Systematic palaeontology (vertebrate palaeontology)

New observations on the Late Miocene–Early Pliocene Lutrinae (Mustelidae: Carnivora, Mammalia) from the Middle Awash, Afar Rift, Ethiopia

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Abstract

New observations on the Late Miocene and Earliest Pliocene mustelids from the Middle Awash of Ethiopia are presented. The Middle Awash study area samples the last six million years of African vertebrate evolutionary history. Its Latest Miocene (Asa Koma Member of the Adu-Asa Formation, 5.54–5.77 Ma) and Earliest Pliocene (Kuseralee and Gawto Members of the Sagantole Formation, 5.2 and 4.85 Ma, respectively) deposits sample a number of large and small carnivore taxa among which mustelids are numerically abundant. Among the known Late Miocene and Early Pliocene mustelid genera, the Middle Awash Late Miocene documents the earliest *Mellivora* in eastern Africa and its likely first appearance in Africa, a new species of *Plesiogulo*, and a species of *Vishnuonyx*. The latter possibly represents the last appearance of this genus in Africa. *Torolutra ougandensis* is known from both the Late Miocene and Early Pliocene deposits of the Middle Awash. The genus *Sivaonyx* is represented by at least two species: *S. ekecaman* and *S.* aff. *S. soriae*. Most of the lutrine genera documented in the Middle Awash Late Miocene/Early Pliocene are also documented in contemporaneous sites of eastern Africa. The new observations presented here show that mustelids were more diverse in the Middle Awash Late Miocene and Early Pliocene than previously documented. ***To cite this article: Y. Haile-Selassie, C. R. Palevol 7 (2008).***

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Résumé

Nouvelles observations sur les Lutrinae (Mustelidae : Carnivora, Mammalia) du Miocène terminal–Pliocène basal de l'Aouache moyen, Bassin de l'Afar, Éthiopie. L'article présente de nouvelles données sur les mustélidés du Miocène terminal et du Pliocène basal de la vallée moyenne de l'Aouache (Éthiopie). Cette région permet d'échantillonner les derniers six millions d'années de l'histoire évolutive des vertébrés africains. Les dépôts du Miocène terminal (Membre Asa Koma de la Formation Adu-Asa, 5,54–5,77 Ma) et du Pliocène basal (Membres Kuseralee et Gawto de la Formation Sagantole, 5,2 and 4,85 Ma, respectivement) ont livré de nombreux taxons de grands et petits carnivores parmi lesquels, les mustélidés sont bien représentés. Parmi les genres connus se trouvent le plus ancien *Mellivora* trouvé en Afrique de l'Est et même en Afrique, une nouvelle espèce de *Plesiogulo* et une espèce de *Vishnuonyx*. Cette dernière pourrait correspondre à l'ultime présence du genre en Afrique. *Torolutra ougandensis* se retrouve sur toute l'étendue des dépôts de l'Aouache moyen. *Sivaonyx* est représenté par au moins deux espèces, *Sivaonyx ekecaman* et *S.* aff. *S. soriae*. La plupart des mustélidés de l'Aouache moyen sont également connus des sites contemporains d'Afrique de

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l'Est. Les nouvelles données présentées ici montrent que les mustélidés du Miocène terminal et du Pliocène basal de cette région étaient plus diversifiés qu'on ne l'avait constaté jusque-là. ***Pour citer cet article : Y. Haile-Selassie, C. R. Palevol 7 (2008).***

1. Introduction

The Middle Awash paleontological study area is located in the Afar region of Ethiopia at the southern terminus of the Afar Rift and northern end of the Main Ethiopian Rift (MER; Fig. 1). The fluvial, lacustrine, and volcanogenic deposits in this area have a thickness of ca. 1 km and sample the last six million years of geological and paleontological history of the region [4,5,23,24,31,32]. The paleontological potential of this area has been recognized since the early 1970s [12–15,27], although intensive geological and paleontological work was carried out beginning in the 1980s with the creation of the Middle Awash paleoanthropological research project led by the late Professor Desmond Clark and Professor Tim White of the University of California at Berkeley [1,4].

Fieldwork conducted in the study area during the last 20 years has refined the geology, geochronology, and paleontology of the Middle Awash study area. The oldest deposits along the western rift margin of the study area are grouped into the Adu-Asa Formation and comprise four members. These are, from the oldest to the youngest, the Saraitu, Adu Dora, Asa Koma, and Rawa Members [31] (Fig. 2).

Radiometric dating has established an age between 6.3 Ma and less than 5.54 Ma for these members [24,31] (Fig. 2). A total of greater than 2200 vertebrate fossil specimens has been collected from these members, most of them from the Asa Koma Member. These specimens represent more than 60 genera in 23 mammalian families, in addition to remains of Aves, Crocodilia, Chelonia, and fishes [4,6]. The lower portion of the Sagantole Formation is divided into the Kuseralee, Gawto, and Haradaso Members. The Kuseralee Member is dated to between 5.2 and 5.5 Ma and the Haradaso Member to between 4.85 and 5.2 Ma [23,24,31].

The carnivore fauna of this succession represents one of the most taxonomically diverse in the latest Miocene of eastern Africa. At least 15 genera in seven families are recognized from the Asa Koma Member of the Adu-Asa Formation (5.54–5.77 Ma) and the Kuseralee Member of the Sagantole Formation (5.2 Ma) [3]. The slightly younger Haradaso Member (4.8–5.2 Ma) has also yielded diverse mammalian taxa including large and small carnivores. This assemblage has not been fully analyzed yet. However, the lutrines are described here.

According to Haile-Selassie and Howell [3], large felids from the Late Miocene of the Middle Awash
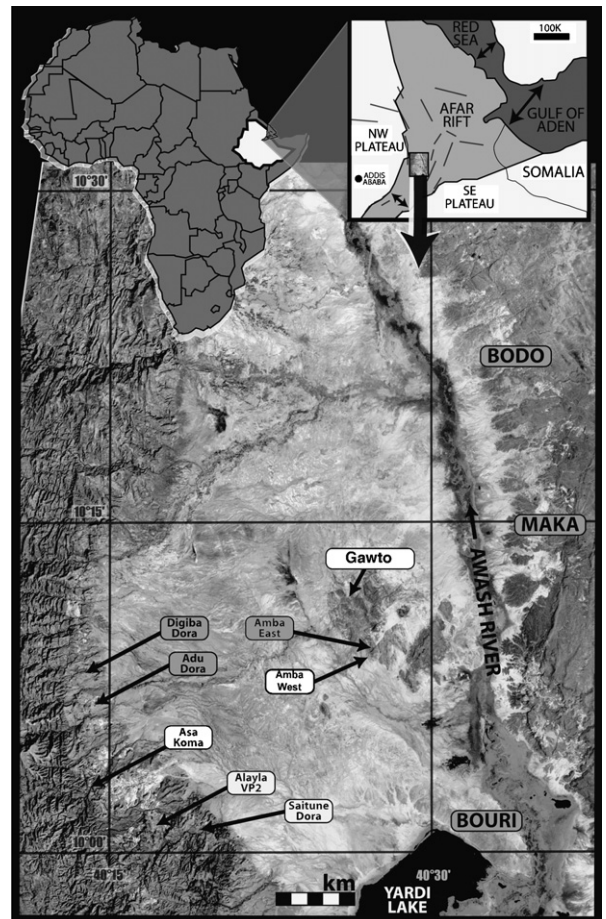

Fig. 1. Location map showing the Middle Awash Late Miocene–Early Pliocene localities described in the text (shown in boxes in white background). Asa Koma, Alayla, and Saitune Dora are located along the western margin of the study area and Gawto and Amba West are in the Central Awash Complex (CAC). Modified from [4].

Fig. 1. Carte montrant les localités du Miocène terminal et du Pliocène basal, discutées dans le texte. Asa Koma, Alayla, et Saitune Dora sont situées le long de la marge occidentale de la région étudiée et Gawto et Amba West sont dans le Complexe central de l'Aouache (CAC). Modifié d'après [4].
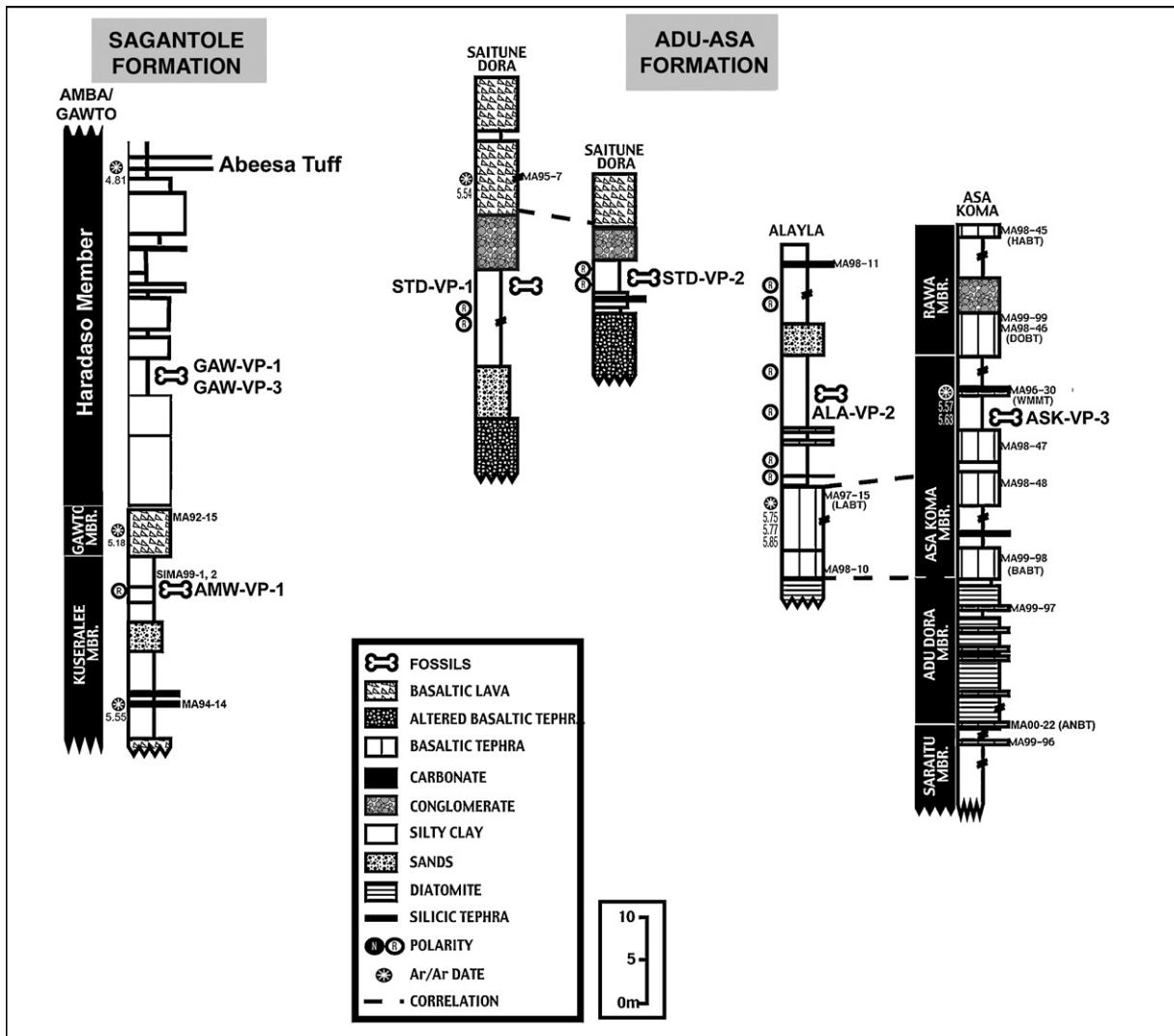
Fig. 2. Stratigraphy and geochronology of the Adu-Asa and Sagantole formations of the Middle Awash. Modified after [4,23,31].
Fig. 2. Stratigraphie et géochronologie des formations Adu-Asa et Sagantole de l'Aouache moyen. Modifié d'après [4,23,31].

include *Machairodus* sp., *Dinofelis* sp., and one large felid unidentified at the genus or species level. One small felid is also present although it has not been identified at the genus or species level because of the fragmentary nature of the remains. Two hyaenid genera, *Hyaenictitherum* and *Hyaenictis* sp. nov., are recognized. These genera are also known from other terminal Miocene sites of Africa. Ursids are represented by one genus, *Agriotherium*, and it is probably larger than *Agriotherium africanum* from Langebaanweg. Mustelids are diverse in the Adu-Asa Formation, with at least four species in four genera. This family includes the earliest record of *Plesiogulo* (*P. botori*), a genus previously known only from slightly younger deposits at Langebaanweg [9]. It is now known also

from contemporaneous or slightly older deposits at Lemudong'o in Kenya [7,11]. *Torolutra ougandensis* was present in both the Asa Koma and Kuseralee members. The genus *Sivaonyx* is recognized by at least one, and possibly two species [3, this paper]. Viverrids are represented by two species in two genera (*Genetta* and *Viverra*). The Herpestid sample includes the earliest record of *Herpestes*, represented by a new species, *Herpestes* sp. nov. and *Helogale* sp. These species were previously known only from Pliocene deposits of eastern Africa. The family Canidae is represented by one species of *Eucyon*, possibly a second species in the latest Miocene of eastern Africa or conspecific with *Eucyon intrepidus* from the Lukeino Formation of Kenya [19].
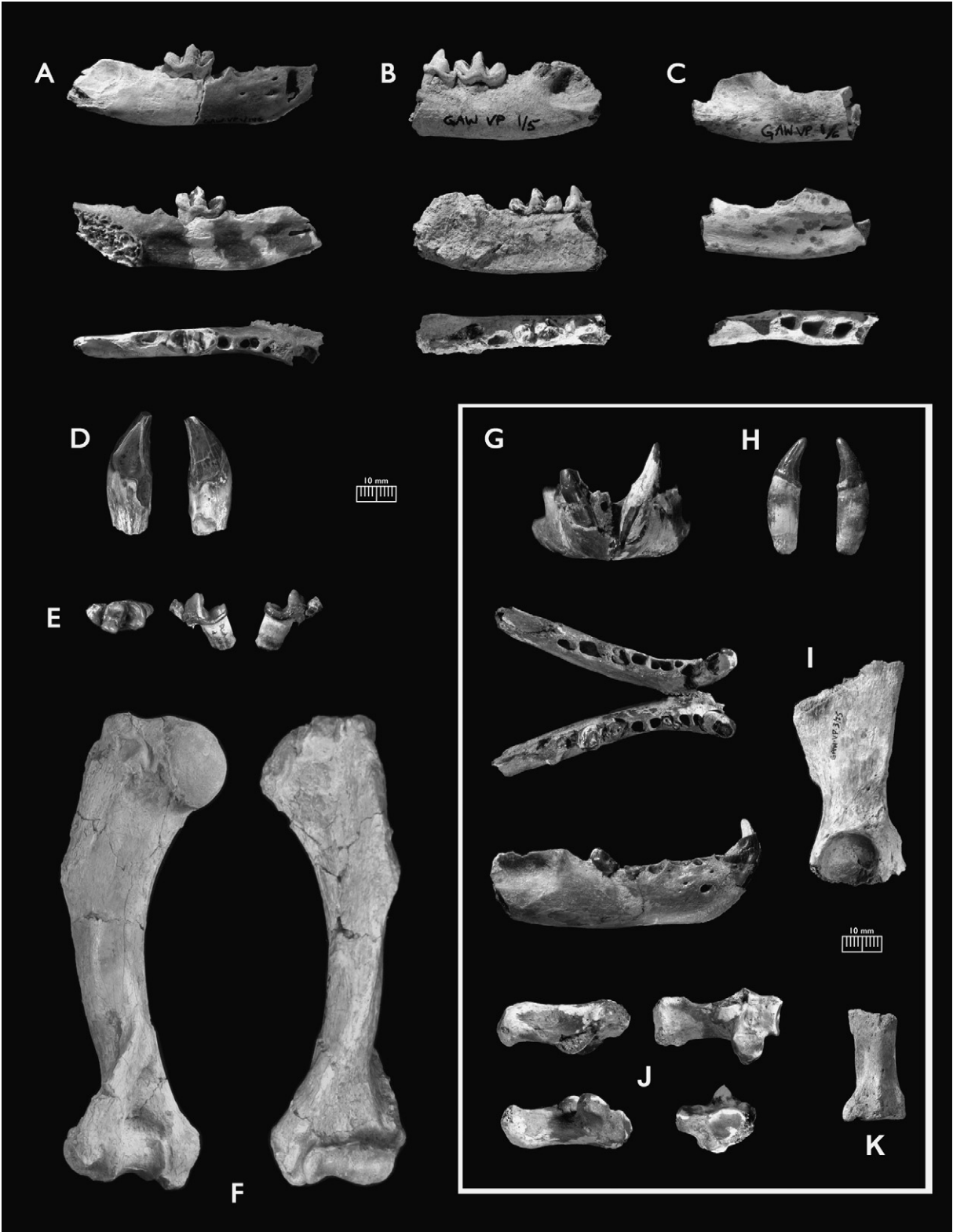
2. Systematics

2.1. Genus Torolutra Petter, Pickford, and Howell 1991

Type species. *Torolutra ougandensis* Petter, Pickford, and Howell 1991.

See [21] for description of the genus and species.

Torolutra ougandensis (Fig. 3).

Referred material. ALA-VP-2/106, left M_1; ALA-VP-2/214, C^1; STD-VP-1/2, left humerus; GAW-VP-1/3, maxillary fragments with left P^3 and right M^1; GAW-VP-1/5, left mandible (P_4-M_1); GAW-VP-1/6, right edentulous mandible; GAW-VP-1/165, left maxillary fragment; GAW-VP-1/173, right C_1; GAW-VP-1/177, right C_1; GAW-VP-3/25, a complete mandible with left and right canines and a distal right M_1, right C^1, pelvic fragment, caudal vertebra, left calcaneum, and proximal MTP fragment; GAW-VP-1/146, right mandible (M_1); WKH-VP-1/32, left edentulous mandible. All dental and mandibular measurements are given in Table 1.

Localities and horizons. Alayla Vertebrate Locality 2 (ALA-VP-2) and Saitune Dora Vertebrate Locality 1 (STD-VP-1) are located along the western margin of the Middle Awash in the Asa Koma Member of the Adu-Asa Formation (5.54–5.77 Ma). Gawto Vertebrate Locality 1 and 3 (GAW-VP-1 and –3) are in the lower part of the Haradaso Member of the Sagantole Formation (4.82–5.18 Ma).

2.1.1. Description

Haile-Selassie and Howell [3] assigned ALA-VP-2/106, ALA-VP-2/214, and STD-VP-1/2 to Lutrinae gen et sp indet. Full descriptions are also presented there and will not be repeated here. However, detailed comparison subsequent to the completion of Haile-Selassie and Howell [3] has revealed that these specimens belong to an early species of *Torolutra*. ALA-VP-2/106 and ALA-VP-2/214 possibly belong to the same individual

largely due to the proximity of their discovery and similar coloration. ALA-VP-2/106 is metrically and morphologically similar to M_1s of specimens assigned here to *Torolutra ougandensis* and also to M_1s of the species from Nkondo [21] and Lukeino [19]. Morphology of the humerus (STD-VP-1/2) shows aquatic adaptation and its size is similar to younger specimens assigned to the species and also to extant large size lutrines.

GAW-VP-1/5 is a left mandible anteriorly broken at the P_4 root level. The ascending ramus is missing. It is morphologically similar to all the mandibles assigned here to cf. *Torolutra ougandensis*. The teeth are preserved from P_4-M_1. The P_4 is double-rooted with a tall main cusp. There is an accessory cusp distal to, and attached to, the main cusp. The accessory cusp is half as long as the main cusp. Its overall dental morphology and metrics are very similar to the Siwaliks lutrine, *Vishnuonyx chinjiensis* [22]. The distal tubercle is low but well-developed. The P_4 has a strong buccal cingulum and a weaker lingual cingulum. The M_1 is complete. The paraconid is the largest cusp, followed by the paraconid, whereas the metaconid is the smallest. The paraconid is apically worn. The paraconid and protoconid are separated by a deep, slit-like notch, and a buccal wear facet is present on both cusps. At its base, the M_1 is surrounded by a cingulum. Talonid cusps are not distinguishable. The flat and relatively low talonid slopes lingually. The M_1 is morphologically identical with specimens such as GAW-VP-1/146 and GAW-VP-3/25. The cusp proportions of these specimens are also similar.

GAW-VP-1/6 is the posterior half of a right edentulous mandible, morphologically similar to the other mandibular specimens described here but slightly shallower. This specimen appears to belong to a young individual.

GAW-VP-3/25 is a complete mandible with left and right canines and a distal right M_1. The symphysis is extremely receding and hence, distally elongate. Preserved root sockets indicate the presence of P_2 and M_2. The M_2 is single-rooted and sloping. The left C_1 is

Fig. 3. Middle Awash specimens assigned to *Torolutra ougandensis*. Lateral, medial, and occlusal views (top to bottom) of A. GAW-VP-1/146, right mandible (M_1). B. GAW-VP-1/5, left mandible (P_4-M_1). C. GAW-VP-1/6, right edentulous mandible. D. Medial and lateral views of ALA-VP-2/214, C^1. E. Occlusal, buccal, and lingual views of ALA-VP-2/106, left M_1. F. Posterior and anterior views of STD-VP-1/2, left humerus. G. Mandible of GAW-VP-3/25, (top to bottom) symphysial, occlusal, and lateral views. H. C^1 of GAW-VP-3/25, labial and lingual views. I. Innominate fragment of GAW-VP-3/25. J. Left calcaneous of GAW-VP-3/25, (clockwise) lateral, dorsal, anterior, and medial views. K. Caudal vertebra of GAW-VP-3/25.

Fig. 3. Spécimens de l'Aouache moyen attribués à *Torolutra ougandensis*. Vues latérale, médiale et occlusale (de haut en bas) de A. GAW-VP-1/146, mandibule droite (M_1). B. GAW-VP-1/5, mandibule gauche (P_4-M_1). C. GAW-VP-1/6, mandibule droite édentée. D. Vues médiale et latérale de ALA-VP-2/214, C^1. E. Vues occlusale, buccale et linguale de ALA-VP-2/106, M_1 gauche. F. Vues postérieure et antérieure de STD-VP-1/2, humérus gauche. G. Mandibule de GAW-VP-3/25, (de haut en bas) vues symphysaire, occlusale et latérale. H. C^1 de GAW-VP-3/25, vues labiale et linguale. I. Fragment non désigné de GAW-VP-3/25.]. calcanéum gauche de GAW-VP-3/25, (sens horaire) vues latérale, dorsale, antérieure et médiale. K. Vertèbre caudale de GAW-VP-3/25.

Table 1

Dental and mandibular measurements of Middle Awash specimens assigned to *Torolutra ougandensis*. All measurements are in millimetres. Values in parentheses are estimates from preserved parts and/or alveolar measures. * indicates that the measure is a vertical crown height on the distal face. (R) = right. (L) = left.

Tableau 1

Mensurations dentaires et mandibulaires des spécimens de l'Aouache moyen attribués à *Torolutra ougandensis*. Toutes les mesures sont en millimètres. Les valeurs entre parenthèses sont des estimations à partir des parties préservées et/ou des mesures alvéolaires. * indique que la mesure est une hauteur verticale de la couronne sur la face distale. (R) = droit. (L) = gauche.

Specimen number	Element	Mesiodistal length (MD)	Buccolingual breadth (BL)	Crown Height (CH)	M_1 Trigonid length	M_1 Talonid length	Mandibular depth at M_1
GAW-VP-1/1	Mandible (M_1)	13.5	7.2	–	8.2	5.3	15.8
GAW-VP-1/3	LP^3	–	–	–	–	–	–
	RM^1	7.0	10.0	–	–	–	–
GAW-VP-1/5	Mandibular depth	–	–	–	–	–	14.4
	P_4	8.7	5.1	6.8	–	–	–
	M_1	13.4	6.9	–	8.2	5.2	–
GAW-VP-1/146	Mandible (M_1)	13.0	6.7	–	7.9	5.1	13.6
GAW-VP-1/173	Right C_1	7.3	6.5	–	–	–	-
GAW-VP-3/25	Mandibular depth	–	–	–	–	–	15.4 (R), 14.8 (L)
	Left C_1	8.7	6.6	(12.7)*	–	–	–
	Right C_1	8.8	6.5	–	–	–	–
	Right M_1	(15.3)	(7.5)	–	–	5.7	–
	Right C^1	7.6	6.1	12.3	–	–	–

unworn and the apical half of the right C_1 is missing. The mandible is very shallow, with multiple mental foramina. The talonid of the M_1 slopes lingually. A strong cingulum is present on the buccal faces of the protoconid continuing to the talonid. The canine crown is highly convex anteriorly and its base is circled by cingulum except above the labial CEJ. Judging from the sockets, the incisors were small, two on each side. The ascending rami are missing. It has a very deep masseteric fossa extending medially as far as the distal M_2. The left C^1 is an unworn crown with a complete and inflated root. It has incipient vertical wear on its mesial crest. The crown is anteriorly less convex compared to the lower canines. The cingulum is manifested in the same way as in the lowers. Associated postcranial elements include a pelvic fragment, a caudal vertebra, a left calcaneum, and a proximal MTP fragment.

GAW-VP-1/146 is a right mandible with M_1. The root socket for the P_2 is entirely obliterated and the ascending ramus is missing. It has a strongly sloping symphysis. It is morphologically identical with GAW-VP-1/5 and GAW-VP-3/25. WKH-VP-1/32 is a left edentulous mandible with the distal root of the M_1 and M_2 preserved. The preserved morphology of the mandible is similar to the other mandibles referred to *Torolutra*. GAW-VP-1/173 is a complete right C_1 and GAW-VP-1/177 is a right C_1 with a complete root, but missing the apical half of the crown. GAW-VP-1/173 is stouter and lower crowned compared to the other lower canines described above. It also has a strong distal cingulum. However, its morphology is similar in having a distally curved crown relative to the root.

GAW-VP-1/3 comprises maxillary fragments with associated left P^3 and a right M^1 fragment. The P^3 is mesially narrower and distally wider. The main cusp is tall relative to the length of the crown. It is two-rooted and the main cusp is anteriorly slightly convex. The M^1 mesiolingual portion is broken. A strong shelf-like cingulum is present on the buccal side of the paracone and metacone, larger at the former. The crown also has a deep, centrally positioned median valley. The paracone and metacone are of equal height and separated by a V-shaped valley. GAW-VP-1/165 is a left maxillary fragment with the root sockets of the canine and P^2. Its size and morphology best fit with the specimens described above.

2.1.2. Discussion

Haile-Selassie and Howell [3] tentatively assigned specimens ALA-VP-2/106, ALA-VP-2/214, and STD-VP-1/2 to Lutrinae gen. et sp. indet. However, further comparative analysis shows that these specimens belong

to *Torolutra ougandensis*. This species was named by Petter et al. [21] to refer to lutrine specimens from the Nkondo and Nyaburogo Formations of Uganda. More specimens were referred to this species from Plio-Pleistocene sites such as Koobi Fora [30]. The earliest record of this species in Africa possibly comes from 6-7 Ma deposits in Chad. Peigné et al. [20] assigned TM 266-01-194, a mandible with a carnassial, from Toros Menalla of Chad to aff. *Torolutra* sp. The carnassial and mandibular morphology of this specimen is similar to the specimens from the Middle Awash and Lukeino referred to *Torolutra ougandensis*. This might be an indication that the Toros Menalla specimen belongs to the same species. However, the M_1 length (16.0 mm) is slightly larger in the Toros Menalla specimen compared to other *Torolutra* M_1s from eastern Africa. This species appears to have been widespread in central and eastern Africa during the Late Miocene and Early Pliocene. It persisted to the Early Pleistocene deposits of eastern Africa [30]. Although the origin of this species is currently unknown, it probably descended from a Eurasian species similar to *Paralutra* or *Paludolutra*, or from a species similar to the Siwaliks *Vishnuonyx chinjiensis*, particularly based on the P_4 morphology and dimensions. Moreover, the holotype of *Vishnuonyx angololensis* matches, metrically and morphologically, a *Torolutra ougandensis* P^4 from Lukeino [19]. However, it should be noted that Late Miocene Eurasian and African lutrines showed a mosaic of dental features shared among different species of the subfamily [28].

2.2. Genus Sivaonyx Pilgrim, 1931

Type species. *Lutra bathygnatha* Lydekker, 1884.

Other species. *S. lluecai* (Crusafont and Golpe, 1962, *S. africanus* Stromer, 1931, *S. campanii* (Meneghini, 1863), *S. soriae* Morales and Pickford, 2005a, *S. senutae* Morales and Pickford, 2005a, *S. ekecaman* (Werdelin, 2003b), *S. kamuhangirei* Morales and Pickford, 2005a, *S. hendeyi* (Morales, Pickford, and Soria, 2005), *S. beyi* Peigné, Bonis, Likius, Mackaye, Vignaud, Brunet, 2008.

Sivaonyx sp. cf. S. ekecaman.

Referred material. AMW-VP-1/61, lingual two-third of left M^1; GAW-VP-1/58, right M_1; GAW-VP-1/162, right M^1 fragment (Fig. 5).

Localities and horizons. Amba West Vertebrate Locality 1 (AMW-VP-1) is in the Kuseralee Member of the Sagantole Formation and dated to 5.2–5.5 Ma. Gawto Vertebrate Locality 1 (GAW-VP-1) is in the Haradaso Member of the Sagantole Formation and dated

to 4.85–5.2 Ma. These localities are in the Middle Awash study area, Afar Rift, Ethiopia.

2.2.1. Description

AMW-VP-1/61 is the lingual two-thirds of a left M^1 and it is bunodont. The parastyle, paracone and metacone are missing. The paraconule is as large as the protocone and they are almost fused, separated only by a shallow groove. The metaconule is small and positioned close to the metacone position. The area between the preserved cusps and cuspules is a wide, flat basin. The lingual cingulum is strong mesial to the protocone and continues distally, rising to merge with the hypocone. The lingual length at the protocone is 14.1 mm.

GAW-VP-1/58 is a complete bunodont right M_1 crown lacking the roots. The trigonid cusps are separated from each other by V-shaped valleys. The paraconid is the largest cusp, followed in size by the protoconid and metaconid, respectively. The paraconid and protoconid are of equal height and the metaconid is slightly shorter. The protoconid is apically worn and dentine is exposed on its apex. The talonid is wide and the hypoconid and entoconid are well-developed. The accessory cusplet distal to the protoconid is larger than the cusplet behind the entoconid. Additional small cusplets are present on the distal occlusal rim of the talonid. The latter is lingually expanded, particularly at the entoconid level. It has a strong basal cingulum on the buccal side and a weaker one on the lingual side. The talonid basin is positioned low relative to the trigonid, and is deep at its center. Crown morphology is typical of Enhydrini. The crown is 20.4 long and 12.5 wide. The trigonid and talonid lengths are 11.6 and 8.7, respectively.

GAW-VP-1/162 is a left P^4 fragment. Most of the lingual, mesial, and mesiobuccal parts of the crown are missing. The paracone is extremely worn, with a large dentine exposure on its cusp apex. This dentine exposure extends distally to the apex of the metastyle. The crista obliqua of the protocone is preserved and connects to the lingual crest of the paracone to form the distal wall of the anterior valley. The entire metastyle and most of the hypocone are preserved. The hypocone is relatively large. A strong distal cingulum is present and continues lingually around the hypocone and buccally around the metastyle. Although much of its morphology remains absent due to its fragmentary nature, this specimen best matches BAR 566'05 from Lukeino [17].

2.2.2. Sivaonyx sp. cf. S. soriae

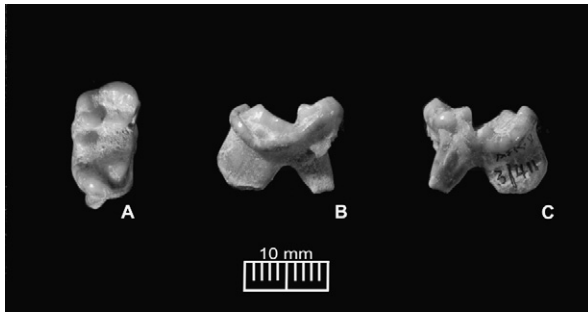Specimen ASK-VP-3/62 is a left P^4 fragment from Asa Koma Vertebrate Locality 3 (ASK-VP-3) located

Fig. 4. A. Occlusal. B. Mesial. C. Distal views of ASK-VP-3/411, right M^1, Middle Awash late Miocene specimen from the Asa Koma Member assigned to Lutrinae gen. et sp. indet. aff. *Torolutra* sp.
Fig. 4. Vues A. Occlusale. B. Mésiale. C. Distale de ASK-VP-3/411, M^1 droite du Miocène supérieur de l'Aouache moyen du membre Asa Koma, attribuée à un Lutrinae gen. et sp. indet. aff. *Torolutra* sp.

in the Asa Koma Member of the Adu-Asa Formation, dated to 5.54-5.77 Ma. ASK-VP-3/62 (Fig. 5) is fragmentary and most of the diagnostic occlusal morphology is not preserved. Although Haile-Selassie and Howell [3] assigned ASK-VP-3/62 to *Sivaonyx* cf. *africanus*, they indicated that it is similar in its preserved parts to speci-

men BAR 1720'00 from the Lukeino Formation assigned to *S. senutae* [17]. The size of ASK-VP-3/62 is large for the latter species and appears to best fit within the size of *Sivaonyx soriae* [17], the larger *Sivaonyx* species from Lukeino, although its P^4 is unknown. Given that size is the only difference described by Morales and Pickford [17] between *S. soriae* and *S. senutae*, and considering the contemporaneity of ASK-VP-3/62 with *Sivaonyx soriae*, it is more plausible to tentatively assign this specimen to *Sivaonyx* sp. cf. *S. soriae*. Discovery of more complete specimens from the Asa Koma Member will refine this tentative identification.

2.2.3. Discussion

Sivaonyx species have always been difficult to distinguish from *Enhydriodon* species in the Late Miocene of Eurasia and Africa [19]. In some cases, upper and lower dentitions of the same taxa were assigned to different species (details discussed in [19]). While the distinction between *Sivaonyx* and *Enhydriodon* species from the Late Miocene/Early Pliocene remains elusive, new discoveries in Africa have increased the sample size
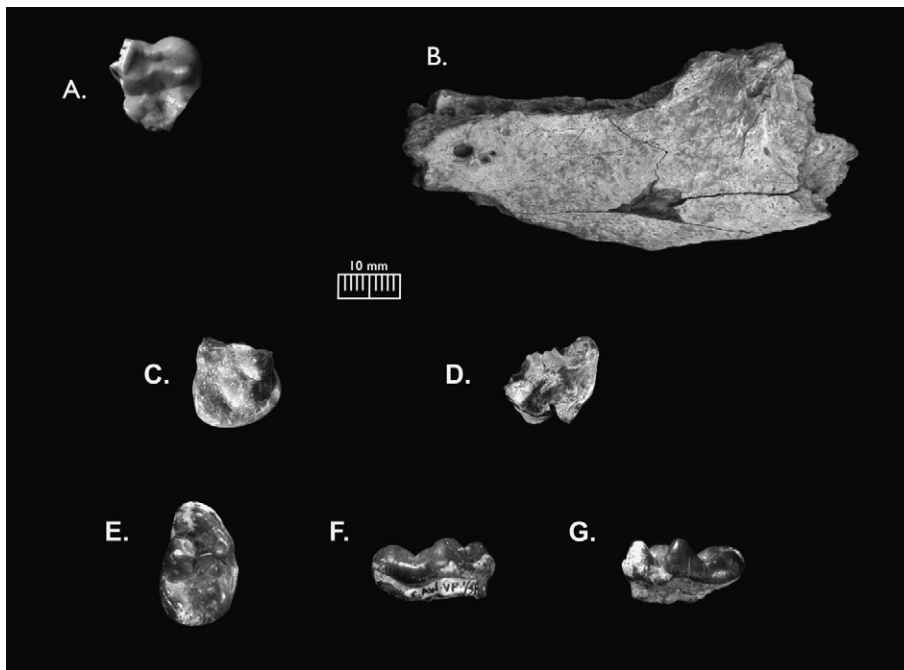

Fig. 5. A. Occlusal view of ASK-VP-3/62, left P^4, *Sivaonyx* sp. cf. *S. soriae* from the Asa Koma Member. B. Lateral view of STD-VP-2/4, left edentulous mandible, Lutrinae gen. et sp. indet. from the Asa Koma Member. C. Occlusal view of AMW-VP-1/61, left M^1, *Sivaonyx* cf. *ekecaman* from the Kuseralee Member; D. Occlusal view of GAW-VP-1/162, left P^4, *Sivaonyx* cf. *ekecaman* from the Haradaso Member. E-F. Occlusal, lingual, and buccal views of GAW-VP-1/58, right M$_1$, *Sivaonyx* cf. *ekecaman* from the Haradaso Member.
Fig. 5. A. Vue occlusale de ASK-VP-3/62, P^4 gauche, *Sivaonyx* sp. cf. *S. soriae* du membre Asa Koma. B. Vue latérale de STD-VP-2/4, mandibule gauche édentée, Lutrinae gen. et sp. indet. du membre Asa Koma. C. Vue occlusale de AMW-VP-1/61, M^1 gauche, *Sivaonyx* cf. *ekecaman* du membre Kuseralee. D. Vue occlusale de GAW-VP-1/162, P^4 gauche, *Sivaonyx* cf. *ekecaman* du membre Haradaso. E-F. Vues occlusales, linguale et buccale of GAW-VP-1/58, M$_1$ droite, *Sivaonyx* cf. *ekecaman* du membre Haradaso.
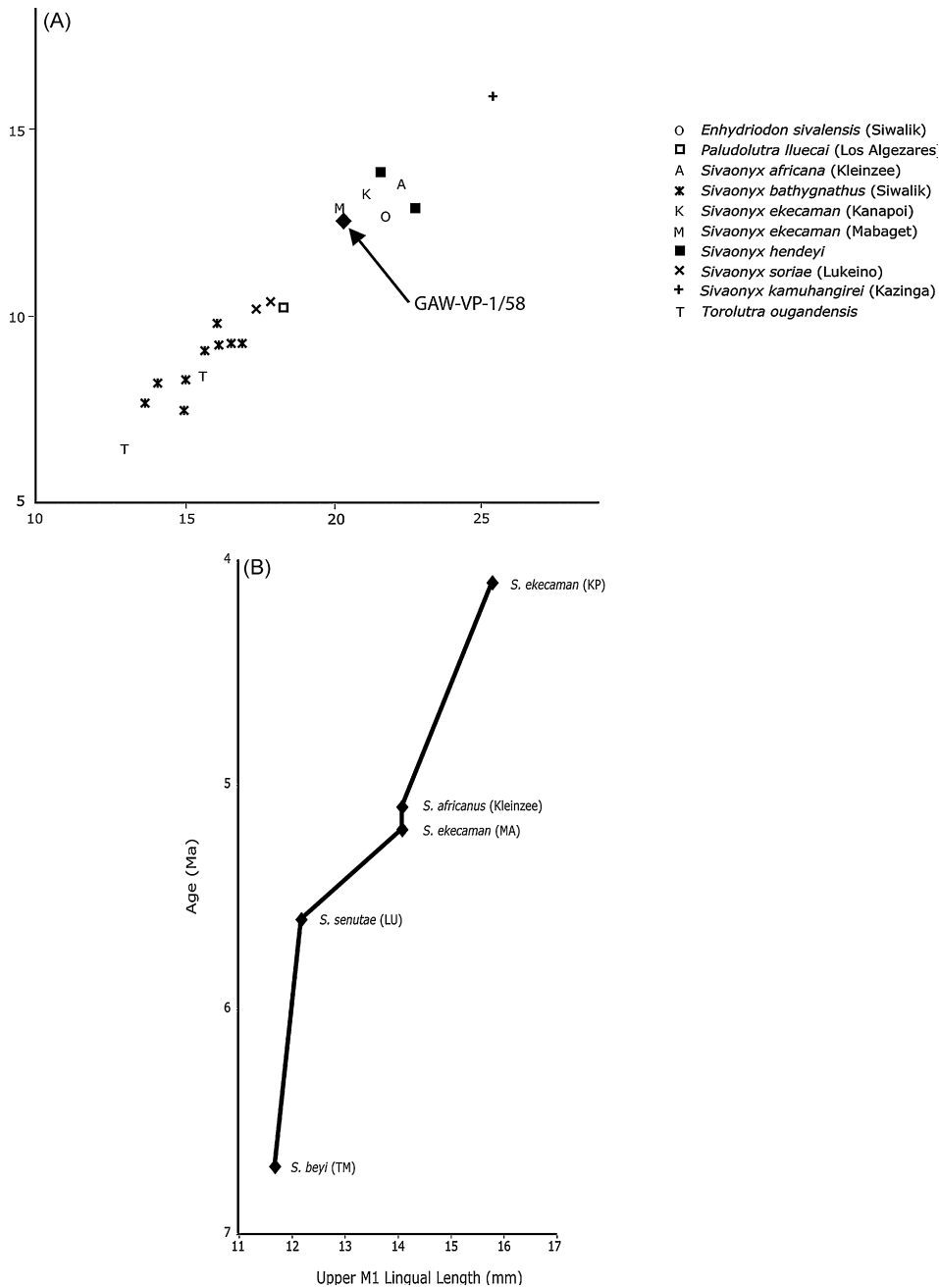
Fig. 6. A. M₁ length/breadth plot showing the placement of GAW-VP-1/58 relative to other lutrine species. Modified after [17]. B. A graph showing an increase in the size of the lingual mesiodistal dimension of the M¹ of *Sivaonyx* species through time.
Fig. 6. A. Diagramme longueur/largeur de M₁ montrant la position de GAW-VP-1/58 par rapport aux autres espèces de lutrinés. Modifié d'après [17]. B. Graphique montrant une augmentation de la longueur mésiodistale linguale de la M¹ des espèces de *Sivaonyx* à travers le temps.

of Enhydrini. These new fossil discoveries resulted in the naming of *Sivaonyx beyi*, a new species from Toros Menalla (Chad) [20], as well as the taxa *Sivaonyx soriae*, *S. senutae*, *S. kamuhangirei*, *S. ekecaman*, and discovery of more *S. africanus* material, all from Plio-Miocene sites in eastern and South Africa [3,17,18,29]. The

Langebaanweg material initially identified as *Enhydriodon africanus* [9] was renamed *Sivaonyx hendeyi* sp. nov. [19]. The new *Sivaonyx* species from Chad, *S. beyi* Peigné et al., 2008, appears to be different from the Lukeino and Middle Awash *Sivaonyx* both in terms of its size and morphology of the upper and lower first molars.

GAW-VP-1/58 from the Middle Awash is morphologically similar to the M_1s of KNM LU 337 and BAR 1984'05 from the Kapcheberek Member of Lukeino Formation. The former specimen was initially assigned to *S. africana* [19] but later reassigned as the holotype of *S. soriae* [17]. AMW-VP-1/61 (M^1) is slightly larger in its size and close to *Sivaonyx ekecaman* from Mabaget (Fig. 6A). It also appears to be larger than BAR 1082'01, a specimen from Lukeino initially assigned to *S. africana* [19] but later reassigned to *S. senutae* [17] (Fig. 6B). However, morphology of the lingual cusps and the talon of AMW-VP-1/61 and BAR 1082'01 is very similar.

The difference between *S. soriae* and *S. senutae* is merely size, with the former being larger [17]. However, their dental morphological similarities or differences have not been documented due to lack of molars from the homologous position. *Sivaonyx beyi* has a M^1 morphologically different from the Lukeino, Middle Awash, and other African *Sivaonyx* M^1 specimens. AMW-VP-1/61 has a lingual length (14.1 mm) larger than both TM 90-00-066 (11.7 mm) [20] and BAR 1082'01 (12.2 mm) [19]. However, it is smaller than the M^1 of *S. ekecaman* from Kanapoi (15.8 mm), which is much younger [29]. One of the evolutionary trends hypothesized for *Sivaonyx* species is an increase in body size [17,18,22] and the lingual breadth of the M^1 tends to support this observation (Fig. 6B). However, the fact that M^1s of *S. beyi* are larger than all other *Sivaonyx* species falsifies this hypothesis. Alternatively, if there was indeed an increase in body size through time, available evidence then challenges the geological age of *S. beyi*. On a more general observation, given the temporal distribution and morphological overlap seen in the currently named Late Miocene/Early Pliocene African *Sivaonyx* species, it appears that they are taxonomically oversplit. Hence, a thorough investigation with increased hypodigm is now required.

2.3. Genus Vishnuonyx Pilgrim, 1932

Type species. *Vishnuonyx chinjiensis* Pilgrim, 1932.
Other species. *Vishnuonyx angololensis* Werdelin, 2003a.
Vishnuonyx sp.
Referred material. GAW-VP-1/1, left mandible (M_1) (Fig. 7).
Locality and horizon. See above.

2.3.1. Description

GAW-VP-1/1 is a left mandible with M_1. It is anteriorly broken at the level of the M_1 mesial root. Posteriorly, a small portion of the root of the ascending ramus is preserved. The masseteric fossa is deep and anteriorly extends to the level of the M_2. The mandible is relatively deep, measuring 15.8 mm at mid-M_1 level. The M_1 is relatively unworn and very strong shearing carnassial. The length and breadth of the M_1 are 13.5 and 7.2 mm, respectively, with a trigonid length of 8.2 mm and talonid length of 5.3 mm. The protoconid is the tallest cusp, followed by the metaconid, although most of the trigonid
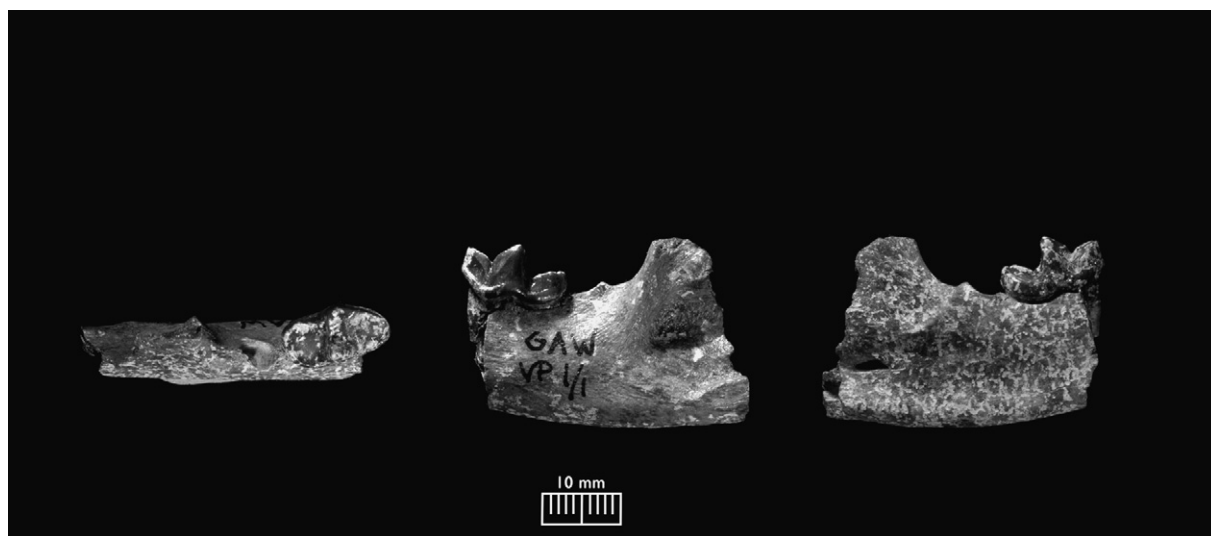

Fig. 7. Occlusal, buccal, and lingual views of GAW-VP-1/1, left mandible with M_1, Middle Awash specimen from the Haradaso Member assigned to *Vishnuonyx* sp.

Fig. 7. Vues occlusale, buccale et linguale de GAW-VP-1/1, mandibule gauche avec M_1, spécimen de l'Aouache moyen du membre Haradaso attribué à *Vishnuonyx* sp.

surface area is occupied by the paraconid. The talonid is set very low and horizontally flat with its buccal occlusal rim slightly higher than its lingual occlusal rim. The talonid is lower than the trigonid, the paraconid and the protoconid are separated by a deep incision. The buccal cingulum is stronger than the lingual cingulum. The root socket preserved behind the M_1 indicates that the M_2 was single-rooted. The mandibular foramen is positioned much farther below the tooth row and is anteroposteriorly long. The insertion for the digastric muscle is broad anteriorly.

2.3.2. Discussion

The earliest *Vishnuonyx* in Africa, which is also contemporaneous with the Siwalik type species of the genus, was documented from the Ngorora Formation of Kenya from deposits dated to ca. 12 Ma [18]. A second species was identified from the latest Miocene Lower Nawata Member of Lothagam, Kenya [28]. These two taxa were recognized based on a single tooth from each species. GAW-VP-1/1 is the most complete mandible of *Vishnuonyx* found in Africa thus far. Its similarity with the Siwaliks *Vishnuonyx chinjiensis*, particularly in the morphology and metrics of the M_1, is striking. The presence of a well-developed shearing surface on the buccal side of the carnassial cusps are characters shared between GAW-VP-1/1 and *Vishnuonyx chinjiensis* Stromer, 1932 as seen in specimen NHM G 4 described from the Siwalik of Pakistan [22]. However, GAW-VP-1/1 is larger than NHM G 4 and further differs from this specimen by having a deeper masseteric fossa and deeper mandible. The relationship between the *Vishnuonyx* from the Middle Awash and Lothagam (*V. angololensis* Werdelin, 2003a) is currently unknown because there is no mandible and/or M_1 known for the latter, or a P^4 known from the Middle Awash. However, Morales et al. [19] indicated that BAR 270'03, a left P^4 that they assigned to *Torolutra ougandensis*, is close in size and morphology to the holotype of *Vishnuonyx angololensis*. This raises two issues: the holotype of *V. angololensis* is either a misidentified *T. ougandensis* specimen, or the genera *Vishnuonyx* and *Torolutra* have dental morphological similarities. However, the Middle Awash *Vishnuonyx* and *Torolutra* specimens appear to have significant differences in their M_1 morphology. Given the similarities in the mandibular and M_1 morphology of *V. chinjiensis* and *Vishnuonyx* sp. from the Middle Awash, it appears parsimonious to infer that the African *Vishnuonyx* are closely related to the Asian *V. chinjiensis* indicating biogeographic relationships between Africa and Eurasia during the Late Miocene. The lack of similar elements to compare GAW-VP-1/1 with the Lothagam *V. angololensis* renders it

difficult to assign the Middle Awash specimen to the latter species. However, the temporal and spatial proximity of the two areas would suggest that they may be conspecific.

2.4. Lutrinae gen et sp. indet aff. Torolutra sp.

Referred material. ASK-VP-3/411, right M^1 (Fig. 4).
Localities and horizons. Asa Koma Vertebrate Locality 3 (ASK-VP-3) is situated in the Asa Koma Member of the Adu-Asa Formation of the Middle Awash study area of Ethiopia, dated to between 5.54 Ma and 5.77 Ma.

2.4.1. Description

ASK-VP-3/411 is a complete right M^1 crown with most of the lingual and mesiobuccal roots, but lacks the distobuccal root. The lingual root is compressed mesiodistally and long buccolingually. The crown is unworn and low. The parastyle is very large. It has a well-developed metastyle buccal to the metacone. The paracone is slightly smaller than the metacone, a bulbous cusp. Immediately lingual to the metacone is a well-developed, rounded metaconule slightly smaller than the metacone. There is no sign of a paraconule and a wide basin separates the paracone and protocone. The rounded protocone is separated from the mesiodistally elongate hypocone by a narrow groove. The mesial cingulum is well-developed particularly at the mesiolingual corner where it ascends to merge with the hypocone.

2.4.2. Discussion

ALA-VP-3/411 (Fig. 4) is morphologically different from, and smaller than, M^1s of most *Sivaonyx* species. It differs from BAR 1082'01, a specimen from Lukeino assigned to *S. africana* [19], later re-assigned to *S. senutae* [17], in the lack of a paraconule, presence of a metastyle, and overall size. It belongs to a lutrine the size of *Aonyx* or modern *Lutra lutra*. This molar is buccolingually long and mesiodistally compressed compared to *Sivaonyx*, *Aonyx*, and *Procyon*. Its proportions are more like *Lutra* in being buccolingually elongate. Most M^1s of *Lutra* species also lack the paraconule and have large parastyles. Unfortunately, upper first molars are unknown for *Torolutra ougandensis* from the Late Miocene or Early Pliocene, and this makes it difficult to assign ASK-VP-3/411 to the species with confidence. The assignment of ASK-VP-3/411 to aff. *Torolutra* sp. is largely based on the presence of this genus in the Asa Koma Member and the fact that it is much smaller than all *Sivaonyx* species known from the Middle Awash. On the other hand, it could also represent the earliest *Lutra* from eastern Africa because the buccolingual elongation

and lack of the paraconule appear to be characters seen in extant *Lutra* species. Further discoveries might refine the taxonomic affinity of this specimen.

2.5. *Lutrinae gen. et sp. indet.*

STD-VP-2/4 (Fig. 5) is a left edentulous mandible from Saitune Dora Vertebrate Locality 2 (STD-VP-2) located in the Asa Koma Member of the Adu-Asa Formation (5.54–5.77 Ma) of the Middle Awash study area. This specimen was assigned to *Sivaonyx* cf. *africanus* by Haile-Selassie and Howell [3]. It was described as a mandible that has all the mandibular characters referable to Lutrinae of a relatively large size, such as *Sivaonyx africanus*. The second molar is single-rooted. The masseteric fossa is deep. Multiple mental foramina are situated below the level of P_3–P_4 [3]. STD-VP-2/4 is morphologically similar to SAM PQL 5000, the type mandible of *Sivaonyx hendeyi*, from Langebaanweg, South Africa [19]. STD-VP-2/4 is more likely to belong to one of the lutrine species dentally identified from the Asa Koma and/or Kuseralee Members. This is warranted by its general lutrine-like mandibular morphology and a single root socket for the M_2. However, due to its morphological overlap with multiple lutrine species, it is more parsimonious to assign it to Lutrinae gen. et sp. indet.

3. Conclusion

The family Mustelidae represents the largest and highly diverse monophyletic group among extant carnivores [33]. Their Mio-Pliocene and Pleistocene fossil record also shows that they were widespread in Africa and Eurasia. The oldest fossil record of the family goes as far back as 24 Ma from France [25]. However, the earliest Lutrinae appears only in the late Middle Miocene of Europe during MN7-8 (13.5-11.1 Ma) [2,25,26]. The tribe Enhydrini appears for the first time in the Late Miocene of Spain from MN12 level dated to 8.0-6.6 Ma [26].

Latest Miocene and Early Pliocene African mustelids are known from a number of sites in the North, central, and eastern Africa. There are at least seven mustelid genera (*Djourabus*, *Sivaonyx*, *Aonyx*, *Plesiogulo*, *Torolutra*, *Mellivora*, and *Enhydriodon*) known from the latest Miocene and Early Pliocene sites of Chad, Kenya, Ethiopia, Uganda, and South Africa [3,9,19-21]. The genus *Djourabus* is currently known only from Toros Menalla, Chad (6-7 Ma), although *Plesiogulo*, *Enhydriodon*, and *Mellivora* have not been documented from this site. *Plesiogulo* was abundant in Asia [16] and North America [8] and is known in Africa from Late Miocene

deposits of Lukeino and Lemudong'o (Kenya) and Middle Awash (Ethiopia), and Early Pliocene deposits at Langebaanweg, South Africa. The genus *Sivaonyx* was widespread in the Latest Miocene deposits of Africa with at least seven putative species named thus far – *S. beyi* from Toros Menalla, *S. soriae*, *S. senutae*, *S. africanus*, *S. ekecaman*, *S. kamuhangirei*, and *S. hendeyi* from the Plio-Miocene deposits of eastern and South Africa. *Torolutra* appears to be ubiquitous in all the sites mentioned above and continues into the Early Pleistocene at Koobi Fora, Kenya [30]. The Middle Awash Early Pliocene also possibly samples the last appearance of *Vishnuonyx* at 4.85 Ma. Its presence in the Middle Awash and older Lothagam deposits may indicate biogeographic ties with Southwest Asia towards the end of the Miocene. The earliest *Enhydriodon* in Africa is currently documented from the Early Pliocene deposits at Langebaanweg [9,19] and later appears at Nkondo (Uganda), Kazinga, Mabaget, and Omo (Ethiopia), and other Pliocene sites [19,30].

Although the Late Miocene and Early Pliocene eastern African mustelid carnivores are poorly known, recent discoveries from Lothagam and Lukeino (Kenya) and the Middle Awash (Ethiopia) have enormously improved our knowledge of this mammalian group by increasing the sample size and adding numerous new taxa to the hypodigm. The Middle Awash Late Miocene carnivore community shares a number of taxa with other contemporary and slightly older and younger sites of eastern Africa such as Lothagam and Lukeino in Kenya. However, it also seems to overlap at the genus level with the carnivores from Toros Menalla (Chad) and Sahabi (Libya) [10], sites otherwise known to have more affinity with northern African and southern European Late Miocene faunas. Continued work will improve the sample sizes and refine our knowledge of the origin of the modern African carnivore community.

Acknowledgments

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