Available online at www.sciencedirect.com

ScienceDirect

C. R. Palevol 7 (2008) 607–627

COMPTES RENDUS
PALEVOL

http://france.elsevier.com/direct/PALEVO/

Systematic palaeontology (vertebrate palaeontology)

The femur of extinct bunodont otters in Africa (Carnivora, Mustelidae, Lutrinae)

Margaret E. Lewis

NAMS-Biology, The Richard Stockton College of NJ, PO Box 195, Pomona, NJ 08240, USA

Received 1st September 2008; accepted after revision 17 September 2008
Available online 12 November 2008

Written on invitation of the editorial board

Abstract

This study compares fossil femora attributed to extinct African bunodont lutrines with extant mustelids and ursids to reconstruct locomotor behavior. Due to the immense size differences among taxa, shape data were used to compare morphology. Based on morphological differences, the fossil femora are suggested to belong to different taxa with different locomotor abilities and habitat preferences. The Langebaanweg femur is the oldest and has a typical mustelid morphology suggesting that it was a locomotor generalist like most mustelids. The West Turkana form is more like extant nonbunodont otters, but much larger, and may have belonged to a semiaquatic taxon. The enormous Omo femur shares some features with truly aquatic taxa (e.g., *Enhydra*) and is the most likely to have been fully aquatic. The same may hold true for the Hadar species as it is most similar to that from the Omo. If these femora truly belong to bunodont lutrines, then they are more diverse in postcranial morphology than in dental morphology. ***To cite this article: M.E. Lewis, C. R. Palevol 7 (2008).***

Résumé

Le fémur des loutres bunodontes fossiles en Afrique (Carnivora, Mustelidae, Lutrinae). Cette étude compare des fémurs de loutres africaines bunodontes fossiles à des mustélidés et des ursidés actuels, afin de reconstituer leur mode de locomotion. À cause des grandes différences de taille entre les taxons, nous avons utilisé les données relatives à la forme pour comparer les morphologies. En se basant sur les différences morphologiques, les fémurs fossiles sont supposés appartenir à différents taxons, avec des capacités locomotrices et des habitats préférentiels différents. Le fémur de Langebanweg est le plus ancien et possède une morphologie typique de mustélidé suggérant une locomotion de type généraliste comme celle de la plupart des mustélidés. La forme de l'Ouest Turkana est plus proche des loutres actuelles non bunodontes, bien que beaucoup plus grande, et peut avoir appartenu à un taxon semi-aquatique. L'énorme fémur de l'Omo partage quelques traits avec des taxons véritablement aquatiques (par exemple, *Enhydra*) et se trouve celui qui a le plus de chances d'avoir été pleinement aquatique. On peut dire la même chose de celui de Hadar qui est proche de celui de l'Omo. Si ces fémurs appartiennent vraiment à des lutrinés bunodontes, il s'ensuit que ceux-ci étaient plus variés dans leur morphologie appendiculaire que dans leur morphologie crânienne. ***Pour citer cet article : M.E. Lewis, C. R. Palevol 7 (2008).***

Keywords: Fossil; Omo; Hadar; West Turkana; Langebaanweg; *Enhydriodon*; *Sivaonyx*

Mots clés : Fossile ; Omo ; Hadar ; Ouest Turkana ; Langebaanweg ; *Enhydriodon* ; *Sivaonyx*

E-mail address: Margaret.Lewis@stockton.edu.

1631-0683/$ – see front matter © 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.crpv.2008.09.010

1. Abbreviations

1.1. Institutions

AMNH	American Museum of Natural History, New York
ENM	Ethiopia National Museum, Addis Abeba
FMNH	Field Museum of Natural History, Chicago
KNM	Kenya National Museums, Nairobi
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
NMNH	National Museum of Natural History, Washington, D.C.
NRM	Swedish Natural History Museum, Stockholm
SAM	South African Museum, Cape Town

1.2. Others

AP	anteroposterior
ML	mediolateral
SI	superoinferior

2. Introduction

Otters have often been divided into two functional groups based on dental morphology: those with bunodont carnassials and those whose carnassials form blades [33,42,56]. The first group is often referred to as "crab-eating otters" and the second as "fish-eating otters", although this is an inaccurate description of their diets [32]. In the original formulation by Pohle [55], the crab-eating otter group included the small-clawed (*Amblonyx*), clawless otters (*Aonyx*), and the sea otter (*Enhydra*), all of whom include crabs in their diet. "Crabotters" were considered by him to belong to a taxonomic group distinct from all other otters. As today's categories are more about dental morphology, the sea otter is the sole "crab-eating otter" as it is the only extant lutrine with bunodont teeth. All other extant lutrines are members of the second group. To reduce confusion, extant otters will be referred to as "bunodont" or "nonbunodont" in this paper.

While both bunodont and nonbunodont lutrines have been found in the fossil record, this paper focuses on bunodont forms from Africa. Confusion exists over which African material should be referred to *Sivaonyx* and which to *Enhydriodon*, reflecting the general uncertainty about these taxa. A smaller form, *Vishnuonyx*, is also present. The taxonomy of all bunodont forms, including those from Eurasia and North America, has been the subject of discussion for some time [8,42,43,52,65,66,69] and will not be dealt with here (a discussion of valid and invalid bunodont taxa by continent can be found in Pickford's review [52]).

Although rare, postcrania presumably belonging to extinct bunodont lutrines are known [1,21,25,33,49,50,53,56]. Assignment to genus in the past has often been based on craniodental material from the same locality. As with the extant lutrines, grouping fossil lutrines solely based on dental morphology obscures the diversity of postcranial morphology present in this group. Despite the great variation in size and morphology, few studies have attempted functional analyses of this material [33,49]. As *Enhydriodon* and *Sivaonyx* are being found at an increasing number of sites in Africa [18,21,25–27,42,43,49,51,59,66], understanding their behavior and ecology becomes critical for reconstructing the past. This paper, therefore, examines the most common postcranial element in the fossil record of African lutrines, the femur, to determine similarities and differences in behavior among extinct forms and among extinct and extant forms with the hope of better understanding the behavior and ecology of these forms. The first descriptions of these femora are also provided.

3. Materials and methods

3.1. Materials and measurements

Linear measurements (functional length, midshaft diameters, and articular dimensions; Table 1) were made of various extant and fossil carnivoran femora. Only free-ranging taxa were used. In addition to lutrines, a range of mustelids and a few ursids were measured for comparison (Table 2). Data on extant, free-ranging, adult taxa were collected at the AMNH, FMNH, KNM, MCZ, NMNH, and NRM.

In this paper, "semiaquatic" refers to a species that spends a significant portion of its time in water and a significant portion out of the water. Almost all extant otters are semiaquatic. "Aquatic" taxa, on the other, spend all or the vast majority of their time in the water. Among extant otters, sea otters (*Enhydra lutris*) and possibly marine otters (*Lontra felina*) are aquatic. Marine otters were not included in the study due to a paucity of material. Information on aquatic and nonaquatic locomotor and postural behavior was taken from the literature [2,7,11,12,14,15,23,32,34–39,41,46–48,60–63,71].

Extant mustelids included ranged in size from the least weasel (*Mustela nivalis*) to the wolverine (*Gulo gulo*). Unfortunately, no living mustelid approaches the size of the larger fossil specimens. The femoral length of the largest fossil (OMO L 183-14), for example, falls within the range of extant lions, tigers, and bears. While the morphology of these specimens is clearly mustelid, ursids were included for comparison as they are more similar in locomotion and posture to mustelids than are large-bodied felids.

Fossil mustelid femora measured are from eastern and southern Africa (Table 3). Data on fossil specimens were collected from specimens housed at the ENM, KNM, SAM, and the laboratory of Prof. F.C. Howell at the University of California, Berkeley. This article also provides the first description of these four femora. Data can be found in Table 4.

3.2. Statistical analyses

Linear measurements were analyzed using both bivariate and multivariate methods. Bivariate plots of ln-transformed data were created. Separate linear regressions were performed on extant lutrines and extant nonlutrine mustelids to assess similarities in scaling trends between these two groups. Fossils were then plotted onto these graphs to determine whether they lay along

Table 1
Code for measurements included in Table 4.
Tableau 1
Les codes pour les mesures sont dans le Tableau 4.

Code	Femoral measurement
1	Functional Length
2	Proximal ML Width
3	Intertrochlear Maximum Width
4	Lesser Trochanter to Lateral Projection of Greater Trochanter
5	Lesser Trochanter to Neck
6	Femoral Head AP Width
7	Femoral Head SI Width
8	Femoral Head ML Width
9	Femoral Neck Minimum Width
10	Femoral Midshaft ML Width
11	Femoral Midshaft AP Width
12	Lateral Condyle ML Width of Distal Surface
13	Medial Condyle ML Width of Distal Surface
14	Lateral Condyle AP Width of Distal Surface
15	Medial Condyle AP Width of Distal Surface
16	Both Condyles Posterior Height
17	Bicondylar Width
18	Biepicondylar Width
19	Distal AP Width
20	Max Intercondylar Notch Width
21	Patellar Groove ML Width

Table 2
Extant taxa arranged by subfamily and average body mass. Body masses are provided for reference and were taken from the literature [12,31,32,34,36–39,46]. Codes are for Table 4 and some figure captions.
Tableau 2
Taxons actuels ordonnés par sous-familles et par moyennes des masses corporelles. Les poids sont donnés à titre indicatif et proviennent de la littérature [12,31,32,34,36–39,46]. Les codes sont ceux du Tableau 4 et des légendes de figures.

Family Subfamily	Code	Species	Common name	Max *n*	Body Mass (kg)
Mustelidae	AMCI	*Amblonyx cinereus*	Small-clawed otter	2	1–5
Lutrinae	HYMA	*Hydrictis maculicollis*	Spotted-necked otter	2	3–9
	LOCA	*Lontra canadensis*	North American river otter	24	5–14
	LULU	*Lutra lutra*	Eurasian river otter	4	5–14
	LOLO	*Lontra longicaudis*	Neotropical river otter	9	5–15
	AOCA	*Aonyx capensis*	Cape clawless otter	2	10–21
	PTBR	*Pteronura brasiliensis*	Giant otter	3	22–34
	ENLU	*Enhydra lutris*	Sea otter	9	15–45
Melinae	TATA	*Taxidea taxus*	American badger	6	4–12
	MELE	*Meles meles*	Eurasian badger	7	10–16
Mellivorinae	MECA	*Mellivora capensis*	Honey badger or ratel	4	7–13
Mephitinae	MEPH	*Mephitis mephitis*	Striped skunk	5	0.7–2.5
Mustelinae	MAAM	*Martes americana*	American pine marten	7	0.3–1.3
	ICST	*Ictonyx striatus*	Zorilla or striped polecat	4	0.4–1.4
	MUNI	*Mustela nigripes*	Black-footed ferret	3	0.8–1.1
	MAMA	*Martes martes*	European pine marten	1	0.8–1.8
	MUVI	*Mustela vison*	American mink	8	0.8–2.3
	MAFL	*Martes flavigula*	Yellow-throated marten	5	2–3
	EIBA	*Eira barbara*	Tayra	11	4–5
	GUGU	*Gulo gulo*	Wolverine	3	7–32
Ursidae	URAM	*Ursus americanus*	American black bear	5	92–270
	URAR	*Ursus arctos*	Brown or grizzly bear	2	70–324
	URMA	*Ursus maritimus*	Polar bear	2	150–500

Table 3
Extinct taxa included in the study. Dates taken from the literature [13,20,22,64,67]. Code refers to Table 4.
Tableau 3
Taxons éteints inclus dans cette étude. Les datations sont prises dans la littérature [13,20,22,64,67]. Les codes sont ceux du Tableau 4.

Specimen #	Code	Site	Member	Age (Ma)
PQ-L 41523	L	Langebaanweg, S. Africa	E Quarry	≈ 5
AL 166-10	H	Hadar, Ethiopia	Sidi Hakoma	3.4–3.28
KNM-WT	W	West Turkana, Kenya	Lomekwi	3.36–2.52
OMO L183-14	O	Omo, Ethiopia	Shungura C	2.85–2.52

lutrine or nonlutrine regression lines or neither. Extant ursids were also added for comparison. Neither ursids nor the fossils were used in calculating the regression equations.

As the specimens varied greatly in size, analyses were conducted on “shape” data. “Shape” data for a given specimen were derived by dividing each variable by a measure of overall element size (i.e., the geometric mean of all linear dimensions) [10,28]. Bivariate plots of ln-transformed overall femoral size versus ln-transformed shape data were used to show how variables change with overall bone size. Shape data were also used in all multivariate analyses.

Two multivariate techniques, cluster and principal component analyses (PCA), were used to investigate functional similarity between species using PAST v. 1.81 [19]. In cluster analysis, a standardized matrix of variables is transformed into a numerical matrix of average distances between each pair of species. As this distance matrix is often difficult to interpret when there are many taxa, further routines are run to summarize the matrix in dendrograms. Cophenetic correlation coefficients (r) measure the agreement between the original

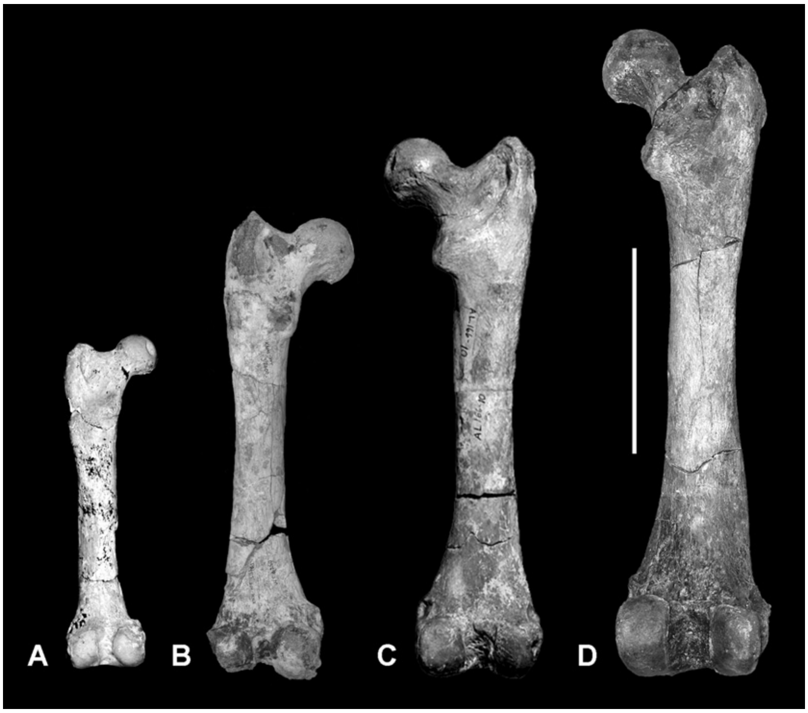

Fig. 1. Posterior view of fossil femora in this study. A. PQ-L41523 from Langebaanweg. B. KNM-WT 37400 (copyright KNM). C. AL 166-10. D. Omo L183-14. Note the wide variation in size and morphology in specimens reported to belong to bunodont otters. Photographs A, B, and D taken by Lars Werdelin. Scale = 100 mm.

Fig. 1. Vue postérieure des fémurs fossiles étudiés ici. A. PQ-L41523 de Langebaanweg. B. KNM-WT 37400 (copyright KNM). C. AL 166-10. D. Omo L183-14. Notez la grande variation de taille et de morphologie sur les spécimens attribués à des loutres bunodontes. Photographies A, B et D prises par Lars Werdelin. Échelle = 100 mm.

Table 4
Measurements of fossils and averages of extant species.
Tableau 4
Mensurations des fossiles et moyennes des espèces actuelles.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
L	164.5	48.6	39.2	38.3	30.3	22.1	20.0	20.9	16.8	20.2	16.9	14.0	16.2	19.6	23.9	19.6	37.8	39.1	35.6	7.4	19.9
W	225.4	65.8	59.5	55.6	46.7	35.2	32.5	27.9	24.5	25.4	21.6	19.3	24.0	26.8	26.4	29.9	60.0	57.3	49.7	9.2	26.2
H	259.9	79.5	70.8	68.2	45.8	36.7	33.4	35.5	24.6	30.1	25.0	23.2	24.5	18.6	23.0	31.9	62.7	62.9	57.6	13.8	24.8
O	326.3	88.5	74.5	68.4	50.1	43.3	38.3	40.3	26.7	36.4	28.9	25.3	25.7	42.8	32.3	34.6	72.4	75.2	68.4	21.1	38.9
AMCI	70.5	17.7	15.7	13.7	12.4	8.5	7.9	8.6	5.8	6.2	5.6	6.2	6.0	8.5	9.6	9.1	15.3	14.7	14.4	3.8	7.3
AOCA	116.3	34.3	26.1	24.5	18.3	15.7	14.1	15.9	12.6	12.5	10.7	9.9	9.3	12.8	16.0	17.1	25.9	28.6	26.6	6.8	11.5
ENLU	115.2	46.6	34.5	33.1	22.5	20.7	18.8	19.2	14.5	19.2	15.3	12.3	13.3	14.3	17.9	21.8	35.9	35.4	32.7	10.2	14.7
LOCA	79.4	24.1	20.6	19.9	16.3	12.5	11.2	11.8	9.8	9.7	7.9	8.2	8.5	11.2	12.5	13.0	23.4	22.6	20.4	6.1	10.1
HYMA	61.6	17.6	14.0	13.5	10.5	9.2	8.8	9.1	7.5	6.8	5.6	7.1	5.4	7.5	8.4	9.7	16.7	16.5	15.6	4.4	6.8
LULU	74.8	21.0	17.1	16.0	12.5	10.5	9.6	9.9	8.1	7.6	6.5	6.8	6.6	8.0	10.1	11.5	18.5	18.8	17.3	4.4	9.2
LOLO	71.1	20.6	17.5	16.1	13.2	10.4	9.7	10.2	8.2	8.1	6.7	7.2	7.1	9.8	10.4	11.2	18.7	18.7	17.3	4.8	8.4
PTBR	104.6	34.6	28.1	27.2	21.1	16.5	14.8	15.3	13.3	14.8	11.6	11.7	11.2	13.8	16.0	17.0	31.5	30.5	28.0	7.8	15.4
MELE	109.4	30.9	22.6	21.2	17.8	14.0	12.7	14.7	11.2	9.9	8.4	8.4	9.1	11.1	11.9	12.8	23.1	23.2	22.1	5.6	10.1
TATA	101.7	30.0	24.3	22.3	18.3	13.9	11.9	14.4	12.2	9.5	8.1	7.6	9.9	10.7	13.0	12.5	23.5	24.1	20.5	5.4	11.1
MECA	116.9	30.3	22.9	20.6	17.2	15.0	14.2	15.0	11.9	10.1	9.4	9.4	9.7	12.5	14.9	13.9	24.9	24.8	22.4	5.4	11.5
MEPH	66.6	19.0	17.0	16.6	12.8	10.0	9.3	9.7	8.9	6.3	5.6	5.6	5.4	6.3	7.5	8.5	14.2	15.0	12.3	3.4	8.3
MAFL	89.9	17.2	13.9	12.4	10.1	8.9	8.2	8.6	7.0	6.2	6.1	5.8	5.9	8.5	8.8	8.7	16.2	15.6	13.9	4.6	7.6
EIBA	104.7	21.0	16.8	15.7	13.1	11.2	10.3	10.8	9.4	7.6	7.3	7.3	7.1	9.9	10.5	10.6	19.6	18.8	16.7	5.1	9.3
GUGU	144.3	38.1	31.5	28.8	22.4	18.4	15.9	18.4	14.6	11.8	11.1	12.3	11.1	15.6	16.5	17.1	32.8	32.3	29.2	8.6	15.3
ICST	55.5	13.0	10.4	9.6	8.5	6.7	6.1	6.5	5.7	4.7	4.4	4.1	4.5	6.6	7.0	6.5	11.5	11.1	10.0	2.7	4.8
MAAM	64.2	12.3	9.1	8.4	6.4	6.0	5.4	6.0	4.7	4.2	4.0	4.2	3.9	6.0	6.3	6.4	11.2	10.7	10.0	3.0	5.1
MAMA	74.5	14.4	11.7	11.4	8.2	6.7	6.4	7.3	5.6	4.6	4.5	5.7	6.8	5.5	6.4	7.3	13.2	12.7	11.6	3.7	6.4
MUNI	51.0	12.9	8.8	8.7	6.3	6.0	5.7	6.3	4.6	4.0	3.9	3.9	4.0	5.4	5.8	6.3	10.7	10.2	9.3	2.0	4.6
MUVI	45.7	11.1	8.3	7.6	6.0	5.2	4.9	5.3	4.3	3.8	3.3	3.8	3.3	4.8	5.3	5.4	9.6	9.4	9.5	2.7	4.4
URAM	326.9	81.3	65.8	56.9	52.7	37.8	32.7	38.1	31.5	29.1	23.2	23.5	24.9	23.2	32.0	31.1	62.3	62.3	56.1	14.4	29.2
URAR	374.3	85.9	76.0	61.6	63.7	43.4	37.5	44.1	33.3	29.9	25.2	26.9	25.1	28.4	40.4	38.1	65.3	66.7	59.7	14.5	28.2
URMA	424.1	109.9	95.0	79.5	73.0	55.7	45.9	55.9	46.9	37.9	30.7	36.5	36.3	33.7	43.3	41.1	92.0	96.5	78.4	19.7	49.7

See Tables 1–3 for taxa and measurement codes.

distance matrix dissimilarity values and those implied by the dendrogram and thus provide an indicator of the strength of the dendrogram [17,58]. PCA is an ordination technique where variation among species in multidimensional space is summarized in a space of lower dimensionality such as two or three dimensions [54].

To better determine nonlength related morphological similarity among taxa, functional length was also removed from the data set and the geometric mean recalculated. The data were broken into regional subsets (e.g., proximal and distal) and restandardized by the subset geometric mean to examine whether a particular region of a fossil specimen bore a resemblance to that of a given extant species, even if the overall femoral morphology did not.

Multivariate analyses were initially run with separate sexes for taxa known to be sexually dimorphic in body mass. As sexes consistently fell together in all cases, species averages are presented in the results for these taxa.

4. Description of the fossil material

While taxonomic issues are beyond the scope of this paper, the various taxonomic assignments of these specimens will be discussed briefly. While two of the included specimens have not been mentioned previously in the literature, two undescribed specimens have received attention. All fossils can be found in Fig. 1, while extant lutrine femora can be found in Fig. 2 for comparison.

4.1. PQ-L 41523

Hendey [21] assigned two mandibles from Langebaanweg, PQ-L 9138 and PQ-L 50000, to *Enhydriodon africanus*, a species named by Stromer from Kleinzee [59]. With the mandibles, he tentatively placed this femur (Fig. 1A), right and left distal radii (PQ-L 50001a,b) and an astragalus (PQ-L 50117, now known to be an aardvark) in this taxon. In his opinion, the femur was similar to *Aonyx capensis* in everything but size.

PQ-L 41523 was referred to a new species, *E. hendeyi,* when the Langebaanweg mandible, PQ-L 50000, was designated the type specimen [43]. Morales and Pickford [42] later referred this species to *Sivaonyx*. This specimen has also been a source for comparison to the femur of *Sivaonyx beyi* [49], a specimen that will be discussed in detail below.

PQ-L 41523 is much smaller and older than the other femora in this study. The head is rounded and projects anteriorly and superiorly. The neck and head are not angled as far superiorly as in Omo L 183-14 and AL 166-10. The head projects further superiorly than the greater trochanter. The lesser trochanter is large and projects enough inferomedially that it can be seen in anterior view, although not to the degree seen in L 183-14 and AL 166-10. The shaft is short and stout.

The distal end looks a little different from the younger specimens. The patellar groove is twisted so that it angles laterally as it moves distally. This angulation is reflected in the superior border whose most proximal point is the lateral end. The medial edge of the groove is much more projecting than the lateral edge. In anterior view, the medial edge actually projects further inferiorly than the lateral edge due to the angulation of the groove. A second difference is that medial condyle is not enlarged in comparison to the size of the left condyle, although both are large. A final difference is that the shaft does not widen appreciably before the distal end. Overall, this specimen is most similar to KNM-WT 37400, albeit smaller.

4.2. KNM-WT 37400

This femur from West Turkana (Fig. 1B) is associated with a proximal fibula. Additional large lutrine postcranials that probably belong to this species will be discussed elsewhere. The femur is cracked and the distal end has been damaged. The distal end has split down the center, so distal ML measurements may be overestimated. This specimen is extremely small in comparison to the teeth of *Enhydriodon* from this site and is much smaller than Omo L 183-14 and AL 166-10. It is larger than PQ-L 41523.

The head is large and rounded, as in all the fossil femora in this study. The head is distinct from the neck and the neck has a “waist”. The angle of the neck is similar to most large carnivorans and differs from L 183-14 and AL 166-10 in not angling as far superiorly.

The greater trochanter is large and projects to a great degree anteriorly. The superior end projects only slightly above the level of the head. The greater trochanter is broken posteriorly. The intertrochanteric fossa is deep and short. Neither the intertrochanteric crest nor the fossa continues all the way to the lesser trochanter. The crest for the adductors runs inferiorly from the greater trochanter and moves medially onto the posterior surface of the shaft about a third of the way down the shaft. At this point it continues as a ridge that peters out just inferior to midshaft.

The posterior surface of the shaft is relatively flat. The narrowest part of the shaft is just below midshaft. However, there does not seem to be the inflation seen in the larger fossil specimens. The patellar groove is wide

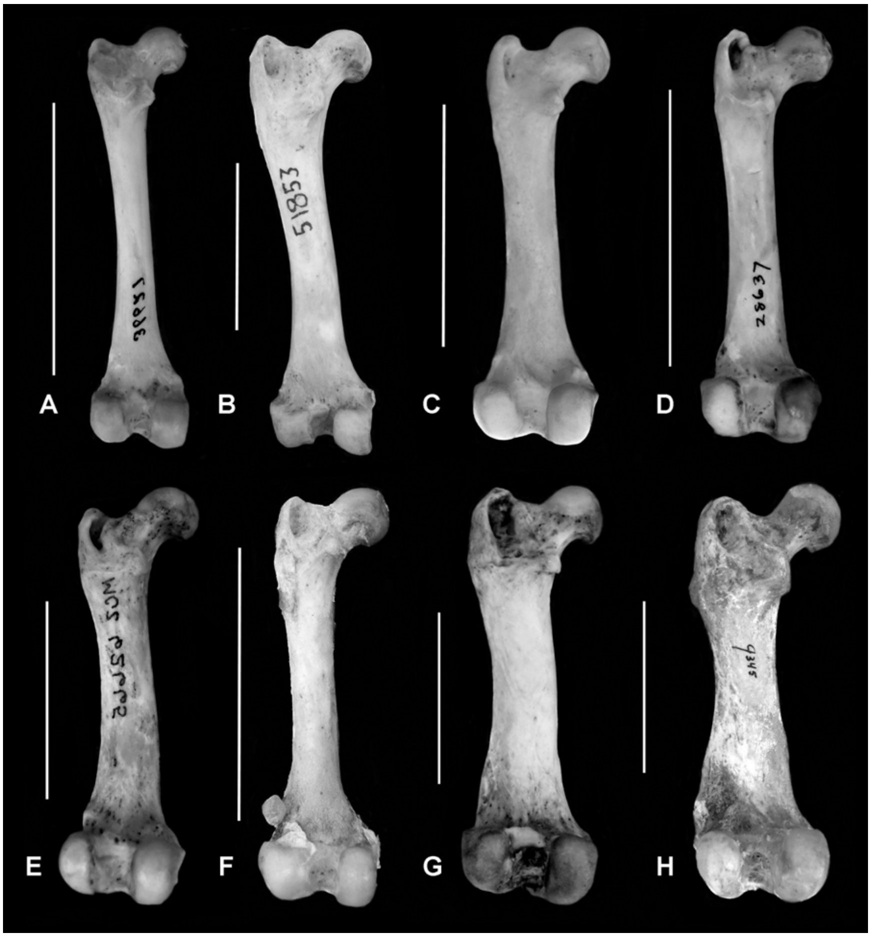

Fig. 2. Posterior view of extant lutrine femora. A. *Amblonyx cinereus* (MCZ 36627). B. *Aonyx capensis* (AMNH 51853). C. *Lontra canadensis* (MCZ 39657). D. *Lontra longicaudis* (MCZ 28637). E. *Lutra lutra* (MCZ 62665). F. *Hydrictis maculicollis* (AMNH 51825). G. *Pteronura brasiliensis* (MCZ 27868). H. *Enhydra lutris* (MCZ BOM 9345). A and E are right femora whose photos have been flipped to facilitate comparison. Note the distinct morphology of *Enhydra*. Photographs A, C–E, G, H copyright MCZ. Scale = 50 mm.

Fig. 2. Vue postérieure de fémurs de loutres actuelles. A. *Amblonyx cinereus* (MCZ 36627), B. *Aonyx capensis* (AMNH 51853), C. *Lontra canadensis* (MCZ 39657), D. *Lontra longicaudis* (MCZ 28637), E. *Lutra lutra* (MCZ 62665), F. *Hydrictis maculicollis* (AMNH 51825), G. *Pteronura brasiliensis* (MCZ 27868), H. *Enhydra lutris* (MCZ BOM 9345). A et E sont des fémurs droits dont les photos ont été inversées pour faciliter les comparaisons. Notez la morphologie distincte d'*Enhydra*. Photographs A, C–E, G, H copyright MCZ. Échelle = 50 mm.

and flat and the medial edges are broken. The lateral condyle is much smaller than the medial. The medial condyle is large and projects much more posteriorly than the lateral condyle.

4.3. AL 166-10

This complete right femur (Fig. 1C) is well preserved for the most part and is one of several large lutrine postcranial specimens from Hadar. The head is oriented anterosuperiorly, although not quite to the degree of Omo L183-14. The lateral lip formed by greater trochanter down the lateral side of the shaft is sharp and rugose. The lesser tuberosity is positioned more medially and projects much more medially than in WT 37400 or PQ-L 41523. As such, it is similar to Omo L 183-14.

The intertrochanteric fossa is extensive, as in Omo L 183-14. The tubercle on the medial border is extremely large and extends medially across the posterior surface of the neck to the articular surface of the head. This large tubercle makes the neck appear in line with the posterior edge of the head in superior view.

The shaft is relatively robust. The medial condyle is located medially with respect to the shaft. The lateral condyle is located more in line with the shaft and only slightly laterally displaced from it. The medial condyle extends slightly further distally than the lateral condyle. On the anterior surface, the medial lip of the patellar groove is partially missing, as is the surface just anterosuperior to the medial epicondyle. The lateral surface is well preserved. The distal end shows four large canine punctures.

The patellar groove extends slightly above the level of the superior edge of the condyles. The medial edge extends further proximally than the lateral edge. The articular surface, therefore, slopes upwards from the lateral lip to the medial lip.

As in most mustelids, the distal end is relatively compressed anteroposteriorly in comparison to similarly-sized felids or other more specialized, cursorial carnivores. The lateral condyle is very short and curved anteroposteriorly. A large pit for the origin of extensor digitorum longus occurs posterior to the posterior edge of the shaft and just inferior to the superior edge of the condyle. Just posteroinferior to this is a pit for the popliteus that indents the lateral edge of the lateral condyle. The fabellar pit on the lateral side is smaller and shallower than that on the medial. However, the area of attachment for the lateral head of gastrocnemius is quite rugose and excavated. The medial condyle extends further posteriorly from the shaft than the lateral condyle. The sides of the medial condyle are parallel along the posterior surface and tapering closer together towards the most distal anterior surface. The lateral epicondyle does not project laterally beyond the lateral condyle for the most part. The medial epicondyle projects further medially than the condyle and is in line with the oblique set of the condyle.

4.4. Omo L183-14

This femur (Fig. 1D) is part of a group of postcranial specimens that Howell and Petter [24,25,27] referred to *Enhydriodon* sp. nov. along with deciduous and permanent dentition. Howell and Petter noted that this species is far larger than previously recorded species of *Enhydriodon*, an observation that still holds true. The material that is closest in size to the Omo material is the Hadar material described above, and even that is a bit smaller. Although the distal end of Omo L183-14 is roughly similar in size to *Homotherium*, it is much more robust and the entire specimen is shorter and more robust.

The neck angles steeply more anteriorly and superiorly than in felids and most other nonpinniped carnivorans. The articular surface of the head is also rotated more superiorly. The head is extremely large and rounded. The fovea capitis is large and on the posterior side just distal to the most superomedial point of the head. Although this is not a different placement from *Homotherium*, it does fall closer to the posterior border of the articular surface due to the rotation of the surface superiorly in *Enhydriodon*. The neck is robust in a rounded oval in cross-section.

The lesser trochanter is extremely large and is located on the medial edge of the posterior border. It is not, however, all the way over on the medial side of the shaft. It projects so far medially (more so than posteriorly) that it is easily visible in anterior view.

The greater trochanter is robust and very anteriorly directed. In anterior view, it is pyramidal with the apex point proximally and the base corners oriented medially, anteriorly, and laterally. The anterior projection of the base is robust and extends as far anteriorly as the head. The lateral side of the base does not project as far. In lateral view, the greater trochanter also curves anteriorly.

The intertrochanteric fossa is deep but not relatively long. It extends laterally under the intertrochanteric crest. There is a slight tubercle on the medial side of the fossa. The crest does not extend all the way to the lesser trochanter. The shaft is robust, with the thickest point being slightly medial to the axis of the shaft.

The distal end is robust, but not very thick anteroposteriorly. This is a mustelid characteristic. The patellar groove is wide and very rectangular. The lateral edge extends further proximally than the medial edge. This proximal portion actually curves slightly medially. The lateral edge is distinct from the rest of the femur. The medial edge is slightly eroded, but does not appear to have been as distinct. The superior edge of the patellar groove blends into the shaft, with the exception of the lateral border. With the exception of the proximal extension of the lateral border, the sides of the patellar groove are parallel. The surface of the shaft proximal to the patellar groove is very flat, even more so than in *Homotherium*. There is a slight concavity in this area. The distal shaft is very wide mediolaterally relative to AP width.

In distal view, the medial condyle projects only slightly more posteriorly than the lateral in contrast to the greater projection of the medial condyle of *Panthera*. In posterior view, the lateral condyle is slightly narrower than the medial, but both are roughly rectangular in shape. The intercondylar fossa is rectangular with parallel sides. Neither epicondyle is particularly large, although the lateral is more rugose.

4.5. Comparison with the femur of Sivaonyx beyi

S. beyi from Toros Menalla, Chad includes the partial skeleton, TM 171-01-033 [49]. While I have not seen this material, the right and left partial femora have been

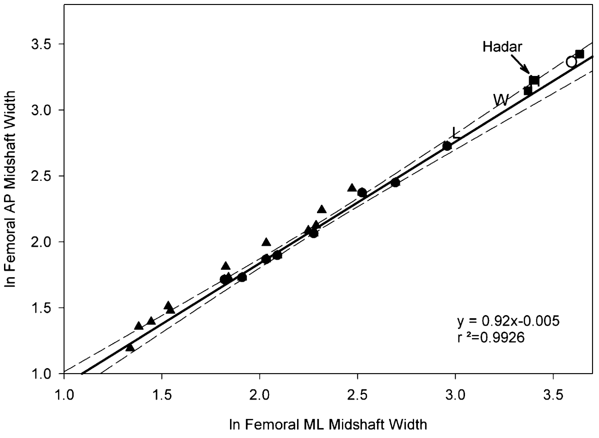

Fig. 3. Bivariate plot of femoral ML against AP midshaft width. On all bivariate plots, both variables are natural logged unless otherwise noted. The regression is based solely on extant lutrine mustelids and extended to both axes. While many nonlutrine mustelids fall outside the 95% CL (dotted lines), the fossils and ursids fall on the line or within the CL. (●) = lutrines, (▲) = nonlutrine mustelids, (■) = ursids, L = Langebaanweg, W = West Turkana, H = Hadar, O = Omo.

Fig. 3. Répartition bidimensionelle de la longueur maximale sur la largeur au milieu de la diaphyse des fémurs étudiés. Chaque point, sauf contre-indication, correspond à des logarithmes. La régression est basée seulement sur les lutrinés actuels et s'étend aux deux axes. Tandis que beaucoup de mustélidés non lutrinés tombent hors de la limite des 95 % (lignes pointillées), les fossiles et les ursidés tombent sur la ligne ou à l'intérieur des limites. (●) = lutrinés, (▲) = mustelidés non lutrinés, (■) = ursidés, L = Langebaanweg, W = West Turkana, H = Hadar, O = Omo.

well-described, figured, and compared to PQ-L 41523 as part of the description of the species. Peigné et al. concluded that PQ-L 41523 was more robust, with a thinner neck, less well-developed trochanters and a shorter intertrochanteric fossa. They also note that PQ-L 41523 has a head that is more proximally oriented as the greater trochanter of *S. beyi* extends above the level of the head. The *S. beyi* femur was also probably larger than PQ-L 41523.

Based on the measurements given, the *S. beyi* femur is much smaller and proportioned differently than West Turkana, Hadar, or Omo specimens presented here. The relative size, location, and projection of the lesser trochanter are very similar to that of the Hadar and Omo femora. However, the shape of the superior edge of the neck and greater trochanter is much more similar to the West Turkana specimen. The fovea capitis appears to be oriented more posteriorly in all of the specimens included here than in *S. beyi*. What is preserved of the entire specimen looks least like PQ-L 41523, although it is not really like any of the femora discussed here.

5. Results

5.1. Bivariate analyses

Lutrine and nonlutrine mustelids often scale similarly with respect to femoral morphology (Fig. 3). While some nonlutrine mustelids are slightly above the 95% CL, they are still scaling in a similar manner. This pattern of similar or parallel scaling among extant taxa was consistent across many measurements when using traditional regression and bivariate plots. On this graph, ursids and the fossils fall either within or on the 95% CL.

Due to the great differences in body size of the extant and extinct taxa, variables were standardized by overall femoral size (i.e., geometric mean) as discussed above. When this is done, patterns obscured by body size differences become apparent, particularly when these standardized variables are graphed against overall femoral size. It must be remembered that the calculation of overall femoral size takes into account all variables, not just length. Conversely, a difference in

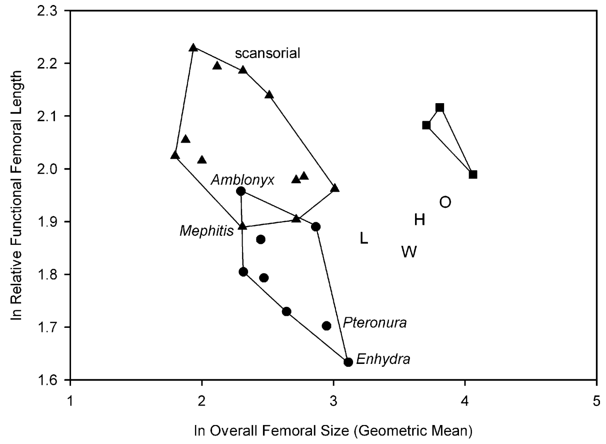

Fig. 4. Bivariate plot of overall femoral size (i.e., geometric mean of all variables) against relative functional femoral length (= functional length/geometric mean). Convex hulls were drawn to delineate major taxonomic or functional groups. Lutrines have relatively shorter femora than nonlutrines despite overlapping in overall femoral size. Scansorial mustelids (EIBA, MAAM, MAFL, MAMA) have the longest femora. The fossils fall within the overlap of lutrine and nonlutrine mustelids. Extant codes in Table 2, key as in Fig. 3.

Fig. 4. Répartition bidimensionelle de la taille générale des fémurs (c'est-à-dire la moyenne géométrique de toutes les variables) sur la longueur relative fonctionelle de ces fémurs (= longueur fonctionelle/moyenne géométrique). Les principaux groupes taxonomiques ou fonctionnels sont délimités. Les lutrinés ont des fémurs relativement plus courts que les autres, en dépit du recouvrement pour la taille générale. Les mustélidés de type scansorial (EIBA, MAAM, MAFL, MAMA) ont les fémurs les plus longs. Les fossiles tombent à l'intérieur du recouvrement des lutrinés et des autres mustélidés. Pour les légendes voir Tableau 2 et Fig. 3.

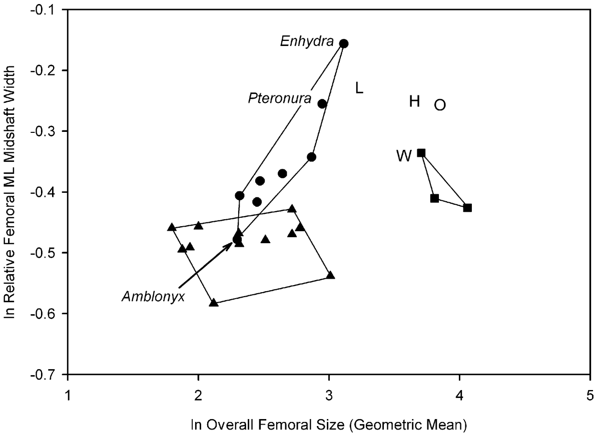

Fig. 5. Bivariate plot of overall femoral size against relative femoral ML midshaft width. Though similar in overall femoral size, lutrines (except the least aquatic *Amblonyx*) have relatively wide midshafts mediolaterally. The two largest extant otters have the relatively widest midshafts. The fossils overlap with extant lutrines. Key as in Fig. 3.

Fig. 5. Répartition bidimensionelle de la taille générale des fémurs sur la largeur fémorale relative au milieu de la diaphyse. Bien que semblables par la taille générale, les fémurs des lutrinés (à l'exception du moins aquatique d'entre eux, *Amblonyx*) sont relativement plus larges médiolatéralement, au niveau médian de la diaphyse. Ceux des plus grandes loutres actuelles ont également la plus grande largeur médiane. Il y a recouvrement des « plots » correspondant aux loutres actuelles. Même légende que la Fig. 3.

overall femoral size between two mustelids with roughly the same femoral length indicates a difference in proportion and/or robusticity of other aspects of the bone (e.g., midshaft, articulations). Geometric means of an element are often used when body mass is unknown [28,40].

Nonlutrine mustelids and lutrines overlap considerably in overall femoral size, but are clearly different in relative proportions. Lutrines have shorter femora in contrast to nonlutrine mustelids relative to overall bone size (Fig. 4). Among lutrines, *Enhydra* has the relatively shortest femur, while *Amblonyx* has the relatively longest one and is more like nonlutrine mustelids. The fossils fall within the zone of overlap between the two extant groups, despite being much larger overall than any extant mustelid. The fossils are clearly distinct from extant ursids in being much shorter relative to overall femoral size.

Extant lutrines also have relatively ML wide femoral shafts in contrast to other mustelids (Fig. 5) and show a tendency for shaft width to increase with overall size. The two largest extant lutrines, *Enhydra* and *Pteronura*, have the relatively widest midshaft widths. Ursids, like nonlutrine mustelids, have a relatively narrow midshaft for their overall size. The fossil taxa are similar in relative midshaft width to the largest lutrines and ursids. Biomechanical expectations, however, would be that these much larger fossil femora would be much wider relative to overall femoral size due to positive allometry. Since they do not meet these predictions, their morphology most likely reflects adaptive differences.

Extant lutrines tend to have relatively large biepicondylar widths (Fig. 6), although they do overlap with nonlutrine mustelids in their distribution. The small-clawed otter, *Amblonyx cinereus*, however, falls outside of the range of all mustelids with its extremely narrow distal end. This is just one of many unusual nonotter-like features of *A. cinereus*. The three largest fossils, like extant lutrines, have a large biepicondylar width. The oldest and smallest, PQ-L 41523, falls with the nonlutrine mustelids. As these fossil femora are much larger than mustelids with similar relative biepicondylar width, this is again contrary to biomechanical expectations and probably reflects adaptive differences.

As a side note, the polar bear, *Ursus maritimus*, has the relatively greatest biepicondylar width. This finding is intriguing as polar bears are reported to use their forelimbs for swimming with the hindlimb trailing behind [2,16]. The terrestrial locomotion of polar bears is similar to that of other large carnivorans [9],

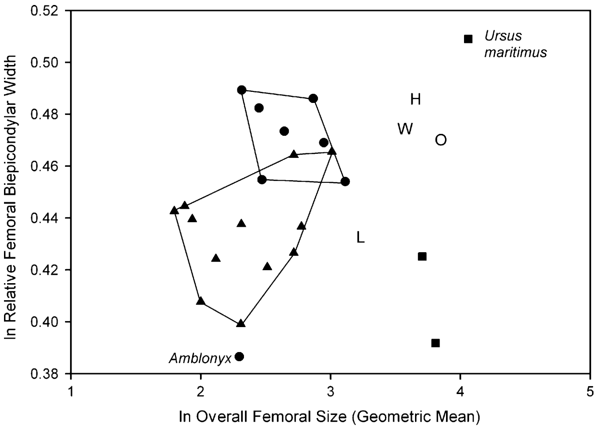

Fig. 6. Bivariate plot of overall femoral size against relative femoral biepicondylar width. Lutrine and nonlutrine mustelids overlap in relative biepicondylar width. The least aquatic otter, *Amblonyx*, falls far away from extant lutrines and below the nonlutrine mustelids. The three largest fossils fall with the otters while the smallest and oldest fall with the nonlutrine mustelids. Key as on Fig. 3.

Fig. 6. Répartition bidimensionelle de la taille générale des fémurs sur la largeur biépicondylienne relative. Il y a recouvrement, pour les fémurs des lutrinés et ceux d'autres mustélidés en ce qui concerne la largeur biépicondylienne relative. Le fémur de la loutre la moins aquatique, *Amblonyx*, figure loin de ceux des loutres actuelles et au-dessous de ceux des autres mustélidés. Les trois fossiles les plus grands tombent dans le champ de ceux des loutres, alors que le plus petit et le plus ancien dans le champ des les mustélidés non lutrinés. Même légende que la Fig. 3.

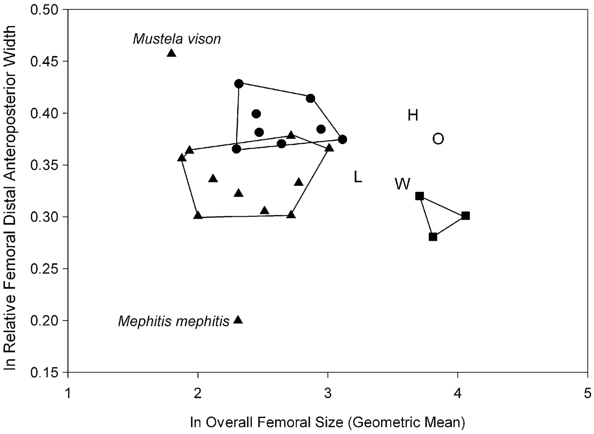

Fig. 7. Bivariate plot of overall femoral size against relative femoral distal AP width. Lutrines have relatively wider distal AP width than most mustelids. The largest fossils fall with lutrines, while the two smaller femora fall with nonlutrine mustelids. Key as in Fig. 3.

Fig. 7. Répartition bidimensionelle de la taille générale des fémurs sur le diamètre distal antéropostérieur. Les fémurs des lutrinés ont un diamètre distal antéropostérieur relativement plus large que celui des autres mustélidés. Les fémurs fossiles les plus grands se regroupent avec ceux des lutrinés, tandis que les deux plus petits se regroupent avec ceux des autres mustélidés. Même légende que la Fig. 3.

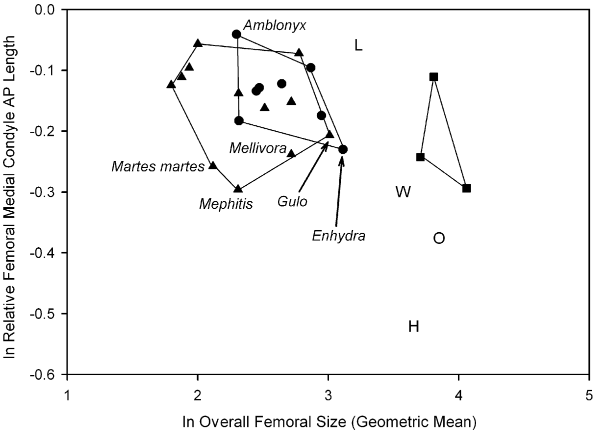

Fig. 8. Bivariate plot of overall femoral size against relative medial condyle AP length. Lutrines, other mustelids, and ursids overlap in their expression of relative condyle length. With the exception of the Langebaanweg femur, the fossils fall at the bottom or below the extant taxa distribution. Key as in Fig. 3.

Fig. 8. Répartition bidimensionelle de la taille générale des fémurs sur le diamètre antéropostérieur du condyle médial. Il y a recouvrement dans l'expression du diamètre relatif du condyle médial pour les lutrinés, les autres mustélidés et les ursidés. À l'exception de celui de Langebaanweg, les fémurs fossiles se trouvent tout en bas, au-dessous de ceux des formes actuelles. Légende comme sur la Fig. 3.

yet, unlike other large carnivorans, their preferred habitat is pack ice [11,45]. Perhaps this feature is related to either transitioning into or out of the water and onto pack ice.

Lutrines also tend to have slightly relatively wider distal femora in the AP direction (Fig. 7). This feature fits with the overall shorter, more robust femur than in most other mustelids or ursids. As with biepicondylar width, the Langebaanweg femur is more like nonlutrine mustelids, as is the West Turkana femur. Note the placement of *Mustela vison*, the American mink. While many mustelids also swim, *M. vison* is a particularly excellent swimmer and can swim underwater for about 30 m and to depths of 5–6 m [46]. *M. vison* swims primarily via alternate limb paddling [70]. Unlike lutrines, however, *M. vison* does not have a particularly wide biepicondylar width.

There are some features where the largest fossil femora are distinct from those of the extant taxa. In general for extants, the AP length of the lateral condyle is relatively constant across overall femoral size (Fig. 8). However, in the three largest fossil femora, the medial condyle is relatively short anteroposteriorly. This may not be size-related, as the ursids are more similar to the extant mustelids. Note the extreme position of the Hadar specimen, AL 166–10. The lateral condyle in this specimen is also extremely short anteroposteriorly, although not to the same degree. In contrast, the Langebaanweg specimen (PQ-L 41523) falls on the opposite end of the extant mustelid range.

5.2. Multivariate analyses

Analyses were first performed on the total standardized data set of extant and fossil lutrines. In the cluster analysis (Fig. 9), the extant taxa cluster somewhat as expected. The river otters cluster together in the middle. The Cape clawless otter, *Aonyx capensis*, clusters with the sea otter, *E. lutris* rather than the small-clawed otter, *Amblonyx cinereus*, a species often included in *Aonyx*. The femora of *Amblonyx* and *Aonyx* are visually quite dissimilar (Fig. 2) and it is not surprising that they do not fall together. The fossil taxa are unlike the extant lutrines, especially the Hadar femur.

In the PCA of all variables (not figured), the first axis expressed 92.41% of the variance. The primary variable driving this axis was functional length, with very little contribution from other variables. The second axis expressed a minute amount of the variance (3.14%).

As mentioned above, analyses were also performed on shape data from regions of the femur. The PCA of the proximal femoral variables (Fig. 10) demonstrates some of the differences between the fossils and between extant lutrines. As with all PCA in this study, the first two axes summarized the vast majority of the variance

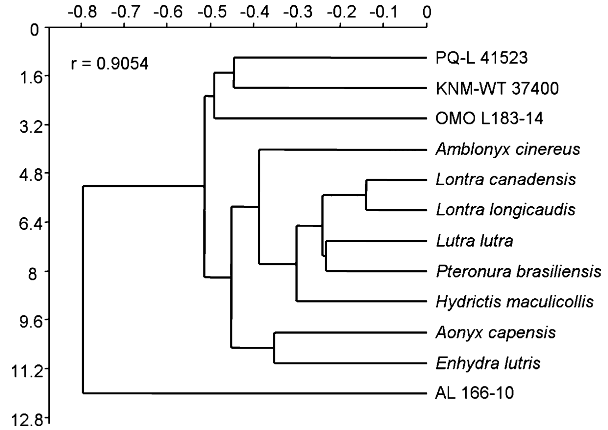

Fig. 9. Results of cluster analysis of all standardized femoral measurements in extant lutrines and fossils. Overall, the four fossils are unlike the extant taxa, with AL 166-10 being unique. The length of the branches with fossil taxa indicates that although they are more like one another than they are like extant taxa, they are still not that similar to one another. For the most part, nonbunodont otters cluster together, with the unusual *Amblonyx* on the outside. *Aonyx* clusters with *Enhydra*.

Fig. 9. Analyse de cluster des mensurations standardisées chez les lutrinés actuels et fossiles. En général, les quatre fossiles analysés diffèrent des taxons actuels, AL 166-10 étant l'exception. La longueur des branches indique que, si les fossiles se ressemblent plus entre eux qu'ils ne ressemblent aux autres, ils ne sont toutefois pas semblables. Les loutres bunodontes sont pour la plupart regroupées, alors que l'*Amblonyx* atypique se situe à l'extérieur. *Aonyx* voisine avec *Enhydra.*

(PC 1 = 49.4%, PC 2 = 32.4%). Measurements involving the lesser trochanter (e.g., intertrochanteric width, length from the lesser trochanter to the lateral projection of the greater trochanter) and the neck drive the first axis, while the proximal ML width and neck width are driving the second. In this figure, all of the fossils except for KNM-WT 37400 fall in the upper right quadrant with the two largest otters and the largest mustelid, *Gulo*. These specimens tend to have the largest intertrochanteric widths (particularly the Hadar femur) and distances from the lesser trochanter to the lateral projection of the greater trochanter. In contrast, KNM-WT 37400 is more similar to *Lontra*, *Amblonyx*, *Mephitis*, and *Taxidea* along the first two principal components. These taxa all share a relatively long distance from the lesser trochanter to the top of the neck.

It is interesting that *Mephitis* and *Taxidea* are within this quadrant. These two genera have the relatively shortest femora among nonlutrine mustelids studied. Functional length was not a part of this PCA, yet there were still similarities between these taxa and *Lontra*.

A cluster analysis forces a dissimilarity matrix to be expressed in clusters or pairs of taxa. As such, it can provide an indication of general similarity. The cluster analysis of the proximal femur had a low cophenetic correlation coefficient ($r = 0.6608$) and thus provided a poor summary of the dissimilarity matrix. As such, it is not considered here.

The cluster analysis of the distal femoral variables (Fig. 11) is extremely strong ($r = 0.9096$). The oldest fossil femur (Langebaanweg) clusters with the extant lutrines. This group then clusters with the West Turkana specimen and then the Omo specimen. The Hadar femur is least like the other femora in distal morphology.

The reason for the distinctiveness of the Hadar femur can be found in the PCA analysis of the distal femur (Fig. 12). The first axis is driven by the AP width of each condyle and biepicondylar width. The Hadar femur has particularly short (AP) condyles, while those on the negative side of the first axis have the largest AP condyle lengths. The second axis is driven primarily by the proximodistal height of the condyles and the width of the patellar groove. Those higher along the second axis have the greatest patellar groove widths, while those lower along the axis have the shortest condyles proximodistally. Three of the fossils fall high along the second axis, while the Hadar femur falls slightly below 0 on this axis. This signal from the distal morphology is strong enough and accounts for some of the distinctiveness of the Hadar femur in the overall analysis discussed above (Fig. 9).

6. Discussion

The four fossils clearly differ in overall morphology from extant lutrines, other mustelids, and ursids. One would predict that as a nonaquatic species evolves to a larger size, it will avoid greater stresses by changing some aspect of its design (e.g., morphology, posture, locomotor behavior) to avoid mechanical failure [3–5]. However, in several cases (e.g., midshaft ML width, biepicondylar width), the fossil femora retained similar proportions to extant lutrines. This morphological similarity suggests that they must have changed some aspect of their locomotion and/or posture if they were terrestrial. Another possibility is that some or all are aquatic or semiaquatic, as the more aquatic the species, the fewer forces engendered by contact with a resistant substrate (e.g., river bank, tree limbs, and rocks). In that case, body size presumably affects morphology as one might need to alter morphology to maintain efficiency while propelling the larger body mass through water. Such changes would presumably have more to do with altering muscle size and/or

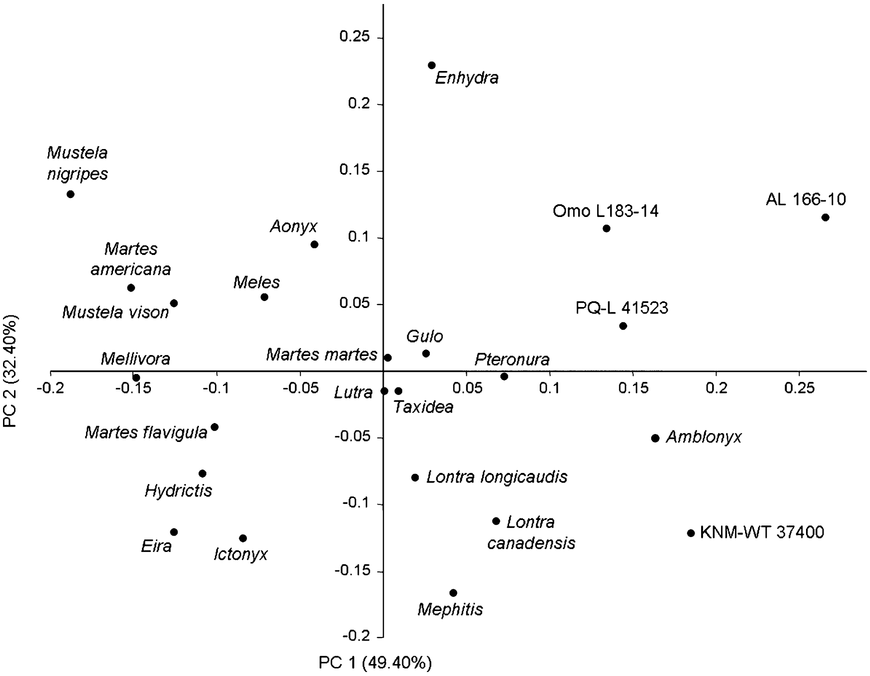

Fig. 10. Results of PCA of standardized proximal femoral variables in extant mustelids and fossils. Taxa in the right upper quadrant tend to have the largest intertrochanteric widths (particularly the Hadar femur) and distances from the lesser trochanter to the lateral projection of the greater trochanter. Taxa in the lower right quadrant share a relatively long distance from the lesser trochanter to the top of the neck.

Fig. 10. Analyse en composantes principales des variables standardisées du fémur proximal chez les mustélidés actuels et fossiles. Les taxons situés dans le quadrant supérieur droit tendent à avoir la plus grande largeur intertrochantérienne (en particulier celui de Hadar) et la plus grande distance relative entre le petit trochanter et la projection latérale du grand. Les taxons situés dans le quadrant droit inférieur partagent une plus grande distance relative entre le petit trochanter et le sommet du col.

leverage than with features associated with weight-bearing.

The fossils also differ from one another in both size and morphology. The Omo and Hadar femora are more alike than they are to the other two specimens despite the differences in size between the two. In the variables considered above, the Hadar specimen was the most extreme in condylar morphology. The West Turkana specimen has a distal end that is more similar to extant lutrines than the other fossil femora. It is also shorter relative to its overall femoral size than the other fossils. While the West Turkana and the Langebaanweg specimens were most similar overall, they differ in many respects. For a given variable, the Langebaanweg specimen was more likely to fall with generalized mustelids than with any other group.

The question then becomes, what is the meaning of these differences? It is clear that these specimens are not merely enlarged versions of extant mustelids, whether lutrine or not. While increasing body size probably plays a role in shaping the morphology of these femora, these fossils do not always follow allometric trends seen in extant taxa.

7. Aquatic and semiaquatic adaptations in the femur

Otters exhibit a range of swimming behaviors whose usage is determined by water depth and displacement pattern [14]. In a study of North American river otters [14], *Lontra canadensis*, alternate hindlimb paddling occurred at the surface when swimming in a straight line and dorsoventral undulation was used for submerged swimming. Quadrupedal or forelimb paddling was used for maneuvering. In contrast, *Enhydra* undulates the lumbosacral and caudal spine dorsoventrally in combination with simultaneous strokes of the hindfoot as its primary means of swimming quickly [29,61,71]. At slower speeds only the hindlimbs and tail are involved. *Enhydra* is also more buoyant than river otters. When resting on its back, the hindlimbs may be used alternately to propel the animal in a straight line. The expanded foot is moved caudally by extension of the knee and ankle during the propelling stroke. At the end of the stroke, the limb is moved cranially by flexing these joints [61]. Tarasoff et al. do not mention femoral movement, as the femur of *Enhydra* is hidden within loose skin.

No otter oscillates a true hydrofoil (pectoral, pelvic or caudal), as seen in pinnipeds, sirenians, and cetaceans [15]. Hydrofoils provide the most efficient means of swimming. Most otters have long tails that are not particularly efficient during swimming. However, *Enhydra* has reduced its tail length [61] and *Pteronura* has broadened its tail [14]. *Enhydra* also has more of the hindlimb contained within loose body skin than most other otters [61]. Shortening and widening the tail and encasing portions of the lower limb in loose skin are presumably evolutionary steps towards usage of the caudal end of the body as a hydrofoil.

In a study using landmark analysis of mustelid humeri, ulnae, femora, and tibiae, Schutz and Guralnick [57] demonstrated that the morphology of the femur and ulna of aquatic mustelids is not as differentiated from other mustelids as is that of the humerus and tibia. They found that the femora of lutrines were shorter and the greater trochanter and gluteal tuberosity were more robust than in other mustelids, findings that are supported by the present paper.

Schutz and Guralnick grouped *Enhydra*, *Lutra*, and *Lontra* together in their aquatic group and did not consider them separately. However, it is clear that the femoral morphology of *Enhydra* is unlike that of other otters (Fig. 2). While many mustelids may swim, they are locomotor generalists. Only the sea otter, *E. lutris*, and to some degree the marine otter, *L. felina*, are truly aquatic. Therefore, examining the postcrania of other aquatic carnivorans, namely the pinnipeds, can be instructive in understanding morphology associated with aquatic behavior.

Among the three families of pinnipeds, the otariids (fur seals and sea lions) and odobenids (walruses) are most like aquatic mustelids in their terrestrial posture. Otariids and odobenids use their hindlimb for weight-bearing locomotion on land. In contrast, the phocid hindlimb extends posteriorly and cannot be brought under the body to bear weight during terrestrial locomotion, thus the orientation of the femur relative to the os coxae is quite different. Otariids rely on pectoral oscillation for locomotion, while phocids and odobenids rely on pelvic oscillation [15].

Pinniped femora (Fig. 13), in general, are short, relative to their body size, as in otters. The fovea capitis is difficult to see as this group has lost the round ligament [2]. The shaft has become compressed anteroposteriorly to a degree not seen in extant mustelids. The condyles, in particular, are very short anteroposteriorly, a feature seen to a lesser degree in the West Turkana, Omo and especially the Hadar femora.

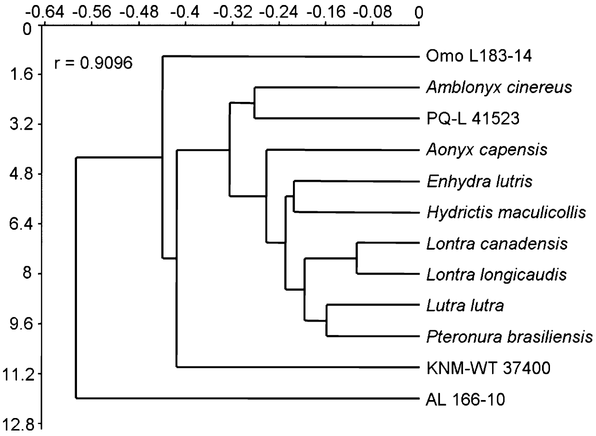

Fig. 11. Results of cluster analysis of standardized distal femoral variables in extant lutrines and fossils. The distal femur does not discriminate between aquatic and semiaquatic extant taxa. The fossils, with one exception, fall outside of the clusters of extant lutrines. The Langebaanweg femur falls with the unique *Amblonyx*.

Fig. 11. Analyse de cluster des mensurations standardisées des variables du fémur distal chez les lutrinés actuels et fossiles. Cette région ne permet pas de discriminer les taxons actuels aquatiques et semiaquatiques. Les fossiles, à une exception près, sont extérieurs aux regroupements des lutrinés actuels. Le fémur de Languebaanweg se retrouve avec l'unique *Amblonyx*.

Most significantly, pinnipeds have reoriented their head more superiorly relative to the shaft and shortened the neck. What is left of the neck is also angled more superiorly such that the distal border, which is usually inferior, is now medial. The greater and lesser trochanters are extremely enlarged.

Since lutrines use a different form of aquatic or semiaquatic locomotion, one would not expect them to be identical to pinnipeds. For truly aquatic forms, such as *Enhydra*, one would expect some similarities to pinnipeds due to the shared femoral posture (posterior extension) during undulation.

Enhydra and the Omo and Hadar fossils are similar in some ways to the pinniped morphology described above (note that some of these features were not quantified in the present study as angles were not included). The Omo fossil expresses this morphology to the greatest degree with the superiorly oriented articular surface of the head, shortened neck (to a lesser degree than pinnipeds), enlarged greater and lesser trochanters, and the inferior border of the neck having become more medial. *Enhydra* and the Hadar femur have enlarged trochanters, but the head and neck are not rotated superiorly to the same degree. *Enhydra* and the Omo and Hadar femora also share a feature not seen in pinnipeds: a well-excavated superior portion of the neck. The West Turkana specimen has a shortened neck, but has not

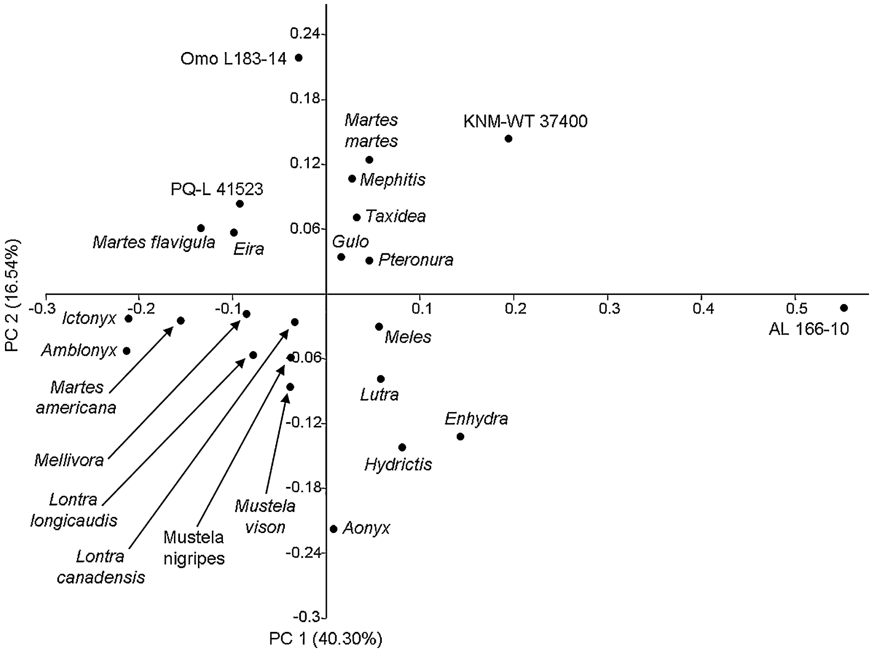

Fig. 12. Results of PCA of standardized distal femoral variables in extant mustelids and fossils. PC 1 is driven by the AP width of each condyle and biepicondylar width. Those with the largest condyles fall towards the negative side of the axis. PC 2 is driven primarily by the proximodistal height of the condyles and the width of the patellar groove. Those higher along the second axis have the greatest patellar groove widths, while those lower along the axis have the shortest condyles proximodistally.

Fig. 12. Analyse en composantes principales des variables standardisées du fémur distal chez les mustélidés actuels et fossiles. La CP 1 est commandée par le diamètre antéropostérieur de chaque condyle et par la largeur biépicondylienne. La seconde l'est surtout par la hauteur proximodistale des condyles et la largeur du sillon de la patella. Les sujets qui se projettent les plus hauts le long du second axe possèdent les plus grandes largeurs du sillon, tandis que ceux qui se trouvent les plus bas ont les hauteurs proximodistales les plus faibles.

reoriented the head or enlarged the lesser trochanter. The Langebaanweg specimen has none of these features.

Among other extants, only the giant otter, *Pteronura*, shows any similarity to *Enhydra*. *Pteronura* has enlarged the greater trochanter and has a relatively short, mediolaterally wide shaft. The lesser trochanter is not enlarged to the degree seen in *Enhydra* and is within the size range of other extant otters. The giant otter, as the name implies, is quite large and is the longest otter, reaching up to 2 m in length [32]. However, despite its length, it is not as heavy as *Enhydra*. These morphological similarities may be due not only to *Enhydra* and *Pteronura* being the two largest extant otters, but also to similarities in the structure of their habitat. *Enhydra* swims in deep ocean water, while *Pteronura* prefers the deeper regions of lakes [6,32]. All other nonbunodont otters prefer shallower areas along the margins of bodies of water [32]. While no laboratory analyses have been done of the locomotion of *Pteronura* as they have for other otters, one would predict that they might include more undulation and *Enhydra*-like movements on a daily basis than the typical river otter.

Having a superiorly oriented head and neck, as seen in the Omo fossil and to a lesser degree in *Enhydra*, changes the orientation of the entire femur with respect to the os coxae. This reorientation changes both rotatory ability and muscle leverages. Rather than the femur being relatively valgus and moving parasagittally, as in terrestrial cursorial mammals, or more varus, as in ambulatory mammals, the femur can be rotated posteriorly more easily. In fact, *Enhydra* has been shown to bring its hindlimb further superiorly past the tail when swimming for increased thrust, while other otters only bring their hindlimb to the level of the tail [61].

Enhydra has a large lip on the ilial portion of the acetabulum (arrow in Fig. 14). When *Enhydra* swims ventrum down or when it is terrestrial, this lip would be anterior and slightly superior. This lip prevents hyperflexion and excessive medial rotation. There is little to no lipping of the ilial portion of the acetabulum in other otters.

Enhydra also has widened, laterally flaring iliac blades in the ossa coxae such that the proximal half of the ilium projects laterally at roughly a 135° angle from the main axis of the rest of the os coxae (Fig. 14).

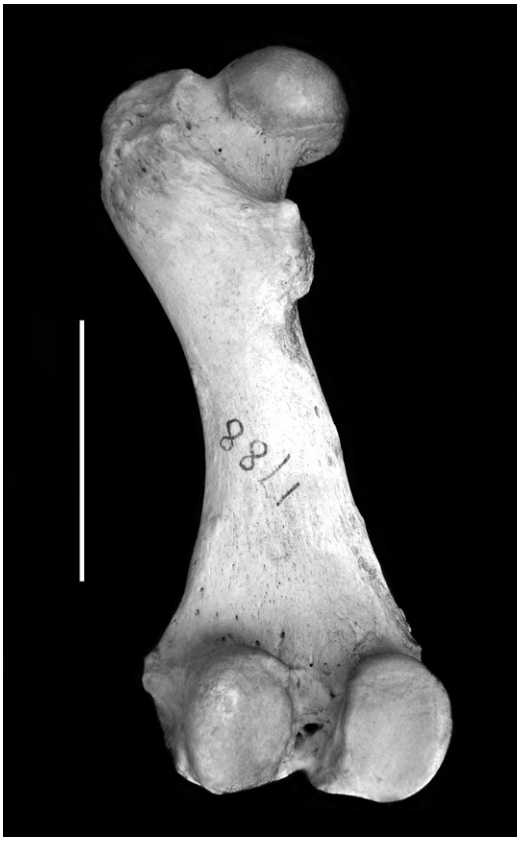

Fig. 13. Posterior view of the femur of the northern fur seal, *Callorhinus ursinus* (MCZ BOM 1788), an otariid pinniped. Note the enlarged greater and lesser trochanters, the short neck, and superiorly oriented head. Copyright MCZ. Scale = 50 mm.

Fig. 13. Vue postérieure du fémur de l'otarie nordique à fourrure, *Callorhinus ursinus* (MCZ BOM 1788), ordre des Pinnipedia. Notez l'agrandissement des deux trochanters, le col raccourci et la tête orientée vers le haut. Copyright MCZ. Échelle = 50 mm.

This flaring not only provides a wider surface area of attachment for muscles, but also a radical change in the orientation of those muscles. Several muscles attach to the iliac blade including the iliocostalis and longissimus lumborum on the internal surface and the gluteus medius on the external surface. The longissimus lumborum is an important extensor of the lumbosacral region of the vertebral column. Presumably, having broader, everted ilia increases the leverage for this group muscle and would create more powerful dorsoventral undulation in this region of the spine. The iliocostalis lumborum is important in lateral flexion, which is important for turning, but not a component of rectilinear movement in sea otters. A somewhat similar ilial morphology in phocine seals has been suggested to be due to the need to increase the surface area of attachment for the iliocostalis lumborum, a muscle that is important for much of the lateral body movements used in swimming in this subfamily [2,30].

In terrestrial mammals, the gluteus medius is the strongest extensor of the hip and an abductor [44]. The insertion point for the gluteus medius, the greater trochanter, is also enlarged in *Enhydra*. The greater trochanter also serves as the insertion point for the piriformis and the gluteus profundus, which support the actions of the gluteus medius. Perhaps *Enhydra* ilial morphology also helps to increase the powerstroke from the hindlimbs during undulation or while changing direction. Extension is apparently a very important part of *Enhydra* locomotion as the gluteal tuberosity (= third trochanter) is larger in *Enhydra* than in any other extant otter (it is also enlarged in the Omo femur, although it projects posteriorly and not laterally). This tuberosity is the site of attachment for the gluteus superificialis, another hip extensor. One should note that the lesser trochanter is also quite enlarged in *Enhydra*. This is the insertion point for the iliopsoas, an important flexor of the hip used during the recovery phase of locomotion.

In contrast to *Enhydra*, other extant otters have nonflaring ilia that are very similar to nonlutrine mustelids.

Fig. 14. Ossa coxae of *Enhydra lutris* (AMNH 215274). Arrow indicates lipping on the ilial portion of the acetabulum. In anatomical position, this lip would be anterosuperior. Note that the iliac blade flares laterally unlike in other otters. Scale = 100 mm.

Fig. 14. Os coxal de *Enhydra lutris* (AMNH 215274). La flèche indique le bourrelet sur l'aile iliaque de l'acétabulum. En positon anatomique, cette lèvre serait antérosupérieure. Notez que l'aile iliaque s'étend latéralement contrairement à celle des autres loutres. Échelle = 100 mm.

The size of the greater trochanter varies and the lesser trochanter is prominent, but not as enlarged. The gluteal tuberosity is discernible, but not enlarged. These differences may reflect the fact that undulation is not a dominant form of locomotion in these otters.

Unfortunately, no os coxae were found with the femora included in this study. One might predict that the Hadar and Omo femora would be associated with ossa coxae more similar to those of *Enhydra* based on the morphology of the head, neck, and greater trochanter. The West Turkana and Langebaanweg specimens would probably have been associated with ossa coxae like other lutrines. In fact, *S. beyi*, a species that has been reconstructed as not being particularly aquatic (see Figure 7 in Peigné et al. [49]), from the published photographs appears to have had the nonflaring ilia like river otters given what remains of the fragmentary os coxae.

Of the four fossil femora included in this study, it is clear that the Langebaanweg specimen is least likely to be aquatic in the manner of *Enhydra*. In some features, it appears more like nonlutrine mustelids. As a good generalist, it is possible that it was semiaquatic, like extant river otters, or occasionally aquatic, like many nonlutrine mustelids.

The West Turkana specimen is also relatively generalized. Among the fossils, the West Turkana specimen has the shortest functional length relative to overall bone size. In that manner, it is most similar to extant lutrines. The condyles are also relatively short anteroposteriorly and the neck is short. Overall, this specimen could easily have belonged to a semiaquatic form.

The largest fossil, Omo, does have a few features that may be indicative of more aquatic behavior: the superiorly oriented head, more sharply angled neck, and enlarged trochanters. While the Hadar femur has not reoriented the head, it does have enlarged trochanters. The Omo and especially the Hadar femora also had relatively anteroposteriorly short condyles (also seen in the West Turkana femur), although not to the degree seen in otariids. However, this is not a feature expressed in *Enhydra* or other less fully aquatic otters.

Could the rotation of the head and angling of the neck in the Omo specimen be due to the need to transmit increased forces due to their much larger body weight than extant mustelids? This feature is present to a lesser degree in the much smaller *Enhydra*. Among carnivorans, it is not seen in any extant ursid (including pandas), nor is it seen in felids, including large, extinct machairodont forms such as *Homotherium*. Although not recognized until now, among extinct bunodont otters, it is present in *Enhydritherium terraenovae* (see Figure 7 in Lambert [33]), but not in the larger *S. beyi* (see Figure 7 in Peigné et al. [49]). While I have not surveyed all extinct large mustelids, this does not seem to be a feature found in any specimen except *some* of those potentially belonging to bunodont lutrines. Granted, not many mustelids approach the size of the Hadar and Omo specimens. Even the large mustelid from Lothagam, *Ekorus ekakeran* (which also lacks this feature), has a femur that is only slightly longer than the West Turkana femur and is more gracile. Thus, it appears that this feature is more likely to be due to locomotor adaptation than body size within this group.

The Omo and Hadar femora do have some features that would argue against aquatic behavior along the lines of *Enhydra*. Both fossils have the relatively long functional lengths for their overall femoral size. Otters, with the exception of *Amblonyx cinereus*, tend to have short, robust femora, with the largest otters *Enhydra* and *Pteronura* taking this trend to the extreme. Among nonlutrine mustelids, the most scansorial taxa have the longest femora relative to overall bone size. The two fossils fall in the middle with the majority of lutrines and nonlutrine mustelids. Whether their femora are long relative to their body size for a lutrine or whether their femora are simply gracile relative to their overall body size for a lutrine cannot be determined as body size is unknown. In either case, this does not preclude aquatic behavior as they are certainly within the range of extant otters.

In sum, the two smallest femora from Langebaanweg and West Turkana, while large, can be reconstructed as locomotor generalists. The West Turkana form appears more like lutrines than the Langebaanweg form and was probably semiaquatic. In the Langebaanweg form, this behavior cannot be ruled out. The two largest specimens (Omo and Hadar) are unusual both in their size and in their morphology. They are clearly engaging in locomotion unlike any extant mustelid. While the morphology of the proximal end points to more aquatic behavior than in most lutrines, the relative length to overall size is more similar to that of generalist mustelids, including semiaquatic lutrines. Future study of the less common postcranial elements of bunodont otters from Omo and Hadar may help to resolve this mystery.

8. Behavior and ecology of extinct bunodont lutrines in Africa

While it is not reasonable to reconstruct the behavior and ecology of a taxon solely on femoral morphology, some remarks can still be made. If the larger taxa were aquatic to the degree of *Enhydra*, they may have preferred the deepwater lakes searching for a variety of foods. While narrow streams and river banks may be favored habitats of extant otters such as *Lutra* [32], a gigantic, more aquatic otter might not be able to maneuver as well in such an area. Today, the largest "fish otter", *Pteronura* (giant otter), prefers clear, black water which is usually the larger, fish-rich areas [6,32]. Moderately large size would not preclude the use of river banks in species that were more semiaquatic (e.g., the West Turkana species).

Of course, as mustelids, these species probably came out of the water as even *Enhydra* does. Among otters, *A. cinereus*, the small-clawed otter, spends the most time away from the river. This relatively long-limbed otter often forages for invertebrates at night away from the river bank in damp vegetation, while other sympatric species of otter remain in the river [32]. *Amblonyx* has not been reported to dive or fish in deeper waters [32], and so represents the opposite extreme from *Enhydra* in being the least aquatic otter.

It should be noted that while *Enhydra* is often thought of being predominantly durophagous, other types of foods such as fish and cephalopods can be important components of the diet. Kenyon [29] found that 50% of the stomach contents of over 300 sea otters were fish, with only 37% of the contents being mollusk and 11% sea urchin. Freshwater otters, despite being referred to as "fish otters", also consume a wide range of foods. The giant otter, *Pteronura*, has been known to eat tapir dung, invertebrates extracted from the mud, and even small vertebrates (bird, small mammal, snake, small caimans, and turtles) [32]. *Amblonyx* and *Aonyx* prefer crabs and other invertebrates even without bunodont teeth [32].

Pickford [52] has suggested that *Enhydriodon* was a molluscivore based on the reinforced anterior snout dentition, powerful masticatory musculature, and the possession of bunodont teeth with thick enamel. In his analysis, the breadth–length relationship of m1 was found to discriminate between otters whose primary prey was shellfish and those whose primary prey was fish. Both *Sivaonyx* and *Enhydriodon* have a breadth–length relationship suggesting shellfish predation. However, Pickford suggests that those taxa with thick enamel (in his analysis, all *Enhydriodon* and African *Sivaonyx*) would have preyed on harder more abrasive food like freshwater mollusks. Pickford, therefore, suggests that *Enhydriodon* preyed extensively, although not exclusively, on freshwater mollusks.

Larger, extinct bunodont otters may have foraged for a wide variety of foods in addition to their primary prey. Bunodont teeth may have allowed them to deal with larger fish with harder external coverings (e.g., catfish) or even other vertebrates as seen in *Pteronura*. *Enhydritherium*, a bunodont otter from North America, has been shown to have extremely powerful neck muscles, which Lambert [33] suggested were used to hold on to extremely large fish. Bunodont dentition would not have prevented the intake of a large amount of softer foods, as seen in sea otters today, and may have been useful for dealing with relatively large fish.

9. Conclusions

The four fossil femora exhibit very different morphologies. The differences in morphology and extreme differences in size among the four specimens suggest that they each belong to a different species. While one might speculate that the Omo femur is male and the Hadar femur is female, this is extremely unlikely. In the Omo femur, the head is angled more superiorly, the neck is shorter, and the distance between the greater and lesser trochanter is much shorter relative to overall size than in the Hadar femur. The condyles of the Hadar femur are unique.

The two largest specimens, Omo L183-14 and AL 166-10, have a morphology that is most consistent with an aquatic lifestyle. Given their respective ages, it is possible that the Omo species evolved from the Hadar form. This would have required an increase in size along with an increase in the relative length of the bone. The head would become angled more sharply superiorly and the relative size of the intertrochanteric length would shrink. The condyles, however, would have had to enlarge somewhat.

The West Turkana specimen looks more like a much larger version of a river ("fish") otter, but with a higher greater trochanter, shorter neck and an increased ridge running from the greater trochanter to the gluteal tuberosity. This femur could certainly have belonged to a lutrine, whether bunodont or not. If not a bunodont otter, this individual is much larger than any known nonbunodont lutrine in Africa such as *Torolutra*. The dating of this specimen overlaps with both the Hadar and Omo specimens. While it could represent the ancestral form relative to the more derived Hadar and Omo specimens, it may also simply be another large otter living in eastern Africa during the Pliocene. To evolve from the West Turkana form into the other two would require an increase in overall size, a reorientation of the head and neck more superiorly, a slight increase in neck length, and an increase in size and medial projection of the lesser trochanter.

Whether any of the above specimens belong to *Enhydriodon* or to *Sivaonyx* or to something different is unclear. Association with dental material is unclear, although it is most parsimonious to assume that they are the same taxon as any similarly-sized lutrine dental material found from the same locality and geological age. Full description of these new taxa will be left for a later paper [68].

The oldest specimen, PQ-L 41523, from Langebaanweg is more like a generalized mustelid than any of the other taxa. It is certainly possible that it is a primitive bunodont otter. The morphology is generalized enough that it could be ancestral to the others.

In sum, there are multiple species of large mustelid present in Africa during the Neogene. The four femora presented here are not firmly associated with dentition, but are definitely mustelid. While there is no clear picture of how these species might be related, it is certain that they were not engaging in exactly the same forms of locomotion. If they do belong to bunodont lutrines, then they appear to be more diverse in postcranial morphology than in dental morphology. The oldest (Langebaanweg) appears the most generalized, the West Turkana form is more like extant river otters, and the two largest forms (Omo and Hadar) are unique in both their extreme size and morphology, with features that point to aquatic behavior. The increasing number of identifications of large mustelids, both lutrine and nonlutrine, in the fossil record points to the importance of these taxa for understanding Neogene paleoecology. How might an otter (or a nonlutrine mustelid) with a femur within the size range of extant lions interact with other taxa? One of the limits of the present study was the lack of information on specific locomotor behavior across all extant lutrine and nonlutrine mustelid taxa. Only further functional studies of extant morphology and of the morphology of other craniodental and postcranial specimens of extinct mustelids will help determine whether these enormous mustelids were feared predators or gentle giants, rarely seen outside of the lake.

Acknowledgments

This paper is dedicated to the memory of Professor F.C. Howell with gratitude to him for many things including allowing Lars Werdelin and me to study the Omo material in his lab. I would also like to thank Professor L. de Bonis and Professor F.C. Howell for the invitation to join the NSF Analytical Working Group on Phylogeny, Paleobiogeography and Paleoecology of Carnivores Related to Hominid Origins, Revealing Hominid Origins Initiative (RHOI) and the invitation to participate in the associated RHOI workshop. Comments made by participants were an important component in the creation of this manuscript.

The CCRH of Ethiopia and the Governments of Ethiopia and Kenya made this study possible by giving me permission to study material housed in Addis Abeba, Ethiopia and Nairobi, Kenya. I would also like to thank M. Avery, J. Chupasko, J. Flynn, L. Gordon, M.G. Leakey, R. MacPhee, E. Mbua, N. Mudida, M. Muungu, K.E. Reed, N. Simmons, R. Thorington, and E. Westwig for permission to study material in their care. M.R. Lague provided invaluable discussions and other assistance, while L. Werdelin was kind enough not only to comment on the study, but also to supply photos of the West Turkana, Langebaanweg, and Omo femora. This research was supported by grants from the LSB Leakey Foundation to ML and K.E. Reed, NSF, Sigma Xi, Stockton Distinguished Faculty Fellowships and a Stockton CDC Grant.

References

[1] A. Berta, G.S. Morgan, A new sea otter (Carnivora: Mustelidae) from the Late Miocene and Early Pliocene (Hemphillian) of North America, J. Paleontol. 59 (1985) 809–819.

[2] A. Berta, J.L. Sumich, Marine Mammals: Evolutionary Biology, Academic Press, San Diego, 1999, 494 p.

[3] B.C.R. Bertram, A.A. Biewener, Differential scaling of the long bones in the terrestrial Carnivora and other mammals, J. Morphol. 204 (1990) 157–169.

[4] A.A. Biewener, Allometry of quadrupedal locomotion: the scaling of duty factor, bone curvature and limb orientation to body size, J. Exp. Biol. 105 (1983) 147–171.

[5] A.A. Biewener, C.R. Taylor, Bone strain: A determinant of gait and speed? J. Exp. Biol. 123 (1986) 383–400.

[6] S.K. Carter, F.C.W. Rosas, Biology and conservation of the giant otter *Pteronura brasiliensis*, Mamm. Rev. 27 (1997) 1–26.

[7] T.W. Clark, E. Anderson, C. Douglas, M. Strickland, *Martes americana*, Mamm. Spec. 289 (1989) 1–8.

[8] M. Crusafont Pairó, J.M. Golpe, Nuevos hallazgos de lútridos aonicoides (*Sivaonyx*, *Enhydriodon*) en el Pikermiense Español (Cuenca de Teruel), Notas Comun. Inst. Geol. Minero Esp. 67 (1962) 5–16.

[9] A.I. Dagg, The walk of large quadrupedal mammals, Can. J. Zool. 57 (1979) 1157–1163.

[10] J.N. Darroch, J.E. Mosimann, Canonical and principal components of shape, Biometrika 72 (1985) 241–252.

[11] D.P. DeMaster, I. Stirling, *Ursus maritimus*, Mamm. Spec. 145 (1981) 1–7.

[12] J.A. Estes, *Enhydra lutris*, Mamm. Spec. 133 (1980) 1–8.

[13] C.S. Feibel, F.H. Brown, I. McDougall, Stratigraphic context of fossil hominids from the Omo Group deposits: northern Turkana basin, Kenya and Ethiopia, Am. J. Phys. Anthropol. 78 (1989) 595–622.

[14] F.E. Fish, Association of propulsive swimming mode with behavior in river otters (*Lutra canadensis*), J. Mammal. 75 (1994) 989–997.

[15] F.E. Fish, Transitions from drag-based to lift-based propulsion in mammalian swimming, Am. Zool. 36 (1996) 628–741.

[16] V. Flyger, M.R. Townsend, The migration of polar bears, Sci. Am. 218 (1968) 108–116.

[17] H.G. Gauch Jr., Multivariate Analysis in Community Ecology, Cambridge, New York, 1982, p. 298.

[18] Y. Haile-Selassie, G. WoldeGabriel, T.D. White, R.L. Bernor, D. Degusta, P. Renne, W. Hart, E.S. Vrba, S.H. Ambrose, F.C. Howell, Mio–Pliocene mammals from the Middle Awash, Ethiopia, Geobios 37 (2004) 536–552.

[19] Ø. Hammer, D.A.T. Harper, PAST: Palaeontological Statistics software package for education and data analysis, Palaeont. Elect. 4 (2001) 1–9.

[20] J. Harris, F.H. Brown, M.G. Leakey, Stratigraphy and Palaeontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya, Contrib. Sci., Nat. Hist. Mus. Los Angeles 399 (1988) 1–128.

[21] Q.B. Hendey, Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaanweg, South Africa, Ann. S. Afr. Mus. 76 (1978) 329–357.

[22] Q.B. Hendey, Palaeoecology of the Late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context, Ann. S. Afr. Mus. 84 (1981) 1–104.

[23] C.N. Hillman, T.W. Clark, *Mustela nigripes*, Mamm. Spec. 126 (1980) 1–3.

[24] F.C. Howell, Overview of the Pliocene and Earlier Pleistocene of the Lower Omo basin, southern Ethiopia, in: C.J. Jolly (Ed.), Early Hominids of Africa, St. Martin's Press, New York, 1976, pp. 85–130.

[25] F.C. Howell, G. Petter, Carnivora from Omo Group Formations, Southern Ethiopia, in: Y. Coppens, F.C. Howell, G.L. Isaac, R.E.F. Leakey (Eds.), Earliest Man and Environments in the Lake Rudolf Basin: Stratigraphy, Paleoecology, and Evolution, University of Chicago Press, Chicago, 1976, pp. 314–331.

[26] F.C. Howell, G. Petter, Indications d'âge données par les Carnivores de la formation d'Hadar (Éthiopie orientale), C. R. Acad. Sci. Paris, Ser. D 282 (1976) 2063–2066.

[27] F.C. Howell, G. Petter, Diversification et affinités des carnivores pliocènes du groupe de l'Omo et de la formation d'Hadar (Éthiopie), Bull. Soc. geol. France 7 (1979) 289–293.

[28] W.L. Jungers, A. Falsetti, C. Wall, Shape, relative size, and size-adjustments in morphometrics, Yrbk. Phys. Anthropol. 38 (1995) 137–161.

[29] K.W. Kenyon, The sea otter in the eastern Pacific ocean, North American Fauna 68 (1969) 1–352.

[30] J.E. King, Seals of the World, Oxford University Press, London, 1983.

[31] J. Kingdon, East African Mammals, Volume IIIA: Carnivores, University of Chicago Press, Chicago, 1977.

[32] H. Kruuk, Otters: Ecology, Behaviour and Conservation, Oxford University Press, Oxford, 2006, 265 p.

[33] W.D. Lambert, The osteology and paleoecology of the giant otter *Enhydritherium terraenovae*, J. Vert. Paleontol. 17 (1997) 738–749.

[34] S. Larivière, L.R. Walton, *Lontra canadensis*, Mamm. Spec. 587 (1998) 1–8.

[35] S. Larivière, *Mustela vison*, Mamm. Spec. 608 (1999) 1–9.

[36] S. Larivière, *Lontra longicaudis*, Mamm. Spec. 609 (1999) 1–5.

[37] S. Larivière, *Aonyx capensis*, Mamm. Spec. 671 (2001) 1–6.

[38] S. Larivière, *Lutra maculicollis*, Mamm. Spec. 712 (2002) 1–6.

[39] S. Larivière, *Amblonyx cinereus*, Mamm. Spec. 720 (2003) 1–5.

[40] M.E. Lewis, M.R. Lague, Interpreting sabertooth cat (Carnivora; Felidae; Machairodontinae) postcranial morphology in light of scaling patterns in felids, in: A. Friscia, A. Goswami (Eds.), Carnivora: Form, Function, and Phylogeny, Cambridge University Press, Cambridge (in press).

[41] C.A. Long, *Taxidea taxus*, Mamm. Spec. 26 (1973) 1–4.

[42] J. Morales, M. Pickford, Giant bunodont Lutrinae from the Mio–Pliocene of Kenya and Uganda, Estud. Geol. 61 (2005) 233–246.

[43] J. Morales, M. Pickford, D. Soria, Carnivores from the Late Miocene and Basal Pliocene of the Tugen Hills, Kenya, Rev. Soc. Geol. Esp. 18 (2005) 39–61.

[44] R. Nickel, A. Schummer, E. Seiferle, J. Frewein, H. Wilkens, K.-H. Wille, The Anatomy of the Domestic Animals. Volume 1. The Locomotor System of the Domestic Mammals, Springer-Verlag, Berlin, 1986, 499 p.

[45] R.M. Nowak, Walker's Marine Mammals of the World, The Johns Hopkins University Press, Baltimore, 2003, 264 p.

[46] R.M. Nowak, Walker's Carnivores of the World, The Johns Hopkins University Press, Baltimore, 2005, 313 p.

[47] M. Pasitschniak-Arts, *Ursus arctos*, Mamm. Spec. 439 (1993) 1–10.

[48] M. Pasitschniak-Arts, S. Larivière, *Gulo gulo*, Mamm. Spec. 499 (1995) 1–10.

[49] S. Peigné, L. De Bonis, A. Likius, H. Taisso Mackaye, P. Vignaud, M. Brunet, Late Miocene Carnivora from Chad: Lutrinae (Mustelidae), Zool. J. Linn. Soc. 152 (2008) 793–846.

[50] G. Petter, Carnivores des régions de Nkondon et de Kisegi-Nyabusosi (Rift occidental, Ouganda), in: B. Senut, M. Pickford (Eds.), Geology and palaeobiology of the Albertine Rift Valley, Uganda–Zaire. Volume II: Palaeobiology, CIFEG Occasional Publications, Orléans, 1994, pp. 207–215.

[51] G. Petter, M. Pickford, F.C. Howell, La loutre piscivore du Pliocène de Nyaburogo et de Nkondo (Ouganda, Afrique orientale): *Torolutra ougandensis* n. g., n. sp. (Mammalia, Carnivora), C.R. Acad. Sci. Paris, Ser. II 312 (1991) 949–955.

[52] M. Pickford, Revision of the Mio–Pliocene bunodont otter-like mammals of the Indian Subcontinent, Estud. Geol. 63 (2007) 83–127.

[53] G.E. Pilgrim, Catalogue of the Pontian Carnivora of Europe, British Museum (Natural History), London, 1931, p. 174.

[54] R. Pimentel, Morphometrics, Kendall/Hunt, Dubuque, Iowa, 1979, p. 276.

[55] H. Pohle, Die Unterfamilie der Lutrinae, Archiv für Naturgeschichte, Jahrg. 85, Abt. A 9 (1919) 1–249.

[56] C.A. Repenning, *Enhydra* and *Enhydriodon* from the Pacific coast of North America, Bull. Florida State Mus. 20 (1976) 305–315.

[57] H. Schutz, R.P. Guralnick, Postcranial element shape and function: assessing locomotor mode in extant and extinct mustelid carnivorans, Zool. J. Linn. Soc. 150 (2007) 895–914.

[58] P. Sneath, R. Sokal, Numerical Taxonomy, WH Freeman, San Francisco, 1973, p. 573.

[59] E. Stromer, Reste süsswasser- und landbewohnender Wirbeltiere aus den Diamantfelden Klein-Namaqualandes (Südwest-Afrika), Sitzungsberichte der bayerischen Akademie der Wissenschaften zu München 1931 (1931) 17–47.

[60] F.J. Tarasoff, Comparative aspects of the hind limbs of the river otter, sea otter and seals, in: R.J. Harrison (Ed.), Functional Anatomy of Marine Mammals, 1, Academic Press, London, 1972, pp. 333–359.

[61] F.J. Tarasoff, A. Bisallon, J. Pierard, A.P. Whitt, Locomotory patterns and external morphology of the river otter, sea

otter, and harp seal (Mammalia), Can. J. Zool. 50 (1972) 915–929.

[62] M.E. Taylor, Locomotor adaptations by carnivores, in: J.L. Gittleman (Ed.), Carnivore Behavior, Ecology, and Evolution, Cornell University Press, New York, 1989, pp. 382–409.

[63] W.P. Taylor, The problem of aquatic adaptation in the Carnivora, as illustrated in the osteology and evolution of the sea otter, Univ. Calif. Publ. Bull. Dept. Geol. 7 (1914) 465–495.

[64] R. Walter, The age of Lucy and the First Family: single crystal ^{40}Ar/^{39}Ar dating of the Denen Dora and lower Kada Hadar Members of the Hadar Formation, Ethiopia, Geology 22 (1994) 6–10.

[65] L. Werdelin, Mio–Pliocene Carnivora from Lothagam, Kenya, in: M.G. Leakey, J.M. Harris (Eds.), Lothagam: The Dawn of Humanity in eastern Africa, Columbia University Press, New York, 2003, pp. 261–678.

[66] L. Werdelin, Carnivores from the Kanapoi hominid site, Turkana Basin, northern Kenya, Contrib. Sci. 498 (2003) 115–132.

[67] L. Werdelin, M.E. Lewis, Plio–Pleistocene Carnivora of eastern Africa: species richness and turnover patterns, Zool. J. Linn. Soc. 144 (2005) 121–144.

[68] L. Werdelin, M.E. Lewis, K.E. Reed, A revision of the bunodont otters of Africa (Mammalia, Mustelidae, Lutrinae) (in preparation).

[69] G.F. Willemsen, A revision of the Pliocene and Quaternary Lutrinae from Europe, Scripta Geolog. 101 (1992) 1–115.

[70] T.M. Williams, Locomotion in the North American mink, a semiaquatic mammal. I. Swimming energetics and body drag, J. Exp. Biol. 103 (1983) 155–168.

[71] T.M. Williams, Swimming by sea otters: adaptations for low energetic cost locomotion, J. Comp. Physiol. 164 (1989) 815–824.