

## GIANT BUNODONT LUTRINAE FROM THE MIO-PLIOCENE OF KENYA AND UGANDA

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### ABSTRACT

Three new species of bunodont otters are described from the Mio-Pliocene of East Africa. They are provisionally attributed to the genus *Sivaonyx* Pilgrim, 1931. The species described are *Sivaonyx soriae*, nov. sp. and *Sivaonyx senutae* nov. sp. from the Latest Miocene Lukeino Formation (Kenya) and *Sivaonyx kamuhangirei* nov. sp. from the Pliocene of Kazinga and Warwire (Uganda). Additional material of the species *Sivaonyx ekecaman* (Werdelin, 2003) is described from Sagatia, Mabaget Formation (Kenya). The systematics of the new tribe Enhydriodontini are discussed and we report the presence of evolutionary tendencies in the bunodont African otters: increase in body size, modification of the carnassial teeth. In particular in the P4/ the protocone becomes well separated from the paracone, at the same time that an anterior valley develops.

### RESUMEN

Se describen tres nuevas especies de nutrias bunodontas del Mio-plioceno de Africa oriental. Provisionalmente se adscriben al género *Sivaonyx* Pilgrim 1931. Las especies descritas son *Sivaonyx soriae* nov. sp. y *Sivaonyx senutae* nov. sp. del Mioceno final de la formación Lukeino (Kenia), y *Sivaonyx kamuhangirei* nov. sp. del Plioceno de Kazinga y Warwire (Uganda). También se describen nuevos fósiles de Sagatia, formación Magabet (Kenia) atribuibles a la especie *Sivaonyx ekecaman* (Werdelin, 2003). Se discute la sistemática de la nueva tribu Enhydriodontini y se señala la presencia de dos tendencias evolutivas en las nutrias bunodontas africanas: incremento de talla y modificación de las carníceras. Especialmente del P4/ en el que el protocono se va separando del paracono, al mismo tiempo que se desarrolla un valle en posición anterior.

### Introduction

Late Miocene and Early Pliocene otters from East and South Africa have been described on several previous occasions (Hendey, 1974; Morales *et al.*, 2005; Petter *et al.*, 1991; Stromer, 1931; Werdelin, 2003). Recent field research in Uganda and Kenya has resulted in the collection of additional informative material which throws light on the radiation that these bunodont African otters experienced during this period (Fig. 1).

In previous studies authors tended to attribute the African bunodont otter fossils to *Enhydriodon* but whereas the new material supports the ultimate derivation of the African bunodont otters from forms

similar to the Indian Late Miocene ones, it is now clear that once this group of otters arrived in Africa it experienced a major radiation culminating in species that differ markedly from the Indian group. It is also clear that the European bunodont forms such as *Paludolutra* and other genera such as *Tyrrhenolutra* should not be ignored in the study of these bunodont otters, since the dentognathic adaptations appear to be somewhat similar, although the evolutionary pathways are evidently divergent. The adaptations were probably related to dietary shifts, with several otter lineages independently developing bunodont dentitions and robust mandibles related to a change in diet from predominant piscivory to one dominated by shellfish (crustaceans and molluscs).

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Age	Uganda	Kenya	South Africa	Species
4	Kazinga Warwire	Kanapoi		<i>Sivaonyx ekecaman</i> <i>Sivaonyx kamuhangirei</i> <i>Sivaonyx kamuhangirei</i> <i>Sivaonyx africanus</i>
5		Magabet	Klein Zee Langebaanweg	<i>Sivaonyx ekecaman</i> <i>Sivaonyx hendeyi</i>
6		Lukeino		<i>Sivaonyx senutae</i> <i>Sivaonyx soriae</i>
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Fig. 1.—East and South African localities that have yielded remains of large bunodont otters.

There were two major evolutionary trends in the African bunodont otters - an increase in size over time and modification of the morphology of the carnassials and neighbouring teeth, whereby with the passage of geological time the protocone of the P4/ became more detached from the paracone, at the same time that accessory cusplets developed and an anterior valley in the P4/ appeared, among other features.

There has long been confusion about the exact status of the genera *Enhyriodon* and *Sivaonyx* (Colbert, 1935; Falconer, 1868; Lydekker, 1884, 1885; Matthew, 1929; Morales *et al.*, 2005; Pilgrim, 1931, 1932; Prasad, 1970; Verma & Gupta, 1992; Willemsen, 1992, 1999) aggravated by the fact that the holotype of the type species of the former is a snout with maxillary dentition, while that of the latter is a mandible with a very poorly preserved m/1. There are at least four kinds of bunodont otters in the Indian subcontinent, Europe and Africa. Because of breakage and wear of the teeth in the Indian type specimens, it is still not clear whether the type mandible of *Sivaonyx bathygnathus* really represents a genus different from *Enhyriodon*. Verma & Gupta (1992) for example listed the holotype of *S. bathygnathus* in their hypodigm of *Enhyriodon sivalensis* as a 'hypotype' of the species. Even when erecting the genus *Sivaonyx*, Pilgrim (1931) wrote "If *Lutra bathygnathus* were only known from its holotype there would be little justification for not including it in the genus *Enhyriodon*". Indeed, it is clear from the diagnosis of the genus *Sivaonyx*, that the deci-

sion to erect it was based predominantly on the morphology of the upper carnassial. As Pilgrim (1931, p. 75) wrote "the genus *Sivaonyx* is mainly based on the characters of this tooth (ie the P4/, N° GSI D 157), as diagnosed". Most of the difficulties subsequently encountered in the literature originate from Pilgrim's decision to include *bathygnathus* in *Sivaonyx* as the type species.

Bunodont, giant otters were widespread during the Late Miocene and Early Pliocene, having been recorded in North America (Repenning, 1976) and Europe (Alcalá, 1994; Crusafont-Pairó & Golpe, 1962a, b; Hürzeler, 1987; Meneghini, 1863; Pilgrim, 1931; Villalta & Crusafont, 1945; Willemsen, 1992, 1999) as well as Africa (Hendey, 1974; Morales *et al.*, 2005; Petter *et al.*, 1991; Stromer, 1931; Werdelin, 2003). The otter from Wadi Natrun, Egypt, (Stromer, 1921) has sometimes been included in either *Sivaonyx* or *Enhyriodon* (Geraads *et al.*, 2004), but it is neither very large nor particularly bunodont, and its affinities lie more with the piscivorous otters such as *Lutra* than with the crab-eating or molluscivorous ones (Willemsen, 1992).

### Geological context

The bunodont otters from Africa derive from Late Miocene and Early Pliocene strata in East and South Africa. Figure 1 lists the localities and approximate ages of the material. Mentions in faunal lists which are based on undescribed or mis-

identified fossils have been omitted from the table. The sites concerned are Omo, Garba IV (Melka Kunture) (Geraads *et al.*, 2004) and the Ada-Asu and Sagantole Formations (Haile-Selassie *et al.*, 2004). The generic affinities of *Enhydriodon aethiopicus* Petter, 2004 (in Geraads *et al.*, 2004) require restudy. It is probable that the tooth from Garba IV belongs to *Pseudocivetta ingens*, a civet, rather than to *Enhydriodon* (Petter & Howell, 1977, Fig. B). Indeed, the tooth from Omo (Omo 33-354) mentioned in this paper figures in the hypodigms of both species. Howell & Petter (1976, 1979) mention the presence of *Enhydriodon* sp. at Omo Members B and C, Hadar Member SH, DD, and Amado in Ethiopia, and Koobi Fora, Kenya, but the material was not figured and no measurements were provided. Behrensmeyer (1976) recorded the presence of *Enhydriodon* sp., at Kanapoi, Kenya, confirmed by Werdelin (2003) as the species *Enhydriodon ekecaman*. Savage (1978) referred this material to *Enhydriodon pattersoni* but without designating a type specimen, and without providing a diagnosis, a figure or measurements. The name was repeated by Turner *et al.*, 1999, but it is evidently a *nomen nudum* (Werdelin, 2003).

#### Remarks on the validity of the the tribe Enhydrini, Carnivora

There is clearly a classificatory problem with the tribe name Enhydrini, as it has been applied to two different groups of animals, otters and gyrid coleopterans. According to McKenna & Bell, 1997, Enhydrini was erected by Gray, 1825 (spelled Enhydrina in 1825) for a group of Phocidae, later included in Mustelidae (Gray, 1865). The same name was proposed for a group of Gyrinidae, Coleoptera, by Régimbart, 1882. Without entering into all the details, the authors simply raise the issue, without trying to solve it. What is clear is that the tribe Enhydrini Sokolov, 1973, for otters cannot be valid, as the name is predated in the work of at least two other authors.

We consider that the genus *Enhydra* belongs to a separate tribe from the Siwalik and African bunodont otters, and we accordingly propose a new tribe Enhydriodontini for extinct bunodont otters, a tribe which includes the genera *Vishnuonyx* Pilgrim, *Sivaonyx* Pilgrim, *Enhydriodon* Falconer and *Paludolutra* Hürzeler, but which excludes *Enhydra*. *Tyrrhenolutra* Hürzeler does not belong to this tribe either, but is closer to Enhydrini (sensu Gray, 1825). The diagnostic characters of species within the Enhydriodontini are summarised at the end of the paper (Fig. 6).

#### Order Carnivora Bowdich 1821 Family Mustelidae Fischer de Waldheim 1817 Subfamily Lutrinae Bonaparte 1838 Tribe Enhydriodontini nov. Genus *Sivaonyx* Pilgrim, 1931

**Type species:** *Sivaonyx bathygnathus* Lydekker, 1884.

**Other species:** *Sivaonyx africanus* (Stromer, 1931), *Sivaonyx hendeyi* (Morales *et al.*, 2005), *Sivaonyx ekecaman* (Werdelin, 2003), *Sivaonyx kamuhangirei* nov. sp., *Sivaonyx senutae* nov. sp. and possibly *Sivaonyx hessianus* (Lydekker, 1890).

#### *Sivaonyx soriae* nov. sp.

##### Synonymy:

p1975 *Enhydriodon* cf. *llucai* Villalta & Crusafont Pairó, 1945. Pickford, p. 284.

p2005 *Sivaonyx africana* (Stromer, 1931). Morales *et al.*, pp. 53-55, Fig. 6I, 9D.

**Holotype:** KNM LU 337 + 338, right mandible with symphysis. (Morales *et al.*, 2005 Fig. 6I).

**Paratype:** Bar 1984'05, left m/1 (Figs. 2G, 3A).

**Diagnosis:** Small-medium sized *Sivaonyx*, mandible with p/2 biradicate. m/1 with crescentiform paraconid, located in an antero-buccal position. Protoconid conical, bigger than the metaconid, but lower than it. Antero-lingual valley of the trigonid open lingually. Protoconulid well developed. Talonid long and wide, with a deep central valley bordered by peripheral cusplets of which the hypococonid is the largest. Small hypoconulid in posterior position. Entoconid crescentiform and extends to the base of the metaconid. Strong basal cingulum lingually.

**Differential diagnosis:** *Paludolutra llucai*, from the Turolian of Spain (Alcalá, 1994), is more primitive due to the retention in the m/1 of a protoconid which is higher than the metaconid and the weaker development of the entoconid. In these same features *Sivaonyx soriae* differs from *Torolutra ougandensis*. The size of the new species is intermediate between *S. bathygnathus* and *Sivaonyx senutae* nov. sp.

**Derivatio nominis:** The species name honours our late colleague Dr Dolores Soria.

**Description:** BAR 1984'05 left m/1, has low but quite robust cuspids. The paraconid is crescentiform and located in an antero-buccal position. The protoconid is conical, and is bigger than the metaconid but lower than it. Internally, they are united by two crests which approach the anterior valley of the trigonid which remains open lingually. A protoconulid is well developed on the posterior cristid of the protoconid.

The talonid is long and wide, with a deep central valley bordered by peripheral cusplets of which the hypoconid is the largest. A small hypoconulid occurs in a posterior position. The entoconid is crescentiform and extends to the base of the metaconid. There is a strong basal cingulum lingually and anteriorly which fades out at the base of the metaconid.

The m/1 measures L = 17.5 mm; W = 10.6 mm (Fig. 4).

Other material of this species was described by Morales *et al.*, 2005.

**Discussion:** The new lower molar from the Lukeino Formation described above introduces some doubt into the attribution of the mandible KNM LU 337+338 to *Sivaonyx africanus* by Morales *et al.*, 2005. The two teeth are similar in size and morphology. In comparison with the holotype of *S. africanus* the molar BAR 1984'05 is smaller and has a narrower, more triangular trigonid, in which the paraconid is not located in such an anterior position, in consequence of which in the Baringo tooth the valley between the metaconid and paraconid is wider and remains open lingually.

#### *Sivaonyx senutae* nov. sp.

##### **Synonymy:**

p2005 *Sivaonyx africanus* (Stromer, 1931). Morales *et al.*, pp. 53-55, Fig. 6G, 6H, 9E, 9F.

**Holotype:** Bar 1720'00, left P4/. (Figs. 2B, 3E).

**Paratype:** Bar 1082'01, right M1/. (Fig. 2H).

**Diagnosis:** *Sivaonyx* of medium-large size. P4/ with occlusal outline almost square. Parastyle moderately strong. Paracone voluminous, without any incision separating it from the metastyle, which is small. Protocone strong, rounded and well separated from the paracone, with a small cusplet backing onto its base. Hypocone somewhat smaller than the protocone, well separated from both the protocone and the paracone-metastyle. Cingulum strong, completely surrounding the tooth. M1/ with metacone small with respect to the paracone, and internally displaced. Protocone strong and in an anterior position, flattened central valley. Lingual cingulum very strong and elevated.

**Differential diagnosis:** *Sivaonyx senutae* differs from *S. hendeyi* by its smaller size, and the different morphology of the P4/. In the P4/ of *S. hendeyi* there is a small notch between the paracone and metastyle. The buccal cingulum is stronger, joining the metastyle and parastyle. The protocone is more separated from the paracone. The hypocone is lower and extensive, contacting the protocone and closing the tooth lingually. The median valley of the tooth is wide. *S. senutae* is larger than *S. soriae*.

**Derivatio nominis:** The species name honours Professor Brigitte Senut, co-leader of the Kenya Palaeontology Expedition.

**Locality:** Kapcheberek, Lukeino Formation, Baringo District, Kenya.

**Description:** These fossils were already described by Morales *et al.*, (2005) where they were attributed to *Sivaonyx africanus*. However, closer comparison of the material with *S. africanus* (Figs. 2 I,Q,P) from Klein Zee (M1/ in Stromer, 1931) and *S. hendeyi* from Langebaanweg (Hendey, 1978; Morales *et al.*, 2005) reveals that not only are they smaller than these species, but they are also somewhat divergent morphologically. These specimens are too large to belong to the other species from Lukeino, *Sivaonyx soriae*, known by lower m/1 and a lower jaw.

Measurements of the teeth are Bar 1720'00, left P4/ (L = 14.8 mm, B = 15 mm). Bar 1082'01, right M1/ (L = 12.3, B = ca. 18 mm) (Fig. 4).

#### *Sivaonyx hendeyi*

(Morales, Pickford & Soria, 2005)

**Holotype:** PQ-L 50000 left mandible with p/4-m/2 and associated P4/ (Hendey, 1978, Fig 9A, 10) (Figs. 2 D, O, 3 C, F).

**Type locality:** Langebaanweg, South Africa.

**Age:** Lower Pliocene.

**Original diagnosis:** *Enhydriodon* of large size, dentition bunodont, m/1 with talonid occupied by an enormous hypoconid surrounded by a hyperdeveloped entoconid. P4/ with well developed cingulum, strong parastyle and relatively poorly developed hypocone.

**Emended diagnosis:** *Sivaonyx* of medium to large size. m/1 robust, with the paraconid in the shape of a dune, located in an antero-lingual position. Protoconid higher than the metaconid, with complicated morphology. Anterior valley of the trigonid closed. Protoconulid very well developed. Talonid short and very wide, dominated by an extensive but relatively low hypoconid. p/4 with very robust and high posterior cuspid located in a buccal position, with a small lingual platform. P4/ with sub-quadrate outline. Paracone-metastyle compressed transversely, with a small notch between them. Parastyle of medium size. Buccal cingulum strong joining the metastyle and parastyle. Protocone well separated from the paracone but joined to it by a crista obliqua which touches the lingual crest of the paracone. Anterior valley present, but of modest dimensions. The hypocone is low and extensive, contacting the protocone and closing the tooth lingually. The median valley of the tooth is wide.

**Discussion:** We think that *S. hendeyi* and *S. africanus* are very close, but there are some differences between them; mainly the development of the basal cingulum of the p/4 and m/1, more developed in *S. hendeyi*, and to a lesser degree the morphology of the talonid of m/1, that is more flattened in *S. africanus* (Fig. 2 P). The separation of the paraconid-metaconid is also greater in *S. africanus*, and the morphology of the paraconid which is somewhat bunodont in *S. hendeyi*.

***Sivaonyx ekecaman* (Werdelin, 2003) =  
*Enhydriodon* sp. Morales, Pickford & Soria, 2005**

**Type locality:** Kanapoi, Kenya.

**Locality:** Sagatia, Mabaget Formation, Baringo District, Kenya.

**Material:** BAR 1231'01, left P3/ (Sagatia, Mabaget Formation); BAR 416'00, left m/1 (Mosionin, Mabaget Formation); BAR 720'03, fragment of left mandible (Sagatia, Mabaget Formation); BAR 566'05, left P4/ (Sagatia, Mabaget Formation); BAR 567'05, left m/1 (Sagatia, Mabaget Formation).

**Description:** BAR 1231'01 (Morales *et al.*, 2005, Fig. 9, I) is a left P3/. It is almost circular in occlusal outline, with an incisiviform aspect. It has a conical main cusp, somewhat bunodont, with a smooth, low posterior crest, a wide anterior platform, and the tooth is completely surrounded by a basal cingulum.

BAR 566'05 is a left P4/ (Figs. 2, E, 3 G). The occlusal outline is subquadrate, the paracone is massive with a rounded external wall and which has three crests emanating from its summit; a short anterior one which contacts the posterior crest of the parastyle basally, another short one that is separated from the metastyle by a deep notch, and a lower third one which contacts the internal crest (crista obliqua) of the protocone. The metastyle is short, also massive, but retains a certain amount of transverse compression. The parastyle is well developed, almost attaining the size of the metastyle. A strong buccal cingulum joins the metastyle to the parastyle. The protocone is well separated from the paracone, and is high and large, but is not as big as the paracone. A crista obliqua contacts the lingual crest of the paracone. Between this crest and the lingual wall of the paracone and parastyle there is a deep valley which receives the posterior cuspid of the p/4 during occlusion. The posterior crest of the protocone is subdivided, forming an extra cusplet between the protocone and hypocone. The hypocone is high and conical, with a small anterior crest, a second somewhat larger one which resembles a posterior cingulum reaching the base of the metastyle. Lingually the hypocone is quite extensi-

ve, but does not fill the medial valley of the tooth, but does divide it into two deep parts, an anterior one which occludes with the paraconid, and a posterior one occluding with the protoconid of the corresponding lower tooth. The lingual cingulum of the protocone is fine.

BAR 720'03 (Morales *et al.*, 2005, Fig. 9, G) is a fragment of left mandible with the incompletely erupted p/4 and the trigonid of the m/1 (Fig. 2, K). The trigonid of m/1 is wide with low pyramidal cusps. The paraconid is in an anterior position and has a small paraconulid close to it. The protoconid is the largest of the three cusps, and has a small but distinct protoconulid attached to it posteriorly. The metaconid is higher than the paraconid and is pyramidal. The trigonid valley is wide and completely surrounded by the main cusps. The p/4 is robust and in occlusal view is subtriangular with rounded corners. The main cusp is pyramidal and there is a small anterior cusplet, which emerges from the cingulum, and a posterior one which is high and displaced buccally. There is a wide basal platform disto-lingually. The tooth possesses a strong basal cingulum.

BAR 416'00, is a left m/1 (Morales *et al.*, 2005, Fig. 9, H) (Fig. 2, L). Only the trigonid is preserved. Outstanding is the strength of the protoconid, which is low, with swollen posterior and interior crests. The paraconid is located in a very anterior position, and is separated from the protoconid by a wide valley. The buccal cingulum is strongly developed. The trigonid measures ca 14 mm long and ca 12 mm wide.

BAR 567'05, is a left m/1 (Figs. 2, J, 3 B). The tooth is robust with a dune-shaped paraconid located in an anterior position. The protoconid is massive, bigger than the metaconid, but lower than it. Internally these two cusps are united by two crests which close the anterior valley of the trigonid. A well developed protoconulid occurs on the posterior protoconid crest. The talonid is short and very wide, with a deep central valley surrounded by four peripheral cuspid of which the hypoconid is the largest. A hypoconulid that is subdivided into two cusplets is located in a posterior position. The entoconid is also subdivided and extends to the base of the metaconid. There is a strong basal cingulum anteriorly and lingually which fades out at the base of the metaconid.

Measurements of the teeth are left P3/ (L = 10 mm; W = 8.5 mm); left P4/ (L = 14.7 mm; W = 17.5 mm), left p/4 (L = 11.1 mm; W = 8.4 mm), left m/1 trigonid (W = 12.8 mm), left m/1 (L = 20.1 mm; W = 13.0 mm (Fig. 4).

**Discussion:** Part of the material mentioned above was attributed by Morales *et al.*, 2005 to *Enhydriodon*

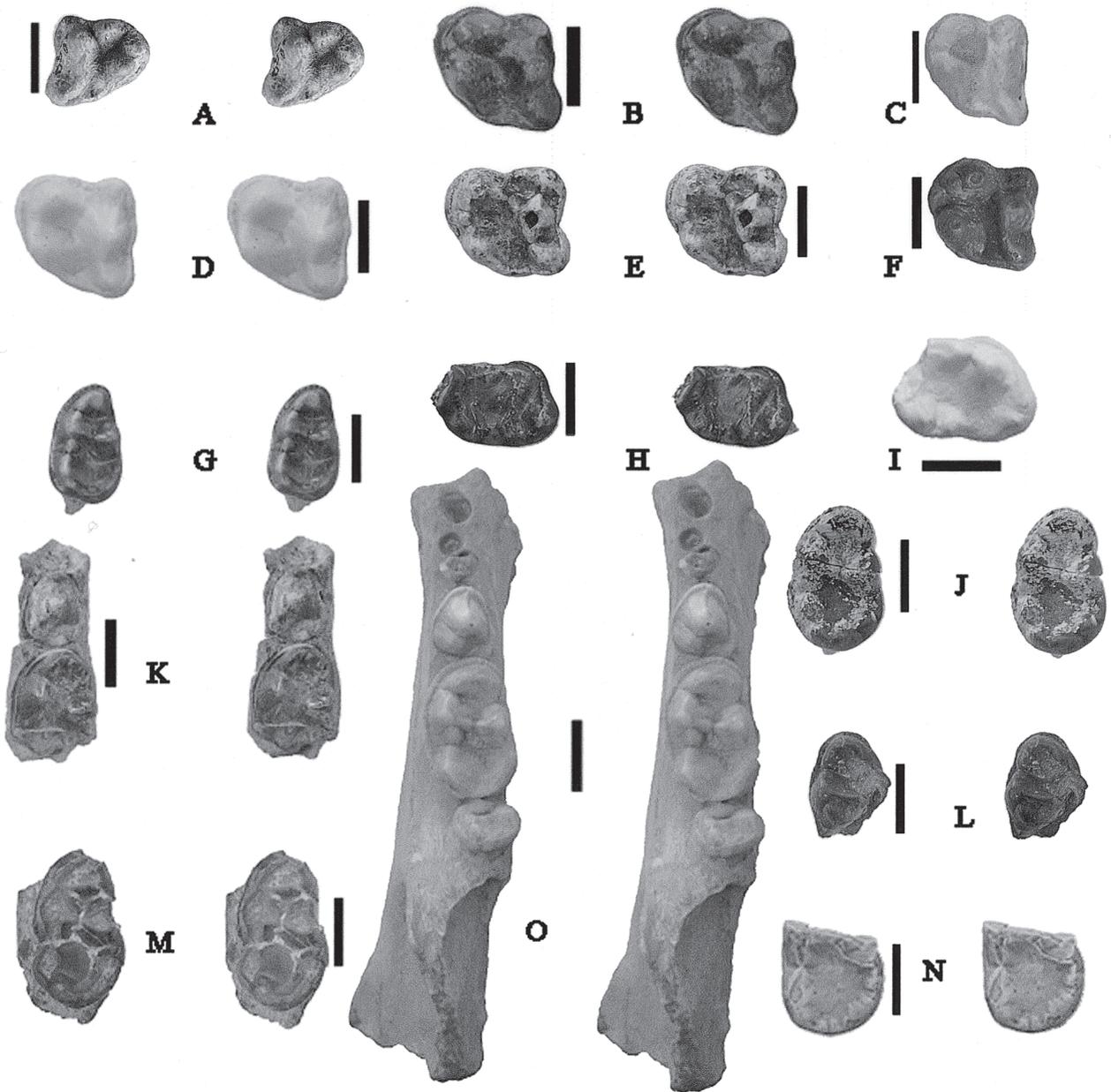


Fig. 2A-O.—Bunodont otters from Africa, India and Europe (scale: 10 mm). A) *Paludolutra lluecai* from Conclud, Spain, right P4/, stereo occlusal view of cast; B) *Sivaonyx senutae* sp. nov. Bar 1720'00, from Lukeino, Kenya, holotype left P4/, stereo occlusal view; C) *Sivaonyx bathygnathus* M 12352 from Hasnot, Pakistan, left P4/, occlusal view of cast of holotype; D) *Sivaonyx hendeyi*, PQL 50000 from Langebaanweg, South Africa, left P4/, stereo occlusal view of cast; E) *Sivaonyx ekecaman* Bar 566'05, from Sagatia, Kenya, left P4/, stereo occlusal view; F) *Enhyriodon falconeri* M 4847, from the Siwalik Hills, India, holotype left P4/, occlusal view; G) *Sivaonyx soriae* sp. nov. Bar 1984'05, from Lukeino, Kenya, paratype left m/1, stereo occlusal view; H) *Sivaonyx senutae* sp. nov. Bar 1082'01, from Lukeino, Kenya, paratype right M1/, stereo occlusal view; I) *Sivaonyx africanus* 1930 XI 1 from Klein Zee, South Africa, right M1/, occlusal view of cast; J) *Sivaonyx ekecaman*, Bar 567'05 from Sagatia, Kenya, left m/1, stereo occlusal view; K) *Sivaonyx ekecaman*, Bar 720'03 from Sagatia, Kenya, left p/4 half m/1 in mandible, stereo occlusal view; L) *Sivaonyx ekecaman*, Bar 416'00 from Mosionin, Kenya, anterior part of left m/1, stereo occlusal view; M) *Sivaonyx kamuhangirei* sp. nov. unnumbered specimen from Kazinga, Uganda, holotype left m/1, stereo occlusal view; N) *Sivaonyx kamuhangirei* sp. nov. NK 1988'89 from Warwire, Uganda, paratype talonid of left m/1, stereo occlusal view of cast; O) *Sivaonyx hendeyi* PQL 50000 from Langebaanweg, South Africa, left mandible, stereo occlusal view of cast of holotype.

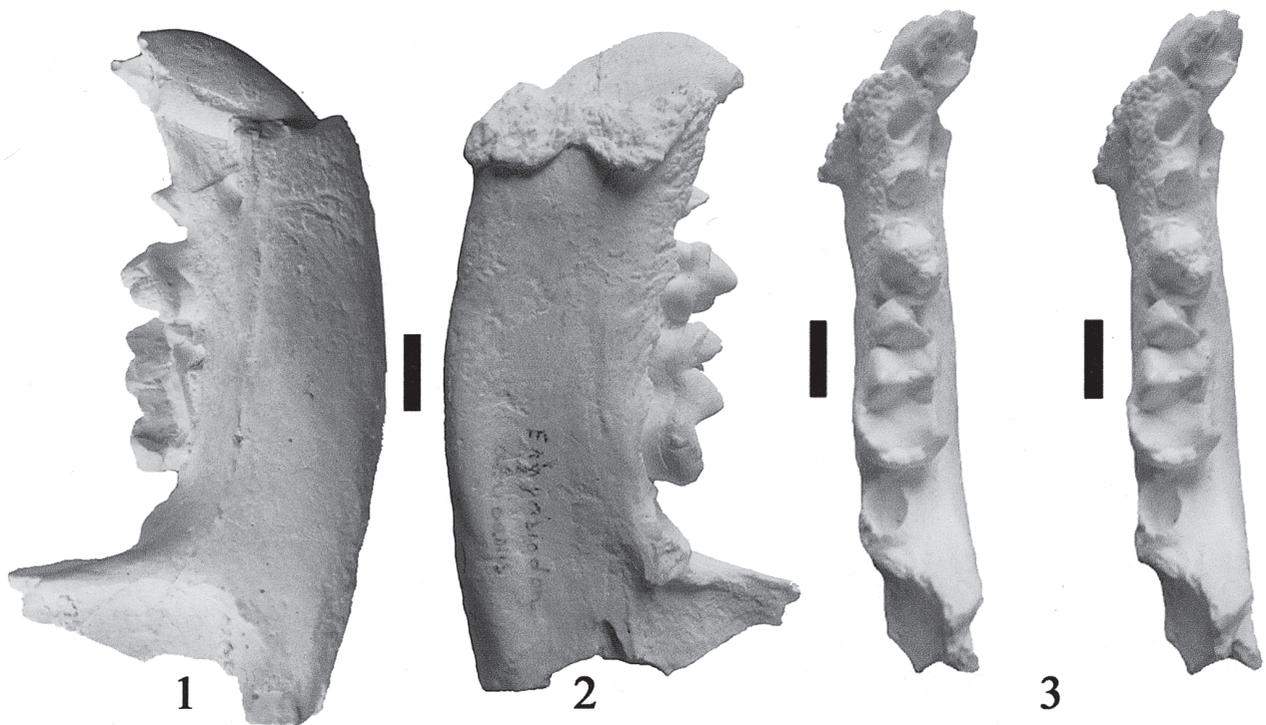


Fig. 2P.—*Sivaonyx africanus* 1930 XI 1 from Klein Zee, South Africa, right mandible, 1) lingual view, 2) buccal view of cast, 3) stereo occlusal view of cast.

*don* sp., but with the discovery of a P4/ of the species we now consider that it is closer to *Sivaonyx* than to *Enhyriodon*. This is confirmed to a great extent by examination of the P4/ of the Mabaget otter (see below) and that of the Langebaanweg species (Hendey, 1978) both of which differ from the Indian species *Enhyriodon falconeri* and *Enhyriodon sivalensis* but are closer morphologically to *Sivaonyx*. There are differences from *Sivaonyx* including the greater degree of bundonty and the larger dimensions, but the underlying morphology and disposition of the cusps are closer to *Sivaonyx* than to *Enhyriodon*. It is possible that these African bundont otters belong to a distinct genus, but for the time being we prefer to class them with *Sivaonyx*.

The new teeth described here lead us to differentiate this form from the *Sivaonyx* specimen from the Lukeino Formation which has a P4/ with a smaller parastyle, more sectorial paracone and metastyle, with barely any sign of a notch between them. The protocone is smaller and is located close to the paracone, without developing an anterior valley. Finally the hypocone is less voluminous and the internal valley of the tooth is continuous and not subdivided.

In comparison with *Sivaonyx hendeyi* the differences between the P4/s are minor, but quite clear. In certain measure, *S. hendeyi* shows a morphology intermediate between that of the Lukeino *Sivaonyx* and that of *S. ekecaman*. In *S. hendeyi* there is an incipient notch between the paracone and parastyle, but it has conserved a sectorial morphology (albeit quite blunt). The parastyle is small, but the protocone is equal to that of *Sivaonyx ekecaman*, being well separated from the paracone, making room for an incipient anterior valley. In contrast the hypocone appears to be less developed, although it is extensive and its anterior crest developed to the extent of closing the lingual wall of the tooth where it contacts the protocone. This morphology differs not only from the Lukeino *Sivaonyx* but also from *Sivaonyx ekecaman*. Likewise there are significant differences in the morphology of the m/1. In *S. hendeyi* the trigonid and talonid are about the same width, whereas in *Sivaonyx ekecaman* the difference in width is notable. The protoconid of *S. hendeyi* is very complex in contrast with the relatively simple situation in *Sivaonyx ekecaman*. But above all, there are differences in the morphology of the talonid, which in *S. hendeyi* is dominated by a large hypoco- nid and a strong entoconid making the central

valley small and narrow, differing greatly from the wider, deeper valley in *Sivaonyx ekecaman*.

The P4/ of *Sivaonyx ekecaman* is morphologically different from that of the bunodont viverrid *Pseudocivetta ingens*, although both are rather bunodont and roughly square in occlusal outline (Petter, 1969).

### *Sivaonyx kamuhangirei* nov. sp.

**Synonymy:** 1991, large non fish-eating otter. Petter *et al.*, p. 949.

**Type locality:** Kazinga, Uganda.

**Holotype:** left m/1 (Figs. 2 M, 3 D).

**Paratype:** NK 1988'89, talonid of left m/1 from Warwire, Uganda (Fig. 2 N).

**Derivatio nominis:** The species name honours Dr Ephraim Kamuhangire, Director of the National Museum of Uganda.

**Diagnosis:** Large *Sivaonyx* in which the protoconid of m/1 is larger than the metaconid. Talonid large and very wide, dominated by a vast hypoconid and a strong entoconid, which makes the central valley small and narrow with low relief.

**Differential diagnosis:** It differs from other species of the genus by its greater dimensions. It differs from *S. africanus* and *S. ekecaman* by the lower relief of the talonid cuspids and from *S. hendeyi* by the much flatter talonid valley.

#### **Description:**

*Kazinga.* Left m/1 is a large tooth, the largest known among the bunodont otters. The cuspids are quite worn and the base of the paraconid and metaconid are damaged. The tooth is robust, with the paraconid located in an anterior position. The protoconid is massive, being bigger than the metaconid. Internally these two cusps are united by two crests which close the anterior valley of the trigonid. The talonid is big and very wide, dominated by a huge hypoconid and a strong entoconid which make the central valley small and narrow with weakly pronounced relief. There is a strong basal cingulum buccally and anteriorly.

The tooth measures (L = 26.0 mm; W = 15.9 mm; Fig. 4).

*Nkondo:* NK 1988'89 is a fragment of left m/1 comprising the talonid and the rear part of the trigonid (Petter *et al.*, 1991). Its dimensions are comparable to the molar described above and the cuspids of the talonid are less worn. The talonid is dominated by a low but extensive hypoconid and a crescentiform entoconid which borders the lingual part of the talonid and which has various incisions giving it a beaded appearance. The talonid valley is narrow with low relief.

The talonid measures (W = 14.4 mm).

**Discussion:** The dimensions of these two teeth are markedly greater than the largest of the previously described African bunodont otters such as *Sivaonyx africanus*, *Sivaonyx hendeyi*, *Sivaonyx soriae* nov. sp. and *Sivaonyx senutae* nov. sp. from Lukeino and *S. ekecaman*. Morphologically *S. kamuhangirei* is rather divergent from these species, differing from *S. africanus* and *Sivaonyx soriae* by the lower relief of the cuspids of the talonid, a feature in which it approaches *S. hendeyi*, although in *S. kamuhangirei* the relief of the hypoconid is even lower and the talonid valley notably flatter.

**General discussion:** In our opinion the otters described here, together with the species *S. hendeyi* and *Sivaonyx africanus* (Stromer, 1931), comprise a homogeneous group which can be classified into a single genus. The shared features that unite these species are the position of the protocone in the P4/ which is far from the paracone, and the development of an anterior valley near the junction of the protocone and paracone. In *S. africanus* these characters are present but weaker than in *S. hendeyi* and *S. ekecaman*, the three species forming a morphocline with respect to these features. Hendey (1978) already noted a similar trend in the Langebaanweg, South Africa, otters from Beds 3aS (higher crown, less bulbous cusps) and 3aN (lower crowned and more bulbous cusps). It should be noted that the talus (PQL 50117) tentatively attributed to *Enhydriodon africanus* by Hendey (1978) belongs to *Orycteropus* (Pickford, 2005).

Comparison of the P4/ of these three species with the Italian Late Miocene otters (Hürzeler, 1987) and with *Paludolutra lluecai* from Spain (Figs. 2 A, 6 B) (Alcalá, 1994; Morales *et al.*, 2005) reveals a clearly different structure of the P4/ which in *Paludolutra campanii* and *Paludolutra maremmana* (the latter is extraordinarily close to *P. lehmani* from Spain which we consider is a synonym of *P. lluecai*) possesses a protocone which is close to the paracone, resembling the structure of the P4/ of more usual mustelids (*Mustela*, *Martes*, etc.), consequently there is no development of an anterior valley near the junction of the protocone and paracone, and only a cingulum united to the parastyle.

The differences between *Paludolutra* and *Sivaonyx bathygnathus*, judging from the P4/ of the latter species described by Pilgrim (1931) (Fig. 2, C) are the same as those pointed out above. *S. bathygnathus* has a protocone far from the paracone and there appears to be an anterior valley. Because of this we classify the four sub-Saharan species in the genus *Sivaonyx*.

Differences from *Enhydriodon* are more difficult to establish. Traditionally, this genus has been envi-

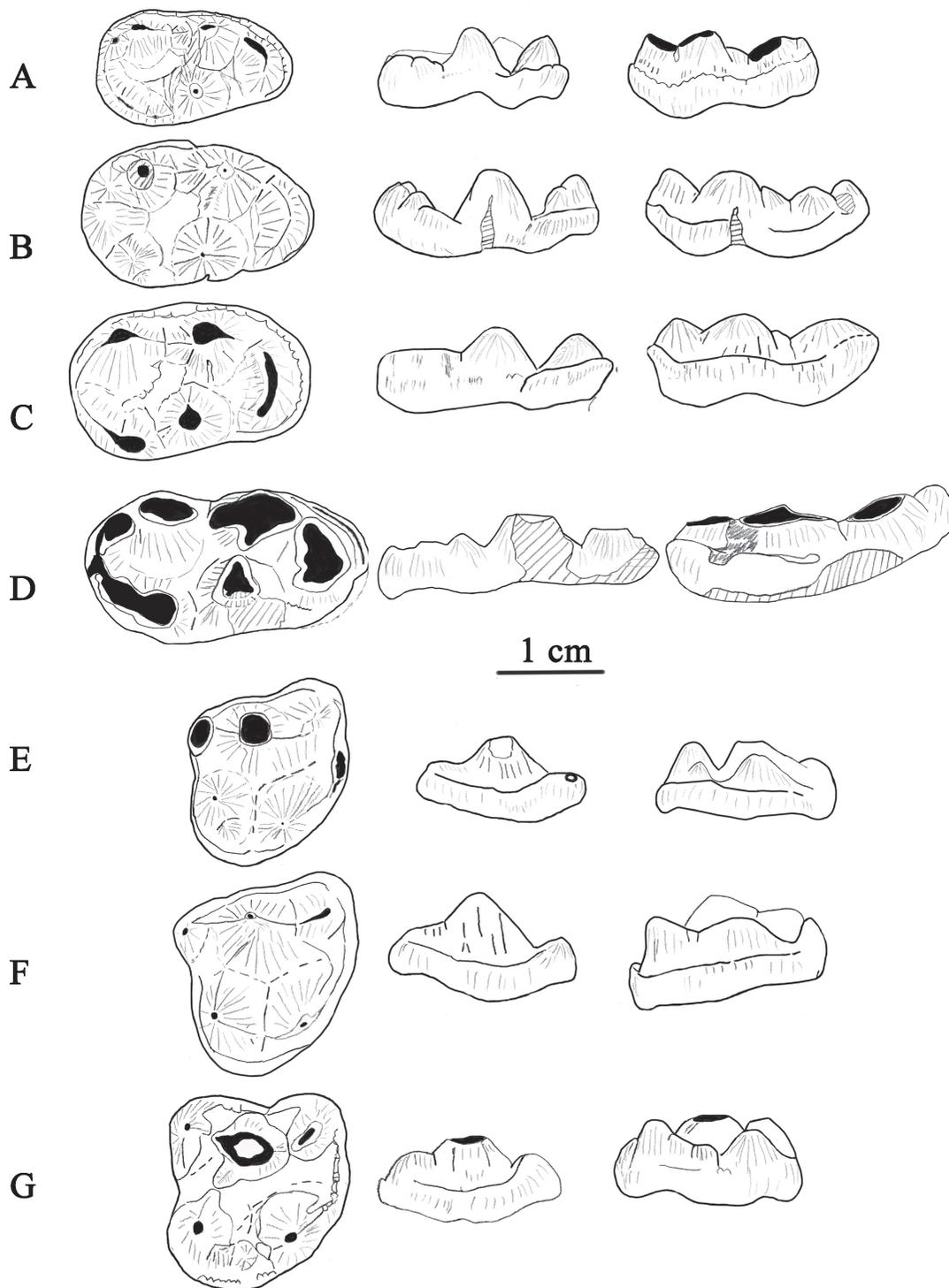


Fig. 3.—Bunodont otters from Africa. A) *Sivaonyx soriae* sp. nov. Bar 1984'05, from Lukeino, Kenya, paratype left m/1, occlusal, lingual and buccal view; B) *Sivaonyx ekecaman*, Bar 567'05 from Sagatia, Kenya, left m/1, occlusal, lingual and buccal view; C) *Sivaonyx hendeyi* PQL 50000 from Langebaanweg, South Africa, left mandible, occlusal, lingual and buccal view of cast of holotype; D) *Sivaonyx kamuhangirei* sp. nov. unnumbered specimen from Kazinga, Uganda, holotype left m/1, occlusal, lingual and buccal view; E) *Sivaonyx senutae* sp. nov. Bar 1720'00, from Lukeino, Kenya, holotype left P4/, occlusal, buccal and lingual view; F) *Sivaonyx hendeyi*, PQL 50000 from Langebaanweg, South Africa, left P4/, occlusal, buccal and lingual view of cast; G) *Sivaonyx ekecaman* Bar 566'05, from Sagatia, Kenya, left P4/, occlusal, buccal and lingual view.

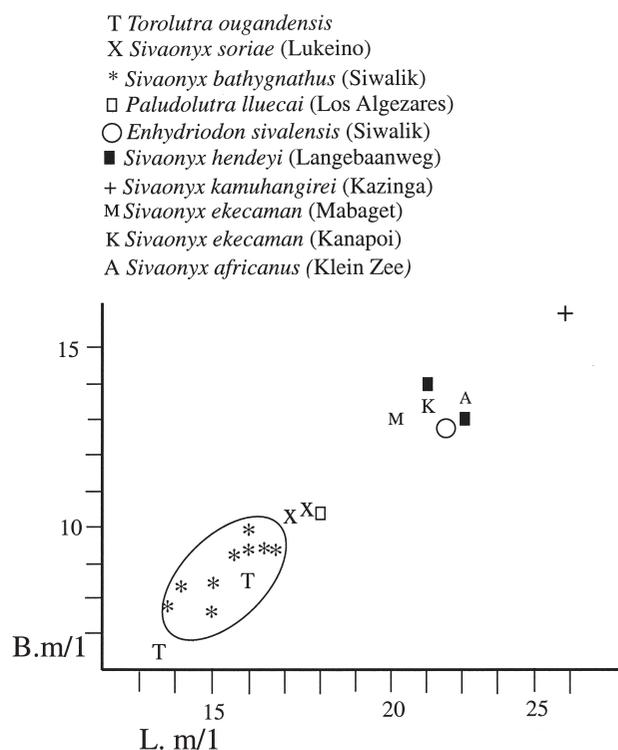


Fig. 4.—Plot of length/width relationship of m/1 of *Torolutra*, *Paludolutra*, *Sivaonyx* and *Enhydriodon* species.

saged as descending from *Sivaonyx*, but available data render this vision difficult to demonstrate satisfactorily. *Enhydriodon falconeri* and *Enhydriodon sivalensis* (Pilgrim, 1931; Matthew, 1929; Willemssen, 1999) reveal a notable mastoidisation of the P4/ especially reflected in the size and robustness of the hypocone of the P4/ (Fig. 2, F). These two species possess the protocone close to the paracone. This, combined with the hyperdevelopment of the hypocone, could give rise to the characteristic morphology of *Enhydriodon*. In general the P4/ of *Enhydriodon* is wider than long, whereas in *Sivaonyx* the P4/s are longer than wide.

The relationships of the African bunodont otters to those from the Yuanmou Basin, Yunnan, China (Fang Qian, 1993) attributed to *Enhydriodon*, remain to be discerned. The same applies to the North American species (Repenning, 1976). Willemssen (1992, 1999) aligned the North American material with *Paludolutra*.

Of the African species described here *S. ekecaman* is the one that shows the greatest amount of mastoidisation of the P4/, and moreover the tooth is wider than long. (in *S. hendeyi* from Langebaanweg, the mastoidisation is weaker and the length and breadth of the tooth are similar). However, *S.*

*ekecaman* has a moderately developed hypocone, almost the same size as the protocone, which makes the occlusal outline clearly different from that of other species of *Sivaonyx*. It seems likely that the African forms do not have a close relationship with *Paludolutra* (a more primitive group) but are instead related to *Sivaonyx*, a genus to which several species show convergences.

None of the African otters (for the moment) possess P4/s with morphology similar to that of *Enhydriodon*. This is clearly observable in the morphology of *E. falconeri* which combines a strong conical protocone close to the paracone with an enormous hypocone which occupies almost 2/3 of the lingual part of the tooth (Fig. 2, F). In addition the external cusps, paracone and metastyle are quite conical.

In the position and shape of the protocone, *Enhydriodon* and *Paludolutra* appear to be closer to each other than either is to *Sivaonyx*. However they differ from each other by the different development of the hypocone of P4/ and the sectorial morphology of the paracone-metacone.

For these reasons we prefer to recognise three groups of bunodont otters, firstly Indian *Enhydriodon falconeri* (Fig. 2, F) and *Enhydriodon sivalensis* (the latter species requires revision), secondly in Europe there is the genus *Paludolutra* represented by *Paludolutra campanii* and *Paludolutra lluecai* (Fig. 5), which differ from *Sivaonyx senutae* nov. sp. by the separation between the protocone and paracone (very short in *Paludolutra* and wide in *S. senutae*). Because of these differences we consider that *S. senutae* does not fit comfortably into either *Paludolutra* or *Enhydriodon*. Thirdly, there is the *Sivaonyx* lineage with both Indian and African species.

Taking into account the wide separation of the protocone and paracone in *S. senutae* and the material from South Africa originally attributed to *Enhydriodon hendeyi* it is likely that the African fossils may belong to *Sivaonyx* but this raises another problem. The major trouble is that the holotype of *Sivaonyx* (a fragmentary mandible with broken m/1) is inadequate. However, if we accept that the P4/ described by Pilgrim (1931, 1932) belongs to *Sivaonyx bathygnathus*, then it is clear that this genus differs not only from *Enhydriodon* but also from *Paludolutra*. It differs from *Enhydriodon* by the weaker development of the hypocone and by the more sectorial paracone-metastyle. It differs less from *Paludolutra*, as shown in the drawing by Pilgrim (1931) where it appears that the paracone and protocone of *Sivaonyx* are widely separated (Fig. 2, C). It is thus possible that it is close to the morphology in P4/, BAR 1720'00.

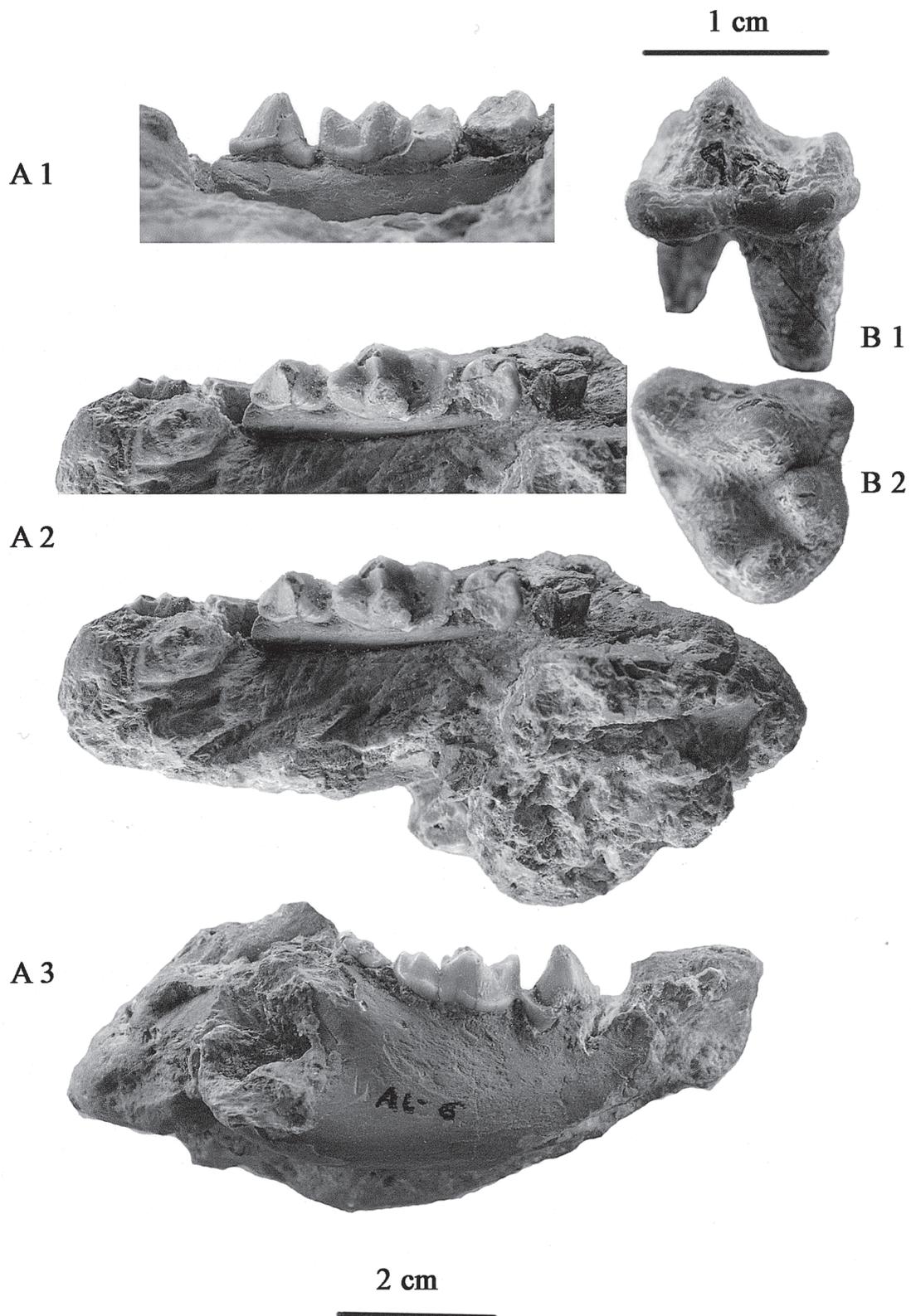


Fig. 5.—*Paludolutra lluecai* from the Middle Turolian of Spain. A) AL-6 Holotype. Left mandible from Los Algezares, Teruel. 1) lingual view, 2) stereo occlusal view, 3) buccal view; B) Right P4/ from Concud, Teruel. 1) buccal view, 2) occlusal view.

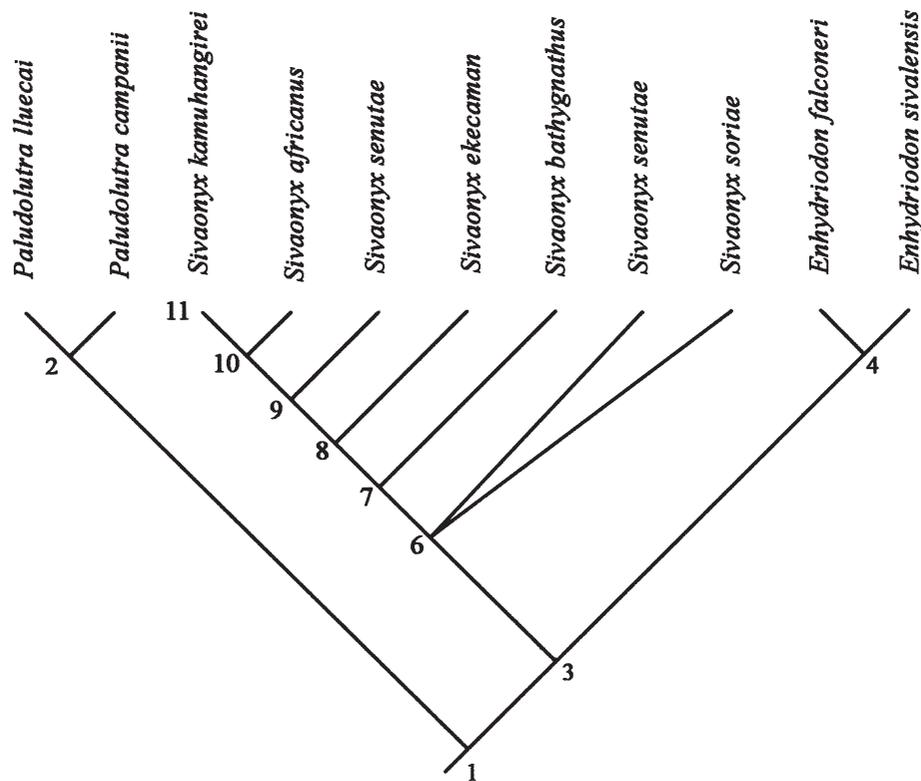


Fig. 6.—Proposed phylogeny of bunodont otters. 1) Enhydriodontini: m/1 talonid enlarged, with entoconid and hypoconid developed. P4/ with conical protocone; 2) *Paludolutra*: plesiomorphic genus; 3) m/1 with low trigonid, parastyle present, development of anterior valley and hypocone strong, P4/ with strong hypocone and subquadrangular occlusal outline; 4) *Enhydriodon*: P4/ with protocone and hypocone hyper-developed and bunodont trend of the paracone-metastyle blade, Strong parastyle; 5) *Sivaonyx*: P4/ with protocone well separated from paracone and development of an anterior valley; 6) Paracone-metastyle blade of the P4/ with notch; 7) P4/ with bunodont paracone-metastyle blade and strong parastyle; 8) M1/ with metacone small with respect to the paracone, and internally displaced. Protocone strong and in an anterior position, flattened central valley; 9) m/1 talonid short and very wide, dominated by an extensive but relatively low hypoconid; 10) m/1 with enlarged trigonid, with the paraconid in the shape of a dune, located in an antero-lingual position; 11) m/1 talonid valley flattened, large size.

In conclusion we attribute the African bunodont otter fossils to the following taxa.

Lukeino BAR 1984'05. *Sivaonyx soriae* nov. sp.

Lukeino BAR 1720'00. *Sivaonyx senutae* nov. sp.

Sagatia BAR 566 and 567'05, Kanapoi. *Sivaonyx ekecaman* (Werdelin, 2003).

Kazinga and Warwire. *Sivaonyx kamuhangirei* nov. sp.

Klein Zee. *Sivaonyx africanus* (Stromer, 1931).

Langebaanweg. *Sivaonyx hendeyi* (Morales *et al.*, 2005).

The detailed phylogenetic relationships between the various bunodont otters is not clear, and will remain so until a revision of the Siwalik material is done. If we accept that *Sivaonyx* is valid, and that it is different from *Paludolutra*, then we consider that all the African forms may have been derived from *Sivaonyx* (if evidence to the contrary becomes avail-

able, then a new genus may be necessary for the African forms). This group of bunodont otters is very homogeneous with the exception of *Sivaonyx ekecaman* which possesses features that in principal could be considered typical of *Enhydriodon*, such as the bunodont morphology of the paracone-metastyle blade and the large dimensions of the P4/. However, as pointed out above, there are other characters that align the species more closely to *Sivaonyx*, and we are inclined to accent this option. Both possibilities imply that there are convergences. Figure 6 shows our preferred phylogeny.

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