Late Miocene Carnivora from Chad: Lutrinae (Mustelidae)

STÉPHANE PEIGNÉ[1,2]*, LOUIS DE BONIS[1], ANDOSSA LIKIUS[3], HASSANE TAÏSSO MACKAYE[3], PATRICK VIGNAUD[1] and MICHEL BRUNET[1]

[1]*Université de Poitiers, UFR SFA, UMR 6046 'Géobiologie, Biochronologie et Paléontologie humaine', 40 Avenue du recteur Pineau, F-86022 Poitiers cedex, France*
[2]*Muséum national d'Histoire naturelle, Département Histoire de la Terre, USM 0203/UMR 5143 'Paléobiodiversité et Paléoenvironnements', 8 rue Buffon CP 38, F-75231 Paris cedex 05*
[3]*Université de N'Djamena, BP 1117, N'Djamena, Chad*

We describe extensive Late Miocene fossil Lutrinae from Toros-Menalla, Chad. A minimum of four species are present in this fossiliferous area. Such a large number of species, diverse in size and dental morphology, is significant and unique in the fossil record of the subfamily Lutrinae in the Neogene of Africa. Two new taxa are described, ***Sivaonyx beyi* sp. nov.** and ***Djourabus dabba* gen. nov. sp. nov.**; the two other species, which are represented by more fragmentary remains, are assigned to Lutrinae indet. aff. *Torolutra* sp. and Lutrinae indet. aff. *Aonyx* sp. *Sivaonyx beyi* is the best known of the species. It is represented by many dental remains and a subcomplete skeleton. Postcranial characters of this species are not particularly specialized. It is interpreted here as a terrestrial predator with poorly developed aquatic adaptations. Fossils of otters are known from ten different localities at Toros-Menalla, each of which yielded a single individual of one or two species. The presence of four morphologically distinct otters in the area is indicative of a palaeoenvironment with a relatively well-developed freshwater system of lakes and/or rivers. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, **152**, 793–846.

ADDITIONAL KEYWORDS: Africa – aquatic adaptation – *Sivaonyx* – systematics.

INTRODUCTION

The Djourab desert of Chad has been surveyed by the Mission paléoanthropologique franco-tchadienne (MPFT) since 1994. Perilacustrine, for the most part poorly cemented sandstone sediments of the fossiliferous sector of Toros-Menalla (TM) have yielded about 15 000 fossil specimens of late Miocene age, including *Sahelanthropus tchadensis*, the earliest known hominid nicknamed 'Toumaï' (see data for the TM 266 site in Brunet *et al.*, 2002, 2005; Vignaud *et al.*, 2002). Toros-Menalla now includes about 400 sites, of which more than 60 have produced remains of carnivorans. Preliminary study

of this material has revealed a rich and diverse carnivoran fauna of which only a few taxa have been studied and described up to this time (de Bonis *et al.*, 2005, 2007a, b; Peigné *et al.*, 2005a, b).

Here we describe material assigned to the Lutrinae (Mustelidae) from Toros-Menalla. The Mustelidae is the most diverse family of the Carnivora, with more than 60 extant species (Wilson & Reeder, 1993). The fossil record of the family in Africa is less complete than it is in Asia or North America but, interestingly, it includes a great number of lutrines. At Toros-Menalla, otters are the most abundant mustelids, with at least four species. There is only one additional non-lutrine mustelid known from the area. The material described here is remarkable in including a partial skeleton of a very large species that has no extant equivalent. Previous studies describing

*Corresponding author. E-mail: peigne@mnhn.fr

postcranial anatomy of fossil otters are rare in the literature (but see Hendey, 1978; Willemsen, 1980a, b; Lambert, 1997), which has motivated a detailed description and comparison of the material presented here.

MATERIAL AND METHODS

ABBREVIATIONS

Institutions: BAR: fossils from Baringo District, Community Museums of Kenya; BMNH: Natural History Museum, London; BSP: Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; GSI: Geological Survey of India, Calcutta; KNM: Kenya National Museums, Nairobi; MNCN: Museo Nacional de Ciencias Naturales, Madrid; MNHN CG and MNHN A: 'Catalogue Général' and 'Anatomie', collections de mammalogie, Muséum national d'Histoire naturelle, Paris; NK: fossils from Nkondo, Uganda National Museum, Kampala; SAM PQ-L: collections from Langebaanweg, South African Museum, Cape Town; TM: fossils from Toros-Menalla, CNAR (Service des collections), N'Djamena (during the study temporarily in University of Poitiers, UMR 6046 Géobiologie, Biochronologie et Paléontologie humaine); UF: Vertebrate palaeontology collection, Florida Museum of Natural History, Gainesville, Florida.

Measurements: On the mandible: Ldistc-m2 (or -m1), length between distal margin of canine alveolus and distal margin of m2 (or m1) alveolus; Lp2-m2, length between mesial margin of p2 alveolus and distal margin of m2 alveolus; Tp3 (or Tm1), maximum thickness of the hemimandible below the main cuspid of p3 (or m1 protoconid); Hp3-4, minimum depth of the hemimandible between the lingual alveolar margin between p3-p4 and the ventral margin of the hemimandible (other H are similarly defined; see Peigné & Heizmann, 2003: fig. 2). On dentitions: L, maximum length; W, maximum width; Wtal, m1 talonid width; Wmax, maximum width of m1 (= W or Wtal if talonid is wider than trigonid); LtrigoM and LtrigoP, m1 trigonid length at the level of the metaconid or the protoconid; Hmeta, m1 metaconid height, i.e. shortest distance from metaconid tip to enamel/dentine junction (see Peigné & Heizmann, 2003: fig. 3); Hproto, m1 protoconid height, measured as Hmeta; Llab, M1 labial mesiodistal length; Lling, M1 lingual mesiodistal length; Wdist, M1 distal transverse width; MlingDlab, maximum distance between mesiolingual corner and distolabial corner on M1; MlabDling, maximum distance between mesiolabial corner and distolingual corner on M1. On postcranial bones: acet, acetabulum; ant, anterior; AP, anteropos-terior; art, articulation; D, diameter; DBL, dorsal body length of caudal vertebrae; dist epi, distal epiphysis; FctL, functional length; IS, index of slenderness calculated as in Maynard Smith & Savage (1956); L, length; max, maximum; min, minimum; lat, lateral; ML, mediolateral; NF, nutrient foramen; pat, patella; post, posterior; prox epi, proximal epiphysis; TH, total height of caudal vertebrae body, measured from the ventral face margin of the body and the dorsal margin of the postzygapophyses; t.m and l.d., teres major and latissimus dorsi; W, width.

MEASUREMENTS

Dental and postcranial measurements were taken with vernier callipers to the nearest 0.1 mm. Functional lengths of long bones follow the measurements of Hildebrand (1952). For definitions of dental and postcranial measurements, see 'abbreviations' above. The identification of muscular insertions in our descriptions is based mainly on Davis (1964), Evans (1993) and Barone (1986, 2000). Nevertheless, more specific anatomical studies dealing with otters or other mustelids constitute a significant source of osteological and/or myological data for our comparisons (e.g. Hall, 1926, 1927; Fischer, 1942; Howard, 1973, 1975; Stains, 1976; Leach, 1977).

MATERIAL

Specimens of extant Lutrinae used in comparisons are listed in Appendix 1. Taxonomy follows Wilson & Reeder (1993). To avoid confusion, we abbreviate *Lutra*, *Lontra*, and *Lutrogale* as *Lu*., *Lo*. and *Lutro*., respectively, and *Aonyx* and *Amblonyx* as *Ao*. and *Am*., respectively.

Extinct otters have also been studied, especially middle–late Miocene and early Pliocene taxa. Our comparison database includes taxa from three main areas: east Africa (material from Lukeino for specimens of *Sivaonyx*, courtesy of Dr Morales, MNCN), South Africa (fossils of *Sivaonyx* from Klein Zee and Langebaanweg), and Siwalik Hills of India and Pakistan (species of *Enhydriodon*, *Sivaonyx*, *Vishnuonyx*) stored at the NHM, London. Data on fossils are mainly first hand, although, when necessary, data from previous literature have been used.

SYSTEMATIC PALAEONTOLOGY

CARNIVORA BOWDICH, 1821
CANIFORMIA KRETZOI, 1943
ARCTOIDEA FLOWER, 1869
MUSTELIDAE FISCHER, 1817
LUTRINAE BONAPARTE, 1838
SIVAONYX PILGRIM, 1931

Type species: Sivaonyx bathygnathus (Lydekker, 1884).

Other included species: S. *africanus* Stromer, 1931, S. *beyi* sp. nov., S. *ekecaman* Werdelin, 2003, S. *hendeyi* Morales, Pickford & Soria, 2005, S. *kamuhangirei* Morales & Pickford, 2005, S. *soriae* Morales & Pickford, 2005 (= S. *senutae* Morales & Pickford, 2005; see comparisons and discussion).

Comments: The generic assignment of the Chadian material is based on the great resemblance with other species of the genus in the mandibular and dental morphology. This includes, for example, a highly robust mandibular corpus, a reduction of the premolars, a short, wide p4, an m1 with a low trigonid with cuspids of approximately equal height, deeply separated paraconid and metaconid, a talonid wider than the trigonid, a large hypoconid crest, a shallow talonid basin, a low but distinct entoconid ridge, a cingulid marked on the labial side that may extend on to the lingual side of the paraconid, and an M1 with a strong metaconule. *Sivaonyx* and *Paludolutra* [*sensu* Morales & Pickford, 2005; i.e. including *P. campanii*, *P. lluecai* (= *P. lehmani*) and *P. maremmana*] are mainly distinguished by the characters of the upper carnassial (Morales & Pickford, 2005). Furthermore, *Sivaonyx* differs from *Paludolutra* in having an M1 with a strong metaconule, a distinct notch separating the paraconule and the protocone, a wider and more robust p4, and a more bunodont m1 (see, for example, the m1 of *P. lluecai*; Morales & Pickford, 2005: fig. 5).

SIVAONYX BEYI SP. NOV.

Holotype: TM 171-01-033, partial skeleton of one individual including: fragment of left edentulous hemimandible, fragment of right hemimandible with distal root of p3, p4 (broken) and damaged m1, proximal fragment of left and right scapulae, subcomplete left humerus and two distal fragments of right humerus, proximal fragment of left ulna and complete right ulna, subcomplete left radius, proximal fragment of diaphysis of right radius, right scapholunar, left magnum, right Mc III, fragment of right Mc II, and left Mc I, II, III, fragments of undetermined metapodials, seven fragmentary caudal vertebrae (Cd 2, 4, 5, 7, 10, 11 and 12), fragment of left hip including acetabulum, left femur lacking distal epiphysis and diaphysis of right femur, left tibia lacking the proximal epiphysis and diaphysis of right tibia, left astragalus, left navicular, left Mt II and IV, incomplete right Mt II, III and IV, five proximal phalanges.

Type locality: TM 171, Toros-Menalla fossiliferous area, Chad; late Miocene.

Etymology: From 'beyi', meaning large in the Goran language.

Referred specimens: TM 31-99-001, distal fragment of right humerus; TM 74-99-015, left calcaneum; TM 90-00-066, right M1; TM 172-05-001, subcomplete right hemimandible with damaged m1; TM 219-01-001, anterior fragment of mandible with canine root and p1-3 roots; TM 247-01-005, fragment of right hemimandible with m1; TM 355-02-002, fragment of left hemimandible with fragment of canine, p2-3 roots, fragment of p4, subcomplete m1.

Geographical and stratigraphical distributions: Chad: Toros-Menalla fossiliferous area (TM 74, 90, 171, 172, 219, 247, 355), late Miocene (*c*. 7 Ma).

Diagnosis: Large species of *Sivaonyx* (*c*. 60 kg) with two lower incisors only, and in having a postcranial skeleton displaying only a few characters related to an aquatic adaptation.

Differential diagnosis: Differs from S. *bathygnathus* in being larger, which may be related to the presence of a much thicker and taller mandible, and in having a much more robust (L/W ratio lower) and shorter p4 compared with m1. Differs from S. *soriae* in its larger size, having only two lower incisors, an M1 that is transversely more elongated with a mesiodistally less extended lingual cingulum and more distantly located metacone and metaconule. Differs from S. *hendeyi* in having an m1 with a talonid that is wider than the trigonid and being less bunodont, which implies a deeper carnassial notch, smaller and less transversely orientated paraconid, shorter and more erect metaconid, and metaconid and protoconid proportionally taller relative to m1 length. Furthermore, the femur of S. *hendeyi* is more robust, has a thinner neck and a larger head that is more proximally orientated, less developed trochanters and less extended trochanteric fossa. Differs from S. *africanus* in having an M1 that is less robust, more transversely elongated with a less expanded lingual cingulum, a crest-like metaconule extending mesially, p4 longer relative to m1 length and a shorter and more erect metaconid on m1. Differs from S. *ekecaman* in having a less bunodont m1, which includes a greater elongation, a less robust and more erected metaconid, a shorter talonid, and a much more transversely elongated M1 with taller cusps, no parastyle, more developed paracone and a much more expanded lingual cingulum. Differs from S. *kamuhangirei* in its smaller size and by a more reduced and less transversely orientated paraconid on m1. Differs from *Sivaonyx* sp. from Wadi Natron in

having a proportionally more elongated m1. The case of *Sivaonyx senutae* will be discussed below.

Description (Figures 1–7, Tables 1–5)
Mandible (Figs 1, 2, Table 1): The mandible is very stoutly built, with a thick, tall and curved corpus so that the hemimandibles are posteriorly diverging, as in *Aonyx capensis*. There are several mental foramina in variable positions below the premolars. In all of the specimens, the largest one is below the diastema between p3 and p4 in the dorsal half of the corpus, while 3–6 additional foramina are present below p1 and p2. In the individuals that completely preserve the chin (TM 355-02-002, Fig. 1E–G, TM 219-01-001), there is a distinct ventral apophysis prolongating the symphysis. The latter is deeply indented, dorsoventrally tall and anteroposteriorly short. Muscular attachments for the masticatory muscles (Mm. tem-

Table 1. Comparisons of mandibular measurements in bunodont fossil and extant Lutrinae

Mandible	Ldistc-m2	Ldistc-m1	Lp2-m2	Tp3	Tm1	Hp3-4	Hp4-m1	Hm1-2	Hm2-dist
Fossil taxa									
Sivaonyx beyi									
TM 172-05-001	59.5	51.8	59.5		16		28	27	32.8
TM 355-02-002	59	48	55.5	14.5	13.4	29.6	27	28.5	32.5
TM 171-01-033*	60	50	60.5	15.7	13.8	30.5	30.5	29.5	32.4
TM 247-01-005					13.7				
Sivaonyx hendeyi									
SAM PQ L 5000*	56.5				13.9	26.3			31.4
SAM PQ L 9138					17.6		31.7		37.4
Sivaonyx bathygnathus									
GSI D 33*		39.4					20		
BMNH M 16929					11	20.2	19		
BMNH M 13175					9.7		19	19.7	
BMNH M 15397					11		25.4		
Sivaonyx africanus									
BSP 1930-XI-1*	59	50	56.8	14.8	14.4	26.8	27.4	27.8	32
Djourabus dabba									
TM 293-01-006 & 053*			17.8	16.4			39		
Extant bunodont taxa									
Amblonyx cinereus									
MNHN CG 1884-10			30		7.5				
Aonyx capensis									
MNHN CG 1897-982			45		10	17.1	16.3	17.2	18.5
MNHN A 1914			43		9.6				
MNHN A 1899					10.5				
MNHN A 3388			43						
Aonyx congicus									
MNHN CG 1947-31			37		8.3	18.6	16.8	17	20
MNHN CG 1973-65			35		8.1	16	16.5	16.8	19.2
MNHN CG 1966-216			35		8.4				
Lutrogale perspicillata									
MNHN CG 1962-1646			39.2		9.1				

Except for the type of *S. bathygnathus* (data are from Lydekker, 1884), data are from personal measurements.
*Holotype.

Figure 1. *Sivaonyx beyi* **sp. nov.**, photographs of the lower dentition. TM 171-01-033, holotype: fragmentary left hemimandible in A, lingual view, B, labial view, and fragmentary right hemimandible with subcomplete p4 and damaged m1 in C, labial view and D, dorsal view. TM 355-02-002: fragmentary left hemimandible with fragment of p4, subcomplete m1 in E, labial view, F, lingual view, and G, dorsal view. TM 172-05-001: subcomplete right hemimandible with damaged m1 in H, labial view, I, lingual view, and J, dorsal view. TM 247-01-005: fragment of right hemimandible with m1 in K, labial view, L, lingual view, and M, dorsal view. Scale bar = 10 mm.
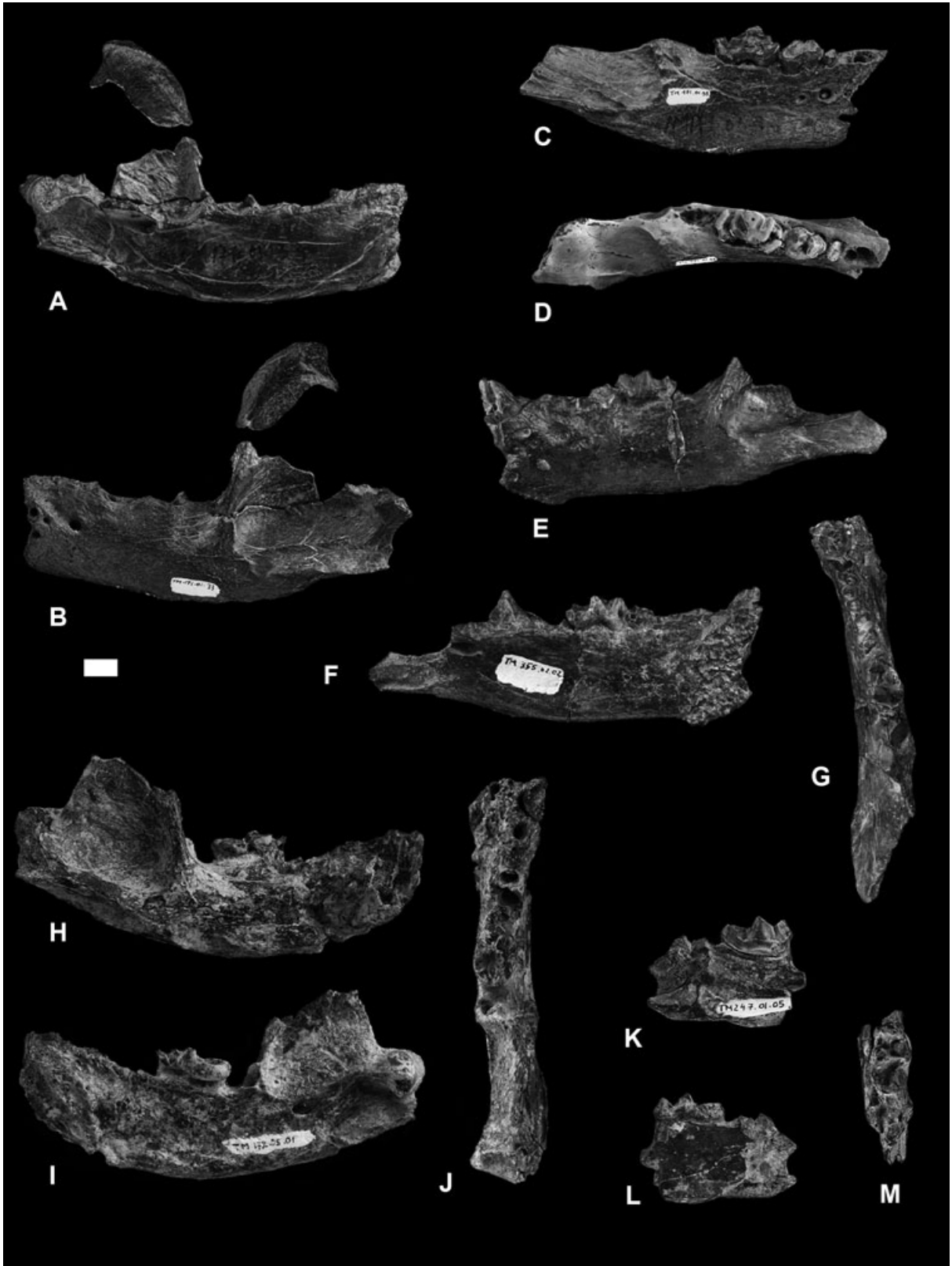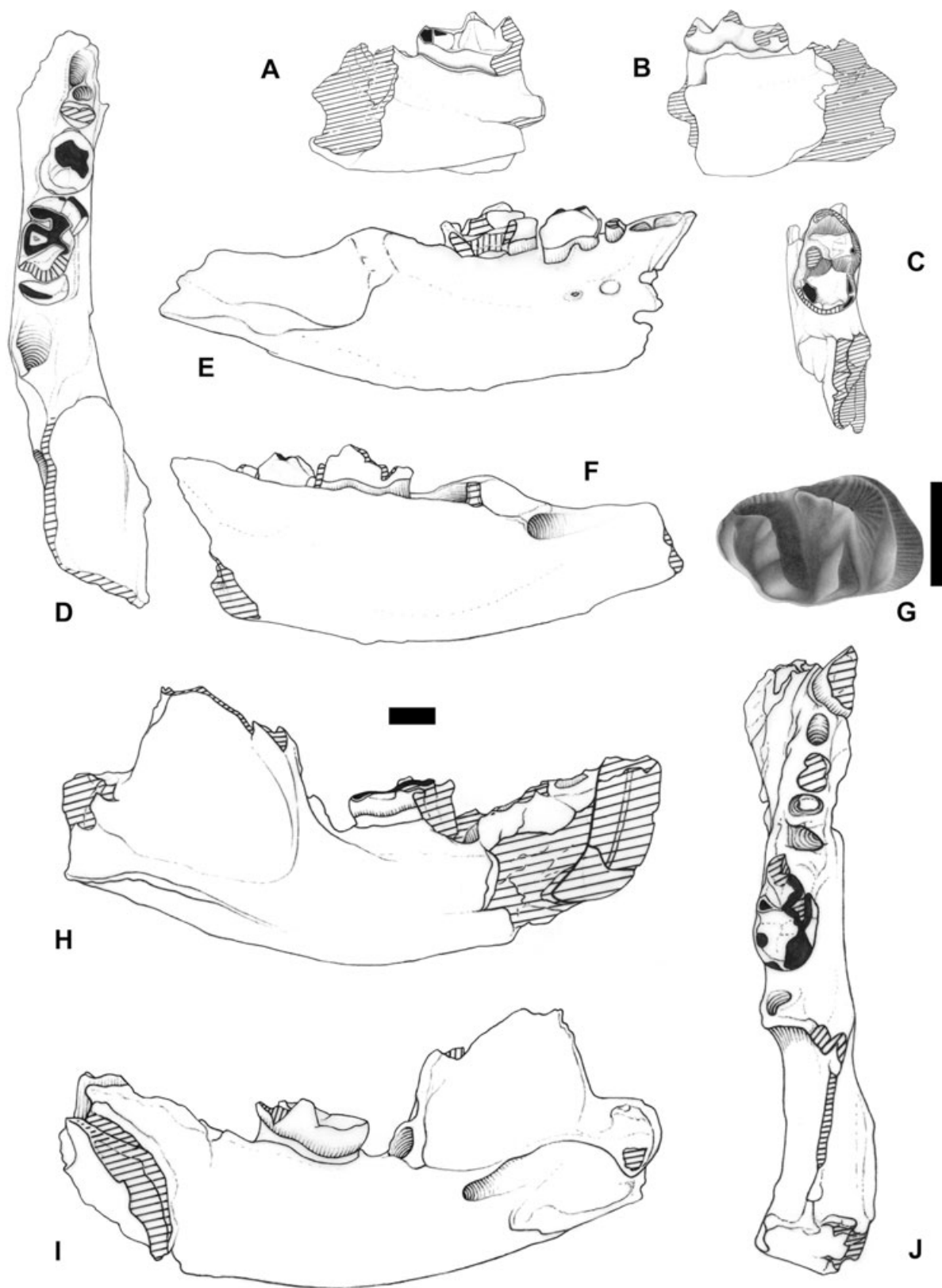
Figure 2. *Sivaonyx beyi* **sp. nov.**, drawings of the most significant dental remains. TM 247-01-005: fragment of right hemimandible with m1 in A, labial view, B, lingual view, and C, dorsal view. TM 171-01-033, holotype: fragmentary right hemimandible with subcomplete p4 and damaged m1 in D, dorsal view, E, labial view, and F, lingual view. TM 90-00-066: right M1 in G, occlusal view. TM 172-05-001: subcomplete right hemimandible with damage m1 in H, labial view, I, lingual view, and J, dorsal view. Scale bars = 10 mm.

poralis, masseter, zygomaticomandibularis and pterygoideus) are strongly developed. The attachments for the Mm. masseter and temporalis are particularly deep, suggesting great strength in these adductors during mastication, which may be related to a diet based on relatively hard items, as in *Aonyx capensis*. The masseteric fossa is deep and large, although anteriorly not reaching the level of m2; it is ventrally bounded by a strong and laterally projected masseteric ridge. This suggests a strong development of the M. masseter profundus and M. zygomaticomandibularis, the latter of which is regarded as a part of the former by some students (Turnbull, 1970; Gorniak, 1986; Evans, 1993; Barone, 2000). Ventrolaterally to the masseteric ridge, the mandible surface is relatively flattened. This area, where the M. masseter superficialis inserts, is also particularly wide and elongated compared with that in other carnivorans, as it extends backwards to the angular process and forward to nearly below the anterior margin of the masseteric fossa. The coronoid process is incompletely preserved on the available material. The anterior rim of the process is nearly vertically orientated (i.e. nearly at right angles relative to the alveolar plane). A fragment of the tip of the process is preserved on the left hemimandible of the type. It is rather triangular-shaped and has a thin posterior rim, and an anteriorly thick dorsal rim; the tip also has a convex lateral side and a deeply excavated medial side for the attachment of the M. temporalis profundus. The attachment area for the deepest fibres of the M. temporalis profundus is also strongly marked on the medial side of the coronoid process. This area is delimited (1) ventrally, by a horizontal crest that runs from the mandibular condyle to the posteroventral corner of the m2 alveolus; (2) anteriorly, by an even stronger, roughly vertical crest located just posterior or posteroventral to the m2 alveolus. The ventral surface of the corpus is also marked by the attachment area of the M. digastricus. It is clearly distinct on TM 171-01-033, TM 172-05-001 and TM 355-02-002 where it extends from slightly posterior to the mandibular foramen forward to at least beneath m1; the insertion is about 50 mm in total length. The lateral boundary of this insertion area is prominent and crest-like. This insertion is extended more medially than laterally; moreover, it narrows anteriorly and enlarges posteriorly, where it extends dorsally on the medial surface of the mandible. The elongation

and extension of the M. digastricus insertion is rather similar to that in *Enhydra lutris* and unlike *Lontra canadensis* (Scapino, 1976). The tip of the angular process is not preserved, but it is likely that it was short. A large insertion area for the M. pterygoideus medialis is visible on the medial surface of the angular region, extending dorsally to the ventral rim of the condyle and anteriorly to a level about 1 cm posterior to the mandibular foramen.

Dentition (Figs 1, 2, Tables 2, 3): The dentition is poorly preserved in the material, with only p4 and m1 being nearly complete. The shape and location of the alveoli or roots of the other teeth provide some information, however. Two individuals (TM 219-01-001 and TM 172-05-001, Figs 1H–J, 2H–J) have only two lower incisors, with i1 presumably being absent as in *Enhydra lutris* (Estes, 1980). As in extant otters, the incisor alveoli are transversely compressed, that of i3 being larger and more labially located than that of i2. The anterior part of the chin is not preserved in TM 355-02-002 (Fig. 1E–G), but one incisor alveolus is visible along the symphyseal face. Given its location, this alveolus is that of i2, while that of i1 is probably absent. Only a fragment of the root and/or the base of the crown of the canine is available in some individuals (TM 172-05-001, TM 355-02-002, TM 219-01-001). The tooth was large and the root poorly curved. The number of premolars is variable in the sample from Toros-Menalla. In TM 171-01-033 (Figs 1A–D, 2D–F) and TM 172-05-001 p1 is absent and p2 is single-rooted. Nevertheless, the left hemimandible of the former displays evidence of alveolar resorption at the level of p1 and p2, which suggests these teeth may have fallen out during the animal's life. TM 219-01-001 and TM 355-02-002 both have a tiny p1 alveolus that is closely applied against, and partly coalescent with, the canine alveolus; in these individuals p2 had two nearly fused roots and was obliquely orientated, the mesial root being labial. In all of the available specimens the p3 was short and double-rooted. Its roots are preserved in TM 355-02-002, TM 172-05-001 and TM 171-01-033, being partly fused in the last two; the distal one is markedly larger than the mesial one and is mesiodistally compressed. The p4 is preserved on the right hemimandible of the holotype TM 171-01-33, though the main cuspid is broken off. The tooth is short and distally very wide; it was
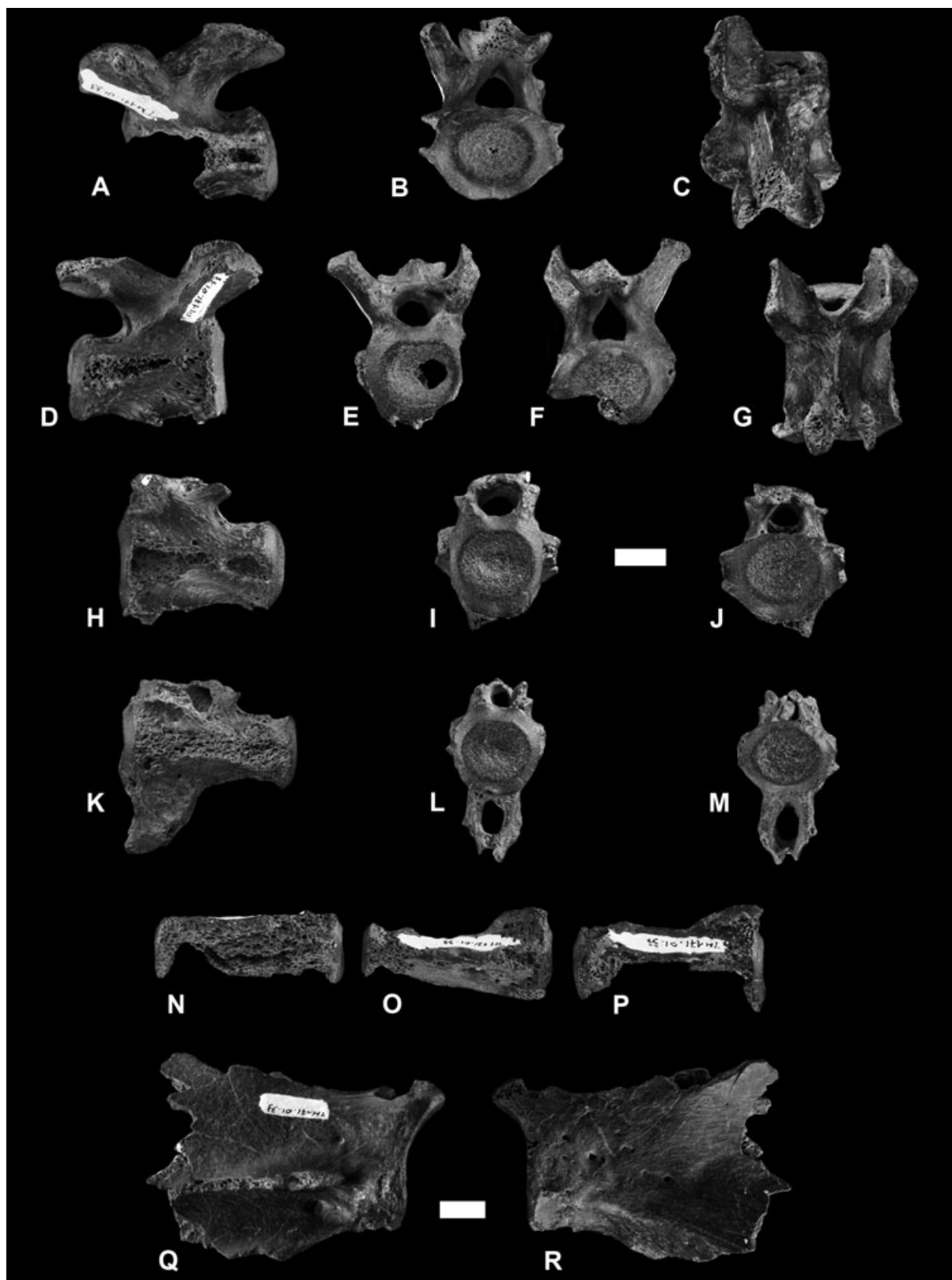
Figure 3. *Sivaonyx beyi* **sp. nov.**, photographs of vertebrae and scapula. TM 171-01-033, holotype: 2nd caudal vertebra in A, left lateral view, B, posterior view, and C, dorsal view; 4th caudal vertebra in D, right lateral view, E, anterior view, F, posterior view, and G, dorsal view; 5th caudal vertebra in H, left lateral view, I, anterior view, and J, posterior view; 7th caudal vertebra in K, left lateral view, L, anterior view, and M, posterior view; N, O, P: right lateral view of 12th, 11th, and 10th caudal vertebra, respectively; proximal fragment of right scapula in Q, lateral view and R, medial view. Scale bars = 10 mm.
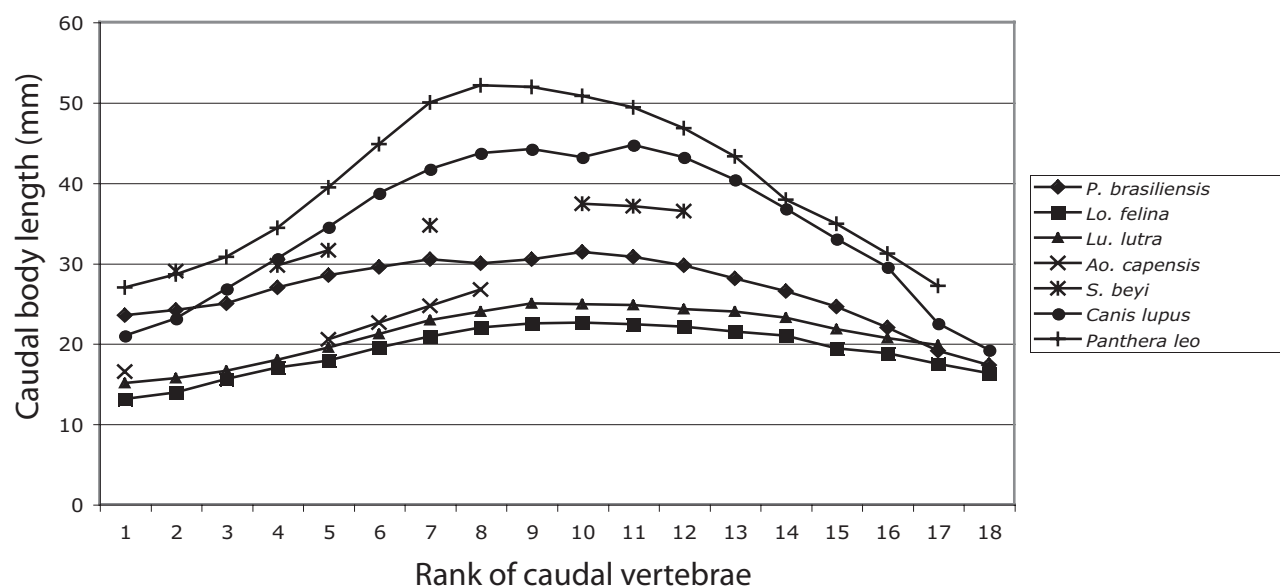

Figure 4. Vertebral profile of Lutrinae: diagram of caudal vertebrae body length in relation to their rank in extant Lutrinae and *S. beyi* **sp. nov.** See text for comments.

probably taller than m1, judging by a comparison with other specimens preserving the latter (e.g. TM 247-01-005, Figs 1K–M, 2A–C). There is no mesial accessory cuspid, but a distal, incompletely preserved one was certainly well developed, closely appressed to the main cuspid, and labially placed. A prominent crest extends from the distolingual face of the main cuspid, as in, for example, *Lutrogale perspicillata* (MNHN CG 1962-1646). The lower carnassial is nearly complete in TM 247-01-005, TM 355-02-002 and TM 172-05-001. It is a low and wide tooth. The paraconid is only slightly lower than the protoconid and has a slightly backwardly orientated mesial face, a cingulid that may be marked (e.g. TM 355-02-002) and an almost transversely orientated distal face. Labially, the basal half of the distal face of the protoconid is occupied by a prominent vertical crest. The metaconid is a prominent cuspid that reaches approximately the same height as the protoconid; it is separated from the paraconid by a deep and wide V-shaped valley; it has a somewhat oblique distal face; it is slightly distal to the protoconid, from which it is separated by crests forming a V-shaped valley prolonged by a short notch. The

talonid is long and wide, slightly wider than the trigonid; it is poorly basined and located mainly distally to the metaconid. All of the cuspids of the talonid are more or less worn in the available material. The hypoconid forms a large labial crest, which has a lingual slope that occupies more than one-half of the talonid width; it is separated from the distal crest of the protoconid by a small notch. The wear pattern of the talonid indicates that a small hypoconulid was probably present in TM 247-01-005, as was a small entoconid in TM 172-05-001, TM 355-02-002 and TM 247-01-005. The cingulid is strongly developed only along the labial face (e.g. TM 247-01-005), but it may extend on the lingual face of the paraconid (e.g. TM 355-02-002). The m2 alveolus is large, particularly in TM 355-02-002 (9.5 mm long and 5.5 mm wide), oval-shaped and lingually located; because this tooth is located at the base of the ascending branch, its alveolar plane is orientated almost anteriad in TM 172-05-001.

The single preserved upper tooth is an isolated M1 germ with unworn cusps (TM 90-00-066; Fig. 2G, Table 3). The tooth is transversely elongated, the mesial and distal faces being approximately parallel.

Figure 5. *Sivaonyx beyi* **sp. nov.**, photographs of the long bones of the forelimb and scapholunar. TM 171-01-033, holotype: subcomplete left humerus in A, anterior view, B, posterior view, and C, medial view; subcomplete right ulna in K, lateral view, L, medial view, M, anterior view, and N, posterior view; subcomplete left radius in H, proximal view, I, anterior view, and J, posterior view; right scapholunar in F, proximal view and G, distal view. TM 31-99-001: referred distal fragment of humerus in D, anterior view and E, posterior view. Scale bars = 10 mm.

The paracone and metacone are trenchant, the former being much longer but clearly lower than the latter. The protocone and paraconule form a mesially curved blade; both have a nearly vertical mesial face and are separated by a notch; the paraconule is slightly smaller than the protocone. There is a prominent metaconule located on the distal border, separated from the metacone by a V-shaped valley. There is no crest linking the metaconule and the protocone. The lingual cingulum is developed, extended somewhat distally, with a tilted-up rim. The cingulum is also present along the mesial and labial borders and is very wide labially to the paracone.

Postcranium (Figs 3–7, Tables 4–6): Most of the available postcranial bones belong to one individual, TM-171-01-033. Only a few vertebrae were preserved, but none completely. The only remaining element of the cervical, thoracic and lumbar vertebral segments is a small fragment that preserves the anterior and posterior articular processes and a part of the dorsal arch with the basis of the spinous process. The articular surfaces of both processes are orientated at about 45° relative to the sagittal axis, which may correspond to one of the last cervicals or the first thoracic vertebrae. Except for its large size, a detailed comparison with extant taxa is not possible. Seven caudal vertebrae are variably preserved (Fig. 3A–P). It is possible to determine their position based on a comparison with extant otters (*P. brasiliensis*, *Lo. felina*, *Lu. lutra*). In *Lu. lutra* only the first eight or nine caudal vertebrae are complete, i.e. have transverse and spinous processes and a complete vertebral arch enclosing a long vertebral canal. Four of the caudal vertebrae preserved in TM-171-01-033 display all or a part of these morphological traits. The three others are poorly preserved but certainly represent more posteriorly located vertebrae. The position of the caudal vertebrae can be determined using several morphological characters observed in extant species, of which only a few are available in the Chadian fossil otter. In extant otters, the length of the vertebral body (measured along the dorsal rim) increases from the first to the ninth or tenth vertebra depending on the species (*P. brasiliensis*, *Lu. lutra*, *Lo. felina* are used here), but the length does not differ much from the ninth to the eleventh caudal. As the vertebral body lengthens, it also becomes smaller in diameter and the posterior section (which may be markedly dorsoventrally flattened in the first caudals) becomes more rounded. Furthermore, the posterior articular process becomes more reduced in size and less laterally projected, and the spinous process is present on the first six caudals only, then becomes reduced further posteriorly. Figure 4 presents the hypothetical position of the preserved caudal vertebrae of TM-171-01-033 based on their body length (Table 4) to fit the vertebral profile obtained from the extant species. Thus, given their shape and body length, we infer that the preserved caudal vertebrae of the Chadian species most probably represent the second, fourth, fifth, seventh, tenth, eleventh and twelfth ones. This ordering is consistent with the aforementioned characters, especially the diameter, size of the body, and development and lateral projection of the posterior articular processes. The second caudal vertebra (Fig. 3A–C) consists of the posterior part of the body and most of the dorsal half. The body is short but wide, with a posterior part that is dorsoventrally flattened; the surface of the latter is convex externally but slightly depressed in its centre. The vertebral foramen is large and the vertebral canal is 17 mm long; its anterior opening is wider than high while this is the opposite for the posterior opening. The anterior articular process (or prezygapophysis) is large and thick; the articular surface is large, oval-shaped, anteroposteriorly elongated and strongly concave in its medium part. The mammillary process is not well preserved but was certainly small. The tip of the spinous process is not preserved; its anterior rim is thick and strongly backwardly orientated. The posterior articular process (or postzygapophysis) is much more reduced and less laterally projecting than the anterior one; it is oval, anteroposteriorly elongated, and its surface is flat to slightly convex, being ventrolaterally orientated. Transverse processes are not preserved. In comparison with the second one, the fourth caudal (Fig. 3D–G) vertebra is better preserved, lacking only a part of its ventral half. It differs in having a longer body, and more reduced articular processes, with the posterior ones being much less laterally projecting, slightly larger mammillary processes, a thinner spinous process and a less dorsoventrally flattened anterior opening of the vertebral canal. The anterior face of the body, which is not preserved on the second caudal, is here rounded and its surface is similar to that of the

Figure 6. *Sivaonyx beyi* **sp. nov.**, photographs of the magnum, metacarpals and phalanges. TM 171-01-033, holotype: left magnum in A, proximal view, B, medial view, and C, distal view; left Mc I in D, proximal view, G, dorsal view, and H, medial view; left Mc II in E, proximal view, I, dorsal view, and J, lateral view; right Mc III in F, proximal view, K, dorsal view, and L, lateral view; indeterminate proximal phalanges in M, N, O, P, Q, dorsal view and in R, S, T, U, V, ventral view. Scale bars = 10 mm.

posterior face of the body: smooth, externally convex and centrally depressed. The transverse processes are not preserved; they are 7 mm thick at their posterior base. Most of the fifth caudal vertebra body, the vertebral canal and the dorsal arch are preserved (Fig. 3H–J); articular and transverses processes are broken off. The shape and surface of the anterior and posterior articulation of the body are like those of the other caudals. On the ventral side of the anterior face, there are some fragments of a haemal arch (or chevron bone), which protects the median coccygeal artery; there is no visible suture between either side of the haemal arch and the body. The seventh caudal (Fig. 3K–M) is represented by most of the body, a part of the dorsal arch and the vertebral canal, and most of the haemal arch. This vertebra differs from the preceding ones in having a longer but smaller-diameter body and a smaller but equally long vertebral canal. The haemal arch is well preserved and completely fused to the body. It is particularly long basally (extending about half of the length of the body) and is ventrally extended (nearly the height of the body). The two branches of the arch are transversely compressed, curved forward and tapering ventrad; their lateral surface is smooth and presents a low horizontal crest at mid-height. The three other caudal vertebrae are more fragmentary (Fig. 3N–P); they retain only a part of the body, including the anterior and posterior face, and a small part of the vertebral and/or haemal arches. The body length of these caudals is greater than the more anterior ones while the diameter of their body is more reduced. In addition, the body length and diameter decrease from the tenth to the twelfth caudal.

Only the proximal extremity of both scapulas is preserved (Fig. 3Q, R), including the glenoid fossa, the neck and a small portion of the scapular spine. The glenoid fossa is oval (L/W ratio of 0.69), piriform and anteriorly narrow, although less so than in ursids (Davis, 1964: 91) and extant otters. The articular surface is excavated, with a moderately developed supraglenoid tubercle. A small, rounded, smooth and slightly concave area for the attachment of the tendon of the M. biceps brachii is present on this tubercle. The coracoid process is vestigial. The preserved portion of the scapular spine is rather uninformative, illustrating that, at least proximally, the supraspinous fossa was anteroposteriorly more extended than the infraspinous fossa. The surface of the infras-pinous fossa is concave and its outer rim is relatively raised, while the surface of the supraspinous fossa is flat or slightly concave. Both the lateral and the medial surfaces of the scapula display a pair of nutrient foramina placed more or less adjacent to the spine. The medial face is mostly occupied by the subscapularis fossa, which is slightly depressed. Just ventral to the glenoid fossa, there is a deep and elongate groove for the insertion of the tendon of the long head of M. triceps brachii.

Most of the left humerus is preserved (Fig. 5A–C); a portion of the head and the greater tuberosity are broken off. The right humerus is only represented by its distal quarter. We also provisionally assign to the species a distal fragment of humerus TM 31-99-001 (Fig. 5D, E); it is not perfectly preserved, especially the lateral epicondyle, but this individual is undoubtedly smaller than the holotype (see Table 5) and has a supracondylar crest that is not as laterally extended distally as in TM 171-01-033. In comparison with most of the extant otters, the humeral epiphysis of the type of *S. beyi* is overall relatively straight, though it is slightly curved laterally and, in its proximal half, backwards. Thus, the marked anteroposterior curvature observed on most extant species is indistinct in the fossil otter. The diaphysis is transversely compressed and marked by strong ridges. The deltoid crest is distinct and fused with the pectoral ridge in the proximal half of the humerus, about 80 mm from the head (i.e. approximately 45% of the total length of the bone); the area for the attachment of the M. deltoideus is slightly depressed and rugose. It elongates and widens proximolaterad. The pectoral ridge is much stronger than the deltoid crest and present almost throughout the length of the diaphysis. The lateral epicondylar crest is proximodistally very developed and laterally very expanded; its outer rim makes a gentle curve. The anterior face of the crest is concave (insertion area for the M. brachialis and the extensors of the wrist and the digits) and the posterior one convex (insertion area for the M. anconeus). Another well-delimited muscular scar is the attachment area for the Mm. teres major and latissimus dorsi, which forms a proximodistally elongated, 25-mm-long groove on the medial face of the diaphysis; the distal extremity of this attachment is at the level of the distal extremity of the deltopectoral crest. The humeral head is only partially preserved, which pre-

Figure 7. *Sivaonyx beyi* **sp. nov.**, photographs of the hind-limb bones. TM 171-01-033, holotype: Fragmentary left innominate in A, lateral view and B, medial view; fragment of left femur in F, anterior view and G, lateral view; fragment of right femur in H, anterior view; fragment of left tibia in C, distal view, D, anterior view, and E, posterior view; left astragalus in I, dorsal view, J, ventral view, K, distal view, and L, lateral view; left navicular in V, lateral view, W, proximal view, X, distal view, and Y, dorsal view; left Mt II in M, proximal view and N, anterior view; left Mt IV in O, proximal view, P, anterior view, and Q, lateral view. TM 74-99-015: referred left calcaneum in R, medial view, S, distal view, T, dorsal view, and U, ventral view. Scale bars = 10 mm.

vents us from giving a precise description. Only the base of the lesser tuberosity is preserved; it was certainly large and is separated from the greater tuberosity (not preserved) by a wide intertubercular (or bicipital) groove in which glides the tendon of the M. biceps brachialis. The articulation of the distal epiphysis is wide. The capitulum is transversely very extended on the anterior face; it is relatively flat and displays a shallow groove on which the coronoid process of the radius slides. The trochlea is narrow and relatively deep, with a steepened medial lip. The olecranon fossa is deep, distally wide and has a triangular shape. Distomedially to the fossa and to the trochlea, there is a very deep fossa extending distally in a rugose trough for the attachment of the olecranon ligament. The entepicondylar foramen is large and slightly proximodistally elongated; a heavy bar limits it. The radial fossa is deep and wide. The lateral epicondyle is much less laterally extended than the medial one, but it is anteroposteriorly developed and prominent due to the distal extension of the epicondylar crest. The attachment of the M. anconeus on the posterior surface of this crest is extended distally, well beyond the distal margin of the olecranon fossa. The lateral surface of the lateral epicondyle is the area of origin for the tendons of the extensors and supinators of the elbow, and of the carpus and digits; the distinction between them is not clear on the specimen, specifically because the margin of the distal part of supracondylar crest and of the lateral epicondyle is damaged. The medial epicondyle is well developed and triangular though it does not extend as much as in, for example, *Pteronura brasiliensis*, whose epicondyle has a square outline: here, it is laterally and slightly posteriorly orientated. Except for its posterodistal part, the medial epicondyle is well preserved in the material. The M. triceps brachii medialis inserts on the proximal half of the posterior side, which is slightly depressed and has a ridged medial rim. In extant carnivorans, the anterior face and medial rim of the epicondyle are more complex and support closely placed insertions for flexors and pronators of the forearm. The exact location of the insertion or origin of each of these muscles has been described and/or illustrated in many carnivorans, including mustelids (e.g. Fischer, 1942; Howard, 1973; Leach, 1977).

There are obvious problems of homology looking at the muscle name used in the literature, which complicates myological identification and comparisons. The M. palmaris longus, which apparently displays a great variation in location and presence/absence, is an appropriate example. It is said to be absent in the domestic cat and dog in some publications (Evans, 1993; Barone, 2000; Sebastiani & Fishbeck, 2005), but there is some confusion about the homology of this muscle between humans and other animals [i.e. here the carnivorans (Spoor & Badoux, 1986)]; Evans (1993: 340) also mentions this homology. The homologous muscle to the M. palmaris longus of humans is the M. flexor digitorum superficialis in Carnivora. Actually, most of the myological descriptions of carnivorans that we use mention the presence of this muscle either as the M. palmaris longus (e.g. Hall, 1926, 1927; Fischer, 1942; Davis, 1964; Howard, 1973) or as the M. flexor digitorum superficialis (e.g. Leach, 1977; Evans, 1993; Barone, 2000), which reinforces the idea that these two names deal with the same muscle. Here, we base our identification primarily on the myology of the extant otters *Enhydra lutris* and, especially, *Lontra canadensis*, for which myological descriptions are available (Fischer, 1942; Howard, 1973). With the homology being clearly established, the precise location of every insertion is not easy in our fossil material, because sandblasting of the bones partly deletes the outline of insertions. We propose the following tentative topography. As in all carnivorans, the small area present on the proximal part of the medial rim of the medial epicondyle is for the origin of the tendon of the M. pronator teres. Immediately distally, there is a rounded and similarly sized insertion area, presumably for the tendon of M. flexor digitorum superficialis. Laterally, a shallow crest separates the latter from a clearly distinct insertion area, to which we assign the tendon of the M. flexor carpi radialis; it is 6.5 mm wide and 4.5 mm high. Finally, the incompletely preserved area posterior and distal to the latter may be the insertion area for one of the tendons of the M. flexor digitorum profundus and/or that of the M. flexor carpi ulnaris. The distalmost part of the epicondyle is not preserved.

The right ulna lacks only the anterior portion of the extremity of the olecranon (Fig. 5K–N). The left ulna

Table 2. Comparisons of lower teeth measurements (mm) and proportions of extant and extinct bunodont Lutrinae

Lower dentition	cL	W	p4L	m1W	L	W	Wtal	L/Wmax	LtrigoM	LtrigoM/L	Hmeta	Hmeta/L	Hproto	Hproto/L
S. beyi														
TM 172-05-001					22.8	13.4		1.70	14.2	0.62	8.0	0.35		
TM 355-02-002			12.2		20.0	11.6		1.72			7.3	0.37		
TM 171-01-033*			12.4	9.5	20.3									
TM 247-01-005					21.5	12.7		1.69	14.0	0.65	7.5	0.35	9.3	0.43
S. sp.														
no number[1]					22.0	13.0	14.0	1.57						
S. ekecaman														
KNM-KP 10034*[2]			11.3	8.4	21.2	13.5		1.57	11.5	0.54				
BAR 72003						12.8			13.4		6.5		7.6	
BAR 416'00														
BAR 567'05[3]					20.1	13.0		1.55						
S. soriae														
KNM LU 337 & 338*[4]	9.6	7.7			17.6	10.5		1.68						
KNM LU 614[4]														
BAR 1984'05[4]					17.5	10.6		1.65						
S. hendeyi														
SAM PQ L 5000*			12.3	9.5	21.3	13.1	12.8	1.63	14.2	0.67	7.0	0.33	7.9	0.37
SAM PQ L 9138				10										
S. kamuhangirei														
no number*[4]					26.0	15.9		1.64						
NK, 1988'89[4]						14.4								
S. bathygnathus														
GSI D 33*[5]			9.1	6.5	17.5	9.2		1.90						
BMNH M 16929			10.0		15.6	9.3		1.68	10.3	0.66	6.7	0.43	7.0	0.45
BMNH M 13175					15.6	9.0		1.73						
BMNH M 15397					18.5	11.0		1.68	11.9	0.64	6.4	0.35	7.4	0.40

S. africanus													
BSP 1930 XI 1*		12.0	9.1	22.2				14.0	0.63	7.2	0.32		
Djourabus dabba													
TM 293-01-006 & 053*	13.4	10.0		20.9	14.7	14.1	1.42	14.6	0.70				
Enhydriodon cf. *falconeri*													
BMNH-M 12350				21.6	12.5		1.73	14.5	0.67				
Enhydritherium terra.													
UF 100000[6]				15.9	9.3	10.4	1.53						
UF 18928*[7]				17.1	11.2		1.53						
UF 32001[7]				15.8	10.3		1.53						
UF 68001[7]		12.0	6.4	16.1	7.5		2.15						
Amblonyx cinereus													
MNHN CG 1884-10	5.1	3.8	4.6	13.4	8.0	8.2		8.7					
Aonyx capensis													
MNHN CG 1897-982	8.7			19.9	11.0		1.81	12.15	0.61	7.15	0.36		
MNHN A 1914	8.7	6.5	6	17.8	10.7		1.66	11.4	0.64	7		9.7	
MNHN A 1899	9.2	7	6.6	18.7	11.4		1.64	12.0	0.64				
MNHN A 3388	8.7	7	6.6	18.5	11.8		1.57	11.6	0.63	6.3	0.34	8.5	10.8
Aonyx congicus													
MNHN CG 1947-31	9.6	6.85	4.7	14.0	7.8		1.79	9.0	0.64				
MNHN CG 1973-65	9	6.6	4.7	14.7	8.05		1.83	8.8	0.60				
MNHN CG 1966-216	8.9	6.55	4.4	13.5	7.15		1.89	8.6	0.64	4.3	0.32	4.7	
MNHN CG 2005-612				14.7	8.4		1.75	8.8	0.60				
Lutro. perspicillata													
MNHN CG 1962-1646	7.8	6.4	6	16.5	10.3		1.60	10.6	0.64	5.7	0.35		

*Holotype; *S., Sivaonyx*; *terra., terraenovae*; *Lutro., Lutrogale.*
Personal measurements, except: [1]from Stromer (1920); [2]from Werdelin (2003); [3]from Morales & Pickford (2005); [4]from Morales *et al.* (2005); [5]from Lydekker (1884); [6]from Lambert (1997); [7]from Berta & Morgan (1985).

Table 3. Comparisons of measurements of M1 (mm) in bunodont extant and fossil Lutrinae

	Llab	Lling	Llab/Lling	Wdist	Lling/Wdist	MlingDlab	MlabDling
Sivaonyx beyi							
TM 90-00-066	11.7	11.7	1.00	17.3	0.68	16.5	20.0
S. soriae							
BAR 1082′01	11.0	12.2	0.90			15.6	18.2
S. ekecaman							
KNM-KP 10034 (holotype)	12.1	15.8	0.77	19.0	0.83		
S. africanus							
BSP 1930-XI-1 (holotype)	13.0	14.1	0.92	18.8	0.75	17.1	
Lutrogale perspicillata							
MNHN CG 1962-1646	10.6	11.5	0.92			12.7	16.9
Amblonyx cinerea							
MNHN CG 1884-10	8.8	9.3	0.95			11.1	13.0
MNHN CG 1879-198	8.8	9.4	0.94			10.3	13.0
Aonyx congicus							
MNHN CG 1947-31	8.7			9.9		9.6	12.6
MNHN CG 1973-65	8.4	8.75	0.96	10.25	0.85	10.15	14.1
Aonyx capensis							
MNHN CG 1897-982	12.0	12.3	0.98	14.5	0.85	14.4	18.9
MNHN A 1914	11.8	12.8	0.92			14.7	18.5
MNHN A 1899	12.0	13.8	0.87			15.6	19.3
MNHN A 3388	13.0	13.9	0.94			15.2	19.3

Data are personal except for *S. ekecaman*, from Werdelin (2003).

consists of its proximal third only, and the olecranon is no better preserved than in the right ulna. The ulna is a robust bone. Except for the extremity of the olecranon, which turns mediad, the bone shaft is rather straight. The olecranon is relatively long and thick, with a squared distal outline, and displays relatively well-marked muscular attachments and insertions (Fig. 3K–N). Its anterodistal part is unfortunately not preserved. On the posterior part of the distal face somewhat medially, the insertion area for the tendon of the long head of the M. triceps brachii is rounded, deeply marked and extends somewhat distally on the lateral face; it is located anteroproximally to the insertion of the lateral head of the triceps, which lies on the posterolateral side of the olecranon. The latter is about 30 mm long and proximodistally extended, with its distal extremity tapering off. Proximally, the crest-like, lateral rim of this insertion limits the insertion of the tendon for the M. anconeus. A low ridge separates the triceps lateralis insertion from that of the M. flexor digitorum profundus. The insertion of the medial branch of the triceps is not clearly visible, due to the poor preservation of the medial rim of the olecranon. Just distal to the triceps insertions on the medial face, there is a depressed and extended insertion for the tendon of the ulnar head of the M. flexor carpi ulnaris. Just opposite to it on the lateral face of the olecranon, the insertion for the M. anconeus is shallow in comparison; its distal rim is, however, distinct as a low ridge that is nearly perpendicular relative to the long axis of the ulna. This low ridge separates the anconeus insertion from that for the M. abductor pollicis longus. On the left ulna, the latter area is distinctly depressed from the level of the semilunar notch to that of the interosseus tubercle, while the area of insertion for the M. extensor digiti I and II (formerly M. extensor pollicis longus et indicis proprius; Evans, 1993), which lies just posterior to it, is convex, with a distal rim at the level of the middle of the semilunar notch. On the medial face of the olecranon, the insertion for the M. flexor digitorum profundus is well delimited. Proximally, it has an adjacent, oblique boundary with the insertion for the medial head of the triceps, then runs distad between the ulna crest-like posterior rim and the insertion for the tendon of M. brachialis (and, probably, that of one muscle of the pectoral group; see discussion below). Distally, a prominent crest marks its anterior limit (with the insertion of the M. pronator quadratus). The semilunar notch is well rounded. In anterior view, it presents a transverse constriction in its middle part. The anconeal process is wide and laterally particularly prominent; the medial articular surface is more inclined proximad than the lateral surface. The lateral coronoid process is very reduced and located strictly laterally, while the medial coronoid process is prominent and anteriorly projected. The

Table 4. Comparisons of the length of caudal vertebra body in Lutrinae and some non-lutrine carnivorans

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17	C18
S. beyi sp. nov.																		
TM 171-01-033		29		29.7	31.6		34.7			37.4	37.1	36.5						
P. brasiliensis																		
A 1918	23.5	24.2	25	27	28.5	29.5	30.5	30	30.5	31.4	30.8	29.7	28.1	26.5	24.6	22	19.1	17.3
Lo. felina																		
CG 1995-185	13.1	13.9	15.6	17	17.9	19.5	20.9	22	22.5	22.6	22.4	22.1	21.5	21	19.4	18.8	17.5	16.3
Lu. lutra																		
CG 1996-2466	15.1	15.7	16.6	18	19.5	21.2	22.9	24	25	24.9	24.8	24.3	24	23.2	21.8	20.7	19.8	
Ao. capensis																		
CG 1883-1561	16.5				20.5	22.6	24.7	26.7										
Canis lupus																		
CG 2005-79	21	23.1	26.8	30.6	34.5	38.7	41.7	43.7	44.2	43.2	44.7	43.2	40.4	36.8	33	29.5	22.5	19.2
Panthera leo																		
CG 1954-2	27	28.6	30.8	34.4	39.4	44.8	50	52.1	51.9	50.8	49.4	46.8	43.3	37.9	34.9	31.2	27.2	

The measurements serve for the vertebral profile of Figure 4.

radial notch is weakly concave; it faces almost exactly laterally. Just distal to the trochlear notch on the anterior part of the medial face, the area of insertion for the tendon of the M. brachialis is large and depressed, about 30 mm long proximodistally and as wide as 7 mm; it is limited posteriorly by a marked, thick ridge. It is clear that there are two distinct insertion areas. The most anterior and distal insertion area is for the tendon of the M. brachialis. This is also much more proximodistally extended than the second insertion area, which is located on the neck of the coronoid process and is more or less rounded in outline. According to Howard (1973), the tendons of the Mm. pectoantebrachialis and deltoideus (the latter is called M. clavobrachialis by Howard) are attached in this second area in *Enhydra lutris* while the insertions of these muscles are both placed on the anterior face of the humerus in *Lontra canadensis* (Fischer, 1942). In fact, the M. pectoantebrachialis is not mentioned in most of the anatomical sources we used and therefore it is not clear with what muscle of the pectoralis group the pectoantebrachialis is homologous. According to Howard (1973: 432), this muscle is 'the most superficial of the pectoral muscle group' and arises from the sternum, starting from the manubrium anteriorly and extending posteriorly to the level of the second rib. This muscle probably corresponds to the M. pectoralis transversus of other authors (e.g. Barone, 2000). Whatever the name of this muscle, in other mustelids (*Spilogale*, *Mephitis*, *Martes*, *Taxidea*; Hall, 1926, 1927; Leach, 1977), ursids (Davis, 1964), various additional wild (*Potos*, *Paradoxurus*, *Caracal*; Beswick-Perrin, 1871) and domestic carnivorans (*Felis* and *Canis*; Evans, 1993; Barone, 2000), neither the pectoral muscles nor the deltoid attach on the ulna. The M. pectoantebrachialis is, however, described in the domestic cat (Wischnitzer, 1993; Sebastiani & Fishbeck, 2005), where it attaches on the antebrachium fascia. The identity of the attachment adjacent to that of the M. brachialis in TM-171-01-033 is therefore unclear. Regardless, the size and depth of the entire area supports the attachment of the strong flexors of the elbow. The interosseus tubercle is very prominent and located at mid-shaft. In its distal third, the diaphysis displays marked crests that clearly delimit a flat, 10-mm-wide insertion area for the M. pronator quadratus; the crest between this insertion and that for the M. flexor digitorum profundus is particularly prominent, but distally does not reach the level of the articulation for the radius. The styloid process is large, and the articulation for the scapholunar is slightly larger than that for the radius. Both articulations are prominent and separated by a deep and wide notch.

The left radius is nearly complete (Fig. 5H–J), displaying small cracks and lacking some fragments of the two epiphyses, including the part distal to the

Table 5. Comparisons of postcranial measurements (mm) and indexes of **S. *beyi* sp. nov.** with extinct and extant taxa: vertebrae and thoracic limb

	S. beyi		*Enhydrit. terra.*	*P. brasiliensis*	*Lu. lutra*	*Lo. felina*	*Lutro. persp.*
	TM 171-01-033	TM 31-99-001	M. A. R.	A 1918	CG 1996-2466	CG 1995-185	CG 1960-3670
Condylobasal L of skull				151.5	122	107.2	
Lm1	20.5		15.9	18.4	13.75	15.5	
Caudal vertebrae							
C2 DBL	29			24.2	15.7	13.9	
C2 TH	33			24.3	15.1	16.2	
Scapula							
articulation: APD	35			24.8	18.5	17.8	18.5
articulation: MLD	24.3			16.3	11.3	10.9	11.3
neck: min APD	30.7			22	16	14.3	16.1
Humerus							
FctL	178		109	98.8	87.8	80	84.2
L (trochlea-dist margin of V-deltoid)	103.6			39	46.5	45	46.5
L prox (boundary epicondylar crest-trochlea)	81.5			38.6	35.5	28	30.2
prox epi: APD	49			30.6	23	21.3	22.3
dist epi: max MLD	53.3	46.5	42	36.4	30.5	27.8	26.3
dist epi: max APD	24.5	23.3		17.5	12.8	13	13.1
dist epi: max MLW art. on ant. face	36.7	31.3		22.5	19.5	16.5	15.3
min APD trochlea	14.8	14		11	8	7.6	8.2
min MLD dia	16			9	8.1	7.1	7.1
APD same level	23			14.2	14.5	12.2	9.5
APD at mid-FctL	16.5			14.2	14.5	7.2	7.3
MLD at mid-FctL	24			9.2	8.1	12.2	9.8
Fct L/ML max D of dist epi	3.34			2.71	2.88	2.88	3.20
IS	1.10			0.97	0.84	0.94	1.34
L (head-t.m and l.d. insertion)	80.50			51.00	40.50	37.00	37.50
Ulna							
max L	185		116	99.5	86	80.1	83.6
Olecranon L	43.7			33	20.2	21.5	19.4
Shaft L	149.3			76.8	67.5	59.9	65.8
L (dist epi-dist rim osseus tubercle)	80			25	30	28.5	31.5
Olecranon proportion	0.29			0.43	0.30	0.36	0.29

Radius					
max L (= FctL)	146	87	74.2	64.2	56	62.6
prox epi: MLD	22		15	12.2	11.5	12
prox epi: APD	16.1		10.2	8.6	7.5	
dist epi: MLD	33.6*		22.1	14.8	13.4	13.6
dist epi: APD	19*		14	10.8	9	10.1
L (dist epi-dist rim radial tuberosity)	114		54.2	48.5	43.1	50.4
Scapholunar						
body: MLW	18.5		15.5	10.6	10	
body: APW	17.5		13	8.3	8	
max MLW (incl. post. tubercle)	23.6		16.5	12.2	10.5	
max APW (incl. post. tubercle)	22		15	11	9.5	
Metacarpals						
Mc I max L	37.50		24.80	16.80	15.50	
Mc II max L	48.80		35.00	22.20	20.70	
Mc III max L	55.8		40.1	28.6	25.1	
Mc IV max L			42	29.9	26.4	
Mc V max L			34.50	22.70	20.60	
Ratio Mc III to limb L	0.147		0.188	0.158	0.156	
Ratio of Mc III to Mc I	1.49		1.62	1.70	1.62	
Ratio of Mc III to Mc II	1.14		1.15	1.29	1.21	
Ratio of Mc III to Mc IV			0.95	0.96	0.95	
Ratio of Mc III to Mc V			1.16	1.26	1.22	
Ratio of Mc II to Mc I	1.30		1.41	1.32	1.34	
Ratio of Mc II to Mc IV			0.83	0.74	0.78	
Ratio of Mc II to Mc V			1.01	0.98	1.00	
Ratio of Mc IV to Mc I			1.69	1.78	1.70	
Ratio of Mc IV to Mc V			1.22	1.32	1.28	
Ratio of Mc V to Mc I			1.39	1.35	1.33	
Ratio of Mc II to limb L	0.13		0.17	0.13	0.13	
Ratio of Mc I to limb L	0.10		0.13	0.10	0.10	
Brachial Index	0.82	0.80	0.75	0.73	0.70	0.74
FctL radius/Lm1	7.12	5.47	4.03	4.67	3.61	
FctL humerus/Lm1	8.68	6.86	5.37	6.39	5.16	
FctL radius/C2 DBL	5.03		3.07	4.09	4.03	
FctL humerus/C2 DBL	6.14		4.08	5.59	5.76	

*Estimated value.

Data are personal, except those for *Enhydritherium terraenovae*, from Lambert (1997). Abbreviations: *Enhydrit. terra., Enhydritherium terranovae*; M.A.R., Moss Acres Racetrack; *persp., perspicillata*.

Table 6. Comparisons of postcranial measurements (mm) and indexes of **S. beyi sp. nov.** with extinct and extant taxa: pelvic limb

	S. beyi sp. nov. TM 171-01-033	cf. Aonyx sp. TM 219-05-001	S. hendeyi PQL 41523	E. terra. M.A.R.	P. bras. A 1918	Lu. lutra CG 1996-2466	Lo. felina CG 1995-185	Lutro. persp. CG 1960-3670	Ao. capensis CG 1883-1561
Condylobasal L skull					151.5	122	107.2		
Lm1	20.5			15.9	18.4	13.75	15.5		
Hip									
max acet D	32				21.0	16.0	14.6		21.0
min acet D	30.5				19.8	15.3	12.7		17.8
Femur									
L max	195	129	165		99	92.5	79.2	83.4	112.5
FctL	182.3	122.7	154.3	123	93	86.5	72.4	77.9	107.0
AP head D		17.8			17	13.3	11.7	12.8	15.2
prox epi: MLW		38.1			35	26.9	24.7	26	34.4
dist epi: MLW		34			30.5	24.5	20.9	22.9	28.8
dist epi: APW		31.4			27.5	22.2	18.5	22.9	26
APW pat art		16.3			14.5	10.7	9.1	9.8	13
neck: max D	19.7	15	16.6		13.5	9.8	8.7	10.7	13
neck: min D	14.3	11.3	10		9.5	7.7	6.1	7.3	9.2
MLD at mid-FctL	21	15.1	20.2		14	10.2	9.7	10.5	10.5
APD at mid-FctL	17.3	13.1	16.4		10.8	8	7	8.3	9.7
min MLD dia	21	15			14	10.2			
APD same level	17.3	13			10.8	7.9			
IS	1.16	0.97	0.92		0.73	1.17	0.98	0.89	1.43
Tibia									
FctL	178–210			125	122	101	85.8	100.5	124.1
prox epi: MLW					32	24.7	21.7	24.2	30
prox epi: APW					25.5	21.3	16.3	20.2	25
dist epi: MLW					24.1	17.4	16.5	20	22.5
dist epi: APW					17.8	13	12	13.4	15.5
MLD at mid-FctL	16.6				9.5	9.8	5.9	6.8	8.5
APD at mid-FctL	21				14.3	15.6	8	10.7	10.6
Crural Index	0.98–1.15			1.02	1.31	1.17	1.19	1.29	1.16
FctL femur/Lm1				7.74	5.05	6.29	4.67		
FctL tibia/Lm1				7.86	6.63	7.35	5.54		
FctL radius/FctL tibia	0.69–0.82				0.61	0.64	0.65	0.62	

Calcaneum					
max L	60	41.5	29.5	25	39.5
dist MLW	31.5	25.2	16	15	22
min MLW body	9.6	8.2	4.9	4.3	6
Astragalus					
max L	34.9	27	18.7	17.6	24.6
L of lat condyle	28.5	20	13.8	12.9	17
max ML dia head	18	13.7	10.1	8.6	
min ML dia neck	12.7	11.8	8	6.2	
Metatarsals					
Mt I max L		30.7	24.1	23.3	
Mt II max L	56.1	45.7	35.7	31.3	
Mt III max L	61	54.5	41.9	35.1	
Mt IV max L	63	57.8	44.1	38	
Mt V max L		52	36.5	32.5	
Ratio Mt I to limb L		0.11	0.10	0.12	
Ratio Mt II to limb L	0.12–0.13	0.17	0.15	0.16	
Ratio Mt III to limb L		0.20	0.18	0.18	
Ratio Mt IV to limb L	0.14–0.15	0.21	0.19	0.19	
Ratio Mt V to limb L		0.19	0.16	0.17	
Ratio Mt I to Mt IV		0.53	0.55	0.61	
Ratio Mt II to Mt IV	0.89	0.79	0.81	0.82	
Ratio Mt III to Mt IV	0.97	0.94	0.95	0.92	
Ratio Mt V to Mt IV		0.90	0.83	0.86	
Ratio Mt I to Mt III		0.56	0.58	0.66	
Ratio Mt II to Mt III	0.92	0.84	0.85	0.89	
Ratio Mt V to Mt III		0.95	0.87	0.93	
Ratio Mt I to Mt II		0.67	0.68	0.74	
Ratio Mt I to Mt V		0.59	0.66	0.72	
Ratio Mt II to Mt V		0.88	0.98	0.96	

Data are personal, except those for *Enhydritherium terraenovae*, from Lambert (1997). Abbreviations as in Table 4 and: *bras.*, *brasiliensis*; *E. terra.*, *Enhydritherium terraenovae*.

ulnar articulation and the articular circumference of the head only. The right radius is represented by a short fragment of the diaphysis. The proximal epiphysis is mediolaterally elongated (mediolateral diameter = 22 mm; anteroposterior diameter = *c*. 16 mm) and weakly depressed, especially laterally. The articular surface with the radial notch of the ulna is curved, although incompletely preserved. On the anterior margin, a small coronoid process is present. It is somewhat medially positioned relative to the mid-width of the head. The neck is only slightly antero-posteriorly compressed. The radial tuberosity is on the posteromedial surface of the diaphysis, located relatively proximally; this tuberosity, on which the tendon of the M. biceps brachii inserts, is highly developed and has a strongly indented circular surface that is about 10 mm in diameter. The interosseus tuberosity lies on the posterolateral surface of the diaphysis. It is strongly marked, with the distal half being very rugose; it is 6–7 mm wide and 25 mm long and its proximal rim reaches the level of the distal rim of the radial tuberosity. Distally, the diaphysis curves backwards and becomes semicircular in section, with the lateral side being rounded and the medial one rather flat. The latter, which is the area of insertion for the M. pronator quadratus, is particularly widened distally, being up to 17 mm in width mediolaterally. Posteriorly, the lateral and medial sides of the diaphysis meet at an acute angle, resulting in a strong, crest-like posterior face. The diaphysis is anteriorly rounded, with an attachment surface for the M. supinator extending distally as far as two-thirds the length of the epiphysis; unlike *P. brasiliensis* or *Lu. lutra*, the distal limit of the insertion is poorly rugose and not prominent. Just laterally, the groove for the tendons of the Mm. extensor carpi radialis brevis and longus is wide but poorly marked; however, on the anterior face of the distal epiphysis, this groove is more marked and wide. The distal epiphysis does not show the grooves for the tendons of the M. abductor pollicis longus and M. extensor digitorum communis, because its medial and lateral sides are damaged. The styloid process is incompletely preserved, but was developed and medially extended, offering a large surface for the attachment of the tendon of the M. brachioradialis and the radiocarpal ligaments. The articulation for the ulna is widely separated from that for the scapholunar; it is large and prominent, to a greater extent distally, with a depressed surface that faces posterolaterally. The articulation for the scapholunar is well preserved except for its posterolateral margin. This articular surface is only slightly transversely elongated, being somewhat more anteroposteriorly than mediolaterally extended; it is roughly triangular, with a posterior extremity pointing backwards. As mentioned above,

the anterior face displays a marked groove for the tendons of M. extensor carpi radialis; the lateral rim is markedly convex, while the medial rim is slightly concave. The centre of the articular surface is depressed.

The right scapholunar (Fig. 5F, G) and the left magnum (Fig. 6A–C) represent the carpus. Both are relatively well preserved but show small cracks in some places. The proximal face of the scapholunar is almost entirely occupied by the articular surface for the distal epiphysis of the radius. It is mediolaterally weakly extended, hence having a square shape, and is entirely convex. The scapholunar tubercle is long and posteromedially projected; it is proximodistally developed and the groove for the tendon of the M. flexor carpi radialis is shallow. The distal face of the scapholunar is divided into two approximately equal parts by a prominent ridge. The medial half includes the articular surfaces for the trapezoid and trapezium. The former is very extended and very steep, facing distomedially; it is not concave as in most carnivorans, but mostly convex, with only its posteromedial part being slightly concave. The articular surface for the trapezium is a very reduced, transversely narrow and fully concave area; it lies anterior to the trapezoid surface and extends slightly on the posteromedial face of the scapholunar tubercle. On the lateral half of the distal face of the scapholunar we distinguish three articular surfaces corresponding to the three lateralmost carpal bones of the distal row, the magnum (or capitate), the unciform (or hamate) and the pyramidal (or ulnar or triquetrum). The articular surface for the magnum is the most concave; it forms a narrow surface that is wider posteriorly than anteriorly, does not extend to the anterior margin of the scapholunar and is distally orientated. A low ridge separates this articulation from that for the unciform, which is, by comparison, less depressed, wider anteriorly than posteriorly and does not extend as far posteriorly. The unciform surface is distally and to a small degree laterally orientated. Between these two surfaces, the posterior rim of the bone has a strong tubercle. Posterolateral to the articulation for the unciform, there is small, crescent-shaped surface for the articulation of the pyramidal; this surface forms a gentle curve and is mainly laterally orientated.

On the left magnum the articulation for the Mc III is strongly concave, narrow and slightly more transversely extended anteriorly than posteriorly. The articulation for the scapholunar is narrow; it is strongly convex in its proximal part but its anterior slope is nearly straight. The articular surface does not extend far posteriorly. Nevertheless, it extends somewhat laterally and, to a greater extent, medially. On the medial face, the distal margin displays an elon-

gated articular surface for the Mc II that is anteriorly large and convex, and posteriorly more reduced but elongated and slightly depressed. Just proximal to the posterior part, there is a small, triangular and roughly flat surface for the trapezoid. The distal margin of the lateral face displays two articular surfaces for the unciform. Typically, the dorsal articulation is extended and the ventralmost one is very reduced; the two surfaces are connected distally.

Several metacarpals are preserved. From the left hand, we have complete Mc I (Fig. 6D, G, H), II (Fig. 6E, I, J) and III. A complete Mc III (Fig. 6F, K, L) and a distal fragment of Mc II represent the right hand. A fragment of metapodial representing either Mc V or Mt I is also preserved. It lacks the head and base, the diaphysis is short, curved and tapers off distally. It is roughly rounded in cross-section but becomes to a small degree anteroposteriorly compressed distally. Given the shortness of the shaft, this is not a central metapodial. The Mc I, which is described below, is totally different and the Mt V, by analogy with that of extant otters, is expected to be much longer. Except for their epiphysis, the Mc V and Mt I are similar, their shaft being nearly the same length in for example, *Lutra lutra*, *Pteronura brasiliensis* and *Lontra felina* (see Tables 5, 6). The posterior rim of the base of the Mc I is not preserved; the base is extremely developed compared with the head. Although the articular surface for the trapezium is very small on the scapholunar, it is fairly large on the Mc I; it is very convex and has an anterior rim that is oblique relative to the long axis of the shaft. The latter is approximately round in section. Though it is incompletely preserved, the head was probably very reduced. The base of the Mc II is asymmetrical, the medial articular surface being more developed than the lateral one; the proximal articular surface for the trapezoid is narrow, about the width of the proximal shaft and is only slightly transversely wider anteriorly; the posterior rim has slightly rounded angles. The medial articular surface is located for the most part anteriorly, where it is proximodistally extended. In this part, there is no visible distinction between two articular surfaces and therefore we cannot estimate the relative proportion of the proximalmost portion articulating with the magnum and the distalmost portion articulating with Mc III; the articular surface then extends slightly backwards along the proximal margin of the base. The anterior corner of the medial face is not preserved, and hence the articular surface for the trapezium is not visible. The shaft is weakly curved, to a greater extent proximally. The insertion for one of the tendons of M. extensor carpi radialis longus is well pronounced and crest-like, located medially on the anterior face at approxi-

mately one-third of the length. The shaft becomes increasingly anteroposteriorly compressed distally. The head is wide and anteriorly well rounded; it is slightly asymmetrical, with a slightly more reduced medial part. The sagittal crest is well developed posteriorly and the sesamoid fossa is shallow. The Mc III is much longer than the Mc II. The base is narrow and its medial and lateral margins gently converge posteriorly; the lateral margin is slightly concave in proximal view. Medially, the articulation for the Mc II is proximodistally elongated and somewhat proximally orientated. The lateral face of the base displays two articular surfaces separated by a deep trough. The surface for the Mc IV is similar in shape to the articulation for Mc II, although it is anteroposteriorly more extended; the posterior articular surface is smaller than the anterior one, anterodorsally elongated and located along the margin of the magnum surface. The insertion for the tendon of the M. extensor carpi radialis brevis is located just distal to the base; it is very deep and much more pronounced than that for the long branch of this muscle on Mc II, extending to approximately one-third of the length of the diaphysis. The latter is distally more compressed than in Mc II. The head is more symmetrical but its sagittal crest is less prominent than that of Mc II.

Only five proximal phalanges are preserved (Fig. 6M–V). They obviously belong to different digits but it is almost impossible to determine whether they belong to the pes or manus. All of them are relatively long and have a dorsoventrally compressed, poorly curved shaft. The base is generally stronger than the head and the diaphysis is less compressed proximally than distally. The base of three of the phalanges is stronger than in the others due to an enlarged flexor face, which is marked by strongly rugose attachment surfaces; these phalanges also show a markedly rough surface distally for the attachment of the proximal digital annular ligament that encloses the various branches of the tendons of the flexors of digits.

The small fragment of the left hip that is preserved includes the nearly complete acetabulum with the anterior part of the ischion and the dorsal part of the ilion neck (Fig. 7A, B). The acetabulum is almost perfectly rounded and displays a lunate surface that is more expanded anteriorly than posteriorly. The acetabular notch is wide and deep. Just anterodorsal to the acetabular margin, the insertion for the tendon of the M. rectus femoris forms a deep and wide groove. The ilion neck is very short but thick, and the iliac spine displays a shallow ischiatic notch. The ischiatic spine is poorly convex. The ischion is mediolaterally flattened; it has a medial surface softly depressed; both the ventral and the dorsal rims are

sharp, but the former is the thinnest. The obturator foramen does not extend anteriorly beyond the middle of the acetabulum.

Neither of the femurs is complete. The left one, which is the better preserved, lacks the distal and anterior portion of the head, the anterior face of the greater trochanter, and the distal epiphysis (Fig. 7F, G); the right femur lacks the proximal epiphysis and most of the distal one, representing only the posterior part of the lateral condyle and the intercondyloid fossa (Fig. 7H). The two femurs allow us to estimate the minimum total length of the bone at 195 mm and, consequently, slightly less for the minimum functional length. The fovea capitis of the femur is located medially. The greater trochanter extends slightly beyond the femoral head; its lateral face is slightly flattened and anteroposteriorly extended. The attachment surface for the tendons of most of the extensors of the hip joint and rotators of the femur (Mm. gluteus medius and profundus, and M. piriformis) is large and proximodistally elongated. The attachment for the M. gluteus superficialis is located very distally, even distal to the lesser trochanter; it consists of a distinct, rugose elliptical area (identified as a 'third trochanter' by Evans, 1993). The trochanteric fossa is oval, deep and proximodistally extended. The lesser trochanter is large, posteromedially orientated and markedly distal to the fossa, which results in a large attachment area for the M. quadratus femoris located between the fossa and the lesser trochanter. Distal to the lesser trochanter, the shaft is straight and somewhat anteroposteriorly compressed. The lateral femoral crest is prominent throughout half of the shaft length. The lateral condyle is narrow and the intercondyloid fossa is wide. The origin for the main head of the M. peroneus digiti quinti is a small rounded depression just proximal to the condyle on its lateral face. The insertion for the tendon of the M. popliteus, near the distal rim of the lateral face of the condyle, is about the same size and morphology. Only the posterior part of the insertion for the tendon of the M. extensor digitorum longus is visible; it is located between, but slightly anterior to, the insertions for the two aforementioned muscles. There is a contradiction between Fischer (1942) and Howard (1975) relative to the attachments of these muscles. According to the former, the M. peroneus digiti V attaches on the fibula and the M. peroneus longus on the femur, whereas it is the opposite in Howard (1975). In pinnipeds also, the M. peroneus longus arises completely or partly from the distal part of the femur (e.g. Howell, 1929; Mori, 1958; Bryden, 1971; Piérard, 1971). However, we follow Howard (1975), as M. peroneus longus never attaches on the femur in other carnivorans, such as bears (Davis, 1964), domestic dogs (Evans, 1993) and many other mustel-

ids (Hall, 1926, 1927). Comparing the insertions of these muscles in non-lutrine carnivorans raises questions about the homology of the M. peroneus digiti V. Previous authors (e.g. Hall, 1926, 1927; Fischer, 1942; Davis, 1964; Howard, 1975; Barone, 1986, 2000; Evans, 1993) recognize the Mm. peroneus (or fibularis) longus and brevis, but the third muscle of the peroneus group is variably named M. peroneus digiti V, M. peroneus quinti brevis, M. peroneus tertius or M. fibularis tertius (as in humans), which all refer to the same muscle; the M. peronaeus (sic) intermedius or quartus mentioned in *Potos flavus* (Beswick-Perrin, 1871) may also be the same muscle. In addition, the synonymy of the M. extensor digitorum lateralis and M. peroneus digiti V in domestic carnivorans is also clear in the myological description of the domestic dog in Barone (1986: fig. 395; 2000: 963) and Bourdelle & Bressou (1953: 452), and in that of the domestic cat through a comparison of Barone (2000: fig. 459) and Wischnitzer (1993: 187, 189) who give the names M. extensor digitorum lateralis and M. peroneus tertius, respectively, to exactly the same muscle. Additional support of this synonymy can be found in Evans's (1993) anatomical description of the dog, which uses the name 'M. extensor digitorum lateralis', and in many other descriptions of carnivoran myology, which include only either one or the other of these names but never both of them. Thus, a third branch of the M. peroneus is also present in pinnipeds (M. peroneus digiti V: Howell, 1929; M. extensor digitalis lateralis: Bryden, 1971; Piérard, 1971), in ursids (M. peronaeus tertius; Davis, 1964), in the domestic cat (M. peroneus tertius; Wischnitzer, 1993), in viverrids (M. peroneus tertius in *Genetta genetta*, *G. tigrina*; Taylor, 1976), in herpestids (M. peroneus tertius in *Herpestes ichneumon*, *Ichneumia albicauda*; Taylor, 1976), and in many mustelids, with additional information on its relative weight (M. peroneus digiti quinti in *Enhydra lutris*, *Lutra lutra*, *Vormela peregusna*, *Martes foina* and *Meles meles*; Gambarjan & Karapetjan, 1961) or its anatomy (M. peroneus quinti brevis in *Mephitis mephitis*, *Martes americana* and *Taxidea taxus*; Hall, 1926, 1927). In almost all of these descriptions, however, the origin of this muscle is located on the fibula or tibia, unlike in *Enhydra*. The origin of the tendon of the M. peroneus digiti V on the lateral condyle of the femur in *Enhydra* would therefore be unique among carnivorans, if confirmed by dissections.

The left tibia is the best preserved (Fig. 7C–E); it lacks the proximal quarter and fragments of the medial and lateral face of the distal epiphysis. Only the distal part of the popliteus depression is preserved and it occupies almost all of the posterior face of the diaphysis; a small nutrient foramen is also visible medially on this face. The tibial crest is thick

and extended distally. The small elliptic attachment area for the tendon of the M. semitendinosus is located somewhat medially on the distal part of the crest. The distal two-thirds of the interosseus face are marked by a crest, which forms the anterior and lateral limits of the insertion area for the M. tibialis posterior. The latter is a very elongated insertion on the distal two-thirds of the diaphysis; distally it occupies almost the entire lateral half of the posterior face and then gradually tapers proximally. A discrete ridge marks the medial limit of this insertion and separates it from the wide attachment for the M. popliteus. The medial malleolus is short but mediolaterally thick, and is slightly laterally orientated. The distal epiphysis is wide. The articulation for the astragalus is shallow; a low ridge separates the two parts of the articular surface, each of which articulates with the astragalar condyles. The lateral articular surface is less depressed than the medial one and faces distolaterally, while the medial one is orientated distally only.

Preserved tarsal bones include the left astragalus and navicular of TM 171-01-033. We also assign to the species a left calcaneum (TM 74-99-015; Fig. 7R–U). The latter fits perfectly with the astragalus of TM 171-01-033 (Fig. 7I–L), which indicates similar body size for the two individuals. The lutrine characters of the calcaneum are distinct on TM 74-99-015. The cuboid articular surface is small and oval, being mediolaterally expanded, and markedly depressed. Relative to the long axis of the tuber, the cuboid facet is orientated somewhat medially. Lateral to the facet, the trochlear process (coracoid process in Davis, 1964: 120; peroneal tubercle in Fischer, 1942: 17) forms a massive, distally hooked shelf; it is proximodistally long, extending beyond the cuboid facet distally, and reaching the distal part of the proximal articular surface proximally; the process then continues proximally as a low crest, which is probably the dorsal limit of the attachment of the M. quadratus plantae. The lateral face of the distal extremity of the process is proximodistally extended and marked by a deep groove. This portion is usually flat or slightly convex in extant otters. It is worth noting that a similarly grooved trochlear process has been observed in pinnipeds (e.g. *Odobenus rosmarus*, *Callorhinus ursinus* and *Eumetopias jubatus*). An additional difference from extant species is the presence of a deep and wide groove on the ventral face of the process; it is ventrally limited in its distal part by the tubercle for the long plantar ligament, and in its medium part by a smaller tubercle that is probably the ventral attachment of the annular ligament maintaining the tendinous bundle. According to Davis (1964), the trochlear process is the area of attachment for the Mm. extensor digitorum brevis

and quadratus plantae. However, according to Fischer (1942) and Howard (1975), in otters the M. quadratus plantae attaches on nearly the entire lateral surface of the calcaneum (see above). The groove on the lateral aspect of the distal calcaneum may therefore serve for various ligaments or tendons related to the musculature of the lateral calcaneum such as the tendons for the Mm. calcaneometatarsalis and the tendons of the various branches of the M. peroneus. Although the insertion origins and attachments of the latter vary slightly between *Lo. canadensis* and *E. lutris*, their path is similar in both species. In particular, the tendons of the Mm. peroneus longus and brevis probably pass through the groove that is present laterally on the trochlear process and we may thus infer a similar pattern in the fossil species. In pinnipeds, Howell (1929: 100) and Mori (1958: 227) state that the lateral groove of the prominent trochlear process serves for the tendon of the M. peroneus longus; it is less clear in Piérard (1971: 101), who mentions that the tendon of the M. peroneus longus runs in a 'groove on the lateral aspect of the calcaneus'. On the ventral face of the distal calcaneum of TM 74-99-015, the tubercle for the attachment of the long plantar ligament is ventrally proximodistally developed. The medial articular surface is supported by a very laterally projected sustentaculum tali; the surface is small, rounded and softly depressed; it is extended anteriorly but it is not clear whether there is a small anterior articular surface. The presence of the latter in extant species is variable (Stains, 1976). On the ventral surface of the sustentaculum, the groove for the tendon of the M. flexor hallucis longus is not distinct. The proximal articular surface is smooth and moderately convex compared with the extant taxa; it has its maximum height in the middle and does not extend much proximally. The groove that separates the medial and proximal surfaces is wide. The tuber is relatively long and transversely compressed, though it thickens proximally. The extremity of the tuber is not perfectly preserved but it was certainly poorly grooved; it slopes distally so that the ventral corner is anterior to the dorsal corner. The medial tubercle of the tuber is more developed than the lateral one, which is nearly absent. The area of attachment of the tendon for the M. gastrocnemius extends ventrad in the form of a well-developed tubercle, which probably also serves for the insertion of the M. calcaneometatarsalis, as in *Lo. canadensis* (Fischer, 1942: fig. 34). From comparisons that were done within other extant otters, this tubercle has been observed in *Aonyx capensis* (MNHN CG1883-1561).

The left astragalus lacks the ventral and dorsal margins of the head, a part of the astragalus tubercle and the distal margin of the medial condyle (Fig. 7I–

L). The astragalus body is wide while the trochlea is very shallow, as in *P. brasiliensis*. The articular surface for the tibia is as wide as it is long and does not extend far proximally. The proximal extremity is occupied by the astragalar tubercle, which is large and protrudes ventrally, although breakage prevents us from observing its full extent. On the proximal face of the tubercle, just ventrally to the articular margin, there is a large astragalar foramen and several additional small foramina. The medial condyle is distally short and does not reach the distal extension of the lateral one; distally its articular surface does not extend on the medial face. The neck is long and distomedially orientated. The neck and the head are dorsoventrally compressed and the navicular articular surface is strongly convex. The latter does not contact the articulation for the calcaneum on the ventral face. Nevertheless, there is a small articular facet for the cuboid on the ventrolateral face of the neck. The fibular articular surface can be seen on approximately the distal half of the lateral surface of the body; it is dorsoventrally very tall and its smooth surface is ventrally strongly depressed, with a laterally projecting ventral rim. The ventral surface of the astragalar body displays two distoproximally elongated articular surfaces separated by a deep groove in their distal two-thirds; the medioproximal third of the face is occupied by the astragalar tubercle. These articular surfaces diverge distally; the lateral one is wider than the medial and ventrolaterally orientated, while the medial surface tapers off proximally and is strictly ventrally orientated. The medial surface is proximally more extended than in *Lu. lutra*, *Lo. felina* or *P. brasiliensis*, and is also strongly concave in its proximal part.

The left navicular is complete (Fig. 7V–Y). It is dorsoventrally elongated and proximodistally compressed. The proximal surface is almost entirely occupied by the articulation for the astragalus, which is elliptical and deep. The ventrolateral tubercle is small and distally slightly protruding. The distal face displays three articular surfaces. The largest is for the proximal surface of the ectocuneiform. It is gently depressed and occupies the dorsolateral part of this face; it is dorsolaterally orientated and makes a slightly obtuse angle with the articular surface for the mesocuneiform, from which it is separated by a ridge. The relatively small angle (approximately 90°) between these two surfaces is a marked difference from *Ao. capensis*, *P. brasiliensis*, *Lo. felina* and *Lu. lutra*, in which the angle is much more opened. The remaining distal articular surfaces of the navicular are located along the medial rim of the bone. That for the mesocuneiform is slightly ventral to the ectocuneiform surface; it is dorsoventrally elongated and nearly flat, though the dorsal and ventral margins are

visible. The articular surface for the entocuneiform is even more elongated but is smaller, less dorsoventrally extended and slightly convex. A small facet for the cuboid is present on the navicular. It is slightly convex, located on the dorsolateral face of the bone and makes a slightly obtuse angle with the ectocuneiform articular surface.

Five complete or nearly complete metatarsals are preserved in TM-171-01-033: the right Mt II, III and IV, and the left Mt II (Fig. 7M, N) and IV (Fig. 7O–Q). Compared with extant otters, all of them are proportionally shorter and have a more robust shaft; the latter is proximal, mediolaterally compressed, but distally it becomes gradually dorsoventrally compressed. The Mt II has a triangular section in the proximal half and a triangular proximal articular surface; distally the shaft is more compressed laterally than medially. The base is similar to that in extant otters: it is dorsoventrally elongated, triangular with a pointed ventral extremity, its surface being concave, with a proximally prominent lateral rim. The head of the Mt II is slightly asymmetrical and is not different from that of any one of the other lateral or medial metapodials. The base of the Mt III is not preserved. The length, morphology and shape of the distal portions of the lateral articulations with Mt IV support its assignment to the Mt III. In contrast with that of Mt II or IV, the head is roughly symmetrical and transversely more elongated, which are additional arguments for the anatomical identification of this bone. The left Mt IV is complete except for the ventral part of the proximal articular surface. The base is wide and the articulation projects laterally, which results proximally in a marked concavity of the lateral side of the bone. The proximal articular surface is dorsoventrally elongated; the lateral surface, which articulates with Mt V, is depressed anteriorly but nearly flat posteriorly. On the medial face of the base, the small elliptical articular surface for the Mt III is less prominent and closer to the proximal surface than in *Lu. lutra*, *Lo. felina* and *P. brasiliensis*.

Comparisons with fossil taxa
Fossil otters are relatively common in the late Miocene of Eurasia and Africa and most of them can be assigned to one of the aforementioned extant tribes. Recently, however, bunodont species of the genera *Enhydriodon*, *Sivaonyx*, *Vishnuonyx* and *Paludolutra*, which were previously included in the tribe Enhydrini (see Willemsen, 1992), have been assigned to a new tribe, the Enhydriodontini, by Morales & Pickford (2005). As pointed out above, however, the distinction between tribes based on dental morphology only is not in agreement with the classification based on molecular analyses. In our opinion, the

creation of another tribe including *Sivaonyx*, to the exclusion of *Aonyx*, does not help to clarify the interrelationships of the Lutrinae. In such a scheme, genera such as *Aonyx* and *Sivaonyx* are classified in two different tribes, while their dentitions and mandibles are morphologically very similar.

The material from Chad shows a closer resemblance to other extinct bunodont taxa of Africa than to any other taxa. These African species are now assigned to the genus *Sivaonyx* (Morales & Pickford, 2005), which is therefore the assignment that we give to the Chadian material. Valuable comparisons require that we first address the following issues: (1) the significance of the size and morphological variations displayed by the Chadian material; (2) the support for the presence of two species of the genus in the Lukeino Formation and, consequently, the number of valid species of *Sivaonyx* in Africa; and (3) the significance of the evolutionary trends suggested by Morales & Pickford (2005), i.e. increasing size and morphological modifications of carnassials over time.

We have noted that the reduction of the premolars is stronger in TM 171-01-033 and TM 172-05-001 than in the other individuals from this area; they lack p1, but a single-rooted p2 and a p3 with two partially fused roots are present. If they had been found elsewhere, these specimens would possibly have been assigned to a distinct species. However, the material assigned to *S. beyi* comes from geologically contemporaneous sites in the same fossiliferous area, and, other than this reduction in premolars, TM 171-01-033 and TM 172-05-001 do not show any significant differences relative to the other TM specimens. Such variation in the occurrence of already reduced teeth (e.g. p1, p2), is well known in mustelids such as *Martes* spp. (Wolsan, Ruprecht & Buchalczyk, 1985) and *Meles meles* (Szuma, 1994). Nevertheless, the absence of p1 in TM 171-01-033 and TM 172-05-001, which are both old individuals as shown by their strong tooth wear pattern, may be misinterpreted. In fact, P1/p1 are frequently lost during the animal's life, and the alveolus is then resorbed so that these teeth may look like they were congenitally absent (Wolsan, 1989); the absence of p1 and p2 in the left tooth row of TM 171-01-033 probably results from this process. Observations of extant individuals used in comparisons, especially those of the species of *Aonyx* (although our sample is not large) also show a significant amount of variation in the presence of P1/p1 and P2/p2. In *Aonyx congicus*, P1s/p1s are absent in MNHN CG 1947-31 and MNHN CG 1966-216, but P1s are present in MNHN CG 1973-65 and MNHN CG 2005-612; in *A. capensis*, P1s/p1s are absent in MNHN CG 1897-982 and MNHN A 1899 but P1s are present in MNHN A 1914, while in MNHN A 3388 the left P1

only is absent (the right P1 and the p1s are present). Moreover, P1 is also known to often be absent in *Lo. felina* and completely lacking in *Amblonyx cinereus* and *Enhydra lutris* (Van Zyll de Jong, 1972). The P2/p2 are present in all observed *Aonyx* specimens, except that p2s are absent in MNHN A 1899 (*Aonyx capensis*) and the left p2 in MNHN CG 1966-216 (*A. ?congicus*). We conclude that the sample from TM probably illustrates intraspecific variation and therefore represents a single species.

In their review of the giant African bunodont otters, Morales & Pickford (2005) recognize six species of *Sivaonyx* of which two are known from Lukeino, *S. soriae* and *S. senutae*. The presence of two morphologically very similar species in Lukeino is questionable, especially when the only mentioned difference is body size, with *S. senutae* being the larger. No direct comparison can be made between these species, as one is based on lower carnassials (Lm1 = 17.5–17.6 mm in *S. soriae*) while the other is known from upper teeth only (LP4 = 14.8; LM1 = 12.3 in *S. senutae*). However, it is possible to estimate Lm1 in *S. senutae* (or LP4 in *S. soriae*) from an Lm1/LP4 ratio calculated for the holotypes of *Sivaonyx hendeyi* (SAM-PQ L 5000) and *S. ekecaman* (KNM-KP 10034), which are both known from lower and upper carnassials. This ratio is 1.26 in *S. hendeyi* and 1.28 in *S. ekecaman*, which results in estimates of Lm1 in *S. senutae* of 18.65–18.95, respectively. Taking into account the size range in the TM sample (or in most of the extant species), the size difference between *S. senutae* and *S. soriae* is not great enough to indicate a specific distinction. These species must be regarded as synonyms, with the first one created, *Sivaonyx soriae*, being the valid name. Therefore, in the comparisons below, the material assigned to *S. senutae* will be discussed under the name *S. soriae*.

According to Morales & Pickford (2005), African bunodont otters show two major evolutionary trends: an increase of size over time and a morphological modification of carnassials. The material described here displays a relatively great variation of size, Lm1 ranging from approximately 20 to 22.8 mm. The size range of the Chadian species thus encompasses the size range of the three most recent species of *Sivaonyx*, *S. ekecaman*, *S. hendeyi* and *S. africanus*. By contrast, the type species *S. bathygnathus* and *S. soriae* are distinctly smaller and *S. kamuhangirei* larger than the Chadian species, but only the former may be stratigraphically older than the Chadian *Sivaonyx* (see below). Hence, the latest Miocene and Pliocene *Sivaonyx* species are either much smaller than (*S. soriae*), similar in size to (*S. ekecaman*, *S. hendeyi*, *S. africanus*) or larger than (*S. kamuhangirei*) *Sivaonyx beyi*. This does not support the postulated increase of size over time in *Sivaonyx*.

We acknowledge that, between *S. bathygnathus* and *S. ekecaman*, the morphology of m1 has been modified. However, more information on intraspecific variation is required to assess the evolutionary significance of this trend.

Comparison with Sivaonyx bathygnathus, type species of the genus Sivaonyx (Lydekker, 1884): This species is based on a fragmentary left hemimandible with partial p4, m1, and alveoli of c and p1-p3 (GSI D33) illustrated by Lydekker (1884: pl. 27, fig. 3), then re-drawn and figured by others (Pohle, 1919: pl. 2, fig. 2; Matthew, 1929: fig. 8). The origin and age of the type material are not precisely known. It is well known that fossil specimens from the Siwaliks of India and Pakistan collected during the 19th and early 20th centuries are generally not precisely located, and that mention of general stratigraphical units such as 'Dhok Pathan Stage' are of limited use, because they do not necessarily correspond to the 'Dhok Pathan Formation' and were often confused with lithostratigraphical units (Barry, 1995). Recent investigations on the Potwar plateau have resulted in a better understanding of the geology, stratigraphy, chronology and other features of the Siwalik sequence (Barry *et al.*, 2002), and have yielded a large amount of fossils of mammals, including new material of fossil otters of the genera *Sivaonyx* and *Vishnuonyx*. On the Potwar plateau, *S. bathygnathus* ranges in age from 10 to 6.2 Ma. If this range includes more than one species, *S. bathygnathus* would be the stratigraphically latest and the largest. The holotype comes from Hasnot and presumably from the upper limit of the range (J. Barry, pers. comm., March 2007). If so, *S. bathygnathus* could be more or less contemporaneous with the late Miocene species of the genus, including *S. beyi*. That the type species is much smaller than our material is additional support for the lack of a trend toward increased size over time. The studied sample of *S. bathygnathus* does not include the holotype, but we have studied specimens from Siwalik Group rocks of Pakistan previously described by Pilgrim (1931) that come from two geographical areas on the Potwar Plateau, near Dhok Pathan and Tatrot-Hasnot (see Appendix 1 for detailed description and geographical origin of specimens). Study of this material indicates considerable similarity with our sample. The m1 has a very similar morphology and proportions, with a low trigonid with cuspids of approximately equal height, the paraconid, however, being slightly lower than the two other cuspids; the paraconid and metaconid are deeply separated; the talonid is wider than the trigonid, and has a large hypoconid crest, a shallow basin and a low but distinct entoconid ridge; the cingulid is marked on the labial side and may extend on the lingual side of the paraconid. The illustration known and description of the holotype also provides some information. The m1 width of this specimen is not provided by Lydekker (1884) but, from the illustration, we conclude that m1 is much narrower than those from Toros-Menalla (see also measurements inferred by Pohle, 1919: 26); oddly, however, the L/Wmax ratio of m1 in the type specimen is much greater than in the sample of *S. bathygnathus* used here (see Table 2), which may indicate either great variability in the proportions of this species or a poor quality illustration, which underestimates this measurement. The p4 of the holotype is damaged, but its outline shows a wide distal part; based on measurements taken from an illustration (Lydekker, 1884: pl. 27, fig. 3), however, the p4 of *S. bathygnathus* is much less robust (large L/W ratio) and shorter compared with the m1 length than in the Chadian material (Table 2). An additional, more prominent difference between *S. bathygnathus* and our material is size. Not only are the teeth of *S. beyi* larger, but the mandible is much thicker and taller than in the type species (Table 1).

Comparison with S. soria: This African species is much smaller than the Chadian material. Moreover, it retains three lower incisors. The M1 of *S. soriae* displays all of the features that we find in TM 90-00-066, which supports the generic assignment of the latter. However, compared with the Chadian specimen, the tooth from Lukeino is clearly less transversely elongated, has a mesiodistally more extended lingual cingulum, and has a metaconule and metacone that lie closer to each other.

Comparison with S. hendeyi: The lower carnassial of *S. hendeyi* is distinct from the corresponding tooth in our material. The Langebaanweg tooth has a talonid that is narrower than the trigonid and is more bunodont than in the Chadian species, which includes a set of characters such as a greater width, a shallower carnassial notch, an enlarged and more transversely orientated paraconid, an enlarged metaconid with less steepened mesial and distal faces, and a protoconid and metaconid that are proportionally lower relative to m1 length (Table 2); most of these features are also differences between the South African species and the other late Miocene species, *S. soriae* and *S. bathygnathus*. The relative height of the trigonid cuspids in *S. hendeyi* is similar to those in the extant species of *Aonyx*. With the exception of *S. beyi*, *S. hendeyi* is the only species of the genus for which postcranial bones have been described. Hendey (1978) assigned several postcranial specimens to the species, based on their similarity to the corresponding bones of *Aonyx capensis*. We have studied only the femur

(SAM-PQ L 41523) in detail; the astragalus mentioned by Hendey (1978) belongs to *Orycteropus afer* (Pickford, 2005). If correctly assigned, the femur provides further support for a specific distinction with the *Sivaonyx* material from Chad. This bone differs from that of TM 171-01-033 in being more robust (e.g. similar cross-section at mid-height but a much smaller total length, Table 6) and in having a larger head that is more proximally orientated, which partly results in a lower greater trochanter in comparison with the head; in addition the two trochanters are more reduced, especially the lesser one, the trochanteric fossa is proximodistally less extended, the femoral neck is anteroposteriorly thinner and the fovea capitis is more posteriorly located.

Comparison with S. africanus: The holotype includes a right M1 and right hemimandible with p4-m1 from the early Pliocene of Klein Zee (BSP 1930-XI-1). We have studied these specimens on the basis of casts in the MNHN palaeontological collection. The size of this specimen is within the range of the TM sample. The M1 of *S. africanus* displays the general cusp pattern already observed in *S. soriae* and TM-90-00-066. However, it is more robust and is less transversely elongated than in the latter, having a mesiodistally more expanded lingual cingulum; the metaconule is cusp-like and does not extend mesially in the form of a crest as in *S. beyi*. In the lower dentition of *S. africanus*, the p1 is lost and the p2 and p3 are single-rooted, with the latter displaying two fused roots. The p4 is morphologically very similar to that of *S. beyi* (TM 171-01-033) but is shorter relative to m1 length. On the carnassial of the specimens from Chad, the metaconid is shorter and thus appears more erect, having more steepened mesiolingual and distolingual margins. In this character, *S. beyi* is closer to *S. soriae* while *S. africanus* has a morphology intermediate between that of *S. ekecaman* and that of *S. hendeyi* (see Morales & Pickford, 2005: fig. 3).

Comparison with S. ekecaman: The proportions of the m1 in *Sivaonyx* are rather conservative, with the exception of *S. ekecaman*. The lower carnassial of this species is particularly wide and its talonid is long compared with other species of *Sivaonyx* (Table 2). Additional differences are a more robust, enlarged metaconid in *S. ekacaman* which results in relatively less steep mesial and distal faces of this cusp in lingual view than in *S. beyi* (and *S. soriae*). The holotype from Kanapoi also includes the single known M1 of the species (Werdelin, 2003) and confirms clear distinctions although the heavy wear pattern has obliterated some details on the Kenyan tooth. Compared with TM 90-00-066, the M1 of *S. ekecaman* is

much less transversely elongated and has lower cusps, a distinct and large parastyle, a proportionally more reduced paracone, and a much more extended lingual cingulum (see ratio Llab/Lling in Table 3). The above features of *S. ekecaman* are consistent with the hypothesis of Morales & Pickford (2005) that this species shows the greatest amount of mastoidization in the genus.

Comparison with S. kamuhangirei: This species is known only from an isolated m1 from Kazinga and an m1 talonid from Warwire (Morales & Pickford, 2005: fig. 2M, N). These specimens differ from our material in their larger size and in having an enlarged and more transversely orientated paraconid, which thus is closer to the metaconid than in the Chadian species. One diagnostic feature of this species mentioned by Morales & Pickford (2005) may be the presence of a protoconid that is larger than the metaconid, but this is difficult to determine due to the heavy wear of the m1 of the holotype.

Comparison with Sivaonyx sp. from Wadi Natron, Pliocene of Egypt: Stromer (1920: fig. 11) described and assigned an isolated m1 from Wadi Natron to *Lutra* aff. *capensis*. Howell & Petter (1979) assigned this tooth to *Enhydriodon africanus*, now referred to as *Sivaonyx*. We agree that this tooth is clearly to be related to the African species now assigned to the genus *Sivaonyx*. Its specific assignment is more problematic, however, and we recommend an open taxonomy for this specimen. The m1 from Wadi Natron is incomplete but, on the basis of the measurements of Stromer (1931), it is similar in length to that of *S. beyi*, *S. ekecaman*, *S. hendeyi* and *S. africanus*. The tooth is clearly wider than those from Toros-Menalla. The proportions and morphology are not very different from those of the other mentioned species, which are also roughly contemporaneous with the Egyptian tooth, i.e. earliest Pliocene.

Comparison with 'Enhydriodon' sp. from Nkondo, Uganda: In their reassignment of the African *Enhydriodon* species to the genus, Morales & Pickford (2005) did not discuss the systematic position of the postcranial material assigned to these species. Some of this material has been discussed in this paper when its specific assignment is known. A distal fragment of a right humerus from Nkondo was described and assigned to *Enhydriodon* sp. by Petter (1994: pl. 1, fig. 4). The generic assignment was based on the large size of the specimen, which is 35 mm wide distally. It is not that large, however, as the bone from Nkondo does not reach the size of the humerus of *P. brasiliensis* (distal width of humerus = 36.4) and is markedly smaller than that of *S. beyi* (distal

width = 53.3). If correctly assigned to the Lutrinae, this bone may therefore belong to a smaller-sized species of *Sivaonyx* or to a different genus.

Comparisons with extant taxa

In the literature, the Lutrinae may or may not be divided into tribes. In the latter case, the subfamily is frequently divided into three tribes (Lutrini, Aonyxini and Enhydrini) by morphologists (see Willemsen, 1992) on the basis of different dental and/or cranial morphologies. The species in each tribe have essentially similar diets, though these may vary greatly geographically and seasonally in some species and/or populations, depending on the availability of prey. The Lutrini includes species of *Lutra*, *Lontra*, *Lutrogale* and *Pteronura*; they generally have sharp and relatively tall teeth with cutting blades and they feed mainly on fish (Carter & Rosas, 1997; Larivière & Walton, 1998; Larivière, 1999a, 2002), but some species such as *Lutrogale perspicillata*, *Lontra provocax* and *Lo. felina* also feed on invertebrates (crustaceans and/or bivalves) (Larivière, 1998, 1999b; Hwang & Larivière, 2005). The Aonyxini (or Aonychini) includes the species of *Aonyx* and *Amblonyx*. They have wider and more robust teeth than in Lutrini, and feed mainly on crabs, including in their diet a variable amount of fish (Larivière, 2001a, b, 2003; Somers & Nel, 2003; Emmerson & Philip, 2004; Parker, Burchell & Bernard, 2005). The Enhydrini is represented by only one extant genus and species, *Enhydra lutris*, which differs from other extant taxa in its wide and low teeth with blunt cusps and no shearing blades, which is related to its diet predominantly based on bivalves and sea urchins; however, a greater dietary variability than in other otters is observed in this species (Kruuk, 2006). An alternative classification based on morphology exists (Van Zyll de Jong, 1987), which supports the Enhydrini and a separation between Old World (genus *Lutra*) and New World (genus *Lutra*) river otters, the former being associated with *Lutrogale* and *Pteronura*, the latter with the clawless otters. Whatever the morphology-based classifications, they are not supported by recent molecular studies (Koepfli & Wayne, 1998; Marmi, López-Giráldez & Domingo-Roura, 2004; Fulton & Strobeck, 2006), which all propose a different arrangement where three clades are recognized: (*Lontra*) + (*Lutra*, *Aonyx*, *Amblonyx*, *Enhydra*) + (*Pteronura*). Contra Fulton & Strobeck (2006), the Aonyxini as defined by Van Zyll de Jong (1991), which includes *Lontra* but not *Lutra* (see above), is not supported by molecular data. The molecular studies thus suggest that the Lutrini, Enhydrini and Aonychini may be based on morphological convergences rather than apomorphies. Consequently, we do not use any tribe names.

Mandible and lower dentition: The mandible and lower dentition of the fossil specimens from Chad described here are incomplete, but they are metrically and morphologically clearly distinct from those extant otters. One of the most prominent differences is the very large size of the fossil species. None of the extant species reaches such a size; even postcranial bones of *P. brasiliensis*, which may reach a total length of up to 2 m (Kruuk, 2006), are small compared with those of the Chadian otter (see Tables 5, 6, for comparative measurements). In addition to the size, the presence of only two lower incisors distinguishes *S. beyi* from all extant species except *Enhydra lutris*. Compared with the otter from Toros-Menalla, the species of *Lutra*, *Lontra* and *Pteronura* used in comparisons have among other things a sharper dentition with cutting edges on the teeth, a shorter and more gracile p4, an m1 talonid with a taller and more trenchant hypoconid crest and a low lingual border. These extant species also have a much more gracile mandible. The dentition of *Lutrogale perspicillata* is stouter than in *Pteronura*, *Lutra* and *Lontra*, and looks more like that of *Sivaonyx beyi*. In comparison, however, the smooth-coated otter has a shorter p4 relative to m1 length and with a vestigial distal accessory cuspid, an m1 with a narrower and triangle-shaped trigonid, paraconid–protoconid blades forming a more opened angle, and a talonid that is wider relative to the trigonid. The dentition of *Enhydra lutris* is morphologically completely different from that of the TM species, with robust and very blunt cuspids adapted to a durophagous diet. The greatest dental resemblance to the material from Toros-Menalla is found in extant *Aonyx* spp., the clawless otters, in particular *Aonyx capensis*. The carnassial of this species is only slightly smaller than that in the Toros-Menalla material (Table 2; and see Pohle, 1919: 141). The morphologies of the mandible and lower carnassial are rather similar. Thus, the m1 is low and wide, bunodont, and has a tall metaconid and a wide, poorly basined talonid with a wide hypoconid. However, there are also clear differences, especially in M1 and the postcranial skeleton (see below). In the lower dentition, p4 of the species of *Aonyx* is much less stout and shorter relative to m1 length (more so in *A. capensis* than in *A. congicus*; Table 2).

Upper dentition: The single upper tooth assigned to the Chadian species is an M1 (TM 90-00-066). Its assignment to *Sivaonyx* is based on comparisons with the species of *Sivaonyx* whose M1 is known (e.g. *S. soriae*, *S. ekecaman*, see above). The labial part is similar to that of the M1 of extant lutrines, except that the labial cusps are more prominent than in *Lutrogale perspicillata*, and much more so than in

Enhydra lutris. The lingual part presents many differences, however, of which only the most prominent ones are listed here. Compared with TM 90-00-066, the crest formed by the protocone and protoconule is proportionally taller in *Lutra* spp., *Lontra* spp. and *Pteronura brasiliensis*; the distinction observed in the fossil species between the protocone and the paraconule is generally absent or poorly marked in *Lutra* spp., *Lontra* spp., *P. brasiliensis*, *Amblonyx cinereus* and *Aonyx* spp.; there is generally no metaconule in *Lutra* spp., *Lontra* spp., *P. brasiliensis* and *Ao. congicus*, whilst it is variably present but never as developed as in the Chadian species in *Lutro. perspicillata*, *Ao. capensis* and *Am. cinereus*. TM 90-00-066 is also much more transversely elongated than in *Lutro. perspicillata*, *Am. cinereus* and *Aonyx* spp. (Table 3).

Postcranium: The difference in size is much greater in the postcranial bones than in the teeth (Tables 4–6), which indicates that *S. beyi* has relatively small teeth relative to its body size. The femur of *Sivaonyx* from Chad is nearly twice as long as that of *Aonyx capensis* or *Pteronura brasiliensis*, while m1 length is only slightly greater. Detailed analysis reveals further and deeper differences with extant otters. Measurements and the most common indexes of the postcranial bones are presented in Tables 5, 6. We mention here the most prominent differences, which are then discussed with regard to the functional morphology and the locomotion of *Sivaonyx beyi*.

Besides their much larger size, the caudal vertebrae of *Sivaonyx beyi* present some differences from those of the extant otters (*P. brasiliensis*, *Lo. felina*, *Lu. lutra*, *Ao. capensis*). On both the second and the fourth caudal vertebrae of *S. beyi*, the spinous process was more posteriorly located (nearly between the posterior articular processes) and has a markedly backwardly orientated basal anterior rim. In the four extant species examined, the spinous process is more or less vertical and is clearly anterior to the posterior articular processes. In the fossil species, the anterior part of the body is less dorsoventrally flattened than in *P. brasiliensis*; furthermore, the vertebral canal is less dorsoventrally compressed than in *Lu. lutra* and *P. brasiliensis*. The same differences are found on the fourth caudal of the fossil species. In addition, the posterior part of the body of this vertebra is more dorsoventrally compressed in *S. beyi*, *Ao. capensis*, *Lu. lutra* and *P. brasiliensis* than in *Lo. felina*. In the fossil, the posterior articular processes are dorsally more projecting, the caudal vertebral notch being much higher and deeper than in the extant species. In the fifth vertebra of *S. beyi* the vertebral canal is shorter and much less dorsoventrally compressed, and the caudal vertebral notch much deeper, than in the extant species. Unlike other otters, there are no

haemal arches in *Ao. capensis*. Only reduced haemal processes are present in the seventh and eighth caudals. On C4, C5 and C7, the vertebral body is somewhat mediolaterally compressed in its anterior part, and then becomes gradually dorsoventrally compressed posterad (the width of the body is more than 1.3 times its height). The anterior part of the second caudal of *S. beyi* is not preserved, but its posterior part is like that of the other caudals. The same general morphology of the body is found in the extant otters, especially *Ao. capensis*. However, it occurs only in the three first caudals in *Lo. felina*, the four first ones in *Lu. lutra* and the five first ones in *P. brasiliensis*. Posteriorly, the vertebral body becomes much less dorsoventrally compressed in its posterior part and its cross-section is then nearly round. The primary difference between the giant otter and the other species examined here is that the vertebral body of the first caudals is flattened throughout its length. All of these extant otters are known to have a long, basally flattened tail. This is particularly true of *Pteronura brasiliensis*. The main effects of this widening of the tail are: (1) to provide a larger surface of attachment for flexors and depressors of the tail, notably the Mm. sacrocaudalis ventralis lateralis and medialis; and (2) to extend the area used for propulsion during the vertical movements used in a rapid locomotion. The further widening of the anterior part of the caudal body in *P. brasiliensis* suggests an even more extended surface for muscle attachment. The giant otter is the fastest swimming of the extant species and the only one to pursue its prey rapidly over relatively long distances (Kruuk, 2006), the tail then taking an important role in the hunting. Being of such importance, the tail in otters is generally more developed in diameter than in other carnivores. Thus, in *Felis catus* or *Canis familiaris*, the caudals are less developed (e.g. spinous process small or absent, body proportionally much shorter, being as wide as it is long in the 1st caudal of the dog; Evans, 1993), and they are reduced more rapidly to simple rods posteriorly. We have made the same observations on *Canis lupus* (MNHN CG 2005-279) and *Panthera leo* (MNHN CG 1954-2) (i.e. spinous process present on the first caudal of the former only, anterior caudals more reduced, etc.). In addition, in these two species, the vertebral profile obtained by plotting vertebral body length against caudal rank (Fig. 4) is very different from that of otters, including the extinct otter from Chad; the canid and felid profiles have much greater amplitudes, showing a more extreme increase in the body length up to approximately the tenth caudal. In species of *Lontra*, *Lutra*, *Pteronura*, *Lutrogale* and *Amblonyx*, the tail is usually thickened at its base, which has to be correlated with the enlargement and dorsoventral flattening of the first caudals. These

species also have a longer tail than in *E. lutris* (30–50% of the total length of the animal vs. 20–25%; Tarasoff *et al*., 1972; Kenyon, 1981; Larivière, 2003; Hwang & Larivière, 2005; Nowak, 2005) though the tail of *Amblonyx cinereus* is said to be shorter than in *Lutra*, *Lutrogale* and *Pteronura* (Willemsen, 1980b: 312). In *Pteronura*, the tail was observed to be an active locomotor organ used to propulse the body, especially during rapid locomotion through dorsoventral sinusoidal movements (Tarasoff *et al*., 1972; Tarasoff, 1972). Although the tail is said to be flattened in *Lo. felina* (Kruuk, 2006), only the three first caudal bodies are dorsoventrally flattened, which indicates that the shape of the vertebral body and the external shape of the tail do not strictly correlate to each other. The specimens of *Lo. felina*, *Lu. lutra* and *P. brasiliensis* studied here possess haemal processes or arches on some caudals. The presence of these elements supports a greater vascularization of the tail. The haemal arch protects the median coccygeal artery and the development of these arches probably also provides extended surface of muscular attachment (Taylor, 1914), especially for the (common) tendons of the Mm. sacrocaudalis ventralis lateralis and medialis, as in the dog (Evans, 1993: 316). In comparison with the other otters, the tail of *Enhydra lutris* is more reduced, dorsoventrally flattened and of uniform width throughout its length (Kenyon, 1981); it is also shorter, which results from both the reduction in the number of caudals (18–21 instead of 24–25 in other species; Taylor, 1914; Fischer, 1942) and the shortening of the caudal bodies, which are even shorter than in a much smaller species such as *Lo. canadensis* (Taylor, 1914: figs 7, 8). There are no haemal processes or arches on the caudals of *E. lutris*. The reduction of the tail, its flatness and the absence of haemal arches on the caudals may be related to the aquatic adaptation of *E. lutris*, which uses its tail more as a rudder or a scull than as a propulsive organ according to Taylor (1914); other authors report, however, that the tail also participates in the propulsion in the sea otter (e.g. Tarasoff *et al*., 1972; Tarasoff, 1972; Kenyon, 1981). It appears that the large size of the caudals (body of the 2nd caudal is as long as that of a female *Panthera leo* MNHN CG 1954-2, m1 length = 22.9, which corresponds to a body mass of approximately 100 kg based on the regression analysis for Felidae proposed by Van Valkenburgh, 1990: appendix table 16.6), the flattening of the caudal bodies, the great development of at least the first seven caudals (e.g. with developed articular processes and spinous process), and the presence of strong haemal arches at least as far back as the tenth caudal, support the presence of a powerful muscular, basally flattened tail in *S. beyi*. The length of the tail cannot be estimated, however, nor the total number of caudals. In comparison with the extant species of otters studied here, the TM otter also has a greater number of caudals with a posteriorly flattened body, which may indicate a more powerful musculature related to the large size of the animal. The development of depressor and levator muscles suggests that the tail had an active role in the life of the fossil otter. That the tail was used as a propulsive organ in the aquatic locomotion of *S. beyi*, as in its extant relatives, is therefore probable. However, it is important to note that a long, powerful and flattened tail is not a prerequisite for swimming. *Enhydra lutris* spends most of its time in the water and has a short, slender tail compared with that of other otters; the surface of the hind feet is greatly increased, which is related to the fact that the main propulsive elements in this animal are the hind feet, not the tail, and that swimming rapidly is not a necessity (Taylor, 1914; Tarasoff, 1972). Having only a few flattened caudals as in *Lontra felina* does not preclude this animal from being completely adapted to the sea (its vernacular name is 'marine otter') and from having an externally flattened tail (Kruuk, 2006: 18). Moreover, caudals frequently have a flattened vertebral body in carnivorans, despite the fact that they are not adapted to an aquatic life. Finally, outside the Lutrinae, there are accomplished swimming carnivorans that do not show any evidence of aquatic adaptations on their skeleton (e.g. *Ursus maritimus*, *Atilax paludinosus*, *Cynogale bennetti*, *Mustela vison*; Taylor, 1989).

With only a fragment of the scapulas preserved in TM 171-01-033, it is difficult to estimate the development of the shoulder muscles in this species. The fossil species is rather similar to the extant otters studied here and displays only slight differences that may be due to individual variation. Thus, the proximal part of the scapula, especially the glenoid cavity, in *S. beyi* is slightly broader than in the extant species, which have an ML/AP diameter ratio similar to that of bears (Table 5; see Davis, 1964: 91). In addition, the supraglenoid tubercle of *Sivaonyx* from Chad is less prominent than in *Lu. lutra*, the coracoid process is vestigial as in all of the extant species except in *Lo. felina*, where it is slightly more developed, and the attachment area for the tendon of the M. triceps longus is more developed and deeper than in *P. brasiliensis*. The absence of a developed scar on the supraglenoid tubercle of the scapula may indicate a lighter attachment of the tendon of the M. biceps brachii, and therefore a lesser development of this muscle. No conclusions can be drawn, however, because there is no direct relationship between the development of the biceps insertion on the scapula and its size in carnivorans such as *Canis lupus*, *Ursus arctos* and *Panthera leo* (Bryant & Seymour, 1990). On the other hand, the development of the radial

tuberosity, as in *S. beyi*, is correlated with the development of this muscle. The more developed attachment area for the long head of the M. triceps is not necessarily evidence for better swimming ability than in *P. brasiliensis*. The very large size of the fossil species itself implies a much greater development of the supporting muscles of the body, e.g. the M. triceps brachii, which prevents the elbow from collapsing when bearing weight.

The humerus of *S. beyi* is more slender than that of the extant species except that of *Lutro. perspicillata*. The index of slenderness based on the minimum cross-sectional area of the epiphysis (Table 5; for calculation of the index, see Maynard Smith & Savage, 1956) indicates that the smooth-coated otter has the most slender humerus among the extant otters used here. The most striking difference between the fossil and the extant species is the lack of strong curvature of the diaphysis in the former. In living otters, the anterior face of the humerus is strongly curved in its proximal two-thirds, corresponding to the area where the main flexors of the humerus inserted (Mm. latissimus dorsi and teres major, assisted by Mm. pectoralis and deltoideus). This curvature is very strong in *Enhydra lutris* (Howard, 1973: figs 63, 65), *Lu. lutra* and *Lo. felina*, slightly less pronounced in *Lutro. perspicillata* and *P. brasiliensis*, while it is nearly absent in *Sivaonyx beyi*. The strong curvature of the humerus provides a better mechanical strength for resistance against flexion (Willemsen, 1992). Another prominent difference observed in the material is the relative development of the deltoid and pectoral crests, and the distal extent of these crests. They are much less developed in *Sivaonyx beyi* than in *Lo. felina* and the deltoid tuberosity is also more reduced in the fossil material than in *Lu. lutra*. The crests are relatively reduced in *P. brasiliensis*. The development of these crests does not correlate with their distal extension in our sample. Thus, in *Sivaonyx* from Chad, the deltopectoral crest is as distally extended as in *Lu. lutra*, *Lo. felina* and *Lutro. perspicillata* but much less than in *P. brasiliensis*. The relative position of the insertion area of the main flexors of the humerus (Mm. teres major and latissimus dorsi) is about the same in *Sivaonyx*, *Lutra*, *Lontra* and *Lutrogale* (and probably in *Enhydra* as well; Howard, 1973: fig. 65); in *Pteronura*, this insertion is located slightly more distally than in these genera, which suggests a more powerful flexion in the giant otter than in the other species. Powerful flexion being related to swimming ability, the absence of curvature of the humerus shaft in *Sivaonyx beyi* suggests a lesser swimming ability in this species. The epicondylar crest is somewhat more proximally extended in *Sivaonyx beyi* than in *P. brasiliensis* and *Lu. lutra*, and much more than in *Lutro. perspicillata* and *Lo. felina*. This crest is also laterally very developed in the fossil and extant species except *P. brasiliensis*. The resulting greater development of the muscular attachment for the M. anconeus and the extensors of the wrist and digits is probably related to the large size of *S. beyi*. The ratio of the functional length to the maximum mediolateral distal width of the humerus shows that the distal epiphysis is relatively much wider in *P. brasiliensis*, and to a lesser extent in *Lutra lutra* and *Lontra felina* than in *Lutrogale perspicillata* and *Sivaonyx beyi* from Chad. In the two species, this mainly results from a lesser development of the medial epicondyle, the main consequence being reduced leverage of the flexors and pronator of the carpus and manus. The medial epicondyle is also proximodistally more developed in the giant otter than in the other species, in particular *Lo. felina*. In the distal articulation, the capitulum is mediolaterally more extended in the Chadian species than in *P. brasiliensis* and *Lutro. perspicillata*, and less rounded than in all of the other species discussed here, which indicates reduced ability to supinate the forearm. The olecranon fossa of the fossil otter is more proximally extended and deeper, and the radial fossa more pronounced than in the extant species. Interestingly, as in the fossil otter, we found a very deep fossa and groove for the attachment of the olecranon ligament in *Lo. felina* and *Lutro. perspicillata*. In *Lu. lutra* and *P. brasiliensis*, the insertion of the ligament is clearly distinct but much less pronounced and shallower than in the other species. In the fossil, the presence of a strong olecranon ligament, which limits the maximal flexion of the elbow joint (Engelke *et al.*, 2005), may also help to prevent the elbow from collapsing when bearing weight.

As the main area of attachment of the triceps complex, the relative length of the olecranon is an important parameter. Thus, the longer the olecranon, the larger the leverage of the extensors of the elbow. Conversely, a relatively short olecranon allows for a more rapid but less powerful extension of the elbow joint (Maynard Smith & Savage, 1956). In fossorial, aquatic and graviportal animals, the olecranon tends to be longer than in cursorial forms. Because not every element of the forelimb is preserved, we use the method of Van Valkenburgh (1985) rather than that of Maynard Smith & Savage to estimate the leverage of the triceps muscles in the otters compared here. Table 5 shows the proportion of the olecranon in fossil and extant otters; for comparisons, we also calculate this proportion in one specimen of *Meles meles* (0.26; personal data), *Vulpes vulpes* (0.18; personal data), *Martes foina* (0.18; uncatalogued specimen of GBPH), *Canis familiaris* (0.21; collections M. Brunet) and *Orycteropus afer* (0.49, uncatalogued specimen of GBPH); our measurements for *M. meles* and *V. vulpes*

are consistent with the data of Van Valkenburgh (1985). It appears that in *S. beyi*, *Lu. lutra* and *Lutro. perspicillata*, the leverage of the triceps is lower than in *Lo. felina*, and much lower than in *P. brasiliensis*; it remains, however, greater than in semifossorial carnivorans such as the badgers (Van Valkenburgh, 1985: appendix 2). By far the greatest leverage is seen in the aardvark. The olecranon of *Sivaonyx* also displays a weak medial deviation while in the extant otters (especially in *P. brasiliensis* and *Lu. lutra*), the posterior tip of the olecranon is strongly medially extended, which provides a larger attachment area and leverage for the triceps muscles, especially for the long head. The radial notch of the fossil ulna is weakly concave as in the extant species, but is more laterally orientated than in the studied extant otters except *Lu. lutra*. Such an orientation allows for more rotation, which is then unadapted for running. This is consistent with the curvature observed on the radial head. However, the acute angle between the anterodistal rims of the radial notch and the coronoid process on the ulna suggests that the range of pronation/supination was not extensive in *S. beyi*, which is in accordance with the capitulum shape of the humerus (see above). The interosseus tubercle is located much more proximally in the extinct otter than in the studied extant ones, and more so in *P. brasiliensis* than in other river otters. It is also extended, as on the radius, which indicates that the interosseus membrane was developed. Distal to the ulnar notch, and especially in the distal quarter of the shaft, the ulna is transversely very flattened in *P. brasiliensis* compared with the other taxa, including *S. beyi*. Correlative with this flatness, the area of attachment of the M. pronator quadratus is more reduced in the giant otter, is orientated more medially and has a posterior bounding ridge that is much less prominent than in other taxa. The need for developed pronators, as inferred in *S. beyi*, is related to the use of manus in a prone or semi-prone position (Taylor, 1974). In *P. brasiliensis*, pronation may have been more limited than in the other studied species. In the extinct otter, the posterior face of the distal half of the shaft is not marked by a crest, as in all the studied extant species. Distally, the two articular surfaces for the radius and the scapholunar are well developed and well separated in *S. beyi*, as in *Lu. lutra* or *Lutro. perspicillata*. In comparison, the distal ulna of *P. brasiliensis* displays two surfaces that are nearly in contact, and that of *Lo. felina* has a reduced articular surface for the radius.

The radius of all species is markedly bowed anteroposteriorly, especially in its distal half. This curvature may be related to a plantigrade posture and the ability to supinate the manus, as stated for viverrids (Taylor, 1974). In medial view, the maximal convexity is across the distal rim of the attachment for the M. supinator. This limit is very prominent in the extant species except in *Lutro. perspicillata*, and the supinator attachment surface extends more distally in *Lu. lutra*, *Lo. felina* and *P. brasiliensis* than in *Lutro. perspicillata* and *S. beyi*. As on the ulna, the interosseus tuberosity is more prominent and more proximal in *S. beyi* than in the extant species, except *Lutro. perspicillata*, which may be related to the need to avoid dislocating the radial head in the open radial notch of the ulna. There is no difference in the location of the radial tuberosity. The groove for the tendons of the Mm. extensor carpi radialis brevis and longus is more marked in *Lu. lutra* and *Lo. felina* than in *Lutro. perspicillata* and *S. beyi*; this groove is not visible in *P. brasiliensis*. The brachial index of *S. beyi* is 0.82, which is that of a generalized carnivoran (Davis, 1964). It is much greater than in the extant otters used here. Comparison of ratios of radius and humerus lengths to m1 length or 2nd caudal body length (the teeth being relatively smaller in the fossil species, another reference measurement would be better) reveals that the great brachial index of *S. beyi* results mainly from a relatively longer radius (and, to a lesser extent, to a relatively slightly longer humerus) compared with the extant species. Due to their aquatic adaptations, extant otters have reduced forelimbs, and especially the forearm (Davis, 1964: 35–37). The radius being more elongated in *S. beyi* and the radial tuberosity being located as in the extant species implies less strength in the M. biceps brachii in the fossil compared with the extant species. The smaller reduction of the forearm and the less powerful flexion of *S. beyi* supports the hypothesis that its aquatic adaptations are less pronounced than in extant otters.

As in the other otters, the proximal surface of the scapholunar is completely convex in *Sivaonyx* from Chad, which allows for a great degree of flexion at the wrist. It is noteworthy that the posteromedial part of the articular surface for the radius is slightly concave in *Lo. felina*, which probably limits movements in the anteroposterior plane and implies an ulnar deviation of the manus in flexion, as noted for other carnivorans (Yalden, 1970). In the fossil otter, the scapholunar is narrower and therefore the proximal surface looks more squared than rectangular and transversely extended, which probably limits the degree of radial and ulnar deviation. Another prominent difference is the longer and larger posterior tubercle and its marked projection posteromediad in *S. beyi*. In *Lu. lutra*, *Lo. felina* and *P. brasiliensis*, this tubercle is usually shorter and smaller, and is orientated more medially than posteriorly. In carnivorans this tubercle bears a small articular surface for the radial sesamoid and is the attachment area for some ligaments,

notably the radial collateral ligament. The articular facet in extant otters is small and located slightly distally on the medial face of the tubercle. In *S. beyi*, the facet is barely visible but seems to be in the same position, though slightly more posteriorly orientated. Regardless, the radial sesamoid was small in the fossil species. On the distal face of the scapholunar, the most prominent differences include the shape, the orientation and the extension of the articular surface for the trapezoid. In *S. beyi*, this surface is narrower and more steeply sloped medially, and its surface displays an extended convexity and a reduced concavity, which suggests a more medial orientation of the Mc II (and probably of the Mc I) than in the extant species. The articulation for the magnum is less dorsoventrally extended and shallower than in *Lu. lutra* and *Lo. felina*; it extends further toward the flexor side of the scapholunar. On the magnum, the proximal articular surface, very convex in all carnivorans and responsible for the mid-carpal flexion (Yalden, 1970), is less convex and less sloped anteriorly than in *Lu. lutra*, *Lo. felina* and *P. brasiliensis*. The mid-carpal flexion in the fossil otter may have been less marked than in its extant relatives. The magnum does not display any other marked differences from that of the living otters.

In the manus, one of the main differences between *S. beyi* and the living otters is the relative proportions of the metacarpals (see Table 5). We did not have access to the metacarpals of *Lutro. perspicillata*, but Willemsen (1980b: table 5) provides postcranial measurements of this species. The Mc IV is the longest metacarpal in *P. brasiliensis*, *Lu. lutra* and *Lo. felina*, but this metacarpal is not preserved in TM 171-01-033. The difference in length between the Mc IV and Mc III is not great in the extant otters used here (5% or less; Table 5), while according Tarasoff *et al.* (1972) the length of these two metacarpals is equal in river otters. We thus use the length of the Mc III to estimate the length of the manus compared with total limb length (= functional length of humerus + radius + Mc III). It would have been much better to include scapula length in this proportion due to the importance of this bone in the movement of the forelimb (e.g. Lilje, Tardieu & Fischer, 2003), but this measurement is not available in our fossil material. This ratio shows that *Sivaonyx* from Chad has the shortest Mc III in our sample, though the difference from *Lu. lutra* and *Lo. felina* is not great. In the giant otter, this distal element is absolutely much longer than in the other species. In comparison with total limb length, the Mc I and Mc II have the same proportion in *Sivaonyx beyi*, *Lutra lutra* and *Lontra felina*, but are relatively longer in *Pteronura brasiliensis*. Comparisons of the metacarpals to each other indicate that the Mc I of the fossil otter is distinctly

longer compared with the Mc III than in the extant otters, while the Mc II of the Chadian species and *P. brasiliensis* is much shorter in comparison with Mc III than that of *Lu. lutra* and *Lo. felina*.

The proportions and the relative lengths of the proximal phalanges preserved in TM 171-01-033 are difficult to compare with those of the extant otters without knowing their exact location in the manus or pes. The proportions of the metacarpals of the fossil otter are difficult to interpret in terms of aquatic adaptations since otters do not use their forelimbs to swim; in addition, in a strictly aquatic otter such as *Enhydra lutris*, the metacarpals and phalanges are more reduced than in river otters (Taylor, 1914). That the Mc III of the Chadian species is shorter in comparison with the limb length than in river otters is probably partly due to the lengthening of the radius (and to a lesser extent of the humerus), but the Mc I and II do not document the same trend, which shows that the shortening of Mc III is real in *S. beyi*. Overall, the latter has relatively short metacarpals. Moreover, Mc I and II were possibly more medially orientated based on the orientation of their articular surface.

On the hip bone, the acetabulum in the fossil otter is nearly circular (the greatest, anteroposterior diameter 30.8, the smallest, dorsoventral diameter 28), as in *Lu. lutra* and *P. brasiliensis* but unlike *Lo. felina* and *Ao. capensis*, which have a more elliptical acetabulum. The posterodorsal part of the lunate surface of the acetabulum is less extended in the fossil species than in all of the extant species except *Lo. felina*, which results in a posteroventrally more opened acetabular fossa in the latter and in the Chadian specimen.

The fovea capitis of the femur is located medially. Jenkins & Camazine (1977) have demonstrated that fovea position is an indicator of a more or less abducted posture of the femur. Using the same measurements (see Jenkins & Camazine, 1977: fig. 9) is difficult as the femoral head is not fully preserved. Nevertheless, the fovea certainly was nearer the 'equator' of the head than in *Lu. lutra* and *Lo. felina*, and in a posterior location relative to the 'meridian'. The articular surface of the femoral head does not extend on the proximal surface of the neck as in *Ao. capensis* and *Lo. felina* (extension less important in the latter than in the former). The margins of the articular surface (preserved posteriorly) and the position of the fovea capitis in the fossil otter indicate an abducted posture of the femur, though less so than in *Ao. capensis*, *Lu. lutra* and *Lo. felina*. The greater trochanter extends slightly above the femoral head, in contrast to that of *Lu. lutra*; this enhances the surface of attachment for Mm. gluteus medius, profundus and piriformis, which are extensors of the femur. In a

generalized mammal, these muscles, which have a small moment arm, are responsible for high-speed movements. The enlargement and proximal extension of their attachment area increases the moment arm of these muscles. In the fossil otter, movements imparted by these muscles were then slightly more powerful but less rapid than in *Lu. lutra*. The trochanteric fossa and the lesser trochanter of *S. beyi* are much more developed than in *Ao. capensis*, and, to a lesser extent, than in *P. brasiliensis*. The lesser trochanter is also more medially projected than in the extant species and more distally located than in *P. brasiliensis*, which enhances the moment arm, and therefore increases the power of the M. iliopsoas. As in the extant otters, the shaft is anteroposteriorly compressed in TM 171-01-033 but much less so than in *P. brasiliensis*. Table 6 presents the index of slenderness for the femur (calculated as in the humerus; Maynard Smith & Savage, 1956). Since the femur of *S. beyi* is incomplete, we estimate its functional length using the mean ratio of the functional length to the total length of the femur in extant species, which is approximately 0.935. As expected from the general shape of the bone, the femur of *P. brasiliensis* is much more robust than in any other otter observed here, which results from the strong widening of the shaft. The index of slenderness of the femur of the fossil otter is similar to that of *Lu. lutra* (1.17), the two species having a relatively robust femur compared with that of *Lutro. perspicillata*, and especially *Ao. capensis*. The latter has the most slender femur. As a comparison, we calculate this index for the femur of the European badger (*Meles meles*), which shows it to have a less robust femur than in most otters, including *S. beyi*, though it is still more robust than that of *Ao. capensis*. Interestingly, however, the femoral shaft of *Meles meles* has a totally different cross-sectional shape, with a slight mediolateral compression strongly contrasting with the anteroposteriorly flattened shaft of the otter femur. The lateral supracondylar tuberosity for the attachment of the tendon of the lateral head of the M. gastrocnemius is well marked in *Lu. lutra*, *P. brasiliensis* and *Sivaonyx beyi*. It is much deeper, more marked, and more proximally located in *P. brasiliensis* than in the other species, indicating that the lateral head of the M. gastrocnemius is much stronger and has a greater moment arm than the medial head compared with the above-mentioned species. In the otter from Toros-Menalla, the insertion area for the lateral head of the gastrocnemius was less marked than in the giant otter, but in a similar proximal position; this insertion is also more marked on the left femur than on the right one in our fossil individual. Just distal to the insertion of the lateral head of the M. gastrocnemius, there is a small depressed area for the insertion of the

tendon of the M. flexor digitorum superficialis (= Mm. plantaris + flexor digitorum brevis in Fischer, 1942; Howard, 1975; see Barone, 2000: 935–937), a muscle that is at its origin closely associated with the lateral head of the gastrocnemius. In the extant otters, this small insertion is also present, more or less depressed but in the same position. The articular facet for the sesamoid associated with the lateral head of the M. gastrocnemius is not always clearly distinct. It is a small, relatively flat area on the proximolateral side of the lateral condyle in *Lu. lutra*, *Lo. felina* and *Lutro. perspicillata*; it is not visible in *P. brasiliensis* and the corresponding area is poorly preserved in *S. beyi*. In *Ao. capensis*, it is extended laterally and the condyle then displays a proximolateral prominence not seen in the other species, including the extinct one. The articular fact for the medial sesamoid on the medial condyle is only visible in *Lutro. perspicillata* and *P. brasiliensis*. The proximalmost part of the intercondyloid fossa is preserved in the fragmentary femur of *S. beyi*; it is not different from that of the extant species, displaying the usual pits for the attachment of the ligaments of the joint cavity, i.e. the cranial cruciate ligament on the medial face of the lateral condyle and, slightly more proximally, the meniscofemoral ligament on the lateral face of the medial condyle.

The tibia of *S. beyi* is not complete; the distal extremity displays marked differences from the tibias of the extant species. In the fossil specimen the medial malleolus is short and slightly medially orientated, which contrasts with the longer and distally orientated one observed in the living species of *Pteronura*, *Lutra*, *Lontra* and *Lutrogale*. The tibioastragalar articulation was probably less well constrained to an anteroposterior axis in *S. beyi*. The muscular attachments are similar to those found in most extant otters except *P. brasiliensis*. In the latter there is a very prominent crest separating the insertion areas for the Mm. tibialis posterior and popliteus, which extends the insertion area of both muscles; there is no crest in *S. beyi* nor in the other extant species. In the giant otter, the insertion of the M. popliteus is also more extended and much more medially orientated. The medial astragalar articular surface is shallower in *Sivaonyx* from Chad than in *Lu. lutra*, *Lo. felina* and *Ao. capensis*; it is like that of *Lutro. perspicillata* and slightly deeper than in *P. brasiliensis*. The limbs of otters are much shorter than in terrestrial carnivorans (Davis, 1964: table 2). Nevertheless, in otters the distal elements (zeugopode and autopode) of the hind limb are lengthened in comparison with the proximal element (stylopode), which results from their aquatic locomotion. The crural or femorotibial index is a good indicator of this kind of locomotion. In otters the tibioradial index is also

markedly distinct from that of most carnivorans (see Davis, 1964: table 1) and indicates a much longer tibia relative to the radius. We calculated these indexes for the extant otters we used in our comparisons on the basis of the functional lengths of bones. Our values are slightly greater than Davis' who used the total length of bones, which in the case of the femur is greater than the functional length. Crural index is generally distinctly greater than 110 in otters. None of the extant terrestrial carnivorans displays such a difference between tibia and femur length, although some species may have a tibia that is clearly longer than the femur, as in, for example, the felids *Acinonyx jubatus* and *Uncia uncia* (Gonyea, 1976) and the canid *Chrysocyon brachyurus* (Davis, 1964). In otters the radius is clearly less than two-thirds of the tibia length, which corresponds to a tibioradial index of less than 0.65. The total and functional lengths of the tibia are unknown in *Sivaonyx beyi*. Given the functional implication of tibia lengths and to calculate the crural and tibioradial indexes, we estimate this measurement in the fossil species. One of the preserved attributes that may serve to predict tibia length in this specimen is the nutrient foramen placed on the posterior face approximately at the junction of the proximal and middle thirds of the bone. In extant otters, the distance between the distal border of the tibia and this foramen ranges from 56 to 66% of the total length. The same distance in *S. beyi* being 118 mm, the functional length of the tibia would range from 210 to 178 mm, which results in a femorotibial index of 1.15–0.98 and a tibioradial index of 0.69–0.82. If these estimates actually represent a maximum range for the fossil species, then its tibia is not as lengthened as in extant otters. In carnivorans adapted to aquatic locomotion, the femur becomes the shortest segment of the hind limb at the expense of the tibia/ulna and, especially, the foot; shortening the femur results in more powerful extensors of the stifle joint and lengthening the tibia provides extended attachment for the flexor/extensors of the ankle and foot (Tarasoff, 1972). In the Chadian *Sivaonyx*, the tibia was as long as or longer than the femur, but certainly less so than in extant otters. This is additional evidence that the aquatic adaptations of the fossil Chadian species were less developed than in its extant relatives.

As stated in the descriptive section, the calcaneum of *S. beyi* resembles that of the extant otters. The trochlear process is larger in the fossil otter. There are also small differences regarding the proportions of the tuber calcanei, which is the longest and narrowest in *Ao. capensis*, and mediolaterally thickest in *P. brasiliensis*. We find the greatest similarities between the astragalus of the fossil species and that

of *Lu. lutra*. Our fossil material displays some differences, however, such as a longer neck, a shallower trochlea and a less posteriorly extended tibial articular surface, a more depressed and distolaterally extended articular surface for the fibula, and, on the distal face, a medial calcaneal articular surface that is posteriorly more extended and does not contact the navicular surface. One difference between the fossil and the extant species, with the exception of *Lo. felina*, is the presence of an elongated articular surface for the cuboid in the former, on the ventral edge of the lateral face of the neck. There is no articulation or clear contact between the cuboid and the astragalus in *Ao. capensis*, *P. brasiliensis* and *Lu. lutra*. In *Lo. felina*, which has a longer astragalar neck than in the other extant species, just as in the fossil otter from Chad, there is also a clear contact between the astragalus and the cuboid, but this surface is located ventrolaterally on the neck. There is probably a relationship between the presence of a long astragalar neck, which then extends well beyond the cuboid facet of the calcaneum, and the presence of an articular contact between the astragalus and the cuboid. On the cuboid of *Lo. felina*, the corresponding facet is along the proximal rim of the medial face and makes an obtuse angle with the articular surfaces for the calcaneum and mesocuneiform; it is distoproximally more extended in its dorsal part, then tapers ventrally. Except for its general shape, the navicular of *S. beyi* displays important differences from those of the extant species, especially regarding the distal face. Thus, in the fossil species, the angle between the ectocuneiform and cuboid surfaces is slightly more open and that between the ectocuneiform surface and those for the other cuneiforms is much less open than in the extant species. This supports a more divergent direction for the Mt I and II.

Except for the differences mentioned in the descriptive part, the metatarsals of *S. beyi* have a similar morphology to those of the extant species. However, as for the metacarpals, there are interesting proportional differences. In the fossil specimen, only the total lengths of the Mt II and IV are preserved; the total length of Mt III is estimated at approximately 61 mm, which is slightly shorter than the Mt IV (see Table 6). The metatarsals preserved in the fossil species, Mt II, III and IV, are then shorter relative to limb length (= functional length of femur + functional length of tibia + length of Mt IV) than in the extant species for which metatarsals are available (*Lu. lutra*, *Lo. felina* and *P. brasiliensis*). Among the latter species, the giant otter has the longest metatarsals. The lengthening of the distal part of the hind limbs, especially the foot, characterizes fully aquatic carnivorans such as the sea otter and pinnipeds. The

greater lengthening of the metatarsals in *P. brasiliensis* is consistent with the overall morphology of this animal (e.g. lengthening of the tibia), which displays distinct aquatic adaptations. In the fossil species, Mt II is less reduced relative to Mt III and Mt IV than in the extant species, especially compared with the giant otter. Moreover, the Mt IV of the Chadian fossil otter is only slightly longer than Mt III, while the difference is greater in the studied extant species. It is worth noting also that in comparison with the other metatarsals (but not compared with the hind limb length) the Mt I is much more reduced in *P. brasiliensis* and *Lu. lutra* than in *Lo. felina*, and that the Mt V is longer compared with the other metatarsals and limb length in *P. brasiliensis* than in the two other extant otters. In *Enhydra lutris*, the Mt V actually becomes the longest metatarsal, which may indicate that the elongation of this bone in the giant otter is related to aquatic adaptations.

Discussion

Even in the absence of well-preserved dentitions, the species from Toros-Menalla is assigned to the genus *Sivaonyx* (*sensu* Morales & Pickford, 2005) with some confidence. Differences in body size, mandibular stoutness, proportions of M1, relative size and breadth of p4, and morphology of m1 suggest a specific distinction of the Chadian material, for which we propose the name *Sivaonyx beyi* sp. nov. We found the greatest resemblance between this species and *S. africanus*, although the specimen from Wadi Natron may also have a close relationship to *S. beyi* when additional material is found. *Sivaonyx beyi* is the most common otter in Toros-Menalla and is found throughout the area.

Body size: Metric comparisons with extant otters of known body mass show a marked size difference between the fossil and the extant otters. Postcranial measurements of *Sivaonyx* from Toros-Menalla are much greater than those of the two largest extant species (*Pteronura brasiliensis* and *Enhydra lutris*), which are also the largest extant mustelids, with a maximum body mass of 35 and 45 kg, respectively (Estes, 1980). The specimen of *P. brasiliensis* used here is probably not a large individual, as its m1 is smaller than the other studied individuals, which are represented only by craniodental material. Nevertheless, the calcaneum of the Chadian species is about 60 mm in total length while the maximum length of that of *P. brasiliensis* and *E. lutris* is about 45 mm (Stains, 1976); as a comparison, the calcaneum of *S. beyi* is the length of that of the female individuals of *Ursus americanus* (Stains, 1973). Estimating the body mass of the Chadian fossil otter is difficult. First, the dentition of this species is smaller than that of the

Table 7. Estimates of body mass of **S. *beyi* sp. nov.**

Regression based on:	Parameter used for **S. *beyi* sp. nov.**	Estimate of body mass (kg)
Mustelidae (from V.V. 1990)	m1 length:	
	min Lm1	30.60
	max Lm1	48.50
Total Carnivora (from Anyonge, 1993)	long bone FctL:	
	humerus	30.50
	femur	21.40
	mean	25.95
from Egi (2001) generalized terrestrial group	total area at mid-FctL of:	
	humerus	92.80
	femur	44.60
	tibia	34.00
	mean	57.13
pooled terrestrial group	humerus	55.00
	femur	62.04
	tibia	52.20
	mean	56.41
semifossorial terrestrial group	humerus	31.60
	femur	81.70
	tibia	67.00
	mean	60.10
	general mean	57.88

V.V., Van Valkenburgh; pooled terrestrial group in Egi (2001) includes generalized, semifossorial and semi-aquatic taxa of her study.

extant species in comparison with its postcranial bones. Thus, the m1 length of *S. beyi* is about the same as in *Ao. capensis* while the postcranial bones of the former are nearly twice the length of those of the latter (this is similar when comparing *S. beyi* with *P. brasiliensis*). Consequently, body mass estimates based on m1 lengths are probably underestimated for *S. beyi* (minimum–maximum range is 30–48 kg; see Table 7). Second, extant otters have much shorter limbs than other, non-aquatic carnivorans. It is then not surprising that body mass estimates based on length of humerus and femur are even lower than those obtained from m1 length (30.5 and 21.4 kg, respectively; Table 7). In our opinion, estimates based on long bones or m1 lengths are unrealistic considering the difference size between the skeleton of *S. beyi* and that of known extant or fossil giant species of otters. Moreover, m1 and long bone lengths are not good predictors of body mass because they give larger errors for estimates (see Egi, 2001). Estimates based on cross-sectional properties of long bone shaft are considered to be the best body mass estimators. Here mid-shaft section area of the long bones (humerus, femur and tibia) is used to estimate the body mass of *S. beyi*. We use the regression equations of Egi (2001);

this author provides a regression equation for different locomotor type: arboreal, scansorial, terrestrial and cursorial taxa. We made the *a priori* assumption that *S. beyi* belongs to the terrestrial locomotor group, which includes short-legged species. In Egi (2001), the terrestrial taxa are divided into generalized terrestrial taxa (the herpestids *Herpestes edwardsii* and *Ichneumia albicauda*, the mustelid *Galictis vittata*, the mephitid *Spilogale putorius* and the viverrid *Viverra zibetha*), terrestrial semifossorial taxa (the mustelids *Conepatus mesoleucus*, *Ictonyx striatus*, *Meles meles*, *Melogale personata*, *Taxidea taxus* and the mephitid *Mephitis mephitis*), and semi-aquatic terrestrial taxa (the herpestid *Atilax paludinosus*, and the mustelids *Lontra canadensis* and *Mustela vison*). Egi (2001: table 5) only provides the regressions based on the two first categories (generalized and semifossorial), and a regression based on the total sample of terrestrial taxa. We followed the method of this author (Egi, 2001: 511) to infer an average estimate and range of body mass for the Chadian species (Table 7). There is a great variation in the estimates obtained from the different bones; nevertheless, whatever the locomotor group to which the Chadian *Sivaonyx* is assigned, means of estimates from different bones are close to each other, ranging from 56.4 to 60.1 kg. Even including fossil taxa, *Sivaonyx beyi* is among the largest known otters; other species of *Sivaonyx* such as *S. kamuhangirei* certainly reached an even greater size. At the very least, the Chadian *Sivaonyx* is much larger than presumed giant fossil otters for which postcranial bones are known, such as *Megalenhydris barbaricina* from the Pleistocene of Sardinia (Willemsen & Malatesta, 1987) or *Enhydritherium terraenovae* from the late Miocene and early Pliocene of North America (Lambert, 1997). The presumed giant size of the former must be nuanced, however; its humerus is *c.* 120 mm long, which is longer than in the specimen of *P. brasiliensis* used here, but the tibia length (122–125 mm) of *M. barbaricina* is approximately that of *P. brasiliensis* and *Ao. capensis*. It is therefore probable that the limbs of this fossil species were different in proportion but that its size was not much greater than that of the giant otter or even the largest specimens of the Cape clawless otter. Dental measurements are consistent with our hypothesis, as m1 length of *M. barbaricina* is 17.7 mm while it is 17.8–19.9 in our sample of *Ao. capensis* ($N = 4$) and 18.4–20 in our sample of *P. brasiliensis* ($N = 4$). The size of *Enhydritherium terraenovae* was inferred to be similar to that of the extant sea otter (Lambert, 1997). The length of the humerus, radius, ulna and tibia of the specimen from Moss Acres Racetrack site, Florida (Lambert, 1997), is about 60% (60–70% for the tibia) and that of the femur is 67.6% of the

corresponding measurement in *S. beyi*; another tibia assigned to a larger specimen from Palmetto fauna, Florida (Berta & Morgan, 1985) is 145 mm long, which is 69–80% of the tibia minimum and maximum estimated lengths of *S. beyi*.

Locomotion: Interpretation of postcranial characters of an extinct species is not easy. Inferences regarding the location, development and, correlatively, the power of muscles from observation of osteological features in fossils need to be tested. In carnivorans, such inferences have been tested by Bryant & Seymour (1990), who concluded that the amount of myological information inferred from osteological characters is greater in carnivorans than in other vertebrates. As recommended by those authors, we base our myological reconstruction of the fossil otter described here on the myology of extant carnivorans, especially mustelids and lutrines when available. Inferring the locomotion of *S. beyi* is not easy. Many postcranial characters are not particularly specialized and indicate it was a terrestrial predator with poorly developed aquatic adaptations. The small number of distinct 'aquatic' characters such as presence of a powerful, large tail, which only has its equivalent in extant otters except *Enhydra lutris*, and proportion of limbs segments, especially the long tibia in comparison with the femur, contrasts with the numerous 'non-aquatic' characters if compared with their development in extant otters, e.g. absence of strong curvature and slenderness of humerus, poor development of humerus medial epicondyle, relatively long radius and lesser lengthening of tibia in comparison with the femur. Some differences between the musculature of *S. beyi* and that of the extant species can be related to the size of the former (e.g. attachment for long head of triceps on scapula more developed, greater development of extensors of digits and elbow joint). If the orientation of the metapodials correlates with the orientation of the digits, then Mc I and II and Mt I and II are more medially orientated than in extant species; this results in an increased surface of the manus and pes, presumably to provide a better support for the body of this large-sized animal.

DJOURABUS GEN. NOV.

Type species: Djourabus dabba sp. nov.

Etymology: After *Djourab*, a Saharan erg located in the Chadian depression, in reference to the location of the fossiliferous arera of Toros-Menalla.

Diagnosis: Genus distinguished by its large size; tall and thick mandibular corpus; m1 bunodont, short, and very broad with a trigonid broader than the
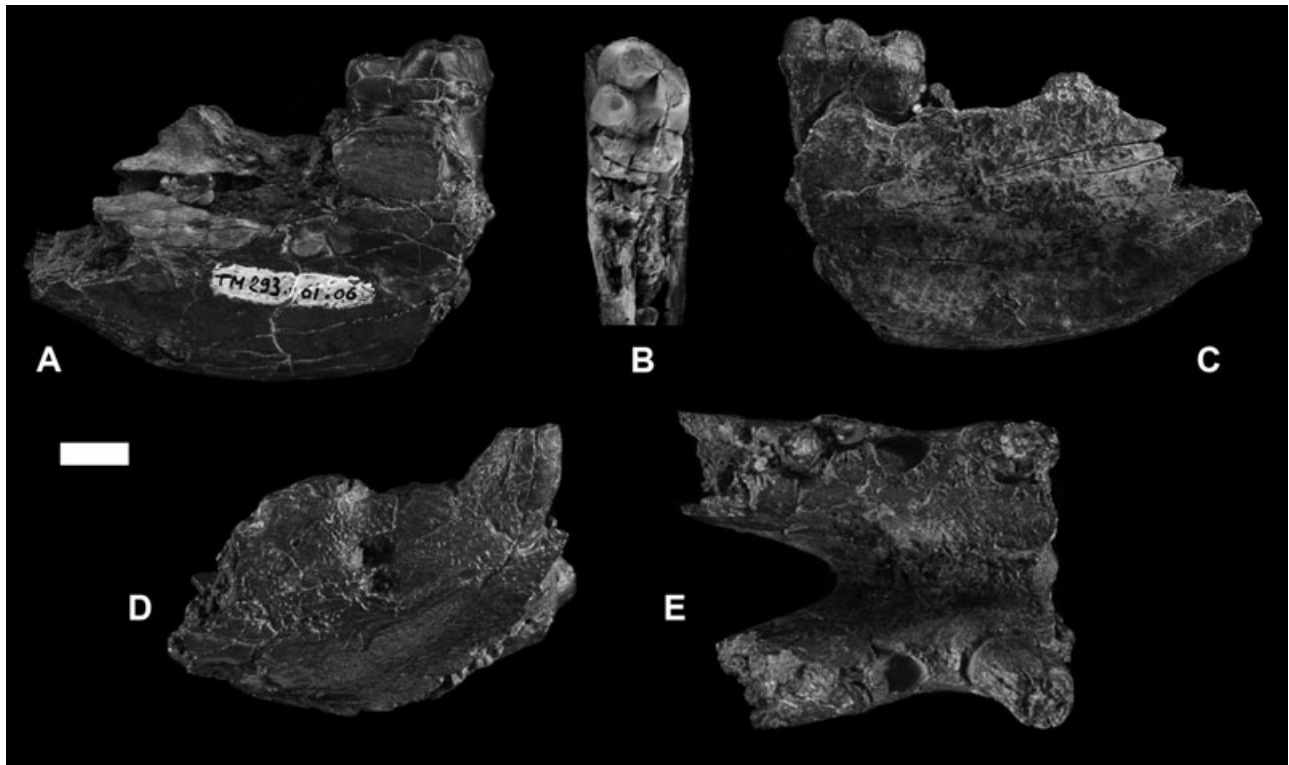
Figure 8. *Djourabus dabba* **gen. nov. sp. nov.**, photographs of the dentition. TM 293-01-006, holotype: fragment of right hemimandible with m1 in A, labial view, B, dorsal view, and C, lingual view; anterior part of the mandible in D, right lateral view and E, dorsal view. Scale bar = 10 mm.

talonid, transversely orientated paraconid shelf, bases of the metaconid and paraconid connate, short; m1 talonid molarized and short, with squared off distal margin and individualized and low entoconid and hypoconid, and cingulid very reduced and restricted to the mesial margin of the paraconid.

Differential diagnosis: Most of these characters distinguish *Djourabus* from all of the extant species, and within bunodont fossil otters, from the species of *Sivaonyx* and *Paludolutra*. *Djourabus* differs from *Enhydritherium* in its larger size, taller mandible, an m1 that is relatively broader with a transversely orientated paraconid, trigonid broader than the talonid, metaconid smaller than the protoconid, and reduced labial cingulid. *Djourabus* differs from *Enhydriodon* in its much broader m1 with more bunodont cuspids, enlarged and more transversely orientated paraconid, metaconid that is closer to the protoconid than to the paraconid and talonid that is shallower with a squared off distal margin.

DJOURABUS DABBA SP. NOV.

Holotype: TM 293-01-006, fragment of right hemimandible with m1, and TM 293-01-053, anterior part of the mandible with left canine (broken), most probably belonging to the same individual (Fig. 8, Tables 1, 2).

Etymology: The specific name comes from 'dabba' meaning 'thick' in the Goran language, in reference to the great width of m1.

Referred material: Only the holotype.

Age and distribution: TM 293 site, Toros-Menalla, late Miocene, Chad.

Description
Mandible (Fig. 8, Table 1): We did not find an anatomical connection between the anterior fragment of the mandible and the fragment of the right corpus bearing m1 because a short piece of the right hemimandible is missing. The mandible is stout and very thick anteriorly; it is narrower posteriorly and very tall. The symphysis is tall and short, and has ventral processes as in *Sivaonyx* species. There is one large mental foramen on the left side below the p2-3 diastema and two slightly smaller ones on the right side in the same position.

Dentition (Fig. 8, Table 2): The canine tip is broken and/or strongly worn and the enamel is poorly preserved; the tooth section is elliptical. A 4.5-mm-long diastema separates the canine from the first cheek tooth. The latter is identified as a single-rooted p2. The presence of a p1 is rare in Lutrinae. When the tooth is present as may occur in species of *Lutra*, *Aonyx* and *Sivaonyx*, it is a minute tooth and its alveolus is very close to or coalescent with that of the canine. The alveolus of p2 is 8.5 mm long and about 7 mm in width. The p3 was double-rooted and obliquely set in the mandible, with the mesial root labial. The mandibular part bearing p4 is not preserved. The m1 is very broad and short; its mesiolabial face is obliquely orientated due to the transverse orientation of the paraconid. The trigonid cuspids are heavily worn and clearly bunodont. There are no distinct crests on the cuspids, which are inflated, especially the lingual face of the paraconid, metaconid and entoconid and the labial face of the protoconid and hypoconid. The trigonid cuspids form a fairly closed triangle and the trigonid basin is small, shallow and widely opened distally. The paraconid is very strong, much stronger than the metaconid, from which it is separated by a V-shaped valley, the bases of the cusps being closely applied to each other; its mesial face is nearly vertical in lingual view and its mesial cingulid is poorly developed. The protoconid is wide and short; it is orientated approximately sagittally; its distal face is strongly oblique. The metaconid is a well-individualized cusp, slightly distal to and widely separated from the protoconid, closer to the paraconid; the cross-section of the cusp is nearly rounded. The talonid is short, slightly narrower than the trigonid and has a distally squared-off occlusal outline. It is molarized, with each distal corner of the talonid being occupied by a low blunt cuspid, an entoconid lingually and a slightly larger hypoconid labially; distally, the two cuspids are separated by a shallow notch. The hypoconid crest is poorly developed and joins the distal face of the protoconid mesially. The talonid basin is shallow and in the centre of the talonid. The cingulid is present only around the mesial base of the paraconid.

Comparisons and discussion
Compared with that of *Sivaonyx* species, the mandible of TM 293-05-053 is stouter, thicker anteriorly and taller posteriorly (Table 1). The m1 is proportionally much broader than in the species of *Sivaonyx*, especially the trigonid, which is broader than the talonid; the width of the lower carnassial in *S. africanus* is not known, however (Table 2). In TM 293-05-006, cuspids are more bunodont, in particular the metaconid, which is more distant from the protoconid and closer to the paraconid than in *Sivaonyx* spp. The

paraconid and protoconid shelves are shorter and the paraconid is much more transversely orientated than in the carnassial of *Sivaonyx*. The talonid of m1 is more molarized, shorter and narrower, with a squared-off distal margin. The cingulid is much more reduced than in species of *Sivaonyx*, and present only on the mesial face of the paraconid; in *S. africanus*, where the labial part is not preserved, this character remains to be confirmed.

Species with a more bunodont dentition belong to the genera *Enhydritherium* and *Enhydriodon*. Compared with *Enhydritherium terraenovae* from the late Miocene – early Pliocene of North America, our material differs in its larger size (m1 length range in *E. terraenovae* is 15.8 to *c*. 18; Berta & Morgan, 1985), taller mandible, its m1, which is relatively broader due to the transverse orientation of the paraconid, trigonid that is broader than the talonid (the opposite is true in *E. terraenovae*), lesser enlargement of the metaconid, which remains smaller than the protoconid in *Djourabus dabba*, and its reduced labial cingulid. We find, however, some similarities, such as the squared-off distal margin of the talonid and the bunodonty.

The comparison between our material and that of *Enhydriodon* (*sensu* Morales & Pickford, 2005) is more problematic. As Morales & Pickford (2005) pointed out, there has been much confusion about this genus, notably because the two known species (the type species *E. sivalensis* and *E. falconeri*) are based on the upper dentition. The lower dentition of *Enhydriodon* remains mostly unknown. An isolated m1 from the Siwaliks was assigned to *E.* sp. cf. *E. falconeri* by Pilgrim (1931: pl. 2, fig. 5) then to *E. falconeri* (Pilgrim, 1932: pl. 2, fig. 15); Pilgrim (1932: 85) also states that he mentioned this tooth under *E.* sp. aff. *E. sivalensis* in one of his previous papers, i.e. Pilgrim (1913: 282). This tooth (BMNH-M 12350, cast of GSI D161) was more recently assigned to *E. sivalensis* on the basis of its large size (Repenning, 1976) but more recently authors have assigned it either to *E. sivalensis* (e.g. Morales & Pickford, 2005: fig. 4) or *E.* cf. *falconeri* (e.g. Willemsen, 1999: table 3). Lydekker (1884: pl. 45, fig. 3) assigned to *E. sivalensis* a second fragment of mandible with the distal part of m1, which is housed in the Ipswich Museum. Both specimens undoubtedly differ from our material. The isolated m1 (BMNH-M 12350) is markedly more elongated than TM 293-01-006; the cuspids are less bunodont, the paraconid is much narrower and in a less transverse orientation, and the metaconid is more widely separated from the paraconid and more closely connected to the protoconid by crests. Finally, on both BMNH-M 12350 and the Ipswich specimen the talonid is basined and its distal margin has a curved occlusal outline, which clearly contrasts with the

squared-off distal margin of the poorly basined, molarized talonid of TM 293-05-006. Despite the clear distinction between our material and the lower teeth previously assigned to *Enhydriodon*, there is no guarantee that these m1s effectively belong to that genus. As pointed out by Pilgrim (1932), BMNH-M 12350 is not very different from the m1 of *Sivaonyx bathygnathus*. In addition, the stratigraphical origin of the material of *Enhydriodon* is unclear. The material assigned to the genus comes from 'Siwalik Hills', but the precise locality is unknown. BMNH-M 12350 comes from around Hasnot, in the Potwar Plateau (Pakistan) and was considered to come from the 'Dhok Pathan Stage', which does not provide much stratigraphic information (see comparisons of *Sivaonyx beyi* with *Sivaonyx bathygnathus*); in the Potwar sequence, the Dhok Pathan Formation spans nearly 7 Myr (10.1 to *c*. 3.5 Ma; Barry *et al.*, 2002). Recent discoveries report the presence of *Enhydriodon sivalensis* from the late Pliocene of India (Verma & Gupta, 1992); the material previously listed as *Enhydriodon* sp. from the *Hexaprotodon* biostratigraphic zone in the Potwar plateau (Pilbeam *et al.*, 1979) is probably not an otter at all (J. Barry, pers. comm.). With an age of *c*. 7 Ma (Brunet *et al.*, 2004), the material from Chad is markedly earlier than the single known, well-dated *Enhydriodon* material. This, and the differences mentioned above, support the generic distinction of TM 293-05-006 and -053. It cannot be ruled out, however, that this material may belong to a form close to *Enhydriodon*, which can only be tested when we find associated upper and lower teeth of this animal.

LUTRINAE GEN. ET SP. INDET. AFF. *TOROLUTRA* SP.

2002 – Lutrinae indet. Vignaud *et al*.: 154.

Referred material: TM 266-01-194, subcomplete left hemimandible with p3, partial p4 and m1, fragment of m2 root (Fig. 9, Table 8).

Age and distribution: TM 266 only, Toros-Menalla, late Miocene, Chad.

Description

Mandible (Fig. 9, Table 8): The anteriormost part of the corpus and the top of the coronoid process are not preserved. The corpus is similar in proportions and robustness to that of the extant species. The posterior part of the mandible, however, displays prominent differences from the extant species, except for the coronoid process, which, though incompletely preserved, does not show any marked differences. Thus, in TM 266-01-194, the condyle is much less transversely developed (see Table 8), i.e. it is similar in width to that of *Lutra lutra* (e.g. MNHN CG 1929-545), whereas the mandible is at least 25% longer than that of this extant specimen. On the other hand, in comparison with *Pteronura brasiliensis* (MNHN CG 1937-888), which has a mandible that is 5% longer, the condyle of TM 266-01-194 is 25% narrower. What is more significant for the masticatory biomechanics is the distance between the carnassial notch and the condyle, which is proportionally longer than in extant Lutrinae. The carnassial is therefore more anterior than in extant species. This lengthening of the posterior half of the mandible is related to several morphological changes, such as the position of the condyle and the anteroposterior development of the masseteric fossa. Thus, compared with extant Lutrinae, the Chadian specimen has a condyle that is distant from the posterior rim of the coronoid process (instead of being closely set against it). The masseteric fossa of TM 266-01-194 is also relatively longer than in, for example, *Lutra* and *Lontra*; the individual of *Pteronura brasiliensis* used here for comparison, which is slightly larger than TM 266-01-194, has a distinctly shorter masseteric fossa. In TM 266-01-194, the fossa is particularly deeply excavated posteriorly, just beneath the condyle, a morphology that has not been observed in extant Lutrinae. The angular process is usually strong and short in extant otters such as *Lontra* and *Lutra*. In TM 266-01-194, it is more reduced and not nearly as prominent posteriorly, as in *Aonyx*. The ventral border of TM 266-01-194 is less markedly convex than in *Lutra* or *Pteronura*. The mandible is 91.5 mm long, which is probably very close to the length of the complete bone.

Table 8. Measurements (mm) of the mandible and dentition of aff. *Torolutra* sp.

Dentition	p3		p4		m1				m2	
	L	W	L	W	L	W	LtrigoP	Wtal	L	W
	6.8	3.8	9.5*		16.0		10.5	7.5	(5.9)	(3.1)
Mandible	Hp3-4	Hp4-m1	Hm1–2	Tp3	Tm1					
	18.0	17.5	19.4	10.1	8.8					

*Estimated value; measurements in parentheses are based on alveolus.
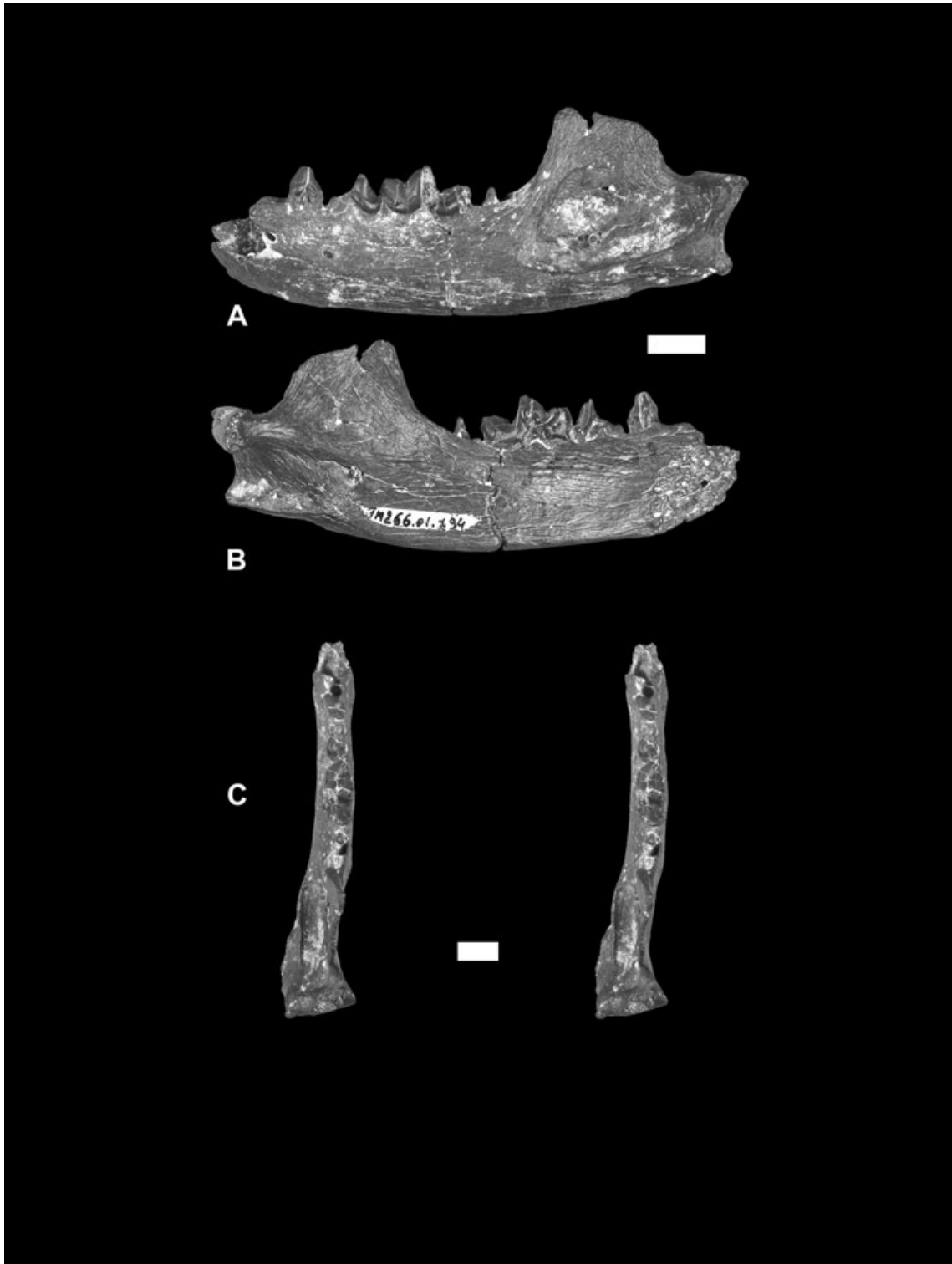See Tables 1 and 3 for abbreviations.

Figure 9. Lutrinae gen. and sp. indet. aff. *Torolutra* sp., photographs of the dentition. TM 266-01-194: subcomplete left hemimandible with subcomplete p4 and m1 in A, labial view, B, lingual view, C, stereophotographs of dorsal view. Scale bars = 10 mm.

Dentition (Fig. 9, Table 8): The teeth are unfortunately poorly preserved. They are overall morphologically very similar to those of piscivorous Lutrinae (e.g. *Lutra*, *Lontra*, *Pteronura*). In TM 266-01-194, the canine alveolus indicates a fairly large tooth, being *c*. 9.5 mm long and 5.5 mm wide. The toothrow is short, measuring 43.5 mm from the anteriormost premolar alveolus to the distal m2 alveolus. There is no diastema between the teeth, which are set closely together as in modern lutrines. In front of p3, there are two alveoli, of which the mesial one is the smallest. In species of *Lutra*, *Lontra* and *Pteronura*, the p2 is double-rooted, the mesial root being more labial than the distal one. In TM 266-01-194, these alveoli probably correspond to a double-rooted p2 with a lingually located mesial root, which therefore has a different orientation than in extant *Lutra* and *Lontra*. The p3 is a relatively large tooth. There is no mesial cuspid as in, for example, *Lo. canadensis*, but a small distal cuspid and a very short heel. The cingulid is developed at least labially; there is a small cingular cusp lingually at the base of the main cusp. Only the distal half of p4 is preserved. The height of the main cuspid cannot be estimated, but the distal accessory cuspid, which is distinct and distolabial, reaches the height of the m1 paraconid in labial view. In *Lu. lutra*, the distal accessory cuspid is more reduced or absent. In *Lontra* (*Lo. canadensis*, *Lo. longicaudis*, *Lo. felina*), a distal accessory cuspid is present, but it is usually lower and does not reach the height of the m1 paraconid. In *Pteronura*, the distal cuspid may be absent (MNHN CG 1937-888, MNHN CG 1981-4) or present and as tall as the paraconid of m1 (MNHN CG 1962-2085). In TM-266-01-194, the cingulid is distinct on the labial face of p4. The talonid of p4 is relatively short and narrower than in *Pteronura* or *Lo. canadensis*. A considerable part of the lingual face, a portion of the protoconid and the distolabial corner of the talonid are not preserved on the carnassial. It is consequently difficult to compare this tooth with that of extant Lutrinae. However, the high hypoconid crest contrasting with the low lingual rim of the talonid support an assignment to the piscivorous otters, which are assigned to the Lutrini. The talonid/trigonid ratio is about 2/3, which is similar to that found in many extant otters. The cingulid is distinct labially but it is not as developed as in *Pteronura*.

Discussion

As pointed out in the description, the species from Toros-Menalla certainly had a piscivorous diet and is clearly distinct from the species of *Sivaonyx* and *Djourabus*. One fossil piscivorous otter, *Torolutra ougandensis*, is known from the late Miocene and Pliocene of Africa (Lukeino; Morales *et al.*, 2005; Nkondo and Nyaburogo formations; Petter, Pickford & Howell, 1991). Courtesy of M. Pickford and J. Morales, we have access to a cast of the holotype of this species and to the recently described material from the Lukeino and Magabet formations (late Miocene to early Pliocene, Kenya; Morales *et al.*, 2005). The Chadian specimen resembles the holotype of *T. ougandensis*. The latter differs, however, in having a longer distal cingulid of p4, an m1 talonid less steepened lingually, and a more extended mandibular symphysis. The species from TM is probably closely related to *Torolutra ougandensis*, but the poor preservation of our material does not allow for an unquestionable specific assignment.

One of the most striking differences between TM 266-01-194 and extant otters (especially piscivorous species) is its mandibular morphology. The lengthening of the posterior part of the mandible results in a longer distance between the condyle (i.e. the fulcrum of the cantilever) and the carnassials, which implies less force in these teeth than in extant otters, and a priori a less powerful bite.

LUTRINAE GEN. ET SP. INDET. AFF. *AONYX* SP.

Referred material: TM 219-05-001, left femur (Fig. 10).

Age and distribution: TM 219 site, Toros-Menalla, late Miocene, Chad.

Description (Fig. 10)

The femur is subcomplete and well preserved except for a part proximomedial to the femoral trochlea, which is absent. Compared with the femur of the extant species, TM 219-05-001 is distinctly longer than that of *Lo. felina* but of similar robustness. It is much smaller, but clearly more robust (lower index of slenderness; Table 6) than the femur of *S. beyi*. The greater trochanter does not extend much beyond the femoral head. The latter is well rounded and the neck is short; the articular surface for the lunate surface of the acetabulum extends on the dorsal and posterior faces of the neck. The trochanteric fossa is narrow but deep, although not as deep as in *Lo. felina*. The lesser trochanter is large, mainly protruding posteriorly; it is barely visible in anterior view. As in other otters, the shaft is anteroposteriorly compressed. A remarkable feature of this specimen is the presence of a proximolateral extension of the lateral femoral condyle for the articulation of the lateral gastrocnemial sesamoid. The femoral trochlea is wide and moderately deep. The intercondyloid fossa has a considerable distolateral extension.

Comparisons and discussion

The femur of TM 219-05-001 is comparable with that of the extant species of otters. Among the latter, we
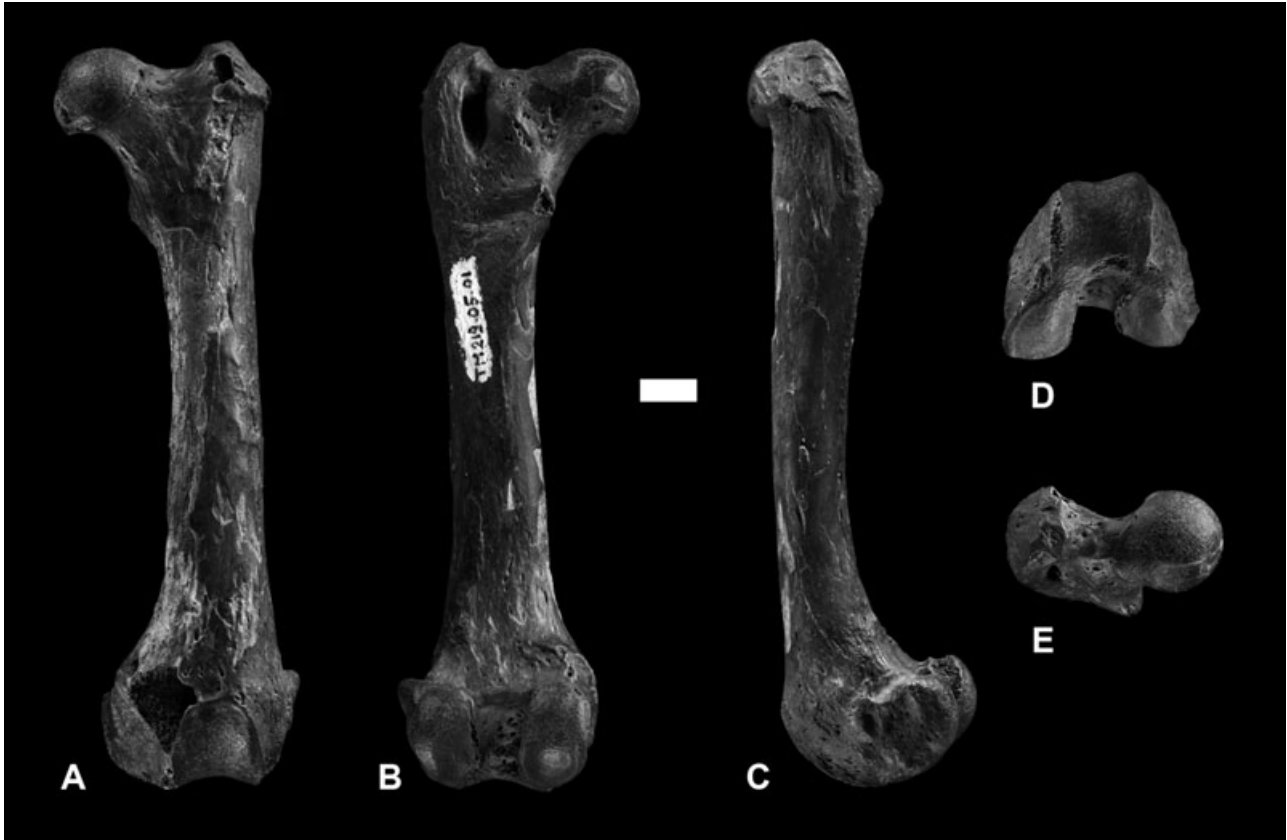
Figure 10. Lutrinae gen. et sp. indet. cf. *Aonyx* sp., photographs of the referred specimen. TM 219-05-001: left femur in A, anterior view, B, posterior view, C, lateral view, D, distal view, and E, proximal view. Scale bar = 10 mm.

found striking similarities to that of *Aonyx capensis*. Characters shared by these two species include (1) the extension of the articular surface of the femur head on the dorsal and posterodorsal face of the neck (character also found to a lesser extent in *Lo. felina*; Fig. 11, right); (2) the shape and location of the trochanteric fossa (also similar to that found in *Lutro. perspicillata*); and the morphology of the distal part of the femur, with (3) an intercondyloid fossa displaying a distolateral extension (Fig. 11, left); and (4) a lateral extension of the articular surface for the lateral gastrocnemial sesamoid (Fig. 11, middle). These four characters are all present in *Ao. capensis* and TM 219-05-001. With the exception that one of these characters may be present in one or the other species, no extant or known fossil species (e.g. *Sivaonyx hendeyi*, *S. beyi*) has a femur displaying all of these characters.

The size and/or morphology of this bone precludes assignment to *S. beyi* sp. nov. or *Djourabus dabba* gen. nov. sp. nov. from Toros-Menalla. Aff. *Torolutra* sp., represented by a mandible, is also known from this area. By comparison, the m1 of this piscivorous species is only slightly longer than that of, for example,

Lo. felina (MNHN CG 1995-185) with femur total length of 79.2; in comparison, the femur of *Ao. capensis* (MNHN CG 1883-1561, femur total length = 112.5) is much larger than in *Lo. felina*. TM 219-05-001, which is 129 mm in total length, cannot be assigned to aff. *Torolutra* sp. from Toros-Menalla and therefore certainly represents a fourth species of otter in this area. We do not know the systematic value of the morphological features shared by this specimen and *Ao. capensis*, but they may indicate a close relationship at generic level at least, as TM 219-05-001 differs from the femur of *Ao. capensis* in being significantly larger and more robust and in having a slightly more anteroposteriorly compressed shaft (Table 6). Although TM 219-05-001 may document a new species of a genus close to *Aonyx*, the known material is inadequate to erect a new name and we therefore prefer to rely on future discoveries of dental or cranial material.

LUTRINAE GEN. ET SP. INDET. AFF. *SIVAONYX* SP. OR *DJOURABUS* SP.

Referred material: TM 266-05-061, fragment of skull, fragment of right maxilla with partial P4.
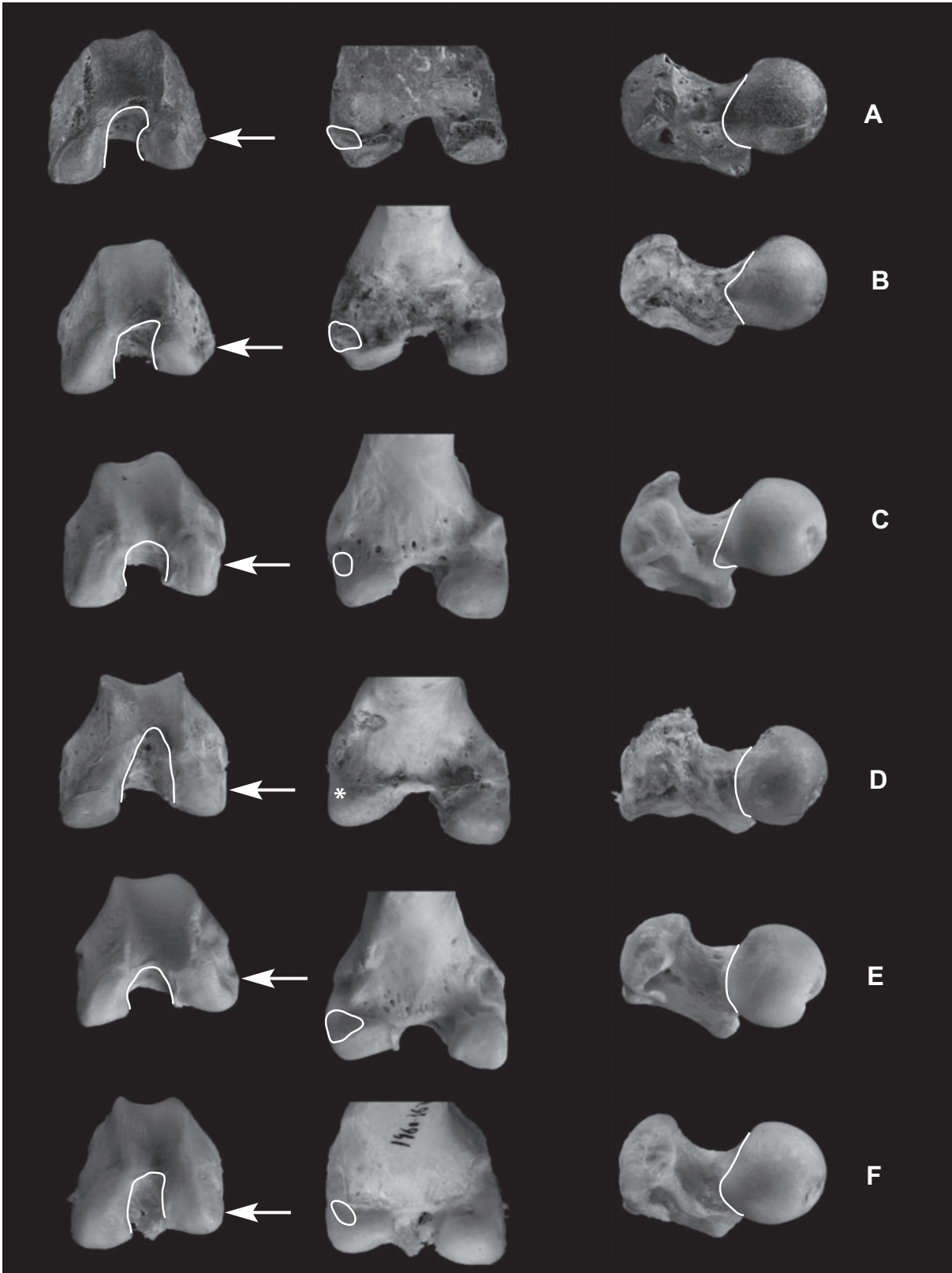
Figure 11. Comparison of the left femur in Lutrinae gen. et sp. indet. cf. *Aonyx* sp. and extant Lutrinae. The distal view in the column to the left shows the shape of the intercondyloid fossa; the proximoposterior view of the distal articulation in the middle column shows the shape and extension of the articulation for the lateral gastrocnemius sesamoid (asterisk shows the approximate location when there is no articular surface); the proximal view in the column to the right shows the lateral and/or posterior extension of the articular surface of the femoral head. The arrow indicates the position of the articulation for the lateral sesamoid, the extension of which is revealed by a strong convexity of the lateral outline of the femur in distal view. A, Lutrinae gen. et sp. indet. cf. *Aonyx* sp. B, *Aonyx capensis*, C, *Lontra felina*, D, *Pteronura brasiliensis*, E, *Lutra lutra* and F, *Lutrogale perspicillata*. All the photographs are to the same scale.

←───────────────────────────────────

Age and distribution: TM 266, Toros-Menalla, late Miocene, Chad.

Description

Skull: The dorsal part of the parietals is preserved, showing a developed sagittal crest. The postorbital constriction is pronounced.

Dentition: The fragmentary right maxilla consists of a piece of P4. It was associated in the field with the skull fragment described above and undoubtedly belongs to the same individual. The labial part of the tooth is preserved, but the cusps are worn and slightly fissured. The tooth is at least 16 mm long; this is an estimate that is probably not far from the actual measurement. The metastyle is much shorter than the paracone, the latter also being taller than the former. It is not possible to state whether a parastyle was present, but the cingulum on the mesial face of the paracone is pronounced. The lingual side of the paracone and metastyle is nearly vertical; lingual to the labial cusps, there is a concave shelf that extends far lingually; it is also extended distally up to the distal end of the metastyle. None of the lingual cusps is preserved. Nevertheless, the lingual root is mostly preserved and indicates a minimum width of 15 mm for P4.

Comparisons and discussion

The assignment of this specimen to the Lutrinae is based on the size and shape of the P4, which is short but very wide and with a short metacone, and also on the presence of a strong sagittal crest and a long and pronounced postorbital constriction. These features distinguish the specimen from the piscivorous otters, *Lutra*, *Lontra* and *Pteronura*, which do not have such a distally wide upper carnassial and/or such a shortened metacone. The P4 of *Torolutra* has been recently described for *Torolutra ougandensis* (Morales *et al.*, 2005) and is of a piscivorous feeding morphotype, with a cutting edge, longer metacone and narrower P4 than in TM 266-05-061. Even if the assignment of the latter specimen remains to be specified, there are undoubtedly two different species of otters at TM 266. As far as we can see, the morphology of TM 266-05-061 (pro-

portion, distal extension of lingual shelf) fits more with that of the large bunodont otters such as *Sivaonyx* or *Djourabus*. Species of both genera are known from Toros-Menalla and *Sivaonyx* spp. are also known from various African localities of late Miocene and early Pliocene age. Dental measurements indicate that TM 266-05-061 was probably slightly larger than, for example, the type of *Sivaonyx senutae* (= *S. soriae*), therefore slightly smaller than *S. beyi*. The generic assignment of TM 266-05-061 remains to be confirmed.

CONCLUSIONS

In the present contribution, at least four species of Lutrinae are described. The presence of such a great number of species, diverse in size and dental morphology, in the fossiliferous area of Toros-Menalla, Chad, is significant and unique in the fossil record of the Cenozoic of Africa. The two new species that are described, *Sivaonyx beyi* and *Djourabus dabba*, are also the best known. Two other species are certainly present in the area, though they are represented by fragmentary remains, and their taxonomy remains to be confirmed. Thus, the dentition of the specimen assigned to aff. *Torolutra* sp. from TM 266 is very different from that of *S. beyi* and *T. dabba*; it is far more similar to that of piscivorous taxa. The femur from TM 219 cannot be assigned to *S. beyi* on the basis of its much smaller size and morphological differences. The size difference also prevents us from assigning this bone to aff. *Torolutra* sp. or *Djourabus dabba*. The single cranial specimen, which is associated with a fragmentary P4, is from TM 266. The size of this specimen and the morphology of P4 indicate it belongs to a bunodont species; however, the material is too fragmentary to assign it with certainty to either of the genera present in Toros-Menalla, *Sivaonyx* or *Djourabus*. Fossils of otters in Toros-Menalla are known from ten localities distributed throughout the area. Two species are known from one individual from TM 266 (aff. *Torolutra* sp. and aff. *Sivaonyx* sp. or *Djourabus* sp.) and TM 219 (*S. beyi* and aff. *Aonyx* sp.); each of the other sites has yielded a single individual of one species. This implies that,

when present, otters were not abundant or not fossilized at Toros-Menalla. Except *Enhydra lutris*, most extant otters spend 75% of their time on land (Kruuk, 2006); they always live near water from which they take their food. The presence of four morphologically distinct otters suggests the presence of a relatively well-developed freshwater system of lakes and/or rivers at Toros-Menalla.

ACKNOWLEDGEMENTS

REFERENCES

Anyonge W. 1993. Body mass in large extant and extinct carnivores. *Journal of Zoology* **231:** 339–350.

Barone R. 1986. *Anatomie comparee des mammiferes domestiques. Tome 1. Ostéologie*. Paris: Editions Vigot.

Barone R. 2000. *Anatomie comparee des mammiferes domestiques. Tome 2. Arthrologie et myologie*. Paris: Editions Vigot.

Barry JC. 1995. Faunal turnover and diversity in the terrestrial Neogene of Pakistan. In: Vrba ES, Denton GH, Partridge TC, Burckle LH, eds. *Paleoclimate and evolution, with emphasis on human origins*. New Haven: Yale University Press, 115–134.

Barry JC, Morgan ME, Flynn LW, Pilbeam D, Behrensmeyer AK, Raza SM, Khan IA, Badgley C, Hicks J, Kelley J. 2002. Faunal and environmental change in the Late Miocene Siwaliks of Northern Pakistan. *Paleobiology Memoirs* **3:** 1–72.

Berta A, Morgan GS. 1985. A new sea otter (Carnivora: Mustelidae) from the late Miocene and early Pliocene (Hemphillian) of North America. *Journal of Paleontology* **59:** 809–819.

Beswick-Perrin J. 1871. On the myology of the limbs of the kinkajou (*Cercoleptes caudivolvulus*). *Proceedings of the Scientific Meetings of the Zoological Society of London* **1871:** 547–559.

de Bonis L, Peigné S, Andossa L, Mackaye HT, Vignaud P, Brunet M. 2005. *Hyaenictitherium minimum*, a new ictithere (Mammalia, Carnivora, Hyaenidae) from the Late Miocene of Toros-Menalla, Chad. *Comptes Rendus Palevol* **4:** 671–679.

de Bonis L, Peigné S, Andossa L, Mackaye HT, Vignaud P, Brunet M. 2007a. First occurrence of the 'hunting hyaena' *Chasmaporthetes* in the late Miocene fossil bearing localities of Toros Menalla, Chad (Africa). *Bulletin de la Société Géologique de France* **178:** 317–326.

de Bonis L, Peigné S, Andossa L, Mackaye HT, Vignaud P, Brunet M. 2007b. The oldest African fox (*Vulpes riffautae* n. sp., Canidae, Carnivora) recovered in late Miocene deposits of the Djurab desert, Chad. *Naturwissenschaften* **94:** 575–580.

Bourdelle E, Bressou C. 1953. *Anatomie regionale des animaux domestiques. IV. Carnivores – Chien et chat*. Paris: Baillière et Fils.

Bowdich TE. 1821. *An analysis of the natural classifications of mammalia, for the use of students and travellers*. Paris: J. Smith.

Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, Beauvilain A, Blondel C, Bocherens H, Boisserie JR, de Bonis L, Coppens Y, Dejax J, Denys C, Duringer P, Eisenmann V, Fanone G, Fronty P, Geraads D, Lehmann T, Lihoreau F, Louchart A, Mahamat A, Merceron G, Mouchelin G, Otero O, Campomanes PP, De Leon MP, Rage JC, Sapanet M, Schuster M, Sudre J, Tassy P, Valentin X, Vignaud P, Viriot L, Zazzo A, Zollikofer C. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* **418:** 145–151.

Brunet M, Guy F, Boisserie JR, Djimdoumalbaye A,

Lehmann T, Lihoreau F, Louchart A, Schuster M, Tafforeau P, Likius A, Mackaye HT, Blondel C, Bocherens H, de Bonis L, Coppens Y, Denys C, Duringer P, Eisenmann V, Flisch A, Geraads D, Lopez-Martinez N, Otero O, Peláez Campomanes P, Pilbeam D, Ponce de León M, Vignaud P, Viriot L, Zazzo A, Zollikofer C. 2004. 'Toumaï', Miocène supérieur du Tchad, le nouveau doyen du rameau humain. *Comptes Rendus Palevol* **3:** 275–283.

Brunet M, Guy F, Pilbeam D, Lieberman D, Likius A, Mackaye HT, Ponce de Leon M, Zollikofer CPE, Vignaud P. 2005. New material of the Earliest Hominid from the Upper Miocene of Chad. *Nature* **434:** 753–755.

Bryant HN, Seymour KL. 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. *Journal of Morphology* **206:** 109–117.

Bryden MM. 1971. Myology of the Southern elephant seal *Mirounga leonina* (L.). *Antarctic Research Series* **18:** 109–140.

Carter SK, Rosas FCW. 1997. Biology and conservation of the Giant Otter *Pteronura brasiliensis*. *Mammal Review* **27:** 1–26.

Davis DD. 1964. The Giant Panda – A morphological study of evolutionary mechanisms. *Fieldiana: Zoology Memoirs* **3:** 1–339.

Egi N. 2001. Body mass estimates in extinct mammals from limb bone dimensions: the case of North American Hyaenodontids. *Palaeontology* **44:** 497–528.

Emmerson W, Philip S. 2004. Diets of Cape clawless otters at two South African coastal localities. *African Zoology* **39:** 201–210.

Engelke E, Koch R, Brunnberg L, Waibl H. 2005. Das Ligamentum olecrani des Ellbogengelenkes bei Hund und Katze. *Kleintierpraxis* **50:** 313–324.

Estes JA. 1980. *Enhydra lutris*. *Mammalian Species* **133:** 1–8.

Evans HE. 1993. *Miller's anatomy of the dog*. Philadelphia: W.B. Saunders Company.

Fischer G. 1817. Adversaria zoologica. *Mémoires de la Société Impériale des Naturalistes de Moscou* **5:** 357–472.

Fischer EM. 1942. *The osteology and myology of the California River Otter*. Stanford: Stanford University Press.

Flower WH. 1869. On the value of the characters of the base of the cranium in the classification of the order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. *Proceedings of the Zoological Society of London* **1869:** 4–37.

Fulton TL, Strobeck C. 2006. Molecular phylogeny of the Arctoidea (Carnivora): effect of missing data on supertree and supermatrix analyses of multiple gene data sets. *Molecular Phylogenetics and Evolution* **41:** 165–181.

Gambarjan PP, Karapetjan WS. 1961. Besonderheiten im Bau des Seelöwen (*Eumetopias californianus*), der Baikalrobbe (*Phoca sibirica*) und des Seeotters (*Enhydra lutris*) in Anpassung an die Fortbewegung im Wasser. *Zoologische Jahrbücher* **79:** 123–148.

Gonyea WJ. 1976. Behavioral implications of saber-toothed felid morphology. *Paleobiology* **2:** 332–342.

Gorniak GC. 1986. Architecture of the masticatory apparatus in eastern raccoons (*Procyon lotor lotor*). *American Journal of Anatomy* **176:** 333–351.

Hall ER. 1926. Muscular anatomy of three mustelid mammals, *Mephitis*, *Spilogale*, and *Martes*. *University of California Publications in Zoology* **30:** 7–38.

Hall ER. 1927. The muscular anatomy of the American badger (*Taxidea taxus*). *University of California Publications in Zoology* **30:** 205–219.

Hendey QB. 1978. Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaanweg, South Africa. *Annals of the South African Museum* **76:** 329–357.

Hildebrand M. 1952. An analysis of body proportions in the Canidae. *American Journal of Anatomy* **90:** 217–256.

Howard LD. 1973. Muscular anatomy of the forelimb of the sea otter (*Enhydra lutris*). *Proceedings of the California Academy of Sciences, 4th Series* **39:** 411–500.

Howard LD. 1975. Muscular anatomy of the hind limb of the sea otter (*Enhydra lutris*). *Proceedings of the California Academy of Sciences, 4th Series* **40:** 335–416.

Howell AB. 1929. Contribution to the comparative anatomy of the eared and earless seals (Genera *Zalophus* and *Phoca*). *Proceedings of the US National Museum* **73:** 1–142.

Howell FC, Petter G. 1979. Diversification et affinités des Carnivores pliocènes du groupe de l'Omo et de la formation d'Hadar (Ethiopie). *Bulletin de la Société Géologique de France, 7e Série* **21:** 289–293.

Hwang YT, Larivière S. 2005. *Lutrogale perspicillata*. *Mammalian Species* **786:** 1–4.

Jenkins FA, Camazine SM. 1977. Hip structure and locomotion in ambulatory and cursorial carnivores. *Journal of Zoology* **181:** 351–370.

Kenyon KW. 1981. Sea otter *Enhydra lutris* (Linnaeus, 1758). In: Ridgway SH, Harrison RJ, eds. *Handbook of marine mammals. Volume 1: the walrus, sea lions, fur seals and sea otter*. London: Academic Press, 209–223.

Koepfli KP, Wayne RK. 1998. Phylogenetic relationships of otters (Carnivora: Mustelidae) based on mitochrondrial cytochrome *b* sequences. *Journal of Zoology* **246:** 401–416.

Kretzoi M. 1943. *Kochictis centennii* n. g. n. sp., ein altertümlicher Creodonte aus dem Oberoligozän Siebenbürgens. *Földtani Közlöny* **73:** 190–195.

Kruuk H. 2006. *Otters: ecology, behaviour, and conservation*. Oxford: Oxford University Press.

Lambert WD. 1997. The osteology and paleoecology of the giant otter *Enhydritherium terraenovae*. *Journal of Vertebrate Paleontology* **17:** 738–749.

Larivière S. 1998. *Lontra felina*. *Mammalian Species* **575:** 1–5.

Larivière S. 1999a. *Lontra longicaudis*. *Mammalian Species* **609:** 1–5.

Larivière S. 1999b. *Lontra provocax*. *Mammalian Species* **610:** 1–4.

Larivière S. 2001a. *Aonyx congicus*. *Mammalian Species* **650:** 1–3.

Larivière S. 2001b. *Aonyx capensis*. *Mammalian Species* **671:** 1–6.

Larivière S. 2002. *Lutra maculicollis*. *Mammalian Species* **712:** 1–6.

Larivière S. 2003. *Amblonyx cinereus*. *Mammalian Species* **720:** 1–5.

Larivière S, Walton LR. 1998. *Lontra canadensis*. *Mammalian Species* **587:** 1–8.

Leach D. 1977. The forelimb musculature of marten (*Martes americana* Turton) and fisher (*Martes pennanti* Erxleben). *Canadian Journal of Zoology* **55:** 31–41.

Lilje KE, Tardieu C, Fischer MS. 2003. Scaling of long bones in ruminants with respect to the scapula. *Journal of Zoological Systematics and Evolutionary Research* **41:** 118–126.

Lydekker R. 1884. Indian Tertiary and post-Tertiary Vertebrata. Vol. 2. Part 6. Siwalik and Narbada Carnivora. *Memoirs of the Geological Survey of India, Palaeontologia Indica Series* **10:** 178–355.

Marmi J, López-Giráldez JF, Domingo-Roura X. 2004. Phylogeny, evolutionary history and taxonomy of the Mustelidae based on sequences of the cytochrome *b* gene and a complex repetitive flanking region. *Zoologica Scripta* **33:** 481–499.

Matthew WD. 1929. Critical observations upon Siwalik mammals (Exclusive of Proboscidea). *Bulletin of the American Museum of Natural History* **56:** 437–560.

Maynard Smith J, Savage RJG. 1956. Some locomotory adaptations in mammals. *Journal of the Linnean Society (Zoology)* **42:** 603–622.

Morales J, Pickford M. 2005. Giant bunodont Lutrinae from the Mio-Pliocene of Kenya and Uganda. *Estudios Geologicos* **61:** 233–246.

Morales J, Pickford M, Soria D. 2005. Carnivores from the Late Miocene and Basal Pliocene of the Tugen Hills, Kenya. *Revista de la Sociedad Geologica de Espana* **18:** 39–61.

Mori M. 1958. The skeleton and musculature of *Zalophus*. *Okajimas Folia Anatomica Japonica* **31:** 203–284.

Nowak RM. 2005. *Walker's carnivores of the world*. Baltimore and London: The Johns Hopkins University Press.

Parker DM, Burchell RK, Bernard RTF. 2005. The diet of Cape clawless otters at two sites along the Bloukrans River, Eastern Cape Province, South Africa. *African Zoology* **40:** 330–334.

Peigné S, Heizmann EPJ. 2003. The Amphicyonidae (Mammalia, Carnivora) from Ulm-Westtangente (MN 2, Early Miocene), Baden-Württemberg, Germany – Systematics and ecomorphology. *Stuttgarter Beiträge Zur Naturkunde Serie B (Geologie und Paläontologie)* **343:** 1–133.

Peigné S, de Bonis L, Andossa L, Mackaye HT, Vignaud P, Brunet M. 2005a. A new machairodontine (Carnivora, Felidae) from the late Miocene hominid locality of TM 266, Toros-Menalla, Chad. *Comptes Rendus Palevol* **4:** 243–253.

Peigné S, de Bonis L, Andossa L, Mackaye HT, Vignaud P, Brunet M. 2005b. The earliest modern mongoose (Carnivora, Herpestidae) from Africa (late Miocene of Chad). *Naturwissenchaften* **92:** 287–292.

Petter G. 1994. Carnivores des régions de Nkondon et de Kisegi-Nyabusosi (Rift occidental, Ouganda). In: Senut B, Pickford M, eds. *Geology and palaeobiology of the Albertine rift valley, Uganda-Zaire. Vol. II: palaeobiology.* Orléans: CIFEG Occasional Publications, 207–215.

Petter G, Pickford M, Howell FC. 1991. La loutre piscivore du Pliocène de Nyaburogo et de Nkondo (Ouganda, Afrique orientale): *Torolutra ougandensis* n. g., n. sp. (Mammalia, Carnivora). *Comptes Rendus de l'Académie des Sciences, Paris, Série II* **312:** 949–955.

Pickford M. 2005. Fossil hyraxes (Hyracoidea: Mammalia) from the Late Miocene and Plio-Pleistocene of Africa, and the phylogeny of the Procaviidae. *Palaeontologia Africana* **41:** 141–161.

Piérard J. 1971. Osteology and myology of the Weddell seal *Leptonychotes weddelli* (Lesson, 1826). *Antarctic Research Series* **18:** 53–108.

Pilbeam DR, Behrensmeyer AK, Barry JC, Shah SMI. 1979. Miocene sediments and fauns of Pakistan. *Postilla* **179:** 1–45.

Pilgrim GE. 1913. The correlation of the Siwaliks with mammal horizons of Europe. *Records of the Geological Survey of India* **43:** 264–326.

Pilgrim GE. 1931. *Catalogue of the Pontian Carnivora of Europe.* London: British Museum (Natural History).

Pilgrim GE. 1932. The fossil Carnivora of India. *Memoirs of the Geological Survey of India, Palaeontologia Indica n.s.* **18:** 1–232.

Pohle H. 1919. Die Unterfamilie der Lutrinae (Eine systematisch-tiergeographische Studie an dem Material der Berliner Museen). *Archiv für Naturgeschichte Abteilung A* **9:** 1–246.

Repenning CA. 1976. *Enhydra* and *Enhydriodon* from the Pacific coast of North America. *Journal of Research of the US Geological Survey* **4:** 305–315.

Scapino R. 1976. Function of the digastric muscle in Carnivores. *Journal of Morphology* **150:** 843–860.

Sebastiani AM, Fishbeck DW. 2005. *Mammalian anatomy: the cat.* Englewood: Morton Publishing Co.

Somers MJ, Nel JAJ. 2003. Diet in relation to prey of Cape clawless otters in two rivers in the Western Cape Province, South Africa. *African Zoology* **38:** 317–326.

Spoor CF, Badoux DM. 1986. Nomenclature review of long digital forelimb flexors in Carnivores. *Anatomical Record* **216:** 471–473.

Stains HJ. 1973. Comparative study of the calcanea of members of the Ursidae and Procyonidae. *Bulletin of the Southern California Academy of Sciences* **72:** 137–148.

Stains HJ. 1976. Calcanea of members of the Mustelidae. Part II, Mellivorinae, Melinae, Mepthitinae, and Lutrinae. *Bulletin of the Southern California Academy of Sciences* **75:** 249–257.

Stromer E. 1920. Mitteilungen über Wirbeltierreste aus dem Mittelpliocän des Natrontales (Ägypten). *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Bayerischen Akademie der Wissenschaften zu München* **1920:** 345–370.

Stromer E. 1931. Reste Süsswasser und Land bewohnender Wirbeltiere aus den Diamantfeldern Klein-Namaqualandes (Südwestafrika). *Sitzungsberichte der Mathematisch-*

Naturwissenschaftlichen Klasse der Bayerischen Akademie der Wissenschaften zu München **1931**: 17–47.

Szuma E. 1994. Quasi-continuous variation of the first pre-molars in the Polish population of the badger *Meles meles*. *Acta Theriologica* **39**: 201–208.

Tarasoff FJ. 1972. Comparative aspects of the hind limbs of the river otter, sea otter and seals. In: Harrison RJ, ed. *Functional anatomy of marine mammals*. London: Academic Press, 333–359.

Tarasoff FJ, Bisaillon A, Piérard J, Whitt AP. 1972. Locomotory patterns and external morphology of the river otter, sea otter, and harpd seal (Mammalia). *Canadian Journal of Zoology* **50**: 915–929.

Taylor ME. 1974. The functional anatomy of the forelimb of some African Viverridae (Carnivora). *Journal of Morphology* **143**: 307–336.

Taylor ME. 1976. The functional anatomy of the hindlimb of some African Viverridae (Carnivora). *Journal of Morphology* **148**: 227–254.

Taylor ME. 1989. Locomotor adaptations by Carnivores. In: Gittleman JL, ed. *Carnivore behavior, ecology, and evolution*, Vol. 1. New York: Cornell University Press, 382–409.

Taylor WP. 1914. The problem of aquatic adaptation in the Carnivora, as illustrated in the osteology and evolution of the sea otter. *University of California Publications, Bulletin of the Department of Geology* **7**: 465–495.

Turnbull WD. 1970. Mammalian masticatory apparatus. *Fieldiana: Geology* **18**: 149–356.

Van Valkenburgh B. 1985. Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology* **11**: 406–428.

Van Valkenburgh B. 1990. Skeletal and dental predictors of body mass in carnivores. In: Damuth J, MacFadden BJ, eds. *Body size in mammalian paleobiology: estimation and biological implications*. Cambridge: Cambridge University Press, 181–205 and appendix.

Van Zyll de Jong CG. 1972. A systematic review of the nearctic and neotropical river otters (Genus *Lutra*, Mustelidae, Carnivora). *Life Sciences Contributions Royal Ontario Museum* **80**: 1–104.

Van Zyll de Jong CG. 1987. A phylogenetic study of the Lutrinae (Carnivora; Mustelidae) using the morphological data. *Canadian Journal of Zoology* **65**: 2536–2544.

Van Zyll de Jong CG. 1991. A brief review of the systematics and a classification of the Lutrinae. In: Reuther C, Röchert R, eds. *Proceedings of the V International Otter Colloquium*. Hankensbüttel: Gruppe Naturschutz GmbH, Habitat 6, 79–83.

Verma BC, Gupta SS. 1992. *Enhydriodon sivalensis*, a giant fossil otter from the Saketi Formation (Upper Pliocene), Siwalik Group, Sirmur district, Himachal Pradesh. *Journal of the Palaeontological Society of India* **37**: 31–36.

Vignaud P, Duringer P, Mackaye HT, Likius A, Blondel C, Boisserie JR, de Bonis L, Eisenmann V, Etienne ME, Geraads D, Guy F, Lehmann T, Lihoreau F, Lopez-Martinez N, Mourer-Chauviré C, Otero O, Rage JC, Schuster M, Viriot L, Zazzo A, Brunet M. 2002. Geology and Palaeontology of the Upper Miocene Toros Menalla hominid locality, Chad. *Nature* **418**: 152–155.

Werdelin L. 2003. Carnivora from the Kanapoi hominid site, Turkana Basin, Northern Kenya. *Contributions in Science* **498**: 115–132.

Willemsen GF. 1980a. Comparative study of the functional morphology of some Lutrinae, especially *Lutra lutra*, *Lutrogale perspicillata* and the Pleistocene *Isolalutra cretensis* – I. *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, Series B* **83**: 289–309.

Willemsen GF. 1980b. Comparative study of the functional morphology of some Lutrinae, especially *Lutra lutra*, *Lutrogale perspicillata* and the Pleistocene *Isolalutra cretensis* – II. *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, Series B* **83**: 310–326.

Willemsen GF. 1992. A revision of the Pliocene and Quaternary Lutrinae from Europe. *Scripta Geologica* **101**: 1–115.

Willemsen GF. 1999. Some remarks on the Enhydrini (Lutrinae) from the Siwaliks, Pakistan. *Deinsea* **7**: 411–418.

Willemsen GF, Malatesta A. 1987. *Megalenhydris barbaricina* sp. nov., a new otter from Sardinia. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B* **90**: 83–92.

Wilson DE, Reeder DM, eds. **1993.** *Mammal species of the world*. Baltimore: Johns Hopkins University Press.

Wischnitzer S. 1993. *Atlas and dissection guide for comparative anatomy*. New York: W.H. Freeman.

Wolsan M. 1989. Dental polymorphism in the genus *Martes* (Carnivora: Mustelidae) and its evolutionary significance. *Acta Theriologica* **34**: 545–593.

Wolsan M, Ruprecht AL, Buchalczyk T. 1985. Variation and asymmetry in the dentition of the Pine and Stone-Martens (*Martes martes* and *M. foina*) from Poland. *Acta Theriologica* **30**: 79–114.

Yalden DW. 1970. The functional morphology of the carpal bones in carnivores. *Acta Anatomica* **77**: 481–500.

APPENDIX 1

LISTS OF SPECIMENS USED IN COMPARISONS

Extant taxa

Skull and dentition of *Pteronura brasiliensis* (MNHN CG 1937-888, MNHN CG 1962-2085, MNHN CG 1981-4), *Lutra lutra* (MNHN CG 1929-545, MNHN CG 1959-209, MNHN CG 1962-1655, MNHN CG 1962-1738, MNHN CG 1996-2466), *Lontra canadensis* (MNHN CG 1901-645), *Lontra longicaudis* (MNHN CG 2001-1291), *Lontra felina* (MNHN CG 1932-3019), *Lutra maculicollis* (MNHN CG 2005-603), *Lutrogale perspicillata* (MNHN CG 1962-1646), *Amblonyx cinereus* (MNHN CG 1884-10, CG 1879-198, MNHN CG 1982-165, MNHN CG 2005-607, MNHN CG 2005-601), *Aonyx capensis* (MNHN A 1899, MNHN A 1914, MNHN A 3388, MNHN CG 1897-982), *Aonyx congicus* (MNHN CG 1947-31, MNHN CG 1966-216, MNHN

CG 1973-65, MNHN CG 2005-612). Complete skeleton, including skull and mandible, of *Pteronura brasiliensis* (MNHN A 1918), *Lutra lutra* (MNHN CG 1996-2466) and *Lontra felina* (MNHN CG 1995-185); long limb bones of *Lutrogale perspicillata* (MNHN CG 1960-3670); vertebral axis, hip, and hind limbs of *Aonyx capensis* (MNHN CG 1883-1561).

Fossil taxa
Siwalik Group of Pakistan and India: Enhydriodon cf. *falconeri*: BMNH-M 12350 (cast of GSI D 161; Pilgrim, 1931: pl. 2, fig. 5; Pilgrim, 1932: pl. 2, fig. 15), isolated right m1. *Sivaonyx bathygnathus*: BMNH-M 16929 (cast of GSI D 156; Pilgrim, 1932: pl. 2, fig. 14), fragment of left hemimandible with fragmentary p4, m1 from Dhok Pathan Stage, Hasnot, Salt Range; BMNH-M 12352 (cast of GSI D 157; Pilgrim, 1932: pl. 2, fig. 16), isolated left P4 from Dhok Pathan Zone, Hasnot, Salt Range; BMNH-M 15397, fragment of right hemimandible with m1 from Tatrot Stage, Punjab (H.M. Sale Collection, presd. by Bormah Oil Co.); BMNH-M 13175, fragment of left hemimandible with m1 from Kamlial, Attock District, Punjab.

Lukeino Formation, Kenya: Sivaonyx soriae: BAR 1720′00 (holotype of *S. senutae*; Morales *et al.*, 2005: figs 6G, 9F), isolated left P4 from Kapcheberek; BAR 1082′01 (paratype of *S. senutae*; Morales *et al.*, 2005: figs 6H, 9E), isolated right M1 from Kapcheberek; BAR 1894′00 (paratype of *S. senutae*), right c from Kapcheberek.

Magabet Formation, Kenya: Sivaonyx ekacaman: BAR 1231′01 (Morales *et al.*, 2005: fig. 9I), isolated left P3 from Sagatia; BAR 416′00 (Morales *et al.*, 2005: fig. 9H), trigonid of left m1 from Mosionin; BAR 720′03 (Morales *et al.*, 2005: fig. 9G), fragment of left hemimandible with p4, trigonid of m1 from Sagatia.

Langebaanweg, South Africa: Sivaonyx hendeyi: SAM-PQ L 50000 (holotype; Hendey, 1978: fig. 9A), fragment of left hemimandible with p4-m2 and isolated left P3 and P4; SAM-PQ L 9138 (Hendey, 1978: fig. 9B), fragment of right hemimandible with distal part of p4; SAM-PQ L 41523 (Hendey, 1978: fig. 11A), left femur.

Klein Zee, South Africa: Sivaonyx africanus: BSP (1930)-XI-1 (holotype; Stromer, 1931), fragment of right mandible with c broken, p4-m1, and isolated M1 (casts studied in MNHN).