



**Lutrinae Bonaparte, 1838 (Carnivora, Mustelidae) from
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Camille Grohé, Kevin Uno, Jean-Renaud Boisserie. Lutrinae Bonaparte, 1838 (Carnivora, Mustelidae) from the Plio-Pleistocene of the Lower Omo Valley, southwestern Ethiopia: systematics and new insights into the paleoecology and paleobiogeography of the Turkana otters. *Comptes Rendus. Palevol*, 2022, 30, pp.681-705. 10.5852/cr-palevol2022v21a30 . hal-03769832

HAL Id: hal-03769832

<https://hal.science/hal-03769832>

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Camille GROHÉ, Kevin UNO & Jean-Renaud BOISSERIE

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Members B and C of the Shungura Formation in the Lower Omo Valley, Ethiopia. Credits: OGRE.

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ISSN (imprimé / print) : 1631-0683/ ISSN (électronique / electronic) : 1777-571X

Lutrinae Bonaparte, 1838 (Carnivora, Mustelidae) from the Plio-Pleistocene of the Lower Omo Valley, southwestern Ethiopia: systematics and new insights into the paleoecology and paleobiogeography of the Turkana otters

Camille GROHÉ

Laboratory Paleontology Evolution Paleoecosystems Paleoprimatology (PALEVOPRIM, UMR 7262 CNRS INEE), University of Poitiers, 6 rue Michel Brunet, 86073 Poitiers (France)
camille.grohe@univ-poitiers.fr (corresponding author)

Kevin UNO

Lamont-Doherty Earth Observatory of Columbia University,
Palisades, New York, 10025 (United States)

Jean-Renaud BOISSERIE

Laboratory Paleontology Evolution Paleoecosystems Paleoprimatology (PALEVOPRIM, UMR 7262 CNRS INEE), University of Poitiers, 6 rue Michel Brunet, 86073 Poitiers (France) and Centre Français des Études Éthiopiennes (CFEE, USR 3137 CNRS), Ministry of Europe and Foreign Affairs, Embassy of France to Ethiopia, PO BOX 5554 Addis Ababa (Ethiopia)

Submitted on 7 February 2021 | Accepted on 25 May 2021 | Published on 5 September 2022

urn:lsid:zoobank.org:pub:F1DCE631-9ED9-4151-A928-A67EB286BB58

Grohé C., Uno K. & Boisserie J.-R. 2022. — Lutrinae Bonaparte, 1838 (Carnivora, Mustelidae) from the Plio-Pleistocene of the Lower Omo Valley, southwestern Ethiopia: systematics and new insights into the paleoecology and paleobiogeography of the Turkana otters. *Comptes Rendus Palevol* 21 (30) : 681-705. <https://doi.org/10.5852/cr-palevol2022v21a30>

ABSTRACT

We describe otter remains (Lutrinae Bonaparte, 1838) from the Plio-Pleistocene of the Lower Omo Valley of southwestern Ethiopia. We report isolated lower and upper teeth of *Torolutra* sp. dated to *c.* 3.3 Ma, dental specimens and a femur of *Enhydriodon* Falconer, 1868, attributed to a new species, dated between *c.* 3.4 Ma and 2.5 Ma, as well as a humerus of Lutrinae indet. dated between *c.* 1.9 Ma and 1.8 Ma. The new species *Enhydriodon omoensis* n. sp. is the largest species of the genus discovered so far. It is even larger than its close relative *E. dikikae* Geraads, Alemseged, Bobe & Reed, 2011, a Pliocene lion-sized otter from the Afar region and potentially from eastern Turkana. Based on stable oxygen and carbon isotope analyses, we found that *Enhydriodon* from the Lower Omo Valley could have been terrestrial and fed on both aquatic and terrestrial prey, acquired by either hunting or scavenging. It filled a unique ecological niche in the past communities co-existing with australopithecines. *Enhydriodon* and *Torolutra* Petter, Pickford & Howell, 1991 went extinct in Africa around the Plio-Pleistocene transition, along with many large-sized and ecologically specialized carnivores. This extinction event could be linked to the many geological, climate, and biotic changes occurring in the eastern African rift during this period, notably the incursion of early hominins into the carnivore guild.

KEY WORDS

Otters,
carnivores,
Africa,
ecological niche,
stable isotopes,
new species.

RÉSUMÉ

Lutrinae Bonaparte, 1838 (Carnivora, Mustelidae) du Plio-Pléistocène de la basse vallée de l'Omo, sud-ouest éthiopien : systématique et nouvelles données sur la paléoécologie et la paléobiogéographie des loutres du Turkana.

Nous décrivons des restes de loutres (*Lutrinae* Bonaparte, 1838) du Plio-Pléistocène de la basse vallée de l'Omo, au Sud-Ouest de l'Éthiopie. Nous rapportons des dents inférieures et supérieures isolées de *Torolutra* sp., datées de *c.* 3,3 Ma, des spécimens dentaires et un femur d'*Enhydriodon* Falconer, 1868, attribués à une nouvelle espèce, datés entre *c.* 3,4 et 2,5 Ma, ainsi qu'un humérus de *Lutrinae* indet., daté entre *c.* 1,9 et 1,8 Ma. La nouvelle espèce *Enhydriodon omoensis* n. sp. est la plus grande espèce du genre découverte à ce jour. Elle est encore plus grande que son proche parent *E. dikikae* Geraads, Alemseged, Bobe & Reed, 2011, une loutre pliocène de la taille d'un lion provenant de la région de l'Afar et potentiellement de l'Est du Turkana. Elle remplissait une niche écologique singulière dans les communautés du passé coexistantes avec les australopithécines. À partir des analyses des isotopes stables de l'oxygène et du carbone, nous avons mis en évidence qu'*Enhydriodon* de la basse vallée de l'Omo devait être terrestre et se nourrir de proies aquatiques et terrestres, acquises par la chasse ou le charognage. *Enhydriodon* et *Torolutra* Petter, Pickford & Howell, 1991 se sont éteintes en Afrique aux environs de la transition Plio-Pléistocène, à la même période que de nombreux carnivores de grande taille et spécialisés d'un point de vue écologique. Cet événement d'extinctions pourrait être lié aux nombreux changements géologiques, climatiques et biotiques associés au rift est-africain durant cette période, notamment à l'incursion des hominines anciens dans la guilda carnivore.

MOTS CLÉS

Loutres,
carnivores,
Afrique,
niche écologique,
isotopes stables,
espèce nouvelle.

INTRODUCTION

The Lower Omo Valley of southwestern Ethiopia is located north of Lake Turkana. It represents the northern part of the large Turkana Depression and it exposes Plio-Pleistocene fluvio-lacustrine sediments on the western side of the Omo River, mainly deposited as the Usno and Shungura formations. The Shungura Formation is exceptional in Africa because it preserves a highly continuous, well-dated, and rich paleontological and archaeological record from about 3.6 Ma to 1.05 Ma. The Usno Formation has a smaller extent and is dated to younger than 4.1 Ma, with fossiliferous levels probably deposited at *c.* 3.3 Ma according to correlations with the Shungura Formation (Heinzlin, 1983). The Omo fauna includes hominins (*Australopithecus* Dart, 1925, *Paranthropus aethiopicus* (Arambourg & Coppens, 1968), *P. boisei* (Leakey, 1959), *Homo* Linnaeus, 1758; e.g. Arambourg & Coppens 1967; Howell & Coppens 1974a, 1976; Boaz & Howell 1977; Suwa *et al.* 1996; Alemseged *et al.* 2002; Dayer *et al.* 2018), as well as many other mammals, birds, turtles, crocodiles, ostracods, and molluscs (e.g. Arambourg 1947; Van Damme & Gautier 1972; Howell & Coppens 1974b, 1974c; Coppens & Howell 1976, 1985, 1987a, 1987b; Heinzlin 1983; Beden *et al.* 1985; Stewart & Murray 2008). Hominin occupation sites also preserve Oldowan lithic industries (Chavaillon 1976; Merick & Merick 1976; Howell *et al.* 1987; Delagnes *et al.* 2011; Maurin *et al.* 2014, 2017).

While the carnivoran faunas from the eastern and western parts of the Turkana Depression are well-known (Werde-

lin & Lewis 2000 for South Turkwell; Werdelin 2003, Werdelin & Manthi 2012, Werdelin & Lewis 2020 for Kanapoi; Werdelin & Lewis 2013 for Koobi Fora), remains of carnivorans from the Lower Omo Valley, uncovered mostly in the 1960s-1970s, are briefly discussed in a few papers (Arambourg 1947; Howell & Coppens 1974b; Petter & Howell 1976, 1977, 1985; Howell & Petter 1976, 1979; Wesselman 1984) and have not been revised since. New fieldwork conducted by the Omo Group Research Expedition (OGRE) since 2006 in the Shungura Formation investigates Omo fossil biodiversity, artefacts, and geology (e.g. Boissérie *et al.* 2008; Delagnes *et al.* 2011; Bibi *et al.* 2013; Maurin *et al.* 2014, 2017; Blondel *et al.* 2018; Dayer *et al.* 2018; Martin *et al.* 2018; Corbé *et al.* 2019), including the carnivoran fossil record. Here we describe specimens of the subfamily Lutrinae recovered in deposits from members B and C and lower part of Member H of the Shungura Formation, dated by radiochronology to 3.44-2.91 Ma, 2.91-2.53 Ma, and 1.9-1.84 Ma, respectively (Feibel *et al.* 1989; McDougall & Brown 2008) and in the Brown Sands deposits of the Usno Formation, dated to *c.* 3.3 Ma (equivalent to horizons B-1/B-2 at Shungura; Heinzlin 1983). Furthermore, we investigate the possible habitat and diet of one of these otters, *Enhydriodon*, using stable oxygen and carbon isotope analyses of fossilized enamel. Finally, we review and discuss the paleobiogeographic history and the patterns of diversification and extinction of the Omo otters in view of the environmental changes that occurred in eastern Africa during the Plio-Pleistocene.

MATERIAL AND METHODS

All the material described here is curated at the National Museum of Ethiopia, Addis Ababa, under the Authority for Research and Conservation of the Cultural Heritage, Ministry of Culture and Tourism, Ethiopia. We used a digital caliper to the nearest 0.1 mm for measurements.

ABBREVIATIONS

Hemimandible

Dm	depth of the mandible under M ₁ ;
Wm	width of the mandible below M ₁ .

Teeth

I ₃	third lower incisor;
L	maximum mesiodistal length;
Ltrigo ling	length of the M ₁ trigonid from the paraconid to the metaconid;
Ltrigo lab	length of the M ₁ trigonid from the paraconid to the protoconid;
M _x	lower molar (x indicating the number of the molar);
M _x	upper molar (x indicating the number of the molar);
MlabDling	maximum distance between the mesiolabial corner and distolingual corner of M ₁ ;
MlingDlab	maximum distance between the mesiolingual corner and distolabial corner of M ₁ ;
P _x	lower premolar (x indicating the number of the premolar);
P _x	upper premolar (x indicating the number of the premolar);
W	maximum linguolabial width;
Wtalo	width of the M ₁ talonid;
Wtrigo	width of the M ₁ trigonid.

Humerus

DT	deltoid tuberosity;
DV	dorso-ventral;
L	maximum length;
LM	latero-medial;
W	maximum width (see Appendix 3 for illustrations of the measurements).

Localities and institutions

AL	Afar Locality, Hadar area, NME;
B	Brown Sands of the Usno Formation, Lower Omo Valley, NME;
BAR	Baringo District;
BMNH-M	Natural History Museum, London, fossil mammals;
BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, Munich;
DIK	Dikika, NME;
F	Shungura Formation, Lower Omo Valley, NME;
L	Shungura Formation, Lower Omo Valley, NME;
GSI NR	Geological Society of India, Northern Region, Lucknow;
KNM	Kenyan National Museums: -ER, East Rudolf (Koobi Fora), -KP, Kanapoi, -LU, Lukeino Formation, Baringo District, -WT, West Turkana;
MNHN	Muséum National d'Histoire Naturelle, Paris;
NME	National Museum of Ethiopia, Addis Ababa;
OMO	Shungura Formation, Lower Omo Valley, NME;
SAM	South African Museum (former Iziko South African Museum, Cape Town: -PQ-L, Quaternary Palaeontology, Langebaanweg's collections, -ZM, Zoology Mammals;

W White Sands of the Usno Formation, Lower Omo Valley, NME.

Other abbreviations

OGRE	Omo Group Research Expedition;
VPDB	Vienna Pee Dee Belemnite.

STABLE ISOTOPE ANALYSIS

To evaluate the habitat and diet of the otters of the Lower Omo Valley, we measured stable oxygen and carbon isotope ratios of fossil tooth enamel in four specimens of *Enhydriodon* (Lutrinae) and eight specimens of other carnivorans (Felidae and Hyaenidae) from the Usno Formation and from members B and C of the Shungura Formation (Fm). We compared oxygen and carbon isotope ratios of *Enhydriodon* to those of terrestrial taxa (felids, hyaenids, bovids, cercopithecids, proboscideans, equids, giraffids, rhinocerotids, suids; n = 306) and semi-aquatic ones (hippopotamids; n = 29), all recovered from the the Usno Fm and members B and C of the Shungura Fm (our data; Souron *et al.* 2012; Bibi *et al.* 2013; Negash *et al.* 2015, 2020; Appendix 1).

Oxygen isotope ratios reflect a taxon's dependence on water (Bocherens *et al.* 1996; Clementz & Koch 2001; Levin *et al.* 2006). Using the new and existing oxygen isotope data for the Omo fauna, we evaluated water dependence of *Enhydriodon* using approaches developed by Clementz & Koch (2001) and Clementz *et al.* (2008). Clementz & Koch (2001) found that extant aquatic and semi-aquatic taxa, including river and sea otters, have significantly lower oxygen isotope standard deviations compared to terrestrial carnivorans. In a second study, Clementz *et al.* (2008) explored the empirical relationship between oxygen isotope ratios of extant hippopotamids (i.e., semi-aquatic mammals) and co-occurring terrestrial mammals. They showed that this relationship could be extended to extinct taxa to evaluate whether they were semi-aquatic. They found $\delta^{18}\text{O}$ values of hippopotamids to be more negative than co-existing large terrestrial mammals, which is described by the linear relationship $\delta^{18}\text{O}_{\text{hippo}} = 0.96 (\pm 0.09) \times \delta^{18}\text{O}_{\text{fauna}} - 1.67 \pm 2.97$ ($r^2 = 0.886$, $p < 0.001$).

Carbon isotopes record the proportion of C₃ and C₄ resources diet (DeNiro & Epstein 1978). In carnivoran enamel, carbon isotopes reflect the diets of their prey (e.g. C₄ grazing, mixed feeding, or C₃ browsing terrestrial herbivores) (e.g. Clementz *et al.* 2009).

Stable isotope sampling protocols and analytical procedures follow those outlined in detail in Uno *et al.* (2018). All samples were pretreated for 30 minutes with an oxidizer (3% bleach) and buffered acetic acid (0.1 M), triple rinsed with Milli-Q ultrapure water, dried overnight, and vacuum roasted at 60°C for two hours prior to acid-hydrolysis in a Kiel IV at 70°C, followed by analysis via dual-inlet on a Thermo Scientific Delta V isotope ratio mass spectrometer. Isotope data are reported as δ -values relative to the Vienna Pee Dee Belemnite (VPDB) standard using permil (‰) notation where $\delta^{13}\text{C}$ ($\delta^{18}\text{O}$) = $(R_{\text{sample}}/R_{\text{standard}} - 1)$, and R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ($^{18}\text{O}/^{16}\text{O}$) ratios in the sample and in the standard, respectively, and the $\delta^{13}\text{C}$ ($\delta^{18}\text{O}$)

value of VPDB is defined as 0‰. Samples were analyzed alongside NBS 19 ($\delta^{13}\text{C} = 1.95\text{‰}$; $\delta^{18}\text{O} = -2.2\text{‰}$). The $\delta^{18}\text{O}$ values were calculated using a temperature-dependent acid fractionation factor of 1.00799 for enamel based on equation 4 in Passey *et al.* (2007).

SYSTEMATIC PALAEONTOLOGY

Order CARNIVORA Bowdich, 1821
Suborder CANIFORMIA Kretzoi, 1943
Superfamily ARCTOIDEA Flower, 1869
Family MUSTELIDAE Fischer, 1817
Subfamily LUTRINAE Bonaparte, 1838

Genus *Enhydriodon* Falconer, 1868

TYPE SPECIES. — *Enhydriodon sivalensis* Falconer, 1868 by original designation.

OTHER INCLUDED SPECIES. — *Enhydriodon africanus* Stromer, 1931, *E. falconeri* Pilgrim, 1931, *E. ekecaman* Werdelin, 2003, *E. hendeyi* Morales, Pickford & Soria, 2005, *E. kamuahangirei* Morales & Pickford, 2005, ?*E. soriae* (Morales & Pickford, 2005), *E. dikikae* Geraads, Alemseged, Bobe & Reed, 2011, *E. afman* Werdelin & Lewis, 2013.

GEOGRAPHICAL AND STRATIGRAPHIC RANGE OF THE GENUS IN AFRICA (Fig. 1). — Late Miocene to early Pleistocene based on the earliest occurrences in the Tugen Hills, Kenya (5.88–5.72 Ma, Lukeino Formation) and in the Middle Awash, Ethiopia (5.77–5.54 Ma, Adu-Asa Formation) and on the latest occurrences in the Turkana Basin, Kenya (c. 2–1.87 Ma, Koobi Fora Formation and c. 2 Ma at Nakoret) and in Pinnacle, Ethiopia (early Pleistocene). Countries: Egypt, Ethiopia, Kenya, Uganda, Chad, South Africa (see Appendix 2 for details).

REMARKS

The attribution of fossil specimens to either *Enhydriodon* or *Sivaonyx* Pilgrim, 1931, its close relative, is problematic and has often been debated (e.g. Pickford 2007; Peigné *et al.* 2008; Werdelin & Peigné 2010; Geraads *et al.* 2011; Valenciano & Govender 2020). The morphological differences between *Sivaonyx* and *Enhydriodon* are difficult to assess because the main differences are carried by the P^4 , unknown in some species, and because the specimens are fragmentary, preventing from observing the intraspecific variation. We consider here that *Sivaonyx beyi* Peigné, Bonis, Likius, Mackaye, Vignaud & Brunet, 2008, the oldest species of *Sivaonyx* in Africa, definitely belongs to this genus, because its dental morphology is very similar to that of the type species *Sivaonyx bathygnathus* (Lydekker, 1884) (e.g. M_1 with a narrow trigonid relative to the talonid, a protoconid higher and larger than the metaconid, a lingual rim of the talonid lower than the labial rim, M^1 with parallel mesial and distal borders, distantly located paracone and metacone, and a trenchant parastyle). However, we consider that all other species of African *Sivaonyx* or *Enhydriodon* (except maybe “*Sivaonyx*” *soriae* Morales & Pickford, 2005) may belong to *Enhydriodon*, based on some dental traits: metaconid higher than the protoconid on M_1 ,

presence of a carnassial notch and one or more cusps between the protocone and the hypocone on P^4 , and/or distolingual expansion on M^1 .

Enhydriodon and/or *Sivaonyx* are recorded in Africa (Stromer 1920; Hendey 1978; Werdelin 2003; Morales & Pickford 2005, 2007; Morales *et al.* 2005; Haile-Selassie 2008; Lewis 2008; Bonis *et al.* 2008; Peigné *et al.* 2008; Geraads *et al.* 2011; Werdelin & Manthi 2012; Werdelin *et al.* 2014; Werdelin & Lewis 2020), in southern Asia (Falconer 1868; Lydekker 1884; Pilgrim 1931; Chow 1961; Qi 1985, 2006; Verma & Gupta 1992; Grohé *et al.* 2013) and in southeastern Europe (Lydekker 1890; Peigné 2016; Koufos *et al.* 2018). *Sivaonyx* originated from southern Asia during the middle Miocene (Grohé *et al.* 2013) and then probably migrated to Europe and Africa during the late Miocene. Other dispersal waves of *Sivaonyx* and/or *Enhydriodon* between Africa and southern Asia could have happened during the Pliocene or Pleistocene, although their number and their polarity are difficult to assess due to the lack of cladistic analysis of these otters. Alternately, it is also possible that the African Plio-Pleistocene *Enhydriodon* evolved from an African *Sivaonyx*, independently from the Asian species of *Enhydriodon*.

From the Miocene to the Pleistocene, two main trends characterized these otters: 1) their teeth became more and more bunodont, a trait observed in other fossil otters (Wang *et al.* 2017); and 2) their body size increased, with some Plio-Pleistocene forms becoming gigantic, reaching the size of a large male lion (e.g. *Enhydriodon dikikae* in Geraads *et al.* 2011; *Enhydriodon dikikae* and Omo *Enhydriodon* in Valenciano *et al.* 2017).

Enhydriodon omoensis n. sp.
(Figs 1–4; Tables 1; 2)

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HOLOTYPE. — P 791-18, right P^4 (unit C-8, Shungura Formation).

REFERRED MATERIAL. — B 426, left I_3 (Usno Formation, correlated with unit B-2 of Shungura Formation); W 8-4S, left P_3 (Usno Formation, equivalent to unit B-2 of Sh. Fm); B 376, right P_4 (Usno Formation, equivalent to unit B-2 of Sh. Fm); L 2-10012, left hemimandible with P_4 and crown base of M_1 (unit B-10, Sh. Fm); L 56-1, left M_1 (unit C-6, Sh. Fm); OMO 18-1972-99, right broken M_1 (unit C-8, Sh. Fm); L 2-148, left M_2 (unit B-10, Sh. Fm); OMO 3/0-10084, left hemimandible with alveolus of M_2 , broken roots of M_1 and posterior root of P_4 (unit B-12, Sh. Fm); L 23-10021, right M^1 (unit C-6, Sh. Fm); W 717, labial fragment of left M^1 (Usno Fm, correlated with unit B-2 of Sh. Fm); L 183-14, right femur (unit C-5, Sh. Fm).

ETYMOLOGY. — Species name is derived from the Lower Omo Valley, where it has been recovered.

DIAGNOSIS. — *Enhydriodon* with at least three lower premolars; P_3 two-rooted, M_1 with a high talonid border, a high hypoconid, a smaller hypoconulid relative to the hypoconid and in distolingual position relative to the latter, an entoconulid higher than the entoconid, and two cusps on the distal border between the hypoconulid and the entoconulid; P^4 with a labial border concave at the level

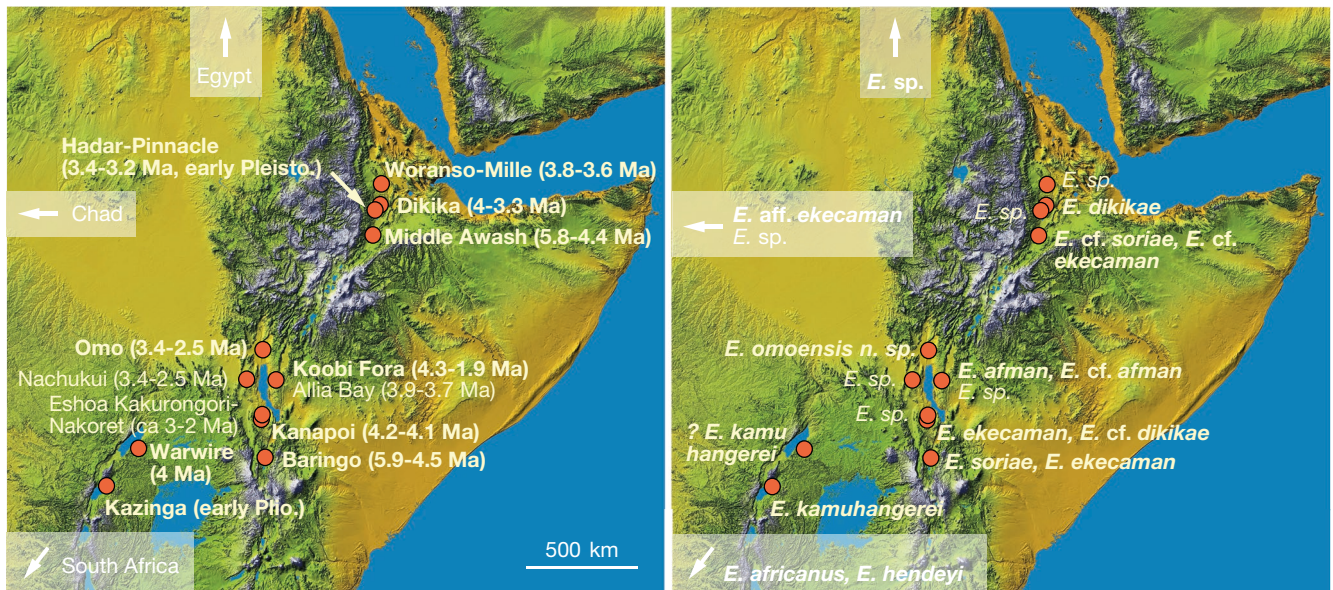


Fig. 1. — Geographical and stratigraphic distribution of *Enhydriodon* Falconer, 1868 in Africa, with a focus on the East African Rift System. Different species occur in the Turkana Basin, the Afar region and the Lake Albert area. References for fossil sites are provided in the main text and in Appendix 2. Abbreviations: *E.*, *Enhydriodon*; *Plio.*, Pliocene; *Pleisto.*, Pleistocene.

of the region between the parastyle and paracone and between the paracone and metastyle, with two post-protocone cusps aligned distolingually with the protocone, the distalmost post-protocone cusp being much smaller than the mesialmost post-protocone cusp, with a short V-shaped notch between the protocone region and the hypocone; M^1 with a large parastyle, closely located paracone and metacone, and an elongated distolingual hypocone; femur with a neck oriented at 40° relative to the longitudinal axis of the diaphysis, a head much higher than the greater trochanter, a strong and very medially oriented lesser trochanter, a diaphysis compressed dorsoventrally with a flat ventral surface, a slightly curved patellar groove, and a medial condyle that does not project much more posteriorly than the lateral condyle.

DIFFERENTIAL DIAGNOSIS. — Differs from *E. soriae* by larger and taller cuspids and cusps, a wider M^1 trigonid, P^4 with two post-protocone cusps, fusion of the post-protocone cusp with the protocone, and a narrow separation between the protocone region and the hypocone, M^1 with closely located paracone and metacone, and a more distal hypocone; differs from *E. ekecaman* by a higher crown on M^1 , a more squared P^4 with the distalmost post-protocone cusp more lingually located relative to the hypocone, M^1 with a smaller parastyle, a larger metaconule, and a less reduced metacone; differs from *E. hendeyi* by less bulbous cuspids and cusps, P^4 with a smaller distal accessory cuspid, M^1 with a smaller paraconid, an entoconulid higher than the entoconid, and presence of an hypoconulid, M^2 with a more distally placed metaconid, P^4 with post-protocone cusps and lacking a mesiolingual cingulum, longer femur with a head that projects further above the level of the greater trochanter, a more medial lesser trochanter, a concave patellar groove, and a medial condyle that projects much less ventrally relative to the lateral condyle; differs from *E. africanus* by a double-rooted P_3 , P^4 with a smaller distal accessory cuspid, M^1 with a shorter and higher metaconid and a higher-crowned talonid, M^1 with a higher protocone relative to the paraconule and a larger and higher hypocone; differs from *E. kamuhangirei* by a larger size; differs from *E. afman* by a double-rooted P_3 , M^1 with an entoconulid higher than the entoconid and the presence of an hypoconulid and cuspids on the talonid distal rim; differs from *E. dikikae* by the presence of P_3 , a more squared P^4 with the

mesialmost post-protocone cusp being more individualized and the distalmost protocone cusp being less individualized, and a femur with a head projecting further above the level of the greater trochanter; differs from *Djourabus dabba* Peigné, Bonis, Likius, Mackaye, Vignaud & Brunet, 2008 by a longer M^1 relative to its width and a wider and longer M^1 talonid relative to its trigonid.

REMARKS

We attribute the specimens described below (two fragmentary hemimandibles, several isolated lower and upper teeth, and a femur) to a single species, as the range of size and morphology is similar with the intraspecific variation ranges observed in extant otters.

DESCRIPTION

Mandible and lower dentition (Fig. 2A-I, K-N; Table 1)

On OMO 3/0-10084 (Fig. 2A), a mental foramen is present below the middle part of the P_4 , closer to the ventral border of the hemimandible than to the dorsal one. The anteriormost part of the masseter fossa is preserved. The masseter fossa is deep and extends towards the M^2 position. The second hemimandible fragment (L 2-10012; Fig. 2F, G) belongs to a different individual. It only preserves the dorsalmost part beneath the P_4 and does not allow a more detailed description of the mandibular morphology.

The I_3 is triangular in shape in occlusal view (Fig. 2B). It has a small cuspid. The lingual cingulid is asymmetrical. It extends from the mesial base of the tooth distoventrally then distodorsally, describing a V shape. The mesial cingulid is in a more dorsal position compared to the distal cingulid (Fig. 2B, C).

The P_3 is almost complete and only lacks its mesialmost and labialmost parts, just at the base of the main cuspid (Fig. 2D, E). It is longer than wide (Table 1). It has two roots.

TABLE 1. — Measurements (in mm) of the lower teeth and hemimandibles of the two species of *Enhydryodon* Falconer, 1868 from the Lower Omo Valley and other African *Enhydryodon*. *, broken or estimation from roots. Own measurements and from: 1, Werdelin (2003); 2, Morales & Pickford (2005); 3, Morales *et al.* (2005); 4, Peigné *et al.* (2008); 5, Geraads *et al.* (2011); 6, Werdelin & Lewis (2013); 7, Valenciano & Govender (2020).

	I ₃	P ₃	P ₄	LM ₁	Ltrigo ling	Ltrigo lab	Wtrigo	Wtalo	M ₂	Dm	Wm
<i>Enhydryodon omoensis</i> n. sp.											
B 426	6.9 × 7	—	—	—	—	—	—	—	—	—	—
W 8-4S	—	10.4 × 8.1	—	—	—	—	—	—	—	—	—
L 2-10012	—	—	18.2 × 13.4	—	—	—	—	—	—	—	—
B-376	—	—	18.7 × 13.8	—	—	—	—	—	—	—	—
L 56-1	—	—	—	32.1	18.1	18.3	17.9	18.3	—	—	—
OMO 18-1972-99	—	—	—	31.7*	—	—	—	19.1*	—	—	—
L 2-148	—	—	—	—	—	—	—	—	10.1 × 12.4	—	—
<i>Enhydryodon</i> sp.											
OMO 3/0 10084	—	—	—	26.4*	—	—	—	11.8*	—	37.9	19.3
<i>E. soriae</i>											
BAR 1984'05 ²	—	—	—	17.5	—	—	—	10.6	—	—	—
KNM-LU 337 (holotype) ³	—	—	—	17.6	—	—	—	10.5	—	—	—
<i>E. hendeyi</i>											
SAM-PQL 50000A (holotype) ⁷	—	7.7* × 5.2*	12 × 9.4	21.3	—	—	—	13.9	8.1 × 10.3	—	—
SAM-PQL-9138 ⁷	—	7.8* × 4.6*	13.8 × 9.9	22.1*	—	—	—	12.8*	9.2* × 7.2*	—	—
<i>E. ekecaman</i>											
KNM-KP 10034B (holotype) ¹	—	—	—	22.1	—	—	—	13.3	—	—	—
BAR 720'03 ²	—	—	11.1 × 8.4	—	—	—	12.8	—	—	—	—
BAR 567'05 ²	—	—	—	20.1	—	—	—	13	—	—	—
<i>E. kamuhangirei</i>											
unnumbered holotype ²	—	—	—	26	—	—	—	15.9	—	—	—
<i>E. africanus</i>											
BSPG 1930 XI 1 (holotype) ⁴	—	—	12 × 9.1	22.2	14	—	—	—	—	—	—
<i>E. afman</i>											
KNM-ER 3110 (holotype) ⁶	—	—	—	26.4	14.9	—	15.8	16.5	—	—	—
<i>E. cf. afman</i>											
KNM-ER 3108 ⁶	—	—	—	—	—	—	—	—	11.8 × 13.9	—	—
<i>E. dikikae</i>											
DIK-56-9 (holotype) ⁵	—	—	16.2 × 11.9	30*	—	—	—	20*	—	—	—
DIK-24-15	—	—	—	26	—	—	—	16.2	—	—	—

The main cuspid is mesially placed relative to the tooth length, with the mesial face being more vertical than the distal one. Two crests extend from its tip to the mesial and distolabial corners of the tooth. The cingulid is well-marked around the tooth, where the base is preserved.

The P₄ (Fig. 2G, H) has an ovoid shape: the tooth is wider distally than mesially, it is longer than wide (Table 1), it has a weak concave outline at the middle of the lingual border and a straight and slightly distolabially oriented distal border. It bears a small mesiolingual accessory cuspid, a prominent main cuspid located mesially relative to the tooth length, and a high and large distal accessory cuspid, just distolabial to the main cuspid (Fig. 2F-H). The tip of the distal accessory cuspid reaches more than half of the height of the main cuspid. Crests are visible on the mesiolingual and distolabial faces of the main and distal accessory cuspids. The cingulid is thick on the mesiolingual side of the tooth, until it reaches the level of the main cuspid tip, and on its distal side, where it encloses a small distolingual unbasined shelf. The small mesial accessory cuspid and the distal border of P₄ are more visible on L 2-10012 (Fig. 2F, G) than on B 376 (Fig. 2H). The distal and mesiolingual borders of P₄ show wrinkles.

The M₁ has a low trigonid, as wide as the talonid, and slightly longer than the latter (Fig. 2I, L-N; Table 1). The paraconid is the lowest trigonid cuspid. It is subdivided into two cuspids in L 56-1 (Fig. 2L, M). The metaconid is placed distally relative to the protoconid and it is higher and shorter than the protoconid. A short and deep U-shaped lingual valley separates the paraconid from the metaconid. The carnassial notch, between the paraconid and protoconid, is shallow. The metaconid bears a mesial and distal bulge at the cuspid midheight (Fig. 2M). A small protoconulid rises from the lower half of the distal face of the protoconid. The protoconulid is separated from the talonid by a sharp notch, which is positioned approximately at the same level as the metaconid base. The M₁ talonid has a shallow basin. On the labial side, it has a strong hypoconid, whose tip aligns with that of the protoconid, and a smaller hypoconulid, located directly distolingual to the hypoconid. On the lingual side of the talonid, the entoconulid is located slightly mesially with respect to the hypoconulid, but distally with respect to the hypoconid. It is as high as the hypoconulid. The entoconid is the most mesial talonid cuspid. It is closer to the lingual border compared to the entoconulid and it is lower than the latter. Two additional small and very low cuspids are present

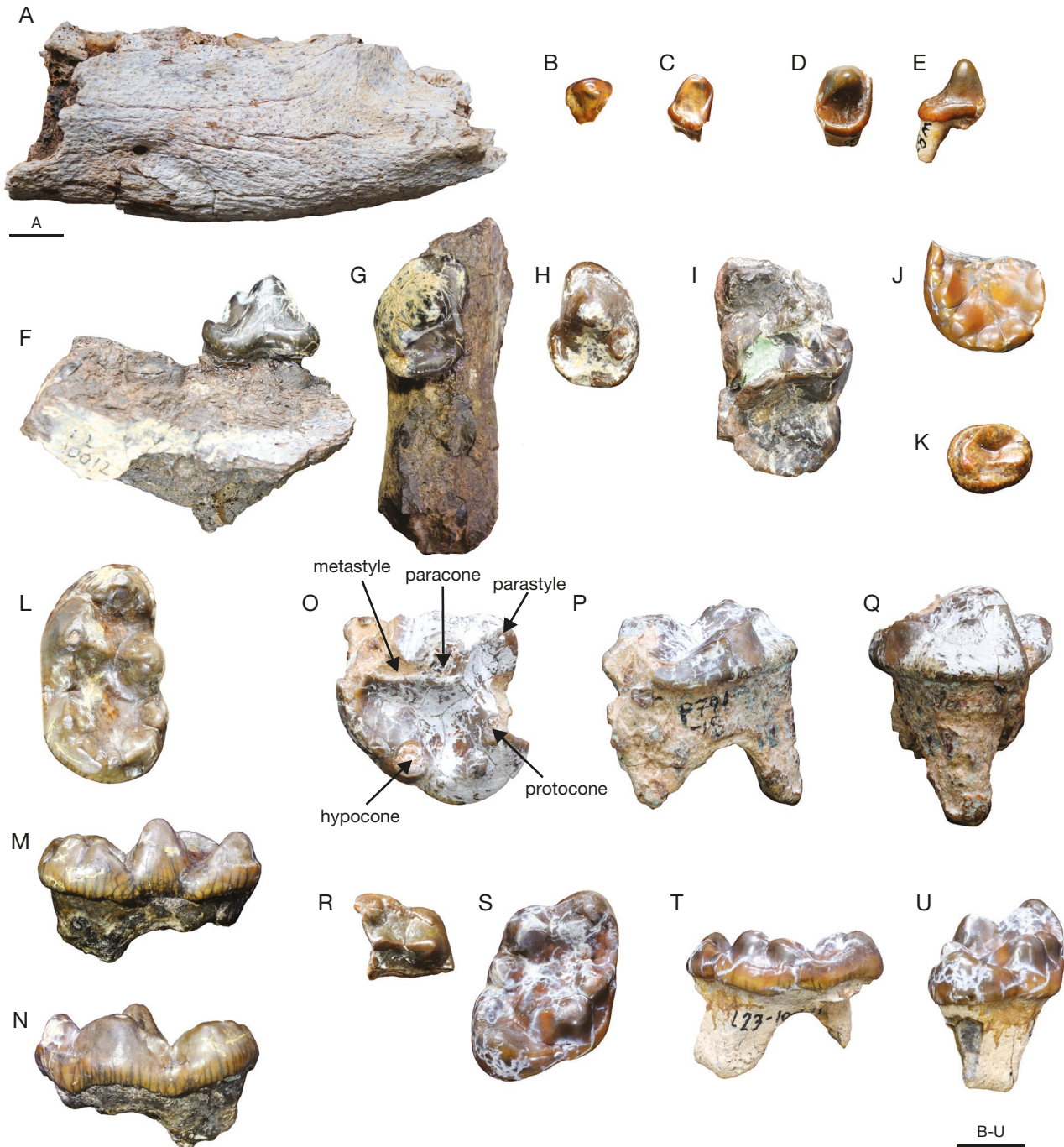


FIG. 2. — *Enhyriodon omoensis* n. sp.: **A**, OMO 3/0-10084, fragment of left hemimandible, in labial view; **B, C**, B 426, left I_3 views: **B**, occlusal; **C**, lingual; **D, E**, W 8-4S, left P_3 views: **D**, occlusal; **E**, lingual; **F, G**, L 2-10012, fragment of left hemimandible with P_4 views: **F**, lingual; **G**, occlusal; **H**, B 376, right P_4 in occlusal view; **I**, OMO 18-1972-99, right M_1 in occlusal view; **K**, L 2-148, left M_2 in occlusal view; **L-N**, L 56-1, left M_1 views: **L**, occlusal; **M**, lingual; **N**, labial; **O-Q**, P 791-18, holotype, right P_4 views: **O**, occlusal; **P**, distal; **Q**, lingual; **R**, W 717, labial fragment of left M_1 in occlusal view; **S-U**, L 23-10021, right M_1 views: **S**, occlusal, **T**, mesial, **U**, lingual. *Enhyriodon* sp.: **J**, OMO 3/0-10011, talonid of right M_1 in occlusal view. Scale bars: A, B-U, 1 cm.

between the hypoconulid and entoconulid, on the distal border of the talonid. The hypoconid is as high as the paraconid. The cingulid is particularly well developed around the paraconid.

The M_2 (Fig. 2K) is wider than long. An oval-shaped mesial contact facet with M_1 is visible. The paraconid is practically indistinct, but a carnassial notch is well visible, even if it is very small and very mesially located. The M_2 protoconid is placed on the distal half of the tooth. The paracristid is very

short between the paraconid and the carnassial notch, but longer between the carnassial notch and the protoconid. The paracristid forms a straight line in front of the carnassial notch and follows the curved labial border behind the carnassial notch. The metaconid is the highest cuspid and points mesially relative to the protoconid. The very shallow protocristid notch is located at the middle of the labiolingual axis of the tooth. The talonid is short, representing less than half of the

TABLE 2. — Measurements (in mm) of the upper teeth of *Enhydriodon omoensis* n. sp. from the Lower Omo Valley and other African *Enhydriodon* Falconer, 1868. *, broken. Own measurements and from: 1, Werdelin (2003); 2, Morales & Pickford (2005); 3, Peigné *et al.* (2008); 4, Werdelin & Manthi (2012); 5, Valenciano & Govender (2020). Measurement of *E. dikikae* Geraads, Alemseged, Bobe & Reed, 2011 based on the left P⁴ and the right M¹.

	P ⁴ L	P ⁴ W	M ¹ L	M ¹ W	M ¹ MlabDling	M ¹ MlingDlab
<i>Enhydriodon omoensis</i> n. sp.						
P 791-18 (holotype)	25.8*	26.7*	—	—	—	—
L 23-10021	—	—	20.6	27.05	28.91	21.23
W 717	—	—	15.1*	12.6*	—	—
<i>E. soriae</i>						
BAR 1720'00 ²	14.8	15	—	—	—	—
BAR 1082'01 ³	—	—	12.2	—	18.2	15.6
<i>E. hendeyi</i>						
SAM-PQL 50000B (holotype) ⁵	16.9	17.4	—	—	—	—
<i>E. ekecaman</i>						
KNM-KP 10034A (holotype) ¹	16.5	—	—	—	—	—
(labial)						
KNM-KP 10034C (holotype) ¹	—	—	15.8	19.8	—	—
BAR 566'05 ²	14.7	17.5	—	—	—	—
<i>E. africanus</i>						
BSPG 1930 XI 1 (holotype) ³	—	—	14.1	18.8	—	17.1
<i>E. dikikae</i>						
DIK-56-9 (holotype)	20.5	22.7	21.4	25.9	—	—
<i>E. cf. dikikae</i>						
KNM-KP 49887 ⁴	18.4	19.5	16.8	23.6*	—	—

M₂ length. A hypoconid is present at the distal border of the tooth, lingually placed with respect to protoconid. The cingulid is thick on the labial side.

Upper dentition (Fig. 2O-U; Table 2)

The P⁴ (Holotype; Fig. 2O-Q) has a large and heavily worn paracone, occupying about one third of the labial side, and located slightly mesially relative to the tooth length (Fig. 2O). It is just distal to a smaller and much lower parastyle. The distolabial corner of the tooth is broken, but the mesial part of the metastyle is preserved, and the outline of the distal border of P⁴ indicates that the metastyle occupied more than half of the tooth length. Two crests extend mesially from the paracone tip: one extends to the parastyle base, the other to the protocone base. Three cusps constitute the protocone region. They are aligned distolingually on the mesiolingual portion of the P⁴. The protocone is as large as the paracone, but lower. Its tip is worn (but less than the paracone one) and is displaced mesially with respect to the paracone and distally relative to the parastyle. A second, high cusp, is present on the distolingual face of the protocone (Fig. 2P-Q). This cusp is higher than the worn hypocone. A third, very small cusp (second and distalmost post-protocone cusp) is present at the base of the distolingual face of the second cusp (mesialmost post-protocone cusp) (Fig. 2P-Q). A notch separates the protocone region from the large hypocone. The hypocone is lower than the paracone. It is also heavily worn so that its relative height compared to the protocone cannot be assessed. It is positioned distally relative to the paracone and is more lingual relative to the protocone. The base of the protocone region extends more lingually than the base of the hypocone. The broad lingual shelf of P⁴ extends until the distal end of the metastyle. The labial outline of P⁴ describes three convex

curves: one around the parastyle, another one around the paracone, and one around the metastyle. We can only observe the mesial part of the latter. The cingulum is well-marked labially and distal to the hypocone.

The M¹ is wider than long and shows a distolingual expansion (Fig. 2S-U). The tooth has bulbous cusps. It has a large parastyle, mesiolabially placed relative to the paracone and about the same height as the latter. The metacone is slightly more distal and higher than the paracone. There is no metastylar region labial to the metacone. A paraconule-protocone blade, close to the mesial border of the tooth, extends lingually and slightly distally. The protocone is higher than the paraconule and a shallow notch separates these two cusps. Two crests extend labially from the paraconule: one extends distally until it reaches a lingual bulge at the base of the paracone, the other one extends mesially to follow the mesial border of M¹ until the base of the parastyle (Fig. 2S). The distolingual border of the tooth is inflated and shows a hypocone, as high as the metacone. A large metaconule is placed in distolingual position relative to the metacone and reaches about half of the metacone height. The metaconule is more labial compared to the paraconule. The cingulum is thick on the mesial and distolingual sides of the tooth.

Postcranium (Fig. 3A-F)

The femur L 183-14 was already described and measured in detail by Lewis (2008: 611, table 4 for measurements, 614 for description). The neck is short and the head is oriented more proximally than medially, as the neck is shifted at around 40° relative to the longitudinal axis of the diaphysis (Fig. 3A). Because of this feature, the lateromedial width of the proximal epiphysis is narrow (Fig. 3E). There is a well-excavated proximal surface along the neck and the medial

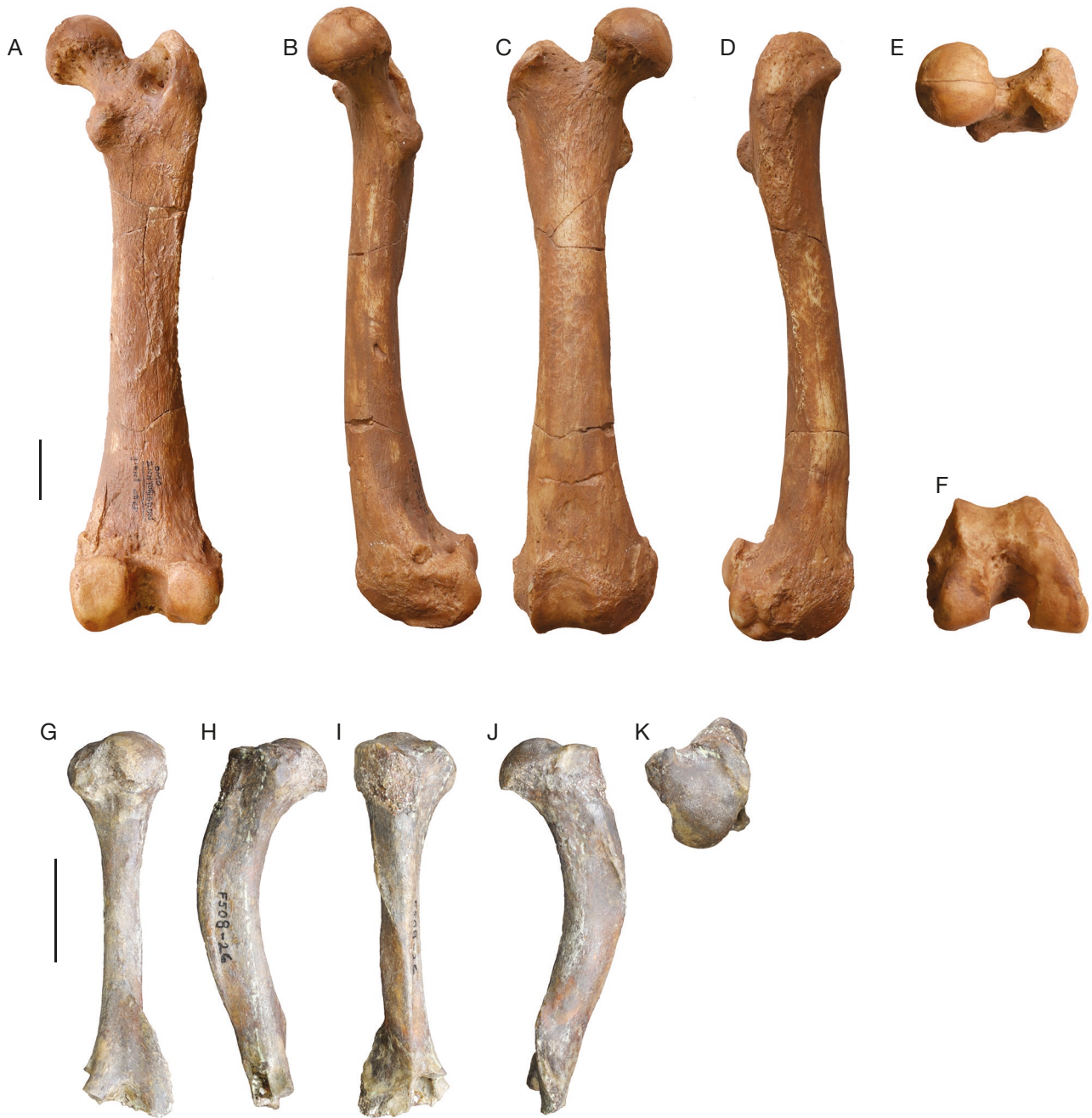


FIG. 3. — **A-F**, *Enhyridodon omoensis* n. sp., cast of L 183-14, right femur views: **A**, ventral; **B**, medial; **C**, dorsal; **D**, lateral; **E**, proximal; **F**, distal; **G-K**, *Lutrinae* indet., F 508-26, right humerus views: **G**, ventral; **H**, medial; **I**, dorsal; **J**, lateral; **K**, proximal. Scale bars: 3 cm.

border of the greater trochanter (Fig. 3A, C). The head is round. The articular surface for the acetabulum slightly extends lateroventrally on the neck (Fig. 3A, E). The fovea capitis is large and is located on the ventromedial side of the head (Fig. 3B). The greater trochanter is bending dorsally (Fig. 3D) and it is lower than the femoral head (Fig. 3A, C). The femur has a short (proximodistally) and deep trochanteric fossa. There is a strong lesser trochanter, which is directed more medially than ventrally, so that it is visible in dorsal view (Fig. 3C). The diaphysis is more compressed anteroposteriorly than lateromedially and its ventral surface is flat. The patellar groove is weakly concave and is slightly

wider mediolaterally than anteroposteriorly (Fig. 3F). The medial condyle is larger than the lateral condyle (Fig. 3A), but it does not extend much ventrally compared to the lateral condyle (Fig. 3F). The intercondylar fossa is rectangular and particularly wide lateromedially. Two pits are present above the lateral border of the lateral condyle and above the medial border of the medial condyle and could correspond to the insertion sites for the lateral and medial heads of the *gastrocnemius* (Fig. 3A, B, D). One large pit is present on the medial epicondyle for the attachment of the medial collateral ligament (Fig. 3B). Several pits are present on the lateral epicondyle: one rather centrally located, where the lateral

TABLE 3. — Measurements (in mm) of the humerus of the Lutrinae indet. from Shungura and remains of *Torolutra* Petter, Pickford & Howell, 1991 from Koobi Fora. *broken. Measurements for Koobi Fora are from Werdelin & Lewis (2013).

	Lutrinae indet.	cf. <i>Torolutra</i> sp.			<i>Torolutra</i> cf. <i>ougandensis</i>
	F 508-26	KNM-ER 4406A	KNM-ER 4406B	KNM-ER 389	KNM-ER 5895T
L	112.4*	—	—	110.7	—
LM W proximal epiphysis	29.6	31.5	—	28.9	—
LM W humeral head	19	21.7	23.3	20.6	—
DV W proximal epiphysis	30.7	33.6	36	30.2	—
L deltoid crest	55.4	—	—	—	—
LM W distal epiphysis	27.3	—	—	—	—
LM W of the shaft at the end of the DT	11.1	—	—	—	—
DV W of the shaft at the end of the DT	18.6	—	—	17.5	15.2

collateral ligament attached, one beneath, closer to the distal border of the epicondyle, where the *extensor digitorum longus* inserted, and two along the ventral margin of the epicondyle, where at least the *popliteus* was present (Fig. 3D).

COMPARISONS

Asian *Enhydriodon*

The first fossils of *Enhydriodon* were found in Asia. Two species, *E. sivalensis* Falconer, 1868 and *E. falconeri* Pilgrim, 1931 were initially recorded from unknown localities of the Siwalik Hills of the Indian Subcontinent, their age being therefore debated. Only one specimen, an isolated m1, which belongs either to *E. falconeri* or *E. sivalensis* (see Peigné et al. 2008), was reported from deposits of the “Dhok Pathan Stage” in Hasnot, Punjab province of northern Pakistan (Pilgrim 1931). The “Dhok Pathan Stage” of the Punjab province is equivalent to the late Miocene-early Pliocene Dhok Pathan Formation, dated from 9.8 Ma to c. 3.5 Ma (Barry et al. 2013). More recently, another specimen from Himachel Pradesh, in India, attributed to *E. sivalensis*, could suggest a late Pliocene age for the species (Verma & Gupta 1992). Here we compare the upper teeth of the Asian *Enhydriodon* to our material as the holotype of *E. falconeri* is an isolated P⁴ and most specimens of the larger *E. sivalensis*, including its lectotype, are partial crania.

The Omo P⁴ differs from that of *E. falconeri* (holotype BMNH-M 4847, left P⁴; Pilgrim 1931: pl. 2, fig. 3-3a; Pickford 2007: 97, fig. 9D) by having a longer metastyle and lower post-protocone cusps, which are oriented on a more distal axis. Because of this last feature, the distalmost post-protocone cusp is far more lingually placed in *E. falconeri* compared to the same cusp in the Omo P⁴. This cusp is also much lower than the mesialmost post-protocone cusp and well-separated from the latter, unlike in the Omo P⁴.

The Omo upper teeth differ from the lectotype of *E. sivalensis* (BMNH-M 37153, a cranium with P⁴-M¹ partially preserved and broken P³; Pickford 2007: 104, fig. 12C) by a less squared appearance of P⁴ and a more developed labial shelf of the paracone and more closely located paracone and metacone on M¹. The P⁴ protocone is lacking on the lectotype, but one cusp is present at the position of the mesialmost post-protocone cusp in the Omo P⁴. In that case, the Omo upper carnassial further differs from that of *E. sivalensis* by having two

post-protocone cusps instead of one. Interestingly, two other crania attributed to *E. sivalensis* by Pilgrim (1932) (BMNH-M 37154 and BMNH-M 37155; Pickford 2007: 104, fig. 12B, D) have a P⁴ morphology different from that of the lectotype. A wide U-shaped valley filled by several small cusps occurs between the protocone and hypocone, differing greatly from our specimen. Other crania attributed to *E. sivalensis* (Lydekker 1884: pl. XXVI, fig. 5; GSI NRV2/468, described by Verma & Gupta 1992, refigured by Pickford 2007: 104, fig. 12A) have not been observed and cannot be compared here.

African *Enhydriodon*

One of the oldest possible *Enhydriodon* species in Africa is *E. soriae* (Morales & Pickford, 2005), originally described as *Sivaonyx soriae* based on remains from latest Miocene deposits of the Lukeino Formation, in Kenya (Morales & Pickford 2005; Fig. 1). It is known by lower and upper dentition, the latter originally assigned to *S. senutae* Morales & Pickford, 2005 in the same paper and re-attributed to *S. soriae* by Peigné et al. (2008). It is a much smaller otter than the species from Omo (Tables 1, 2; Fig. 4), which shows very different morphological features too. The Omo M¹s differ from the M¹ of *E. soriae* by having larger, taller, and more bulbous cusps, closer paracone and metacone, with the distal crest of the paracone and the mesial crest of the protocone of similar lengths (contrary to a distal crest of the paracone much longer relative to the mesial crest of the metacone in *E. soriae*), and an hypocone that is more projected linguo-distally. The Omo P⁴ has also larger and taller cusps, clear concavities on its labial wall, a post-protocone cusp fusing with the distolingual face of the protocone (instead of well-separated cusps in *E. soriae*), two post-protocone cusps (instead of one in *E. soriae*), and it lacks a wide U-shaped valley between the protocone region and the hypocone. The Omo M¹ has a wider trigonid, which approximates the width of the talonid, while the M¹ of *E. soriae* has an oval outline because the trigonid is narrower than the talonid.

Enhydriodon ekecamani Werdelin, 2003 was first described from the early Pliocene fluvio-lacustrine Kanapoi Formation, northern Kenya (Werdelin 2003; Werdelin & Manthi 2012; Werdelin & Lewis 2020), then found in the Mabaget Formation, in the Baringo district of western Kenya (Morales & Pickford 2005; Fig. 1). The Kanapoi material includes complete M₁,

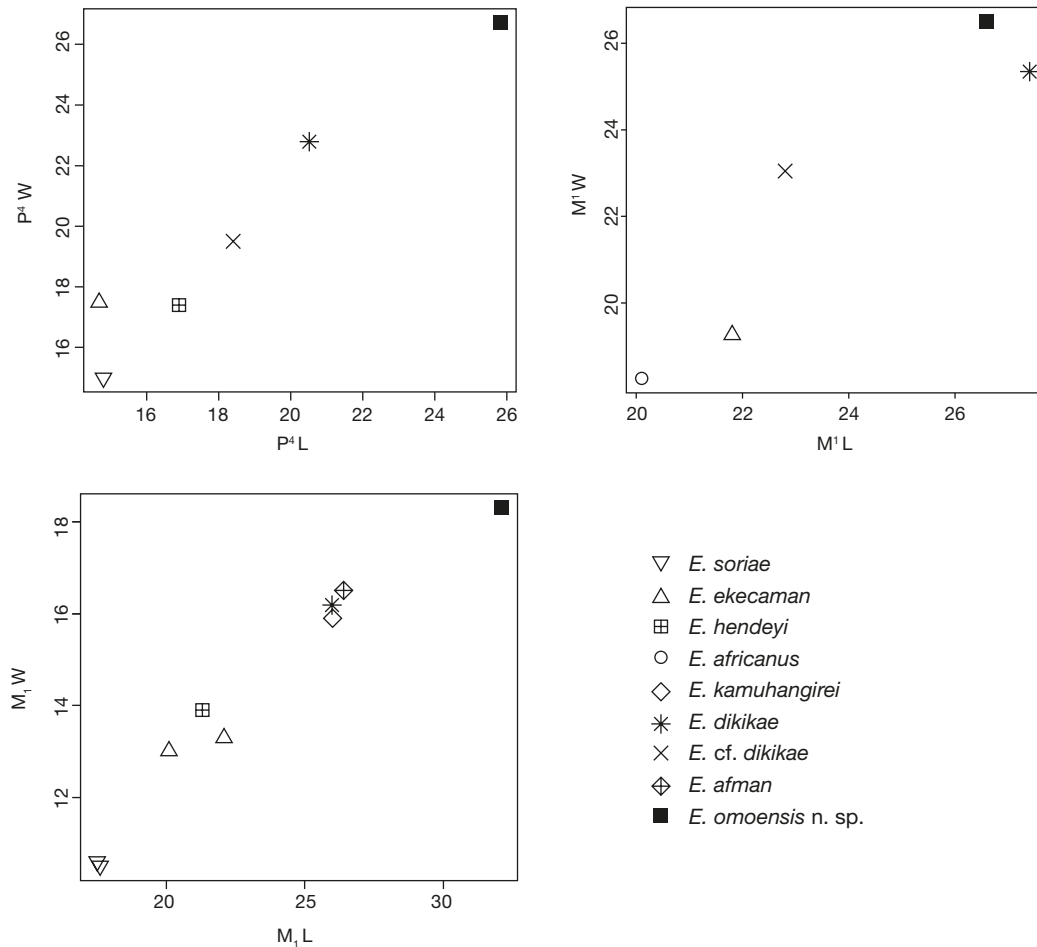


FIG. 4. — *Enhydryodon omoensis* n. sp., the largest species of *Enhydryodon* Falconer, 1868 from tooth dimensions. Biplot of length and width of P⁴, M¹, M₂ of *Enhydryodon*. *Enhydryodon soriae* Morales & Pickford, 2005: BAR 1720'00 (P⁴), BAR 1984'05 (M₁), KNM-LU 337 (M₁, holotype); *E. ekecaman* Werdelin, 2003: BAR 566'05 (P⁴), KNM-KP 10034C (M₁, holotype), KNM-KP 10034B (M₁, holotype), BAR 567'05 (M₁); *E. hendeyi* Morales *et al.*, 2005: SAMP-PQL 50000B (P⁴, holotype), SAMP-PQL 50000A (M₁, holotype); *E. africanus* Stromer, 1931: BSPG 1930 XI 1 (M₁, holotype); *E. kamuhangirei* Morales & Pickford, 2005: unnumbered holotype (M₁); *E. dikikae* Geraads, Alemseged, Bobe & Reed, 2011: DIK-56-9 (P⁴, M₁, holotype), DIK 24-1 (M₁); *E. cf. dikikae*: KNM-KP 49887 (P⁴, M₁); *E. afman* Werdelin & Lewis, 2013: KNM-ER 3110 (M₁, holotype); *E. omoensis* n. sp.: P 791-18 (P⁴, holotype), L 23-10021 (M₁), L 56-1 (M₁). See Tables 1 and 2 for measurements.

M¹ and a partial P⁴, while, in Baringo, specimens comprise a complete P⁴, P³, worn and broken M₁s and a fragmented hemimandible (see Tables 1, 2 and Fig. 4 for measurements). A complete P⁴ from Kossom Bougoudi, Chad, dated to the Mio-Pliocene boundary, assigned to *E. aff. ekecaman* (Bonis *et al.* 2008), is also compared here. Unlike the Omo P⁴, none of the P⁴s from Kanapoi, Baringo, and Kossom Bougoudi show any concave border labially to the parastyle-paracone region. Additionally, the upper carnassial from Baringo is narrower relative to its width (Table 2; Fig. 4), and the distalmost post-paracone cusp is more labially placed compared to that of the Omo carnassial. In *E. aff. ekecaman* from Chad, three cusps are present between the paracone and the hypocone (instead of two in the Ethiopian species); they are smaller and more separated from each other and from the paracone than in the Omo P⁴. Compared to the M¹ from Kanapoi, the Omo M¹ has larger cusps in general (especially the metaconule), a smaller parastyle, a paracone located closer to the metacone and linguodistally to the parastyle (contrary to directly lingual to the parastyle in *E. ekecaman*), a less reduced metacone, and a mesiolingual cingulum that does not extend mesially rela-

tive to the protocone position. Finally, the Omo M₁s have a higher crown and distinctive hypoconid and hypoconulid compared to the lower carnassial from Kanapoi.

Enhydryodon hendeyi from river channel deposits of the Mio-Pliocene Langeberg Quartz Sand (Valenciano & Govender 2020) and Muishond Fontein Pelletal Phosphate members of the Varswater Formation, “E” quarry of Langebaanweg, South Africa, was originally described as *E. africanus* by Hendey (1978). The holotype includes a hemimandible bearing alveolus for P₂, alveoli for P₃ with a remaining distal root, and P₄-M₂ (SAM-PQL 50000A) and an isolated P⁴ (SAM-PQL 50000B), both possibly belonging to the same individual. The hemimandible shows four mental foramina under the P₃ and P₄, unlike in our Ethiopian form. The cuspids are more bulbous than in the material of Omo *Enhydryodon*. Contrary to our taxon, in *E. hendeyi*, the P₄ has a larger distal accessory cuspid; the M₁ has a wider paraconid, poorly differentiated entoconid and entoconulid, with the entoconulid being lower than the entoconid, and no hypoconulid; the M₂ has a more mesially placed metaconid. The P⁴ from South Africa differs

also greatly from the Omo P⁴ by having lower cusps, a thick mesiolingual cingulum, and by lacking post-protocone cusps, showing instead a long and shallow V-shaped valley between the protocone and the hypocone. Additionally, a complete left femur (SAM-PQL 41523), initially attributed to *Enhydriodon africanus* by Hendey (1978), has been reassigned to *E. hendeyi* (Morales *et al.* 2005) and can be compared here with the femur from the Lower Omo Valley. SAM-PQL 41523 is about half the length of L 183-14 (total length of 164.5 mm for SAM-PQL 41523 and 326.3 mm for L 183-14; measurements from Lewis 2008: table 4), the femoral head does not project as far proximally (Lewis 2008: fig. 1A; Valenciano & Govender 2020: fig. 6C), the proximal surface along the neck and the medial border of the greater trochanter is poorly excavated, the proximal epiphysis is wider lateromedially, the lesser trochanter does not project as medially (Lewis 2008: fig. 1A; Valenciano & Govender 2020: fig. 6C, D), the medial condyle projects more ventrally, and the patellar groove is not concave.

Enhydriodon africanus is known by two specimens from the early Pliocene of Klein Zee, Namaqualand of northwestern South Africa: an M¹ and a hemimandible with alveolus for P₂, bases of canine and P₃ crowns, P₄-M₁, and alveolus for M₂ (Stromer 1931: pl. I, figs 3a, b, 4a, c; refigured in Morales & Pickford 2005: 238, 239, fig. 2I, P from MNHN casts, and in Valenciano & Govender 2020: 16, fig. 4D-F from the original holotype). It is similar in size to *E. ekecaman* and *E. hendeyi*, so it is much smaller than the Omo *Enhydriodon* (Fig. 4; Tables 1, 2). In our Ethiopian species, the M¹ has a higher protocone relative to the paraconule and the hypocone is clearly larger and higher than in the South African species. The mental foramen is located under the P₄ in OMO 3/0-10084 while it is present under the P₃ in the holotype of *E. africanus*. The Omo *Enhydriodon* has a two-rooted P₃ (instead of a single-rooted P₃ in *E. africanus*), a smaller distal accessory cuspid on P₄, and an M₁ with a shorter and higher metaconid and higher-crowned talonid, especially lingually, where the entoconid and the entoconulid are separated by a deeper notch. Stromer (1931) also assigned another M₁ from the Pliocene of Wadi Natrun, in Egypt, to *E. africanus*. He first described that specimen as *Lutra aff. capensis* (Stromer 1920), but we agree with him (Stromer 1931) and other authors (Peigné *et al.* 2008) that it belongs to either *Sivaonyx* or *Enhydriodon*. We cannot make relevant comparisons here from the figures of the specimen we have seen (Stromer 1920: fig. 11). Also, because part of the talonid is absent, we cannot evaluate what was its width relative to the trigonid width or the height of its lingual rim relative to the labial rim. Yet those two characters can give indications to determine whether the Egyptian specimen belongs to *Sivaonyx* or *Enhydriodon*. However, this form is smaller than the Omo taxon; it is closer in size to *E. africanus*, *E. ekecaman* and *E. hendeyi*, and larger than *E. soriae*.

Enhydriodon kamuhangirei is represented by very worn M₁s from the early Pliocene of Kazinga and Warwire, Uganda (Fig. 1). The holotype resembles the Omo M₁ in the number and general position of the talonid cuspids, although it is dif-

ficult to assess whether there were two (as in the Ethiopian specimens) or just one cuspid between the entoconulid and the hypoconulid, due to the wear. This species is much larger than *E. ekecaman*, *E. hendeyi* and *E. africanus*, whose sizes are similar. It is still smaller than the Omo otter (Tables 1, 2; Fig. 4). It is also the only *Enhydriodon* recorded on the western branch of the East African Rift.

Enhydriodon afman is recorded from the late Pliocene of the Lokochot Member of the Koobi Fora Formation, northern Kenya (Fig. 1). Although similar in age to some of the Omo otter specimens, and located in the eastern part of the Turkana Basin, which is close to the Lower Omo Valley, it is a smaller species (Table 1; Fig. 4) with a distinct dental morphology. *E. afman* is represented by a hemimandible with alveolus for P₃ and M₂, alveoli for P₄, and M₁, and possibly a few other isolated teeth and bones. The holotype differs from the Omo material by having three mental foramina under P₃-P₄ (although this feature can be variable within species), a single-rooted P₃, an M₁ talonid without hypoconulid and without cuspids on the distal rim, with the entoconid and entoconulid subequal in size, and with a shallower notch separating the entoconid from the metaconid. The description of the M₂ of *E. cf. afman*, from the Tulu Bor Member of Koobi Fora (Werdelin & Lewis 2013), matches the morphological features of the Omo *Enhydriodon*, but probably of other species of the genus too (e.g. *E. hendeyi*). This M₂ is larger than that of *E. omoensis* n. sp. (Table 1).

Enhydriodon dikikae is represented by a cranium and an associated mandible, as well as several isolated lower teeth and postcranial remains. It comes from the early Pliocene of Dikika, in the Lower Awash Valley of Ethiopia (Fig. 1). The Lower Awash otter has smaller tooth dimensions compared to the Omo otter (Tables 1, 2; Fig. 4). However, the M¹ of *E. dikikae* is more elongated than that of *E. omoensis* n. sp. Morphological differences with the Omo *Enhydriodon* are mostly visible on the P⁴ and M₁. The P⁴ of the holotype of *E. dikikae* has a different outline of the labial rim, the latter being only concave at the level of the paracone-metastyle region. The tooth is less square in occlusal view, with different proportions and configuration of the lingual cusps between the protocone and the hypocone compared to the Omo P⁴: the mesialmost post-protocone cusp, at the mid-height of the protocone, is less individualized, and the distalmost post-protocone cusp is well-individualized and closer to the hypocone. The M₁ of the holotype of *E. dikikae* has only one cuspid between the entoconulid and hypoconulid (instead of two cuspids in the Omo M₁s), and this cuspid is closer to the entoconulid, and as high as the hypoconulid. The entoconulid is also higher than the hypoconulid. These features differ from the position and proportion of the talonid cuspids observed in the Omo *Enhydriodon*. Another M₁ attributed to *E. dikikae* (DIK 24-1) shows a different talonid morphology compared to that of the Dikika holotype: the distal rim of the talonid is lower than the labial or lingual cuspids, there are two cuspids distal to the entoconulid, and the entoconid and entoconulid are not well separated. Again, those features are different from what can be seen

in the Omo M_1 s. On the other hand, the bicuspid M_1 paraconid of *E. dikikae* (at least present in DIK 24-1; it is impossible to check its presence in DIK 56-9), mentioned in the species diagnosis, is also present in the Omo *Enhydriodon*. However, it is less pronounced in *E. omoensis* n. sp. and it is a variable feature within the same individual. In fact, a mandible from Hadar (AL 254-1, under study by L. Werdelin and M. Lewis, paper in preparation) shows a left M_1 with a clear bicuspid paraconid, while the right one has a single-cusped paraconid. Finally, *E. dikikae* does not have a P_3 , the first premolar on the dental row of the mandible being a P_4 , unlike in the Omo species. Nevertheless, it is morphologically the closest species to the Omo *Enhydriodon*. In addition to the dental material, Geraads *et al.* (2011) described three epiphyses of femora of *E. dikikae*. They are smaller than the epiphyses of the Omo femur (lateromedial width of the proximal epiphysis is 78.3 mm for DIK 44-1 and 88.5 mm for L 183-14, lateromedial width of the distal epiphysis is 65.5 mm for DIK 44-1 and 75.2 mm for L 183-14; measurements from Lewis 2008: table 4). *E. dikikae* and *E. omoensis* n. sp. share a similar shape of the trochanteric fossa and a very medially oriented lesser trochanter. However, Geraads *et al.* (2011) described a less medially oriented lesser trochanter for DIK 4-1, implying that the orientation of the lesser trochanter is variable among individuals of *E. dikikae*. The proximal femur DIK 44-1 also has a rather deeply excavated proximal surface along the neck and the medial border of the greater trochanter, although not as deep as in the Omo femur. The head only reaches the same level as the greater trochanter and the latter has deeper imprints for the insertion of the hip extensors compared to the Omo femur. Werdelin & Manthi (2012) also described a partial cranium and isolated upper teeth of *E. cf. dikikae* from Kanapoi. Therefore, *E. dikikae* could have been present in both the Afar region and the Turkana Basin during the Pliocene.

Other postcranial and dental specimens of several *Enhydriodon* species are reported from the late Pliocene Sidi Hakoma and Denen Dora members of the Hadar Formation, north of the Dikika research area (Howell & Petter 1979; Lewis 2008; Werdelin & Lewis 2013). The only specimen described so far is the femur AL 166-1 (Lewis 2008). Smaller than the Omo femur (total length of 259.9 mm for AL 166-1 and 326.3 mm for L 183-14; measurements from Lewis 2008: table 4), the lesser trochanter is very medially oriented, as in *E. omoensis* n. sp. As for the Dikika femora, the head only reaches the same level as the greater trochanter and the proximal surface along the neck and the medial border of the greater trochanter is deeply excavated, but not as much as in the Omo femur.

Another Ethiopian occurrence of *Enhydriodon* is reported from the early Pliocene of Woranso-Mille, central Afar region (Werdelin *et al.* 2014; Fig. 1), where a few isolated teeth and postcranial bones were discovered. Unfortunately, we could not compare our material to the P_4 and M_1 s of this locality, and the illustration of one M_1 does not permit us to observe detailed features. We can only note that the Omo M_1 s are larger than those from Woranso-Mille (Werdelin *et al.* 2014: fig. 5).

Finally, other remains of *Enhydriodon* found in several plio-pleistocene localities of Ethiopia and Kenya await description (e.g. Werdelin & Peigné 2010; Werdelin & Lewis 2013; Appendix 2). It is notably the case for specimens of *Enhydriodon* sp. from the late Pliocene of the lower Lomekwi Member of the Nachukui Formation, western Turkana Basin of Kenya, where only the femur has been described by Lewis (2008). Lewis (2008) argued that this femur was very similar to that of *E. hendeyi*, although larger. It is much smaller than the Omo femur (total length of 225.4 mm for KNM-WT 37400 and 326.3 mm for L 183-14; measurements from Lewis 2008: table 4). The femoral head is lower than the greater trochanter. Compared to the Omo femur, the proximal surface along the neck and the medial border of the greater trochanter is poorly excavated, the lesser trochanter does not project as medially, the medial condyle projects more ventrally, and the patellar groove is not concave.

Enhydriodon sp.
(Fig. 2J; Table 1)

MATERIAL. — OMO 3/0-10011, right M_1 talonid (unit B-12, Shungura Formation).

DESCRIPTION AND COMPARISONS

The material is a fragment of M_1 talonid ($W_{\text{talo}} = c. 18$ mm). Compared to *Enhydriodon omoensis* n. sp., it has additional cuspids: one between the entoconid and the entoconulid, three mesial to the entoconid, and three instead of two between the hypoconulid and the entoconulid (Fig. 2J). Whether it could be part of an intraspecific variation within a population, different populations of the same species, or different species cannot be determined. We therefore attribute this specimen to *Enhydriodon* sp. The size of this talonid is comparable to that of *E. omoensis* n. sp. and other large *Enhydriodon*.

Genus *Torolutra*

Petter, Pickford & Howell, 1991

TYPE AND ONLY SPECIES. — *Torolutra ougandensis* Petter, Pickford & Howell, 1991 by original designation.

DIAGNOSIS (translated from Petter *et al.* 1991: 952). — “Mandible with a relatively deep masseteric fossa separated from the ventral margin of the ramus and with the anterior border located behind the alveolus for M_2 ; P_4 robust, with an oval outline, surrounded by a thick and continuous cingulid; M_1 with tall and sharp trigonid cuspids, the protoconid being the tallest trigonid cuspid, a narrow talonid, with a flat and obliquely oriented lingual face of the hypoconid.”

GEOGRAPHICAL AND STRATIGRAPHIC RANGE. — Late Miocene to early Pleistocene based on the earliest occurrences in the Tugen Hills, Kenya (*c.* 5.7 Ma, Lukeino Formation) and in the Middle Awash, Ethiopia (5.77-5.54 Ma, Adu-Asa Formation) and on the latest occurrence in the Turkana Basin, Kenya (1.56-1.38 Ma, Koobi Fora Formation). Countries: Egypt, Ethiopia, Kenya, Uganda (see Appendix 2 for details).

TABLE 4. — $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ data from tooth enamel of *Enhydriodon omonensis* n. sp. and *E. sp.* with specimen IDs, ages, and units in the Shungura Formation (or equivalent for Usno).

Specimen ID	Element	Taxon	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	Age (Ma)	Unit
L 2-10012	Left hemimandible (P ₄)	<i>Enhydriodon omoensis</i> n. sp.	-0.5	-4.7	2.96	B-10
OMO 18-1972-99	right M ₁	<i>Enhydriodon omoensis</i> n. sp.	-3.3	-6.0	2.63	C-8
OMO 3/0-10011	right M ₁	<i>Enhydriodon</i> sp.	-3.2	-9.7	2.91	B-12
W 717	left M ¹	<i>Enhydriodon omoensis</i> n. sp.	2.4	-7.4	3.35	B-2
Mean			-1.2	-7.0	—	—
Standard deviation			2.7	2.1	—	—

Torolutra sp.
(Fig. 5)

MATERIAL. — B 374a, fragment of right M₁; B 374b, fragment of left P₄ (both from Usno Formation, correlated with unit B-2 of Shungura Formation)

DESCRIPTION

B 374a (Fig. 5A-D) lacks the paraconid. The protoconid is high. The metaconid is displaced distally relative to the protoconid and lower than the latter. The talonid (Wtalo = 9.6 mm) is poorly basined, with a high hypoconid and a low entoconid crest (Fig. 5D). The lingual border of the talonid forms an angle of 45° with the distal face of the metaconid. In occlusal view (Fig. 5A), the hypoconid crest is slightly mesiolingually oriented and straight, while the entoconid crest is curved. The cingulid is marked on the labial border of the tooth. B 374b (Fig. 5E-F) is broken mesial to the paracone and lingual to the metastylar blade. The paracone is high (height = 9.2 mm) and sharp and the metastylar blade is relatively short (length = 9.7 mm). The labial border of the tooth is concave. Two well-marked crests extend from the paracone tip, one labially and the other lingually (Fig. 5E). The cingulum is thicker on the labial side than on the distal and lingual ones.

COMPARISONS AND DISCUSSION

The two fragmented teeth were described by Petter *et al.* (1991) as *Torolutra* aff. *ougandensis* because of the slightly larger size of the M₁ (B 374a) relative to that of the holotype of the Ugandan otter. In fact, *Torolutra* Petter, Pickford & Howell, 1991 is an African genus of piscivorous otter, whose material is in need of revision. Indeed, several teeth and postcranial elements from Kanapoi (Werdelin 2003) and cranial, dental and postcranial remains from Koobi Fora (Werdelin & Lewis 2013) are identified as cf. *Torolutra ougandensis* or cf. *Torolutra* sp. Lutrinae indet. aff. *Torolutra ougandensis* is also reported by a fairly complete hemimandible from Toros-Menalla, in Chad (Peigné *et al.* 2008) and by a complete M¹ from the Adu-Asa Formation of the Middle Awash, Ethiopia (Haile-Selassie 2008). It seems that the fossil material of potential *Torolutra* is now important enough in number to reevaluate the taxonomy of these fossils – which is outside the scope of this paper.

REMARK

The dentition of *Torolutra* is reminiscent of that of extant otters with high-crowned and sharp teeth (i.e., *Lutra*, *Lontra*, *Pteronura*), perfectly suited for preying primarily on fish.

Lutrinae indet.
(Fig. 3G-K; Table 3)

MATERIAL. — F 508-26, right humerus lacking the distal epiphysis (lower part of Member H, Shungura Formation).

DESCRIPTION

The humerus (Fig. 3G-K) is broken distally, at the level of the entepicondylar foramen and the olecranon fossa. It has an S-shape in lateral view and is laterally compressed. The head is laterally compressed too and the neck greatly bows ventrally. The lesser tuberosity is lower than the head and is pressed against the dorsomedial surface of the latter. The greater tuberosity reaches the same height as the lesser tuberosity. The greater tuberosity is positioned dorsolaterally to the head and greatly extends dorsally. A narrow and shallow bicipital groove separates it from the lesser tuberosity. The deltopectoral and lateral supinator crests are strong. The proximal border of the entepicondylar foramen is visible. The remaining proximalmost part of the olecranon fossa does not show any supratrochlear foramen.

COMPARISONS AND DISCUSSION

The S-shape laterally compressed diaphysis, the presence of an entepicondylar foramen, the strong supinator crest together with low tuberosities on the proximal epiphysis suggest this specimen belongs to an otter. The size is much smaller than the postcranial material of *Enhydriodon* and is rather reminiscent of a medium-sized otter. Compared to an humerus of the extant African species *Aonyx capensis* (Schinz, 1821) (SAM-ZM 1474), the tuberosities are lower and the lesser tuberosity is more extended dorsomedially. Moreover, contemporaneous humeri of the medium-sized otters *Torolutra* cf. *ougandensis* and cf. *Torolutra* sp. are known from the Upper Burgi and KBS members of Koobi Fora (Werdelin & Lewis 2013). Two of the humeri from Koobi Fora are larger, and two others are smaller than the Omo humerus. However, it is likely that all these remains correspond to species of similar sizes. Morphologically, the

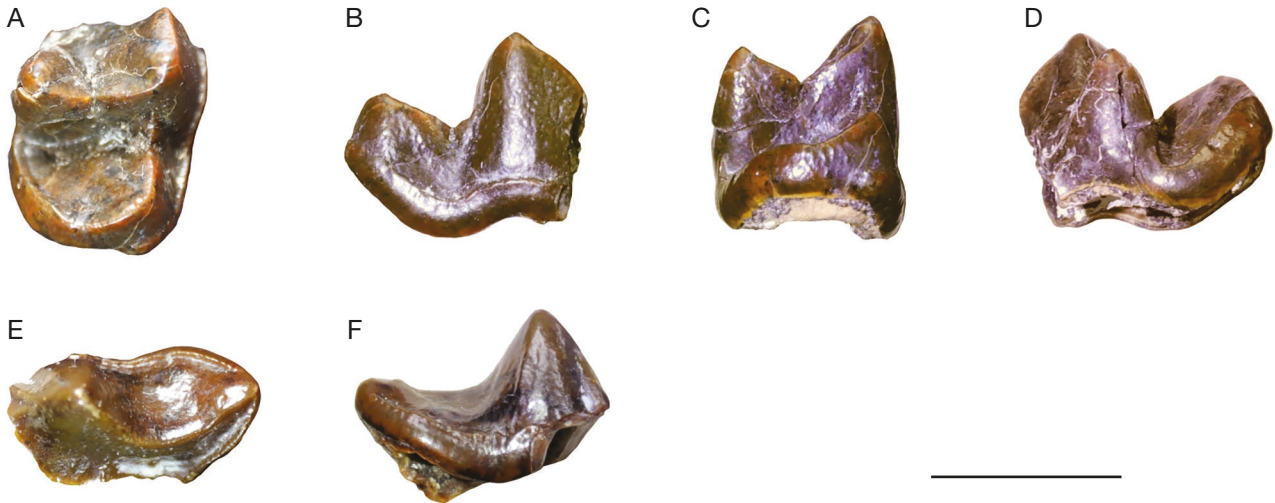


FIG. 5. — *Torolutra* sp.: **A-D**, B 374a, fragment of right M₁ views: **A**, occlusal; **B**, labial; **C**, distal; and **D**, lingual; **E, F**, B 374b, fragment of left P₄ views: **E**, occlusal; **F**, labial. Scale bar: 1 cm.

proximal epiphysis on the Koobi Fora fossils (Werdelin & Lewis 2013: fig. 4.7a-g) resembles that of the Omo specimen. Nevertheless, the distal epiphysis does not have any entepicondylar foramen (Werdelin & Lewis 2013: figs 4.5e, f; 4.7b, c, h-j), unlike the Omo specimen, and the shaft is thicker distally, where the supinator crest emerges (Werdelin & Lewis 2013: fig. 4.7b, c). These morphological differences and the fact that the humerus from the Shungura Formation has not been found in association with the above-described teeth of *Torolutra* render a finer taxonomic attribution premature.

STABLE ISOTOPE ANALYSIS RESULTS

$\delta^{18}\text{O}$ values of four tooth samples of *Enhydrionodon omoensis* n. sp. and *Enhydrionodon* sp. from the Usno Formation and members B and C of the Shungura Formation range from -3.3 to $+2.4\text{‰}$ with a mean value of $-1.2 \pm 2.7\text{‰}$ (Table 4; Fig. 6). Terrestrial mammals from the same members ($n = 306$; Appendix 1) have a similar $\delta^{18}\text{O}$ mean value of $-0.9 \pm 2.9\text{‰}$ (Table 5). Applying the $\delta^{18}\text{O}$ mean value for terrestrial mammals to the equation from Clementz *et al.* (2008), we calculated an expected $\delta^{18}\text{O}$ mean value for a semi-aquatic mammal (based on hippopotamid data) of -2.5‰ , which is lower than the mean value measured for *Enhydrionodon*. Furthermore, the measured $\delta^{18}\text{O}$ mean value for Omo hippopotamids ($n = 29$) is $-4.1 \pm 2.1\text{‰}$, nearly 3‰ more negative than for *Enhydrionodon*. Both the mean and standard deviation of the Omo *Enhydrionodon* $\delta^{18}\text{O}$ values differ from those expected for semi-aquatic mammals and are similar to values found in terrestrial mammals from the same members, such as hyaenids, *Theropithecus* I. Geoffroy Saint-Hilaire, 1843 and deinotheriids (Fig. 6).

$\delta^{13}\text{C}$ values of the four late Pliocene *Enhydrionodon* teeth range from -9.7 to -4.7‰ with a mean value of $-7.0 \pm 2.1\text{‰}$ (1σ) (Table 4; Fig. 6). Therefore, *Enhydrionodon* fed on prey with

C_3 to C_4 diets, with a greater proportion of its diet deriving from prey with C_3 diets. The median $\delta^{13}\text{C}$ value of *Enhydrionodon* is close to those of the other carnivorans from the same members, felids and hyaenids (Fig. 6; Appendix 2).

GENERAL DISCUSSION

ISOTOPE DATA AND PALEOECOLOGY

Extant otters show different degrees of adaptations to aquatic environments. The sea otter, *Enhydra lutris* (Linnaeus, 1758), lives almost exclusively in the water, whereas freshwater otters, such as *Lutra lutra* (Linnaeus, 1758), and to a lesser extent, the marine otter *Lontra felina* (Molina, 1782), spend most of their time on land for resting, breeding, nursing, and traveling between waterways (e.g. Estes 1980; Larivière 1998; Larivière & Walton 1998). Although all extant otters are well adapted for swimming, river otters and the marine otter are more adapted for terrestrial locomotion compared to sea otters (Estes 1980; Larivière 1998), notably in displaying different postcranial morphologies (Taylor 1914; Botton-Divet *et al.* 2016). The postcranial elements of *Enhydrionodon* in the fossil record are scarce and incomplete, so that the interpretation of its morpho-functional features to precisely assess its locomotor habit is challenging. Moreover, different hypotheses exist regarding the degree of aquatic specialization among species of *Enhydrionodon*. For instance, in a review of several African femora, Lewis (2008) suggested that the species from West Turkana (*E.* sp. from Lomekwi) and Langebaanweg (*E. hendeyi*) should be terrestrial generalist mustelids, whereas the Omo and Hadar species (*E. omoensis* n. sp. and *E.* sp., respectively) share more features with the sea otter *Enhydra*. On the other hand, Valenciano & Govender (2020), when assigning new postcranial remains from Langebaanweg to *E. hendeyi*, indicated some similar morphological traits between this otter and the extant clawless otters *Aonyx capensis* and *Amblonyx cinereus* (Illiger, 1815). In another study, Geraads *et al.* (2011)

TABLE 5. — Tooth enamel $\delta^{18}\text{O}$ values for extant and fossil otters, fossil terrestrial mammals and fossil hippopotamids from the Lower Omo Valley, and extant terrestrial carnivores suggesting a terrestrial lifestyle for *Enhydriodon omoensis* n. sp. The most informative variable for % aquatic is the standard deviation (SD) of $\delta^{18}\text{O}$. Extant otters with low SD ($< 1\text{‰}$) are c. 33 to $> 50\%$ aquatic, whereas taxa with higher SD ($> 1\text{‰}$) are not aquatic ($< 5\%$). Mean $\delta^{18}\text{O}$ values are determined by source water. Extant carnivore data from Clementz & Koch (2001); data for Aramis fossil *Enhydriodon* Falconer, 1868 from White *et al.* (2009). Abbreviations: E, estuary; FW, freshwater; KB, kelp bed; T, terrestrial.

Species	Locality	n	Feeding zone	% Aquatic	$\delta^{18}\text{O}$ VPDB			
					mean	min	max	SD
<i>Enhydra lutris</i> (Linnaeus, 1758) Sea otter	Central California, United States	5	KB	$> 50\%$	-3.5	-4.4	-3.0	0.6
<i>Lontra canadensis</i> (Schreber, 1777) River otter	Washington, United States	10	E	c. 33%	-5.0	-6.5	-3.6	0.9
<i>Lontra canadensis</i> (Schreber, 1777) River otter	Oregon, United States	7	FW	c. 33%	-7.7	-7.9	-7.3	0.3
<i>Enhydriodon</i> sp. Large otter	Aramis, Ethiopia	1	unknown	unknown	-7.9	—	—	—
<i>Enhydriodon omoensis</i> n. sp. and <i>Enhydriodon</i> sp. Large otter	Omo, Ethiopia (Members B&C)	4	unknown	unknown	-1.1	-3.3	2.4	2.7
Hippopotamidae	Omo, Ethiopia (Members B&C)	29	T	c. 90%	-4.1	-7.4	2.8	2.1
All mammals – hippos	Omo, Ethiopia (Members B&C)	306	T	$< 10\%$ but variable	-0.9	-8.2	9.0	2.9
<i>Canis latrans</i> Say, 1823 Coyote	Central California, United States	5	T	$< 5\%$	-3.4	-4.5	1.6	3.4
<i>Lynx rufus</i> (Schreber, 1777) Bobcat	Central California, United States	4	T	$< 5\%$	-1.8	-3.1	-0.1	1.2

described several long bones from *E. dikikae* and suggested this species was poorly adapted to an aquatic environment. This hypothesis was based on morphological comparisons between *E. dikikae* and the earliest form of *Sivaonyx*, a terrestrial African predator from which *Enhydriodon* could have originated (see Peigné *et al.* 2008 for details about *Sivaonyx* locomotion). However, Geraads *et al.* (2011) also noted that the partial femora of *E. dikikae* (proximal epiphysis DIK-44-1 and distal epiphysis DIK-41-20) were very similar to a specimen from Hadar (AL-166-10; Lewis 2008). Yet, Lewis (2008) suggested that the epiphyses of the Hadar specimen show clear adaptations to an aquatic environment, while the relative length of its diaphysis is anomalously long for an aquatic mustelid. Therefore, according to those data, there is no consensus about the lifestyle of the different species of *Enhydriodon*; they could have been more terrestrial than extant otters or perhaps, for some of them, as specialized as extant otters for an aquatic lifestyle. Their different postcranial morphologies could reflect postures and/or forms of locomotion that do not exist anymore today.

In order to investigate the preferred habitat of *E. omoensis* n. sp., we used oxygen stable isotopes, as oxygen values can reflect the degree to which a species is dependent on water (Bocherens *et al.* 1996; Clementz & Koch 2001; Levin *et al.* 2006). Surprisingly, $\delta^{18}\text{O}$ values of *Enhydriodon* enamel are not consistent with a semi-aquatic habitat based on three criteria. First, the standard deviation falls outside of the range of extant otters. It is 2.7‰ in *Enhydriodon* but 0.3 to 0.9‰ in extant otters (Table 5). The low standard deviation of $\delta^{18}\text{O}$ values in extant otters include data from *Enhydra lutris* (sea otter) that spend $> 50\%$ of their time in water, and *Lontra canadensis* (Schreber, 1777) (North American river otter) that

spend c. 33% of their time in the water (Clementz & Koch 2001; Table 5). Instead, the standard deviation of *Enhydriodon* $\delta^{18}\text{O}$ values falls squarely within the range of standard deviations measured in extant terrestrial carnivores (1.2 to 3.4‰) with similar sample sizes (Clementz & Koch 2001; Table 5). Second, the mean *Enhydriodon* $\delta^{18}\text{O}$ value (Table 5) is 1.3‰ more positive than what is predicted for a semi-aquatic mammal based on the equation of Clementz *et al.* (2008). Finally, the mean *Enhydriodon* value is 2.9‰ more positive than the mean value measured for hippopotamids from the same members (Fig. 6), even if metabolic differences between otters and hippos certainly exist. Altogether, these results suggest the Omo *Enhydriodon* was not a semi-aquatic otter, *contra* the morphological analysis of its femur by Lewis (2008).

Although it is generally assumed (and rarely investigated) that extinct otters are semi-aquatic, previous studies on postcranial remains suggested that other extinct species of lutrines could have been terrestrial predators (i.e., the late Miocene Chadian *Sivaonyx beyi*; Peigné *et al.* 2008; the late Miocene Spanish *Teruelictis riparius* Salesa, Antón, Siliceo, Pesquero, Morales & Alcalá, 2013 [Salesa *et al.* 2013]). In fact, the $\delta^{18}\text{O}$ median value of the Omo *Enhydriodon* is similar to that of hyaenids from the same time interval. Our $\delta^{18}\text{O}$ results differ from the single specimen of *Enhydriodon* analysed from the older Aramis Member (lower part) of the Middle Awash, which had one of the lowest $\delta^{18}\text{O}$ values of all species sampled, similar to Aramis hippopotamids (White *et al.* 2009). The Aramis *Enhydriodon* is represented by a single sample so that we cannot discuss its range of variation. Furthermore, it is more than a million years older than the Omo form; hence it might belong to a different species, which evolved within a distinct community and could have filled a different ecological niche.

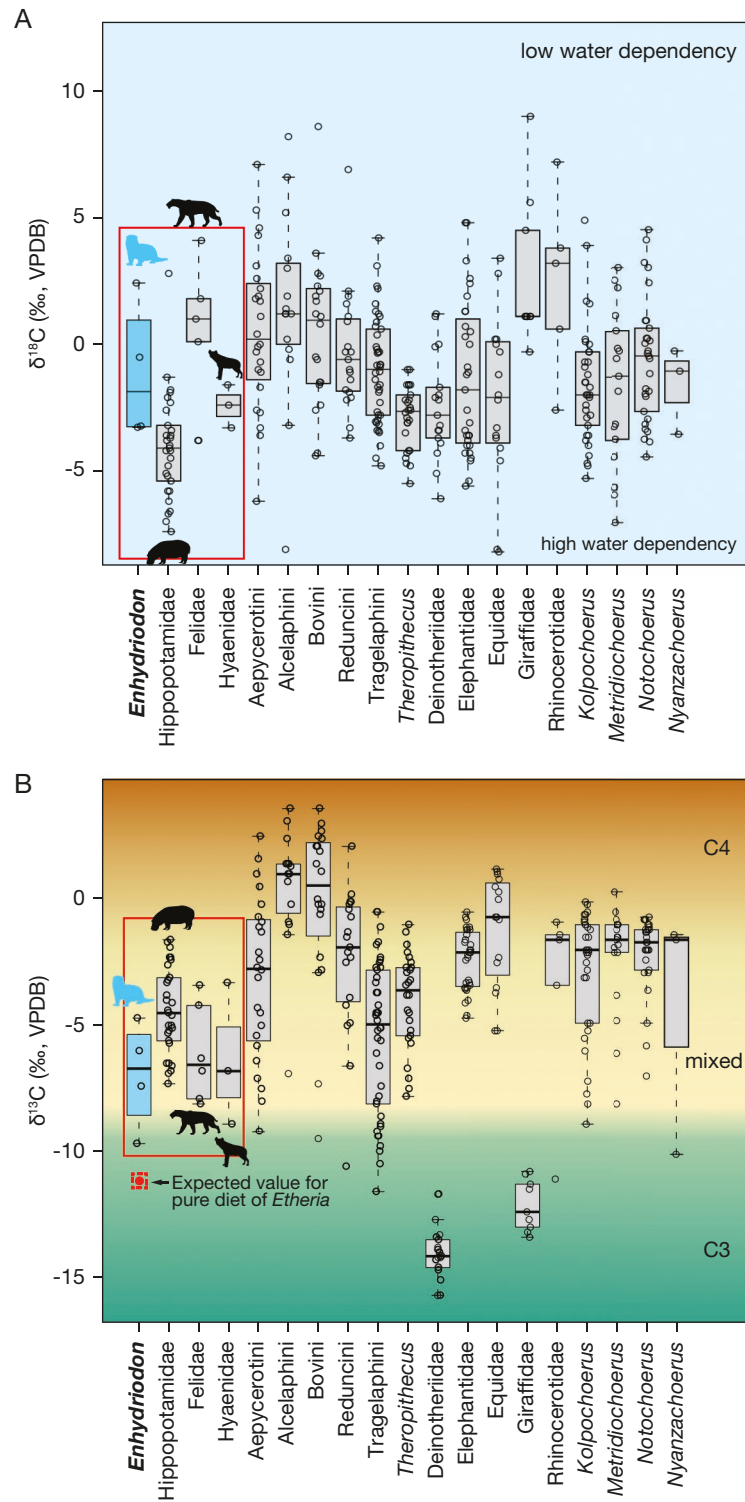


FIG. 6. — **A, B**, Stable oxygen (**A**) and carbon (**B**) isotope values for Omo carnivorans (*Enhyridodon* Falconer, 1868, felids, hyaenids) and herbivore families (Hippopotamidae; Bovidae, by tribe; Cercopithecidae, genus *Theropithecus* I. Geoffroy Saint-Hilaire, 1843; Deinotheriidae, Elephantidae, Equidae, Giraffidae, Rhinocerotidae; Suidae, by genera) from the Usno Formation and the members B and C of the Shungura Formation. Carnivoran data are from this study and herbivore data are from Souron *et al.* (2012), Bibi *et al.* (2013) and Negash *et al.* (2015, 2020) (see Appendix 1 for isotope values). **Bold horizontal lines** in the box and **whisker plots** represent median values, **boxes** represent first and third quartiles, and **whiskers** encompass 1.5x the interquartile range. The $\delta^{13}\text{C}$ isotope value expected for *Enhyridodon* if its diet was based exclusively on the consumption of giant oysters (*Etheria elliptica* Lamarck, 1807) is indicated in **red**. The **red box** underlines the comparisons between otters, terrestrial carnivorans (felids and hyaenids) and hippopotamids (see Stable isotope analysis results and General discussion for details).

TABLE 6. — Tooth enamel $\delta^{13}\text{C}$ values for extant and fossil otters and extant terrestrial carnivorans suggesting an omnivorous, perhaps opportunistic diet for *Enhydriodon omoensis* n. sp. Extant carnivoran data from Clementz & Koch (2001) and Tejada *et al.* (2020) (for *Pteronura brasiliensis* Zimmermann, 1780). Those data are corrected from the extant (–7.8‰) to Plio-Pleistocene (3.4 to 2.5 Ma) $\delta^{13}\text{C}_{\text{atm}}$ value of –6.3‰ based on assumed extant sampling in the 1990s for comparison to the Omo samples (Francey *et al.* 1999; Tipple *et al.* 2010). Data for Aramis fossil *Enhydriodon* Falconer, 1868 from White *et al.* (2009). Abbreviations: **E**, estuary; **FW**, freshwater; **KB**, kelp bed; **T**, terrestrial. Most common diet of extant carnivorans from Bekoff (1977), Estes (1980), Larivière & Walton (1997, 1998), Noonan *et al.* (2017), and the Washington Department of Fish and Wildlife for the Washington population of *Lontra canadensis* (Schreber, 1777) (<https://wdfw.wa.gov/>).

Species	Locality	n	Feeding zone	Diet	$\delta^{13}\text{C}_{\text{corr}}$			
					mean	min	max	SD
<i>Enhydra lutris</i> (Linnaeus, 1758) Sea otter	Central California, United States	5	KB	Sea urchins, bivalves, rock crabs	–4.6	–5.6	–3.7	0.9
<i>Lontra canadensis</i> (Schreber, 1777) River otter	Washington, United States	10	E	Fish	–6.6	–14.4	–4.5	3
<i>Lontra canadensis</i> River otter	Oregon, United States	7	FW	Fish, frogs, crayfish	–15.8	–20.0	–10.0	4.3
<i>Pteronura brasiliensis</i> Zimmermann, 1780 Giant otter	Maynas, Peru	6	FW	Fish	–19.9	–21.1	–17.8	1.3
<i>Enhydriodon</i> sp. Large otter	Aramis, Ethiopia	1	unknown	unknown	–8.2	–	–	–
<i>Enhydriodon omoensis</i> n. sp. and <i>Enhydriodon</i> sp. Large otter	Omo, Ethiopia	4	unknown	unknown	–7.0	–9.7	–4.7	2.1
<i>Canis latrans</i> Say, 1823 Coyote	Central California, United States	5	T	Omnivore	–12.0	–13.0	–10.6	3.4
<i>Lynx rufus</i> (Schreber, 1777) Bobcat	Central California, United States	4	T	Lagomorphs, rodents	–10.3	–15.7	–7.5	1.7

Previous studies inferred a diet based on hard aquatic items for *Enhydriodon*, as its bunodont tooth morphology suggests (Pickford 2007; Lewis 2008; Geraads *et al.* 2011). Indeed, its large, low-crowned, and rather flat teeth are typical of mammals crushing their food, and particularly resemble those of the extant sea otter. Members B and C of the Shungura Formation produced a large number of turtles, catfishes, and molluscs that could constitute potential food items for this otter (e.g. Pickford 2007; Lewis 2008; Geraads *et al.* 2011). Fossils of the giant freshwater oyster *Etheria elliptica* Lamarck, 1807 are frequently found in Miocene to Pleistocene sediments in the Turkana Depression (Feibel 2003, 2011; Vonnhof *et al.* 2013), including members B and C of the Shungura Formation. They tend to build ancient reefs in perennial, agitated waters such as turbulent channels or the margins of freshwater lakes (Van Damme & Gautier 1972; Gautier 1976; Heizelin 1983). *Etheria elliptica* is endemic to Africa and is still present in the extant Turkana system. Its high caloric density (75 kcal/100 g; 12.5% protein by weight) makes it a rich source of protein for the local populations (Ampofo-Yeboah & Owusu-Frimpong 2014) and it could have been a particularly nutritive choice for *Enhydriodon*.

Here we investigated the diet of *Enhydriodon* using carbon stable isotopes and we initially considered *Etheria elliptica* to be the most likely aquatic food source. Because the soft tissues of molluscs reflect their diet, the carbon isotope value of the soft tissues in *Etheria* is dependent on phytoplankton and organic particulates that this mollusc obtains through filter feeding. The bulk tissue $\delta^{13}\text{C}$ value of *Etheria elliptica* from Lake Chad is $-25.7\text{‰} \pm 1.1\text{‰}$ (Kidd *et al.* 2004), falling within the range of C_3 plants in eastern Africa (Cerling & Harris 1999). Assuming this value for the tissue of *Etheria*

in the Lower Omo Valley, a diet of pure oysters would result in an enamel $\delta^{13}\text{C}$ value of -11.3‰ for *Enhydriodon*. This is based on a diet to enamel enrichment value of 13.2‰ using the body mass dependent equation of Tejada-Lara *et al.* (2018) and a $+1.5\text{‰}$ correction for the $\delta^{13}\text{C}$ value of atmospheric CO_2 ($\delta^{13}\text{C}_{\text{atm}}$) from modern values (c. 2000: -7.8‰) to Plio-Pleistocene $\delta^{13}\text{C}_{\text{atm}}$ values (3.4 to 2.5 Ma: -6.3‰) of the fossil specimens. The $\delta^{13}\text{C}_{\text{atm}}$ correction is based on modern atmospheric measurements (Francey *et al.* 1999) and reconstructed values from a high-resolution benthic foraminifera record (Tipple *et al.* 2010). Our results show that the diet of the Omo *Enhydriodon* was certainly not based entirely on *Etheria*, as the carbon values for this otter are c. 2 to 7‰ more positive than the value expected from a pure diet of *Etheria* (Fig. 6). Indeed, $\delta^{13}\text{C}$ values for our sample of *Enhydriodon* fall within the range of mixed C_3 – C_4 feeders, only partly encompassing aquatic organisms feeding on C_3 plants (e.g. some fishes, turtles, and molluscs such as *Etheria*). A wide range of carbon isotope values exists between extant marine, estuarine and freshwater otters (Clementz & Koch 2001; Table 6), indicating that different aquatic foraging zones can lead to different carbon isotope values in tooth enamel. Yet, the $\delta^{13}\text{C}$ standard deviation of the Omo *Enhydriodon* falls outside of the range of the extant freshwater populations of river otters from Oregon (*Lontra canadensis*; Clementz & Koch 2001) and Peru (*Pteronura brasiliensis* Zimmermann, 1780; Tejada *et al.* 2020) (Table 6). The lowest carbon isotope value for *Enhydriodon* (-9.7‰) is 0.3 to 8.1‰ more positive than the highest value for extant freshwater otters (Table 6).

If it was exclusively feeding on aquatic organisms, *Enhydriodon* from the Lower Omo Valley would have had limited time

in the water for foraging or hunting based on its mean and standard deviations of tooth enamel $\delta^{18}\text{O}$ values. Thus, we might consider that the Omo *Enhydriodon* consumed a certain amount of terrestrial prey with a C_4 diet, by either hunting or scavenging. Currently, extant otters can incorporate small mammals, amphibians, reptiles, and birds, to their diet, either opportunistically or depending on seasons and prey availability (e.g. Larivière & Walton 1998 for *Lontra canadensis*; Larivière 2001 for *Aonyx capensis*). To our knowledge, scavenging behaviour has never been observed in extant otters nor has it been suggested for a fossil one, but it should not be excluded. Indeed, the large bunodont dentition of *Enhydriodon* suggests durophagous abilities, hence the possibility to feed on carcasses, maybe in a similar manner as bone-crushing striped and brown hyaenas or wolverines (Rieger 1981; Mills 1982; Pasitschniak-Arts & Larivière 1995).

Given the isotope study results, the ecological niche *Enhydriodon* could have filled in the late Pliocene of the Lower Omo Valley is rather unexpected if we compare to the behaviour of extant otters. This gigantic otter could have been terrestrial and omnivorous, or perhaps opportunistic in its diet, maybe foraging on aquatic organisms and hunting or scavenging terrestrial prey on the shores of the paleo-Omo River or Lake Turkana. Other analyses based on the actual past food consumption of *Enhydriodon*, such as dental microwear analysis, would be helpful to assess the hardness of prey ingested by this peculiar otter. The sample size we used for stable isotope analyses is limited due to the rarity of dental specimens of *Enhydriodon*. Therefore, future analyses of lutrine enamel isotopes and postcrania from the Turkana Basin should be conducted to provide a clearer picture of their ecological niches.

PALEOBIOGEOGRAPHY AND PALEOENVIRONMENT

Based on the morphology of the teeth and the femur, *Enhydriodon omoensis* n. sp. is more closely similar to *E. dikikae*, from the Afar region (and potentially from Kanapoi) than to any other species of *Enhydriodon* within the Turkana Basin. In contrast, the endemism of other mammals that are dependent on aquatic environments, such as the hippopotamids, begins after 2.9 Ma in the rift basins (Boisserie *et al.* 2011). As for some species of *Enhydriodon* (i.e., *E. soriae*, *E. dikikae* and *E. ekecaman*), the same large hippopotamid species is distributed from Afar to Turkana during the late Pliocene (Boisserie 2020; Fig. 1). Faunal similarity analyses of fossil African mammal communities from the southern and northern Turkana Basin, including carnivorans, indicated that they were not closely clustered together (Reed & Lockwood 2001; Werdelin 2008), which could explain patterns of disparity of *Enhydriodon* species. In addition, forms of *Enhydriodon* from the Pliocene of central Chad are close to those of eastern Africa (Bonis, personal comm. on *Enhydriodon* from Koro Toro listed by Brunet *et al.* 1997; Bonis *et al.* 2008 for Kosom Bougoudi).

Enhydriodon diversified into eight known species (and probably more) from the late Miocene to the early Pleistocene, with six of them occurring in the eastern African rift system (Fig. 1).

Werdelin & Lewis (2005) suggested that the multiplicity of drainage systems of paleolakes and paleorivers in the eastern African rift basins during the Plio-Pleistocene could have been responsible for this radiation. We note that *E. omoensis* n. sp. was associated with a wide array of perennial water bodies, as sediments from most of Member B indicate a lacustrine environment, while upper Member B and Member C were dominated by floodplains and associated channels (Heinzelin 1983; Feibel 2011). The same is true for the species of *Enhydriodon* from Kanapoi, present both in lacustrine and riverine environments (Werdelin & Lewis 2020).

While remains of *Enhydriodon* are not found in the Lower Omo Valley after 2.5 Ma, it persisted until around 2 Ma in the Turkana Basin (i.e., Nakoret, Lower Kerio Valley of Kenya; Fig. 1). Moreover, the fossil record of *Torolutra* also extends in the early Pleistocene in the Turkana Basin (i.e., Koobi Fora record; Fig. 1). Working from the assumption that they were semi-aquatic, Werdelin & Lewis (2005) suggested that the extinction of *Enhydriodon* could be linked to hydrographical changes in relation to the gradual aridification of eastern Africa during the Plio-Pleistocene transition. They also noted that the species diversity of eastern African otters shrank after 2 Ma. In the Shungura Formation, humid conditions persisted longer than in the Turkana Basin, with a likely regression of humid-forested environments around 2.8 Ma (e.g. Bibi *et al.* 2013; Blondel *et al.* 2018), and a later shift towards woody grasslands, with < 40% canopy cover, around 1.8 Ma onwards (Cerling *et al.* 2011a, 2011b).

As already pointed out in several papers (e.g. Haile-Selassie 2008: 565, fig. 6; Geraads *et al.* 2011: 451, fig. 5; Werdelin *et al.* 2014: 335, fig. 5) and in this study (Fig. 4), the species of *Sivaonyx/Enhydriodon* tend to increase in size from the late Miocene to the early Pleistocene, with the Omo species being the largest and among the most recent ones (Werdelin *et al.* 2014; Figs 1; 4). Body mass estimates suggest that *E. dikikae* could have weighed between 100 kg and 200 kg (Geraads *et al.* 2011; Valenciano *et al.* 2017) and the larger *E. omoensis* n. sp., more than 200 kg (Valenciano *et al.* 2017), which means it could have weighed more than an extant lion. Several large-sized and specialized taxa, such as saber-tooth felids, also went extinct around the Plio-Pleistocene transition (Werdelin & Lewis 2005, 2013). The intensification of butchery activities or scavenging behavior of early hominins is the primary hypothesis favored for explaining the extinctions of eastern African large carnivorans during the last two million years (Lewis & Werdelin 2007; Werdelin & Lewis 2013; Faurby *et al.* 2020; but see Faith *et al.* 2018 for the lack of evidence of ancient hominin impact on other mammals). Therefore, major changes in climate and biotic interactions seem to have triggered the extinction of African fossil otters, including *Enhydriodon* and *Torolutra*. Further work on the Omo carnivoran paleobiodiversity, paleobiogeography, and paleoecology is still needed to test these hypotheses at a local scale and to understand the evolutionary dynamics of biotic interactions between carnivorans, hominins, and their prey in the past communities of the Lower Omo Valley.

CONCLUSIONS

The Lutrinae from the Plio-Pleistocene of the Lower Omo Valley belong to at least two distinct otters, whose ecologies are very different. *Enhydriodon omoensis* n. sp. is a gigantic terrestrial otter with bunodont teeth, which may have fed on aquatic and terrestrial prey. The much smaller semi-aquatic *Torolutra* sp., similar in size to an extant river otter, probably had a diet based primarily on fish. *Enhydriodon* and *Torolutra* both occur in the Brown Sands of the Usno Formation around 3.3 Ma. *Enhydriodon* is also present further south, in the Shungura Formation, from c. 3.4 Ma to 2.5 Ma. *Torolutra* possibly occurs in the more recent lower part of Member H of the Shungura Formation (c. 1.9–1.8 Ma) too.

The most peculiar otter from the Lower Omo Valley is *E. omoensis* n. sp. Based on our stable isotope analyses and its huge body mass, this otter likely filled a unique ecological niche in the past communities, co-existing with early hominins in the same region from c. 3.4 to 2.5 Ma. While it has been suggested that the extinctions of many large-sized carnivores from eastern Africa during the Plio-Pleistocene, including gigantic otters, were linked to the regional aridification and/or incursion of early hominins into the carnivore guild, further investigations into the paleoecology of carnivores are still needed to evaluate the impact of both abiotic and biotic factors on the evolutionary dynamics of these faunas.

Acknowledgements

This work has been funded by the ANR OLD and the Fondation ARS Cuttoli Paul Appell (the latter to C.G.). It is part of the research program Omo Group Research Expedition (OGRE), also funded by the French Ministry of Europe and Foreign Affairs, the Fyssen Foundation, and the CNRS (INEE). It has been supported by the ARCCH (Ethiopian Authority for Research and Conservation of Cultural Heritage), the CFEE (USR CNRS 3137), and the Embassy of France to Ethiopia. K.T.U. was supported by funding from the Vetlesen Foundation and a fellowship from Columbia University's Center for Climate and Life. This work is based on Omo specimens collected by the IORE (International Omo Research Expedition) and the OGRE. We are grateful to all people who took part to fieldwork with the IORE and OGRE, to the staff of the National Museum of Ethiopia/ARCCH at Addis Ababa, especially the curators in paleontology Tomas Getachew, Getahun Tekle Yemanebirhan, Sahle Selassie, and Gemechis Getane for their help in the collections, as well as to Dawit Seifu for specimen preparation. We thank Kaye Reed and the late William Kimble for giving permission to access the Hadar carnivores for comparative purpose. We would like to deeply thank our dear colleague and friend, the late Stéphane Peigné, who provided photos of some otters compared here. Finally, we are grateful to Robert Asher, Juan Abella and Alberto Valenciano for their comments that helped to improve the quality of our manuscript.

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Submitted on 7 February 2021;
accepted on 25 May 2021;
published on 5 September 2022.

APPENDICES — SUPPLEMENTARY MATERIAL

APPENDIX 1. — $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values for the fauna from members B and C of the Shungura Formation and from the Usno Formation (equivalent to unit B-2): https://doi.org/10.5852/cr-palevol2022v21a30_s1

APPENDIX 2. — Geographical and stratigraphic range of *Enhyriodon* Falconer, 1868 and *Torolutra* Petter, Pickford & Howell, 1991 in Africa: https://doi.org/10.5852/cr-palevol2022v21a30_s2

APPENDIX 3. — Illustration of the anatomical abbreviations for Tables 1-3. **A**, simplified drawings of a hemimandible of an extant otter, *Lontra canadensis* (Schreber, 1777); **B**, teeth of *E. omoensis* n. sp. from Omo; **C**, humerus of Lutrinae indet. from Omo. See also Abbreviations in Material and Methods.

