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Author(s): Denis Geraads, Zeresenay Alemseged, René Bobe, and Denné Reed

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## ENHYDRIODON DIKIKAE, SP. NOV. (CARNIVORA: MAMMALIA), A GIGANTIC OTTER FROM THE PLIOCENE OF DIKIKA, LOWER AWASH, ETHIOPIA

DENIS GERAADS,<sup>\*,1</sup> ZERESEAY ALEMSEGED,<sup>2</sup> RENÉ BOBE,<sup>3</sup> and DENNÉ REED<sup>4</sup>

<sup>1</sup>UPR 2147 du CNRS, 44 rue de l'Amiral Mouchez, 75014 PARIS, France, denis.geraads@evolhum.cnrs.fr;

<sup>2</sup>Department of Anthropology, California Academy of Sciences, San Francisco, California 94118, U.S.A., zalemseged@calacademy.org;

<sup>3</sup>Department of Anthropology, University of Georgia, Athens, Georgia 30602, U.S.A., renebobe@uga.edu;

<sup>4</sup>Department of Anthropology, University of Texas at Austin, Austin, Texas 78712, U.S.A., reedd@mail.utexas.edu

**ABSTRACT**—We describe here a new species of gigantic otter, *Enhydriodon dikikae*, sp. nov., from the Pliocene of Dikika, in the lower Awash valley of Ethiopia. The holotype consists of an associated snout and mandible, and is the most complete fossil specimen of a large bunodont otter. In some features, such as its very large size, the loss of anterior premolars, the tall protocone of P4, and the divided paraconid of m1, this species illustrates the culmination of general trends in this group, but the most remarkable part of its dentition is the broad incisor arch and powerful canine battery. The purported distinction between *Enhydriodon* and *Sivaonyx* is discussed, and the hypothesis of distinct African and Asian lineages is rejected. Postcranial remains confirm that *Enhydriodon dikikae*, sp. nov., was probably mostly terrestrial, but its diet remains uncertain, as none of the suggested preys fully explains the anatomical adaptations and relative abundance of this species.

### INTRODUCTION

The Hadar Formation crops out on both sides of the Awash River in the lower Awash Valley. On the right bank, south and east of the sites of Hadar and Gona, the Dikika Research Project (DRP) explores highly fossiliferous sediments that belong to this sequence, but collections made during the last few years mostly come from the Basal (>3.42 Ma) and Sidi Hakoma (3.42–3.24 Ma) Members (Alemseged et al., 2005, 2006; Wynn et al., 2006, 2008; Campisano, 2007). The most noticeable fossil find made by the DRP is a nearly complete skeleton of a child *Australopithecus afarensis* nicknamed 'Selam' (Alemseged et al., 2006). This extraordinary fossil and other hominin discoveries are associated with a rich mammalian fauna, among which is a new canid species recently described (Geraads et al., 2010). Here, we report new specimens of a gigantic otter, whose remains are found both in the Basal and Sidi Hakoma Members.

**Institutional Abbreviations**—**BMNH**, Natural History Museum, London; **KNM**, Kenya National Museums, Nairobi; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **NME**, National Museum of Ethiopia, Addis Ababa; **Bar**, prefix for specimens from Baringo in the Community Museums of Kenya.

### SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821

Family MUSTELIDAE Fischer, 1817

Genus *ENHYDRIODON* Falconer in Murchison, 1868

**Type Species**—*Enhydriodon sivalensis* Falconer in Murchison, 1868

*ENHYDRIODON DIKIKAE*, sp. nov.

**Type**—DIK-56-9, elements of a skull comprising the snout, part of the orbits, and all upper teeth except I1s and right I2, as

well as part of the lower jaw with left i3, both canines and both p4s, and the talonid of left m1 (Fig. 1, 2, 3D–F).

**Locality**—DIK-56 is located West of the Andalee ridge, in the Meselu drainage of the Dikika research area (coordinates WGS 84, UTM zone 37: E 683768, N 1225048), and stratigraphically belongs to the lower part of the Basal Member of the Hadar Formation; its age is greater than 3.4 Ma, and likely closer to 4 Ma. The specimen is housed in the NME.

**Etymology**—From the site of Dikika, which gave its name to the whole area.

**Referred Specimens**—DIK-24-1 is a piece of left mandibular corpus with m1, from the top of the Basal Member, ca. 3.45 Ma (Fig. 3A–C). DIK-44-1: a proximal left femur (Fig. 4C–D), and DIK-41-20: a distal right femur (Fig. 4E), are both from the base of the Sidi Hakoma Member, ca. 3.35 Ma. DIK-4-1 and DIK-9-1 are poorly preserved distal and proximal left femoral epiphyses with less secured stratigraphic provenience but from the same general area and comparable stratigraphic range, and perhaps belonging to the same individual. DIK-78-1 is a left humerus, from the Sidi Hakoma gastropodite horizon, ca. 3.3 Ma (Fig. 4A–B). All fossils are housed in the NME.

**Diagnosis**—A species of very large size with short and non-prognathic snout; orbit partially closed posteriorly. Broad and robust anterior dental arch, with I3 much larger than I1–I2, and robust canines inserted very laterally on the maxilla. Premolars anterior to P3 and p4 are lost; P4 is broad, with a protocone that is much larger than the hypocone, and located far from the paracone. The M1 is also broad, with a distolingually expanded hypocone. The mandibular corpus is deep, with an almost vertical anterior symphyseal border. The lower m1 has a broadened, subdivided paraconid, and shallow talonid basin.

**Description**—The most striking feature of the holotype is its very large size, more suggestive of a bear than of a modern otter. By comparison with related forms such as *Enhydriodon sivalensis*, or the modern *Enhydra lutris*, the skull of DIK-56-9 is considerably larger with an estimated length of about 25 cm. *Sivaonyx beyi* Peigné et al., 2008, with a m1 length about 2/3 that of

\*Corresponding author.

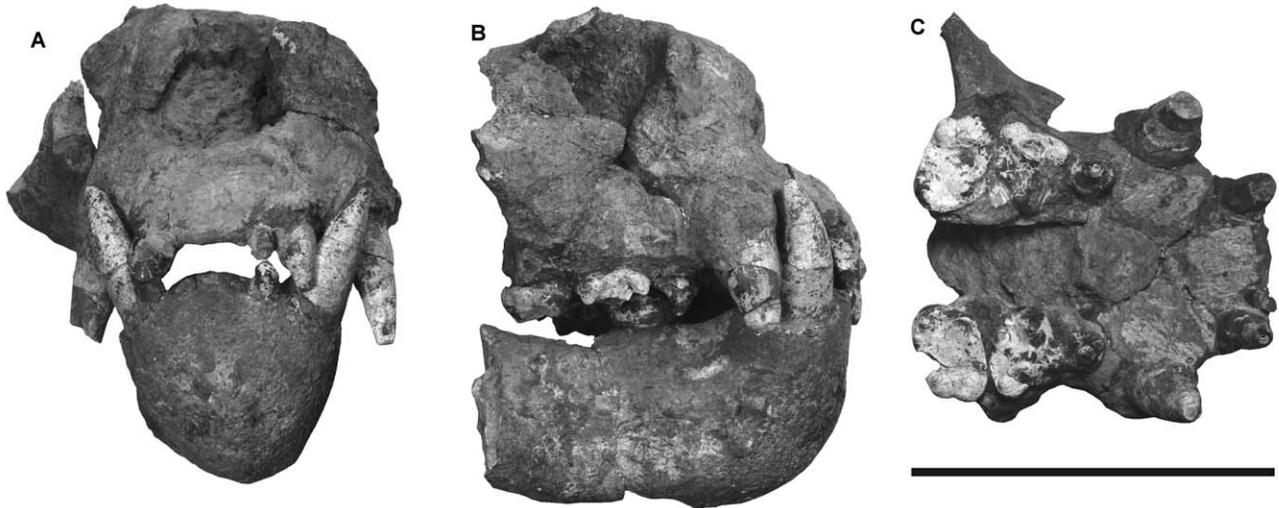


FIGURE 1. *Enhydriodon dikikae*, associated anterior part of the skull and mandible DIK-56-9, holotype, in **A**, anterior and **B**, lateral views; **C**, ventral view of the palate. Scale bar equals 10 cm.

DIK-56-9, was estimated to weigh about 60 kg; thus, taking into account the uncertainties in deriving body weight from m1 length, 100 kg is a minimal estimate for the Dikika otter, and 200 kg perhaps a more likely one.

The skull is broken behind the right postorbital process, and at the level of the left one, and a large flake of bone is missing on the dorsal surface. As a result we do not know whether a sagittal crest was present, but this is likely, because the postorbital process proceeds posteroventrally into a sharp crest, suggesting that the limits of the temporal muscle were well marked. The muzzle is short, with an anterior orbital border located above the posterior part of the canine. Anteriorly, the orbit is bordered by a thick dorsoventrally elongated lacrimal tubercle, protruding anterolaterally. The outline of the nasal aperture is not clear, because the interface between bones in this area and the covering matrix is not well defined, but the missing tips of the nasal bones were probably not very prominent. On the lateral sides of the aperture, the dorsal parts of the maxillae extend farther forward than their ventral parts, so that the part of the premaxillae bearing the incisors projects little rostrally, in contrast to most other carnivores. Overall, the front part of the snout is rather steep, as in modern *Enhydra*. The orbit is relatively small, with a diameter

that is less than the dorsoventral height of the root of the zygomatic arch below. The front wall of the latter (malar region) is oblique, but the posterior one is almost transverse; although incomplete, it is remarkably expanded dorsally behind the orbit, probably almost closing it posteriorly (Fig. 1B). The infraorbital foramen is incomplete, but was very large.

All left teeth from I3 to P4, as well as the right M1, are complete, and the crown base of the left I2 is also preserved, but I1s are missing. Wear is minimal, moderately affecting the tips of I3 and of the P4 hypocone. The most remarkable aspect of the dentition is the strength of the front teeth. The incisor arch is broad and moderately convex. Nothing can be said about I1, but I2 is small, and the distance between the I3s is far too long for four teeth of its size (two I1s and two I2s), so that the central incisors were certainly not closely pressed against each other. The I3s are much larger than I2, conical, somewhat 'hyaenoid' but with two weak keels that are almost medially and laterally located, with a weak lingual cingulum between them. A diastema longer than the I3s separates these teeth from the robust, conical, gently curved canines that have less developed mesiolingual and distal keels, with a faint lingual cingulum between them. They sit very laterally, their lingual border being more laterally placed than

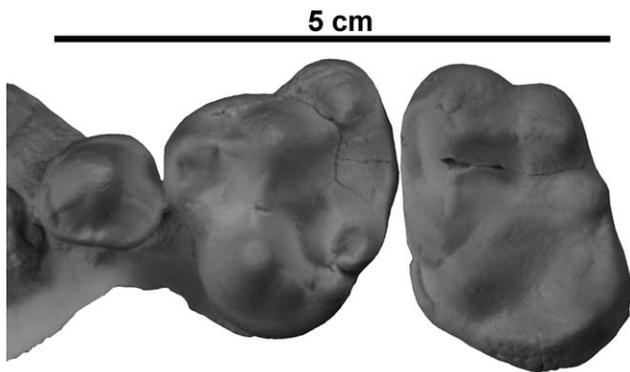


FIGURE 2. *Enhydriodon dikikae*, occlusal view of cast of the holotype; left P3-P4 and right reversed M1.

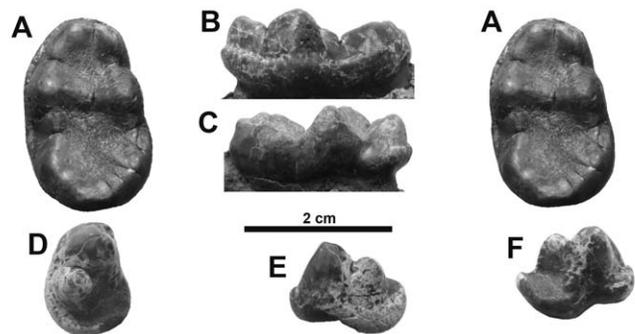


FIGURE 3. *Enhydriodon dikikae*. **A-C**, left lower m1 DIK-24-1 in **A**, stereo occlusal view, **B**, labial view, and **C**, lingual view. **D-F**, p4, DIK-56-9 (part of the holotype), in **D**, occlusal, **E**, labial, and **F**, lingual views.

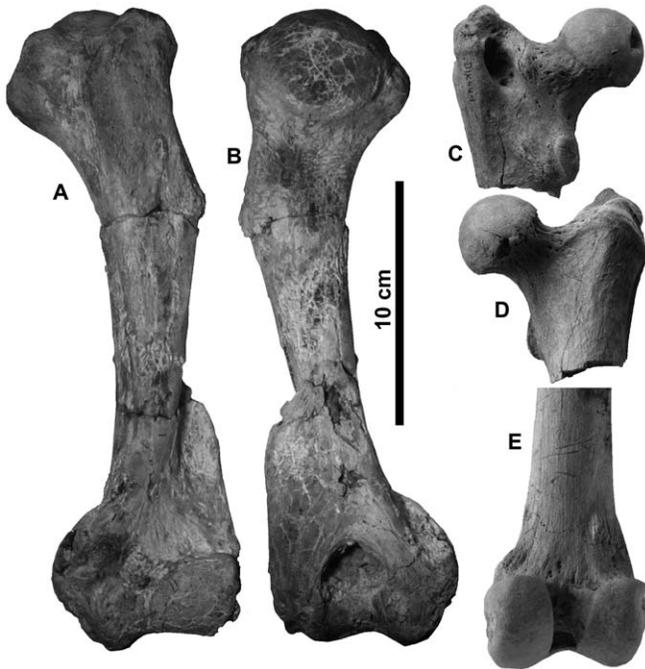


FIGURE 4. *Enhydriodon dikikae*. Referred limb bones. **A–B**, left humerus DIK-78-1 in **A**, anterior and **B**, posterior views. **C–D**, proximal left femur in **C**, posterior and **D**, anterior views. **E**, distal right femur, posterior view.

the lateral sides of I3, and almost as laterally as the labial side of P3. Measurements are given in Table 1.

Both P2s were lacking in life. The post-canine diastema is long (ca. 8 mm), but this is partly due to the lateral position of the canine. P3 consists of a simple conical cusp with basal distal flare, faint mesiolingual and distolabial keels, and is completely circled by a cingulum. P4 is trapezoidal but with a truncated distolingual corner. The paracone is by far the largest labial cusp; it bears a mesial crest connecting to a similar crest descending from the tip of the small parastyle; a distal crest connected to the metastyle, which is similar in size to the parastyle; and a mesiolingual crest directed towards the base of the protocone, but the valley between the paracone and the protocone is quite deep. The protocone is by far the largest lingual cusp; it is even larger than, and almost as high as, the paracone, and much larger and higher than the hypocone (accounting for the apical wear of the latter). A barely distinct accessory cusp closely abuts its distolingual flank, and a second, lower cusp blocks the entrance to the central valley, between protocone and hypocone. The hypocone occupies a relatively labial position, being only slightly more lingual than the protocone (with respect to the labial border of the tooth); a weak crest descends from its tip towards the center of the tooth. There is a faint labial cingulum, but no lingual cingulum. The M1 cusps are all much lower than those of P4; they are all located close to the margins of the tooth, and the lingual ones slope gently towards the center of the tooth, which is relatively flat. The paracone is longer and larger than the metacone, but has no labial expansion, so that the paracone-metacone axis is almost parallel to the labial side of the tooth. At the mesiolingual corner, the protocone and protoconule form a pair of closely positioned subequal tubercles, the protocone being only slightly larger. On the distal margin, the metaconule is small but quite distinct. There is a faint cingulum at the mesial bases of the paracone and protocone, but it expands distolingually into a very large hypocone.

The corpus mandibularis is deep, and the anterior symphyseal region is almost vertical. In both features, it sharply differs from that of the modern *Enhydra*, which has a shallow corpus and a very sloping symphysis. As for the upper jaw, which is broad, the mandible is remarkable for its very broad symphysis, and wide inter-canine distance, quite unusual for an otter. The left i3 is a conical tooth separated from the canine by a diastema, but the incisor alveolar border is too damaged to infer anything about other incisors. The canines are vertically inserted in lateral view, but divergent in front view; they are almost as large as the upper ones with their tips almost reaching the nasal aperture during occlusion. The first post-canine tooth is p4 (Fig. 3D–F), which has an ovoid outline, broader distally, with a main cuspid and a smaller distolabial one, appressed against the main one and with a distinct apex. The distal cingulum is not very robust, but nearly shelf-like distolingually. Of the m1, only the protoconid and part of the talonid are preserved. The latter consists of a shallow basin surrounded by low tubercles, of which only four are preserved, the hypoconid being only slightly larger than the others.

Specimen DIK-24-1 is a left mandibular corpus with a well-preserved m1 (Fig. 3A–C) that is significantly smaller than the incomplete m1 of DIK-56-9. The masseteric fossa almost reaches the level of m2. In comparison to DIK-56-9, where the corpus is of regular depth, DIK-24-1 is definitely deeper below p4 than below m2. On its m1, the trigonid is only slightly narrower than the talonid. The tooth has a broad mesial occlusal outline, because the paraconid is subdivided, forming a strong accessory ‘entoparaconid’ that increases the mesial width of the tooth and is antagonist of the post-protocone accessory cusps of P4. The talonid is similar to that of DIK-56-9, but the basin is slightly deeper and the hypoconid clearly predominant among the 8–10 more or less distinct marginal cuspid. A cingulum circles most of the trigonid, and fills the labial notch between trigonid and talonid. The alveolus shows that m2 was large.

The proximal left femur DIK-44-1 (Fig. 4C–D) and the distal right femur DIK-41-20 (Fig. 4E) were found in the same level, about 50 m apart on a flat area, and could be from the same individual, because their measurements are virtually identical to those of the complete femur AL-166-10 from the Sidi Hakoma Member at Hadar (Lewis, 2008). They are also morphologically very similar to the latter, sharing similar orientation of the head, large tubercle along the neck on the caudal side, medially prominent trochanter minor, and similar disposition of the distal condyles. Specimen DIK-4-1 is a weathered femur, lacking the head and neck. It differs in the orientation of its trochanter minor, which is directed less medially but more caudally. It is likely that all these specimens belong to *E. dikikae*; they are very large but also remarkably slender in comparison with the largest modern otters, *Pteronura* and *Enhydra*. Measurements are given in Table 2.

The humerus DIK-78-1 (Fig. 4A–B) is complete but weathered and its surface is heavily cracked. It is much longer and slightly more robust than that of *S. beyi* Peigné et al., 2008. The deltoid crest forms a strong lateral tubercle. The slightly incomplete lateral supracondylar crest was even longer than in *S. beyi*, but the medial epicondyle is much less prominent; the epitrochlear foramen is limited by a slender bar. The olecranon fossa is small, and more circular than in *S. beyi*. The distal articular surface is much deeper (proximodistally), especially the condyle that has a straight distal border.

**Comparisons and Discussion**—Known for almost a century and a half, large fossil bunodont otters (Enhydriodontini of Morales and Pickford, 2005) are mostly represented by fragmentary material that has been the subject of several studies (Verma and Gupta, 1992; Morales and Pickford, 2005; Morales et al., 2005; Pickford, 2007; Bonis et al., 2008; Peigné et al., 2008). They are known from the late Miocene to the late Pliocene of Africa and southern Asia, records outside these areas being doubtful

TABLE 1. Tooth measurements (in millimeters) of *E. dikikae*.

	I2		I3		Upper C		P3		P4		M1	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD*	BL
DIK-56-9	5.5	9.7	12.4	11.6	16.9	15	12.8	11.3	21	22.6	21.9	25.8
	c		p4		m1							
DIK-56-9			MD	BL	MD	BL	MD	BL				
DIK-24-1			—	—	—	—	ca.30	ca.20				
							26	16.2				

\*Maximum, lingual. **Abbreviations:** MD, mesiodistal; BL, buccolingual.

(Pickford, 2007). Pickford (2007) referred most Plio-Pleistocene Asian forms to *Enhydryodon* Falconer in Murchison, 1868, and the earlier ones to *Sivaonyx* Pilgrim, 1931, and all African forms to the latter. Reexamination of most of the relevant African and Asian material (except those housed in India) suggests, however, that the distinction between an African Plio-Pleistocene lineage and contemporaneous Asian forms is not well substantiated.

The diagnosis of *Enhydryodon* provided by Pickford (2007:185) reads as follows: “Large enhydryodontines 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 distolingually rather than distally, sometimes detached and blocking the lingual opening of the central valley. Upper dental formula 3-1-2-1.”

Bunodonty is a feature that is hard to evaluate objectively; although it is true that latter forms are more bunodont than earlier ones (like *S. bathygnathus* Lydekker, 1884), we did not observe any consistent difference between African and Asian forms in this regard.

Likewise, the difference in size between the protocone and hypocone is often subtle, and can be appreciated on a few specimens only. Yet, some specimens included in *Enhydryodon* by Pickford, such as BMNH M37155, do have a relatively small hypocone; there is a general trend for an increase in protocone size, apparently achieved in part by incorporating previously distinct accessory cups. The centrally oriented ridge on this cusp is missing on *E. falconeri*, as acknowledged by Pickford, but also on the type of *E. sivalensis* (BMNH M37153), whereas it is present in Africa on the Dikika specimens.

The post-protocone cusps are small accessory tubercles that seem to vary randomly from one specimen to the other, and it is hard to distinguish between a ‘post-protocone cusp’ and ‘post-protocone cusplets.’ It may be true that, on the few available specimens, the lingual connection between protocone and hypocone is more cusp-like in Asian *Enhydryodon* than in African forms, but its morphology and orientation seem to result more from the relative size and position of these main cusps than from an intrinsic difference. It is also cusp-like at Dikika.

TABLE 2. Limb-bone measurements (in millimeters) of *E. dikikae*.

	Functional length	Maximum proximal width	Articular AP shaft	Articular distal width	Maximum distal width
Humerus DIK-78-1	268	73	43	57	80
Femur DIK-4-1	ca. 270	—	—	—	61
Femur DIK-41-20	—	—	23	—	—
Femur DIK-44-1	—	78.3	—	—	65.5

**Abbreviation:** AP, anteroposterior.

Very few Asian *Enhydryodon* specimens preserve both the paracone and metastyle, but it is unlikely that the latter could have been almost as large as the former in BMNH M37153 (type of *E. sivalensis*) or BMNH M37154 or M37155 (*E. sivalensis*); only in the type of *E. falconeri* is the metastyle rather large, but even in this specimen it is not larger than in KNM KP-10034 from Kanapoi, type of *Enhydryodon ekecaman* Werdelin, 2003, or in Bar-566’05 from Sagatia referred to the same species but included in *Sivaonyx* by Pickford (2007).

The “deeply concave outer wall to the buccal cusp pair [of P4 ?]” (Pickford, 2007: 185) is observable on a few Asian specimens only (the best one being the type of *E. falconeri*), but we fail to see any significant difference in this regard with African ‘*Sivaonyx*.’

Finally, according to Pickford (2007:101), “*Sivaonyx* possesses a complete premolar row while *Enhydryodon* has lost the anterior upper premolars (presumably reflected in the lower jaw).” As no African fossil preserved the maxillary pieces before the Dikika discovery, this could not be verified in African specimens; however, DIK-56-9 preserves this region and lacks the anterior upper (and lower) premolars, and thus this trait does not distinguish the Asian and African forms.

In conclusion, we are unable to find any diagnostic morphological differences separating the South Asian from African lineages (Pickford, 2007:fig. 18). Cladistic analysis of this whole group would certainly be premature, because several species are known by a few isolated teeth only, and it may be that they should be divided into more than one genus. Yet, because the Dikika form is clearly more similar to *E. sivalensis*, type species of *Enhydryodon* Falconer in Murchison, 1868, than to *S. bathygnathus*, type species of *Sivaonyx* Pilgrim, 1931, we refer it to the former genus.

Several Pliocene and Pleistocene forms of this group have been named. *Enhydryodon dikikae* differs from all of them in (1) its large size, (2) the loss of all premolars anterior to p4, and (3) the division of the m1 paraconid; these characters alone warrant specific distinction. *Enhydryodon sivalensis* of the Siwaliks, probably of Late Pliocene age, is the only species of which we have some knowledge of the skull. The Dikika species differs from it in the subvertical anterior border of the snout, wide arch of the front teeth, and very large size of the canines and associated diastemata. Combination of these features gives its snout a quite different appearance compared to that of the best specimens of *E. sivalensis*, BMNH M37153, M37154, and M37155, whose subnasal region is more prognathic with a more regular arch of the front teeth resulting from the less laterally situated canines, and shorter diastemata. Several other characters distinguish *Enhydryodon dikikae* from all other species:

It differs from *E. sivalensis* in the larger, higher, and more conical protocone of the P4, and weaker post-protocone cusp. We agree with Pickford (2007) that the m1 of this species is illustrated by specimen GSI D161 (of which DG has seen only the cast BMNH M12350); it was called *E. cf. falconeri* by Pilgrim (1931; in the caption of his plate 2) and by Peigné et al. (2008), but its size fits better *E. sivalensis*, because its size is similar to the only other m1 of this species, IPSMG 1949.187 (Pickford,

2007:table 8), whereas the type P4 of *E. falconeri* ( $L = 14.8$ ) is shorter than all P4s of *E. sivalensis* ( $L = 16.7$ – $17.5$ ). The short talonid and rather large and trenchant hypoconid are unlike those of the Dikika m1s. The same is true of the m1 of specimen IPSMG 1949.187 (Pickford, 2007:fig. 12E).

It differs from *E. falconeri* Pilgrim, 1931, also of the Siwaliks, in the larger P4 paracone, and in the much larger, higher, and more lingual protocone of this tooth. Pickford (2007) also assigned to this species the mandible fragment BMNH M15397 that Peigné et al. (2008) referred to *S. bathygnathus*; its m1 is quite distinct in its primitive very high hypoconid, leaving only a narrow central talonid basin.

It differs from *E. africanus* Stromer, 1931, from Klein Zee in Namibia, probably of early Pliocene age, in the less unequal metacone and paracone of the M1 (the latter is broken off at Klein Zee, but was certainly quite large) and in the larger m1 talonid. The ventral border of the mandibular corpus is more convex in *E. africanus*, and was certainly shallower under the canine (Morales and Pickford, 2005:fig. 2P).

It differs from *E. ekecaman* Werdelin, 2003, from Kanapoi, in the much less labially expanded paracone of M1, which forms a robust parastyle at Kanapoi, and in the much shorter lingual part of this tooth, the hypocone being expanded distolingually rather than distally, and the mesiolingual cingulum being weaker. The m1 also has a weaker cingulum, but is otherwise similar. Otters close to *E. ekecaman* have also been reported from several early Pliocene sites: Sagatia in the Mabaget Fm (Morales and Pickford, 2005), Gawto in the Middle Awash (Haile-Selassie, 2008), and Kossom Bougoudi in Chad (Bonis et al., 2008). Bar-720'03 from Sagatia (Morales and Pickford, 2005) is the only one besides DIK-56-9 with an incipient division of the paraconid of m1, but the 'ento-paraconid' remains small, and the paraconid is not shifted labially. All m1s of these forms are little different from each other, and not very different from *E. dikikae* either. The P4 from Kossom Bougoudi is much smaller than the Dikika fossil and its protocone is not so lingually shifted resulting in a narrower tooth, but the height of this cusp and the large paracone resemble DIK-56-9.

It differs from *E. hendeyi* Morales, Pickford, and Soria, 2005, from the early Pliocene of Langebaanweg in South Africa (Hendey, 1978) in the much more distinct and conical lingual cusps of P4, absence of lingual cingulum on this tooth, relatively narrower p4, and higher trigonid cusps on m1 but with a more reduced hypoconid. This species shares with *E. dikikae* a broad m1 paraconid, albeit undivided.

It differs from *S. soriae* Morales and Pickford, 2005, from the latest Miocene of the Lukeino Fm, of which the only known tooth is the m1, in the somewhat shallower talonid basin. The paraconid is narrow on Bar-1984'05, but broader, and thus more like that of *E. dikikae*, on KNM-LU-337 (but linear dimensions of the latter species are nearly twice those of *E. soriae*). Following Peigné et al. (2008), we include in this species *S. senutae* Morales and Pickford, 2005, also from the Lukeino Fm, but represented by upper teeth. The Dikika species differs from it in the more triangular P4, with more lingual protocone and more distal hypocone, and an M1 with less unequal labial cusps, and hypocone more expanded distolingually. Apart from their slightly smaller size, these species differ little from *E. ekecaman*.

It differs from the type m1 of *S. kamuhangirei* Morales and Pickford, 2005, from the early Pliocene of Kazinga in its larger talonid with a much smaller hypoconid, and weaker cingulum. Despite its similar size, this tooth is very distinct from the Dikika form, but the second specimen referred to *S. kamuhangirei*, from Warwire, has a less prominent hypoconid. Bonis et al. (2008) assigned to ?*S. kamuhangirei* a mandible fragment from Kossom Bougoudi, in which a p3 was present, and bearing a p4 that is relatively much smaller than in all other known large fossil otters, unless these authors overestimated the length of m1. In this case,

it would probably be co-specific with the *S. aff. ekecaman* from the same site.

It differs from *S. beyi* Peigné et al., 2008, from the late Miocene of Toros Menalla in Chad in its M1 that is much longer relative to its width because of a much less expanded parastyle but more distally expanded hypocone, in the broader and deeper anterior part of the mandible, slightly wider talonid basin of m1 because of an hypoconid that is more restricted to the margin, and perhaps in the more bunodont cusps. Interestingly, the broad symphysis of *E. dikikae* is reminiscent of that of *Djourabus dabba* Peigné et al., 2008, also from Toros Menalla, but this form has a very distinctive m1, quite unlike those of *Enhydriodon*.

From Member C of the Shungura Fm, Omo, there is a lower carnassial L56-1 that we know only through a photo kindly provided by L. Werdelin. It is about as large as that of DIK-56-9 but its paraconid is undivided. Its trigonid is also differently oriented, with a forwardly placed protoconid relative to the metaconid and paraconid close to the lingual border, and the crests connecting these cusps are poorly developed. In all these features, it differs from *Enhydriodon dikikae*. The Omo femur L183-14 (Lewis, 2008:fig. 1) is also clearly different from the Dikika and Hadar ones in its size and orientation of the head. Several other isolated teeth from Omo labeled *Enhydriodon* belong in fact to the viverrid *Pseudocivetta ingens* Petter, 1967; the same is true of the type specimen of *Enhydriodon aethiopicus* Petter in Geraads et al., 2004, as already noted by Werdelin (pers. comm., 2004) and by Morales and Pickford (2005).

It is clear, therefore, that *E. dikikae* is distinct from all other African bunodont otters, but the (poor) available materials of the latter suggest that there is no major evolutionary break between them. Morales and Pickford (2005:234) postulated that two major evolutionary trends can be discerned in African bunodont otters: increase in size, and change in P4 morphology, with a protocone becoming more distant from paracone. Peigné et al. (2008) raised doubts about the first of these trends but, although size varies at any given time period, the general trend is nonetheless clear, at least during the Pliocene (Fig. 5), and the large size of the Dikika fossils that are among the youngest agree with this. They also confirm the trend towards a more lingual P4 protocone, becoming as lingually positioned as the hypocone, and increasing tooth width.

It is hard to say whether other remarkable features of *E. dikikae* represent the culmination of other evolutionary

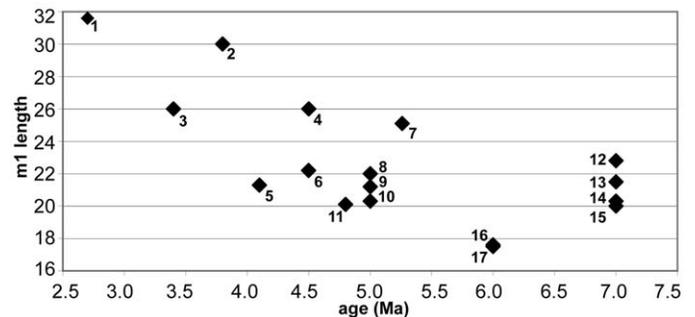


FIGURE 5. Plot of m1 length in various African fossils previously referred to *Sivaonyx* and *Enhydriodon*, to show the general trend in size increase. Some of the ages are approximate. 1: Omo L-56-1 (from a photo provided by L. Werdelin); 2: DIK-56-9 (length is an estimate, but this tooth was significantly larger than DIK-24-1); 3: DIK-24-1; 4: Kazinga (Morales and Pickford, 2005); 5: Kanapoi (Werdelin, 2003); 6: Klein Zee (Stromer, 1931); 7: Kossom Bougoudi (Bonis et al., 2008); 8: Langebaanweg L9138 (Hendey, 1978); 9: Langebaanweg L50000 (Hendey, 1978); 10: Gawto (Haile-Selassie, 2008); 11: Sagatia (Morales and Pickford, 2005); 12–15: Toros-Menalla (Peigné et al., 2008); 16: Lukeino LU-227 (Morales, Pickford and Soria, 2005); 17: Lukeino Bar1984'05 (Morales and Pickford, 2005).

trends, because the skull and anterior dentition are so poorly known in other species. Yet the short snout and enlarged canine/incisor complex are clearly more derived than those shown by *E. sivalensis*, the only form for which this part is documented.

#### ECOLOGY AND DIET

Lewis (2008) performed a detailed comparative study of the femur of extinct African bunodont otters, observing that this bone is more diverse in its morphology and proportions than would be expected from the dental remains. She concluded that the Hadar femur AL-166-10, which is similar to the Dikika ones, shows both aquatic and non-aquatic adaptations; the Dikika femora are much more slender than those of modern truly aquatic *Pteronura* and *Enhydra*. On the humerus, the medial epicondyle is still weaker than in *S. beyi*, which Peigné et al. (2008) consider as a terrestrial predator, and we may infer from these bones that *E. dikikae* was probably mostly terrestrial. At Dikika, levels that yield *Enhydriodon* contain numerous fossils of aquatic species (fishes, crocs, and hippos) but also purely terrestrial forms; detailed paleoecological analyses of the fossil assemblages, in progress, together with increased samples, might tell us more about preferred faunal associations.

The large jugal teeth with expanded crushing parts point to a diet consisting mostly of hard food; indeed, whatever its degree of terrestriality, it is unlikely that such a large animal would have been swift enough to catch fast-swimming fish. Pickford (2007) suggested that Siwalik bunodont otters fed upon bivalves, by crushing their shells with the incisors; he also noted that the curvature of the incisor arch (in front view) is similar to that of the shell of the bivalve *Lamellidens* found in the same beds. Similarly sized bivalves of the genus *Aspatharia* (*Chambardia*) are present (Wynn et al., 2008; Munro, pers. comm. 2009), but rare, at Dikika, and one would expect a more abundant prey, especially of that small size, for a carnivore that is relatively common. In any case, Pickford's interpretation leaves the powerful canines useless in food processing, and the high cusps on some jugal teeth (especially the paracone of P4) also make it unlikely that the crushing function was restricted to the front teeth. Other mollusks are smaller still, and their consumption would not require such a formidable battery of teeth. Crabs can also be discarded as a significant part of the diet, because none has been found at Dikika (but of course they do not preserve as well as mollusks), and because it is also unlikely that their biomass could have supported a large population of gigantic otters; Pickford also noted that the enamel of these African forms was too thick for cancrivorous animals. Lewis (2008) suggested that they ate catfishes and these are abundant at Dikika, and some of them are able to survive in shallow poorly oxygenated waters, and are thus an easy target for carnivores. However, only the armored skull would really need robust teeth to be crushed, whereas the fleshy body, although it bears bony spines, may even be eaten by lions that lack any crushing component in the dentition (Kingdon, 1977). But catfishes are hard to kill and the ability to inflict serious injuries to their skull would certainly be helpful. Other animals with armored exoskeleton, such as juvenile crocodiles and turtles, or ostrich eggs, could also be considered, although once the carapace is broken, robust teeth are no longer needed. None of these potential preys is fully satisfactory, and fail to explain the extinction of these giant otters before the end of the Pliocene.

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