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Some remarks on the Enhydrini (Lutrinae) from the Siwaliks, Pakistan

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Some material of *Enhydriodon sivalensis*, *E. falconeri* and *Sivaonyx bathygnathus* from the Siwaliks is described. The species are compared to other Enhydrini. It is concluded that *Sivaonyx* represents a primitive lineage within the Enhydrini and that it is phylogenetically related to the widespread *Enhydriodon lluecai* group.

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INTRODUCTION

In 1986, I had the opportunity to study the holotype of *Enhydriodon sivalensis* and some other enhydrine otters from the Siwaliks, Pakistan. In this paper, I will describe the material and give some thoughts on enhydrine taxonomy and phylogeny. A thorough revision of the Enhydrini is badly needed, but that will have to include a study of the abundant new material from African localities. All measurements were taken according to the standard given in Willemsen (1992), see Figure 1, and are given in millimeters. The following abbreviations are used:
Ltal = talonid length
Ltri = trigonid length
Wtal = talonid width
Wtri = trigonid width
Lb = buccal length
BM = British Museum (Natural History)
GSI = Geological Survey of India

DESCRIPTION

Subfamily Lutrinae
Tribe Enhydrini
Genus *Enhydriodon* FALCONER, 1868

Enhydriodon sivalensis FALCONER, 1868

In 1868, Falconer described the genus and species based on three partial skulls from the Siwaliks, all in the British Museum (Natural History). Matthew (1929) designated the most complete skull, M 37153, as holotype. The other two, M 37154 and M 37155, are lectotypes. The holotype is a highly arched skull. The intertemporal constriction is broad, caudally slightly converging. The muzzle is short and broad in all three specimens, but in M 37155 it is broader than in the other two specimens (Table 1). In M 37154, the intertemporal region is not converging, while it does so slightly in M 37155.

Dentition

I1 is small, I3 relatively strong. The canine is large. In the holotype and in M 37155, no P2 was present. In M 37154, a very small P2 alveole can be seen. So, P2 was either absent or vestigial. Even P3 is relatively small. P4 has a quadrangular outline rather than the triangular outline which is characteristic of most lutrines. The tooth is slightly wider than

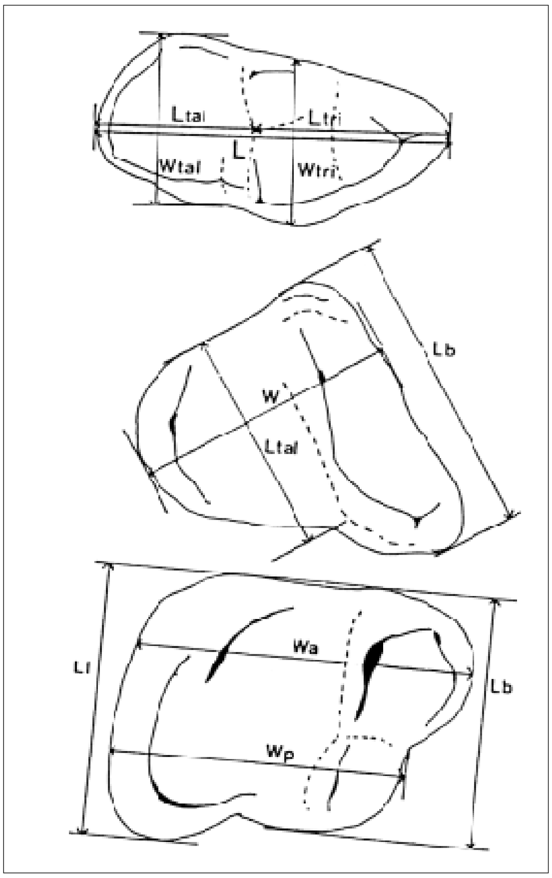

Figure 1 Measurements (from top to bottom) of m1, P4 and M1. From Willemsen (1992).

long. In all three specimens, the trigon is damaged. Nevertheless, it can be seen that all cusps are well developed and blunt. M 37155 shows a large paracone with a well-developed parastyle. All specimens show a large, conical protocone. The protocone is not as large as the more elongated paracone, as can be seen from M 37154 and M 37155. Those specimens show even a large, conical hypocone, which is as large as the protocone. Between the two cusps, a small cuspule can be seen in both specimens. This cuspule continues anteriorly as a cingulum. The talon does not show a concave basin as many lutrines do. M1 is only partially known from M 37155, where the anteriolingual part is preserved. It shows the paracone, which is split in two cusps (see Pilgrim 1932: p. 83).

Enhydriodon falconeri PILGRIM, 1931

Pilgrim (1931) described the species. The holotype, an upper carnassial (BM M 4847), may be the specimen belonging to a smaller species mentioned by Falconer (1868: 336). The specimen is indeed somewhat smaller than the known *E. sivalensis* specimens. It is not as broad as in *E. sivalensis*. The paracone is conical in shape, not connected with the metacone by a ridge. The metacone is smaller than the paracone. There is a well-developed parastyle, which is relatively more developed than in *E. sivalensis*. As in the latter, the talon does not form a basin. The protocone is divided into two cusps, a larger one and lingually of it, a smaller one. The two cusps clearly form one cone. Even the hypocone is conical in shape. It is as large as the two cusps, forming the protocone, together. The additional lingual cuspule between protocone and hypocone is relatively larger than in *E. sivalensis*.

genus *Sivaonyx* PILGRIM, 1931
Sivaonyx bathygnathus (LYDEKKER, 1884)

The holotype is a left mandible with m1, GSI no 33 (Lydekker 1884: pp. 193 ff, plate 27). In the collection of the British Museum there are two specimens, M 15397 and M 13175, as well as two casts, M 16929 (cast from GSI no D 156) and M 12350. All are left mandibular fragments with m1. The mandibles are very stout and the ramus is high, especially in M 15397. The carnassial is very much like *Aonyx capensis* but the mandible is much more robust than in the latter species. In all studied specimens, the talonid is slightly shorter than the trigonid. In M 15397, the paraconid is the largest cuspid, the metaconid is smallest and lowest. The paraconid is situated on the median axis, but the outline of the tooth is not bilaterally symmetrical. The cingulum around the paraconid goes on along the protoconid and the hypoconid. Both protoconid and metaconid fall steeply posteriorly. The metaconid does not have an accessory

Table 1 Skull measurements of *Enhydriodon sivalensis.*

	M 37153	M 37154	M 37155
Dorsal length	ca 165		
Interorbital width	>33	38,3	3,7
Width between postorbital processes	26,5		
Nose length		ca 50	ca 53
Intertemporal width		ca 36	ca 30,6
Intertemporal length	ca 36		
Cranial width	ca 97		
Heigth squama occipitalis from for magnum	42,1		
Muzzle width above canines	ca 52	57,9	70,4

posterior cuspid, contrary to *E. lluecai*, nor does the protoconid have one, The tooth is broad, the talonid is slightly broader and shorter than the trigonid. The hypoconid is large, larger than in *Aonyx capensis*. At the inner edge of the talonid two cuspids can be distinguished. The m1 in M 13175 is very worn and does not show many details (Fig. 2). M 16929 is much like M 15397. The condition of the cingulum is the same. The hypoconid is, though smaller, more like in *Aonyx capensis*. The lingual edge of the talonid does not show any cuspids. M 12350 is the cast of a very large m1, but the tooth is heavily damaged. Pilgrim (1931) also assigns a P4 from Hasnot to this species, mainly on the basis of its size. From his description and figure it is impossible to say whether this is right.

DISCUSSION

The extinct Enhydrini genera *Enhydriodon*, *Sivaonyx* and *Vishnuonyx* were all originally described from the Siwaliks. *Vishnuonyx* is the oldest genus and the least advanced. Its P4 has still the typical triangular outline of most lutrines, but the protocone and hypocone are still separate cusps. The genus seems to be a good candidate for an ancestral Enhydrini. It is described from the Chinji formation (Pilgrim, 1932), which can be dated at about 12 to 14 My (Pilbeam *et al.* 1977). Wessels *et al.* (1982) referred a rodent fauna from Chinji to the Early Astaracian (MN 6).

Enhydriodon apparently had a wide geographical distribution (see Tables 2 and 3 for measurements). The genus has different species in Europe, Africa and North America. The most widespread seems to be the *E. lluecai* lineage. *E. lluecai* De Villalta & Crusafont, 1945 is known from some Turolian localities in Spain (De Villalta & Crusafont 1945, Crusafont & De Villalta 1951). Only lower dentition was described. In 1962, Crusafont & Golpe (1962) described *Sivaonyx lehmani* on an upper P4 from Teruel. Probably, resemblances to the P4 from Hasnot, referred to *S. bathygnathus* by Pilgrim (1932) led them to describe this new *Sivaonyx*. As Repenning (1976) pointed out, there are however differences. Important differences are the prominent parastyle and the prominent hypocone in the Hasnot specimen. *S. lehmani* lacks a parastyle and the hypocone is present only as a pair of small cusps on the hypoconal crest. Repenning (1976) considered *S. lehmani* and *E. lluecai* to be conspecific. Willemsen (1992) and Alcala

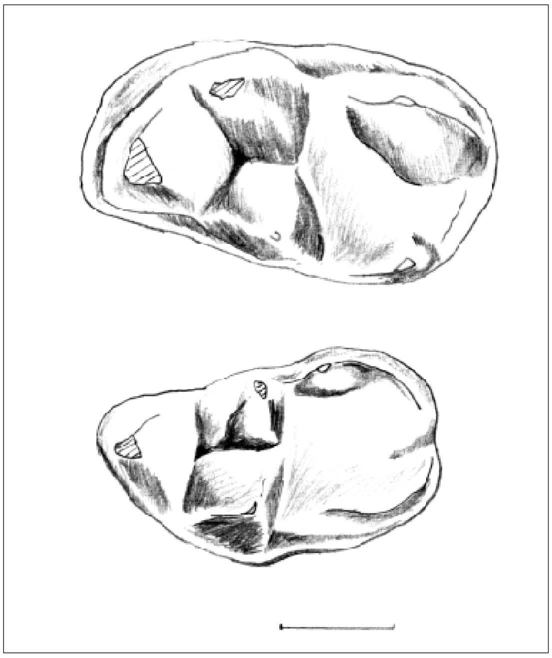

Figure 2 *Sivaonyx bathygnathus* m1 British Museum M 13175 (upper) and cast GSI D156 (lower). Scale = 5mm

(1994) are of the same opinion. Repennings conclusion is confirmed by his findings from California, which he described as *Enhydriodon* cf. *E. lluecai*. He described both the lower and upper carnassial, the upper carnassial being very similar to the Teruel specimen and the lower carnassial only showing minor differences.

E. lluecai represents a lineage with large geographical distribution, being present in both Europe, North America and also in Africa (Lukeino, Kenya, see Pickford 1975). P4 has not yet become as broad and as robust as in later species. The outline is still triangular rather than square. The Hasnot P4 has a similar form, but less stout cusps and, as mentioned before, it has a prominent parastyle and hypocone. The lack of a parastyle is seen in all known European and American *Enhydriodon* P4 (Repenning 1976, Hürzeler 1987).

Table 2 Upper dentition measurements, compared to some measurements from literature.

	P3 L	P3 W	P4 Lb	P4 Ltal	P4 W	M1 Lb	M1 Ll	M1 We
Enhydriodon sivalensis								
BM M37153	10,0	9,8	15,6	14,1	18,7	13,5	ca 15,3	ca 18,7
BM M37154	10,8	10,0	17,3	17,2	19,0			
BM M37155	9,7	8,1	17,0	15,9	18,5			
Surgeons 777A (Pilgrim 1931)			17,6		19,4			
E. falconeri								
BM M4847			16	14,6	15,7			
E. lluecai								
La Algezares (Crusafont&Golpe 1962)			13,0		12,8			
UCMP 32972 (Repenning 1976)			13,6		15,0			
E. n.sp.								
UCMP 184083 (Repenning 1976)			14,5		15,7			
E. campanii								
Mus Siena holotype sin (Hürzeler 1987)			16,1		15,0			
Mus Siena holotype dex (Hürzeler 1987)			16,0		15,2			
Mus Siena paratype (Hürzeler 1987)			14,0		14,5			
E.maremmana								
Pisa, holotype (Hürzeler 1987)			15,1		12,8			
Sivaonyx bathygnathus								
BM 12352 (cast GSI D157)			14,3	13,5	13,2			
Vishnuonyx chinjiensis								
BM M12351 (cast GSI D223)			12	5,2	9,3			

Paludolutra maremmana HÜRZELER, 1987 shows great resemblance to *E. lluecai*. It was described from the insular fauna from Grosseto in Italy. Hürzeler (1987) considered it rightfully to be ancestral to *Enhydriodon campanii* MENEGHINI, 1862, which he included in his new genus *Paludolutra*. I have pointed out earlier (Willemsen 1992: p. 93) that a generic separation of *E. lluecai* and *P. maremmana* is not tenable and that *E. lluecai* does fit in the genus diagnosis of *Paludolutra*, given by Hürzeler (1987). *P. maremmana* clearly represents the same widespread lineage as *E. lluecai*. Whether a generic separation of this whole lineage indeed is justified can only be decided after a thorough study of all available Enhydrini material, including the abundant but yet undescribed African material. For the moment, I prefer to retain all forms within the genus *Enhydriodon*. The resemblance of *P. maremmana* and *E. lluecai* is such, that the latter must be considered to be ancestral to the former. There is probably no phylogenetic relationship between *P. maremmana* and *Tyrrhenolutra helbingi* HÜRZELER 1987.

The two Indian *Enhydriodon* species do definitely form a lineage, separated from the *E. lluecai* group, which includes *E. maremmana*, *E. campanii* and *E.* n. sp. from California, described by Repenning (1976). The Indian lineage is characterised by the enlarged number of cusps on the P4, the large and blunt cusps, the well-developed parastyle, which is very small or absent in the *lluecai* group.

The relationship of *Sivaonyx bathygnathus* with the other species is somewhat problematical. The species, based on a lower jaw with m1, was originally placed within the genus *Lutra* (Lydekker 1884: pp. 193 ff). Pilgrim (1931: p. 74) proposed the genus *Sivaonyx*, in which he also placed *Lutra hessica* LYDEKKER, 1890 from Eppelsheim. Pohle (1919: p. 26) put the species in the genus *Potamotherium*, on the basis of the presence of p1 in the lower jaw. This tooth is normally absent in lutrines. Pohle (1919) noted, however, strong

Table 3 Lower dentition measurements, compared to some measurements from literature.

	m1 L	m1 Ltri	m1 Ltal	m1 Wtri	m1 Wtal	m1 W	m1 W/L
Sivaonyx bathygnathus							
BM M15397	18,6	9,8	8,8	10,9	11,0	11,0	0,59
BM M13175	15,5	8,8	6,7	8,4	8,9	8,9	0,57
GSI D250 (Pilgrim 1931)	16,4					9,1	0,55
GSI D249 (Pilgrim 1931)	14,2					8,3	0,58
GSI D156 (Pilgrim 1931)	16,0					9,4	0,59
BM M16929 (cast GSI D156)	16,0	9,0	7,0	9,0	9,1		
Enhydriodon cf falconeri							
GSI D161 (Pilgrim 1931)	21,6					12,7	0,59
BM 12350 (cast GSI D161?)	21,8	12,8	9,8	11,9	12,1	12,1	
E. africanus							
Stromer 1931	22,0					>12	
E. lluecai							
La Algezares (Vill.&Crus. 1945)	17,5					10,0	0,57
Los Mansuetos (Crus.&Golpe 1962)	16,0					9,5	0,59
Vishnuonyx chinjiensis							
GSI D245 (Pilgrim 1931)	11,7						

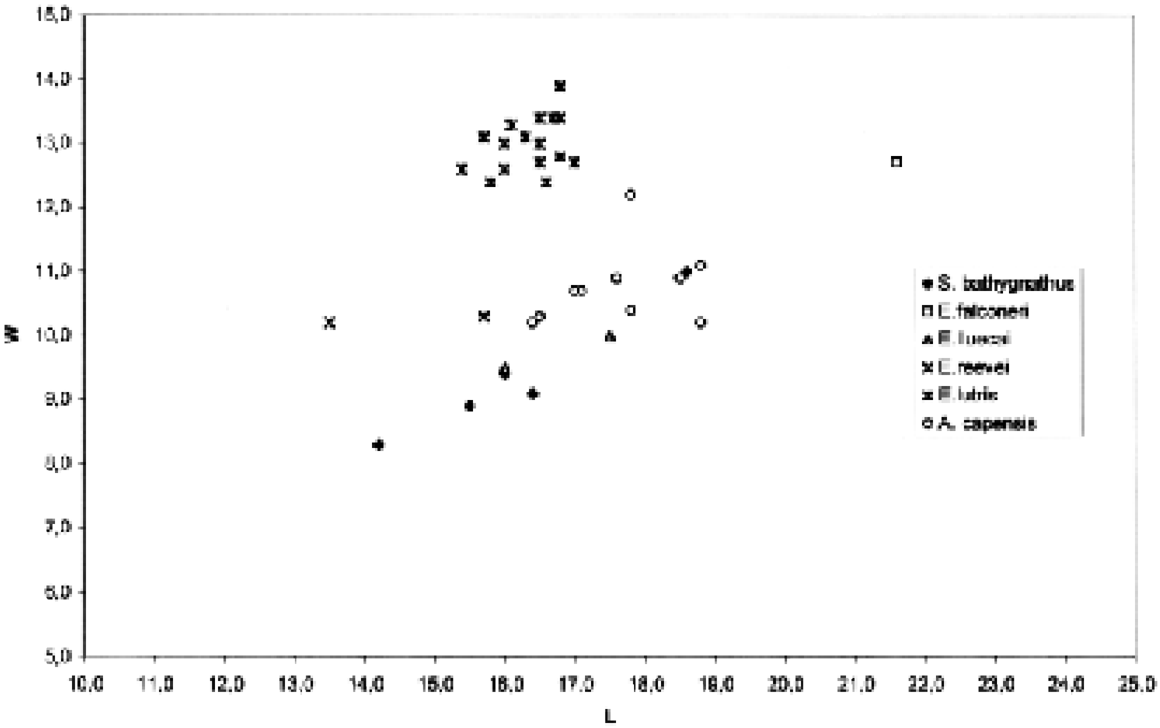

Figure 3 Length and width of m1 of some lutrines.

similarities to *Aonyx*. Pohle (1919), like many others, considered *Potamotherium* to be a primitive lutrine, ancestral to the whole subfamily. During later years, several authors have expressed doubts about this and I have placed it in a mustelid subfamily of its own, noting that *Potamotherium* may be related to the Phocidae rather than the Lutrinae (Willemsen 1992: pp. 8, 79; see also Savage 1957, De Muizon 1982). *Sivaonyx* on the other hand, is beyond doubt a lutrine. All known specimens are from Hasnot and probably have an Upper Vallesian or Lower Turolian age (Willemsen 1992, Pilbeam *et al.* 1977), except for one of the studied specimens, M 15397 in the British Museum, which is from Tatrot and thus of Late Pliocene age (Barry *et al.* 1982). It seems thus that the species represents a lineage, which was present during most of the Pliocene. Even if the P4 from Hasnot, referred to *S. bathygnathus* by Pilgrim (1932), shows differences from *E. lluecai*, as mentioned above and as pointed out by Repenning (1976), the overall structure suggests some relationship to *E. lluecai* and related species. The more triangular outline and the less bunodont character compared to *E. falconeri* and *E. sivalensis* remind of the *lluecai* group. If Pilgrim is right in referring the P4 to *Sivaonyx*, this would suggest a relationship of this genus to the *E. lluecai* group.

I pointed out earlier (Willemsen 1992) that even the m1 of *S. bathygnathus* reminds of *E. lluecai*. In both cases, the paraconid is placed on the median axis of the tooth. The outline of the tooth is, however, more symmetrical in *E. lluecai*. There are also differences. One difference is the secondary cuspid posterior to the metaconid. This is not present in the *S. bathygnathus* specimens I studied, but it is present in both the Teruel and the Californian specimens of *E. lluecai* (Repenning 1976). This secondary cuspid is unusual in lutrines. The m1 of *E. lluecai* has a relatively short talonid. Villalta & Crusafont (1945) especially point this out. They give a ratio Ltrig/Ltal of 1.91 for the Teruel specimen. According to

Pilgrim (1931), the talonid and the trigonid are approximately equal in length in *S. bathygnathus*. The four specimens studied by myself show a slightly shorter talonid than trigonid, with a ratio of 1.11 to 1.31, which is about the same as in *Aonyx capensis*. Much depends however on exactly how talonid and trigonid lengths are measured. According to the figures in Repenning (1976) the talonid of *E. lluecai* is not as short as suggested by the above-mentioned ratio. Repenning (1976) mentions that *S. bathygnathus* is characterised by a 'noticeably narrow, elongate m1'. My own observations do not confirm this. The width/length ratio does not differ from whether *E. lluecai*, the specimen referred to *E. falconeri* or *Aonyx capensis* (see Table 3 and Figure 3).

Differences in m1 between *S. bathygnathus* and *E. lluecai* are apparently less than suggested by Repenning. To this comes the difficulty in separating lutrines on the basis of m1 only. Pilgrim (1932) described an m1, which he referred to *E. falconeri* on the basis of its size. It differs in structure from *S. bathygnathus*, but not too much. Pilgrim stated that the genera could not be separated on the basis of m1 alone (Pilgrim 1932: p. 87). I noted myself a strong resemblance of the m1 of *Sivaonyx* and *Aonyx*. It are other characteristics that separate the genera. *Sivaonyx* is characterised by a very stout and high mandibular ramus, which is typical for even *Enhydriodon*. An important characteristic is the presence of p1. This is unusual in lutrines and it can be regarded a primitive character. This clearly separates *Sivaonyx* from *E. lluecai*.

I would suggest that *Sivaonyx* represents a primitive lineage within the Enhydrini, retaining the presence of p1. Similarities with *E. lluecai* suggest a relationship with this group, which may have evolved from, or have a common origin with, *Sivaonyx*. *E. lluecai* and related forms reached both Europe, Africa and North-America. On the Pacific coast it eventually gave rise to *Enhydra* (see Willemsen 1992). The *E. falconeri*/*E. sivalensis* group seems to have had a more restricted geographic distribution.

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