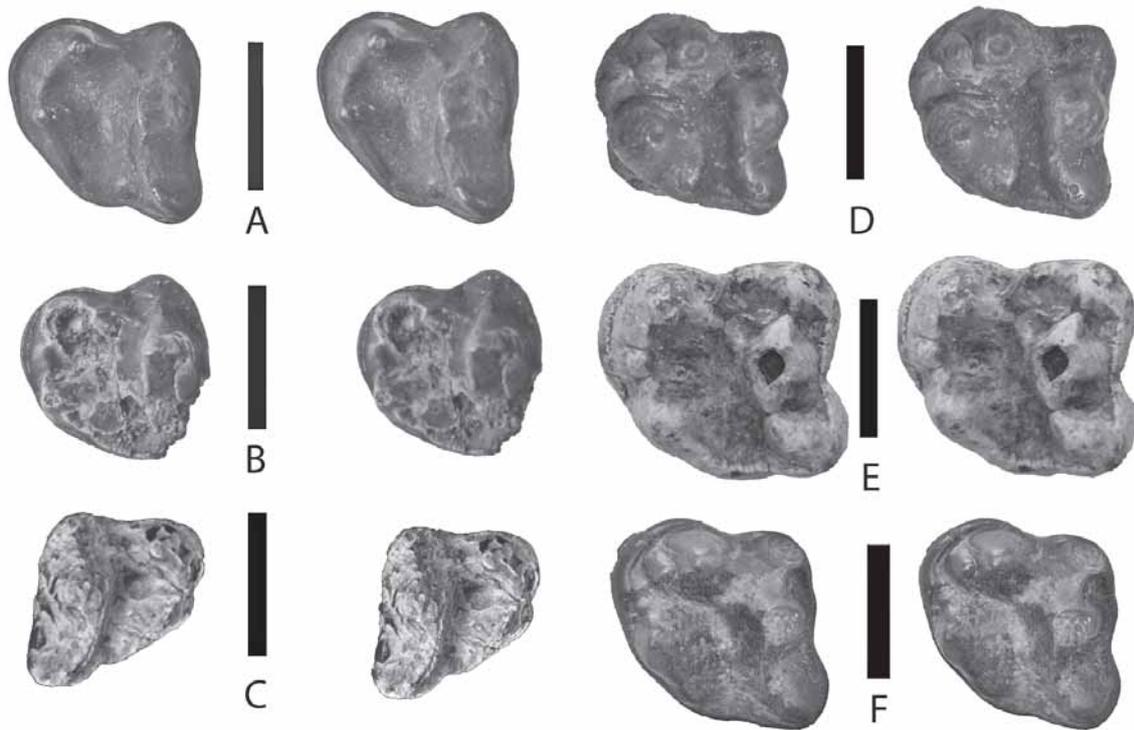
Fig. 9.—*Sivaonyx* and *Enhydriodon* P4/s in stereo occlusal views, A) GSI D 157, *Sivaonyx bathygnathus* left P4/ from Hasnot, Pakistan; B) GSI K13/15, *Sivaonyx bathygnathus* left P4/ from Hasnot, Pakistan; C) GSP 4616, *Sivaonyx gandakasensis* right P4/ from Gandakas, Pakistan; D) M 4847, *Enhydriodon falconeri* holotype left P4/ from the Siwalik Hills, India; E) Bar 566'05, *Sivaonyx ekecaman* left P4/ from Sagatia (Mabaget Formation) Kenya; F) Bar 1720'00, *Sivaonyx senutae* left P4/ from Lukeino, Kenya (scale bars : 10 mm).

Table 3.—**Measurements of the P4/ of *Sivaonyx gandakasensis* from Pakistan and *Sivaonyx bathygnathus* from China and Pakistan (e = estimated measurement)**

Specimen	Length P4/	Breadth P4/	Locality	Species	Data from
GSP 4616	13.5	11.5	Gandakas	*S. gandakasensis*	Own data
IVPP V 6886.3	13.0	13.8	Lufeng	*S. bathygnathus*	Qi, 1983
IVPP V 6886.4	13.2	13.5	Lufeng	*S. bathygnathus*	Qi, 1983
GSI D 157	14.5	13.4	Hasnot	*S. bathygnathus*	Own data
GSI K13.14	14e	13.4	Hasnot	*S. bathygnathus*	Own data

157) in that the lingual cingulum is not as strongly developed, being little more than a slight wrinkle in the enamel surface. Furthermore, the hypocone in GSI D 157 is swollen producing a more bunodont cusp, the posterior crest of which is directed less obliquely, so that the rear of the tooth is wider than in GSP 4616. Another specimen in the Calcutta Museum GSI K13.14 from Hasnot (personal observation) although slightly damaged and eroded, is morphometrically similar to GSI D 157, and consequently belongs to *S. bathygnathus* rather than to *S. gandakasensis*.

Measurements of the teeth are provided in table 3.

Dental occlusion

In occlusion, the parastyle of the P4/ contacts the lingual surface of the paraconid of the p/4. The protocone of P4/ bites against the lingual surface of the

paraconid of the m/1 and the posterior cingular shelf of the p/4, while the apex of the paraconid of m/1 fits into the anterior valley between the parastyle and protocone of the P4/. The hypocone of P4/ occludes with the trigonid basin of the m/1, and the central valley between the buccal and lingual cusp pairs of the P4/ is filled during occlusion by the buccal portion of the paraconid and the anterior half of the protoconid of m/1. The lingual surface of the buccal cusps of the P4/ shear against the buccal surface of the paraconid and protoconid. The metaconid, posterior accessory cusplet and talonid of the m/1 bite against the M1/.

Although the P4/ and m/1 in *Sivaonyx gandakasensis* retain some shearing function, the overall aspect is one of a crushing dentition.

Discussion

The newly available fossils reveal that there were at least three enhydriodontine taxa represented in the Hasnot, Tatrot, Kaulial and Gandakas stratigraphic interval (*Sivaonyx gandakasensis*, *Sivaonyx bathygnathus*, and *Enhydriodon falconeri*) most specimens of which were hitherto identified as *Sivaonyx bathygnathus*. It is almost certain that these three species did not exist at the same time, but instead succeeded each other through the stratigraphic column. If this is so, then the main evolutionary trends consisted of augmentation in size and increase in bunodonty.

The species *Sivaonyx gandakasensis* was not recognised by Pilgrim (1932) although one of the fossils now included in it was identified by him as *Sivaonyx bathygnathus*, albeit with some hesitation (Pilgrim, 1932, p. 89, GSI D 249). Even though the sample of the latter species was extemely restricted it was curious in possessing teeth with indications of both crushing and sectorial functions, but the damage to and advanced wear on some specimens obscured the original morphology which hindered their interpretation. The sample from Kaulial and Gandakas clarifies the situation somewhat, as it reveals that all this material should be assigned to a single species. The species *S. gandakasensis* is smaller than *S. bathygnathus*, and all the fossils attributed to it are older than the collection attributed to *S. bathygnathus*. It is therefore possible that *S. gandakasensis* could be ancestral to *S. bathygnathus*. *Sivaonyx gandakasensis* is larger and more bunodont than *Vishnuonyx chinjiensis*, but the basic

structure of the dentition and mandible indicates that the latter species could be the precursor of the former.

Heavy occlusal wear on some of the fossils (M 13175) reveals that the cheek teeth of *Sivaonyx gandakasensis* were exposed to the action of abrasive particles while chewing, perhaps sand grains or fragments of shell adhering to the food. It is unlikely that the carnassials were used for crushing molluscs, but crustaceans could have been included in the diet. Similar heavy wear in the lower carnassial is known in *Sivaonyx kamuhangirei* from Kazinga, Uganda (Morales & Pickford, 2005a).

GSI K47.710 from Haritalyangar (Prasad, 1970, Pl. 4, fig. 2) requires restudy, as the published illustrations (which are poorly reproduced) suggests that it may not be the same as the P4/ of *Sivaonyx*, recalling by its occlusal outline, an upper molar. Searches in the GSI and the Indian Museum in Calcutta in 2007, failed to reveal its existence there, and for the time being I am inclined to remove this record from the hypodigm of *Sivaonyx bathygnathus*.

Fossils from Lufeng and Leilao, China, attributed to *Sivaonyx bathygnathus* appear to be typical of the species (Qi, 1983, 1985, 2006) the slightly broader measurements of the P4/ possibly being due to different ways of measuring the specimens.

On the basis of the dimensions of m/1, the body weight of *Sivaonyx gandakasensis* is estimated to have been about 4-8 kg.

Species *Sivaonyx bathygnathus* (Lydekker, 1884)

Diagnosis : Large species of the genus *Sivaonyx* with slightly sectorial aspect to P4/ and m/1, but showing talonid basin broader than trigonid.

Synonymy :
v1884a - *Lutra bathygnatha* sp. nov.,   Lydekker, 193, 193bis, 194, Pl. 27, figs 3, 4.
1884b - Lutra bathygnatha Lydekker, Lydekker, 135.
1885 - Lutra bathygnatha Lydekker, Lydekker, 11.
1910 - Lutra bathygnatha Lydekker, Pilgrim, 199.
1913 - Lutra bathygnatha Lydekker, Pilgrim, 282, 291.
1919 - Potamotherium bathygnathus (Lydekker), Pohle, 26.
v1929 - *«Lutra» bathygnathus* (Lydekker), Matthew, 448, 470, fig. 8.
v1931 - *Sivaonyx bathygnathus* (Lydekker), Pilgrim, 74, Pl. 2, figs. 4, 4a.

pv1932 - *Sivaonyx bathygnathus* (Lydekker), Pilgrim, 60, 88-93, Pl. 2, figs. 14, 16, Pl. 4, fig. 1. (specimens D 156, D 250, D 33, D 157).

v1935 - *Sivaonyx bathygnathus* (Lydekker), Colbert, 99-101, fig. 48.

pv1999 - *Sivaonyx bathygnathus* (Lydekker), Willemsen, pp. 413-413, fig. 2, bottom frame.

non pv1999 - *Sivaonyx bathygnathus* (Lydekker), Willemsen, pp. 414, fig. 2, top frame.

?1970 - *Sivaonyx bathygnathus* (Lydekker), Prasad, 18-20, Pl. 4, figs. 3, 4 (specimen K47.710).

?1932 - *Sivaonyx bathygnathus* (Lydekker), Pilgrim, p. 60, 89 (specimen GSI D 249).

?1970 - *Sivaonyx bathygnathus* (Lydekker), Prasad, 18-20, Pl. 4, figs. 3, 4 (specimen K47.708).

non v1970 - *Sivaonyx bathygnathus* (Lydekker), Prasad, 18-20, Pl. 4, figs. 3, 4 (specimen K29.469).

Type specimen : GSI D 33, left mandible with p/4-m/1 and alveoli of c/1- p/3 (Lydekker, 1884a, pp. 193-194, Pl. 27, figs. 3-4; Pohle, 1919, p. 26).

Type locality : Hasnot, Punjab, Pakistan.

Additional material :
AM 19509, right mandible with m/1 from Hasnot, Pakistan (Colbert, 1935, p. 99, fig. 48).
GSI D 34, edentulous mandible fragment from Punjab (Lydekker, 1884a; Matthew, 1929, p. 470, fig. 8).
GSI D 244, mandible with p/4 from Hasnot, Pakistan (Pilgrim, 1932, p. 89, Pl. 4, figs. 1, 1a).
GSI D 156, mandible with p/4-m/1 from Hasnot, Pakistan (Pilgrim, 1932, p. 89, Pl. 2, fig. 14) (cast in NHM M 16929) (fig. 8A).
GSI D 157, left P4/, from Hasnot, Pakistan (Pilgrim, 1931, p. 75, Pl. 2, figs. 4, 4a; Pilgrim, 1932, p. 89, Pl. 2, figs. 16, 16a) (fig. 9A).
GSI D 250, right mandible with talonid basin of m/1 from Hasnot, Pakistan (Pilgrim, 1932, p. 89) (fig. 8B) (Cast in NHM).
GSI K13.14, left P4/ from Hasnot, Pakistan (fig. 9B).

Localities and stratigraphic range : Hasnot, Late Miocene (Dhok Pathan Zone).

Historical review

Lydekker (1884a) erected the species *Lutra bathygnathus* on the basis of a partial left mandible with p/4-m/1 and the alveoli of the canine, p/1-p/3 (specimen GSI D 33) from the Hasnot area, Potwar Plateau, Pakistan (Lydekker, 1884a, pp. 193-194, Pl. 27, figs. 3, 3a). A second edentulous mandible fragment possessing the alveolus for m/2 (GSI D 34) was included in the species. Lydekker (1884b, 1885) published additional notes on the material. Pilgrim (1910, 1913) briefly mentioned the existence of the specimens, and Pohle (1919) attributed them to the genus *Potamotherium* on the basis of the presence of p/1 in the mandible, despite the numerous morphological differences between the teeth of the two. Matthew (1929, fig. 8) re-illustrated the type specimen and suggested a comparison with *Brachypsalis* rather than *Potamotherium*.

Extending this line of argument, and in an attempt to resolve the debate about the taxonomic position of the specimens, Pilgrim (1931, p. 74, Pl. 2, figs. 4, 4a) erected the new genus *Sivaonyx*, adding an upper carnassial to the hypodigm. The generic diagnosis was based primarily on the morphology of the P4/ because, as Pilgrim pointed out «If *Lutra bathygnathus* were only known from its holotype there would be little justification for not including it in the genus *Enhydriodon*». The attribution by Pilgrim of the P4/ (GSI D 157) to the same species as the holotype mandible was based mainly on its discovery locus. But the presence of other otter-like species from the same stratigraphic interval raises the possibility that the P4/ belongs to a species different from the holotype. In the Hasnot-Tatrot area, there is now clear evidence for the presence of three species of large otter-like mammals which differ in size and morphology. Unfortunately, because the m/1 in the holotype of *S. bathygnathus* lacks the apices of the two rear cusps of the trigonid, it is not clear whether it represents a bunodont form, in which case it should be referred to *Enhydriodon*, or whether it was slightly more sectorial, in which case its attribution to *Sivaonyx* would be upheld. The difference in size between these two species is not very great. The dimensions of the m/1 in GSI D 33 are lower than those of the *Enhydriodon falconeri* from Tatrot (M 15397) but are the greatest among the fossils attributed to *Sivaonyx*. Subsequent researchers have almost invariably been troubled by the fact that the holotype of *S. bathygnathus* is a mandible, whereas its diagnostic characters are defined largely on the upper carnassial.

Measurements of the teeth are provided in table 4.

Table 4.—**Dimensions (in mm) of the first lower molar and mandibular depth beneath m/1 in bunodont Siwalik otter-like mammals (e = estimated measurement)**

Specimen	Attribution	Length m/1	Breadth m/1	Depth of mandible beneath m/1
IPSMG 1949.187	*Enhydriodon sivalensis*	22e	13e	31.5
GSI D 161	*Enhydriodon sivalensis*	21.6	13.1	—
NHM M 15397	*Enhydriodon falconeri*	18.6	10.9	25.4
GSI D 33	*Sivaonyx bathygnathus*	17.1	9.7	19.2e
GSI D 34	*Sivaonyx bathygnathus*	—	—	20.6
GSI D 156	*Sivaonyx bathygnathus*	16.0	9.4	18.7
GSI D 250	*Sivaonyx bathygnathus*	16.4e	9.1	18.8
AM 19509	*Sivaonyx bathygnathus*	16.5	9.5	—
GSI D 244	*Sivaonyx bathygnathus*	—	—	21.9
GSI D 249	*Sivaonyx gandakasensis*	14.4	8.6	18.1
NHM M 13175	*Sivaonyx gandakasensis*	15.3	9.0	19.7
GSP 4225	*Sivaonyx gandakasensis*	15.0	7.9	15.5e
WIHG RF 24/18	*Vishnuonyx chinjiensis*	—	—	11 (beneath p/4)
GSI D 245	*Vishnuonyx chinjiensis*	11.7	6.3	—
NHM G 4	*Vishnuonyx chinjiensis*	13.0	7.4	17

Table 5.—**Measurements (in mm) of dentition and mandibles of *Sivaonyx bathygnathus* (Lydekker, 1884a) from Pakistan and China (Qi, 1983) (*re-measured by the author)**

Specimen	GSI D 156	GSI D 250	GSI D 244*	GSI D 33*	GSI D 34*	Lufeng V6886.8 + 13	Lufeng V6886.9	Lufeng V6886.10
Length of canine	—	—	9.8	—	—	6.4	—	—
Breadth of canine	—	—	6.4	—	—	5.0	—	—
Length of p/1	1.9	—	—	—	—	—	—	—
Length of p/2	5.5	—	5.5	—	—	4.3	—	—
Breadth of p/2	—	—	—	—	—	3.6	—	—
Length of p/3	7.1	—	6.4	—	—	5.6	5.3	—
Breadth of p/3	—	—	—	—	—	4.0	4.1	—
Length of p/4	9.7	—	10.3	—	—	8.8	8.4	8.8
Breadth of p/4	5.8	—	6.4	—	—	6.0	6.0	6.5
Length of m/1	16.0	16.4	—	17.1	—	15.9	—	—
Breadth of m/1	9.4	9.1	—	9.7	—	9.0	—	—
Depth of mandible beneath m/1	18.7	18.8	21.9	—	20.6	—	—	—
Thickness of mandible at m/1	10.7	9.6	10.9	—	10.4	—	—	—

In 1932, Pilgrim described additional material of the species from Hasnot and Kamlial (Pilgrim, 1932, pp. 88-93, figs. 14, 16, Pl. 4, fig. 1). It should be noted that Pilgrim misread the label of specimen GSI D 249, which in fact was collected near Kaulial and not Kamlial, an important point considering the different stratigraphic contexts of the two localities. Colbert (1935, fig. 48) illustrated another specimen of *Sivaonyx bathygnathus* from the upper part of the Hasnot section (stated to be in the Tatrot Zone).

In 1970, Prasad attributed additional material from Haritalyangar, India, to *Sivaonyx bathygnathus*, but some of the fossils are not lutrine (K29.469 for example, which is a viverrid with possible affinities to *Paradoxurus* and/or *Pseudocivetta*) and some that may belong to the subfamily Lutrinae

(GSI K 47.707, GSI K 47.708, GSI K 47.710) are too poorly illustrated to provide convincing evidence of their presence at the site. Without being able to re-examine the original fossils, which could not be traced during my visit to the GSI, Calcutta, in 2007, I have decided to omit the Haritalyangar fossils from the hypodigm of *Sivaonyx*.

Measurements of the teeth are provided in table 5.

Discussion

Although the type specimen of *Sivaonyx bathygnathus* is a lower jaw, the decision to create the genus *Sivaonyx* was based largely on the morpho-

Table 6.—**Measurements (in mm) of the p/4 and m/1 of *Sivaonyx bathygnathus* (Lydekker, 1884a) from the Indian Subcontinent and China and *Sivaonyx gandakasensis* sp. nov. from Pakistan**

Specimen	Length p/4	Breadth p/4	Length m/1	Breadth m/1	Locality	Species	Data from
GSI D 33	—	—	17.1	9.7	Hasnot	*S. bathygnathus*	Own data
GSI D 156	9.7	5.8	16.0	9.4	Hasnot	*S. bathygnathus*	Pilgrim, 1932
GSI D 244	10.1	6.4	—	—	Hasnot	*S. bathygnathus*	Pilgrim, 1932
GSI D 250	—	—	16.4	9.1	Hasnot	*S. bathygnathus*	Own data
AM 19509	—	—	16.5	9.5	Hasnot	*S. bathygnathus*	Colbert, 1935
IVPP V6886.8	8.8	6.0	—	—	Lufeng	*S. bathygnathus*	Qi, 1983
IVPP V6886.9	8.4	6.0	—	—	Lufeng	*S. bathygnathus*	Qi, 1983
IVPP V 6886.10	8.8	6.5	—	—	Lufeng	*S. bathygnathus*	Qi, 1983
IVPP V 6886.13	—	—	15.9	9.0	Lufeng	*S. bathygnathus*	Qi, 1983
PDYV 1585	8.7	5.0	—	—	Leilao	*S. bathygnathus*	Qi, 2006
GSI D 249	—	—	14.4	8.6	Kaulial	*S. gandakasensis*	Own data
GSP 4225	8.7	6.3	15.0	7.9	Gandakas	*S. gandakasensis*	Own data
NHM M 13175	—	—	15.3	9.0	Kaulial	*S. gandakasensis*	Own data

logy of the P4/. As Pilgrim (1931) pointed out, the lower jaws that he had at his disposal showed little difference from that of *Enhydriodon* and, for the time being, one must only hope that Pilgrim is proven right in his assertion that the P4/ described by him does indeed belong to the same species as the lower jaw.

With the newly available material described here it is possible to document differences between the mandibles of *Sivaonyx* and *Enhydriodon*. *Sivaonyx* possesses a complete premolar row while *Enhydriodon* has lost the anterior upper premolars (presumably reflected in the lower jaw). The mandible of *Enhydriodon falconeri* is foreshortened in comparison with that of *Sivaonyx gandakasensis*. The morphology of the m/1 is approximately similar in the two genera, although the cusplets round the margin of the talonid basin tend to be discrete in *Enhydriodon* whereas in *Sivaonyx* they are usually joined together to form two elongate cusps.

Pilgrim (1932) indicated that one of his specimens (GSI D 249, from Kaulial) was smaller than other jaws attributed to *Sivaonyx bathygnathus*. GSP 4225 from Gandakas is also smaller than the ensemble of fossils from Hasnot, underlining the specific distinction of these geologically earlier specimens.

The Lufeng, China, sample identified as *Sivaonyx bathygnathus* by Qi (1983, 1985) appears to be similar to the Siwalik material. A p/4 from Leilao (Qi, 2006) also seems to accord in dimensions and morphology with *S. bathygnathus*. The Lufeng fossils indicate that the proposed association between P4/ and m/1 suggested by Pilgrim (1932) is indeed likely to be correct.

Willemsen (1999, fig. 2, top frame) included NHM M 15397 (mislabelled as NHM M 13175) in *Sivaonyx bathygnathus*, but I consider that this specimen is too large to belong to this species, but is the appropriate size to belong to *Enhydriodon falconeri*.

Examination of the holotype of *Lutra hessica* Lydekker, 1890, from Eppelsheim, Germany, reveals that it is extremely similar to *Sivaonyx bathygnathus* (Lydekker, 1884a) as was already indicated by Pilgrim (1931). Indeed, its morphology and dimensions fall within the range of variation of *S. bathygnathus*, and it is possibly a synonym of this species. The discovery of an upper carnassial of the German form would resolve this question.

Measurements of the teeth are provided in table 6.

Although the premolar row in *Sivaonyx bathygnathus* is complete, the crowding of the teeth and the oblique orientation of the p/2 indicate that the species was engaged on a trend towards shortening of the jaw, as exemplified by *Enhydriodon*. The m/2 is in the process of losing its anterior root (?) and its crown is raised upwards and pushed anteriorly towards the m/1. The p/1 is small and single rooted, and could have been lost in some individuals. The p/2 is obliquely oriented, carried to extreme in *Enhydriodon*. The p/4 and m/1 both show expansion of their distal parts, and the dentition shows enhanced adaptations to crushing, and a diminution of the sectorial function.

On the basis of the dimensions of the m/1, the body weight of *Sivaonyx bathygnathus* was probably about 9-11 kg, slightly lighter than *Aonyx capensis*, the body weight of which ranges from 11-21 kg (Larivière, 2003).
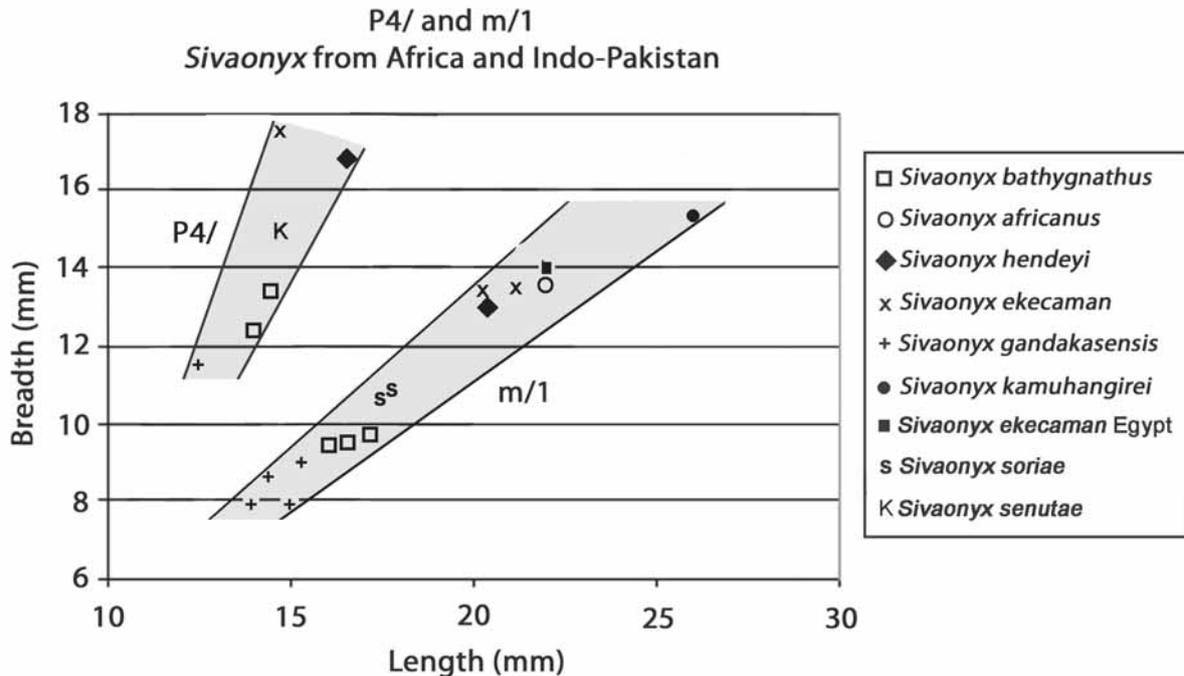
Fig. 10.—Metric comparison of P4/ and m/1 of *Sivaonyx* species from Indo-Pakistan and Africa.

The known Siwaliks species of *Sivaonyx* are smaller than any of the African species thus far described (fig. 10). This is probably due to the fact that all the known African specimens are younger than those from the Indian subcontinent. Otters are not yet known from African deposits between 11 and 6 million years old.

A note on GSI K 29.469 previously attributed to Sivaonyx bathygnathus

GSI K 29.469, a mandible with the rear half of p/3, and complete p/4-m/1 from Haritalyangar, was tentatively attributed to *Sivaonyx bathygnathus* by Prasad (1970) but apart from its dimensions, it differs markedly from other specimens of this genus. The p/4 is a tall trenchant blade with a slender, diminutive posterior cusplet almost in line with the main cusp, unlike the lower crowned, more inflated, bundont p/4 of *Sivaonyx* in which the posterior cusp is inflated and is offset buccally considerably more. Prasad (1970) erroneously reported that the distal cusplet of the p/4 was higher than the main cusp. Furthermore, in *Sivaonyx* the cingulum encircles the entire tooth but it is discontinuous in K 29.469, in

particular on its buccal and lingual sides, and the enamel is smooth, rather than coarsely wrinkled as in *Sivaonyx*. The m/1 of K 26.469 differs from those of *Sivaonyx* by its much more rounded, more inflated and smoother cusps, the deeper incision between the paraconid and protoconid, which lingually overhangs the trigonid basin rather than being vertical, the lingual spout of the trigonid basin is narrow V-shaped rather than U-shaped as in *Sivaonyx* and other enhydriodontines, the metaconid is somewhat taller than the other two trigonid cusps, the lingual talonid cusp is almost as large as the buccal talonid cusp, and the posterior accessory cusplet immediately behind the protoconid is vestigial. There is a large distal interstitial facet for the m/2. The mandible possesses a single mental foramen beneath the p/2-p/3, unlike *Sivaonyx* and *Vishnuonyx* which possess two or even three mental foramina beneath the premolar row (one each beneath p/2, p/3 and p/4) or *Enhydriodon* in which there is one beneath the p/4 (condition unknown for the anterior part of the premolar row, since no specimen preserves this portion of the jaw). In some of these features the Haritalyangar fossil resembles the bunodont African viverrid *Pseudocivetta ingens* (Petter, 1967) and the morphology of the p/4 and
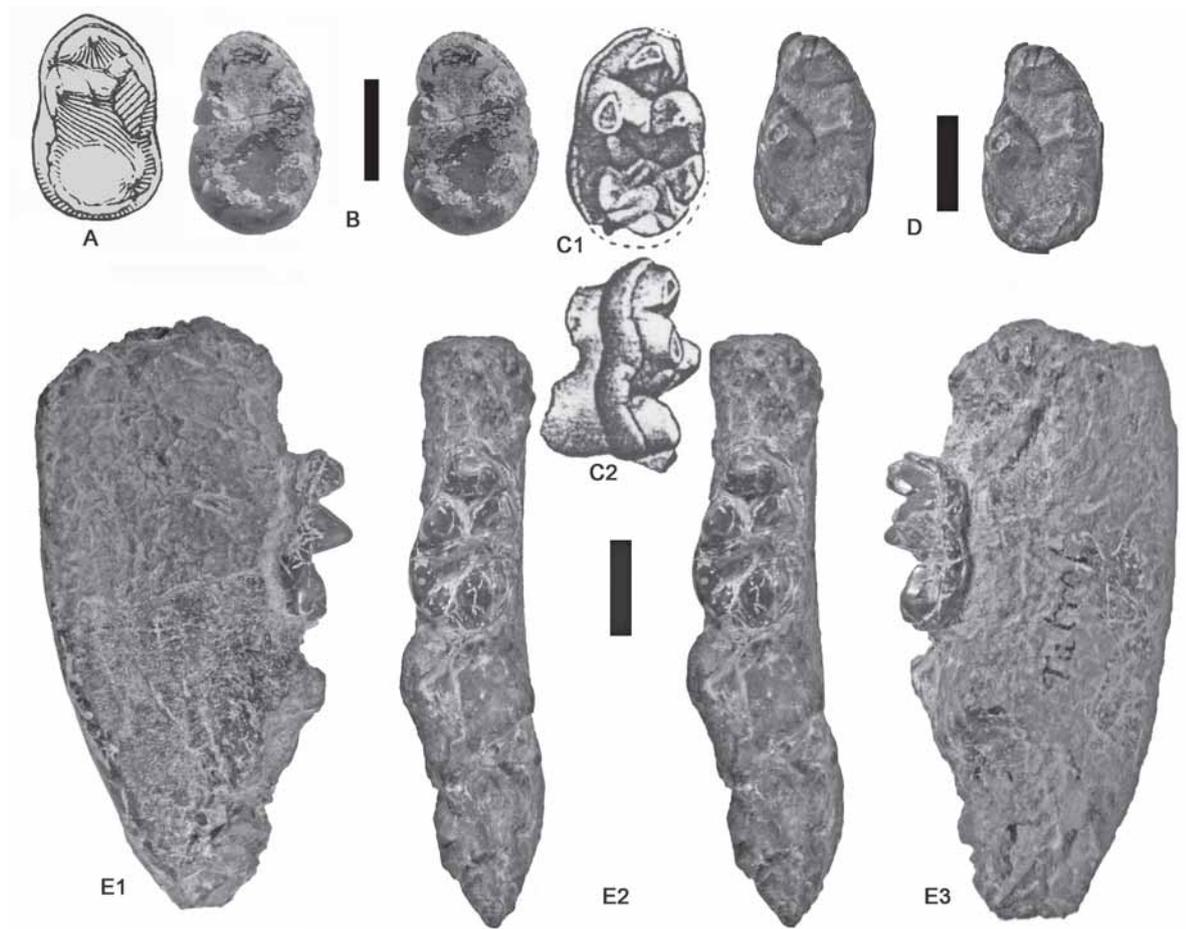
Fig. 11.—*Sivaonyx* and *Enhydriodon* lower dentition, A) Shakou, China, otter, right m/1, occlusal line drawing from Chow, 1961, attributed to *Enhydriodon* cf *falconeri*; B) Bar 567'05, *Sivaonyx ekecaman* right m/1 from Sagatia, Kenya, (stereo occlusal view); C) right m/1 from Wadi Natrun, Egypt, figured by Stromer (1920, fig. 11) C1) occlusal view, C2) buccal view; D) GSI D 161, *Enhydriodon sivalensis*, right m/1 from Hasnot, Pakistan (stereo occlusal view); E) NHM M 15397, *Enhydriodon falconeri* right mandible containing m/1 (E1 – lingual, E2 – stereo occlusal and E3 – buccal views) (scale bars : 10 mm).

m/1 show some similarities to those of extant *Paradoxurus hermaphroditicus*.

All these features lead me to withdraw GSI K 29.469 from the Lutrinae and to transfer it to Viverridae.

Genus *Enhydriodon* Falconer, 1868

Type species : *Enhydriodon sivalensis* Falconer, 1868

Synonymy :
1835 - *Amyxodon* nom. nud., Falconer & Cautley, p. 707.
1839 - *Amyxodon* nom. nud., Royle, vol. 1, p. 31.
1868 - *Enhydriodon* (*Amyxodon*) Falconer & Cautley, Falconer, vol. 1. p. 331.

Diagnosis : Large enhydriodontines with extremely bunodont dentition. Hypocone of P4/ larger than protocone and conical with low centrally directed ridge; post-protocone cusp conical and usually separated apically from the protocone; metastyle almost as voluminous as the paracone. Deeply concave outer wall to the buccal cusp pair. Only two upper premolars present. Parastyle large and low. Post-protocone cusplets oriented linguo-distally rather than distally, sometimes detached and blocking the lingual opening of the central valley. Upper dental formula 3-1-2-1.
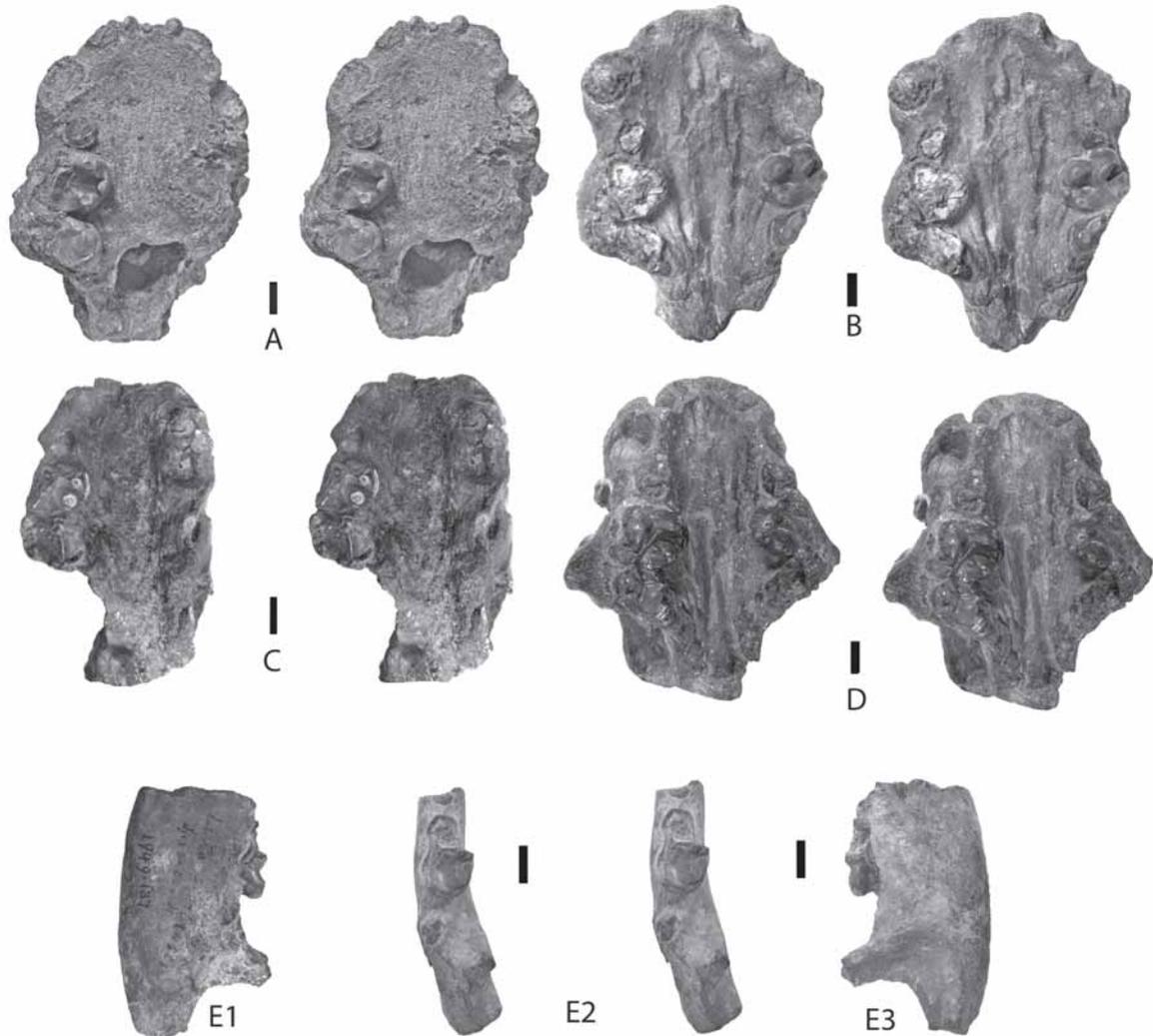
Fig. 12.—*Enhydriodon sivalensis*, A) GSI NRV2/468, snout from Saketi, India in stereo palatal view; B) NHM M 37155, snout from Siwalik Hills, India in stereo palatal view; C) NHM M 37513, snout from Siwalik Hills, India in stereo palatal view; D) NHM M 37154, snout from Siwalik Hills, India in stereo platal view; E) IPSMG 1949.187, right mandible with part of m/1 from Siwalik Hills, India (E1 – lingual, E2 – stereo occlusal and E3 – buccal views) (scale bars : 10 mm).

Species *Enhydriodon falconeri* 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 linguo-distally, 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 m/1 trigonid narrow U-shaped.

Synonymy :
v1929 - *Enhydriodon* sp., Matthew, p. 472, Text fig. 11.
v1931 - *Enhydriodon falconeri* sp. nov., Pilgrim, pp. 54, 56, Pl. 2, figs. 3, 5.
v1932 - *Enhydriodon falconeri* Pilgrim, Pilgrim, pp. 60, 85-88, Pl. 2, fig. 15.
v1999 - *Sivaonyx bathygnathus* (Lydekker), Willemsen, pp. 413, fig. 2, top frame (M 15397 mislabelled as M 13175).
non1961 - *Enhydriodon* cf *falconeri,* Chow, 164-167, fig. 1.
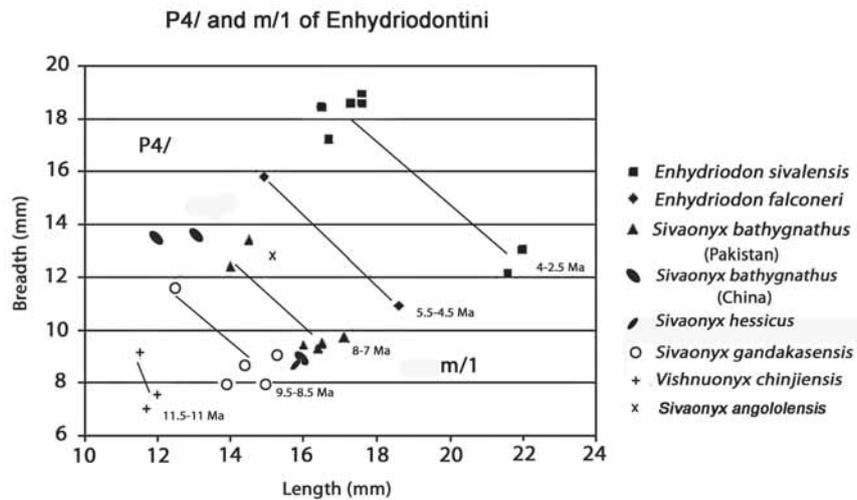
Fig. 13.—Metric comparison of P4/ and m/1 of various species of Enhydriodontini omitting the very large African species of *Sivaonyx*.

non1913 - Enhydriodon sp. aff. *sivalensis* (Lydde-ker), Pilgrim, p. 282.

Type specimen : M 4847, left P4/ (fig. 9D).

Type locality : Siwalik Hills, India.

Additional material :
NHM M 15397, right mandible with m/1 from Tatrot (Sale collection in NHM, London) (fig. 11E).

Localities and stratigraphic range : Siwalik Hills, Hasnot and Tatrot, Latest Miocene (Tatrot Zone).

Description

The two specimens attributed to *Enhydriodon fal-coneri* have been described on previous occasions. Matthew (1929) and Pilgrim (1932) described and figured the P4/ whereas Willemsen (1999, fig. 2, top frame) illustrated the m/1 in mandible NHM M 15397, but attributed the specimen to *Sivaonyx bathygnathus*. The catalogue number that he provi-ded for this tooth (NHM M 13175) belongs to anot-her specimen, a left mandible which has a more deeply worn carnassial.

There is little to add to the existing descriptions, save to point out that the lingual opening of the tri-gonid basin of the m/1 is somewhat more pinched in than it is in *Enhydriodon sivalensis* (fig. 11) and the hypoconid is more voluminous than it is in *Siva-*

onyx bathygnathus. Metrically the specimens fall in between *Sivaonyx bathygnathus* and *Enhydriodon sivalensis* (fig. 13).

Discussion

Enhydriodon falconeri is in many ways an inter-mediate form between *Sivaonyx bathygnathus*, which is smaller and *Enhydriodon sivalensis*, which is bigger (fig. 13) as has been noted on several pre-vious occasions (Matthew, 1929; Pilgrim, 1932; Willemsen, 1999). The P4/ is closer morphologi-cally to *E. sivalensis* than to *Sivaonyx bathygnathus* by its more bunodont cusps, its expanded protocone with accessory distal cusplet, enlarged bunodont hypocone, more rounded paracone and metastyle and prominent parastyle. The m/1 is however, more similar to that of *Sivaonyx bathygnathus*, with the lingual opening of the trigonid basin more pinched in than it is in *E. sivalensis* and its less well develo-ped marginal cusps in the talonid.

There can be little doubt that *E. falconeri* repre-sents a form transitional in body size and dental morphology between *Sivaonyx bathygnathus* and *Enhydriodon sivalensis*.

Chow (1961) attributed a right mandible with m/1 and m/2 from Shakou (Yuanmo, China) to *Enhydriodon* cf *falconeri*. The m/1 is appreciably larger than that of *E. falconeri*, plotting out close to East African *Sivaonyx ekecaman* and South African *Sivaonyx hendeyi*. Chow (1961) reported that the

Table 7.—**Measurements (in mm) of the teeth of *Enhydriodon falconeri* from the Indian Subcontinent and a specimen from China attributed to *Enhydriodon* cf *falconeri* (Chow, 1961)**

Specimen	Tooth	Length	Breadth	Locality	Data from
NHM M 4847	P4/	14.9	15.8	Siwalik Hills	Own data
NHM M 15397	m/1	18.6	10.9	Tatrot	Own data
Chow, 1961	m/1	20	13	Shakou (Yuanmo)	Chow, 1961

Chinese fossil is slightly smaller than *E. falconeri*, but in fact it is larger than the only available m/1 of the latter species. Its length corresponds to *E. sivalensis*, but the crown is distinctly broader than m/1s of the latter species (two specimens known). Furthermore, the lingual opening of the trigonid is pinched in, and not broad and U-shaped as it is in *E. sivalensis*. It is possible that the Shakou fossil belongs to a large species of *Sivaonyx*, rather than to *Enhydriodon*.

On the basis of the dimensions of m/1, the body weight of *Enhydriodon falconeri* is estimated to have been about the same as that of *Aonyx capensis*, with a mean of ca 16 kg.

Measurements of the teeth are provided in table 7.

Species *Enhydriodon sivalensis* Falconer, 1868

Diagnosis : Large species of *Enhydriodon* with post-protocone cusplets directed distally rather than linguo-distally, often one of them detached and blocking the lingual opening of the central valley. Hypocone with a low but wide centrally directed ridge leading into the central valley.

Synonymy :
v1868 - *Enhydriodon sivalensis* nov. gen. nov. sp., Falconer, pp. 331-338, Pl. 27, figs. 1-5.
1868 - *Enhydriodon ferox* sp. nov., Falconer, p. 552.
1880 - Enhydriodon sivalensis Falconer, Bose, p. 134.
v1884a - *Enhydriodon sivalensis* Falconer, Lydekker, pp. 195-201, Text fig. 2, Pl. 27, fig. 5.
1885 - Enhydriodon sivalensis Falconer, Lydekker, p. 196.
v1913 - *Enhydriodon* sp. aff *sivalensis* Falconer, Pilgrim, p. 282.
v1929 - *Enhydriodon sivalensis* Falconer, Matthew, p. 471, Text fig. 9.
v1931 - *Enhydriodon* sp. aff. s*ivalensis* Falconer, Pilgrim, p. 54, Pl. 2, fig. 5, 5a, 5b (specimen GSI D 161).

v1932 - *Enhydriodon sivalensis* Falconer, Pilgrim, pp. 83-85.
pv1932 - *Enhydriodon* cf *falconeri* Pilgrim, Pilgrim, pp. 60, 85-86 (specimen GSI D 161 only).
v1992 - *Enhydriodon sivalensis* Falconer, Verma & Gupta, pp. 31-35, Text fig. 2, Pl. 1.
v1999 - *Enhydriodon sivalensis* Falconer, Willemsen, pp. 411-413.
v2002 - *Enhydriodon sivalensis* Falconer, Verma, Mishra & Gupta, pp. 70-71, Pl. 14.

Lectotype : NHM M 37153, skull from the Siwalik Hills, India (Matthew, 1929, p. 471) (fig. 12C).

Additional material :
RCS 777A, snout from the Siwalik Hills, India. Royal College of Surgeons (probably destroyed) = GSI D 103 casts in the GSI, Calcutta and Lucknow, India.
M 37154, snout from the Siwalik Hills, India (fig. 12D).
M 37155, snout from the Siwalik Hills, India (fig. 12B).
GSI NRV2/468, snout from the Saketi Formation, India (fig. 12A).
GSI D 161, right m/1, from near Hasnot, Punjab, V. Rao coll. (cast in NHM M 12350) (fig. 11D).
IPSMG 1949.187, right mandible fragment from the Siwalik Hills, India, Ipswich Museum, England (fig. 12E).

Localities and stratigraphic range : Siwalik Hills, Saketi, India : Middle to Late Pliocene (Pinjor Zone).

Description

IPSMG 1949.187 is a right mandible fragment (fig. 12E) from the Siwalik Hills, India broken in front of the m/1 (Lydekker, 1884a, Pl. 45, fig. 3, 3a). The specimen is attributed to *Enhydriodon sivalensis* on account of its dimensions and the morphology of the talonid of the lower first molar.

Table 8.—**Measurements (in mm) of the teeth of *Enhydriodon sivalensis* (all measurements are by the author; e = estimated measurement)**

Specimen	Tooth	Length	Breadth	Locality
GSI NRV 2/468	I1/ right	2.7	3.4	Saketi
GSI NRV 2/468	I2/ right	4.6	4.5	Saketi
GSI NRV 2/468	I2/ left	5.1	5.5	Saketi
GSI NRV 2/468	I3/ root right	8	7	Saketi
GSI NRV 2/468	I3 root left	10	10	Saketi
GSI NRV 2/468	C1/ root right	15	13.1	Saketi
GSI NRV 2/468	C1/ root left	16	12.8	Saketi
GSI NRV 2/468	P3/ right	10.2	9.6	Saketi
GSI NRV 2/468	P4/ right	17.3	18.6	Saketi
GSI NRV 2/468	M1/ right	14.0e	20.3e	Saketi
NHM M 37153	P4/ right	16.7e	17.2e	Siwalik
NHM M 37154	P4/ (left & right)	17.6	18.9	Siwalik
NHM M 37155	P4/ left	18.2e	18.5	Siwalik
GSI RCS 777A cast	P4/ left	16.5	18.4	Siwalik
GSI RCS 777A cast	P4/ right	17.6	18.6	Siwalik
GSI RCS 777A cast	M1/ right	14.3	19.7	Siwalik
GSI RCS 777A cast	M1/ left	14	20	Siwalik
GSI D 161	m/1 right	21.6	12.7	Hasnot
IPSMG 1949.187	m/1 right	22e	13e	Siwalik

Although the specimen is a fragment, it is useful because it is the only known lower jaw of the species. Falconer (1868) mentioned the existence of a mandible with m/1 and m/2, but the specimen was subsequently identified as *Canis cautleyi* by Bose, 1880.

The Ipswich mandible is robust with a depth beneath m/1 of 31.5 mm and a thickness of 13.2 mm. The masseteric fossa is deep and bordered by sharp margins, terminating anteriorly below the alveolus of the m/2. There is a linear series of small pits a short distance below the alveolar margin on the buccal surface, which probably correspond to the buccinator insertion. These pits are arranged in circular groups, and not in a line as in other otters.

The m/1 is severely damaged, but judging from the roots and what remains of the talonid, its dimensions would have been about 22 mm long by about 14 mm broad. The talonid of m/1 is broad, basin-shaped, with a prominent crescentic buccal cusp group separated by a short gap from the posterior accessory cusplet of the protoconid, which is the only part of the trigonid preserved. There is a low buccal cingulum. The lingual part of the talonid is broken, but the most distal of the lingual cusplet group is preserved. At the rear of the talonid there is a distinct contact facet for the m/2. The m/2 alveolus is ovoid with a lingual indentation.

The upper cheek dentition and snout of *Enhydriodon sivalensis* have been described on several

occasions (Falconer, 1868; Lydekker, 1884a; Pilgrim, 1932; Verma & Gupta, 1992) and it is thus not necessary to redescribe these parts of the fossils. The anterior dentition, in contrast, has received less attention, mainly because most specimens lack the crowns of these teeth. However, the specimen described by Verma & Gupta (1992) contains the right I1/, both I2/s and the roots of both I3/s. The I1/ is the smallest of the upper incisors, and the I3/ is the largest. In this specimen, wear has advanced to the stage where the pulp canal of the I2/ is exposed, whereas it is not yet visible in the I1/ (fig. 14A). The wear surface of the upper incisor battery is thus concave from side to side, unlike the wear pattern in other otters, including *Enhydra lutris*, in which the cutting edge of the teeth is almost straight. The concave profile of the incisor battery in *Enhydriodon* is presumed to have been enhanced by attrition during incisive preparation of durable food items (fig. 14A).

Measurements of the teeth are provided in table 8.

Discussion

Matthew (1929, Text fig. 9) selected M 37153 as the lectotype of the species *E. sivalensis*, a relatively complete skull but with damaged dentition. The composite illustration of the upper dentition
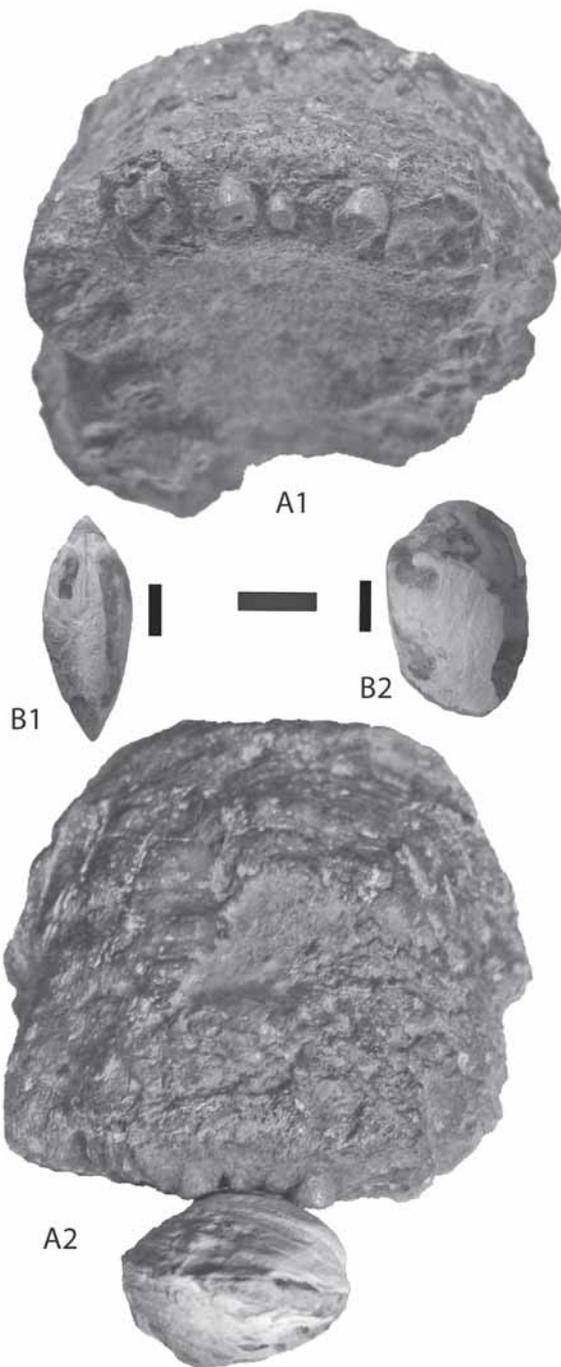
Fig. 14.—Anterior dentition of *Enhydriodon sivalensis*, GSI NRV2/468 and its possible prey the bivalve *Lamellidens*. A1) oblique antero-ventral view of snout showing deeply worn and curved occlusal surface of the upper incisors, exposing the pulp canal in the right I2/; A2) anterior view of snout with a complete doublet of the bivalve *Lamellidens jammuensis* placed in occlusal position; B) *Lamellidens jammuensis* (B1 – umbonal view, B2 – lateral view) (scale bars : 10 mm).

that he published is misleading in a number of features. Firstly, out of the four snouts known at the time of his research only one possessed an alveolus in front of the P3/ and lingual to the canine. Lydekker (1884a) considered that the alveolus in the only specimen that does have one could represent the alveolus of a deciduous tooth or that the P2/ had a tendency to fall out early. The P3/ of *Enhydriodon sivalensis* possesses two roots, the condition being clearly expressed in the snout described by Verma & Gupta (1992) in which the P3/ is present on the right side, while its crown is missing on the left exposing its two roots. Secondly, the morphology of the P4/ and M1/ in Matthews' illustration does not correspond to any of the specimens, but is a chimera. In particular, it does not match the best preserved dentition (RCS 777A) illustrated by Lydekker (1884a) nor does it agree with the morphology of the lectotype.

On the basis of the dimensions of m/1, the body weight of *Enhydriodon sivalensis* is expected to be greater than that of *Aonyx capensis* (range 11-21 kg) and a figure of 22-25 kg or more would not be unreasonable.

Diet of Enhydriodon

It has often been written that extinct bunodont otters preyed mainly on shellfish (molluscs and crustaceans) (Willemsen, 1992). However, little direct evidence has been put forward in support of this hypothesis, the proposal being based principally on analogy with extant bunodont otters which include such items in their diet; *Enhydra*, the sea otter which preys on abalone and other marine bivalves, and *Aonyx*, which eats mainly freshwater crabs.

The durophagous dentitions of the two extant taxa are superficially similar to each other in the sense that both are bunodont and have low rounded cusps in the posterior dentition, but it is clear that molluscivores (*Enhydra*) possess considerably thicker enamel caps than otters that prey mainly on crustaceans (*Aonyx*). The extinct genus *Enhydriodon* possessed thick enamel in the posterior dentition, and on this basis one would expect it to have been molluscivorous rather than cancrivorous. Indian species of *Sivaonyx* in contrast, combine a shearing function of the carnassials with overall crown bundonty akin to the structure observed in cancrivores such as *Aonyx capensis*. They were thus

more likely to have preyed on crustaceans than molluscs, although bivalves could have been included in the diet if left in the sun to open from heat stress, a technique employed by *Amblonyx*. Pliocene African species of *Sivaonyx* in contrast possessed thick enamel in the carnassials, and the shearing function is almost defunct, indicating that they probably preyed more on molluscs than on crabs. The heavy occlusal wear observed on the teeth of *Sivaonyx kamuhangirei* (Morales & Pickford, 2005a) from western Uganda provides evidence in support of the view that its food items were extremely abrasive, perhaps due to shell fragments or sand grains adhering to the food.

Until recently, there was no satisfactory way of throwing light on the question, all the available specimens being damaged in the parts that would have helped elucidate the matter. However, a snout of *Enhydriodon* described by Verma & Gupta (1992) preserves part of the upper incisive row in a moderately advanced state of wear, the second incisors having the pulp canal exposed (fig. 14A). Both third incisors in this specimen are broken off at cervix level, but judging from their root diameters, the central incisors were the smallest of the incisor battery, and the third incisors were the largest, recalling canines by their dimensions, a point already made by Falconer (1868) who even proposed the name *Amyxodon* for the genus on account of the grossly enlarged third incisors.

In this snout, the occlusal surface of the incisor battery is concave from I3/ to I3/. This curvature is due to two main factors, morphological and abrasional. The I1/s are the smallest and lowest crowned incisors and the I3/s are the largest and highest crowned, the cervical level of the incisor row being almost planar. Thus even in the unworn state, the incisor battery of *Enhydriodon* would have had a concave occlusal surface, similar in shape and function to the concave functional surface of a pair of nut crackers. With use, the concave surface is enhanced by wear, eventually taking on the profile of the main food item. In the snout described by Verma & Gupta (1992) wear has proceeded to the stage where the central incisor is worn to the point where the crown is almost flat, but the pulp cavity is not exposed. The I2/s are worn to such an extent that the pulp cavities are exposed, but the crowns are higher than those of the I1/s, and the wear facets dip towards the I1/. Both I3/ crowns are unfortunately broken, but it is clear that the roots of these teeth are implanted at an angle to the occlusal surface, diverging apically into their alveoli, thereby directing forces mesially during biting.

A comparable deeply concave dental occlusal surface has already been described for the molluscivorous creodont, *Teratodon*, by Pickford (1995) except that in that case it is the premolar rows (both upper and lower) that show the concave occlusal surface. It was suggested that *Teratodon* preyed on the large achatinid land snail *Achatina leakeyi*, the body whorl of which has a similar radius of curvature to the concave profile of the premolar row. *Teratodon* shifted the main chewing muscles forwards over the premolar row so that power was delivered just behind the area of action of the «nut cracker-like» concave occlusal profile, as in a pair of nut crackers. The sea otter, *Enhydra*, uses stones to break open its prey items, and it thus does not show the concave occlusal profile in its incisor battery that occurs in *Enhydriodon*.

It should be noted that the wear on the incisors in the only individual of *Enhydriodon* in which these teeth are preserved, is considerably more advanced than it is in the cheek dentition, indicating that shell opening was carried out by the front teeth, and that only the soft parts (possibly with some attached shell fragments and/or sand grains) were then passed into the mouth for chewing and swallowing.

On this basis, it is to be expected that when a lower incisor row of *Enhydriodon* is found, its occlusal surface will also be concave from mesial to distal, as in the upper incisor battery. In addition, as in *Teratodon*, the chewing muscles of *Enhydriodon* have shifted forwards so that they are close to the zone of maximal pressure of the «nut cracker», except that in this genus, because the teeth involved in breaking open the mollusc shells are the incisors, this zone is appreciably further forwards than it is in the creodont. The masseteric fossa is deep and extends forwards to the level of the m/2. The snout region of *Enhydriodon* is amazingly robust, even by lutrine standards (figs. 14, 15) and the groove for the upper lip retractor musculature is deep and wide.

Having said this, it remains to determine the possible prey items of *Enhydriodon*. Molluscs are commonly found in the Siwalik freshwater molasse, regardless of the age of the sediments (Chinji to Pinjor : Middle Miocene to Plio-Pleistocene). A number of papers has been written on the taxonomy of these molluscs (Mathur, 1998; Srivastava & Arora, 1983) which reveal that the freshwater bivalves *Parreysia* and *Lamellidens* are widespre-
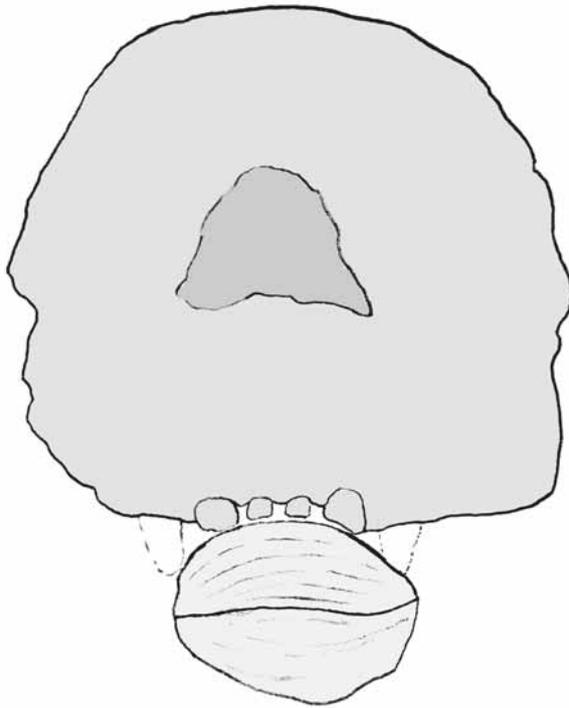
Fig. 15.—Line drawing illustrating the anterior view of the snout of *Enhydriodon sivalensis* with upper I3/s reconstructed, in occlusion with a possible prey species, the bivalve *Lamellidens jammuensis*. The nasal cavity is shaded dark grey. Note the extremely robust premaxillae and maxillae.

ad, common and persist throughout the entire Siwalik sedimentary column (15 – 2 Ma). *Lamellidens* is a medium-sized bivalve with strong shells which are often reinforced by distinct radial growth lines, although ribs and spines have not been recorded. *Parreysia* possesses reinforced v-shaped radial growth lines. The umbo of *Lamellidens jammuensis* is inflated somewhat, so that the shell presents a characteristic radius of curvature from articulation to shell edge. The radius of curvature of adult *Lamellidens* shells (fig. 14B) is similar to the profile of the concave occlusal surface of the incisor row in *Enhydriodon* (figs. 14B, 15). *Parreysia* has a similar radius of curvature, whereas none of the large freshwater gastropods from the Siwaliks do, including fossils attributed to *Scala* (Srivastava & Arora, 1983) (more properly attributed to *Brotia*).

The most primitive known member of the Enhydriodontini, *Vishnuonyx chinjiensis*, previously known from extremely limited material, is now known by a mandible with alveoli of the canine, p/1-p/3, and the crowns of p/4-m/2 in excellent condition, which indicate that the species included alot of fish in its diet, even though its main adaptation was for eating shellfish, and as such possessed a dentition that resembles in several ways those of other piscivorous otters, including a trigonid that is much higher than the talonid, a well developed shearing facet on the buccal aspect of the paraconid and protoconid, and a deep incision between these two cusps. However, there are signs that *Vishnuonyx* was already including shellfish in its diet on a regular basis, as shown by the presence of a raised lingual margin in the talonid of m/1, a robust double-cusped p/4, a mandible that is deeper beneath m/1 than the length of this tooth, the relatively broad m/1 (fig. 16) and the deep masseteric fossa which extends anteriorly to terminate beneath the m/2.

The trend towards bunodonty and durophagy in Enhydriodontini is thus considered to have commenced towards the end of the Middle Miocene (Chinji deposits) on the basis that it is at this level that the earliest indications (ie *Vishnuonyx*) of the dental evolutionary trajectory that culminated in *Enhydriodon* has been observed. In the case of *Vishnuonyx*, the carnassials are still predominantly shearing teeth, but show the beginning of a trend towards the bunodonty which is exemplified in *Sivaonyx* and taken to extremes in *Enhydriodon*. *Vishnuonyx* was too small and its teeth too delicate for it to have crushed mollusc shells. Indian species of *Sivaonyx* probably preyed predominantly on crustaceans, and it was with the emergence of *Enhydriodon* that all the elements were in place for a predominently mollusc-opening behaviour to emerge : large body size with reinforced anterior snout dentition and musculature powerful enough to open bivalve shells, and bunodont, thick-enamelled cheek dentition adapted for chewing food to which hard shell fragments may still be adhering. It is therefore suggested that *Enhydriodon* preyed extensively on bivalves such as *Lamellidens* (fig. 14B) and *Parreysia* which are common in the deposits which have yielded these large otter-like mammals (Srivastava & Arora, 1983).

This dietary hypothesis is supported by a consideration of the length-breadth relationships of the m/1 in otters of known diet. *Lutra* (Heggberget & Moseid, 1994) *Lutrogale* (Mason & MacDonald, 1986) and *Pteronura* (Carter & Rosas, 1997; Eisenberg, 1989; Emmons, 1990; Laidler, 1982; Nowak,
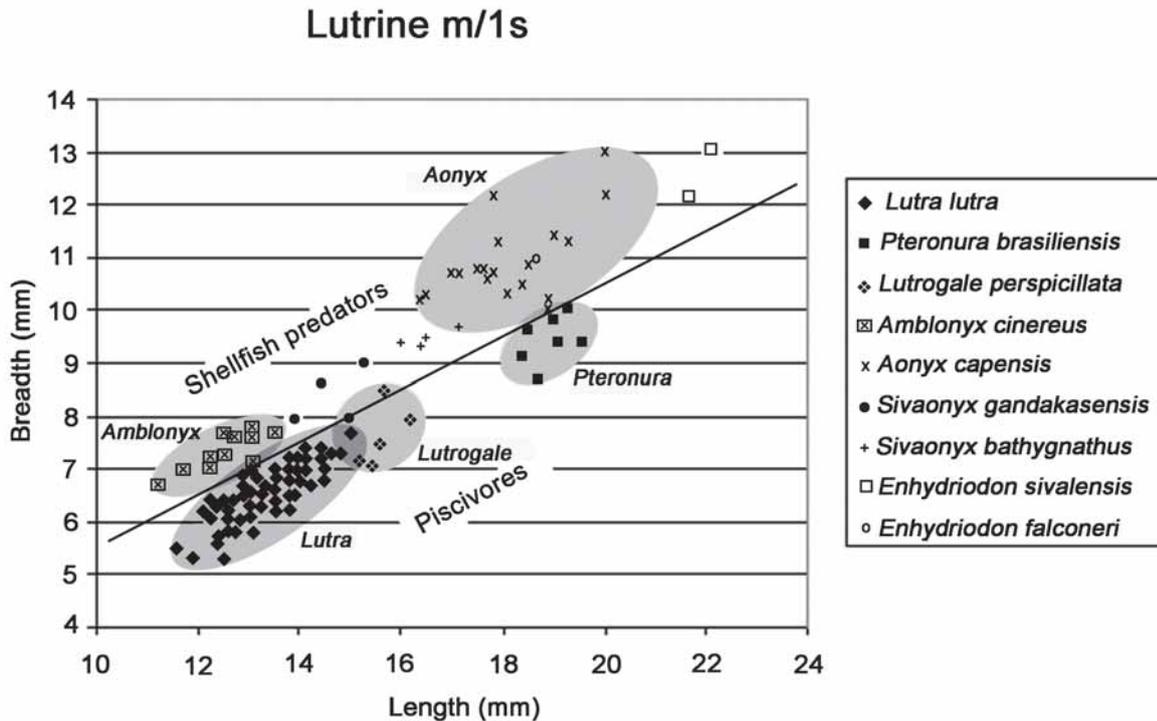
Fig. 16.—Length-Breadth relationships in the first lower molar of otters reflects the dominant prey category. Piscivores (below the sloping line) possess narrower molars whereas cancrivores and molluscivores (above the sloping line) have broader molars. *Vishnuonyx*, *Sivaonyx* and *Enhydriodon* have broad m/1s suggesting that they preyed predominantly on shellfish.

1991) are predominantly piscivorous and they possess relatively narrow lower carnassials. In contrast*, Amblonyx* (Kruuk *et al*., 1994; Foster-Turley, 1992; Timmis, 1971) and *Aonyx* (Butler, 1994; Donnelly & Grobler, 1976) possess broader m/1s (fig. 16) and these two otters prey predominantly on shellfish, crabs in particular. Otters are opportunistic feeders, such that piscivores will occasionally prey on crabs and other items, just as cancrivores will eat fish when it is available and easy to catch. The breadth-length relationships of the m/1 thus reflect the main dietary adaptation. On this basis *Vishnuonyx*, *Sivaonyx* and *Enhydriodon*, which possess broad m/1s, would be expected to have preyed predominantly on shellfish (they fall above the sloping line in fig. 16 that separates piscivores from the otters that prey mainly on shellfish). Within this broad category, otters with thickened molar enamel would presumably be preying on harder and more abrasive food items than those with thinner enamel. If this is so, then *Enhydriodon* would have been preying mainly of molluscs,

whereas Indian species of *Sivaonyx* and *Vishnuonyx* would probably have been predominantly cancrivorous. Pliocene species of *Sivaonyx* with thick enamelled molars, such as *S. ekecaman*, *S. africanus*, and *S. kamuhangirei*, may have been molluscivores (Morales & Pickford, 2005a).

Evolutionary trends in Indian Enhydriodontini

There are several clear evolutionary trends discernible in the Enhydriodontini of the Indian subcontinent. The first development, which effectively led to the separation of the tribe from the other lutrine-like mustelids consisted of the widening of the zone between the protocone and paracone in the P4/. Other lutrines have the protocone close to the paracone and separated from it by a steep-sided valley with a V-shaped bottom. As a consequence, in most lutrines, the protocone is near the midline of the tooth, as in other otters, but in enhydriodonti-

nes the protocone is located much closer to the lingual margin of the crown and further from the paracone. As a result there is a widening of the valley that separates it from the paracone, and the bottom of the valley is broadly U-shaped. Thus, even in the small *Vishnuonyx* from Chinji, this derived morphology is present. Concurrently with this change in the morphology of the P4/, the talonid of the lower m/1 became broader than the trigonid. Linked to this repositioning of the protocone was the increase in size of the talon of the P4/ with development of a cusplet distal to the protocone and on the marginal ridge of the talon, herein called the hypocone. In *Enhydriodon*, accessory cusplets split from the protocone on its disto-lingual side.

A second obvious trend was an overall increase in size with the passage of time. Starting with *Vishnuonyx chinjiensis* in the Middle Miocene, which had an m/1 in the region of 12 mm long, successive species possess m/1s which were 13.9-15 mm (*Sivaonyx gandakasensis*) 16-17.1 mm (*Sivaonyx bathygnathus*) 18.6 mm (*Enhydriodon falconeri*) and about 22 mm (*Enhydriodon sivalensis*) (fig. 13).

A third observable trend is an overall increase in bunodonty in the lineage. *Vishnuonyx* has the talonid basin of m/1 much lower than the trigonid, which has sharp pointed cusps and a well-developed carnassial function of the paraconid and protoconid, indicating that it was probably still predominantly piscivorous. In *Sivaonyx* in contrast, the talonid basin is not much lower than the trigonid, the cusps of which are more bundont, even though some sectorial function is still evident in *Sivaonyx gandakasensis*. In *Enhydriodon*, the trend to bunodonty is taken to its extreme, with the sectorial function almost completely suppressed, and the crushing function predominant.

A fourth trend is a reduction in the quantity of premolars. *Vishnuonyx* and *Sivaonyx* both possess four premolars in the mandible, but in *Sivaonyx gandakasensis* the p/1 is single rooted and small and the p/2 is slightly rotated in the jaw, suggesting the emergence of a trend towards shortening of the mandible, a suggestion bolstered by the observation that the m/2 is raised above the level of the other cheek teeth, and has an occlusal surface that dips towards the talonid basin of the m/1. By the *Enhydriodon* stage, the trend of mandibular shortening had reached an extreme, with the upper premolars reduced to two, the snout becoming so short that the front of the P3/ is located lingually to the rear of the

upper canine, the diastema between the two teeth being oriented bucco-lingually rather than antero-posteriorly.

A fifth trend, but not demonstrable in detail due to imperfections of the fossil record, was the enlargement of the third upper incisor into a canine-like tooth. In most otters in which the upper incisor battery is known, the third incisors are only marginally bigger than the first and second ones. *Enhydriodon* has extremely heterodont incisors, as was already pointed out by Falconer (1868) and we take this to be a derived state. Until upper incisor rows of *Vishnuonyx* and *Sivaonyx* are found, however, we will remain in the dark concerning the timing of I3/ enlargement in this lineage of otter-like mammals. However, it is interesting to note that the Oligocene mustelid *Potamotherium*, often attributed to Lutrinae, already possessed an enlarged I3/, and it is possible that I3/ enlargement was inherited from a precursor such as *Potamotherium*.

All these evolutionary trends were probably related to a single long term behavioural change, which was evidently a shift in diet from piscivory to one including crabs and eventually predominantly molluscs, in particular bivalves which were opened using the incisors. Concomitantly, there was an anterior shift of the biting musculature.

Enhydriodontines from Mainland Asia

Enhydriodon cf *falconeri* has been reported from Yunnan, China, (Chow, 1961) on the basis of a mandible containing m/1 and m/2 whereas *Enhydriodon* sp., is listed from the Rostov area, southern Russia, (Titov *et al*., 2006) but no details of the latter discovery are yet available. The specimen from Yuanmo (Chow, 1961, fig. 1) has a foreshortened trigonid, with a narrow U-shaped lingual opening to the trigonid basin and the metaconid is more anteriorly positioned than the protoconid (fig. 11A). In *Enhydriodon* this opening tends to be wide and U-shaped, the trigonid is more antero-posteriorly elongated and the metaconid is distally positioned with respect to the protoconid (fig. 11D). Further material is required to settle the affinities of the Yuanmo fossil, but judging from the relative proportions of the trigonid and talonid, and the disposition of the trigonid cusps with respect to each other, it is probably more closely related to African *Sivaonyx ekecaman* and *Sivaonyx hendeyi* than it is to *Enhydrio-*

don. The deposits from which this specimen came (Chow, 1961) are younger than Lufeng and Leilao (Qi, 2006; Qian, 1993) (fig. 18) and the specimen is more similar in dimensions and morphology to mid-Pliocene *Sivaonyx ekecaman* from Kenya (fig. 11B) than to *Enhydriodon falconeri*.

Sivaonyx bathygnathus is known from a number of specimens from Lufeng (Qi, 1983, 1985; Qiu & Qiu, 1995) and a lower p/4 from Leilao (Qi, 2006). These fossils are slightly smaller than most of the material from the Siwaliks attributed to *Sivaonyx bathygnathus*, but are larger than specimens of *Sivaonyx gandakasensis*.

Despite the fact that it is known only by post-cranial remains, mention is made of *Semantor macrurus* Orlov (1933) a late Miocene or perhaps basal Pliocene aquatic mammal from the deposits near Pawlodar, Irtysh River, Western Siberia. The relationships between this species and Enhydriodontines will remain obscure until either cranio-dental remains of *Semantor* are found, or post-cranial bones of *Sivaonyx* or *Enhydriodon* are discovered. The species is discussed here because de Muizon (1982) thought that it might be the sister taxon of *Potamotherium*, itself possibly the sister taxon of Lutrinae. The extremely short femur, elongated tibio-fibula and autopode indicate that its affinities probably lie with Pinnipedia, as was concluded by Orlov (1933).

European Enhydriodontini

Enhydriodon

For many years specimens from the lignite mines of Tuscany, Italy, were attributed to *Enhydriodon* (Forsyth Major, 1873; Meneghini, 1863). However, Hürzeler (1987; Hürzeler & Engesser, 1976) following observations by Lydekker (1884a, 1884b) Matthew (1929) and Pilgrim (1931, 1932) revealed that the material differed sufficiently greatly from this genus to warrant erection of a new one, *Paludolutra*, a view which has found general acceptance. Because of the close proximity of the protocone to the paracone in *Paludolutra*, the Tuscan genus does not belong to *Enhydriodon*, despite the fact that for many years it was included in it (Forsyth Major, 1873; Weithofer, 1888, 1889; Repenning, 1976). Furthermore, *Paludolutra* possesses three upper premolars, whereas most individuals of *Enhydriodon* possesses only two, and the third upper incisor

is large, but not as enlarged and canine-like as that of *Enhydriodon sivalensis*.

Pilgrim (1931) created the species *Enhydriodon* (?) *latipes* on the basis of some post-cranial remains of a large lutrine from Pikermi, Greece and Cucuron, France. The generic attribution of these fossils can only be determined when associated dental remains are discovered. They might represent *Paludolutra* rather than *Enhydriodon*. Thus on available evidence, the genus *Enhydriodon* does not occur in Europe. The Greek and French post-cranial remains are highly divergent from those of *Semantor macrurus* from Pawlodar, Western Siberia (Orlov, 1933).

Sivaonyx

In 1931, Pilgrim transferred to *Sivaonyx* a mandible from Eppelsheim, Germany, initially identified as *Lutra hessica* (Lydekker, 1890). By doing so, Pilgrim greatly expanded the known geographic range of the genus to include not only the Indian subcontinent, but also Europe. But because of the poor nature of the type specimen of *Sivaonyx bathygnathus*, it could not be demonstrated clearly that the European species was in fact similar to or different from the Indian one. Tobien (1955) for instance removed the German specimen from *Sivaonyx*. However, re-examination of the specimen in the Natural History Museum, London (NHM M 27486) reveals that it possesses the derived morphology of *Sivaonyx* such as the broad talonid with a raised rim on the lingual margin, and the mandible beneath m/1 deeper than the length of the m/1. Thus, even though the material is scanty, it supports Pilgrim's attribution of the specimen to *Sivaonyx*. Its morphology and dimensions are similar to those of *S. bathygnathus*, and it may in fact be a synonym of this species. Thus, out of all the fossils known from the Miocene of Europe, the only one that is likely to belong to *Sivaonyx* is the Eppelsheim jaw (*Sivaonyx hessicus*) (fig. 17).

The type specimen of *Sivaonyx lehmani* from Spain (Crusafont-Pairo & Golpe, 1962a, 1962b) a P4/, does not possess the enlarged parastyle which occludes with the accessory cusplet in the p/4 (Morales & Pickford, 2005a). Since this is an important functional adaptation in *Sivaonyx*, it is doubtful that the Spanish specimen can be kept in the genus *Sivaonyx*. Its protocone is close to the
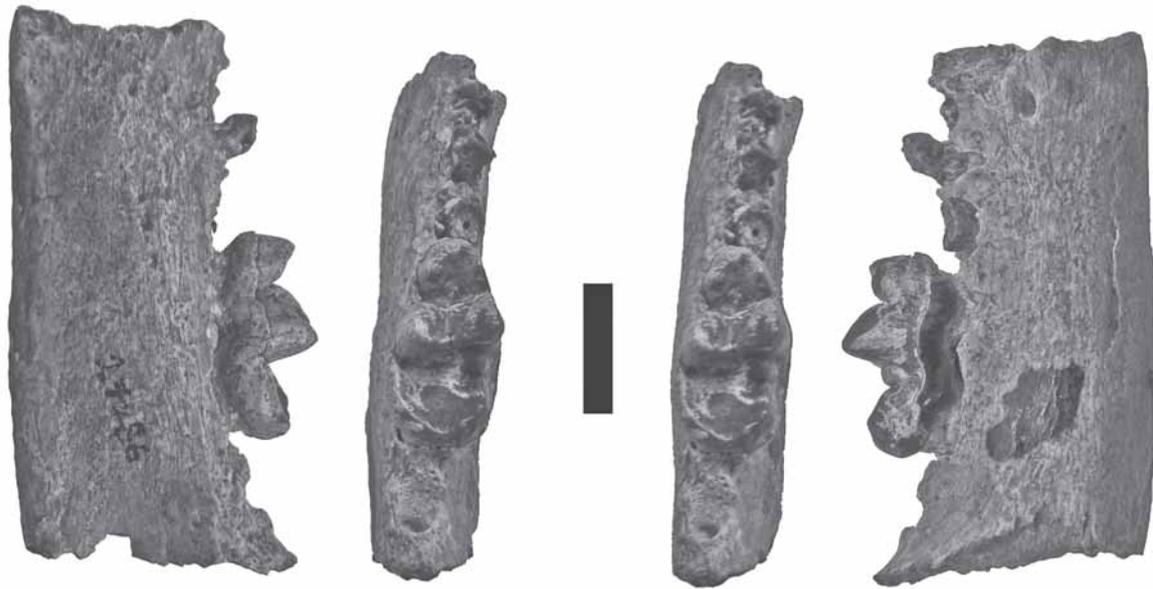
Fig. 17.—*Sivaonyx hessicus* (NHM M 27486) holotype right mandible containing m/1 from Eppelsheim, Germany (from left to right-lingual, stereo occlusal and buccal views) (scale bar : 10 mm).

paracone, unlike that of *Sivaonyx* in which the two cusps are separated by a wide valley. Its metastyle is somewhat inflated, unlike the more blade-like metastyle of *Sivaonyx*. The hypocone of the Spanish fossil is clearly behind the level of the paracone, and disto-lingual to the protocone, unlike the more anteriorly and buccally positioned hypocone in *Sivaonyx*. It is close in morphology to *Paludolutra maremmana* Hürzeler, 1987, but is slightly smaller. In particular, the protocone is close to the paracone and the valley between these cusps is narrow. The protocone is thus near the centre of the anterior margin of the tooth, rather than near the lingual margin. The post-protocone crest is developed into a large cusp separated from the protocone by a valley and is lingually positioned. The hypocone is enlarged but bucco-lingually compressed, and is oriented obliquely. The occlusal outline of the crown is thus more triangular than quadrangular. In all these respects the Spanish species is closely similar to *Paludolutra campanii*, and it probably belongs to this genus.

Paludolutra

Villalta & Crusafont-Pairo (1945) created the species *Enhydriodon lluecai* for a mandible from

Los Algezares, and later Crusfont-Pairo and Golpe-Posse (1962a) added material from Los Mansuetos and Concud, Spain, but the specimens differ markedly in morphology from *Enhydriodon* and agree more closely with *Paludolutra*. In 1962, Crusafont-Pairo & Golpe (1962b) created the species *Sivaonyx lehmani* on the basis of an isolated upper carnassial from Rambla de Valdecebro II, in the type sequence of the Turolian land mammal age of Spain, but this tooth differs markedly from the P4/ of *S. bathygnathus* and even from that of *Enhydriodon*, and probably represents the upper carnassial of *Paludolutra lluecai*.

Hürzeler & Engesser (1976) erected the genus *Paludolutra* for the species *Enhydriodon campanii* from the Late Miocene of Tuscany, Italy. Hürzeler (1978) added the species *Paludolutra maremmana* to the genus. Willemsen (1999) reduced the rank of *Paludolutra* making it a subgenus of *Enhydriodon*, but the differences in dental morphology are sufficient to indicate full generic differentiation, the view accepted by Morales & Pickford (2005a).

An interesting point about *Paludolutra campanii* concerns the upper canines, which possess a cingulum that is located well above the cervix, and that has a jagged edge, above which the crown enamel is unevenly and finely fluted (Hürzeler, 1987, fig. 4a)

akin to the morphology observed in *Potamotherium*. This feature suggests possible affinities between the two genera.

Tyrrhenolutra

Hürzeler (1987) erected the genus *Tyrrhenolutra* for fossil otters from Baccinello level V 1 (MN 12 Italy) and included it within the *Aonyx*-group, but also considered that it might be ancestral to *Paludolutra*. Willemsen (1992, Appendix) included this genus in the tribe Enhydrini, but excluded it from the phylogenetic schemas in the same paper (Willemsen, figs. 22, 24). However, in the text (Willemsen, 1992, p. 93) he wrote that «*If we consider* E. lluecai *ancestral to the* Paludolutra-*lineage from Tuscany, which is difficult to deny,* Tyrrhenolutra *has a somewhat isolated position The dentition is much less robust than in the* Enhydriodon/Paludolutra *forms. It might represent an earlier branch of the* Enhydriodon *group. Another possibility would be a relationship with* Paralutra». Its m/1 plots out in the range of metric variation of extant *Amblonyx cinereus*, suggesting that it was probably preying on shellfish (fig. 16). In view of the uncertain status of this genus, it is not included in the Enhydriodontini as defined in this paper, even though McKenna & Bell (1997) classified it in the Enhydrini. *Tyrrhenolutra* is not related to *Torolutra* from East Africa (Petter *et al*., 1991) which was a piscivorous otter with narrow m/1 (fig. 16) (Morales *et al*., 2005).

African Enhydriodontini

Vishnuonyx

Morales & Pickford (2005b) described an upper carnassial of *Vishnuonyx* from the Middle Miocene Ngorora Formation of Kenya (figs. 18, 19). This genus was already listed by Hill *et al*. (1985) but its material basis was never described. The Ngorora fossil is closely allied to the type species *Vishnuonyx chinjiensis*, and its presence in deposits of similar age to those where it has been reported in the Indian subcontinent reveals that the tribe Enhydriodontini was widespread even during the early stages of its existence.

Werdelin (2003b) described an isolated right P4/ (KNM LT 23948) from the Lower Nawata Forma-

tion, Lothagam, Kenya, and attributed it to *Vishnuonyx*. The specimen is similar in size to P4/s of *Sivaonyx bathygnathus* (fig. 13) from which it differs in minor ways. The hypocone is slightly less lingually positioned than in the P4/ of this species described by Pilgrim (1932), in this respect being more similar to specimen GSI K 13.14 and to the P4/ of *Sivaonyx gandakasensis*. The enlarged parastyle of the Lothagam specimen which is about half the height of the paracone, is similar to that of the Indian species of *Sivaonyx*, and different from the low parastyle in the P4/ of *Vishnuonyx chinjiensis* (fig. 3), which reveals that the Kenyan species was engaged on the trend towards cusp enlargement and enhanced bunodonty that is well expressed in Indian species of *Sivaonyx* and only in an incipient way in *Vishnuonyx*. The lingual shelf behind the protocone terminates beneath the metacone slightly further back than it does in *Vishnuonyx chinjiensis*, whereas in *S. bathygnathus* it ends further to the rear (fig. 9). Thus, whereas this tooth has some resemblance to *Vishnuonyx*, in terms of derived morphology of the parastyle, the slightly expanded lingual shelf, and the strength and position of the hypocone, it is considered more likely to represent *Sivaonyx* than *Vishnuonyx*. Additional material is required to settle the matter in a satisfactory way. The Lothagam tooth is intermediate in age between *Sivaonyx gandakasensis* and *Sivaonyx bathygnathus* (fig. 18).

Sivaonyx

The genus *Sivaonyx* is represented in Northern, Eastern and Southern Africa where several species of various sizes occur (Hendey, 1978; Howell, 1972; Morales *et al*., 2005; Morales & Pickford, 2005a; Stromer, 1920). An isolated and slightly damaged left m/1 from Wadi Natrun (Stromer, 1920, figs. 11, 11a) has the broad talonid with a raised lingual rim and the complete buccal cingulum typical of *Sivaonyx* species (fig. 11C). This tooth, which was attributed to *Lutra* aff? *capensis* by Stromer (1920) is similar in dimensions and morphology to *Sivaonyx ekecaman* from Kanapoi and Sagatia, Kenya (Morales & Pickford, 2005a; Werdelin, 2003a).

Pilgrim (1932) mentioned an otter m/1 from Wadi Natrun, Egypt, attributed by Stromer (1920) to *Lutra* aff. *hessica*. If the species determination were correct, then this would suggest the presence
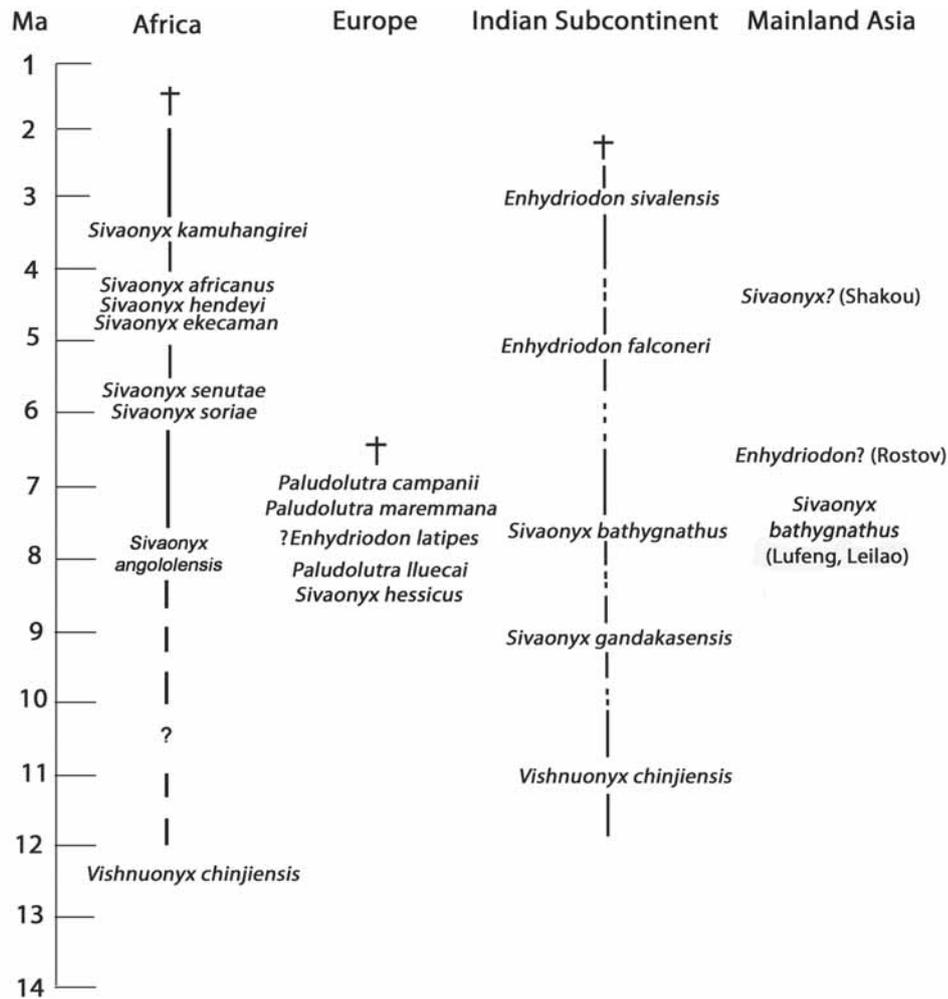
Fig. 18.—Résumé of the geochronologic distribution of African, European and Asian bunodont otter-like mammals.

of the genus *Sivaonyx* at the site, since *S. hessicus*, the Eppelsheim species, likely belongs to this genus. However, the talonid in the Egyptian specimen (Stromer, 1920, figs. 10, 10a) is short and narrow and has no lingual cusplet, and it is more likely that this particular tooth belongs to *Torolutra*, rather than to *Sivaonyx*. The tooth is 16.8 x 9.5 mm which is close in dimensions to *Torolutra ougandensis* (Petter *et al*., 1991). An otter mandible from Wadi Natrun (Egypt) first described by Stromer (1913) as *Lutra libyca*, is much smaller than *Torolutra ougandensis* (dimensions of m/1 : 11.6 x 6 mm) and it is indeed likely to belong to *Lutra* judging from the shape of the trigonid and the short talonid without a lingual talonid cusp. Its m/1 plots out at

the small end of the range of variation of *Lutra lutra*. There were thus three species of otter at Wadi Natrun, two piscivores, and one molluscivore.

Enhydriodon was first reported from Africa by Stromer (1931) on the basis of a mandible and upper molar from Late Miocene deposits at Klein Zee, Namaqualand, South Africa (figs. 18, 19). The species *Enhydriodon africanus* has long been accepted as a genuine member of the genus. In 1974, Hendey described important specimens from Langebaanweg, South Africa, which he took to confirm the presence of the genus in South Africa (bicuspid p/4, protocone of P4/ well separated from the paracone, etc.) but the ensemble has recently been transferred to the genus *Sivaonyx* by Morales
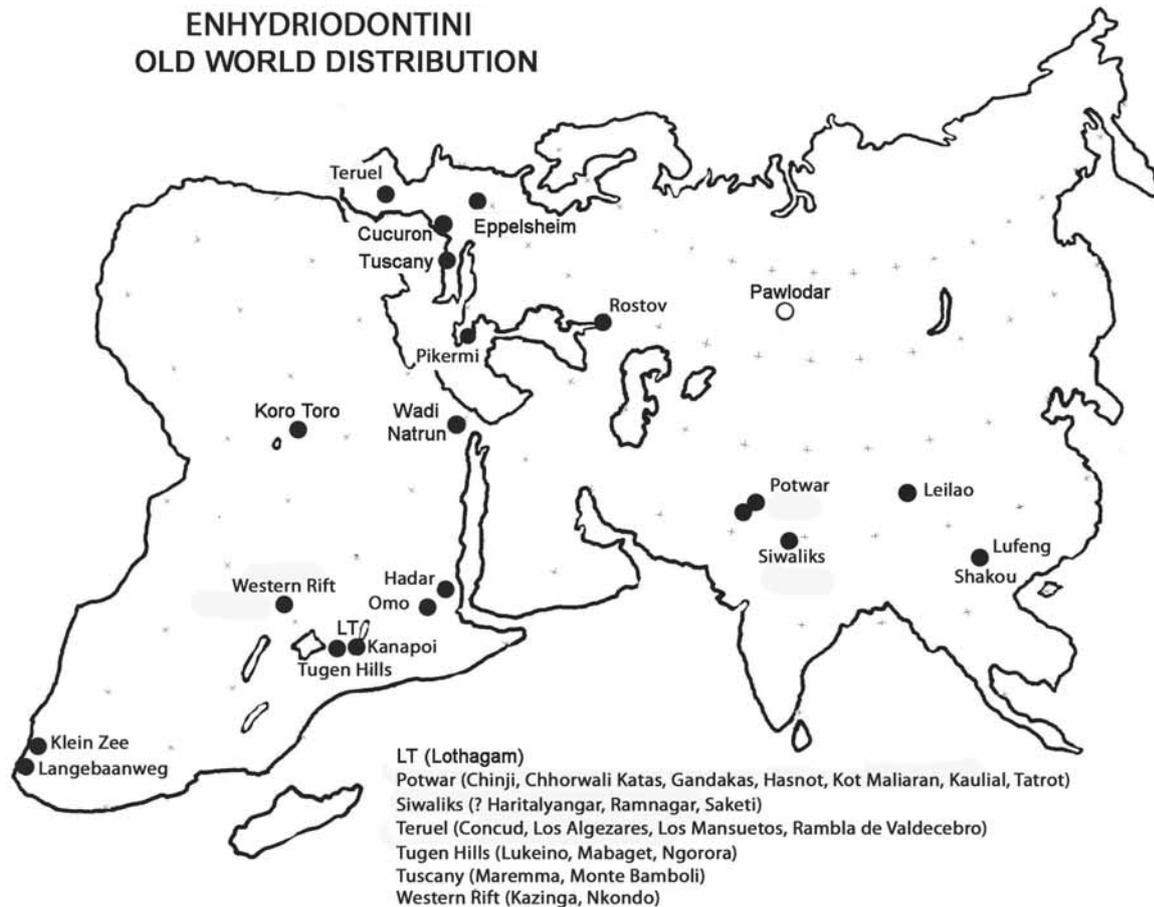
Fig. 19.—Old World geographic distribution of Neogene and Quaternary bunodont otter-like mammals. Pawlodar is the type locality of *Semantor macrurus*, of which the dentition is unknown but which might possibly be remotely related to *Enhydriodon* (de Muizon, 1982). Pikermi and Cucuron yielded postcranial remains which Pilgrim (1931) attributed with hesitation to *Enhydriodon*.

& Pickford (2005a) on the basis of the morphology of the P4/ and m/1.

Enhydriodon has been reported from several localities in East Africa (Haile-Selassie *et al*., 2004; Howell & Petter, 1976, 1979; Patterson *et al*., 1970; Petter *et al*., 1991; Pickford, 1975) (figs. 18, 19) but until recently no detailed descriptions were published. Werdelin (2003a) described the fossils from Kanapoi, Kenya, and Morales & Pickford (2005a) provided descriptions of material from Baringo District, Kenya, and the Western Rift Valley, Uganda, while Petter (in Geraads *et al*., 2004) described a specimen from Melka Kunturé, Ethiopia, that she used to create the species *Enhydriodon aethiopicus*. However, the latter record, along with material from Omo (Howell & Petter, 1976) attributed to the same species, turns out to belong to *Pseudocivetta ingens*, a Viverridae (Morales & Pickford, 2005a). Fossils from Kanapoi described by Werdelin (2003a) as *Enhydriodon ekecaman* were transferred to the genus *Sivaonyx* by Morales & Pickford (2005a). Giant otters have been reported to occur in Chad (Brunet *et al*., 1998) but details have not yet been published.

American fossil bunodont otters

Although there have been reports of the presence of *Enhydriodon* in California (Repenning, 1976) and Florida (Berta & Morgan (1985) (fig. 20) the fossils were said to be more similar to the Spanish
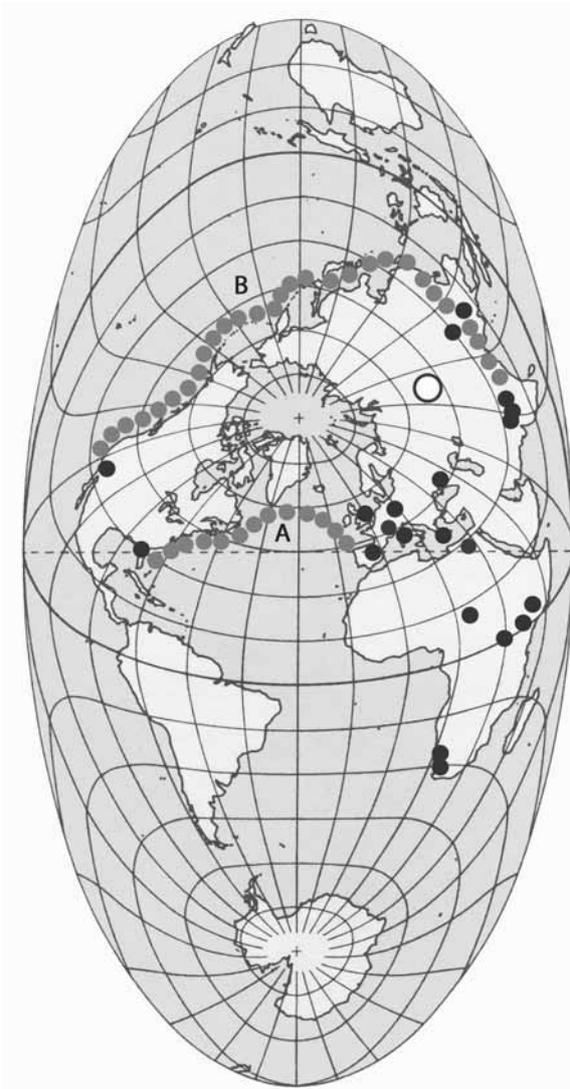
Fig. 20.—Distribution of Mio-Pliocene and Pleistocene bunodont otter-like mammals in the Old and New Worlds. Bartholomew's Atlantis Projection (Equal Area) on which alternative dispersal pathways can be appreciated A) the Circum-Atlantic route between Spain and Florida (Berta & Morgan, 1985) and B) the Indo-Pacific northern rim between India-China and California via the Aleutian-Bering sector (Repenning, 1976). (Black dots – fossil bunodont lutrine localities; grey dots – possible dispersal pathways). (Pawlodar (open circle) yielded *Semantor* which has been interpreted as possibly being quite closely related to *Enhydriodon* (de Muizon, 1982)).

Enhydriodon lluecai (=*Paludoloutra lluecai*) than to either *E. sivalensis* or *E. falconeri* (Alcala, 1994; Berta & Morgan, 1985; Willemsen, 1999). Berta & Morgan created the genus *Enhydritherium* for these otters, and included the Spanish species *lluecai* in

it. Inspection of the figures in Berta & Morgan (1985) and Lambert (1997) reveal that the lower carnassials of *Enhydritherium* are more bunodont than those of *Paludolutra lluecai* and that the trigonid of the m/1 is shorter relative to the talonid, which possesses a higher lingual rim than in the Spanish species. In contrast, Repenning (1976) made a logical case that some of the Californian material, especially the P4/ UCMP 32972 (fig. 21) was closer to what is now known as *Paludolutra lluecai* than it is to any of the Indian specimens attributed to *Sivaonyx* or *Enhydriodon* and this indeed appears to be the case, save for the fact that the Californian species has a deep incision between the paracone and metacone, and the European species does not. A question that arises is whether the Californian material really belongs to *Enhydritherium terraenovae*. The P4/ from the partial skeleton found at the Moss Track Racetrack site in Florida attributed to the latter species (Lambert, 1997) is poorly preserved and deeply worn, and it is difficult to make a convincing case that it is the same as the Californian fossil.

The isolated tooth attributed to *Enhydriodon* sp. nov., by Repenning (1976) (USNM 184083) (fig. 21B) is larger and more bunodont that the one that he identified as *E.* cf *lluecai* (UCMP 32972) but the layout of the cusps is similar in the two, and differs from the situation in *E. sivalensis*. Its parastyle is reduced whereas that of *Enhydriodon* is large. The hypocone is small and is located far from the lingual edge of the tooth and to the bucco-distal side of the post-protocone cusp, whereas in *Enhydriodon,* the hypocone is the largest cusp in the tooth, and its base forms the lingual margin of the crown. The post-protocone cusp in the Californian specimen is as large or larger than the hypocone and is almost the same size as the protocone, but in *Enhydriodon*, this cusplet is considerably smaller than the hypocone and protocone. Finally, the paracone and metacone form a blade in *Enhydriodon*, but are separated by an incision in USNM 184083. The two bunodont lutrines from California, (UCMP 32972; USNM 184083) are, in my opinion, more closely related to *Paludolutra* than to *Enhydriodon*, but resolution of their status requires more substantial fossils.

It should be noted that de Muizon (1982, fig. 6) considered that the large antero-lingual cusp in USNM 184083 (fig. 21) was a mastoidized 'lingual cusp of the lutrine crest' that is separated from the paracone by a valley, that the central of the three

lingual cusps was the protocone, and that the distal one was the hypocone. If this interpretation is correct, then the cusp layout would be markedly different from that in *Sivaonyx* and *Enhydriodon*, both of which retain a crest-like 'lutrine crest' attached to the paracone, a large anteriorly positioned protocone, the post-protocone crest of which gives rise to secondary cusplets distolingually which are separated from the hypocone by a valley. Thus, even though both genera possess mastoid cusps in the P4/, the mastoidization in the two is not homologous.

The relationships between the extant sea otter, *Enhydra lutris*, and fossil otters such as *Enhydritherium terraenovae* from North America and *«Enhydra» reevei* from England (Newton, 1890; Willemsen, 1990) (fig. 21F) remain to be elucidated satisfactorily, even though the question has been evoked by many authors ever since Pohle (1919). The description of a fossil species, *Enhydra macrodonta*, from the Late Pleistocene of California (Kilmer, 1972) does not throw much light on the matter (Estes, 1980).

Interpretations by Berta & Morgan (1985) de Muizon (1982) Lambert (1997) and Willemsen (1992) supported a sister group arrangement between the Californian fossils and *Enhydriodon*, a suggestion already made by Pohle (1919) for the extant sea otter and *«E.» reevei*. If there is a relationship between *Enhydra lutris* and *«Enhydra» reevei*, then it is a remote one. In *E. lutris* the metaconid of the m/1 is the largest of the trigonid cusps and the paraconid is reduced, whereas in *«E.» reevei* the protoconid is the largest cusp in the trigonid (fig. 21F) and the paraconid is not greatly reduced. The hypoconid dominates the talonid in the m/1 of *Enhydra*, extending across the midline three quarters of the way towards the lingual margin of the tooth, whereas in *«E.» reevei*, the hypoconid is small and is confined to the buccal rim of the talonid, and it is the lingual talonid cusplet that is enlarged. It is perhaps more likely that *«Enhydra» reevei* is closer phylogenetically to *Sivaonyx* than to either *Enhydra* or *Enhydriodon*.

In the P4/ of *Enhydra*, the incision between the paracone and metacone is present, despite the advanced mastoidization of the cusps, in contrast to the same tooth in *Enhydriodon*, *Sivaonyx* and *Paludolutra* in which the incision is reduced such that the paracone and metacone form a blade-like cusp. Furthermore, *Enhydra* does not possess a hypertrophied third upper incisor like that of *Enhydrio-*
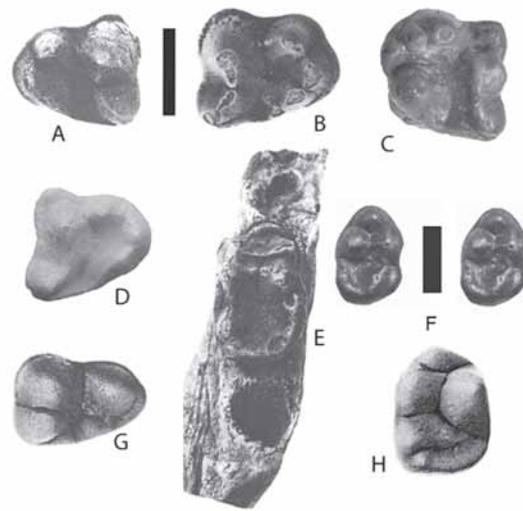

Fig. 21.—Comparison of upper and lower carnassials of North American and Eurasian bunodont otter-like mammals in occlusal view. A) *Enhydritherium terraenovae* left P4/ (UCMP 32972); B) *Enhydriodon* sp. nov. right P4/ (USNM 184083); C) holotype left P4/ of *Enhydriodon falconeri* (NHM M 4847); D) *Paludolutra lluecai* right P4/ from Concud, Spain; E) *Enhydritherium terraenovae*, left mandible containing m/1 (UCMP 32970); F) *«Enhydra» reevei*, right m/1 from England; G) *Enhydra lutris* right P4/; H) *Enhydra lutris* left m/1 (A, B, E-H are modified from Repenning, 1976) (scale bar : 10 mm).

don, an important feature of the Indian genus, probably related to the processing of prey items (see above). For these reasons, it is considered that there is not a particularly close relationship between these North American and Eurasian bunodont otter lineages, represented in fig. 23 by the decision to classify the North American forms in a different tribe from the Old World ones.

In Willemsen's (1992) schema, *Vishnuonyx chinjiensis* represents the beginning of a radiation which gave rise to three lines, one in the Indian subcontinent (*Sivaonyx bathygnathus*, *Enhydriodon falconeri*, *Enhydriodon sivalensis*), one in Europe (*Enhydriodon lluecai*, *Enhydriodon maremmana*, *Enhydriodon campanii*) and a third in North America (*Enhydriodon* cf *lluecai* from California, *Enhydriodon* sp. nov. from California, and *Enhydra lutris*). At heart, the question is whether the bunodont dentitions of the North American otters evolved convergently with those of the Old World or whether the similarities in morphology and dimensions represent shared derived characters. Until this question can be reasonably answered, then hypotheses about dispersal pathways - Circum-Atlantic (Spain

to Florida : Berta & Morgan, 1985) or Bering Straits (India to California, via China : Repenning, 1976) or both – will be difficult to support (fig. 20).

Origin of the Enhydriodontini

The origin of the Enhydriodontini is as murky as that of the subfamily Lutrinae. Historically, many authors have included late Oligocene *Potamotherium* Geoffroy, 1833, in the Lutrinae (Matthew, 1929; Savage, 1957) but Willemsen (1992) discussed the question in depth and showed that this was far from being firmly established. Matthew (1929) considered that *Enhydriodon* was not a true lutrine, and that therefore it could not be closely related to *Potamotherium* which he did consider to be a lutrine. De Muizon (1982) proposed a closer phylogenetic relation of the Lutrinae with the Mephitinae and Mustelinae than with Melinae, and proposed that Phocidae, rather than Lutrinae, might be descended from a *Potamotherium*-like form (de Muizon, 1982, fig. 1; Savage, 1957). With the recent distancing of *Potamotherium* from Lutrinae (*sensu stricto* = Lutrini + Aonychini) the relationship between the latter genus and enhydriodontines warrants re-investigation.

Re-examination of *Potamotherium* specimens from St-Gérand-Le-Puy suggests that it represents a form that could be related to enhydridontines. Such a possibility was strongly denied by Matthew (1929) on the grounds that *Potamotherium* was an otter, whereas he argued that *Enhydriodon* was not, but then, if *Potamotherium* is not an otter, then it could, after all, be related to *Enhydriodon*. The lengthy span of time (some 8-10 million years) that separates *Potamotherium* from the earliest known enhydriodontine means that details of the transition, if indeed it represents the ancestral group, will be difficult to determine. The mandible would have to become more robust, the m/2 would have to be raised above the level of the talonid of the m/1, and the post-protoconid cusp in p/4 would have to shift buccally (fig. 22). Unlike most otters, the talonid of m/1 of *Potamotherium valletoni* from St-Gérand-Le-Puy possesses a raised lingual rim forming a separate cusplet, in a position analogous to the lingual talonid cusp in *Vishnuonyx* and *Sivaonyx*.

In the upper dentition there are several features that attract our attention. The P4/ of *Potamotherium* has a more developed internal talon than occurs in

Paralutra (Ginsburg, 1968) and in unworn specimens it sometimes forms a low cusp separated from the protocone by a shallow valley (fig. 22) (in worn specimens the distinction between these two cusps is not always evident as they fuse together into a single facet quite early in wear, suggesting that the diet of the genus was quite abrasive, possibly including crabs) (Savage, 1957). This low post-protocone cusplet is located on the lingual margin of the crown as in *Vishnuonyx* and *Sivaonyx* and as such it could announce the development of the distinct cusplet (hypocone) that typifies enhydriodontines. However, the P4/ of *Potamotherium* is much broader bucco-lingually relative to crown length than that of *Vishnuonyx*. Also as in enhydriodontines, the parastyle in the P4/ of *Potamotherium* is enlarged and well separated from the paracone and there is a distinct lutrine crest (de Muizon, 1982). The I3/ of *Potamotherium* is substantially larger than the first and second incisors (Savage, 1957, fig. 2). Could this upper incisor heteromorphy presage the grossly enlarged I3/ which occurs in *Enhydriodon* (condition unknown if *Sivaonyx* and *Vishnuonyx*)? The canines of *Potamotherium* are characterised by an unusual basal collar or cingulum which has a jagged margin that is some distance above the cervix, and is closer to the apex anteriorly than posteriorly. Extant otters do not possess such a cingular structure, and the condition in most enhydriodontines is unknown. However, the Tuscan species *Paludolutra campanii* has a somewhat similar canine morphology (Hürzeler, 1987) which could provide evidence of relationship to *Potamotherium*. These possibilities can only be addressed satisfactorily when the fossil record of Early and Middle Miocene otter-like carnivores improves. What does appear plausible is that the separation between Enhydriodontini on the one hand, and the Lutrini + Aonychini on the other, possibly occurred during the Oligocene. A résumé of the various groups of otter-like mammals is provided in fig. 23, which reveals that there is still alot to be determined concerning the details of enhydriodontine and lutrine phylogeny.

It is worth mentioning that *Semantor macrurus* from the Latest Miocene (possibly MN 13 or MN 14) of Western Siberia (Orlov, 1933; 1936) was located on de Muizon's cladogram (de Muizon, 1982, fig. 1) as a potential sister taxon to *Potamotherium*, both being classified by him in the Semantoridae, next to Phocidae on the one hand (more derived), and *Enhydra + Enhydriodon*, on the other (more primitive). *Semantor* is represented only by
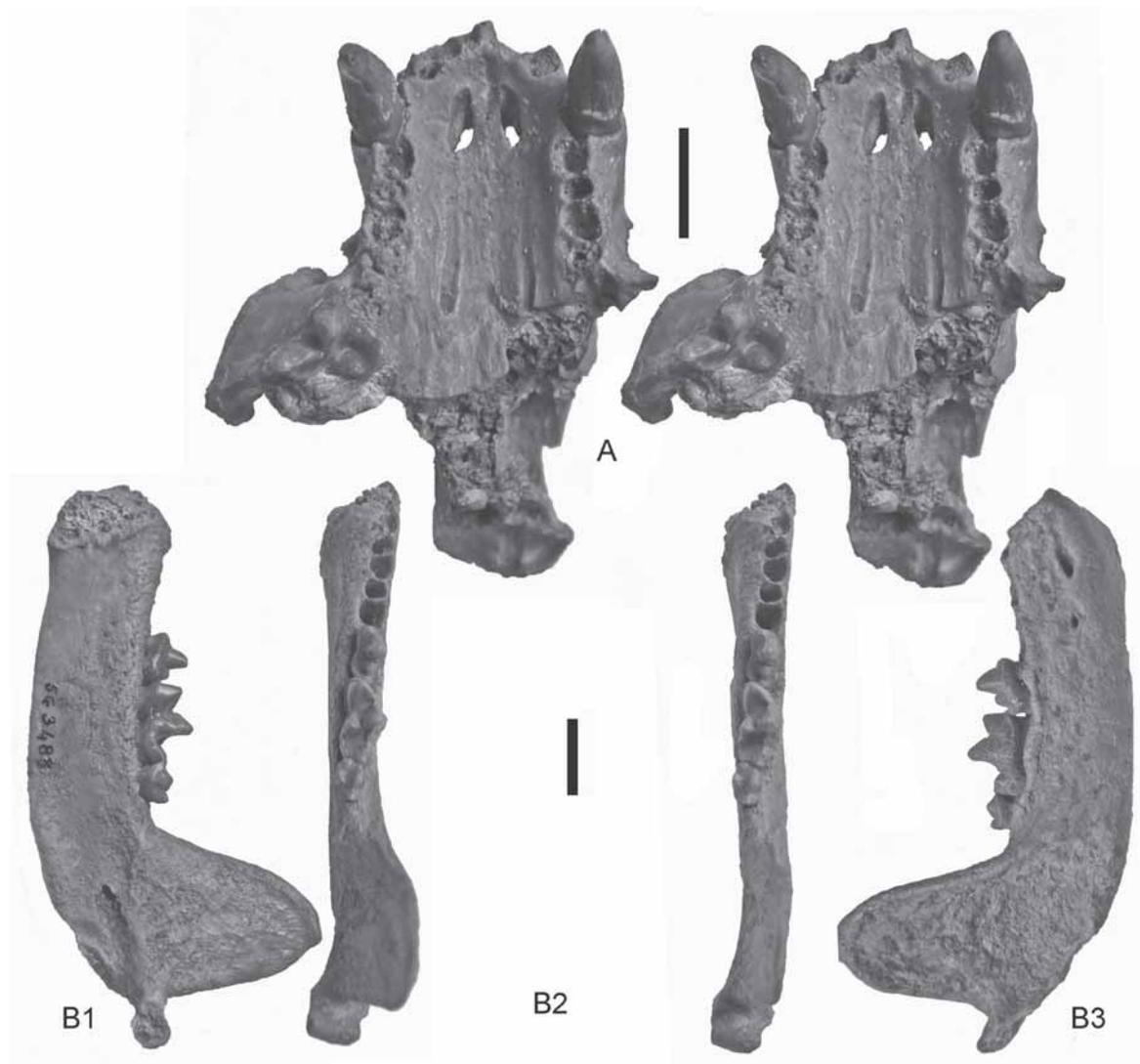
Fig. 22.—*Potamotherium valletoni* from St-Gérand-Le-Puy, France, A) snout (MNHN SG 3487) in stereo palatal view, B) mandible (MNHN SG 3488) right mandible in B1) lingual, B2) stereo occlusal and B3) buccal views (scale = 10 mm).

the sacrum, pelvis, hind limbs and caudal vertebrae, and it is therefore not possible to compare directly with *Enhydriodon* which is known only from cranio-dental remains. The little post-cranial evidence that is available for *Sivaonyx hendeyi* (Hendey, 1978) indicates that it and *Semantor macrurus* possessed widely divergent femoral morphology from which it is deduced that enhydriodonts and semantorids are not likely to be as closely related as implied by de Muizon (1982).

For Willemsen (1992) the oldest known lutrine is *Mionictis* from MN 4-5 of Europe (Ginsburg, 1968)

a genus represented in North America by three species (*M. letifer*, Cook & MacDonald, 1962; *M. elegans*, Matthew, 1924 and *M. incertus* Matthew, 1924). Old World species of *Mionictis* were transferred to two genera, *Adroverictis* and *Lartetictis* by Ginsburg & Morales (1996) and classified in Melinae. *Mionictis* is unlikely to be ancestral to enhydriodontines because it does not possess a p/1 (present in *Vishnuonyx* and *Sivaonyx*) and the trigonid of m/1 is wide open lingually, the metaconid slopes distally rather than being almost vertical and the post-protoconid cusp seems to be vestigial or
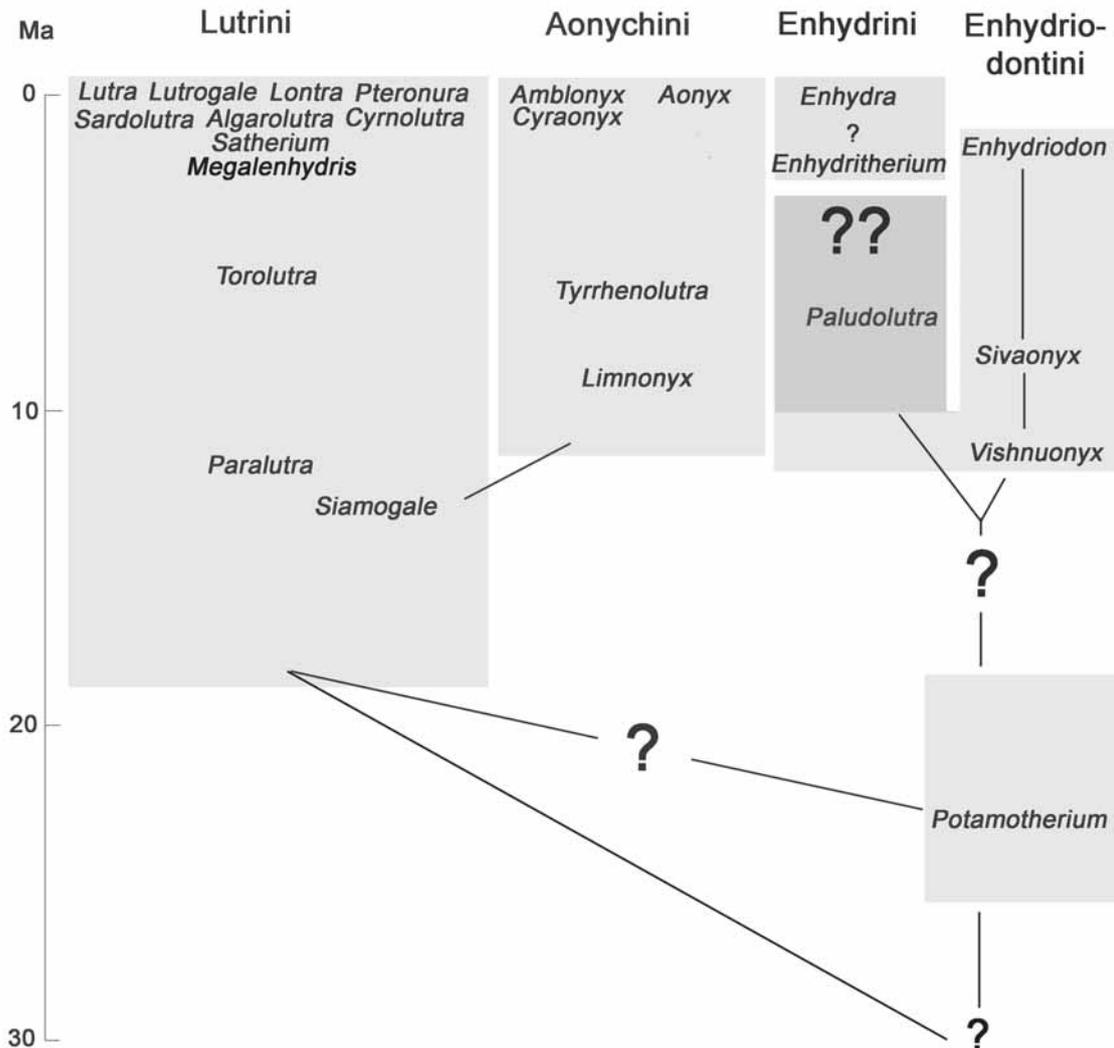
Fig. 23.—Hypothesis of groups of Neogene and Quaternary otter-like carnivores. The Enhydriodontini seem to have been distinct since at least the late Middle Miocene. *Vishnuonyx* shares some dental features with *Potamotherium*, as does *Paludolutra*. A dichotomy is hypothesised to have occurred in this tribe during the Middle Miocene, between the *Vishnuonyx - Sivaonyx - Enhydriodon* lineage on the one hand, and the *Paludolutra* lineage on the other. The relationship of *Enhydritherium* to Enhydriodontini is far from certain. Most authors have linked *Enhydra* with *Enhydriodon* on the basis of the mastoidisation of its cheek teeth, but cusp homology suggests that mastoidization occurred independently in the New World and Old World groups, reflected in the decision to classify it and *Enhydritherium* in the tribe Enhydrini rather than Enhydriodontini. True otters (Lutrini) have a longer fossil record than Enhydriodontini, and Aonychini a shorter fossil record than Lutrini. The large number of genera of Lutrini in the Pleistocene and Recent is due partly to the high diversity found in the Mediterranean Islands. Gaps in the fossil record hinder interpretation of the relationships between and within the groups.

absent. *Mionictis*, as was pointed out by Willemsen (1992) has a number of meline characters in the dentition, which was one of the reasons why Ginsburg (1968) originally classified it in the Melinae. Later (Ginsburg *et al*., 1983) it was transferred to the Lutrinae, a move accepted by Willemsen (1992) on the basis of the «*many characters in common with* Paralutra». *Paralutra jaegeri*, the oldest known member of the genus, is unlikely to represent the ancestor of *Vishnuonyx* as it is too young geologically to fulfil this role (Helbing, 1936). The dentition of other species of *Paralutra*, such as *Paralutra garganensis* Willemsen (1983) is substantially different from that of any enhydriodontine.

Another possible descendent of *Mionictis* is *Siamogale*. *Siamogale thailandicus* (Ginsburg *et al.*, 1983) is suitably positioned chronologically and geographically to have played a role in the evolution of *Vishnuonyx* but its m/1 is low crowned and elongated with a long talonid, it has a long metaconid sloping posteriorly and the enamel is heavily wrinkled. Such morphology contrasts strongly with that of the m/1 in *Vishnuonyx*, in which the trigonid is high, the m/1 not particularly elongated, with the metaconid almost vertical posteriorly and the enamel smooth to lightly wrinkled, and it is concluded that the two genera are not closely related.

Conclusions

Recent fossil discoveries in the Indian Sub-continent and Africa have increased the sample of Mio-Pliocene bunodont otter-like mammals available for study. Because difficulties have been encountered concerning the taxonomy of these mustelids (some type material is inadequate) it was necessary to re-examine the fossils from Indo-Pakistan where three of the genera were originally defined. This revision throws light on aspects of the taxonomy of the tribe Enhydriodontini, but does not resolve all the nomenclatural problems, which can only be achieved with an improvement of the fossil record. A new species of *Sivaonyx* is created for otter-like fossils from the base of the Late Miocene of Pakistan, which are morphometrically intermediate between *Vishnuonyx chinjiensis* from Chinji levels, on the one hand, and *Sivaonyx bathygnathus* from the end of the Late Miocene, on the other (fig. 18). By the very end of the Miocene, the molluscivorous lineage *Enhydriodon* evolved and then persisted until the end of the Pliocene, after which it went extinct. In Africa, *Sivaonyx* increased in body size and developed extremely bunodont dentitions independently of *Enhydriodon*.

The evolution of the Enhydriodontini encompassed several trends. Firstly there was an increase in body size with the passage of geological time (fig. 13) beginning with the small species *Vishnuonyx chinjiensis* from the end of the Middle Miocene, which was about the same dimensions as the Asian small-clawed otter, *Amblonyx cinereus* which has a body weight of about 3 kg, culminating in the giant species *Enhydriodon sivalensis* the skull of which was about the size of a wolf's (*Canis lupus*) and it could have weighed 25

kg or more. In between these extreme forms there occurred two species of *Sivaonyx*, *S. gandakasensis* from the base of the Late Miocene, and *S. bathygnathus* from the later part of this epoch (fig. 18) and *Enhydriodon falconeri*. The dental evidence indicates that the augmentation in body size was accompanied by a change in diet, with the Middle Miocene species being predominantly piscivorous, but including some crustaceans and molluscs in its diet, followed by the genus *Sivaonyx* which was probably a more committed carnivore, and ending with the genus *Enhydriodon*, which was predominantly a molluscivore with the robust dentognathic equipment and sufficient muscle power capable of opening bivalve shells using the front teeth and not having to leave them on land to open in the sun.

What is still not clear from the fossil record, is the group from which enhydriodontines evolved. Perhaps the most plausible ancestor from morphological and chronological points of view is *Potamotherium*, an Oligocene otter-like carnivore, often included in Lutrinae, but more recently affiliated with other mustelid subfamilies and even with Phocidae (de Muizon, 1982). If this suggestion proves to be correct, then the divergence between enhydriodontines and other otters (Lutrini, Aonychini) may have taken place during the Oligocene, or earlier (fig. 23).

Enhydriodontini were widespread from Middle Miocene time onwards, being represented in Africa and the Indian Subcontinent about 13-12 Ma (figs. 18, 19). From the end of the Middle Miocene their history in India is more complete than it is in Africa, where few Late Miocene localities have yielded otters. However, fossil enhydriodontines belonging to the genus *Sivaonyx* have been collected in North Africa from deposits of basal Pliocene age and from East Africa from deposits ranging in age from 6 – 2 Ma. The largest described African species, *S. kamuhangirei*, defined on the basis of fossils from the Western Rift Valley, Uganda, was considerably larger than the largest species known from India, *Enhydriodon sivalensis*, and its body weight could have exceeded 100 kg. It is expected that some of the undescribed Late Pliocene forms from Ethiopia (Howell & Petter, 1979; Werdelin & Lewis, 2005; Wynn *et al.*, 2006) represented by very large post-cranial remains, would have been even larger than *S. kamuhangirei*.

Enhydriodontines seem to have been tropical to subtropical in their distribution, since, apart from records in Germany (ca 50°N) and another in sout-

hern Russia (ca 47°N) they have not been reported at latitudes further north than 35°30'N (fig. 19). Even in the case of *Sivaonyx hessicus* from Germany, it is likely that, at the time (ca 9 Ma) this part of the world enjoyed a sub-tropical climate, as did southern Russia at the end of the Miocene (ca 8-7 Ma) and the same was the case for the Chinese deposits that have yielded *Sivaonyx* (Liu & Pickford, 2007).

ACKNOWLEDGEMENTS

References

Alcala, L. (1994). *Macromamiferos neógenos de la fosa de Alfambra-Teruel*. Instituto de Estudios Turolenses-Museo Nacional de Ciencias Naturales, CSIC, 554 p.

Barry, J., Johnson, N., Raza, S.M. & Jacobs, L. (1985). Neogene mammalian faunal change in southern Asia : Correlations with climatic, tectonic, and eustatic events. *Geology*, 13: 637-640.

Barry, J., Lindsay, E. & Jacobs, L. (1982). A biostratigraphic zonation of the Middle and Upper Siwaliks of the Potwar Plateau of Northern Pakistan. *Palaeogeogr. Palaleoclimat. Palaeoecol*. 37: 95-130.

Berta, A. & Morgan, G.S. (1985). A new sea otter (Carnivora, Mustelidae) from the Late Miocene and Early Pliocene (Hemphillian) of North America. *J. Paleontology*, 59: 809-819.

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

Bose P.N. (1880). Undescribed fossil carnivores from the Sivalik Hills in the collection of the British Museum. *Quart. J. Geol. Soc. London*, 36: 119-136.

Brunet, M., Beauvilain, A., Geraads, D., Guy, F., Kasser, M., MacKaye, H., MacLatchy, L., Mouchelin, G., Sudre, J. & Vignaud, P. (1998). Tchad: découverte d'une faune de mammifères du Pliocène inférieur. *C. R. Acad. Sci. Paris*, 326: 153-158.

Butler, J. (1994). Cape clawless otter conservation and a trout river in Zimbabwe : a case study. *Oryx*, 28: 276-282.

Carter, S. & Rosas, F. (1997). Biology and conservation of the Giant Otter, *Pteronura brasiliensis*. *Mammal Review*, 27: 1-26.

Chow, M.C. (1961). The discovery of *Enhydriodon* at Yuanmo and its application toward the correlation of Late Tertiary Mammal-bearing sediments in Eastern Yunnan Province. *Vertebrata PalAsiatica*, 19: 164-167.

Colbert, E.H. (1935). Siwalik Mammals in the American Museum of Natural History. *Trans. Amer. Philos. Soc.* 28: 1-401.

Cook, H.C. & MacDonald, J.R. (1962). New Carnivora from the Miocene and Pliocene of western Nebraska. *J. Paleontology*, 36: 560–567.

Crusafont-Pairo, M. & Golpe, J.-M. (1962a). Présence dans le Miocène d'Espagne de Mustélidés connus à l'est sur les bords de la Tethys. *C. R. Acad. Sci. Paris*, 254: 2807-2809.

Crusafont-Pairo, M. & Golpe, J.-M. (1962b). Nuevos hallazgos de lútridos aonicoides (*Sivaonyx*, *Enhydriodon*) en el Pikermiense Español (Cuenca de Teruel). *Notas Comm. Inst. Geol. Min. Esp*. 67: 5-16.

De Muizon, C. (1982). Les relations phylogénétiques des Lutrinae (Mustelidae, Mammalia). *Geobios Mém. Spec*., 6: 259-277.

Donnelly, B. & Grobler, J. (1976). Notes on food and anvil using behaviour by the Cape clawless otter, *Aonyx capensis*, in the Rhodes Matopos National Park, Rhodesia. *Arnoldia, Rhodesia*, 7: 1-8.

Eisenberg, J. (1989). *Mammals of the Neotropics*. Vol. 1, University of Chicago Press, Chicago, 550 p.

Emmons, L. (1990). *Neotropical Rainforest Mammals : A Field Guide*. University of Chicago Press, Chicago, 295 p.

Estes, J. (1980). *Enhydra lutris*. *Mammalian Species*, American Society of Mammalogists, 133: 1-8.

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.

Falconer, H. & Cautley, P.T. (1835). Synopsis of fossil genera and species from the upper deposits of the Tertiary strata of the Sewalik Hills, in the collections of the authors. *J. Asiatic Soc. Bengal*, 4: 707.

Forsyth Major, C. (1873). Les faunes des vertébrés de Monte Bamboli (Maremmes de la Toscane). *Atti Soc. Ital. Sci. Nat*. 15: 290-303.

Foster-Turley, P. (1992). Conservation aspects of the ecology of Asian small-clawed otters on the Malay Peninsula. *International Union for the Conservation of Nature, Otter Specialist Group Bulletin*, 7: 26-29.

Geraads, D., Eisenmann, V. & Petter, G. (2004). The large mammal fauna of the Oldowan of Melka Kunture. *Studies on the Early Paleolithic Site of Melka Kunture, Ethiopia*. 2004: 169-192.

Geoffroy, E., St Hillaire (1833). Considérations sur les ossements fossiles de l'Auvergne. *Revue encyclopédique*, 59: 80.

Ginsburg, L. (1968). Les mustélidés piscivores du Miocène français. *Bull. Mus. Nat. Hist. Nat.,* 40: 228-238.

Ginsburg, L., Ingavat, R. & Tassy, P. (1983). *Siamogale thailandica*, nouveau Mustelidae (Carnivora, Mammalia) néogène du Sud-Est asiatique. *Bull. Soc. Géol. France* N° Spéc. 25: 953-956.

Ginsburg L. & Morales, J. (1996). *Lartetictis* et *Adroveric-tis*, nouveaux genres de Melinae (Mustelidae, Carnivora, Mammalia) du Miocène de l'Ancien Monde. *Bull. Mus. Nat. Hist. Nat., Sci. Terre, Paléontol. Géol. Minéral.*, 18: 663-671.

Gray, J.E. (1825). Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera appertaining to each tribe. *Ann. Philos. NS* 10: 337-344.

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

Haile-Selassie, Y., Woldegabriel, G., White, T., Bernor, R., Degusta, D., Renne, P., Hart, W., Vrba, E., Ambrose, S. & Howell, F. (2004). Mio-Pliocene mammals from the Middle Awash, Ethiopia. *Geobios*, 37: 536-552.

Heggberget, T. & Moseid, K. (1994). Prey selection in coastal Eurasian otters, *Lutra lutra*. *Ecography*, 17: 331-338.

Helbing, H. (1936). Die Tertiären Wirbeltiere des Steinheimer Beckens : Die Carnivoren des Steinheimer Beckens. A. Mustelidae. *Palaeontographica* Suppl. Band 8: 1-56.

Hendey, Q.B. (1974). The late Cenozoic Carnivora of the southwestern Cape Province. *Ann. S. Afr. Mus.,* 63: 1-369.

Hill, A., Drake, R., Tauxe, L., Monaghan, M., Barry, J., Behrensmeyer, K., Curtis, G., Jacobs, B., Jacobs, L., Johnson, N. & Pilbeam, D. (1985). Neogene palaeontology and geochronology of the Baringo Basin, Kenya. *J. Human Evol.,* 15: 749-773.

Howell, F.C. (1982). Preliminary observations on Carnivora from the Sahabi Formation (Libya). *Garyounis Sci. Bull. Spec. Issue*, 4: 49-61.

Howell, F.C. & Petter, G. (1976). Indications of age from the carnivores of the Hadar Formation (Eastern Ethiopia). *C. R. Acad. Sci. Paris*, 282: 2063-2066.

Howell, F. & Petter, G. (1979). Diversification et affinités des Carnivores pliocènes du groupe de l'Omo et de la formation d'Hadar (Ethiopie). *Bull. Soc. Géol. Fr.,* 21: 289-293.

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

Hürzeler, J. & Engesser, B. (1976). Les faunes de mammifères du Bassin de Baccinello (Grossetto, Italie). *C. R. Acad. Sci. Paris*, 283: 333-336.

Johnson, G.D., Opdyke, N. & Nanda, A.C. (1983). The Magnetic Polarity Stratigraphy of the Siwalik Group at Haritalyangar (India) and a new last appearance datum for *Ramapithecus* and *Sivapithecus* in Asia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.,* 44: 223-249.

Kilmer, F. (1972). A new species of sea otter from the late Pleistocene of northwestern California. *Bull. South. California Acad. Sci.,* 71: 150-157.

Kruuk, H., Kanchanasaka, B., O'Sullivan, S. & Wanghongsa, S. (1994). Niche separation in three sympatric otters, *Lutra perspicillata*, *L. lutra* and *Aonyx cinerea* in Huai Kha Khaeng, Thailand. *Biological Conservation*, 69 : 115-120.

Laidler, L. (1982). Bring back the giant. *New Scientist*, 23 : 825-828.

Lambert, W. (1997). The osteology and paleoecology of the giant otter *Enhydritherium terraenovae*. *Jl Vert Paleont.*, 17: 738-749.

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

Liu, Jian-Hui & Pickford, M. (2007). Comparison of European and Chinese Late Miocene Suidae: Implications for Biostratigraphy and Palaeoecology *Vert. PalAsiat.*, 45: 59-73.

Lydekker, R. (1884a). Indian Tertiary and Post-Tertiary Vertebrata : Siwalik and Narbada Carnivora. *Mem. Geol. Surv. India, Palaeontologica indica*, Ser 10, 2: 178-355.

Lydekker, R. (1884b). *Catalogue of Siwalik Vertebrata in the Indian Museum, Part 1: Mammalia*. London, British Museum (Natural History).

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

Lydekker, R. (1890). On a new species of otter from the lower Pliocene of Eppelsheim. *Proc. Zool. Soc. London*, 1890: 3-5.

Mason, C. & MacDonald, S. (1986). *Otters: Ecology and Conservation*. Cambridge University Press, New York, New York, 236 p.

Mathur, A.K. (1998). Additional molluscan fauna and taxonomic review of molluscs from the Siwalik Group and Terrace deposits, Himachal Pradesh, Punjab and Haryana. *Geosci. J.*, 19: 34-75.

Matthew, W.D. (1924). Third contribution to the Snake Creek Fauna. *Bull. Amer. Mus. Nat. Hist.*, 50: 59–210.

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

McKenna, M. & Bell, S. (1997). *Classification of Mammals above the Species Level*. New York, Columbia University Press. 631 p.

Meneghini, G. (1863). Descritzione dei resti di due fieri trovati nelle Ligniti mioceniche di Montebamboli. *Atti Soc. Ital. Sci. Natur.*, 4: 17-55.

Morales J. & Pickford, M. (2005a). Giant bunodont Lutrinae from the Mio-Pliocene of Kenya and Uganda. *Estudios Geol.*, 61 : 233-246.

Morales, J. & Pickford , M. (2005b). Carnivores from the Middle Miocene Ngorora Formation (13-12 Ma) Kenya. *Estudios Geol.*, 61: 271-284.

Morales, J., Pickford, M. & Soria, D. (2005). Carnivores from the Late Miocene and Basal Pliocene of the Tugen Hills, Kenya. *Rev. Soc. Geol. España*, 18: 39-61.

Nanda, A.C. (1981). Occurrence of the Pre-Pinjor Beds in the vicinity of Chandigarh. *Proc. Neogene/Quaternary Boundary Field Conference, India, 1979*: 113-116.

Nanda, A.C. (1994). Upper Siwalik Mammalian faunas from Chandigarh and Jammu Regions with comments on certain faunal discrepancies. *Proc. 1st South Asia Geological Congress, February 23-27, 1992, Islamabad, Pakistan. Geology in South Asia,* 1: 39-45.

Nanda, A.C. (1997). Comments on Neogene/Quaternary Boundary and associated faunas in the Upper Siwalik of Chandigarh and Jammu. *1st Regional Geosas Workshop on Quaternary Geology of South Asia, Anna University, Madras*: 120-136.

Nanda, A.C. (2002). Upper Siwalik mammalian faunas of India and associated events. *J. Asian Earth Sci.*, 21: 47-58.

Nanda, A.C. & Sehgal, R.K. (1993). Siwalik Mammalian faunas from Ramnagar (J&K) and Nurpur (H.P.) and lower limit of *Hipparion*. *J. Geol. Soc. India*, 42: 115-134.

Nanda, A.C. & Sehgal, R.K. (2005). Recent advances in Palaeontologic and Magnetostratigraphic aspects of the Siwalik Group of Northwestern Himalaya. *Himalayan Geol.*, 26: 93-102.

Newton, E.T. (1890). On some new mammals from the Red and Norwich Crags. *Quart. J. Geol. Soc. London*, 46: 444-453.

Nowak, R. (1991). *Walker's Mammals of the World*. Johns Hopkins University Press, Baltimore.

Orlov, J.A. (1933). *Semantor macrurus* (Ordo Pinnipedia, Fam. Semantoridae Fam. Nova) aus dem Neogen Ablagerungen Westsiberiens. *Trudy Palaeozool. Inst. Moscow & Leningrad*, 2: 165-262.

Orlov, J.A. (1936). Fundort der Hipparionfauna am Irtysch in der Stadt Pawlodar (W. Siberien). *Trudy Palaeozool. Inst. Akad. Nauk SSSR*, 5: 155-169.

Patterson, B., Behrensmeyer, A.K. & Sill. W.D. (1970). Geology and fauna of a new Pliocene locality in northwestern Kenya. *Nature*, 226: 918-921.

Petter, G. (1967). Petits carnivores villafranchiens du Bed I d'Oldoway (Tanzanie). *Coll. Int. C.N.R.S., Paris 1966, Problèmes actuels de Paléontologie (Evolution des Vertébrés),* 163: 529-538.

Petter, G. & Howell, F.C. (1977). Diversification des civettes (Carnivora, Viverridae) dans les gisements pléistocènes de l'Omo. *C. R. Acad. Sci. Paris,* 284: 283-286.

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.

Pickford, M. (1975). Late Miocene sediments and fossils from the Northern Kenya Rift Valley. *Nature*, 256: 279-284.

Pickford, M. (1988). Revision of the Miocene Suidae of the Indian Subcontinent. *Münchner Geowiss. Abh.,* 12: 1-91.

Pilgrim, G.E. (1910). Notices of new mammalian genera and species from the Tertiaries of India. *Rec. Geol. Surv. India*, 40: 63-71.

Pilgrim, G.E. (1913). Correlation of the Siwaliks with mammal horizons of Europe. *Rec. Geol. Surv. India*, 43: 264-326.

Pilgrim, G.E. (1931). *Catalogue of the Pontian Carnivora of Europe in the Department of Geology*. London, 174 p.

Pilgrim, G.E. (1932). The fossil Carnivora of India. *Mem. Geol. Surv. India, Palaeontologica indica*, 18: 1-232.

Pilgrim, G.E. (1934). Correlation of ossiferous sections in the upper Cenozoic of India. *Amer. Mus. Novitates*, 704: 1-5.

Pillans, B., Williams, M., Cameron, D., Patnaik, R., Hogarth, J., Sahni, A., Sharma, J., Williams, F. & Bernor, R. (2005). Revised correlation of the Haritalyangar magnetostratigraphy, Indian Siwaliks: implications for the age of the Miocene hominoids *Indopithecus* and *Sivapithecus*, with a note on a new hominoid tooth. *J. Human Evol.*, 48: 507-515.

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

Prasad, K.N. (1970). The vertebrate fauna from the Siwalik Beds of Haritalyangar, Himachal Pradesh, India. *Palaeontologica indica*, 34: 1-55.

Qi, GuoQin (1983). Description of Carnivora fossils from Lufeng. *Acta Anthropologica Sinica*, 2: 11-20.

Qi, GuoQin (1985). A preliminary report on Carnivora from the *Ramapithecus* locality, Lufeng, Yunnan. *Acta Anthropologica Sinica*, 4: 33-43.

Qi, GuoQin (2006). Carnivora. *In*: Qi, G.Q. & Dong, W., (eds). *Lufengpithecus hudienensis* Locality. Beijing: Science Press, 158-176 (Chinese with English summary).

Qian, F. (1993). Physical geography and regional geology. *In* : Qian, F. & Zhou, G. *et al.* (eds). *Stratigraphy and Paleontology of the Yuanmo Basin, Yunnan Province, China*. Translated version, Northern Arizona University, 1-8.

Qiu, Zhanxiang & Qiu, Zhuding (1995). Chronological sequence and subdivision of Chinese Neogene mammalian faunas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.,* 116: 41-70.

Ranga Rao, A., Agarwal, R.P., Sharma, U.N., Bhalla, M.S. & Nanda, A.C. (1988). Magnetic polarity Stratigraphy and vertebtrate palaeontology of the Upper Siwalik Subgroup of Jammu Hills, India. *Journal Geological Society of India*, 31: 361-385.

Régimbart, M. (1882). *Dytiscides nouveaux de la collection du musée royal de Leyde*, Leyden, 10 p.

Repenning, C.A. (1976). *Enhydra* and *Enhydriodon* from the Pacific Coast of North America. *J. Res.U.S. Geol. Surv.* 4: 305-315.

Royle, J.F. (1839). *Illustrations of the Botany and other branches of Natural History of the Himalayan Mountains,* London. l: 31 p.

Savage, R. (1957). The anatomy of *Potamotherium*, an Oligocene lutrine. *Proc. Zool. Soc. London*, 129: 151-244.

Sehgal, R.K. & Nanda, A.C. (2002a). Age of the fossiliferous Siwalik sediments exposed in the vicinity of Nurpur, District Kangra, Himachal Pradesh. *Current Science*, 82: 392-395.

Sehgal, R.K. & Nanda, A.C. (2002b). Palaeoenvironment and Palaeoecology of the Lower and Middle Siwalik Subgroups of a part of Northwestern Himalaya. *Journal Geological Society of India*, 59: 517-529.

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.

Srivastava, J.P. & Arora, R.K. (1983). On the occurrence of fossil molluscs in the Tatrot rocks (Pliocene) near Saketi, Sirmur District, Himachel Pradesh. *J. Palaeont. Soc. India*, 28: 112-113.

Stromer, E. (1913). Mitteilungen über Wirbeltierreste aus dem Mittelpliocän des Natrontales (Ägypten) 1. Affen und 2. Raubtiere. *Zeitschr. D. Geol. Ges.,* 65: 350-371.

Stromer, E. (1920). Mitteilungen über Wirbeltierreste aus dem Mittelpliocän des Natrontales (Ägypten) 5. Nachtrag zu 1. Affen. 6. Nachtrag zu 2. Raubtiere. *Sitzber. Bayer. Akad. Wiss.,* 1920: 345-370.

Stromer, E. (1931). Reste Süsswasser und Land bewohnender Wirbeltiere aus den Diamantfeldern Klein-Namaqualandes (Südwest Afrika). *Sitz. Math. Naturw. Abt. Bayer. Akad. Wiss.*, 1: 17-47.

Swainson, W. (1835). On the natural history and classification of quadrupeds. In: *The Cabinet Encyclopaedia conducted by the Rev. Dionysius Lardner*. London, Longman, Rees, Orme, Brown & Longman. 397 p.

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

Titov, V.V., Tesakov, A.S., Danilov, I.G., Danukalova, G.A., Maschenko, E.N., Panteleev, A.V., Sotnikova, M.V. & Sychevskaya, E.K. (2006). The first representative vertebrate fauna from the Late Miocene of southern European Russia. *Doklady Akademii Nauk*, 411: 715-717.

Tobien, H. (1955). Neue und bekannte Carnivoren aus den unterpliozänen Dinotheriensanden Rheinhessens. *Notizbl. Hess. Landesamt. Bodenforsch. Wiesbaden,* 83: 7-31.

Verma, B.C. & Gupta, S.S. (1992). *Enhydriodon sivalensis*, a giant fossil otter from the Saketi Formation (Upper Pliocene) Siwalik Group, Sirmur District, Himachal Pradesh. *J. Palaeont. Soc. India*, 37: 31-36.

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

Villalta, J.F. & Crusafont-Pairo, M. (1945). *Enhydriodon lluecai* n. sp. el primer lútrido del pontiense Español. *Bol. Real. Soc. Esp. Hist. Nat.,* 43: 383-396.

Weithofer, K.A. (1888). Alcune osservazione sulla fauna delle ligniti di Casteani e di Montebamboli (Toscana). *Boll. Com. Geol. Italia,* 19: 363-368.

Weithofer, K.A. (1889). Über die tertiären Landsäugetiere Italiens. *Jahrb. Geol. Reichsanst. Wien*, 39: 55-82.

Werdelin, L. (2003a). Carnivores from the Kanapoi Hominid site, Turkana Basin, northern Kenya. *Contributions to Science*, 498: 115-132.

Werdelin, L. (2003b). Mio-Pliocene Carnivora from Lothagam, Kenya. *In*: Leakey, M. & Harris, J.M., (eds) *Lothagam: The Dawn of Humanity in Eastern Africa*, Columbia, Columbia University Press, 261-328.

Werdelin, L. & Lewis, M. (2005). Plio-Pleistocene Carnivora of eastern Africa : species richness and turnover patterns. *Zool. J. Linn. Soc.,* 144: 121-144.

Willemsen, G. (1983). *Paralutra garganensis* sp. nov. (Mustelidae, Lutrinae), a new otter from the Miocene of Gargano; Italy. *Scripta Geol.,* 72: 1-9.

Willemsen, G. F. (1990). A new specimen of the otter Enhydra reevei (Newton, 1890) from the crag of Bramerton, Norfolk. *Bull. Geol. Soc. Norfolk*, 39: 87-90.

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

Willemsen, G. (1999). Some remarks on the Enhydrini (Lutrinae) from the Siwaliks, Pakistan. *Deinsea*, 7: 411-418.

Wynn, J., Alemseged, Z., Bobe, R., Geraads, D., Reed, D. & Roman, D. (2006). Geological and palaeontological context of a Pliocene juvenile hominin at Dikika, Ethiopia. *Nature*, 443: 332-336.