KIRTLANDIA®
The Cleveland Museum of Natural History

December 2007 *Number 56:86–91*

EARLIEST EVIDENCE FOR *ATHERURUS* AND *XENOHYSTRIX* (HYSTRICIDAE, RODENTIA) IN AFRICA, FROM THE LATE MIOCENE SITE OF LEMUDONG'O, KENYA

LESLEA J. HLUSKO
Department of Integrative Biology
University of California, 3060 Valley Life Sciences Building
Berkeley, California 94720-3140
hlusko@berkeley.edu

ABSTRACT

Eleven Hystricidae teeth have been recovered from the mammalian-dominated fossil locality of Lemudong'o, Kenya. This site dates to the late Miocene, making these fragmentary specimens some of the earliest representatives of this family in Africa. As is typical in porcupine systematics, identifications of isolated teeth are based primarily on size. Three taxa are represented: *Xenohystrix* sp. indet., *Hystrix* sp. indet., and *Atherurus* sp. indet. Lemudong'o documents the earliest occurrence of *Xenohystrix* and *Atherurus* in Africa, and is characterized by a relatively wide diversity of porcupines.

Introduction

Porcupines, members of the family Hystricidae, are categorized within the suborder Hystricomorpha of the Rodentia. The hystricomorphs are divided into two geographic and evolutionary groups, the Old World families (e.g., Hystricidae, Thryonomyidae, Petromyidae, and Bathyergidae) and the New World families (often attributed to their own infraorder, the Caviomorpha, including the Erethizontidae, Caviidae, Hydrochaeridae, and others). Based on molecular data, the Old World and New World taxa are estimated to have split between 63 and 46 Ma, and the Hystricidae would have diverged 54–43 Ma from the other Old World hystricomorpha families (Huchon and Douzery, 2001, p. 245).

Extant Old World porcupines typically are categorized into three genera: *Atherurus*, *Trichys*, and *Hystrix* (Kingdon, 1974; Nowak, 1991), although the latter is sometimes divided into *Hystrix* and *Thecurus* (van Weers, 1978). Here, I will follow the taxonomy of Nowak (1991), recognizing only three extant genera.

Old World porcupines have a wide geographic distribution (Kingdon, 1974, p. 679–695; Nowak, 1991, p. 895–900). *Trichys* is found on the Malay Peninsula, Sumatra, and Borneo. *Atherurus* is found in Asia and sub-Saharan Africa. *Hystrix* has the broadest range, and is found in China, Southeast Asia, Indonesia, Indo-Pakistan, the Mediterranean region, and eastern and sub-Saharan Africa.

To date, no fossils of *Trichys* have been found, which may result from their preference for swampy habitats (Lim et al., 1989, p. 23). Fossil specimens attributed to the Asian *Atherurus* have only been published from Pleistocene sites in Asia (van Weers, 2002), and the African *Atherurus* from the late Miocene in Ethiopia (Haile-Selassie et al., 2004). *Hystrix* fossil taxa are much more abundant, and are known from the Miocene through Pleistocene of Asia, Europe, and Africa. The extinct genus *Xenohystrix* is only known from the late Miocene and Pliocene fossil record of eastern and southern Africa (Greenwood, 1955; Howell and Coppens, 1974; Maguire, 1978; Sabatier, 1979; Haile-Selassie, 2001; Haile-Selassie et al., 2004).

The earliest fossils attributable to the Hystricidae date to MN 11/12 and MN 13 (Turolian $\approx$ 8–6 Ma). These early specimens have recently been reviewed and revised by van Weers and Rook (2003) and, therefore, will not be repeated here. However, to briefly summarize the dental evolution, all of the specimens from this early record have been attributed to the genus *Hystrix*. The earliest species is *Hystrix primigenia*, a very large, low-crowned porcupine from sites in southeastern Europe and Asia ranging from MN 11 to MN 13 (8–6 Ma) (Masini and Rook, 1993; Fistani et al., 1997; van Weers and Rook, 2003). *Hystrix depereti* is slightly larger than *H. primigenia* on average and with relatively somewhat taller cheek-tooth crowns. *Hystrix depereti* ranges geographically from Spain to Turkey during the late Miocene and Pliocene (MN 12–MN 15).

Hystrix aryanensis is only known from the Khurdkabul Basin in Afghanistan, dated roughly to the late Miocene (Thomas and Petter, 1986, p. 361). This species is approximately the same size as the extant *H. cristata*, and, therefore, has smaller, but relatively taller-crowned teeth than *H. primigenia*. The relatively taller crowns seen in *H. aryanensis* and *H. depereti* relative to *H. primigenia* show that the marked increase in hypsodonty seen in later forms probably started to develop in the late Miocene.

These early *Hystrix* species are followed by *H. refossa*, which is known from central and southern Europe and Israel and dates from the early Pliocene through the Pleistocene. This species is also much larger than extant *Hystrix* species, approximating the size of *H. primigenia* although it is distinct from this species and *H. depereti* in having more hypsodont cheek teeth.

During the late Pliocene *Hystrix zhengi* is known from two sites in China, Longgupo in the Sichuan Province and the *Gigantopithecus* Cave in Liucheng, Guangxi (van Weers and Zhang, 1999). This species is larger than all extant *Hystrix* species and its hypsodonty is intermediate between the earlier *Hystrix* species in Europe and later *Hystrix*.

The early and middle Pleistocene fossils from China have been separated as two other species with somewhat overlapping size ranges: *H. kiangsenensis* is smaller than *H. magna* and the two species appear to have been sympatric, or at least to have been recovered from the same sites (van Weers and Zheng, 1998). Both of these Chinese species have much more hypsodont cheek teeth than the earlier *H. zhengi* (van Weers and Shaohua, 1998; van Weers and Zhaoqun, 1999).

Another extinct fossil porcupine, *Hystrix lagrelli* is known from the Pleistocene of both Java and China (van Weers, 1995). This species may represent the sister taxon to the extant *Hystrix* species currently found on Sumatra, Borneo, and the Phillipines that comprise the sub-genus *Thecurus* (van Weers, 1995).

The site of Sangiran on Java in Indonesia has yielded three isolated teeth that van Weers attributed to a large porcupine, *Hystrix gigantean*, whose cheek teeth are larger than *H. indica* and *H. africaeaustralis*, and which are extremely hypsodont (van Weers, 1985, p. 118).

The African-porcupine fossil record has received much less attention than those of Europe and Asia, and therefore is less well understood. The earliest fossil evidence for porcupines in Africa is a dP4 from the Lower Nawata beds at Lothagam, Kenya (estimated to be older than 7.44 Ma), attributed to a small *Hystrix* sp. indet (Winkler, 2003, p. 172–3). Other specimens dated to the late Miocene are also quite limited and fragmentary, and include fossils from the Tugen Hills in Kenya that are conferred only to Hystricidae indet. (Pickford, 1975; Winkler, 2002, p. 241), and partial jaw fragments and isolated teeth representative of three genera (*Xenohystrix*, *Hystrix*, and *Atherurus*) from the 5.7–5.2 Ma West Margin sites in Ethiopia (Haile-Selassie et al., 2004).

The Pliocene documents relatively considerable porcupine diversity in Africa. The site of Makapansgat in South Africa yielded very large porcupine specimens that were described as *Xenohystrix crassidens* (Greenwood, 1955). This genus has also been recovered from Laetoli, Tanzania (Denys, 1987, p. 154). Another fairly large porcupine *Hystrix makapanensis* is also known from Makapansgat (Greenwood, 1955, 1958) and Laetoli (Denys, 1987, p. 154). Specimens similar in size to modern *H. africaeaustralis* have been reported from Makapansgat (Greenwood, 1955; Maguire, 1978) as well as from the Omo and Hadar in Ethiopia (Howell and Coppens, 1974; Sabatier, 1979). A much larger, as yet unnamed, species of *Hystrix* is represented by one isolated lower molar in the Kaiyumung Member (4–3.5 Ma) at Lothagam (Winkler, 2003, p. 173). The smallest species of *Hystrix* to date was recovered from Laetoli, Tanzania, *Hystrix leakeyi* (Denys, 1987, p. 149). Although it is small, *H. leakeyi* is larger than any known species of *Atherurus*.

The relationships between these early porcupines and extant species remain unclear due to the fragmentary nature of the fossil record. The majority of known fossils are isolated teeth or fragmentary jaws. Porcupine teeth are known to be extremely variable morphologically even at the population level, and therefore occlusal morphology is not typically taxonomically informative (van Weers, 1995, p. 17; Sen, 1999, p. 432). Most of the species attributions have relied almost solely on tooth crown size (van Weers, 2002, p. 31), which is also less than ideal given that teeth differ in overall size as they wear (Masini and Rook, 1993, p. 84).

Van Weers (1993) noted that *Hystrix* and the beaver *Anchitheriomys* are morphologically similar, and *Anchitheriomys* has been described as a porcupine by some researchers. The fossils from Lemudong'o show distinct hystricid features: the incisors have smooth and not ribbed enamel as do *Anchitheriomys*; and, the cheek teeth have their largest breadth near the occlusal surface, unlike *Anchitheriomys* teeth that are broadest at the base.

There are 11 Hystricidae specimens recovered from Lemudong'o Locality 1, Kenya, a 6-Ma mammalian-dominated fossil site (Ambrose et al., 2003; Deino and Ambrose, 2006; Ambrose, Kyule, and Hlusko, 2007). Based on size criteria alone, there are four hystricid taxa from these deposits. Although these specimens are fragmentary in nature, they provide the earliest fossil evidence for the appearance of *Atherurus* and *Xenohystrix* in Africa, at least 300,000 years earlier than previously known (Haile-Selassie et al., 2004).

Abbreviations

KNM-NK = Kenya National Museum, fossils from the Narok District, including Lemudong'o Locality 1.

Upper-case letters denote maxillary teeth and lower-case letters denote mandibular teeth, following this convention: M2 = maxillary second molar.

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758
Order RODENTIA Bowdich, 1821
Family HYSTRICIDAE G. Fischer, 1817
Genus *ATHERURUS* F. Cuvier, 1829
ATHERURUS species indeterminate
Figure 1D

Referred material

KNM-NK 44892 and KNM-NK 44893, both mandibular incisors.

Remarks

These two specimens were recovered from a sieving operation conducted to recover eroded fossils trapped in a ephemeral small pool of water in the south western edge of the site (Ambrose, Kyle, and Hlusko, 2007; Ambrose, Nyamai, et al., 2007). Therefore, exact stratigraphic provenience is unknown other than that they derive from the 6-Ma deposits at Lemudong'o Locality 1. Given the re-worked nature of this lag, these may represent one individual, although this cannot be confirmed or denied at this time.

These two incisors are smaller than all known species of *Hystrix* (Table 1) and have smooth, rounded enamel unlike lagomorphs and the cane rat *Thryonomys*. KNM-NK 44892 is shown in Figure 1D. These specimens exceed, or almost exceed, the known range of the variation for *Atherurus*. However, they are only

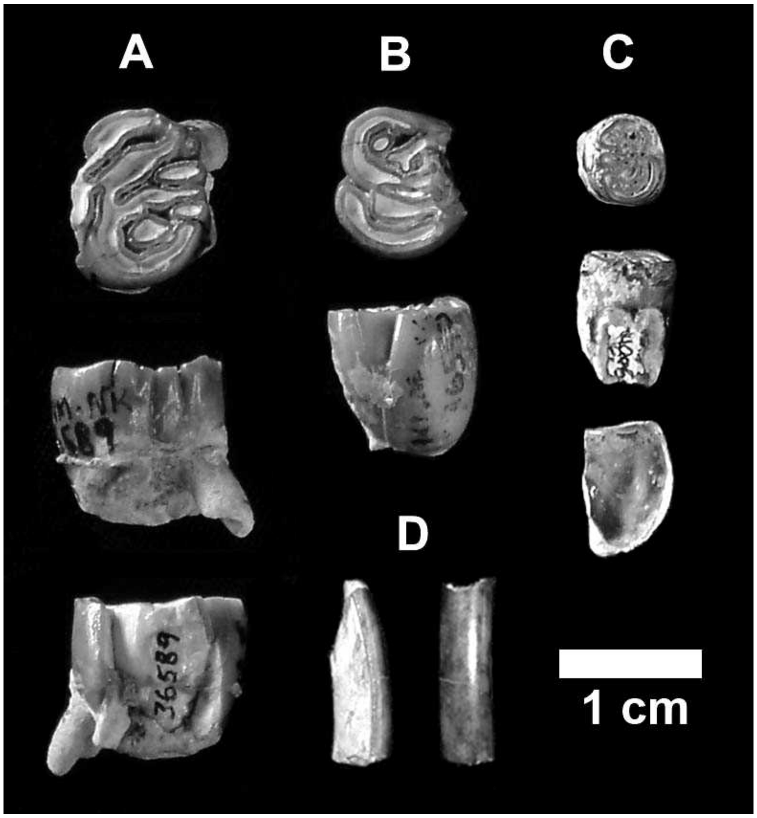

Figure 1. Hystricidae specimens from Lemudong'o Locality 1. A, KNM-NK 36589, left maxillary fourth premolar of *Xenohystrix* sp. indet. in occlusal (mesial is to the top), buccal, and lingual views. B, KNM-NK 36590, right maxillary molar *Xenohystrix* sp. indet. in occlusal and buccal views. C, KNM-NK 44896, right maxillary molar, *Hystrix* sp. indet., in occlusal, buccal and lingual views. D, KNM-NK 44892, mandibular incisor of *Atherurus* sp. indet. in lateral and labial views.

Table 1. Comparison of dental measurements (mm) for various species of Hystricidae and the Lemudong'o specimens.*

Taxon / specimen no.	MD I	LL I	MD i	LL i	MD P4	MD M1/2	MD M3	BL P4	BL M1/2	BL M3
A. macrourus^{1}	2.5–3.0	3.1–4.7	2.5–3.3	3.4–4.3	3.8–5.3	3.4–5.2				
A. karnuliensis^{1}	3.4	4.5	3.2–3.7	3.9–4.3	4.6–6.0	4.7–5.2				
A. africanus^{2}	3.5	4.6			4.9	5.1	4.1	4.6	4.7	4.0
NK 44892			3.8	4.0						
NK 44893			3.7	4.9						
H. leakeyi^{3}						7.0–8.8	7.3		5.2–7.2	6.0
H. africaeaustralis$^{4,\ 5}$	6.3–8.5	6.0–7.4	6.2–8.0	5.0–7.0	8.2–11.0	6.5–9.5	8.0–9.0	7.3–10.5	7.0–9.0	6.5–7.5
H. cristata$^{4,\ 5}$	7.3–8.0	7.0–7.1	6.5–7.5	9.5–10.5	9.5–10.5	8.0–9.0	8.5	9.0	8.0–9.0	7.0
H. primigenia^{6}					10.1–11.5	8.7–10.0	8.0–9.3			
H. depereti^{6}					11.0–12.5	9.2–11.2	8.7–10.0			
NK 36893	7.5									
NK 44896						6.7			6.0	
X. crassidens^{4}	11.5–12.0	10.5–11.0			12.0	10.5–13.0		12.0	12.0	
NK 36589					11.8			n/a		
NK 36590						10.3			n/a	
NK 44771						10.1			8.8	

*MD = mesiodistal length; LL = labiolingual length; BL = buccolingual length; I/i = upper/lower incisor; P = maxillary premolar; M = maxillary molar.

[1] van Weer (2002, p. 31)

[2] measurements of one specimen from the University of California Museum of Vertebrate Zoology (left side)

[3] Denys (1987, p. 150–151)

[4] means from extant specimens taken from Greenwood (1955, p. 81–82), *H. cristata* $n = 2$; *H. africaeaustralis* $n = 7–10$; *X. crassidens* $n = 1–2$

[5] means from Sabatier (1979, p. 94), *H. cristata* $n = 14$; *H. africaeaustralis* $n = 9$

[6] van Weer and Rook (2003, p. 100–101)

Figure 2. *Hystrix* sp. indet. maxillary incisor KNM-NK 36893, in lateral and labial views, from Lemudong'o, Locality 1.

slightly more than half the size of all known *Hystrix* incisors, and, therefore, are referred to the much smaller *Atherurus*.

Genus *Hystrix* Linnaeus, 1758
Hystrix species indeterminate
Figures 1C, 2

Referred material

KNM-NK 36893, a maxillary incisor; KNM-NK 41002, an incisor fragment; KNM-NK 44896, a right maxillary molar.

Remarks

As noted earlier, the occlusal patterns of postcanine porcupine teeth are quite variable even within a population and show little to no consistent morphological change through time. Aside from a family-level identification, isolated cheek teeth cannot be used to differentiate species, and can be difficult to identify to position unless contact wear facets are present (Sabatier, 1979; van Weers, 2002, p. 30–31). However, as these teeth wear, the facets are known to be variably present (change through attrition). Therefore, absence of these facets does not provide positional information. Sabatier (1979, p. 88) and van Weers (2002, p. 30–31) therefore rely only on measurements of dental categories, as is done for the Lemudong'o material in Table 1.

KNM-NK 44896 is a small, relatively unworn brachydont upper molar that does not preserve any interstitial wear facets or root morphology (Figure 1C). The occlusal morphology is typical of the Hystricidae. Measurements are reported in Table 1. The mesiodistal length of this crown falls within the known range of variation for the extant *Hystrix africaeaustralis*; the buccolingual width is smaller and similar in size to *Hystrix leakeyi*. However, the proportions of KNM-NK 44896 do not align it with either species.

KNM-NK 36893 is a fragment of maxillary incisor that falls at the low end of the range of variation for extant *H. cristata* and at the middle for *H. africaeaustralis* (Figure 2, Table 1). Therefore, based on size, it is considered conspecific with KNM-NK 44896. KNM-NK 41002 is an incisor fragment too broken to measure, but almost identical in size and morphology to KNM-NK 36893. These three specimens represent an as yet indeterminate small species of brachydont *Hystrix*.

Genus *Xenohystrix* Greenwood, 1955
Xenohystrix species indeterminate
Figure 1A–B

Referred material

KNM-NK 36589, a left maxillary fourth premolar; KNM-NK 36590, a right maxillary molar; KNM-NK 41052, a fragment of left maxillary molar; KNM-NK 44771, a left maxillary third molar.

Remarks

KNM-NK 36590 is a very large brachydont right maxillary first or second molar (Figure 1B, Table 1). The crown is damaged on the buccal surface and preserves no root morphology. It is slightly smaller (0.2 mm) than the smallest known maxillary first/second molar of *Xenohystrix crassidens* from Makapansgat, South Africa (Greenwood, 1955).

KNM-NK 36589 is a left maxillary fourth premolar with three roots (Figure 1A, Table 1). The lingual side of the crown is damaged so a maximal buccolingual width cannot be measured. This premolar crown falls within the size range of *Xenohystrix crassidens* as well.

These two crowns were collected in 1995, during the first year of collection at Lemudong'o Locality 1. During that field season, exact stratigraphic provenience and proximity between specimens were not being recorded. However, these two specimens have close field numbers (98 and 102), suggesting that they were collected at the same time and close to each other spatially. Therefore, it is likely that KNM-NK 36590 may represent the same individual as KNM-NK 36589.

KNM-NK 44771 is more complete and represents a left maxillary third molar similar in size to KNM-NK 36590 (Table 1). Like KNM-NK 36589 and KNM-NK 36590, this tooth is also brachydont.

These specimens from Lemudong'o also fall within the size range of *H. depereti* from Europe, ranging from Spain to Turkey, see Table 1 (van Weers and Rook, 2003). At this time, I refer the Lemudong'o specimens to *Xenohystrix* until the phylogenetic relationship between *H. depereti* and *Xenohystrix* is resolved. It is quite possible that they are congeneric or conspecific.

KNM-NK 41052 is broken and cannot be measured accurately. However, it is extremely similar in size and morphology to these other three crowns and is, therefore, included in the same taxon.

Family Hystricidae
Genus and species indeterminate

Referred Material

KNM-NK 44894 and KNM-NK 44895, both cheek-tooth fragments.

Remarks

These two fragmentary teeth are fairly large and brachydont. However, they are too broken to confidently assign to either *Hystrix* sp. indet. or *Xenohystrix* sp. indet.

Discussion

The hystricid assemblage from Lemudong'o Locality 1 consists of only isolated and fragmentary dental specimens. However, these preserve enough anatomy to indicate that they represent three species from three genera, *Atherurus*, *Hystrix*, and *Xenohystrix*. These fragments represent the earliest occurrence of both *Atherurus* and *Xenohystrix* in Africa. This predates the previously reported earliest occurrence by more than 300,000 years (Haile-Selassie et al., 2004).

Xenohystrix is an extinct genus found only in southern and eastern Africa to date. There is one recognized species of this genus, *X. crassidens*, which has been recovered from deposits at Makapansgat in South Africa (Greenwood, 1955; Maguire, 1978), Laetoli in Tanzania, and Hadar in Ethiopia (Sabatier, 1979; Denys, 1987). This species lived between 3.7 and 2.5 Ma (Denys, 1987, p. 154) and is found at fossil sites also yielding specimens of two species of early hominids, *Australopithecus afarensis* and *A. africanus* (Maguire, 1978; Sabatier, 1979; Denys, 1987). Although this species has a fairly wide geographic range, Maguire (1978, p. 144) suggests that *X. crassidens* was a soft-diet, forest-dwelling form, based on its brachydont dentition and restriction within South Africa to only Members 3 and 4 at Makapansgat (and is not seen at other fossiliferous localities).

Extant species of East African *Hystrix* tend to be most common in hilly, rocky country but are highly adaptable and are found in all types of habitats (Kingdon, 1974, p. 692; Nowak, 1991, p. 897–900). *Hystrix* adults often live in burrows dug by aardvarks, caves, or crevices exposed along river edges. These porcupines are nocturnal and terrestrial, and can swim well. Their diet includes bark, roots, tubers, rhizomes, bulbs and fallen fruits, and sometimes they will eat insects and small vertebrates. Although they are known to frequently gnaw on bones (e.g., Plug and Keyser, 1994), they only rarely eat carrion.

The extant African brush-tailed porcupine (*Atherurus africanus*) is found in Gambia, western Kenya, southern Zaire, and many places in between. Currently, *Atherurus africanus* is only found in forests (Kingdon and Howell, 1993, p. 232). These small porcupines have long bodies with short limbs; like *Hystrix*, *Atherurus* is nocturnal and can swim; their diet consists of green vegetation, bark, roots, tubers, and fruit (Kingdon, 1974; Emmons, 1983; Nowak, 1991).

The limited hystricid assemblage from Lemudong'o Locality 1 indicates that 6 million years ago this area was inhabited by a taxonomically diverse range of porcupines, ranging from the very small *Atherurus* to the large *Xenohystrix*. The primary habitat indicated by the presence of these organisms in extant ecologies is a forested or relatively closed environment, with the possibility of more open habitats nearby. By extrapolation, the fossil assemblage from Lemudong'o Locality 1 may well sample a similar habitat.

Acknowledgments

I would like to express my appreciation to the Office of the President, Kenya, for authorization to conduct research in Kenya; the Archaeology and Palaeontology Divisions of the National Museums of Kenya for staff assistance and facilities; the Maasai people for permission, access, and assistance. Many thanks to the University of California at Berkeley's Museum of Vertebrate Zoology for access to extant comparative material. Y. Haile-Selassie and T. White for helpful discussions and advice. Thanks also to L. J. Flynn and L. Rook for thoughtful comments on an earlier version of this manuscript. Financial support was provided by the L.S.B. Leakey Foundation, the University of Illinois Center for African Studies and Research Board, National Science Foundation grant SBR-BCS-0327208, and the National Science Foundation HOMINID grant Revealing Hominid Origins Initiative BCS-0321893.

References

Ambrose, S. H., D. Kyule, L. J. Hlusko, A. Deino, and M. Williams. 2003. Lemudong'o: A new 6 ma paleontological site near Narok, Kenya Rift Valley. Journal of Human Evolution, 44:737–742.

Ambrose, S. H., M. D. Kyule, and L. J. Hlusko. 2007. History of paleontological research in the Narok District of Kenya. Kirtlandia, 56:1–37.

Ambrose, S. H., C. M. Nyamai, E. M. Mathu, M. D. Kyule, and M. A. J. Williams. 2007. Geology, geochemistry, and stratigraphy of the Lemudong'o Formation, Kenya Rift Valley. Kirtlandia, 56:53–64.

Bowdich, T. E. 1821. An Analysis of the Natural Classifications of Mammalia, For the Use of Students and Travelers. J. Smith, Paris. 115 p.

Cuvier, F. 1829. Dictionnaire des Sciences Naturelles, 59:1–520.

Deino, A., and S. H. Ambrose. 2007. ^{40}AR/^{39}AR dating of the Lemudong'o late Miocene fossil assemblages, southern Kenya Rift. Kirtlandia, 56:65–71.

Denys, C. 1987. Fossil rodents (other than Pedetidae) from Laetoli, p. 118–170. *In* M. D. Leakey and J. M. Harris (eds.), Laetoli: A Pliocene Site in Northern Tanzania. Oxford University Press, New York.

Emmons, L. H. 1983. A field study of the African brush-tailed porcupine, *Atherurus africanus*, by radiotelemetry. Mammalia, 47(2):183–194.

Fischer de Waldheim, G. 1817. Adversaria zoologica. Memoires de la Société Impériale des Naturalistes du Moscou, 5: 357–428.

Fistani, A. B., P. P. Pavlakis, and N. Symeonidis. 1997. First discovery of *Hystrix primigenia* Wagner from the late Miocene to early Pliocene deposits of Shahinova, Berat, South-West Albania. Annalen des Naturhistorischen Museums in Wien, Serie a Mineralogie und Petrographie Geologie und Palaeontologie Anthropologie und Praehistorie, 98:155–172.

Greenwood, M. 1955. Fossil Hyracoidea from the Makapan Valley, Transvaal. Palaeontologia Africana, 3:77–85.

Greenwood, M. 1958. Fossil Hystricoidea from the Makapan Valley, Transvaal: *Hystrix makapanensis* nom. nov. for *Hystrix major* Greenwood. Annals and Magazine of Natural History, 13:365.

Haile-Selassie, Y. 2001. Late Miocene mammalian fauna from the Middle Awash Valley, Ethiopia. Unpublished Ph.D. dissertation, University of California, Berkeley. 425 p.

Haile-Selassie, Y., G. WoldeGabriel, T. D. White, R. L. Bernor, D. DeGusta, P. R. Renne, W. K. Hart, E. Vrba, S. H. Ambrose, and F. C. Howell. 2004. Mio-Pliocene mammals from the Middle Awash, Ethiopia. Géobios, 37:536–552.

Huchon, D., and E. J. P. Douzery. 2001. From the Old World to the New World: a molecular chronicle of the phylogeny and biogeography of hystricognath rodents. Molecular Phylogenetics and Evolution, 20(2):238–251.

Howell, F. C., and Y. Coppens. 1974. The faunas of fossil mammals of the Plio-Pleistocene formations of Omo in Ethiopia (Tubulidentata, Hyracoidea, Lagomorpha, Rodentia, Chiroptera, Insectivora, Carnivora, Primates). Comptes Rendus Hebdomadaires des Seances de L'Academie des Sciences Serie de Sciences Naturelles, 278(19):2421–2424.

Kingdon, J. 1974. East African Mammals Volume II Part B (Hares and Rodents), p. 343–704. Academic Press, New York.

Kingdon, J., and K. M. Howell. 1993. Mammals in the forests of eastern Africa, p. 229–241. *In* J. C. Lovett and S. K. Wasser (eds.), Biogeography and Ecology of the Rain Forests of Eastern Africa. Cambridge University Press, New York.

Lim, B. L., L. Ratnam, and S. Anan. 1989. Study of the small mammals in Taman Negara with special reference to the rat lung-worm. The Journal of Wildlife and Parks, 8:17–30.

Linnaeus, C. von. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tenth edition. Laurentii Salvii, Holmiae, Stockholm. 824 p.

Maguire, J. M. 1978. Southern African fossil porcupines. South African Journal of Science, 74:144.

Masini, F., and L. Rook. 1993. *Hystrix primigenia* (Mammalia, Rodentia) from the Late Messinian of the Monticino gypsum quarry (Faenza, Italy). Bollettino della Società Paleontologica Italiana, 32(1):79–87.

Nowak, R. M. 1991. Walker's Mammals of the World, 5th edition, Volume I. Johns Hopkins University Press, Baltimore. 642 p.

Pickford, M. 1975. Late Miocene sediments and fossils from the Northern Kenya Rift Valley. Nature, 256:279–284.

Plug, I., and A. W. Keyser. 1994. Haasgat Cave, a Pleistocene site in the central Transvaal: geomorphological, faunal and taphonomic considerations. Annals of the Transvaal Museum, 36(9):139–145.

Sabatier, M. 1979. Les rongeurs des sites à hominidés de Hadar et Melka-Kenture (Ethiopie). Thesis, Académie de Montpellier, Université des Sciences et Techniques de Languedoc.

Sen, S. 1999. Family Hystricidae, p. 427–434. *In* E. Rössner and K. Heissig (eds.), The Miocene Land Mammals of Europe. F. Pfeil, Munich.

Thomas, H., and G. Petter. 1986. Révision de la faune de mammifères du Miocène Supérior de Menacer (ex-Marceau), Algérie: discussion sur l'Âge du gisement. Géobios, 19(3):357–374.

van Weers, D. J. 1985. *Hystrix gigantea*, a new fossil porcupine species from Java (Rodentia: Hystricidae). Senckenbergiana Lethaea, 66:111–119.

van Weers, D. J. 1993. Teeth morphology and taxonomy of the Miocene rodent *Anchitheriomys suevicus* (Schlosser, 1884), with notes on the family Hystricidae. Proceedings of the Royal Netherlands Academy of Arts & Sciences, 96(1):81–89.

van Weers, D. J. 1995. The fossil porcupine *Hystrix lagrelli* Lönnberg, 1924 from the Pleistocene of China and Java and its phylogenetic relationships. Beaufortia, 45(2):17–25.

van Weers, D. J. 2002. *Atherurus karnuliensis* Lydekker, 1886, a Pleistocene brush-tailed porcupine from India, China and Vietnam. Paläontologische Zeitschrift, 76(1):29–33.

van Weers, D. J., and L. Rook. 2003. Turolian and Ruscinian porcupines (genus *Hystrix*, Rodentia) from Europe, Asia and North Africa. Paläontologische Zeitschrift, 77(1):95–113.

van Weers, D. J., and S. Zheng. 1998. Biometric analysis and taxonomic allocation of Pleistocene *Hyxtrix* specimens (Rodentia, Porcupines) from China. Beaufortia, 48(4):47–70.

van Weers, D. J., and Z. Zhang. 1999. *Hystrix zhengi* n. sp., a brachyodont porcupine (Rodentia) from early Nihewanian Stage, early Pleistocene of China. Beaufortia, 49(7):55–62.

Winkler, A. J. 2002. Neogene paleobiogeography and East African paleoenvironments: contributions from the Tugen Hills rodents and lagomorphs. Journal of Human Evolution, 42:237–256.

Winkler, A. J. 2003. Rodents and lagomorphs from the Miocene and Pliocene of Lothagam, Northern Kenya, p. 169–190. *In* M. G. Leakey and J. M. Harris (eds.), Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York.