Fossil aardvark (*Orycteropus*) from Swartkrans Cave, South Africa

Thomas Lehmann*

The study reported here describes the Pleistocene specimens of *Orycteropus* from Swartkrans in the Sterkfontein Valley, South Africa, and reviews the South African fossil Tubulidentata. The fossils are similar to modern aardvark, but show morphological differences. Although smaller in size than modern specimens, the differences are not considered to be sufficient to warrant the creation of a new species. The South African fossils raise new questions about the ancestors of *O. afer*.

Introduction

Excavations at Swartkrans Cave in the Sterkfontein valley, 70 km southwest of Pretoria, were conducted by C.K. Brain from 1965 to 1986, following the initial work by R. Broom and J. Robinson. These excavations have yielded many hominids, including *Paranthropus robustus* and early *Homo.* The associated fauna includes a diversity of Pleistocene vertebrates from five members defined by Brain.[1] Tubulidentata (aardvark) are represented in Members 1, 2 and 3. The fossils are fragmentary and consist only of postcranial elements. In the published faunal list,[2] these fossils were attributed to *Orycteropus afer* (Pallas 1766). The aim of this article is to describe the Swartkrans specimens before proceeding with phylogenetic, biochronological and palaeobiogeograhical issues. Reference is also made to Tubulidentata remains from Makapansgat. These South African fossils could be the oldest *O. afer* known from Africa.

Order Tubulidentata

The Tubulidentata Huxley, 1872, is represented by a single extant species: *Orycteropus afer* (Pallas, 1766) (the generic name means 'digging foot'). It is a nocturnal animal that burrows relatively deeply in underground shelters. Its diet consists of ants, termites and insect larvae. The aardvark is a good digger that is easily capable of breaking open termite mounds. At present, this species is found only in Africa south of the Sahara.[3]

The order is represented by Miocene fossils from Africa and Eurasia, including up to four genera. The isolation of the order in Africa took place during Pliocene times. The genus *Orycteropus* Geoffroy, 1796, is represented by at least 11 fossil species, found from Pakistan to France. Its last occurrence in Eurasia is represented by the species *O. depereti* Helbing, 1933, from Pliocene deposits of Perpignan in France. Following Patterson,[4] and Brunet and MPFT,[5] and Lehmann *et al.*,[6] the genus *Orycteropus* comprises at least six species in Africa, some of which are tentative identifications. They include *O. minutus* Pickford, 1975 from the Lower Miocene of Songhor, Mfwangano, and Rusinga (Kenya); *O. chemeldoi* Pickford, 1975, from the Middle and Upper Miocene of Ngorora and Fort Ternan (Kenya); *O. mauritanicus* Arambourg, 1959, from the Upper Miocene of Bou Hanifia (Algeria); *O.* sp. nov. from the Mio-Pliocene of Kossom Bougoudi[5,6] (Chad); *O. crassidens* MacInnes, 1956, from the Pleistocene of Rusinga and Kanjera (Kenya); and *O. afer,* the extant species, recognized from the Late Pleistocene of Algeria.[7]

Furthermore, many fragmentary *Orycteropus* fossils could not be attributed to any particular species. *Orycteropus* sp. has been reported from many sites from Lower Miocene to Pliocene in East Africa.[4,8–12] Pleistocene specimens are represented throughout Africa.[13–15] Although the extant species was first reported from a South African type specimen, only fragmentary fossil specimens of the genus *Orycteropus* have been reported from the South African Pliocene deposits of Langebaanweg[16] and Makapansgat.[17] From the latter site, the specimens have been referred to *O.* cf. *afer.*

Geological and environmental context

Swartkrans Cave is a solution cavity in dolomitic limestone.[1] During the early Pleistocene, openings in the roof acted as sediment traps. At least five episodes of deposition occurred, and these have been related to five members.[1]

The age of the Swartkrans infills can be estimated on the basis of macrovertebrate biostratigraphy.[1] It is suggested that Member 1 is 1.8 million years old (Myr), that Member 2 is 1.5 Myr, and that Member 3 is at least 1.0 Myr. The fossil accumulation in Members 1, 2 and 3 are attributable mainly to predators that either brought carcasses of their prey into the cavern itself or preyed on animals that found shelter in the cave. The faunal assemblages from Members 1, 2 and 3 are quite similar to each other, suggesting that no major environmental changes occurred within the corresponding period.[2] The palaeoenvironments are thought to have been associated with highveld grassland savanna, suitable habitat for aardvark. The Blaaubank stream, which runs near the cave, would have been more substantial than at present, surrounded by riverine woodland savanna.[2] At present, many termite mounts are found between the stream and the cave.

Description and comparison

Anatomical comparisons were made of fossil and modern specimens of aardvark from South Africa. For this study, part of the material is housed at the Transvaal Museum, Pretoria. Other aardvark skeletons have been studied at the Bernard Price Institute (BPI) for Palaeontological Research, University of the Witwatersrand, Johannesburg. The abbreviation SKX relates to Swartkrans fossils, and AZ refers to specimens in the Archaeozoological collection at the Transvaal Museum.

Order Tubulidentata Huxley, 1872
Family Orycteropodidae Gray, 1821
Subfamily Orycteropodinae Gray, 1821
Genus *Orycteropus* Geoffroy, 1791

Orycteropus cf. *afer* (Pallas, 1766)

Swartkrans material. Member 1: distal part of right humerus SKX 14261.

Age. Circa 1.8 Myr.

Description and remarks

The right humerus SKX 14261 is represented by its lower third and distal epiphysis (Fig. 1). The capitulum, the trochlea and the entepicondylar foramen are well preserved.

The olecranon fossa is deep, oval-shaped and bounded proximally as in the modern *O. afer* and unlike *O. gaudryi* Major, 1888, from Samos (Greece). The trochlea is large as in all Orycteropodinae and unlike *Plesiorycteropus* Filhol, 1895. Table 1

*Faculté des Sciences et CNRS UMR 6046, Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, Université de Poitiers, 40 Avenue du Recteur Pineau, 86022 Poitiers Cedex, France. E-mail: thomas.lehmann@etu.univ-poitiers.fr

presents the measurements for some Orycteropodidae specimens. These data show that the South African fossil is closer to the Pleistocene species, all of the genus *Orycteropus*, than to Miocene forms like *Myorycteropus* MacInnes, 1956, or *Leptorycteropus* Patterson, 1975. In particular, the distal breadth of SKX 14261 is not significantly distinct from data obtained for *O. afer* and is strictly larger than all other Tubulidentata except *O. crassidens* (Fig. 2). On the other hand, the distal breadth of the Swartkrans humerus is smaller than any described specimen of *O. afer.* Noticeably, the humerus of *O. crassidens* has a much larger distal epiphysis than those of the other *Orycteropus* species from our set of comparisons and is thus clearly distinct from the Swartkrans aardvark. The distal breadth of the humerus is of biomechanical importance. Hildebrand[18] noticed that digging animals presented a large distal epiphysis relative to the humerus length. Unfortunately, this length cannot be measured on this fossil.

Fig. 1. SKX 14261. Dorsal (**A**), ventral (**B**), and medial (**C**) view of the right humerus. I = insertion surfaces for *Mm. pronator teres, flexor digitorum profundus* and *flexor carpi radialis.* Scale bar = 1 cm.

The proximodistal height of the epitrochlea of SKX 14261 is 24 mm, which is short in comparison with data from modern specimens of *O. afer,* that range between 27.0 and 28.2 mm. In modern specimens, distal epiphysis breadth is twice as large as the epitrochlea height but not in SKX 14261. Thus, the insertion surfaces on the medial side of the epitrochlea are relatively close to each other in the fossil (Fig. 1C). As a result, the total insertion surface for the *Mm. pronator teres, flexor digitorum profundus* and *flexor carpi radialis* is smaller in SKX 14261 than in *O. afer.* These muscles have an important function in the digging habits of *O. afer.*[20]

The capitulum height in the Swartkrans aardvark is similar to the corresponding dimension for the modern aardvark (Table 1).

This study confirms that SKX 14261 belongs to a species of *Orycteropus* that could have been as large as an extant aardvark but with a less powerful forearm. There is no evidence from the humerus that it was less fossorial, as in *Leptorycteropus.* SKX 14261 is here referred to *Orycteropus* cf. *afer.*

Table 1. Comparative biometry (measurements in mm) of the humerus of some Orycteropodinae.

Humerus	Distal breadth†	Height of capitulum
Orycteropus afer (AZ & BPI)	54.2 ± 1.6 (*n* = 10)	17.6 ± 0.9 (*n* = 10)
*O. crassidens**	64.5	
O. gaudryi (AMNH 22762)	40.9	
O. pottieri (PNT 19 & 135)#	36; 35.5	
Leptorycteropus guilielmi (holotype)	26.5	9.1
Myorycteropus africanus§	39.5	
SKX 14261	51.3	17.2

†Distal breadth = distal mediolateral breadth; capitulum height = maximum proximodistal diameter of the capitulum.
*Holotype after MacInnes.[11]
#Pentalophos, after Bonis *et al.*[21] §Holotype, after MacInnes.[11]
Number of observations indicated in brackets. AMNH, American Museum of Natural History, New York; PNT, Pentalophos, Greece.

Orycteropus sp.

Swartkrans material. Member 2: right second phalange V of the foot SKX 1199, distal phalanges of the foot SKX 75 and SKX 498; Member 3: distal phalange of the foot SKX 37832.

Age. 1.5 Myr (Member 2) and at least 1.0 Myr (Member 3).

Description and remarks

Specimen SKX 1199 is complete and similar to its extant counterpart (Fig. 3). Its length is comparable to the corresponding dimension for *O. afer,* but the bone is more slender (Table 2). The proximal and distal dorsoventral heights are significantly different. Unfortunately, very few foot bones of *O. crassidens* have been found but they are similar to those of *O. afer.* Consequently, it is not possible to recognize SKX 1199 as belonging to *O. crassidens* with confidence. The fossil is referred to *Orycteropus* sp.

The distal phalange SKX 75 is a well-preserved specimen probably from the first digit of the foot (Fig. 4). The size of the bone matches dimensions found in other taxa of the genus *Orycteropus* (Table 2). No clear morphological features have been found that could help with more specific identification. However, the phalanx is noticeably more slender than those of extant aardvark. The specimen is thus considered to represent *Orycteropus* sp.

The distal phalange SKX 498 is from the second or third digit of the foot (Fig. 4). This specimen is broken proximally. Precise identification is difficult as left and right second and third distal phalanges are very similar to each other. Dimensions are not useful for species determination as they can match the length but not the width or height of specimens of *O. afer* or *O. gaudryi* (Table 2). In fact, this South African phalange is more slender than the phalanges of the two latter species. SKX 498 is here assigned to *Orycteropus* sp. until other aardvark material is found.

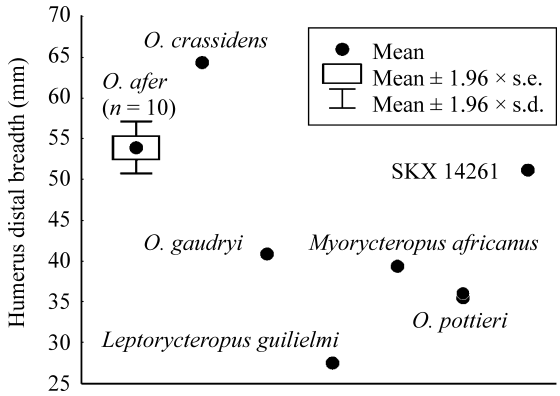

Fig. 2. Comparative distribution of the distal breadth of the humerus in some Orycteropodinae. For references see Table 1.

Table 2. Comparative biometry (measurements in mm) of the posterior phalanges of some Orycteropodinae.

	Phm V L	Phm V Bp	Phm V Hp	Phm V Bd	Phm V Hd	Phd L	Phd Bp	Phd Hp
Orycteropus afer (AZ & BPI)	14.5 ± 0.7 (*n* = 5)	9.5 ± 0.2 (*n* = 5)	9.8 ± 0.4 (*n* = 5)	8.2 ± 0.6 (*n* = 5)	7.6 ± 0.2 (*n* = 5)			
O. gaudryi (AMNH 22762)	11.8	6.6	6.9	5.4	5.2			
O. sp. (KNM-LAET 2711)	11.5	6.7	6.7	6.3	5.2			
SKX 75						16.3	8.5	8.8
SKX 498						18.8 e	7.9 e	7.3 e
SKX 1199	14.1	8.4	7.9	7.1	6.9			
SKX 37832						20 e	11.2	10.1

	Phd											
	II			III			IV			V		
	L	Bp	Hp	L	Bp	Hp	L	Bp	Hp	L	Bp	Hp
O. afer (BPI 155)	24.6	12.3	10.7	22.0	8.9	10.0	21.0	8.3	9.9	18.7	7.8	9.5
O. gaudryi (AMNH 22762)	19.2	8.9	8.8	19.3	7.5	8.3	17.4	6.7	7.7	13.4	5.7	6.9

Phm, medial phalange; Phd, distal phalange; L, maximum length; Bp, proximal mediolateral breadth; Hp, proximal dorsoventral height; Bd, distal mediolateral breadth; Hd, distal dorsoventral height. e, estimated measurements. KNM-LAET, Kenya National Museum, Laetoli site.

The distal tip of SKX 37832 is broken and identification of the Member 3 distal phalanx is difficult (Fig. 4). For instance, dimensions of the bone are slightly smaller than distal phalanx II of *O. afer* and are larger than any of the distal phalanges of *O. gaudryi* (Table 2). As no distal phalanges from other species of the genus have been described so far, it is again sensible to refer SKX 37832 simply to *Orycteropus* sp.

Orycteropus from Makapansgat and Langebaanweg

The earliest occurrences of Tubulidentata in South Africa are in the Pliocene deposits at Langebaanweg and Makapansgat. The specimen from Langebaanweg (*c.* 5 Myr), consisting of a single tooth, was considered as *Orycteropus* cf. *afer,* according to Hendey.[16]

The aardvark fossils from Makapansgat (3.06–3.32 Myr)[21] include cranial remains. The specimens were attributed by Kitching[17] to *Orycteropus* cf. *afer* and were thought to have consisted of a left M^1 and a mandible fragment with broken M_2 and complete M_3.

This new study, including examination of more than 15 adults and juveniles of *O. afer* from South Africa, has led to a revision of Kitching's identification. The Makapansgat material is here considered as a right M^1 and a mandible fragment with broken M_1 and complete M_2. This revised identification is based on the position of the slope on the ventral line of the ramus.

The dimensions of the teeth are not significantly different from corresponding data obtained from extant aardvark. The teeth are as broad but longer than those of Miocene forms like *O. gaudryi* or *O. pottieri* Ozansoy, 1965.

During the Plio-Pleistocene, aardvarks must have become progressively larger to reach the size of the extant form. However, small *O. afer* specimens have teeth that cannot be distinguished by their size from *O. gaudryi* or *O. pottieri.* Notably, the length of the limbs in *O. gaudryi* represents about 75% of that in *O. afer* or *O. crassidens,* while for the teeth this proportion is about 90%. On the other hand, *O. crassidens* and other specimens from East Africa have developed very long molars that are significantly distinct from extant aardvark teeth. Interestingly, the length of the teeth of *O. gaudryi* represents about 75% of that in *O. crassidens.* The comparison between the size of limb bones and teeth

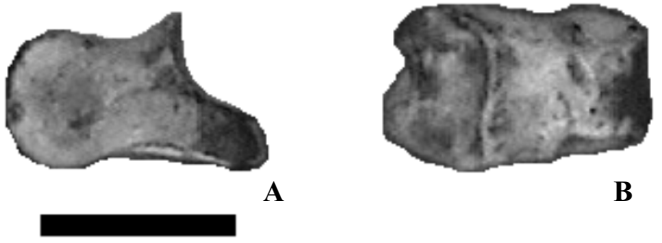

Fig. 3. SKX 1199. Lateral (**A**) and dorsal (**B**) view of the second phalange. Scale bar = 1 cm.

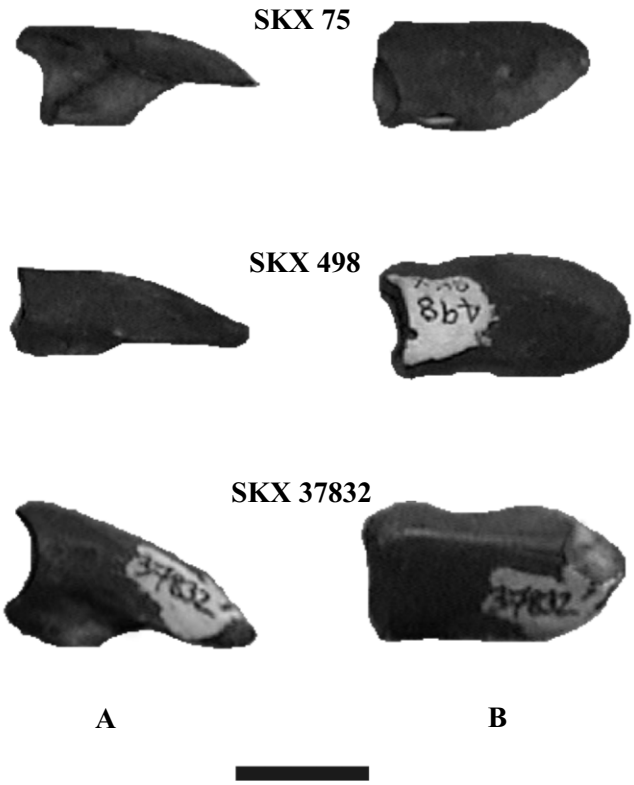

Fig. 4. SKX 75, SKX 498, and SKX 37832. Lateral (**A**) and dorsal (**B**) view of the distal phalanges. Scale bar = 1 cm.

length is therefore important for the determination of species. In the absence of postcranial material from Makapansgat, the view of Kitching[17] is here retained, and all Makapansgat material is referred to *Orycteropus* cf. *afer* until new material is added.

Conclusion

The fossil aardvark from Swartkrans, represented by only postcranial remains, are not sufficiently diagnostic for specific determination. Like the Makapansgat fossil aardvark, they show close similarities to modern South African *O. afer.* However, they are smaller in some respects and this could be related to the general size increase of Tubulidentata during the Plio-Pleistocene in Africa. These fossils show that aardvark of a size similar to that of the extant species was present in South Africa, along with hominids, in the Late Pliocene and Early Pleistocene.

The palaeobiogeography of the African Tubulidentata shows discontinuous distributions. This is due in part to the lack of Tertiary fossiliferous sites from central and west Africa. It appears, however, that *O. afer* is the only continentally widespread species. To the best of our knowledge, the three South African sites (Langebaanweg, Makapansgat and Swartkrans) illustrate the first known occurrences of large aardvarks, close to *O. afer,* in southern Africa. In this respect, it should be noted that, before the emergence of *O. afer,* other large fossil aardvarks occurred at Plio-Pleistocene sites from East Africa.[4,9–11] The widespread distribution of large Tubulidentata in Africa happened prior to the emergence of *O. afer.* The area of origin of the extant species is as yet unknown.

It is striking that Orycteropodinae coexisted with early hominids in Africa since the late Miocene. The list of sites where both taxa can be found is long, including Toros-Menalla,[22] Aramis (T. White, pers. comm.), Lukeino,[10] Laetoli,[11] Olduvai,[14] and the South African sites, which are the subject of this study. Although aardvark material is often fragmentary, new, relatively complete specimens have been found recently in central Africa (Chad).[6] Thus, as our knowledge of the evolution of the Tubulidentata in Africa increases, species in this order may become a useful tool for biochronology, especially at the early hominid localities.

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