Zoological Journal of the Linnean Society, 2009, **155**, 649–702. With 7 figures

Phylogeny and systematics of the Orycteropodidae (Mammalia, Tubulidentata)

THOMAS LEHMANN[1,2]*

[1]*Institut international de Paléoprimatologie, Paléontologie Humaine: Evolution et Paléoenvironnement (IPHEP), CNRS UMR 6046, Université de Poitiers, 40 Avenue du Recteur Pineau, 86022 Poitiers Cedex France*
[2]*Palaeontology Section, Transvaal Museum, P.O. Box 413, Pretoria 0001, South Africa*

Received 19 September 2007; accepted for publication 11 February 2008

The systematics of the order Tubulidentata is poorly known. Its phylogeny has never been thoroughly analysed and only a single review has ever been performed, which was over 30 years ago. This situation has hampered palaeoecological and palaeobiogeographical studies of these Neogene mammals. The present revision of the Orycteropodidae deals with the phylogeny and systematics of all African and Eurasian species over the last 20 Myr. The first comprehensive cladistic analysis of the family is presented here. The results of this analysis, based on 39 coded morphological characters, supplemented by non-coded features taken from all over the skeleton, was used to reconstruct the phylogeny of the order Tubulidentata. Two distinct lineages within the genus *Orycteropus* are recognized and characterized. The new genus *Amphiorycteropus* is subsequently created, in order to harmonize taxonomy and phylogeny. The fossil genera *Leptorycteropus* and *Myorycteropus* are validated, bringing the number of genera in the order Tubulidentata to four. Moreover, within the family Orycteropodidae, the number of confirmed species is now 14. The outcome of this study allows us to propose a consistent palaeobiogeographical scenario for aardvarks. Finally, this revision represents the most comprehensive work on the evolutionary history of the order Tubulidentata to date, and provides a new framework for future studies. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, **155**, 649–702.

ADDITIONAL KEYWORDS: aardvark – Afrotheria – *Leptorycteropus* – Miocene – *Myorycteropus* – *Orycteropus* – Pleistocene – Pliocene – taxonomy.

INTRODUCTION

The first report on aardvarks dates from 1587 when the Portuguese monk João dos Sanctos berthed on the coasts of Mozambique (quoted by von Zimmermann, 1778). He described an animal, called *Inhazaras* by the locals, which had the size and shape of a pig, and which was covered with sparse black hairs. It displayed five toes and four fingers with long nails. It lived underground in burrows, similar to rabbits, and fed on ants. Its skull supported a long and slender snout, as well as long naked ears. More than 400 years later, this description is still the best way to portray this seldom-observed mammal. The first scientific studies conducted on the aardvark date from the second half of the 18th century (Pallas, 1766, 1780). This eutherian mammal was then thought to be congeneric with the South American anteaters (*Myrmecophaga* Linnaeus, 1758). Further studies by Geoffroy St Hilaire (1796) and Cuvier (1817, 1823, 1835) eventually suggested that the aardvark represented a separate genus, and led to its current scientific name: *Orycteropus afer* (Pallas, 1766). However, these authors considered that the aardvark was still in close relationship with the South American mammals. Thus, they classified it as a member of the now obsolete order ‘Edentata’ Cuvier, 1798. During the following century, numerous studies of *O. afer* were performed (e.g. Jäger, 1837; Galton, 1869; Humphey, 1869; Thomas, 1890; Franz, 1908; Broom, 1909a,b; Edgeworth, 1924; Pocock, 1924; Coupin,

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*Senckenberg Forschungsinstitut und Naturmuseum, Abteilung ‘Paläoanthropologie und Messelforschung’, Senckenberganlage 25, 60325 Frankfurt am Main, Germany. E-mail: Thomas.Lehmann@senckenberg.de or bibintom@gmail.com

1926) up until the comprehensive anatomical study (in three parts) by Sonntag (Sonntag, 1925; Sonntag & Woolard, 1925; Le Gros Clark & Sonntag, 1926). This study suggested that the aardvark belongs to an order of its own (Tubulidentata Huxley, 1872), and that it is not related to the Xenarthra. This point of view is now wholly accepted. Save some analyses on the peculiar dental structure of the aardvark (Anthony, 1934; Heuvelmans, 1939), more recent works have focused on its biology and ecology (e.g. Urbain, 1954; Melton, 1976; Willis, Skinner & Robertson, 1992; Taylor, Lindsey & Skinner, 2002; Taylor & Skinner, 2003). Moreover, between 1840 and 1957, 17 doubtful subspecies have been described (see Shoshani, Goldman & Thewissen, 1988), but no real intraspecific variation study was ever performed.

The first fossil aardvark ever described is *Orycteropus gaudryi* Major, 1888 from the Turolian deposits on the Island of Samos (Greece). This discovery was the first of many (especially in Samos) that proved that fossil Tubulidentata lived in Europe and Asia during the Neogene. In 1933, for instance, Helbing and Colbert described new species from France and Pakistan (respectively). Later, Colbert (1941) published an extensive work on *O. gaudryi* and the possible affinities of the Tubulidentata with 'Condylarthra'. Fossil aardvarks were discovered only later in Africa (Dietrich, 1942), and the first comprehensive description of an African fossil species is that of *Myorycteropus africanus* MacInnes, 1956. The intensification of palaeontological research in Africa led to the unearthing of other fossil Tubulidentata. In 1975, Patterson published an article on the known fossil aardvarks, and described a new genus (*Leptorycteropus* Patterson, 1975). This 'conspectus' is the most extensive work carried out on the fossil aardvarks so far. However, additional material has been found in Turkey (Fortelius, 1990; Tekkaya, 1993; Fortelius, Nummela & Sen, 2003; van der Made, 2003), Greece (de Bonis *et al.*, 1994; Sen, 1994), Italy (Rook & Masini, 1994), and Africa (Leakey, 1987; Pickford, 1975, 1994, 1996, 2003, 2005; Milledge, 2003; Lehmann, 2004) during the following 30 years. Also, the fossil record was still generally very fragmentary, with only dental remains and isolated bones, and rarely with skulls or a few incomplete skeletons (found at Lothagam, Rusinga Island, and Samos). This, and the fact that the specimens are disseminated in many museums, has inhibited the long-term research on the phylogenetic systematics of the Tubulidentata.

In 1998, Stanhope *et al.* (1998), following Springer *et al.* (1997), introduced a new clade of mammals based on DNA sequences analysis: the Afrotheria. This supraordinal taxon regroups Elephants, Hyrax, Sirenians, Elephant-shrews, Golden Moles, Tenrecs, and Aardvarks, and is supposed to have appeared and evolved in Africa. Numerous molecular analyses support this clade, whereas fossil records and morphological studies are only beginning to give us arguments in favour of such relationships (see for instance Robinson & Seiffert, 2004; Kjer & Honeycutt, 2007; Murphy *et al.*, 2007; Asher & Lehmann, 2008; Tabuce, Asher & Lehmann, 2008). Thanks to these molecular studies, the aardvarks are well known from a genetic point of view. Moreover, according to Yang *et al.* (2003: 1066), *O. afer* retains a '. . . karyotype that provides strong evidence of the eutherian ancestral state'. These newly proposed high-level phylogenies now need to be tested and completed by morphological analyses. The first step in such long-term research is the revision of the relationships within the concerned mammalian orders.

Recently, the Mission Paléoanthropologique Franco-Tchadienne (MPFT) found the first fossil aardvarks from Central Africa in the Djurab desert, Northern Chad (Lehmann *et al.*, 2004, 2005, 2006). At least five partial skeletons have been preserved, belonging to two different species. For the first time, cranial and post-cranial morphology could be investigated and included in a formal cladistic analysis of the Tubulidentata. Thanks to their relative completeness, these specimens have evoked a new impetus for the study of fossil aardvarks. Therefore, almost all of the fossil aardvarks from Africa and Eurasia have been reconsidered. Moreover, around a hundred skeletons of extant aardvarks have been examined to test morphological variability. Based on these analyses, the aim of this paper is to decipher the relationships of the main clades within the order Tubulidentata, and to propose a systematic revision of the fossil aardvark species.

ORDER TUBULIDENTATA

As shown in the introduction, the study of the aardvarks has its roots in the 18th century. However, Tubulidentata was not recognized as an order on its own until the early 20th century. Furthermore, most of the studies dealing with fossil aardvarks were limited to the description of one species. Patterson (1975, 1978) is the first author to have suggested intraordinal relationships (Fig. 1). In his review, Patterson split the sole family of the order – the Orycteropodidae Gray, 1821 – into two subfamilies. On one hand, the Orycteropodinae, which consists of the African and Eurasian forms (*Leptorycteropus*, *Myorycteropus*, and *Orycteropus* Geoffroy St Hilaire, 1796), and on the other hand, the Plesiorycteropodinae Patterson (1975), represented by a single genus *Plesiorycteropus* Filhol, 1895. The latter taxon is a subfossil from Madagascar known by numerous but fragmentary remains (for instance, no dental remains have been

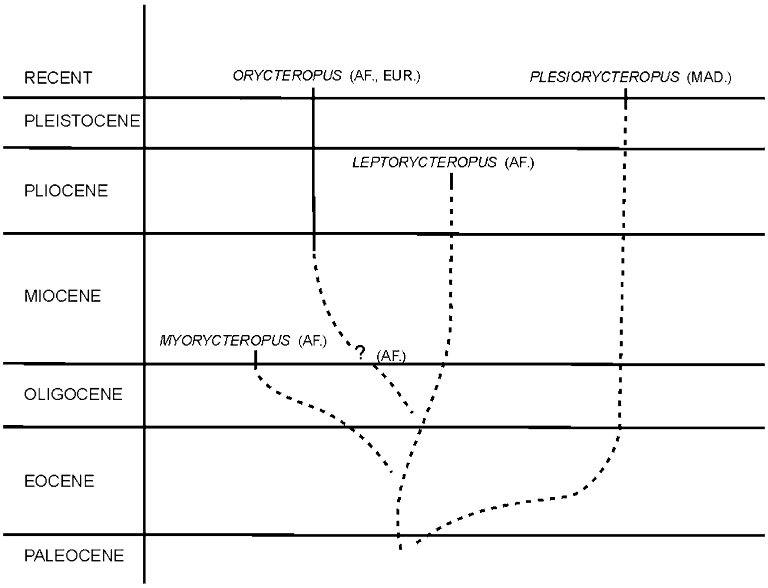


Figure 1. Suggested relationships of the known Tubulidentata genera (modified after Patterson, 1975).

found so far). Following Filhol (1895), Lamberton (1946) and Patterson (1975) suggested that *Plesiorycteropus* was a relative of the aardvarks. However, MacPhee (1994) showed the ambiguities around the phylogenetic relationships of the genus in a cladistical analysis at a high hierarchical level. He concluded his extensive study (MacPhee, 1994: 201) and his '. . . recognition of the distinctiveness of *Plesiorycteropus* by the erection of a new higher taxon to receive it': the new order Bibymalagasia. Thus, the order Tubulidentata is considered in the present study to comprise only one subfamily: the Orycteropodinae.

Within this subfamily, three genera have been described so far. *Myorycteropus* is a Kenyan genus from the Early Miocene of Rusinga and Mfwangano. This form is based on an incomplete skeleton of a juvenile individual, and is monospecific. *Leptorycteropus* is also a Kenyan genus, but from the Late Miocene of Lothagam. Very few specimens of this taxon are known, and they are mostly post-cranial remains. Finally, *Orycteropus* is known from the Early Miocene up to the present day. The extant aardvark belongs to that genus as well as, supposedly, the oldest known fossil Tubulidentata: *Orycteropus minutus* Pickford, 1975. This genus shows the largest biodiversity, with 13 described species widespread from Africa to Eurasia (Lehmann, 2006a). Although they clearly belong to the Orycteropodinae, the relationships between the genera of this subfamily are still poorly known. For instance, Patterson (1975: 216) speculated that the *Orycteropus* and *Leptorycteropus* lineages may '. . . be more closely related to each other than either is to the *Myorycteropus* one' (Fig. 1). Moreover, he agreed with MacInnes (1956) that *Myorycteropus* is too specialized to be involved in the ancestry of *Orycteropus*. Conversely, van der Made (2003) proposed that *Myorycteropus* could be the stem group of the two other genera (Fig. 2). This author also suggested that some *Orycteropus* species should be attributed to *Leptorycteropus* and *Myorycteropus*, thereby demonstrating the absence of well-established systematics for the order. Finally, Pickford (1975, 2004, 2005) simplified the question by assigning all Orycteropodinae to the sole genus *Orycteropus*, without giving substantial evidence to justify this. Taking into consideration all currently available material, the intergeneric relationships are investigated in the present study.

A preliminary cladistic analysis set by Lehmann *et al.* (2005), mostly based on characters found in the literature, demonstrated that the monophyly of the genus *Orycteropus* should be re-examined. Moreover, this analysis was the first to clearly show affinities between an African species, *Orycteropus abundulafus* Lehmann *et al.*, 2005, and a Eurasian species, *O. gaudryi* (Fig. 3). van der Made (2003) and Lehmann *et al.* (2005) performed the only studies that tried to distinguish the relationships between species of Tubulidentata. However, they did not examine the complete fossil record, as it is scattered in many different international institutions, and also because some of the holotypes were inaccessible at the time.

Some fossil specimens not taken into consideration in the present study deserve comments, nonetheless. First, some of the material recovered from the old collection of the Quercy (France) was previously

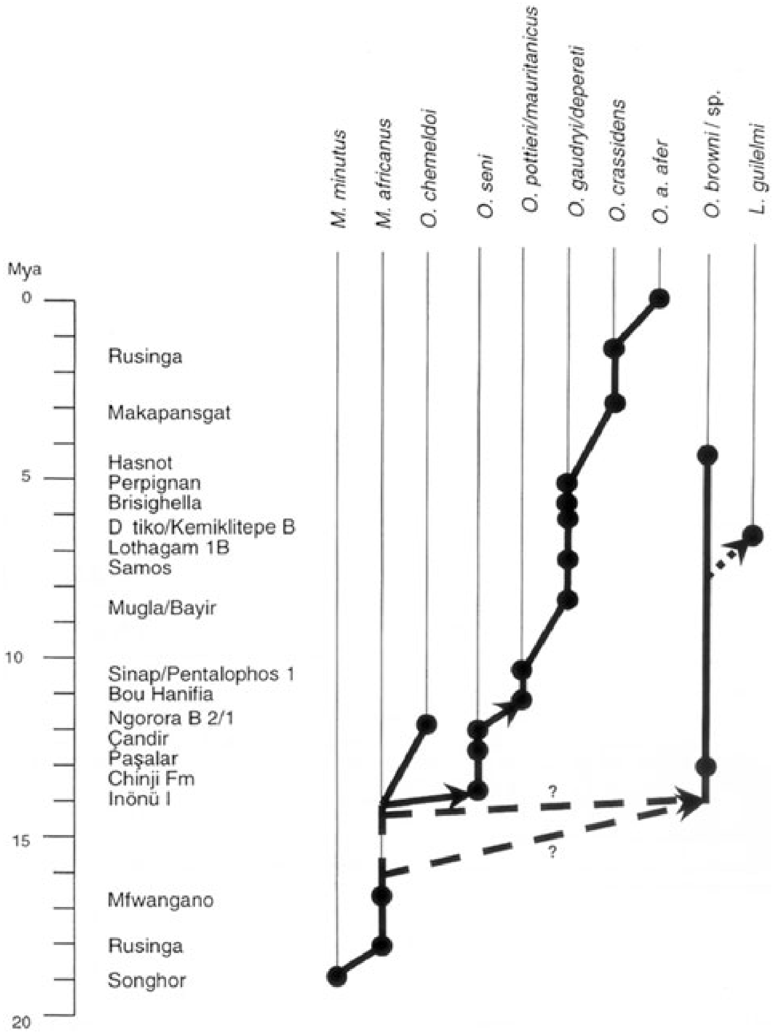


Figure 2. Stratigraphic distribution of different tubulidentates (modified after van der Made, 2003). Localities and their approximate ages in Mya on the left. Thick lines indicate possible ancestor–descendant relationships and arrows indicate possible dispersal events.

assigned to Tubulidentata: *Palaeorycteropus quercyi*, Filhol (1894), *Archaeorycteropus gallicus* Amaghino, 1905, and *Leptomanis edwardsi* Filhol, 1894. The two former specimens (two humeri and a fragment of tibia, respectively) show affinities with the pangolins, but are now usually considered to be both indeterminate eutherians (Patterson, 1975). The latter, a dorsal part of a skull, is usually considered 'faute de mieux' as a manid (Patterson, 1975). However, Thewissen (1985) suggested that *Leptomanis* could be the oldest tubulidentate known so far. It is not the aim of this study to determine the status of *Leptomanis*; a more comprehensive study must be undertaken, as this specimen might speak against the isolated evolution of the Tubulidentata, along with the other Afrotheria, in Africa during the Paleogene. Jepsen (1932) referred a mandible fragment from the Eocene of Wyoming, that he called *Tubulodon taylori* Jepsen, 1932, to the order Tubulidentata. However, further discoveries revealed that *Tubulodon* is rather a palaeanodont (Gazin, 1952; Simpson, 1959). Finally, Alferez *et al.* (1988) described fossil remains at Corcolès (Spain) that they believed were the oldest known Orycteropodidae from Eurasia. However, Pickford & Morales (1998) identified other Spanish remains as belonging to a peculiar lineage of Tayasuidae with tubulidentate microstructure in their cheek teeth roots. They refer the material described by Alferez *et al.* (1988) to that suiform lineage 'being its most derived known member in which the roots of the posterior premolars and molars have become fully tubulidentate, while the anterior premolars have retained their enamel cap and "normal" roots' (Pickford & Morales, 1998: 286).

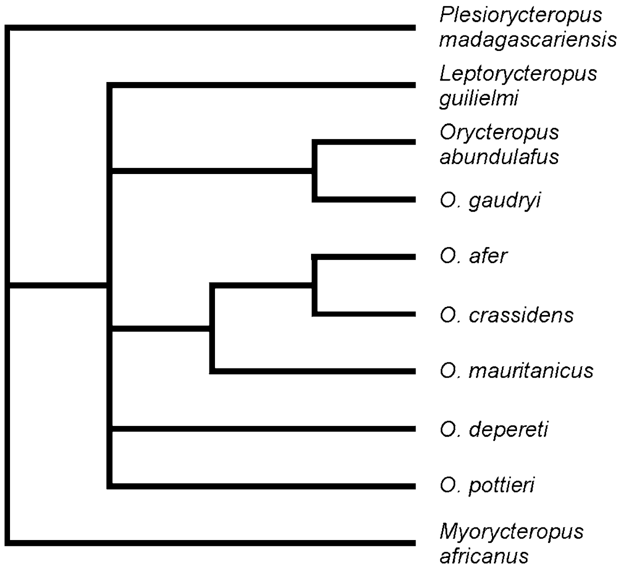


Figure 3. Strict consensus tree of eight most parsimonious trees. Tree length = 45, consistency index (CI) = 0.69, and retention index (RI) = 0.60 (modified after Lehmann *et al.*, 2005).

MATERIAL AND METHODS

This study will reconsider the relationships between the species of the genera *Leptorycteropus*, *Myorycteropus*, and *Orycteropus*. Table 1 shows a list of the fossil tubulidentate taxa considered in this paper. However, only species that have been re-examined by the present author are included in the cladistic analysis. Therefore, and for the first time, all African species (nine), as well as most of the Eurasian ones (four out of six), have been studied, so that only two species (*Orycteropus pottieri* Ozansoy, 1965 and *Orycteropus seni* Tekkaya, 1993) of the 15 recognized have not been considered here. Furthermore, four species (*Orycteropus chemeldoi* Pickford, 1975, *Orycteropus minutus* Pickford, 1975, *Orycteropus pilgrimi* Colbert, 1933, and *Orycteropus browni* Colbert 1933) are known by very fragmentary material, and so they could not be included in the cladistic analysis. However, based on the results of the present study, the affinities of these six species will be discussed. Altogether, over 200 fossil specimens (most of them consist of isolated elements) have been examined. These specimens are housed in the following institutions: American Museum of Natural History (AMNH), New York, USA; Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany; Bernard Price Institut, Johannesburg, South Africa; Centre National d'Appui à la Recherche (CNAR), N'Djaména, Chad; Geological Survey of India, Calcutta, India; Geological Survey of Pakistan, Islamabad, Pakistan; National Earth Science Museum, Windhoek, Namibia; Harvard Peabody Museum, Cambridge, USA; IZIKO South African Museum, Cape Town, South Africa; National Museum of Ethiopia, Addis Ababa, Ethiopia; National Museums of Kenya (NMK), Nairobi, Kenya; Natural History Museum (NHM), London, UK; Naturhistorisches Museum, Basel, Switzerland; Maden Tetkik ve Arama Enstitusu (MTA), Ankara, Turkey; Musée Géologique Cantonal de Lausanne, Switzerland; Museum für Naturkunde, Berlin, Germany; Muséum National d'Histoire Naturelle (MNHN), Paris, France; Museum of Anatolian Civilizations, Ankara, Turkey; Museums of the Aristotle University of Thessaloniki, Greece; Transvaal Museum, Pretoria, South Africa; Uganda Museum, Kampala, Uganda; University of Bonn, Germany; Yale Peabody Museum, Yale, USA. Moreover, several of these fossils were not described before, and numerous fossils were unidentified at the species level. Specimens that are too fragmentary have not been incorporated in the present cladistic analysis, but the affinities of some of them are discussed with regard to the results of this study.

The intraspecific osteological variability of the extant species, *O. afer*, has never been estimated. Again, this might be mostly because the specimens are often scattered in different international institutions, so that it is not easy to gather a sufficient number of material to do such a study. In order to estimate the possible variation range for each character used in this cladistic analysis, a large sample of extant aardvark skeletons (about 120 skulls and 50 post-cranial skeletons, from several African, American, and European museums) originating from different parts of Africa has been examined. The results of this study have been taken into consideration for the extant aardvark, but also, by extension, for the fossil taxa.

Recently, Pickford (2005) described the fossil aardvark remains from Langebaanweg (South Africa). He concluded that these specimens were the earliest fossils attributed to *O. afer*, which means that the temporal distribution of the extant aardvark must be extended from the Late Pleistocene to the Early Pliocene. The Langebaanweg material has been examined for this study, and the validity of this determination has been tested according to the results of the present cladistic analysis.

In 1975, Pickford interpreted the species *Orycteropus crassidens* MacInnes, 1956 (from from Rusinga Island and Kanjera, Kenya) as a subspecies of *O. afer*. Later, the same author (Pickford, 2005) suggested merging the two taxa in the species *O. afer* 'in view of the variability in size and proportions of the teeth and skeletal elements of extant aardvarks', and considering the theoretical difficulties related to fossil subspecies. van der Made (2003) suggested, however, that

Table 1. Fossil Tubulidentata species considered, and references consulted in this study

Species	Main occurrences	Other references
Leptorycteropus guilielmi Patterson 1975	Lothagam, Kenya (U. Mio.)	Milledge, 2003
Myorycteropus africanus MacInnes, 1956	Rusinga Island, Kenya (L. Mio.)	Pickford, 1975
Orycteropus abundulafus Lehmann *et al.*, 2005	Kossom Bougoudi, Chad (U. Mio.)	Lehmann *et al.*, 2006
O. browni Colbert, 1933	Nagri & Dhok Pathan, Pakistan (M. Mio – U. Mio.)	Pickford, 1978
O. chemeldoi Pickford, 1975	Tugen Hills, Kenya (M. Mio.)	
O. cf. *chemeldoi*	Kakara, Uganda (U. Mio.)	Pickford, 1994
O. crassidens MacInnes, 1956	Rusinga Island, Kenya (Ple.)	Pickford, 1975
O. depereti Helbing, 1933	Perpignan, France (L. Plio.)	
O. djourabensis Lehmann *et al.*, 2004	Kollé, Chad (L. Plio.)	Lehmann, 2008b
O. gaudryi Major, 1888	Samos Island, Greece (U. Mio.)	Andrews, 1896; Colbert, 1941; de Beaumont, 1970; Tekkaya, 1993; de Bonis *et al.*, 1994; Sen, 1994
O. mauritanicus Arambourg, 1959	Bou Hanifia, Algeria (U. Mio.)	
O. minutus Pickford, 1975	Songhor, Kenya (L. Mio.)	
O. cf. *minutus* or *O. minutus*	Arrisdrift, Namibia (M. Mio.)	Pickford, 1996, 2003
O. cf. *minutus*	Rooilepel, Namibia (M. Mio – U. Mio.)	Pickford, 1996
O. pilgrimi Colbert, 1933	Nagri & Dhok Pathan, Pakistan (M. Mio – U. Mio.)	Lewis, 1938; Pickford, 1978
O. pottieri Ozansoy, 1965	Sinap formation, Turkey (U. Mio.)	de Bonis *et al.*, 1994; Kappelman *et al.*, 1996; Fortelius *et al.*, 2003.
O. seni Tekkaya, 1993	Çandir, Turkey (M. Mio.)	van der Made, 2003; Fortelius *et al.*, 2003.

Temporal distribution: Mio., Miocene; Plio., Pliocene; Ple., Pleistocene; L., Lower; M., Middle; U., Upper.

the taxon was a valid species. Moreover, Lehmann *et al.* (2005) showed the similitude existing between *O. afer* and *O. crassidens*, but also noticed some distinctive characters that should be investigated further. The holotype and paratype of *O. crassidens* have thus been re-examined, and their validity as a species has been tested.

CLADISTIC ANALYSIS

OUTGROUP

It is difficult to choose an outgroup for the study of the phylogenetic relationships within Tubulidentata, because there is no consensus on the closest sister group of this order. Several hypotheses could be considered, and one of the most intuitive would be a close relationship between Tubulidentata and *Plesiorycteropus*. However, as shown by MacPhee (1994: 198) in his parsimony analyses, '. . . the cladistic position assumed by *Plesiorycteropus* varied significantly among runs' making it impossible to figure out which is the sister taxon of this genus. Those uncertainties about the Malagasy subfossil make it difficult to choose it as the outgroup for the present analysis. As shown by the molecular analyses, Tubulidentata belongs to the clade Afrotheria (see for instance Robinson & Seiffert, 2004; Springer *et al.*, 2004; Kjer & Honeycutt, 2007; Murphy *et al.*, 2007; Tabuce *et al.*, 2008). Nonetheless, the position of the order in this clade is not well established. Several recent studies strongly support a [elephant-shrews + aardvark + tenrecs + golden moles] clade, to the exclusion of paenungulates (elephants, hyraxes, and sirenians) (see, for instance, Waddell *et al.*, 2001, but also see Tabuce *et al.* 2008 for further references). It is not the aim of this paper to resolve the position of the Tubulidentata within the Eutheria, but to establish the intraordinal relationships of the Orycteropodidae taxa known so far. Thus, three extant Afrotherian taxa have been included in the present analysis: a hyrax (*Procavia capensis* (Pallas, 1766)), an elephant-shrew (*Rynchocyon cirnei* Peters, 1847), and a golden mole (genus *Chrysochloris*, based on specimens from the species *Chrysochloris capensis* Lacépède, 1799 and *Chrysochloris stuhlmanni* Matschie, 1894).

CHARACTERS

The cladistic analysis presented in this paper studies the state of 39 adult cranial (18), dental (5), and post-cranial (16) characters in nine species of fossil and extant Tubulidentata, and in three extant Afrotherian taxa. The features are listed and described in the Appendix. All characters are of equal weight and the multistate characters are unordered. Question marks indicate features non-preserved (worn, broken, or missing) on the fossil material. For the purpose of clarity, the characters and their different states are also illustrated (Appendix). Note that some of the characters are taken from the preliminary cladistic analysis of Lehmann *et al.* (2005). However, several of them were based on descriptions found in literature, so that after direct examination of the material, some character states might differ.

RESULTS

The developed data matrix (Table 2) includes 39 characters and 12 taxa, and shows a missing data percentage of 20.7%. This high percentage is explained by the fragmentary state of taxa like *Orycteropus depereti* Helbing, 1933 (known only from a skull), and will be taken into account in the discussions. The analysis was performed using the program PAUP v4b10 (Swofford, 1998), with a branch-and-bound algorithm, on unordered and unweighted characters. All characters are parsimony informative. Three equally parsimonious phylogenetic trees were obtained: with a tree length of 77 steps; consistency index (CI) of 0.6494; and a retention index (RI) of 0.6932. The strict consensus of these trees is given in Figure 4, with the results of a bootstrap analysis (10 000 replicates) and a Decay index for an estimate of the robustness of the clades. The second of the most parsimonious trees (Fig. 5) is chosen to illustrate the character-state changes for each node (ACCTRAN option). The differences between the trees concern the relationships at node G: *O. abundulafus* can be the sister taxon of *O. gaudry* or *Orycteropus mauritanicus* Arambourg, 1959, or is in polytomy with the two other species, as seen in the second most pasimonious tree (Fig. 5). The following discussion is based on these figures.

Orycteropodidae (node A)

The present cladistic analysis suggests that aardvarks are closer to elephant-shrews than they are to golden moles and hyrax. This clade is, however, not strongly supported (bootstrap value < 50%), and there are certainly not sufficient taxa considered to discuss relationships at the supraordinal level. Conversely, this analysis enables the distinction of at least four

Table 2. Character matrix (see Appendix for characters description) used for this cladistic analysis

	Characters																																						
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Procavia capensis	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	2	1	0	–	–	1	1	0	0	0	0	0	2	2	0	1	1	0	0	0	0	0	0
Chrysochloris	0	0	1	0	2	0	0	0	0	0	2	0	0	0	2	0	0	0	0	–	–	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0
Rhynchocyon cirnei	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	–	–	0	0	0	0	0	1	0	3	0	0	1	2	0	1	1	0	0	1
Leptorycteropus guilielmi	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	1	?	?	?	0	0	1	0	?	0	0	?	1	0	0	0	?	0	1	?	1
Myorycteropus africanus	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	0	2	0	?	1	0	1	1	0	?	0	1	0	0	?	?	1	1	1	1
Orycteropus abundulafus	1	0	0	1	0	1	2	1	1	1	1	1	1	1	0	1	2	0	1	1	0	1	1	0	1	0	1	1	0	1	1	1	0	0	1	1	1	0	A
Orycteropus afer	1	0	0	1	1	0	1	0	1	0	2	0	0	0	1	0	1	1	1	0	1	1	1	1	0	1	0	0	1	1	1	0	1	1	2	0	1	0	1
Orycteropus crassidens	1	0	0	1	?	?	1	0	?	?	2	?	0	0	1	0	1	1	1	0	1	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	0	1
Orycteropus depereti	1	0	0	1	0	1	2	0	0	?	1	1	1	1	0	1	?	?	1	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Orycteropus djourabensis	1	0	0	1	1	0	1	0	?	?	2	0	0	0	1	0	1	0	1	0	0	1	1	1	0	1	1	0	1	1	1	0	0	1	2	0	1	0	1
Orycteropus gaudryi	1	0	0	1	0	1	2	1	A	1	1	1	1	1	0	1	2	0	1	1	0	1	1	1	1	1	1	1	?	1	1	1	0	0	1	1	1	0	1
Orycteropus mauritanicus	1	0	?	1	?	1	2	1	1	1	1	?	?	?	0	?	?	?	1	1	0	1	1	?	?	?	?	?	?	?	?	?	1	0	?	1	1	0	1

‘A’ indicates a polymorphism between states 0 and 1. Missing data is indicated by ‘?’. Non-applicable characters are scored as a dash ‘–’.

tubulidentate apomorphies: the extensive mastoid exposure in the occipital region, the tubulidentate microstructure of the teeth, the presence of a pectineal tubercle on the femur, and the mediolaterally curved tibial diaphysis (characters 4, 19, 31, and 37, respectively, all state 1). Moreover, character states that are uninformative for the ingroup relationships of Orycteropodidae, such as the distinct facial extension of the lacrimal (character 1, state 1), the facially situated lacrimal foramen (character 2, state 0), the reduced caudal tympanic process of the petrosal (character 3, state 0), and the prominent astragalar posteromedial process (character 39, state 1) will not be considered in the following discussion. Furthermore, several characters states appear only once within the Orycteropodidae, but are shared with one of the outgroup taxa. Therefore, these characters come out as homoplasies in the analysis. In the following discussions, however, these characters will be regarded as apomorphies when considering the relationships within the ingroup.

Leptorycteropus

The genus *Leptorycteropus* is the sister group of all of the Tubulidentata analysed. In the literature, *Leptorycteropus guilielmi* Patterson, 1975 has frequently been considered as a generalized aardvark, which was less dedicated for digging (e.g. absence of deltoid crest and slender distal epiphysis of the humerus), and whose shorter snout probably shows a less specialized myrmecophagous animal (e.g. Patterson, 1975, 1978; Milledge, 2003), but see systematics discussion). Moreover, Patterson (1975: 201) resumed the description of *L. guilielmi* by putting forward that 'it is, despite its comparatively recent age, primitive in various features . . .'. Those assumptions are in accordance with a basal position for the genus. Conversely, in the preliminary cladistic analysis made by Lehmann *et al.* (2005), although the position of *L. guilielmi* was not resolved, this taxon was not basal, but was associated with the genus *Orycteropus* in the same clade (see Fig. 3). The association of two characters distinguishes *Leptorycteropus* from the other

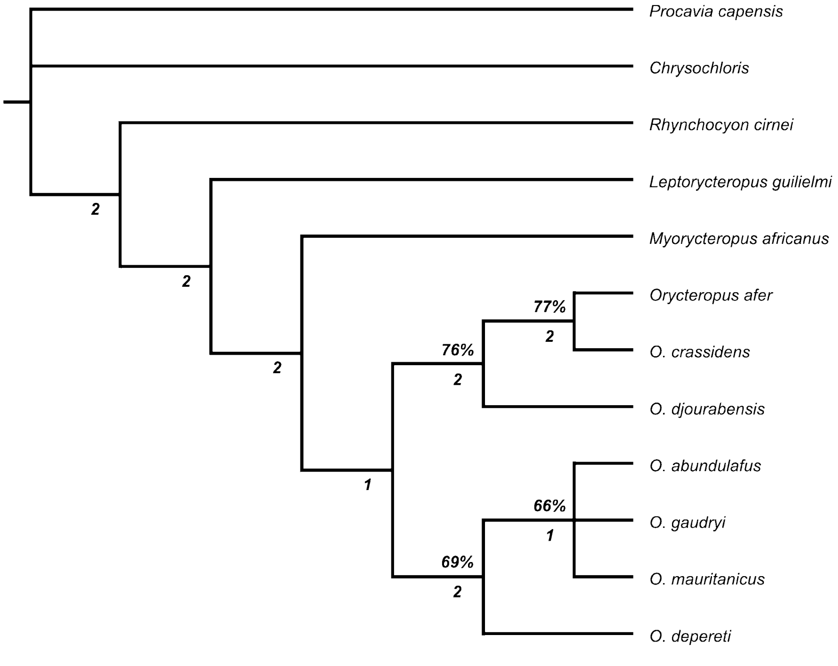
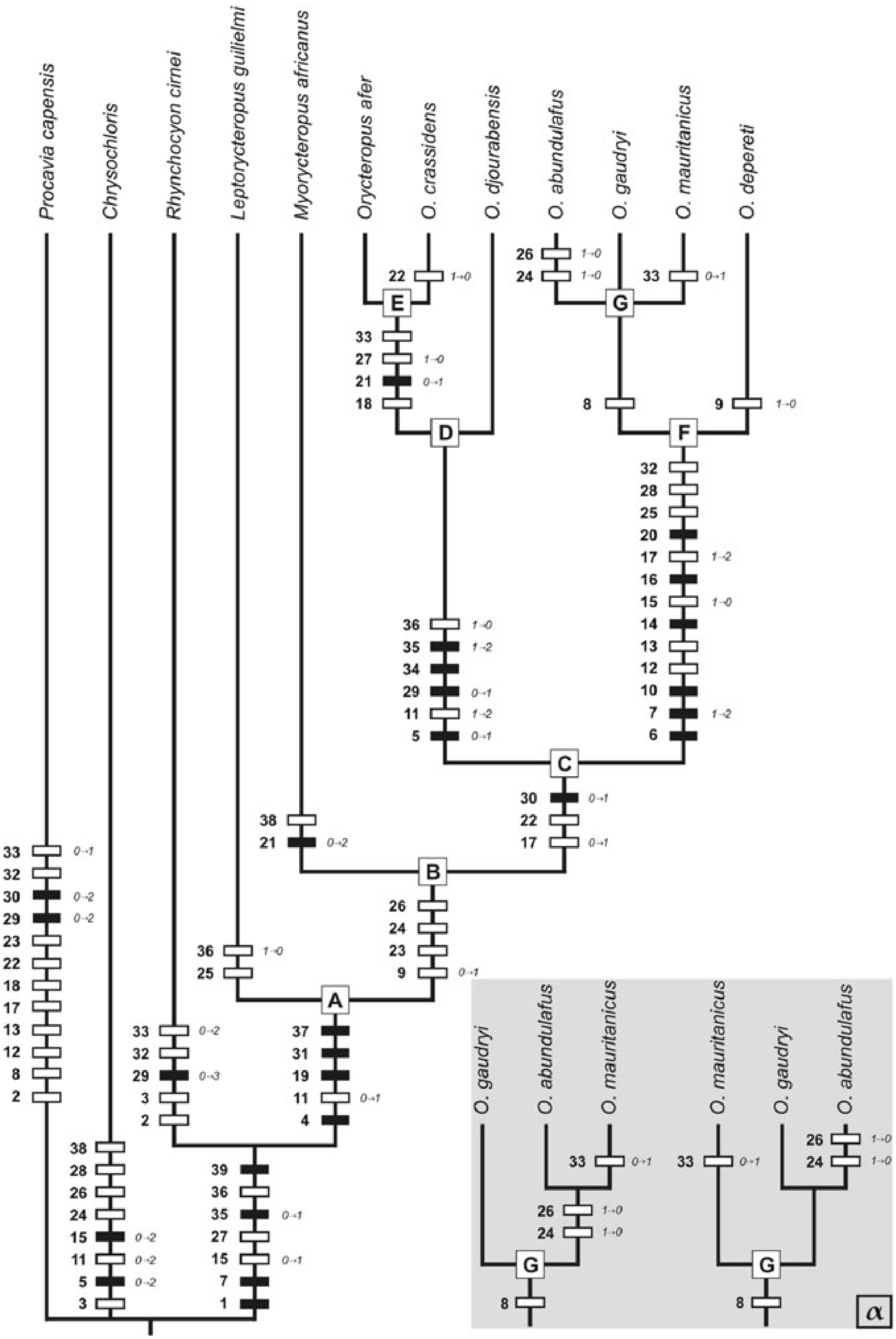


Figure 4. Strict consensus tree of three most parsimonious trees resulting from a branch-and-bound search, PAUP version 4b10. Tree length = 77, consistency index (CI) = 0.6494, and retention index (RI) = 0.6932. The bootstrap values (10 000 replications) for the most robust clades (> 50%) and the decay indices are given above and below the branches, respectively.

Figure 5. Second of the three most parsimonious trees obtained from the cladistic analysis. α, alternative relationships at node G in the two other most parsimonious trees. The numbered boxes indicate the ACCTRAN character state changes (homoplasies are represented by white boxes). The character state is given under the box for multistate characters or reversions. The bold letters are used to symbolize the nodes in the text.


Procavia capensis
Chrysochloris
Rhynchocyon cirnei
Leptorycteropus guilielmi
Myorycteropus africanus
Orycteropus afer
O. crassidens
O. djourabensis
O. abundulafus
O. gaudryi
O. mauritanicus
O. depereti
33 0→1
32
30 0→2
29 0→2
23
22
18
17
13
12
8
2
38
28
26
24
15 0→2
11 0→2
5 0→2
3
33 0→2
32
29 0→3
3
2
39
36
35 0→1
27
15 0→1
7
1
37
31
19
11 0→1
4
A
36 1→0
25
26
24
23
9 0→1
B
38
21 0→2
30 0→1
22
17 0→1
C
36 1→0
35 1→2
34
29 0→1
11 1→2
5 0→1
D
33
27 1→0
21 0→1
18
E
22 1→0
32
28
25
20
17 1→2
16
15 1→0
14
13
12
10
7 1→2
6
F
8
9 1→0
G
26 1→0
24 1→0
33 0→1
O. gaudryi
O. abundulafus
O. mauritanicus
33 0→1
26 1→0
24 1→0
G
8
O. mauritanicus
O. gaudryi
O. abundulafus
26 1→0
24 1→0
33 0→1
G
8
α

Tubulidentata in the present analysis, but each one of these characters is homoplastic, whether considering the Miocene *Orycteropus* or the Plio–Pleistocene *Orycteropus* (character 25, state 1, and character 36, state 0, respectively). Moreover, *L. guilielmi* is the taxon that shows the highest number of missing data in the matrix (23/39), so that the state of only 11 characters (including four constant ones within Tubulidentata) is known both for *Leptorycteropus* and *Myorycteropus*. The reliability of this basal position is thus to be considered with caution.

Myorycteropus + Orycteropus clade (node B)

Only one apormophy, the absence of canines (character 23, state 1), reliably distinguishes this clade from *Leptorycteropus*. The three other state changes at this node are homoplastic within Orycteropodidae (character 9, state 1; character 24, state 1; character 26, state 1). However, on these four features, the state of only two (characters 24 and 26) is known in *Myorycteropus*, and so this clade is poorly supported (the bootstrap index is less than 28%). According to Patterson (1975: 216), ‘the *Orycteropus* and the *Myorycteropus* lineage trended toward acquisition of a fossorial habitus, but they did so in somewhat different ways at different times . . .’. For instance, the majority of the *Orycteropus* species have a broad distal epiphysis of the humerus (character 26, state 1), and have developed a projecting deltoid crest on the humerus (character 24, state 1). These features are also found in *Myorycteropus* in a somewhat more advanced stage. Thus, it is not surprising that those taxa are regrouped in a common clade, mostly on the basis of convergent characters. This clade is not considered a valid one in this analysis, at least not until further material is discovered (see the Discussion).

Orycteropus clade (node C)

This clade contains all of the species of the genus *Orycteropus*. However, this clade is subsequently split in two clades: on the one hand, the Plio–Pleistocene *Orycteropus* (including the extant aardvark), and on the other hand, the Miocene ones (nodes D and F, respectively). The bootstrap index (23.5%) and the decay index (1) do not confirm the validity of this *Orycteropus* clade. Moreover, this clade is supported by only one apomorphy: the mediolateral orientation of the caput femoris (character 30, state 1). In fact, the state of this feature is known for the *Orycteropus* and *Myorycteropus* species, but not for *L. guilielmi*. The lack of data for the latter taxon infers intergeneric relationships that might not be valid (see the Discussion). Therefore, the *Orycteropus* clade (node C) is considered with reserve in this analysis. The species of the genus *Orycteropus* are distributed in the two following clades (nodes D and F).

Plio–Pleistocene Orycteropus clade (node D)

This clade includes three species: *O. afer*, *O. crassidens* and *Orycteropus djourabensis* Lehmann *et al.*, 2004. It is characterized by the acquisition of five apomorphic states of the skull and post-cranial morphology within the Orycteropodidae. On the skull, the temporal lines are low (character 5, state 1), and the post-palatine foramina are caudal to the M^3 (character 11, state 2). On the post-cranium skeleton, the sacrum consists of six sacral vertebrae (character 29, state 1), the proximal epiphysis of the tibia shows a well-developed falciform process (character 34, state 1), and the femur is longer than the tibia (character 35, state 1). Finally, *L. guilielmi* and the Plio–Pleistocene *Orycteropus* share a reversion: their tibial crest is long and ends close to the middle of the diaphysis (character 36, state 0). This high number of apomorphies, combined with a high bootstrap index (76%), shows that this node is better supported than the previous ones. However, the missing data for *Leptorycteropus* and *Myorycteropus* must again be considered here. Figure 6 shows the distribution of the character states supporting nodes D and F. On the five apomorphies found for the Plio–Pleistocene *Orycteropus*, the state of only three is known in *Myorycteropus* or *Leptorycteropus*. More precisely, *Myorycteropus* shows a plesiomorphic character state (36), whereas *Leptorycteropus* presents two plesiomorphic character states (29 and 34) and a convergent one (36). On the other hand, all states of character for the apomorphies discussed here are known for the Miocene *Orycteropus* clade (node F). This observation, combined with the number of apomorphies and the high bootstrap index, suggests that this clade is monophyletic.

Orycteropus afer + Orycteropus crassidens clade (node E)

Among the Plio–Pleistocene *Orycteropus*, the Chadian species *O. djourabensis* appears to be the sister taxon of a clade regrouping *O. afer* and *O. crassidens* (node E). The latter clade is supported by three apomorphies that distinguish these two species from all of the other Tubulidentata: the presence of an incisura mandibulae (character 18, state 1), the deep lingual groove on the upper molars (character 16, state 1), and the perpendicular orientation of the articulation axis of the trochlear notch with regard to the diaphysis of the ulna (character 27, state 0; this state is not the plesiomorphic one within Orycteropodidae). Additionally, *O. afer* shows a large tibial tuberosity (character 33, state 1), as in *O. mauritanicus*, but the state of this feature is not known for *O. crassidens*. Node E is also well

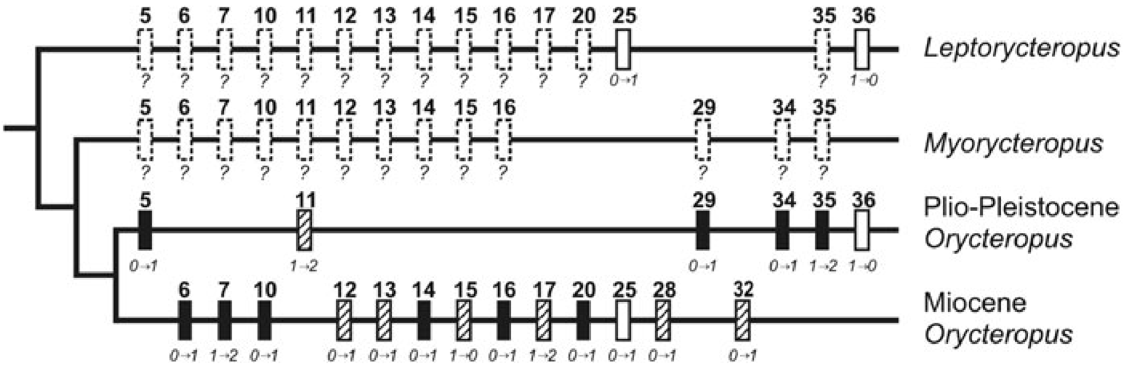


Figure 6. Details of the strict consensus tree showing intergeneric relationships. The distribution of the characters supporting node D (Plio–Pleistocene *Orycteropus*) and node F (Miocene *Orycteropus*) in the strict consensus tree is highlighted. The numbered boxes indicate character state changes: homoplasies are represented by white boxes; apomorphies are represented by black boxes; character states derived and unique in the ingroup (apomorphies within Orycteropodidae), but convergent or plesiomorphic when compared with the outgroup are represented by striped boxes; and unknown character states are represented by dashed boxes. The character state is given underneath the box.

supported according to the bootstrap index (77%). The state of these four characters is plesiomorphic within Orycteropodidae in *O. djourabensis*. This explains the basal position of the Chadian aardvark within the Plio–Pleistocene *Orycteropus* (node D). In this regard, it must be recalled that, excepting the Langebaanweg material, *O. djourabensis* is also the oldest Tubulidentata taxon known from the Pliocene of Africa. As such, given clade E, it may be expected that *O. djourabensis* is a form close to the common ancestor of *O. afer* and *O. crassidens*.

Miocene Orycteropus clade (node F)

This clade includes four species: *O. abundulafus*, *O. depereti* (which is a Pliocene aardvark), *O. gaudryi*, and *O. mauritanicus*. It distinguishes itself from the previous clades by the acquisition of twelve apomorphies distributed all over the skeleton. On the skull, the nuchal line is V-shaped (character 6, state 1), the anterior border of the orbit is situated above the M^2 (character 7, state 2), the palate is slender (character 10, state 1), the post-palatine torus is curved (character 12, state 1), the post-palatine torus is situated at the level of the M^3 (character 13, 1), the pterygoid shows ridges on its lateral wall (character 14, state 1), and the interorbital constriction includes the palatine (character 15, state 0). Moreover, the craniomandibular articulation is concave on the mandible and shows a tubercle on the skull (character 16, state 1), and the mandibular angle is superior to 73° (character 17, state 2). The molars are trapezoidal in shape (character 20, state 1). On the post-cranium, the oblique rim on the radius is blunt (character 28, state 1), and the articular facet for the sesamoid bone of the gastrocnemius muscle on the femur is positioned ventrally to the diaphysis (character 32, state 1). Furthermore, the olecranon fossa on the humerus is triangular (character 25, state 1) in this clade, a feature convergent with *L. guilielmi*. All of these characters are in the plesiomorphic state for Orycteropodidae in the Plio–Pleistocene *Orycteropus* (node D), so that the distinction between the two clades is well supported. On the twelve apomorphies found for the Miocene *Orycteropus*, the state of only four is known in *Myorycteropus* or *Leptorycteropus* (Fig. 6). More precisely, *Myorycteropus* is plesiomorphic for four of these characters (13, 20, 28, and 32), whereas *Leptorycteropus* is plesiomorphic for two of the characters (28 and 32). Moreover, the bootstrap index supports the monophyly of this Miocene *Orycteropus* clade (69%).

Orycteropus abundulafus + Orycteropus gaudryi + Orycteropus mauritanicus clade (node G)

Node G associates the species *O. abundulafus*, *O. gaudryi*, and *O. mauritanicus* in a sister group of the French *O. depereti* on the basis of a single apomorphy: the position of the ventralmost point of the maxillojugal suture above the M^3 (character 8, state 1). *Orycteropus depereti* also presents a homoplastic feature (reversion: absence of palatine groove; character 9, state 0), which is also present in *L. guilielmi*, that none of the three aforementioned species shares. Node G is relatively well supported by the bootstrap index (66%), but not by the decay index (1). It probably suffers from the poorly known anatomy of *O. depereti* and *O. mauritanicus*. For instance, the reversions of the two features that distinguish *O. abundulafus* among the Miocene *Orycteropus* clade (characters 24 and 26) are known in neither of these species. Furthermore, it is possible that one of the post-cranial apomorphies supporting node F is in fact an apomorphy of node G, because its state is not known in *O. depereti*. The relationships between the three species of node G are not resolved, and those uncertainties are responsible for the differences between the three most parsimonious trees obtained in this analysis. The alternatives to the tree presented in Figure 5 consist of the presence of a clade [*O. abundulafus* + *O. gaudryi*] or an African clade [*O. abundulafus* + *O. mauritanicus*] within node G. The latter regrouping is supported by the two homoplasies shown by the Chadian aardvark, but the state is unknown in the Algerian aardvark. No character supports the [*O. abundulafus* + *O. gaudryi*] clade, and *O. gaudryi* is never associated with *O. mauritanicus* in the most parsimonious assumptions. There is no further evidence that could strengthen a close relationship between the two African Miocene *Orycteropus* species. The well-known *O. abundulafus* and *O. gaudryi* actually differ for only two character states (characters 24 and 26), whereas *O. mauritanicus* shows only one character state (convergent) in opposition to both species (character 33, state 1). Therefore, until new specimens of the Algerian aardvark are discovered, the 18 missing states of character will prevent the resolution of the relationships at node G.

DISCUSSION: REVISED PHYLOGENY OF THE ORDER TUBULIDENTATA

The validity of Leptorycteropus

de Bonis *et al.* (1994) and Pickford (2004, 2005) considered, without justification, that *Leptorycteropus* is a junior subjective synonym of *Orycteropus*. This point of view is extreme in regard to the morphological differences between both taxa highlighted in the present study. For instance, the absence of canines (character 23, state 1), the development and lateral projection of the deltoid crest on the humerus, as well as the relative breadth of its distal epiphysis (character 24, state 1 and character 26, state 1, respectively; except for one species nested within the *Orycteropus*), the ventrocaudal projection of the pubis, etc. (see Diagnosis below), are all characters that distinguish *Orycteropus* species from *L. guilielmi*. As discussed below, *O. depereti* and *L. guilielmi* cannot be objectively compared on the basis of their known fossil record. Of the seven features known for both *Leptorycteropus* and *Myorycteropus* (excluding four uninformative characters that are constant in all Tubulidentata), four show different states (characters 24, 25, 26, and 36). In view of such dissimilarities, the genus *Leptorycteropus* is considered valid in this analysis until further specimens are discovered.

The validity of Myorycteropus

Lavocat (1958: 142) expressed some doubts about the validity of the genus *Myorycteropus*, and commented upon the differences observed between *Orycteropus* and *Myorycteropus*: 'On voudrait être assuré qu'elles nécessitent réellement l'admission d'un nouveau genre'. Pickford (1975) also suggests that *Myorycteropus* is not a valid genus, and speaks of '*Orycteropus africanus*'. However, this author did not give much evidence to justify his point of view. Pickford (1975: 79) specified simply that *M. africanus* '. . . shows minor differences in articular facets of the footbones, and the jaw is characterised by a shallow angle between the ascending and horizontal rami. MacInnes (1956) was mistaken in considering the bilobation of the upper third molar to be of generic significance'. I agree with the latter point. In fact, an analysis of the lower and upper M^3 of the extant aardvark ($n > 70$) reveals that their outline can be variably round, grooved on one side, or fully bilobed (intraindividual variations can even be observed). On the other hand, although Pickford (1975) quoted it, he did not take into account the rest of the skeleton of the holotype. For instance, no details concerning the peculiar features of the limbs or of the maxilla were discussed (see below). An analysis restricted to the elements of the hands and the feet would indeed find only differences in size between *Orycteropus* species and *M. africanus*. Pickford (1975) nonetheless specifies that *M. africanus* was an animal more specialized for digging than *O. afer*. According to this author, this specialization shows that the Orycteropodinae experienced a relatively slow evolutionary trend towards a hyperspecialized fossorial way of life. Patterson (1978: 271) found this hypothesis unjustified because the structural and proportion differences shown by the holotype of *M. africanus* indicate '. . . an animal rather differently adapted than *Orycteropus* and certainly not ancestral to it'. The shallow angle between the mandibular rami (character 17, state 0), the outline of the upper molar (character 21, state 2), the orientation of the upper molars perpendicular to the palatine plan (character 22, state 0; this state is not the plesiomorphic one within Orycteropodidae, and is only shared with one other species nested within the *Orycteropus*), the orientation of the caput femoris, the presence of a cnemial tuberosity on the tibia, etc. (see emended diagnosis below for a complete list), and the fact that *M. africanus* was adapted for digging in a more marked way than *Orycteropus* and *Leptorycteropus*, are all characters that justify distinction at the genus level.

The dichotomy within the genus Orycteropus s.l.

Currently, some authors consider *Orycteropus* to be the unique genus of the order Tubulidentata (e.g. Pickford, 1975, 2004, 2005; de Bonis *et al.*, 1994). However, they did not provide convincing evidence to justify this point of view. As discussed above, the genera *Leptorycteropus* and *Myorycteropus* present a significant number of characters that enable us to distinguish them from the genus *Orycteropus*. Besides, Lehmann *et al.* (2005) showed that the monophyly of the latter genus might be doubtful. The present analysis shows up new elements in favour of this suggestion. Indeed, one of the major results of this study is the splitting of the genus *Orycteropus* into two clades: the Miocene *Orycteropus* (including also *O. depereti*) and the Plio–Pleistocene *Orycteropus*. Both clades are recognized and supported by several apomorphies.

The Miocene *Orycteropus* clade consists of *O. abundulafus*, *O. depereti*, *O. gaudryi*, and *O. mauritanicus*. Previous studies had already pointed out possible relationships between some of those species. For instance, on the basis of 'comparable size and structure', Pickford (1975: 80) suggested a relationship between European and Asian fossil aardvarks – *O. browni*, *O. depereti*, *O. gaudryi*, *O. pilgrimi*, and *O. pottieri* – inasmuch as they 'form a closely connected series, which may be referred to as the *O. gaudryi* group'. More recently, Sen (1994) and van der Made (2003) suggested relationships between *O. depereti* and *O. mauritanicus*, as well as between *O. depereti* and *O. gaudryi*, respectively. The present analysis demonstrates, on morphological grounds, that *O. depereti*, *O. gaudryi*, and *O. mauritanicus* are indeed closely related. This study also confirms the close relationship between the penecontemporary *O. abundulafus* and *O. gaudryi* described by Lehmann *et al.* (2005, 2006). Contra to the hypothesis made by Pickford (1975), the '*O. gaudryi* group' should thus also include African species like *O. abundulafus* and *O. mauritanicus*.

Remark: The position of *O. browni*, *O. pilgrimi*, and *O. pottieri* (too fragmentary to be included in the cladistic analysis) with regard to this clade is discussed below.

The Plio–Pleistocene *Orycteropus* clade consists of *O. afer*, *O. crassidens*, and *O. djourabensis*. Lehmann *et al.* (2004) already reported the close relationship between *O. djourabensis* and the extant aardvark. Nonetheless, *O. djourabensis* replaced *O. abundulafus* (a 'Miocene *Orycteropus*' in this analysis) in the Djurab region between 4 and 5 Mya. According to Lehmann *et al.* (2004), these two Chadian aardvarks '. . . are too different to be direct relatives. Furthermore, they are closer to other non-Chadian species than to each other'. (Lehmann *et al.*, 2004: 215). Besides, Lehmann *et al.* (2005) also noticed the close relationship between *O. afer* and *O. crassidens*. Indeed, in their preliminary cladistic analysis, the clade regrouping these two taxa was the best supported by the bootstrap index (Lehmann *et al.*, 2005: fig. 10, clade D). Likewise, in the present analysis, *O. crassidens* is the closest relative to *O. afer*, and a high bootstrap index supports this regrouping (77%). Such strong similarities between *O. afer* and *O. crassidens* led Pickford (1975, 2005) to question the species status of the latter aardvark. Based on the original description by MacInnes (1956), the description given by Lehmann *et al.* (2005) suggested that both species could be distinguished by the angle of the zygomatic arch. However, the comparison of the holotype of *O. crassidens* with a large sample of extant aardvarks showed that this character is variable, and, therefore, that the Kenyan form does not differ by this feature. On the other hand, the present study also shows a convergent character between *O. crassidens* and *M. africanus* – the perpendicular orientation of the upper molars alveoli in respect to the palatine plan (character 22, state 0; this state is not the plesiomorphic one within Orycteropodidae) – that is neither present in *O. afer* nor in any other Tubulidentata. This confirms the hypothesis made by Lehmann *et al.* (2004: 205) that this feature is 'a diagnostic character for *O. crassidens*'. van der Made (2003: 140) described *O. crassidens* as an aardvark that is 'slightly larger than the recent *Orycteropus afer*, but has much larger teeth'. According to this author, these differences in tooth size should justify the specific distinction. In this regard, Lehmann *et al.* (2004: fig. 4) demonstrated that the molars of *O. crassidens* are indeed larger than in *O. afer*. Conversely, the size of the post-cranial elements of the holotype (NHM 21543–NHM 21569) and paratype (NHM M 15412, and associated elements) of *O. crassidens* is comparable with that of the largest specimens of *O. afer*, more precisely the subspecies *O. a. erikssoni* Lönnberg, 1906, *O. a. faradjius* Hatt, 1932, and *O. a. leptodon* Hirst, 1906 (see Table 3). Noticeably, the latter populations usually show smaller teeth than other extant aardvarks, and, a fortiori, *O. crassidens* (Student's t-test, Table 3). Therefore, *O. crassidens* displays a unique set of characters (large post-cranium elements; large molars) that is not present in any population of *O. afer* studied. These features could indicate at least a subspecies level distinction for *O. crassidens*, but I suggest that the additional presence of a character state that is unique among *Orycteropus* species (character 22, state 0) justifies distinction at the species level.

Remarks: Except a talus and some phalanx, no hindlimb elements of *O. crassidens* are known so far. Moreover, the skull of the holotype consists of the left half of the cranium and the two mandibles. In total, 15 character states are missing that could potentially help to further distinguish *O. crassidens* and *O. afer*.

The monophyly of the genus *Orycteropus*, regrouping these two clades, is supported neither by the bootstrap index nor by the decay index in the present analysis. Besides, the *Orycteropus* clade is only sup-

Table 3. Compared measurements (in mm) of the molars and humeri of two extant subspecies of *Orycteropus afer* and *Orycteropus crassidens*

Species	MHL	LM/1	LM/2	LM1/	LM2/
O. a. afer	142.4 ± 11.8 ($n = 15$)	11.8 ± 1.2 ($n = 14$)	12.2 ± 1.3 ($n = 14$)	11.6 ± 0.9 ($n = 12$)	11.4 ± 1.3 ($n = 12$)
O. a. erikssoni & *O. a. faradjius*	172.2 ± 6.7 ($n = 7$)	10.6 ± 1.1 ($n = 9$)	11.3 ± 2.2 ($n = 8$)	9.9 ± 1.2 ($n = 9$)	11 ± 2 ($n = 8$)
Student's t-test	$P < 0.0001$	$P < 0.0030$	ns	$P < 0.0023$	ns
O. crassidens Holotype (NHM 21543 & 21544)		13.1	14.3	11.9	13.7
O. crassidens Paratype (NHM M 15912)	177	14.6		13.9	13.7

MHL, maximum humerus length; LM, mesiodistal length of the molar. Descriptive statistics: mean ± standard deviation; number of observations indicated in brackets; Student's t-test compares the measurements in the two extant subspecies (ns indicates a non-significant test).

ported by one apomorphy (character 30, state 1), the state of which is not known in *Leptorycteropus*. It would be sufficient for this character to be in the apomorphic state in *Leptorycteropus* to break the clade. Considering the apparent dichotomy inside the genus *Orycteropus s.l.*, and the numerous synapomorphies supporting the two branches of this clade, a revision of its taxonomy is required. The extant aardvark, type species of the genus *Orycteropus*, belongs to the Plio–Pleistocene *Orycteropus* clade. This clade is thus considered to represent the redefined genus *Orycteropus* Geoffroy St Hilaire, 1796. On the other hand, the Miocene *Orycteropus* clade, including the Pliocene *O. depereti*, is regrouped around the species *O. gaudryi*. In their preliminary cladistic analysis, Lehmann *et al.* (2005) found that *O. depereti* was placed in polytomy with *Leptorycteropus* and the other *Orycteropus s.l.* This can be explained by the fact that *O. depereti* is only known from a skull, whereas *L. guilielmi* is mostly known from post-cranial material. Only three character states (and one uninformative character, constant in all Orycteropodidae) can be compared between both taxa: two of them are in the plesiomorphic state in both species (8 and 9), whereas the third one (23) is in the plesiomorphic state only for *L. guilielmi*. Conversely, *O. depereti* possesses eight of the twelve apomorphies of the Miocene *Orycteropus*. It is therefore considered a valid member of this clade. The Miocene *Orycteropus* clade, based firmly on synapomorphies, is proposed as a new genus of Orycteropodidae. The present cladistic analysis suggests a parallel evolution between *Orycteropus* and the new genus, but does not resolve the nature of their relationships. Furthermore, except for the basal position of *O. depereti* and *O. djourabensis* in their respective genera, as well as the close relationship between *O. afer* and *O. crassidens*, the relationships between the other species are not yet resolved.

Intergeneric relationships

According to the present cladistic analysis, the clade regrouping *Myorycteropus* and *Orycteropus* is the sister group of *Leptorycteropus*. Such conclusions would contradict the hypothesis made by Patterson (1975) that *Myorycteropus* would assume a basal position in Tubulidentata (see Fig. 1). It would also exclude the possibility for *Myorycteropus* to be, as suggested by van der Made (2003), the stem group of all other aardvarks (see Fig. 2). Besides, the clade [*Myorycteropus* + *Orycteropus*] is not well supported in this analysis, so that this regrouping is likely to be unwarranted. Above all, the paucity of data for the genera *Leptorycteropus* and *Myorycteropus* makes the analysis of the intergeneric relationship difficult (see Fig. 6), and the position of the four genera, relative to each other, thus remains uncertain. As a consequence, it seems more cautious to place these taxa in polytomy with each other.

The revision of the Tubulidentata systematics is linked with the requisite adoption of the present phylogeny that shows a dichotomy within the genus '*Orycteropus*' *s.l.* This reformation can be carried out with the results of the parsimony analysis presented above. However, this approach is not yet sufficient to unravel the intergeneric relationships. More specimens of *Leptorycteropus* and *Myorycteropus* are necessary.

Species excluded from the cladistic analysis

The affinities of the Tubulidentata material that has not been examined directly by the present author (hence based only on literature), or for which the paucity in the fossil record prevented their inclusion in the main analysis, are discussed hereafter. The known character states are presented in Table 4.

Orycteropus afer (?) from Langebaanweg: This form, described by Pickford (2005), is represented by fragmentary material, and only five character states (excluding two uninformative characters constant in all Orycteropodidae) are comparable with other aardvarks in this analysis (see Table 4). Furthermore, the morphological state of these characters is similar to that observed in *O. afer* and *O. crassidens*. Two of them (character 21, state 1 and character 27, state 0) are apomorphies of node D, and thus distinguish the South African material from *O. djourabensis*. However, the orientation of the upper molars alveoli in respect to the palatine plan (character 22), which is diagnostic of *O. crassidens*, is not known in the Langebaanweg form. The material discovered at Langebaanweg consists of teeth and post-cranial elements. Yet, the only post-cranial elements duplicated in both *O. afer* and *O. crassidens* are for the most part not informative (large or medium sized in regard to *O. afer*, but not significantly closer to one or the other species). More disconcerting are the isolated teeth, which can be subdivided according to their size into those closer to *O. afer* and those closer to *O. crassidens*. Therefore, on the basis of the known material, it does not yet seem possible to determine if the Langebaanweg material as a whole belongs to *O. afer* or to *O. crassidens*. I recommend keeping the cautious determination made by Hendey (1973) – *O. cf. afer* – until further material is discovered (see also Lehmann, 2006b).

Orycteropus browni and Orycteropus pilgrimi: In 1933, Colbert described two Pakistani specimens found in two different sites: AMNH 2940 (Nathot) and AMNH 29997 (Hasnot). The first specimen, a fragment of left maxilla, is the holotype of *O. browni*, whereas the second specimen, a left M^1, is the holotype of *O. pilgrimi*. Colbert (1933) considered AMNH 2940 to be an adult individual. However, the cone-shaped teeth and the rounded edges of their smooth occlusal surface are similar to the juvenile conditions found in my study of the extant aardvark. Later, Lewis (1938) described a partial skull of *O. pilgrimi* and, finally, Pickford (1978) reported on additional Pakistani material. Pickford (1978) proposed that *O. pilgrimi* was a junior subjective synonym of *O. browni*, on the basis that AMNH 2940 was a young adult and that AMNH 29997 was an adult individual, which explains the discrepancy of size between the occlusal surface of their respective teeth. I agree with Pickford on this point, and consider, in the present analysis, that *O. pilgrimi* is a junior subjective

Table 4. Character matrix (see Appendix for characters description) for the taxa not used in the main cladistic analysis

Taxa	Characters																						
	3	4	5	6	7	10	11	13	15	16	17	18	19	20	21	23	24	25	27	30	36	38	39
O. afer (?) Langebaanweg	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	?	0	0	?	?	0	1
Orycteropus browni	?	1	?	?	2	1	0	1	0	?	2	?	1	1	0	?	?	?	?	?	?	?	?
Orycteropus chemeldoi	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
Orycteropus minutus	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	1	1
Orycteropus pottieri #	0	1	0	1	?	?	?	?	?	1	1	0	1	1	1	0	1	?	?	1	1	0	1
Orycteropus seni §	?	?	?	?	?	?	?	?	?	?	1	?	1	1	?	?	?	?	?	?	?	?	?

Missing data is indicated by '?'. #In part after the description made by de Bonis *et al.* (1994) and Fortelius *et al.* (2003). §After the description made by Tekkaya (1993); Fortelius *et al.* (2003), and van der Made (2003).

synonym of *O. browni*. Therefore, all material referred to these species has been presently analysed as one taxon.

Orycteropus browni shows eight character states (and two uninformative characters constant in Orycteropodidae), which are comparable with other Tubulidentata (see Table 4). However, none of these informative character states are known in *L. guilielmi*. On their three comparable features, *O. browni* does not share the autapomorphy shown by *M. africanus* on character 21 (state 2), and presents a derived state of character where *M. africanus* shows the plesiomorphic state (character 17, state 2; character 20, state 1). The Pakistani aardvark diverges from the redefined *Orycteropus* for all eight character states (except *O. djourabensis* for character 21, state 1). Conversely, seven of the eight character states are similar in *O. browni* and the new genus. Furthermore, the Pakistani taxon shows six apomorphies of the new genus (character 7, state 2; character 10, state 1; character 13, state 1; character 15, state 0; character 17, state 2; character 20, state 1). *Orycteropus browni* is thus included in this clade in the present study, and, consequently, is assigned to the proposed new genus. *Orycteropus browni* can be distinguished from all other aardvarks, and is thus validated as a separate species, by the unique (within Orycteropodidae) position of its post-palatine foramina (character 11, state 0). Moreover, the anteriormost part of the zygomatic arch starts at the level of the mesial lobe of the M^2 in AMNH 2940 (the holotype of *O. browni*), and in AMNH 29999 (one of the additional specimens determined as *O. browni* by Pickford 1978). Conversely, in most of the species of the new genus, the zygomatic arch starts at the level of the distal lobe of the M^2, whereas, in the redefined *Orycteropus*, *O. depereti*, and *Leptorycteropus*, it starts at the level of the M^3. Thus, this character can be considered as another autapomorphy of the species *O. browni*. In the present cladistic analysis, the state of this feature might be linked to and redundant with the position of the ventralmost point of the maxillojugal suture (character 8), but it must be confirmed on more complete material of *O. browni* before coding it in the character matrix.

Remarks: van der Made (2003) tentatively proposed that *L. guilielmi* might be related to the Asian *O. browni*. It appears that none of the features observed in *O. browni* can be compared with *L. guilielmi*, so that the hypothesis cannot be tested until further material is discovered.

Orycteropus chemeldoi: This taxon, described by Pickford (1975), is only known from very scarce remains (teeth, mandible, and fragments of hand). Therefore, no character state can be compared in the present analysis, except for the presence of tubulidentate teeth (character 19, state 1), which is an apomorphy of the Orycteropodidae. Nonetheless, the lower molars of *O. chemeldoi* present a rectangular shape, as seen in the redefined *Orycteropus* species, *Myorycteropus*, and *O. pottieri*. The species from the new genus are the only ones to show trapezoidal lower molars. Therefore, *O. chemeldoi* is probably not a member of the new genus, but the data is insufficient to determine the exact genus of this taxon. Nonetheless, the unique teeth proportion validates its species status. Note that *M. africanus* and aff. *Myorycteropus minutus* (see below) also show slender lower molars. Moreover, van der Made (2003) suggested that *O. chemeldoi* descended from *M. africanus*. The known data is not sufficient to confirm this point of view. However, until further material is discovered, I recommend placing this taxon in *affinis Myorycteropus*.

Orycteropus minutus: This is the oldest known unquestionable fossil aardvark species so far. It is mainly based on fragments of autopode and two teeth (Pickford, 1975). Therefore, only one character state (besides the tubulidentate tooth structure; character 19, state 1) can be compared with the other Tubulidentata in this analysis: the vertical and negligible cotyloid facet for the medial malleolus of the tibia on the talus (character 38, state 1). *Myorycteropus* shares this derived state, but the redefined *Orycteropus* or the new genus do not. The state in *Leptorycteropus* is not known. van der Made (2003) tentatively joined *O. minutus* to the genus *Myorycteropus*, suggesting that *M. africanus* evolved from '*M. minutus*' in a lineage that increased in size. This point of view is certainly pre-emptive according to the known material. However, until new discoveries are made, this taxon could be placed in *affinis Myorycteropus*. The species status is discussed in detail below.

Orycteropus pottieri: This species presents the highest number of known character states among the species excluded from the analysis (see Table 4). Nonetheless, those characters mostly come from literature, and must thus be used with caution. Moreover, *L. guilielmi* and *O. pottieri* can only be compared for three characters. This explains why the parsimony analyses including the latter taxon are not robust, and have a tendency to disassociate the clades highlighted in the present work. Besides, the affinities of this form at the genus level are difficult to establish. *Orycteropus pottieri* shares no diagnostic state of character with the redefined *Orycteropus*, but shares three diagnostic apomorphies with the new genus (characters 6, 16, and 20). This species is, moreover, in a plesiomorphic state, like the species of the new genus, for one diagnostic character of the redefined *Orycteropus* (character 5). Furthermore, *O. pottieri* shows the same strong development of the deltoid crest on the humerus (character 24, state 1) as the redefined *Orycteropus*, *Myorycteropus*, and the new genus, as well as two other character states that are shared only by the redefined *Orycteropus* and the new genus (character 30, state 1 and character 38, state 0). Conversely, the Eurasian taxon differs from the aforementioned genera for the presence of canines (character 23), which is a plesiomorphic state in Orycteropodidae. Note that *L. guilielmi* also presents this character state. *Orycteropus pottieri* can be distinguished from *Myorycteropus* by at least two derived characters (character 17, state 1 and character 21, state 1). Finally, this Eurasian species shares the deep lingual groove on the upper molars (character 21, state 1) with the clade [*O. afer* + *O. crassidens*], but not the derived condition shown in the mandible of the latter clade: the presence of an incisura mandibulae (character 18).

Pickford (1975) included *O. pottieri* in his '*O. gaudryi* group', which is more or less equivalent to the present new genus, and van der Made (2003) suggested that *O. mauritanicus* might be synonymous with *O. pottieri*. According to the present analysis, the latter species seems to be closer to the new genus than to the redefined *Orycteropus* and *Myorycteropus*. Moreover, the unique fact (except perhaps for *O. seni*) that the lower and upper molars of *O. pottieri* do not show the same shape is rather confusing, but could be a diagnostic character of the species. It is thus not yet possible to reliably decide if *O. pottieri* belongs to the new genus until further material is described or examined. In the meantime, I recommend placing this taxon in *affinis* with the new genus on the basis of the number of apormorphies shared with the species of that genus.

Orycteropus seni: Only a few remains of *O. seni* are known so far. Originally described from a mandible, additional material for that species consisted only of teeth and a few autopode elements. Therefore, only two character states (besides the tubulidentate tooth structure) can be assessed. *Orycteropus seni* shows the same mandibular angle as the redefined genus *Orycteropus* (character 17, state 1), and is thus distinct from *Myorycteropus* and the new genus. Conversely, the outline of the molar is trapezoidal, as in the species from the new genus (character 20, state 1), but is distinct from *Myorycteropus* and the redefined *Orycteropus*. Furthermore, *L. guilielmi* and *O. seni* show no character states that can be compared in that analysis. Such a limited database on this taxon precludes a reliable assignation to one of the genera. However, *O. seni* shares its two character states with *O. pottieri*, unlike any other Orycteropodidae. On that basis, I recommend placing *O. seni*, like *O. pottieri*, in *affinis* with the new genus until further material is discovered.

SYSTEMATIC PALAEONTOLOGY

The new classification proposed below for the Orycteropodidae is based on the foregoing parsimony analysis, but also on the complementary observations discussed previously. The genus *Orycteropus* is redefined and a new genus is proposed. All taxonomical information (spelling, author, date of publication, etc.) follows the comprehensive work of Lehmann (2007). See also this paper for synonymy lists.

CLASS MAMMALIA LINNAEUS, 1758

ORDER TUBULIDENTATA HUXLEY, 1872

FAMILY ORYCTEROPODIDAE GRAY, 1821

GENUS ***AMPHIORYCTEROPUS*** **GEN. NOV.**

Diagnosis: Medium-sized Orycteropodidae (about 65–90% of the general size of the extant aardvark) showing the following apomorphies on the skull: a V-shaped nuchal line; an anterior border of the orbit situated above the M^2; a slender palate; a curved post-palatine torus, moreover situated at the level of the M^3; crests on the lateral wall of the pterygoid; an interorbital constriction, including the palatine; a tubercle on the craniomandibular articulation facet; and molars trapezoidal in shape. On the mandible, a concave craniomandibular articulation surface and a mandibular angle superior to 73°. On the postcranium, a blunt oblique rim as well as a pointed radial (or bicipital) tuberosity on the radius, and a ventrally positioned articular facet for the sesamoid bone of the gastrocnemius muscle on the femur. The genus is also characterized by high temporal lines on the cranium, reduced diastema between the premolars, a short scapular neck, a proximodistally elongated talus, feet longer than hands, and metapodes as well as phalanx more slender, proportionally, than in *Orycteropus*. *Amphiorycteropus* species exhibit a triangular olecranon fossa on the humerus, as in *L. guilielmi*, and a continuous border between the tibial tuberosity and the fibula on the proximal epiphysis of the tibio-fibula, as in *O. djourabensis*. Additionally, they present the following features: a post-palatine foramina situated at the level of the M^3, the absence of an incisura mandibulae, a shallow lingual groove on the upper molar, an articulation axis of the semilunar notch oblique to the diaphysis of the ulna, five sacral vertebrae, no falciform process on the tibiofibula, a short tibial tuberosity, a tibia longer than the femur, and a short tibial crest merging abruptly with the diaphysis.

Remarks: The general size of *Amphiorycteropus* is based on the limb-bone dimensions. The tibia and the cranial elements cannot be taken into consideration here, as their proportions vary between species.

Type species: Amphiorycteropus gaudryi (Major, 1888)

Other forms: In Africa, *Amphiorycteropus abundulafus* (Lehmann *et al.*, 2005), *Amphiorycteropus mauritanicus* (Arambourg, 1959), *Amphiorycteropus* sp. Rooilepel (Pickford, 1996, but see below), *Amphiorycteropus* sp. Saitune Dora (Lehmann, 2008a); and in Eurasia, *Amphiorycteropus browni* (Colbert, 1933), *Amphiorycteropus depereti* (Helbing, 1933), *Amphiorycteropus* cf. *gaudryi* Monticino (Rook & Masini, 1994), *Amphiorycteropus* cf. *gaudryi* Chobruchi (Pavlova, 1915), *Amphiorycteropus* cf. *gaudryi* Maragheh (Major, 1893), as well possibly as aff. *Amphiorycteropus pottieri* (Ozansoy, 1965), aff. *Amphiorycteropus* cf. *pottieri* Sinap (Fortelius *et al.*, 2003), aff. *Amphiorycteropus seni* (Tekkaya, 1993), aff. *Amphiorycteropus* cf. *seni* Paşalar (Fortelius, 1990), and aff. *Amphiorycteropus* cf. *seni* Sinap (Fortelius *et al.*, 2003).

Etymology: The genus name derives from the Greek '*amphi*', meaning 'on both sides', and '*orycteropus*', literally 'digging foot', but also from the genus name of the extant aardvark. This name – 'the aardvark from both sides' – denotes that this genus is for now the only genus of Tubulidentata known from both sides of the Mediterranean sea, i.e. Africa and Eurasia.

Geographic distribution: Kossom Bougoudi (Chad); Bou Hanifia (Algeria); Samos Island, Ditiko, and Euboea Island (Greece); Kemiklitepe, Akgedik-Bayir, Sinap, and Çandir (Turkey); Perpignan (France); Brisighella (Italy); Chobruchi (Moldavia); Maragheh (Iran); Potwar Plateau (Pakistan); as well possibly as Rooilepel (Namibia) and Saitune Dora (Ethiopia).

Temporal distribution: Middle Miocene to Early Pliocene.

Discussion: As noticed by Colbert (1941: 326), the hands of *A. gaudryi* are shorter than its feet: '. . . the third digit in the manus of [*Amphiorycteropus*] *gaudryi* is considerably shorter than the third digit of the pes of that same animal, whereas in *Orycteropus erikssoni faradjius* the length of the third digit of the manus is approximately equal to that of the same digit in the pes'. This is also the case in *A. abundulafus*: the ratio 'length of the longest finger (metapode to intermediate phalanx) on the longest toe' is about 0.82 in the Chadian species, whereas in *O. afer* the ratio is 0.90 ± 0.01 ($n = 10$) (Lehmann *et al.*, 2006: 702). Unfortunately, it cannot be confirmed for *A. mauritanicus* and *A. depereti* because the material is insufficient. Likewise, there exists a difference in the proportion of the metapodes and phalanx between those genera. These elements of the feet and the hands are proportionally broader in *Orycteropus* than in *Amphiorycteropus* (see Lehmann *et al.*, 2005: tables 15, 16). Besides, the length of the metatarsal I and V in *A. abundulafus* and *A. gaudryi* is almost similar to the length of their counterpart in *O. afer* (see Lehmann *et al.*, 2005: table 15).

The creation of a new genus, distinct from genus *Orycteropus*, helps to clarify the relationships between the Miocene species and the Plio–Pleistocene ones. Indeed, as Patterson (1975: 216) described: 'Relationships between the described species of *Orycteropus* are not clear. Tubulidentates first reached Eurasia at some time in the Miocene [. . .] and there may have been independent evolution within the genus in the north. I doubt if [*A.*] *gaudryi* was involved in the ancestry of [*O.*] *afer*, which conceivably could have come from [*A.*] *mauritanicus*, but whether [*A.*] *depereti* descended from [*A.*] *gaudryi* or, as such, reached Eurasia from Africa is uncertain. Progress here must await the discovery of more complete material in both continental areas'. The present phylogenetic systematics analysis highlights the high number of apomorphies supporting the redefined *Orycteropus* and *Amphiorycteropus*. Therefore, it is unlikely that these two genera are ancestral to one another. It would thus contradict the assumption that *A. gaudryi* (or any of the new genus members) gradually evolved into *O. afer* (van der Made, 2003). Moreover, the parsimony analysis implies that *A. depereti* is an early offshoot of the new genus, rather than a descendant of *A. gaudryi*. For more comments about that genus, see the section 'T*he dichotomy within the genus Orycteropus s.l.*'.

SPECIES *AMPHIORYCTEROPUS GAUDRYI* (MAJOR, 1888)

Emended diagnosis: Same as for the genus. Note that *A. gaudryi* is a medium-sized species of *Amphiorycteropus*.

Holotype: There is no defined holotype.

Remarks: As explained by Lehmann (2007), Major (1888) did not specifically define a holotype for '*O. gaudryi*'. In his description, Major (1888: 1180) gave details concerning the skull and foot of the fossil aardvarks discovered in Samos (Greece), but did not give references for that material (probably from several specimens). Nonetheless, the specimens housed at the Musée Géologique Cantonal de Lausanne (Switzerland), where Major worked during that period, most probably represent the type series (or syntype following the International Code of Zoological Nomenclature, Art. 73.2; ICZN, 1999) used by Major. According to the ICZN (Recommendation 73F), a lectotype should be designated among the syntype. Nonetheless, this must be performed in a more specific morphological description, which is beyond the scope of the present article (see Art. 74.7; ICZN, 1999).

Type locality: Adrianos ravine, Mytilinii Basin (Samos Island, Greece).

Remarks: Although the holotype of *A. gaudryi* is not known, the syntypes housed at the Musée Géologique Cantonal de Lausanne all come from 'Adrianos', according to their label (and the original description by Major). This site has been located in the Adrianos ravine by Kostopoulos, Sen & Koufos (2003).

Main occurrences: Quarry 1, 4, and 5 (Samos Island; Greece), Ditiko 1 (Greece), Achmet-Aga near Drazi (Euboea Island, Greece), Kemiklitepe B (Turkey), Akgedik-Bayir near Muğla (Turkey).

Remarks: Colbert (1933, 1941), followed by other authors, quoted Pikermi as an occurrence for *A. gaudryi*. However, I could find no fossil aardvark from this locality in any museum collections. Based on an article written by Woodward (1901), I suggest that no fossil aardvark has been found at Pikermi. Indeed, Woodward (1901) described how, while he was doing some excavation at Pikermi, he visited the site of Achmet-Aga, on Euboea Island (Greece), on the invitation of the manager of the excavations (Franck Noël). The latter thought that the two sites were contemporaneous according to their fauna. Woodward participated in the excavations for some days, and, during this period, they discovered 'part of the skull of a small species of *Orycteropus*, which I was able to preserve and bring for comparison with the skull of the same genus from Samos [studied by Andrews (1896)] now in the British Museum' (Woodward, 1901: 485). In the same article, Woodward (1901) confirmed that Pikermi and Achmet-Aga were of the same age and shared the same fauna. Accordingly, at the NHM, one of the specimens is labelled: 'Skull of *Orycteropus* sp. Drazi, Euboea, presented by Franck Noël, Esq 1901'. I suspect that the amalgam has been made between Woodward, the site he was currently working on (Pikermi), and this discovery of an aardvark skull in Achmet-Aga by him.

Age: Late Miocene (MN11–MN13), more precisely from 7.65 to 5.3 Mya (Kostopoulos *et al.*, 2003)

Additional material: Housed at the AMNH, New York: craniums and mandibles (AMNH 20550, AMNH 20560; AMNH 20561; AMNH 20562, AMNH 20563, AMNH 20694, AMNH 20756, AMNH 22879, AMNH 22979, AMNH 92946); craniums (AMNH 20564, AMNH 20565, AMNH 22980); hemimandibles (AMNH 20800, AMNH 22978A, B, and C, AMNH 23042, AMNH 92947, AMNH 92948); teeth (AMNH 22790); elements of an associated skeleton (AMNH 22762, AMNH field number 1, AMNH field number 4); elements of a left hindlimb (AMNH 22976); left femur (AMNH 22888); metatarsals (AMNH field number 2); metacarpals (AMNH field number 3).

Housed at the MTA, Ankara: hemimandibles (MTA 2574, MTA 2531, M-781).

Housed at the Museums of the Aristotle University of Thessaloniki: hemimandible (DTK-239).

Housed at the Musée Géologique Cantonal de Lausanne: cranium and mandible (260 S.); partial craniums (261 S., 262 S.); endocast (265 S.); hemimandibles (267 S., 280 S., 281 S., 282 S.); fragment of humerus (283 S.); parts of femur (284 S., 285 S.); elements of the foot (259 S., 263 S., 264 S., 278a & b S., 479&480 S., 1029 S., 1268–1272 S.).

Housed at the MNHN, Paris: hemimandible (KTB 94); maxilla fragment (KTB 95); isolated teeth (KTB 96, KTB 97).

Housed at the NHM: cranium and mandible (NHM M. 5690); partial cranium and its endocast (NHM M 8938); partial cranium (NHM 8938); hemimandibles (NHM M 4171, NHM M 4172).

Housed at the University of Bonn: two craniums (Sig. HLMD).

Remarks: The left hemimandible associated with the cranium AMNH 20560 is probably the antimere of the right hemimandible AMNH 20561. So far, no complete skeleton of *A. gaudryi* has been found. The AMNH displays a mounted skeleton (illustrated in Colbert, 1941; Heissig, 1999), but it is a composite, consisting of specimens AMNH 22762 and AMNH 20694, and completed with plaster elements reconstructed by symmetry or moulded on an extant aardvark.

Discussion: The species *A. gaudryi* is the first fossil species of Tubulidentata ever found. Since its description by Major (1888), the number of specimens increased considerably until *A. gaudryi* became the best represented fossil aardvark in the Tubulidentata fossil record. This is why *A. gaudryi* eventually became, along with the extant *O. afer*, an inescapable species of comparison for all studies performed on fossil Tubulidentata. This explains why, among the species of the new genus *Amphiorycteropus*, *A. gaudryi* was chosen as the type species.

As explained by Lehmann *et al.* (2004: 211), Arambourg (1959) misinterpreted the tibial features of *A. gaudryi* because he based his comparative description on a bad cast. Nonetheless, one of Arambourg's conclusions was correct: the tibia of *A. gaudryi* shows a trilobed proximal epiphysis like the species of the genus *Amphiorycteropus* (even *A. mauritanicus*, contra Arambourg, 1959) and *L. guilielmi*. This feature is, however, redundant with the absence of a falciform process, as the presence of this character gives a rather quadrate shape to the epiphysis, as in *O. afer* and *O. djourabensis*.

The locality that yielded the highest number of specimens of *A. gaudryi* is without a doubt the Mytilinii basin, on the Island of Samos (Greece). This Greek island has been the object of intensive palaeontological researches for over a century (Kostopoulos *et al.*, 2003). A recurrent problem faced by modern researchers was to localize and correlate old sites with recent stratigraphy. Indeed, the absence of information concerning the fossils found between 1890 and 1970, combined with the mix-up in the fossils collected from different horizons, did not allow us to 'distinguish evolutionary stages between the faunas of different localities in order to separate biostratigraphic horizons' (Sen & Valet, 1986). In this regard, the observations made by Sondaar (1971) concerning *A. gaudryi* are interesting. In his study of the *Hipparion*, Sondaar (1971) described anatomical dissimilarities between specimens from different localities (quarries). He also quoted other taxa that presented the same pattern of dissimilarities according to their quarries. In particular, Sondaar (1971) measured and compared the upper teeth of *A. gaudryi* (length from M^1 to M^3, and breadth of M^2). This study enabled the distinction of two groups of specimens according to the size of their upper teeth: on the one hand, the specimens from quarry 1 and quarry 4 (Q1 and Q4); on the other hand, the specimens from quarry 5 (Q5). Sondaar (1971): chapter III) suggested that 'the fossil record of Quarry 1 and Quarry 4 contains a similar fauna of *Hipparion* and *Orycteropus* which is different from that of Quarry 5, a difference, which is probably due to age'. This hypothesis has been confirmed by magnetostratigraphic analyses (Kostopoulos *et al.*, 2003): Q4 is dated from MN11 (more precisely between 7.65 and 7.45 Mya), Q1 is dated from MN12 (more precisely between 7.2 and 7.1 Mya), and Q5 is dated from the late MN12 (7–6.7 Mya). Remarkably, so far no discrete features support the differences observed between these fossil aardvarks. Moreover, it is not possible to establish if variations of size in the post-cranial skeleton also existed, because no comparable post-cranial elements are known from the different quarries. It is hazardous to try to distinguish two species from the available material. Therefore, a single aardvark species – *A. gaudryi* – is considered to have been present at Samos in Q1, Q4, and Q5.

SPECIES *AMPHIORYCTEROPUS* CF. *GAUDRYI* MONTICINO

Material (the specimens have not been directly seen by the author): Isolated molars, tarsal bones, metatarsals, and phalanx (BRS4/2; BRS5/2; BRS5bis/5; BRS5/43; BRS5/58; BRS5/69; BRS5/81; BRS5/141; BRS5/142; BRS5/214; BRS5/215; BRS5/216; BRS5/290; BRS25/22; BRS27/22; BRS27/50; BRS27/51) attributed to '*Orycteropus* cf. *gaudryi*' by Rook & Masini (1994).

Locality and age: The specimens have been found in the Monticino Gypsum Quarry (Brisighella, Italy), dated to be from the Late Messinian (MN13: 6.9–5.3 Mya).

Discussion: These fossil aardvarks found in Italy are the westernmost record of Tubulidentata in the Late Miocene of Eurasia. Along with *A. depereti*, they are the two last members of this order in Eurasia known so far. The two tali discovered in this locality show a developed cotyloid facet and a longer proximodistal than mediolateral length. These features are similar to those found in the species of *Amphiorycteropus* (no talus is known for *Leptorycteropus* so far). Moreover, the dimensions of the post-cranial elements match those of the medium-sized species of *Amphiorycteropus*: *A. abundulafus* and *A. gaudryi*. Rook & Masini (1994) did not give any measurements for the teeth, which preclude, for now, a precise determination at the species level. 'However, because of its age and the similarities mentioned, *i.e.* its overall size and the slenderness of its postcranial skeletal elements, [Rook & Masini (1994: 370) attributed] the Monticino material to [*Amphiorycteropus*] cf. *gaudryi*.' A revision of that material is required, noticeably regarding the dental elements.

SPECIES *AMPHIORYCTEROPUS* CF. *GAUDRYI* CHOBRUCHI

Material (the specimens have not been directly seen by the author): A fragment of left maxilla with P^4–M^3 identified as '*Orycteropus gaudryi*' by Pavlova (1915).

Locality and age: The specimen has been found in Chobruchi (GPS: 46°36′1″N, 29°42′30″E) (Moldavia). This site is dated as MN12 (7.43–6.9 Mya).

Discussion: This fossil aardvark is the northernmost record of Tubulidentata in Eurasia so far. Pavlova (1915) described the maxilla as a right maxilla with complete P^4–M^1–M^2 and a fragment of M^3. However, according to the illustration (Pavlova, 1915: fig. 2), these teeth are actually the complete M^1–M^3 and a fragment of P^4 of the left maxilla. The upper molars are diagnostic of the genus *Amphiorycteropus*. Indeed, they show a trapezoid outline and a shallow lingual groove. In the absence of an oblique intracuspal rim or crest on the molars, this specimen is closer to *A. abundulafus* and *A. gaudryi* than to *A. depereti* and *A. mauritanicus*. Further studies are necessary to identify this specimen more accurately. In the meantime, I recommend identifiying it as *A.* cf. *gaudryi*.

SPECIES *AMPHIORYCTEROPUS* CF. *GAUDRYI* MARAGHEH

Material (the specimen has not been directly seen by the author): A single molar (right M_2?) identified as '*Orycteropus gaudryi*' by Major (1893) and probably housed at the NHM, London.

Locality and age: The specimen comes from the Late Miocene of Maragheh, dated to between MN11 and MN12 (around 7.43 Mya after the date of Kostopoulos *et al.*, 2003).

Discussion: The molar described by Major (1893) is curved along its height, and, according to the illustration (Major, 1893), might show a lingual groove that is shallower than the vestibular one. Its outline is, however, trapezoid, as in the species of the genus *Amphiorycteropus*. A precise identification would require further study of the specimen, which I cautiously refer to *A.* cf. *gaudryi* in the meantime.

SPECIES *AMPHIORYCTEROPUS ABUNDULAFUS* (LEHMANN *ET AL.*, 2005)

Emended diagnosis: Middle-sized species of *Amphiorycteropus* (about 70% of the general size of the extant aardvark) that is distinct from the other species of that genus: by its long mandibular symphysis (about 21% of total length), its very broad molars (robustness index of $M_2 > 80\%$), the absence of a lateral projection of the deltoid crest, and the slender distal epiphysis on its humerus.

Remarks: This diagnosis resumes the original and emended ones given by Lehmann *et al.* (2005, 2006) less the features described in the diagnosis of the genus. According to Lehmann *et al.* (2005: 114), the mandibular symphysis of *A. abundulafus* represents 20.8% of the length of the mandible in the holotype. A similar ratio has been calculated for *O. afer* ($n = 55$): it shows that in the extant aardvark the symphysis only represents 17.43% ± 1.53 of the length of the mandible. This ratio is 19.6% for the holotype of *O. crassidens*. Unfortunately, no other fossil taxa show a complete symphysis so far. Therefore, this character is maintained in the diagnosis until more material is discovered. The robustness index compares the maximum breadth and length of the molars. Lehmann *et al.* (2006: table 2) showed that this index was especially high for the lower molars of *A. abundulafus*, but was even more significant for the M_2.

Holotype: KB03-97-214, a sub-complete skeleton of a subadult individual (having reached adult size) discovered in anatomical connection; housed at the CNAR, N'Djaména.

Type locality: KB03 site, Kossom Bougoudi, Djurab desert (GPS: 16°19′–16°20′N, 18°42′–18°43′E) (Chad).

Main occurrences: Type locality and Toros-Menalla fossiliferous sector, Djurab desert (Chad).

Age: Late Miocene; 7 to 5 Ma.

Remarks: The fossiliferous sector of Kossom Bougoudi (hereafter referred to as KB) is dated to around the Mio-Pliocene boundary (Brunet & MPFT, 2000), *c.* 5–5.5 Mya. The evolutionary degree of the mammal assemblage (bovid, anthracotheriid, etc.) from the Toros-Menalla sites (hereafter referred to as TM) yielding aardvarks is similar to that of the 'anthracotheriid unit' defined by Vignaud *et al.* (2002), and is thus *c.* 7-Myr old.

Additional material: Subcomplete and partial skeletons (TM112-00-100; TM255-01-02; TM255-03-01; TM259-02-15; TM266-05-40; TM266-05-55), cranial remains (TM250-01-01; TM266-03-363), femurs (TM92-99-01; TM266-01-89), a radius, and associated elements of hands and feet (TM215-01-130–TM215-01-139), ankles in anatomical connection (TM90-03-20; TM92-01-15), and an isolated metacarpal (TM90-03-14); all housed at the CNAR, N'Djaména.

Discussion: The material attributed to the species *A. abundulafus* includes one very young individual: the almost complete skeleton TM112-00-100. All of the remaining specimens are mainly adults and subadults (like the holotype). This material enabled Lehmann *et al.* (2006) to confirm that the holotype had reached adult size at time of death.

Although a distinct deltoid tuberosity is present on its humerus, there is no prominent and laterally projected deltoid crest in *A. abundulafus*, but instead there is a superficial line. This crest is strong in all other Orycteropodidae except in *L. guilielmi*. Nonetheless, the ventral aspect of the diaphysis of the humerus is flat on its proximal third in *A. abundulafus*, whereas it is rounded in *L. guilielmi*. This difference results from the ventral position of the pectoral crest on the shaft in *L. guilielmi*. Conversely, in *A. abundulafus* and in all other Tubulidentata the pectoral crest is medial to the diaphysis, and forms a flat part with the deltoid crest (or deltoid line in *A. abundulafus*). Although the morphological configuration is somewhat different in *A. abundulafus* and *L. guilielmi*, the weak development of their deltoid crests implies the reduction of the moment arm for the action of the deltoid muscle in both species. The energy expenditure is thus less efficient than for the other Orycteropodidae. In this regard, the acromion process on the scapula (surface of insertion for the deltoid muscle) of *A. abundulafus* is weakly developed, and suggests a deltoid muscle that is rather less important than in other Orycteropodinae. This is best seen when comparing the ratio between the maximum length of the glenoid cavity and the maximum breadth of the acromion process: 88.2% ± 8 in *O. afer* ($n = 31$), 99.4% in the holotype of *M. africanus*, and only 66.8% in the holotype of *A. abundulafus*.

All Tubulidentata specimens discovered at TM are consistent with each other in terms of morphology and size. However, these specimens are biometrically closer to each other than to the holotype of *A. abundulafus* found at the younger KB sector. In fact, the TM specimens display smaller dimensions for their skull, teeth, and, perhaps, elements of the hand than the KB specimen. A similar pattern has been observed at Samos (Greece) for the upper teeth of the species *A. gaudryi* (Sondaar, 1971). Nonetheless, these differences do not justify a species distinction, as all specimens from KB and TM display the discrete diagnostic characters of *A. abundulafus*.

SPECIES *AMPHIORYCTEROPUS BROWNI* (COLBERT, 1933)
(= *ORYCTEROPUS PILGRIMI* COLBERT, 1933)

Emended diagnosis: Small-sized species of *Amphiorycteropus* that can be distinguished from the other species of the genus by the position of its postpalatine foramina at the level of the M^2, and by the root of the zygomatic arch starting at the level of the mesial lobe of the M^2.

Holotype: AMNH 29840, a fragment of left maxilla with M^2 and M^3 of a young individual; housed at the AMNH, New York.

Type locality: Locality 108 of Brown, 1 km south of Nathot (GPS: 32°85′N, 73°21′E), Potwar Plateau (northern Punjab, Pakistan).

Main occurrences: Hasnot, Mathrala, as well as Malhuwala (close to Dhok Pathan), and another imprecise locality (Kamlial or Chinji) on the Potwar Plateau (northern Punjab, Pakistan).

Age: Middle to Late Miocene.

Remarks: The holotype has been found at the base of the Nagri formation, dated to between 11.2 and 9 Mya (Barry *et al.*, 2002). According to Barry *et al.* (2002: appendix 4), the presence of Orycteropodidae is inferred from 14 to 8.1 Mya. Nonetheless, this range includes unpublished specimens and also a 'second very small species of aardvark [. . .], the stratigraphic distribution of which appears to be older than that of [*A.*] *browni*.' (Pickford, 1978: 39), so that additional work on that material is required before assessing an accurate age range for *A. browni* (see below for further details about this second species).

Additional material: Fragments of cranium and mandible (YPM 13901), housed at the Yale Peabody Museum, Yale, USA; isolated left M^1 (AMNH 29997) and right maxilla with M^1–M^3 (AMNH 29999), housed at the AMNH, New York; left metacarpal IV (GSP 11604); mandible fragment with M_2 and M_3 (GSI K13/322) housed at the Calcutta Museum (?).

Remarks: The specimen YPM 13901 could not be found in the collections; instead, I worked on a cast (AMNH 27820). Unfortunately, this cast lacks the mandible and other details. The specimens GSP 11604 and GSI K13/322 (Geological Survey Pakistan and India, respectively) are not housed at the AMNH, and are probably housed in India or Pakistan. The specimen AMNH 29999 described by Pickford (1978) is in fact a cast. This explains why the author (Pickford, 1978: 42) also described 'A right maxilla of very doubtful provenance [. . .] also preserved in Calcutta. It is so similar to [AMNH] 29999 that I thought initially that the American Museum specimen had been donated to the Calcutta Museum'. Moreover, this confusion invalidates the following argument given by Pickford (1978: 41) about a 'strange feature anterior to the M^1', namely that 'It is unlikely that this surface arose merely as an accident of preservation or of damage, as the specimen in Calcutta is virtually identical with that in the American Museum'. The feature might be of taphonomical origin, but it is rough on the cast, and could not be accurately interpreted.

Discussion: As explained before, '*O. pilgrimi*' is considered here as a synonym of *A. browni*. The former holotype of '*O. pilgrimi*' (AMNH 29997) has been successively described as a right M_2 (Colbert, 1933), an M^2 (Lewis, 1938), and an M_2 or an M_1 (Pickford, 1978). The latter author pointed out the mistakes made by Lewis. The study of this tooth shows a curvature along its height (concave on the vestibular side), a flat occlusal surface, subequal lobes, and a shallower lingual groove. These features are very similar to those of the M^1 observed on the cast of YPM 13901. Moreover, the curvature is generally an upper tooth character, and the occlusal surface confirms that the individual was adult (or at least teenager). Therefore, I suggest that the specimen AMNH 29997 is in fact a left M^1. In this hypothesis, the differences between *A. gaudryi* and '*O. pilgrimi*' given by Colbert (1933: 6) – 'straighter [. . .] anterior and posterior edges, and a slightly shallower groove on the lingual side' – fall, and describe rather the diagnostic characters of the genus *Amphiorycteropus*.

Colbert (1933: figs 3, 4) performed several histological sections on the teeth (M^2) of *A. browni* and *A. gaudryi*. This author suggested that the two species diverged for the size of their tubules. However, the tubules compared are not homologous because they are taken from different parts of the tooth section. Lewis (1938: 404) already noticed this problem.

> 'The histological peculiarities of the teeth of [*A.*] *browni* may be due to the location of the section. The writer found that there is histological variation related to the relative distance between the occlusal surface and the proximal growing surface in the molars of *Orycteropus*, and also to the transverse position between the centre and periphery of the tooth. Tangential and radial diameters of the tubules are of little significance unless the position of the tubules is designated, inasmuch as peripheral tubules have greater tangential than radial diameters, medial tubules have greater radial than tangential diameters. Moreover, there appears to be a definite zonation of tubules as to size, the peripheral, central, and medial tubules being increasingly larger in this order.'
>
> (Lewis 1938: 404)

Furthermore, in extant juvenile individuals, the tubules tend to display a more heterogeneous size and shape than in adults (Anthony, 1934). Likewise, the thickness of the wall of these tubules appears to be thicker in juveniles than in adults for a comparable section. In this respect, the dissimilarities observed by Colbert (1933) should be taken with reserve.

The illustration of the specimen YPM 13901 in Lewis (1938): plate 1) presents a mandible in association with the cranium. On this figure, the reconstruction of its right hemimandible suggests an angle between the mandibular rami close to 80°. If this feature is confirmed on the original specimens, it would support the membership of this species to the genus *Amphiorycteropus*. Among this genus, *A. browni* is closer to *A. abundulafus* and *A. gaudryi* than to *A. depereti* and *A. mauritanicus*, for its size.

SPECIES *AMPHIORYCTEROPUS DEPERETI* (HELBING, 1933)

Emended diagnosis: Large species of *Amphiorycteropus* (80% of the size of the extant aardvark for the cranium) with the following deviating features: the absence of a palatine groove, the ventralmost point of the maxillojugal suture caudal to the M^3, a large insertion surface for the Masseter muscle on the zygomatic process of the jugal, and an oblique intracuspal rim on the M^2.

Remarks: The tip of the snout of *A. depereti* is broken, so that the proportion of the palate cannot be calculated and compared with the other species. Nonetheless, the general dimensions of the cranium suggest that, unlike the other species of *Amphiorycteropus*, the palate of *A. depereti* was rather broad. Arambourg (1959) and Patterson (1975) already noted this peculiarity.

Holotype: Rss 55, a complete cranium; housed at the Naturhistorisches Museum, Basel (Switzerland).

Type locality and age: Perpignan (R. & J. Briquetterie Chefdebien, rue de l'Espagne, France). This site is dated from the Early Pliocene, MN15 (Rook & Masini, 1994).

Main occurrences: Type locality only.

Discussion: In *A. depereti*, the intracuspal rim (see Lehmann *et al.*, 2005: 116) is slightly oblique on the M^2, whereas on the M^1, a crest joining the mesial lobe (vestibular side) to the distal one (lingual side) is visible. This crest is probably not an intracuspal rim, as it connects the two lobes. Such a feature is also somewhat observed on the lower molars of the holotype of aff. *A. pottieri*. This is distinct from the situation observed in *A. mauritanicus*, where the intracuspal rims are oblique on the M^1 but transversal on the M^2. Furthermore, the oblique rim on the M^1 of the Algerian aardvark is restricted to the distal lobe of the molar unlike in *A. depereti*.

Amphiorycteropus depereti is the last known species of the genus *Amphiorycteropus*, as well as the last representant of the order Tubulidentata from Eurasia so far. Nonetheless, the cladistic analysis suggests that the French aardvark is in a basal position in its genus. This would imply that *A. depereti* is not the last offshoot of the *Amphiorycteropus* radiation, but is rather the earliest, thereby suggesting a long and undocumented evolutionary history for this species (ghost lineage) extending back to the Upper Miocene. The scarcity of material for *A. depereti* (one cranium) precludes reliable conclusions. The post-cranial elements of that taxon may bear important information. Its inclusion in the genus *Amphiorycteropus* seems, however, certain.

SPECIES *AMPHIORYCTEROPUS MAURITANICUS* (ARAMBOURG, 1959)

Emended diagnosis: Large-sized species of *Amphiorycteropus* (85–90% of the general size of the extant aardvark) that can be distinguished from the other species of the genus by its broad, long, and flat tibial tuberosity, and its very long metatarsals I and V. Furthermore, the longest teeth of its tooth-rows are M_1 and M^1, respectively (resulting in a low robustness index for the M1); the vestibular groove on the upper molars is very deep, and the intracuspal rims on the M^1 are oblique.

Holotype: MNHNP 1951-9-257, a sub-complete cranium; housed at the MNHN, Paris.

Paratype: MNHNP 1951-9-258, a partial left hemimandible.

Remarks: Arambourg (1959) did not indicate if the mandible belongs to the cranium.

Type locality and age: Bou Hanifia 1, near the Ouel el Hammam river (Algeria). This site is dated from the Late Miocene, at around 10.85-Mya (Sen, 1986, 1990).

Main occurrences: Type locality only.

Additional material: A partial right hemimandible (MNHNP 'Spécimen de Suess'); elements of a left hindlimb (tibia, fibula, and tarsals to phalanx) from a single adult individual (MNHNP 1951-9-259; MNHNP 1951-9-260; MNHNP 1951-9-261; MNHNP 1951-9-268; MNHNP 1951-9-271; MNHNP 1951-9-272; MNHNP 1951-9-286, and other phalanges, the labels of which are illegible); partial tibia of a juvenile individual (MNHNP 1951-9-277); proximal phalanx II of the left hand (MNHNP 1951-9-293); proximal epiphyses of the right metacarpals III and IV (MNHNP – illegible).

Remarks: Arambourg (1959) originally described these additional specimens along with the types. However, according to the ICZN (Art. 72.4.6.), as the author did specifically name a holotype and a paratype, the other described specimens are excluded from the type series. The reference number of the talus MNHNP 1951-9-271 is inferred, as the last digit is illegible on the fossil. This reference number is consistent with the original description made by Arambourg (1959: 42): 'un tibia avec tarse en connexion (n^{os} 259, 260, 271, 272)'.

Discussion: A. mauritanicus has often been quoted and used as a comparison taxon in papers dealing with fossil Tubulidentata. Nonetheless, this taxon has not been the object of an extensive study since its original description made by Arambourg (1959). This can be explained by the fact that the fossil material was not accessible for a long period of time (actually, up until May 2004). Most of the authors must have therefore based their analyses on the illustrations and description given by Arambourg (1959) only. This is why some misinterpretations have been carried on until recently, as shown for instance for the tibia by Lehmann *et al.* (2004: 211). Another misinterpretation concerns the talus of *A. mauritanicus*. Arambourg (1959: 48) found the talus of *A. gaudryi* and *A. mauritanicus* to be very similar, except for 'la plus grande longueur totale due au développement plus accentué encore du col et de l'apophyse scaphoïdienne hémisphérique' in the Algerian fossil aardvark. Several authors (Patterson, 1975; Rook & Masini, 1994) followed this description, and considered it to be a diagnostic character of the species: 'The rather narrow astragalus has a relatively longer neck than that of any other orycteropodid in which this bone is known' (Patterson, 1975: 201). However, my direct observation of the talus (MNHNP 1951-9-271) revealed that a fragment of the navicular is still attached to the distal condyle of the talus, and thus artificially increases the length of the talus neck. The true length (proximodistally) of the talus can only be estimated (29.2 mm), but is now relatively comparable with that of the other species of *Amphiorycteropus*.

Amphiorycteropus mauritanicus is the oldest known African species from the new genus *Amphiorycteropus*. van der Made (2003: 139) considered that this species originated in Europe (or even that it was a synonym of aff. *A. pottieri*) and returned to Africa on the basis that 'no possible Late Early or Middle Miocene African ancestral form is known'. Indeed, *A. mauritanicus* does not show any close relationships with the genus *Myorycteropus*. However, the presence in Africa of the undetermined specimens from Rooilepel and Saitune Dora (see below) suggests an earlier presence in Africa for the genus *Amphiorycteropus*. This data is not yet sufficient to ascertain the origin of the genus on that continent, and nor does it completely contradict a possible European origin for *A. mauritanicus*. Nonetheless, this study provides arguments against the synonymy of *A. mauritanicus* and aff. *A. pottieri*. van der Made (2003: 139) thought that 'the available material [of *A. mauritanicus*] does not seem to present important differences with [aff. *A.*] *pottieri*'. Indeed, the two taxa share trapezoid upper molars (a diagnostic apomorphy of *Amphiorycteropus*), as well as the V-shaped nuchal line on the cranium and the short tibial crest, which are two features that are in a different state in the species of the genus *Orycteropus*. However, *A. mauritanicus* differs from the European species by the following derived characters: the shallow lingual groove on its upper molars, the absence of canines, and the fact that the longest teeth of its tooth rows are M_1 and M^1, respectively. Therefore, the two taxa cannot be synonyms (contra van der Made, 2003).

The general size and age of *A. mauritanicus* challenge the classical hypothesis of a gradual increase in size over time for the Tubulidentata taxa (e.g. Patterson, 1975; Pickford, 1975; van der Made, 2003). Indeed, the Vallesian *A. mauritanicus* is about 10% smaller than the extant species, but is larger than the Turolian *A. abundulafus*, *A. gaudryi*, and *L. guilielmi*. Moreover, according to the present study, *A. mauritanicus* belongs to a different genus, and thus a different lineage from the extant aardvark. In *Amphiorycteropus*, the oldest known species, *A. browni* was the smallest species of its genus. Although their phylogenetical relationships are not yet resolved, this species is chronologically followed by *A. mauritanicus*, the largest taxa of the genus. The size decreased again with *A. abundulafus* and *A. gaudryi*, but eventually, *A. depereti* showed a large general size again. Likewise, in the genus *Orycteropus*, the classical trend is not confirmed. First, *O. djourabensis* had a similar-sized skull but shorter limbs than *O. afer*, and then *O. crassidens* was slightly larger than the extant aardvark. It actually appears that the evolutionary history of the order Tubulidentata is more complex than just a general trend towards larger animals.

SPECIES *AMPHIORYCTEROPUS* SP. ROOILEPEL

Material (the specimens have not been directly seen by the author): Elements of a skeleton (RL 4′95) with fragment of mandible, parts of a femur, a tibia, a talus, vertebrae, and phalanx; the distal epiphysis of a metatarsal bone (RL 37′95); and a fragment of a left mandible (RL 43′95), described by Pickford (1996) as '*Orycteropus* cf. *minutus*'. The material is housed at the National Earth Science Museum, Windhoek (Namibia).

Locality and age: The specimens have been found at Rooilepel, close to the Orange River (GPS: 28°17′56″S, 16°35′01″E) (Namibia). Pickford (1996) wrote that the fossil aardvarks have been found in three different stratigraphic levels: 15–14 Mya, 12–11 Mya, and 11–10 Mya, but did not specify in which unit each specimen has been found.

Discussion: The isolated mandible and metatarsal are too fragmentary to enable a reliable identification, and could be placed in Orycteropodidae sp. indet. Nonetheless, they are tentatively associated with the more complete specimen RL 4′95, which shows some remarkable features. No molars are known, but some premolars of unknown position are still present in the mandible. Their size (after Pickford, 1996) is larger than that of the premolars found in Arrisdrift (see below), is close or slightly larger than that in *Myorycteropus* (P_3 and P_4), and is close or slightly smaller than the size of the P_2 and P_3 in *Amphiorycteropus*. Unfortunately, there are no premolars known for aff. *M. minutus*, so far. The Rooilepel premolars are more or less intermediate between *Myorycteropus* and *Amphiorycteropus*. The size of the premolars is nonetheless of only limited value for the identification of the specimens. The talus of that specimen presents, according to Pickford (1996: fig. F), a concave and developed cotyloid facet for the medial malleolus of the tibia. This feature alone helps us to distinguish these specimens from *Myorycteropus*, which shows the derived state for that character (vertical and negligible facet). Therefore, the Rooilepel aardvarks are cautiously attributed to the genus *Amphiorycteropus*, but remain undetermined at the species level until further material is discovered. Pickford (1996) also reported parts of the femur and tibia for that specimen, but only described them briefly. A revision of these elements might give us new clues for the identification of these Namibian aardvarks.

SPECIES *AMPHIORYCTEROPUS* SP. SAITUNE DORA

Material: A sesamoid bone (STD-VP-2/855) and a fourth intermediate phalanx of the foot (STD-VP-2/856), described by Lehmann (2008a) as *Orycteropus* sp. The material is housed at the National Museum of Ethiopia, Addis Ababa.

Locality and age: Saitune Dora (Middle Awash, Ethiopia) from the Asa Koma Member (Adu-Asa Formation) dated from Late Miocene, between 5.77 and 5.54 Mya (WoldeGabriel *et al.*, 2001).

Discussion: Lehmann (2008a) noticed that the material from Saitune Dora appeared to be 'closer to the Late Miocene Chadian [*A.*] *abundulafus* and

European [*A.*] *gaudryi* than to the Plio–Pleistocene West African forms [from the genus *Orycteropus*, n.d.]'. Moreover, the dimensions of these bones are distinct from those of *Myorycteropus*. In consequence, I tentatively refer these Ethiopian specimens to the genus *Amphiorycteropus*.

GENUS AFF. *AMPHIORYCTEROPUS*

SPECIES AFF. *AMPHIORYCTEROPUS POTTIERI* (OZANSOY, 1965)

Emended diagnosis: Orycteropodinae species of medium size (70% of the general size of the extant aardvark), which shares the following diagnostic features with *Amphyorycteropus* taxa: the V-shaped nuchal line on the cranium; a craniomandibular articulation presenting a tubercle on the cranial articulation surface, as well as a concave facet on the mandible; and upper molars that are trapezoid in shape. It also displays the derived mandibular angle between the rami ranging from 60° to 73° of the *Orycteropus* taxa. Moreover, this species is characterized by: the important diastema between the premolars; the rectangular outline of the lower molars (whereas the upper ones are trapezoid); the presence of subequal and deep lingual and vestibular grooves on the upper and lower molars; the short cumulated length of the upper molars; the mandibular symphysis extended backwards, starting between C and P_1; the broad mandibular condyle situated relatively low on the vertical ramus of the mandible, with regard to the lower tooth row; the proximodistally elongated talus; and the presence of a concave and developed cotyloid facet for the medial malleolus of the tibia on the talus. Additionally, aff. *A. pottieri* presents characters that are plesiomorphic for Tubulidentata: the presence of canines; temporal lines situated high on the cranium; the absence of an incisura mandibulae; and the short tibial crest.

Remarks: On the ulna published by de Bonis *et al.* (1994), the orientation of the articulation axis of the semilunar notch seems to be rather perpendicular to the diaphysis, as in *O. afer* and *O. crassidens*. However, the semilunar notch is broken on that specimen, so that this character state can only be estimated until more material is examined directly. The lower M_1 and M_2 of the holotype of aff. *A. pottieri* show transversal intracuspal rims, but also show an oblique crest connecting the mesial and distal lobes. As in *A. depereti*, this feature is certainly not an intracuspal rim (*sensu* Lehmann *et al.*, 2005). In aff. *A. pottieri*, the crest joins the medial lobe (lingual side) to the distal lobe (vestibular side), a reversed situation to that in the French fossil aardvark. Moreover, on the vestibular side of that crest, a shallow groove is visible. This unique character is probably related to a specific wear pattern in aff. *A. pottieri*. Nevertheless, I have directly observed this feature solely on the holotype so far, and further studies on the material are thus required before determining if this is a diagnostic character.

Holotype: MNHN TRQ 1003, a right hemimandible with lower C and P_3–M_3; housed at the MNHN, Paris.

Type locality: Yassiören, in the Sinap Formation (Turkey).

Main occurrences: Pentalophos 1 (Greece) and Sinap Formation (Turkey): localities 12, 72, and 108.

Age: Late Miocene (Vallesian). The sites from the Sinap Formation have been dated to between 10.9 and 8.1 Mya (in particular, localities 12, 72, and 108 have been dated to between 10.1 and 9.6 Mya) (Kappelman *et al.*, 2003).

Additional material (these specimens have not been directly seen by the author): Elements of the cranium (AS.91.423; AS.91.424), fragment of mandible (AS.94.202), isolated molars (AS.92.580; AS.92.581), a fragment of scapula (AS.92.579), and isolated metapodes and phalanges (AS.91.356; AS.91.366; AS.91.415; AS.94.241; AS.94.282; AS.95.176; AS.95.251; AS.95.578; AS.95.700) housed at the Museum of Anatolian Civilizations, Ankara, according to Fortelius *et al.* (2003). A partial cranium (PNT-130), fragments of right and left maxilla from a single individual (PNT-127), right hemimandibles (PNT-128; PNT-129), fragments of humerus (PNT-19; PNT-135), right ulna (PNT-72), left femur (PNT-73), fragment of tibia of a juvenile individual (PNT-?), right talus (PNT-132), associated (?) metacarpals (PNT-61; PNT-62; PNT-63), and isolated phalanx (PNT-64; PNT-133; PNT-134), housed at the Museums of the Aristotle University of Thessaloniki (Greece).

Discussion: The mandibular symphysis starts between the C and the P_1 in the holotype of aff. *A. pottieri*, whereas it starts between the P_1 and the P_2 in *Leptorycteropus*, and starts more rostrally in other Orycteropodidae (at least 10 mm mesially from the P_1 in *Amphiorycteropus* species). The configuration found in aff. *A. pottieri* and *Leptorycteropus* suggests that their symphysis is longer than in the other Tubulidentata, or that their mandible, and so their snout, is shorter. In the former hypothesis, a longer symphysis would strengthen the attachment between the two hemimandibles. In this regard, it is remarkable that these two species are the only Tubulidentata to possess canines, which need a well-built skeletal structure to be active. Likewise, there is a vestibular swelling of the maxilla (respectively, the mandible) at the level of the canine in aff. *A. pottieri* and *Leptorycteropus*. The extension of the maxilla and mandible in front of the canine are not known. Therefore, we cannot yet test the second hypothesis of a shorter snout in aff. *A. pottieri*. The few length measurements available on the fragments of skull show a size close to that of *A. gaudryi* (included in the intraspecific variation range of that species), but shorter than in *A. depereti*.

As explained previously, aff. *A. pottieri* has been tentatively referred to the new genus. This conclusion is in accordance with Pickford (1975), who included '*Orycteropus pottieri*' in his '*O. gaudryi* group' that is roughly equivalent to *Amphiorycteropus* in this work. Conversely, Fortelius *et al.* (2003: 198) suggested that '[aff. *A.*] *pottieri* appears to be quite similar to recent aardvarks [. . .] The differences between [*A.*] gaudryi and *O. afer* seems to be considerably greater . . .'. According to the present cladistical analysis, aff. *A. pottieri* shows indeed more characters in common with *O. afer* than *A. gaudryi* (like the rectangular shape of the lower molars, the presence of a deep lingual groove on the molars, and the same mandibular angle). Nonetheless, a higher number of matching apomorphic features brings together the Turkish species and *Amphiorycteropus*. Until a direct study of the available material from the Sinap Formation can be performed, this identification is maintained.

SPECIES AFF. *AMPHIORYCTEROPUS* CF. *POTTIERI* SINAP

Material (the specimens have not been directly seen by the author): A fragment of metapodial (AS.92.413) and a fragment of distal phalanx (AS.95.1011).

Locality and age: Locality 46 and 49 (respectively) of the Sinap Formation (Turkey). The magnetostratigraphic age estimate for locality 49 is 9.1-Myr old (Kappelman *et al.*, 2003).

Discussion: Fortelius *et al.* (2003) described these specimens and referred them to '*Orycteropus* sp.', given their fragmentary state. Nonetheless, these authors (Fortelius *et al.*, 2003: 198) also remarked that 'faunally, Loc. 49 is very similar to Pentalophos I', which yielded aff. *A. pottieri* specimens. On this basis, and because the genus attribution is still uncertain, I recommend placing these specimens in aff. *A.* cf. *pottieri*.

SPECIES AFF. *AMPHIORYCTEROPUS SENI* (TEKKAYA, 1993)

Emended diagnosis: Orycteropodinae species of medium to small size that concurrently shares the derived mandibular angle ranging from 60° to 73° of *Orycteropus*, and the trapezoid molars of *Amphiorycteropus*. Moreover, this species is unique for the shallow lingual groove on the lower molars, and the relatively short metatarsal II.

Holotype (the specimen has not been directly seen by the author): MTA 2532, a right hemimandible with M_1–M_3, housed at the MTA, Ankara.

Remarks: the holotype is a right hemimandible, as described originally by Tekkaya (1993), and not a left hemimandible (van der Made, 2003).

Type locality and age: Çandir (Turkey). Middle Miocene (MN6): from 15.2 to 12.5 Mya (van der Made, 2003).

Main occurrences: Type locality only.

Additional material (the specimen has not been directly seen by the author): Right metatarsal II (MTA AÇHÜ 1063) housed at the MTA, Ankara.

Discussion: This taxon is the oldest species of Tubulidentata known from Eurasia, so far. It preceded aff. *A. pottieri* (Turkey) and *A. browni* (Pakistan). The relationships between these species are, however, not clear. From the fragmentary material at hand, one can suggest a relationship with aff. *A. pottieri* because they improbably share two characters states found in *Orycteropus* on the one hand, and in *Amphiorycteropus* on the other hand. The only remarkable differences between the two species, so far, are the absence of a lingual groove and the trapezoidal shape of the lower molars in aff. *A. seni*. In his diagram showing possible ancestor–descendants relationships, van der Made (2003: fig. 4) suggested that aff. *A. seni* might be the ancestor of aff. *A. pottieri*. Conversely, Fortelius *et al.* (2003: 198) noted that, in the Sinap Formation, 'it is clear that two temporally successive taxa can be distinguished [. . .] *Orycteropus pottieri* seems to replace *O.* cf. *O. seni* without overlap or evolutionary change'. This material tentatively associated with the Çandir species is described hereafter. The two successive taxa could be aff. *A. seni* and aff. *A. pottieri*, but further material for the former species is required to confirm the existence of a relationship. Regarding *A. browni*, aff. *A. seni* presents at least one derived character that the Pakistani species does not share: the mandibular angle ranging from 60° to 73°. According to the present analysis, the Turkish aardvark, although older, is thus unlikely to be the ancestor of *A. browni*. Nonetheless, the material of both taxa is too fragmentary to resolve their relationship yet.

Tekkaya (1993) also described a proximal phalanx from Inönü (no references, but housed at the MTA, Ankara), aged between 15–16-Myr old (Kappelman *et al.*, 2003), which he could not determine at the species level and referred to '*Orycteropus* sp.' van der Made (2003) suggested that this specimen probably belong to aff. *A. seni*. This material is certainly too fragmentary for an accurate identification, and a direct examination is required.

SPECIES AFF. *AMPHIORYCTEROPUS* CF. *SENI* SINAP

Material (the specimens have not been directly seen by the author): A right M^2 (AS.92.23), a left M^3 (AS.92.810), and a right P_4 (AS.92.23), described by Fortelius *et al.* (2003) as '*Orycteropus* cf. *O. seni*'.

Locality and age: All the specimens come from locality 64 from the Sinap Formation, aged around 10.8-Myr old (Kappelman *et al.*, 2003).

Discussion: Fortelius *et al.* (2003: 198) suggested that because aff. *A.* cf. *seni* 'has asymmetrical upper molars of the usual Eurasian type, [it] could be the basal taxon of the main clade of Eurasian aardvarks, including at least [*A.*] *gaudryi* and [*A.*] *depereti*'. According to the results of the present study, this could be reformulated as aff. *A.* cf. *seni*, which could be the basal taxon of *Amphiorycteropus*. Unfortunately, this hypothesis cannot be tested until further material is discovered.

SPECIES AFF. *AMPHIORYCTEROPUS* CF. *SENI* PAŞALAR

Material (the specimens have not been directly seen by the author): A cheek tooth (1968 VI 795) housed at the Bayerische Staatssammlung für Paläontologie und historische Geologie, München (Germany); a left M^1 or M^2 (?) (G1206), a right M^1 or M^2 (?) (G1207), a fragment of metapodial (G1514), and a third tarsal phalanx (G74), described by Fortelius (1990) as '*Orycteropus* sp.'

Locality and age: Paşalar (Turkey). Middle Miocene (MN6: from 15.2 to 12.5 Mya) (Fortelius, 1990).

Discussion: Gabunia (1956) described a specimen from Belometchetskaya (Russia) as '*Orycteropus* sp.'. van der Made (2003) considered it to be of dubious identity, or not even a Tubulidentata at all (J. van der Made, pers. comm.). If this hypothesis is confirmed, the material from Paşalar is then the oldest record of Tubulidentata remains in Eurasia. Fortelius *et al.* (2003) and van der Made (2003) suggested that the Paşalar material was close to aff. *A.* cf. *seni* from Sinap, and to the species aff. *A. seni*, respectively. Indeed, the molars discovered at Paşalar show a shallow lingual groove and a trapezoidal shape, as in aff. *A. seni*, but unlike aff. *A. pottieri*. Nonetheless, all species from the genus *Amphiorycteropus* share these features. From the illustration given by Fortelius (1990: fig. 1), the molar G1206 could also be a lower molar. If this hypothesis were confirmed, the characters given above would clearly identify this tooth as belonging to aff. *A. seni*. Direct observation of the specimen is necessary for a more accurate determination. In the meantime, these specimens are referred to aff. *A. seni*.

GENUS *LEPTORYCTEROPUS* PATTERSON, 1975

Emended diagnosis: Medium-sized Orycteropodidae with the following autapomorphies: mandibular symphysis extended backwards, starting between P_1 and P_2; pubis oriented medioventrally. It can also be distinguished from the other Orycteropodidae by the combination of the following characters: presence of canines; absence of palatine groove; weak deltoid crest, not projected laterally, olecranon fossa triangular in shape, and slender distal epiphysis on the humerus; sharp oblique rim on the radius; sciatic notch positioned at the level of the acetabulum; sacrum formed by five sacral vertebrae; articular facet for the sesamoid bone of the gastrocnemius muscle at the level of the diaphysis on the femur; absence of a falciform process, as well as presence of an uninterrupted rim of bone between the tibial tuberosity and the fibula on the proximal epiphysis of the tibio-fibula; and a long tibial crest.

Remarks: Different species of aardvark have been described to possess canines: *A. depereti*, *A. mauritanicus*, aff. *A. pottieri*, and *L. guilielmi*. Presumed canines have also been observed in the craniums of juvenile individuals of *O. afer*, but they consist of small rounded dentine masses, and do not pierce the gum. However, as suggested by Lehmann *et al.* (2005: 126): '[*A.*] *depereti* and [*A.*] *mauritanicus* display supernumerary premolars and not canines', as can be observed in the extant form. I consider that a real canine in Orycteropodidae is a large antemolar tooth in front of, and separated from by a diastema, a decreasing (in size) premolar row. Additionally, the maxilla (and, respectively, mandible) shows a slight bulge on the vestibular side of this canine. The general size of *Leptorycteropus* is estimated according to the dimension of the pelvis, which is the sole complete post-cranial element of the hypodigm. The length of the ilion in *L. guilielmi* is about 60% that of its counterpart in *O. afer*.

Type species: Leptorycteropus guilielmi Patterson, 1975.

Geographic distribution: Lake Turkana basin (Lothagam Hill, Kenya).

Temporal distribution: Late Miocene, between 7.4 and 6.5 Mya.

Remarks: This genus is monospecific and known from only one site (Lothagam) so far.

SPECIES *LEPTORYCTEROPUS GUILIELMI* PATTERSON, 1975

Diagnosis: Same as for the genus.

Holotype: KNM-KP 419, partial skeleton; housed at the NMK, Nairobi.

Remarks: The holotype bears a reference number associated with the site of Kanapoi (KP), but it has actually been found in Lothagam (fossil usually labelled LT).

Type locality and age: Lothagam 1, Lothagam Hill, Lake Turkana basin (Kenya). The holotype has been found in the Member B, which corresponds to the Lower Nawata Formation dated to between 7.4 and 6.5-Mya (Leakey & Harris, 2003).

Main occurrences: Type locality.

Additional material: Only some fragments of a femur (KMN LT 28573) have been additionally found in the Lower Nawata Formation of the Lothagam site (Milledge, 2003), and these are housed at the NMK, Nairobi.

Discussion: Patterson (1975: 201) insisted that *L. guilielmi* 'was the most generalized member of the family so far known', and was primitive in various features. Indeed, this author suggested that no osteological structures of the cranium could be associated with a specialized mymecophagous diet. Patterson (1975) quoted, for instance, the well-developed temporal fossa, post-orbital process, and jugal. Furthermore, he considered that the facial region was short, and that 'a rather large canine is present, together with a full complement of cheek teeth', which is the common eutherian condition (Patterson, 1975: 223). First, it is difficult to estimate the development of the temporal fossa on the very fragmentary material. Then, the reduction of the snout and mandible length cannot be confirmed. In fact, in all Orycteropodidae, the teeth are mainly restricted to the rear of the maxilla and mandible. The foremost tooth (canine for aff. *A. pottieri* or premolar for the other species) is then preceded by a long diastema, until the tip of the premaxilla and mandible. The maxilla and mandible of *L. guilielmi* are broken in front of the canine, so that it is not possible to tell the extent of the diastema and whether this species possessed frontal teeth. On the other hand, the mandible presents a symphysis extended backwards that almost reaches the P_2. This can be interpreted as 'an extensive, firm symphysis' (Patterson, 1975: 223), consistent with active canines, or as a normal-sized symphysis shifted backwards because the snout is actually short. Note that in aff. *A. pottieri* the symphysis starts just behind the canine, whereas in *Orycteropus*, as well as in the new genus, the symphysis is situated well in front of the foremost premolar. The presence of both a canine and a firm symphysis is necessary but not sufficient to conclude that *L. guilielmi* used his canines actively. Moreover, in mammals, canines are not only used for the food intake process, but can also be a sexual character (although this is unlikely to be the case here, with respect to the feeble sexual dimorphism shown by the extant aardvark). Therefore, it seems more sensible to merely hypothesize that this species was not a specialized myrmecophagous animal.

The post-cranial elements, on the other hand, reveal more about the habits of *L. guilielmi*. For instance, Patterson (1975: 223) noticed that: 'The limb bones indicate an animal capable of digging but not highly specialized for it'. Indeed, *L. guilielmi* is unique among Orycteropodidae for the structure of its humerus, in particular for the absence of a well-developed deltoid crest and the presence of a strong ventral pectoral crest (see also the discussion for *A. abundulafus*). Moreover, if the femur is rather similar to the one in other taxa (but also see remarks), its pelvis shows some peculiarities. For instance, the reduction of the iliac and ischial bones, as well as the medioventral orientation of the pubis, implies a different distribution of the muscular masses. The back of *L. guilielmi* might have been less powerful than in the extant species, which reinforces the image of a less fossorial animal. This might also induce a less arched back, as suggested in the reconstruction made by Mauricio Anton (Milledge, 2003: fig. 8.12). Despite its comparatively recent age, *L. guilielmi* shows characters that would be expected from a primitive Orycteropodidae. These hypothesis must, however, be confirmed on more complete *Leptorycteropus* material.

Remarks: The femur KNM-KP 419 F of the holotype is consolidated in part with plaster. In particular, the dorsal surface of the diaphysis has been reconstructed with a strong ridge. However, this structure is not consistent with the existing parts of the bone, and must thus be considered incorrect. Furthermore, a revision of the holotype confirms that the element KNM-KP 419 L is not a metacarpal bone, as suggested by Patterson (1975), but is rather the distal epiphysis of the right metatarsal III.

GENUS *MYORYCTEROPUS* MACINNES, 1956

Emended diagnosis: Small-sized genus (50–60% of the general size of the extant aardvark) that is distinct from all other known Orycteropodidae by the shallow lingual groove that is uniquely present on the M^2; the perpendicular orientation, in caudal view, of the upper molars alveoli (except for *O. crassidens*); on the humerus, the proximal extension of its brachial crest above the level of the deltoid tuberosity, the presence of a medial crest next to the entepicondylar crest, and the very important breadth of the distal epiphysis (breadth to length ratio of 46.9%); the presence of a cnemial tuberosity on the tibia; the drop-shaped sustentacular facet, as well as the crescent-shaped, medioventrally to laterodorsally oriented, condyle for the navicular, and the vertical and negligible cotyloid facet on the talus. It also shares the developed and laterally projected deltoid crest common to all Orycteropodidae except *L. guilielmi* and *A. abundulafus*. Some significant features of this genus appear to be primitive: the very shallow angle between the mandibular rami (inferior to 60°), and the mediodorsal to lateroventral orientation, in proximal view, of the caput femoris.

Remarks: This diagnosis merges and complements the original one given by MacInnes (1956), and the emended one given by Pickford (1975). The general size of the animal is probably between 50 and 60% of that of the extant species, based on the length of the limb bones of the holotype. Pickford (1975: 68) followed MacInnes (1956) with this estimation in his diagnosis. Later in the text, however, Pickford (1975: 79) specified that the size of the animal must have been 66% of that of *O. afer* without giving any justification. The autopodes of *M. africanus* are indeed proportionally longer. For instance, the length of the metacarpal V is 84% of that of its extant counterpart, according to MacInnes (1956: 19). Nonetheless, the general size of the animal is more reliably estimated on the basis of the limb bones. As previously discussed, the bilobation of the M_3 and M^3 is now rejected in the diagnosis. Furthermore, MacInnes (1956) and Pickford (1975) suggested that the extent of the third trochanter crest on the diaphysis was a valid character. However, a study of 32 extant aardvark specimens gave values ranging from 8.5 to 15.3%. Although these values are significantly different from the value given for the holotype of *M. africanus* (22.5%) by MacInnes and Pickford, their range of variation shows that this feature is likely to be very variable in other species as well. Moreover, the difficulty to accurately take this measurement further reduces its significance. Finally, no complete femur of *M. africanus* is known, so that the proportional extent of the third trochanter can only be estimated. Therefore, I recommend rejecting it from the diagnostic features.

Type species: Myorycteropus africanus MacInnes, 1956.

Other forms: Myorycteropus cf. *africanus* Kenya (MacInnes, 1956; Pickford, 1975), *Myorycteropus* sp. Arrisdrift (Pickford, 1996, 2003), as well as possibly aff. *Myorycteropus chemeldoi* (Pickford, 1975), aff. *Myorycteropus minutus* (Pickford, 1975), and aff. *Myorycteropus* sp. Napak (Pickford, 1975).

Geographic distribution: Rusinga Island and Mfwangano (Kenya), as well as possibly Arrisdrift (Namibia), Napak (Uganda), and Songhor and Tugen Hills (Kenya).

Temporal distribution: Early Miocene, between 20 and 17 Mya.

Remarks: The possible aff. *Myorycteropus* species '*O. minutus*' and '*O. chemeldoi*' are described below. Moreover, specimens from Arrisdrift (Namibia) and Napak (Uganda) are also referred to this genus 'faute de mieux', and are discussed below.

SPECIES *MYORYCTEROPUS AFRICANUS* MACINNES, 1956

Emended diagnosis: Same as for the genus.

Holotype: NHM M 21500–NHM M 21538 (formerly field number 1264′50): parts of skull, mandible and associated skeleton of a subadult individual (having reached adult size); housed at the NHM, London.

Remarks: The last piece (NHM M 21538) was not mentioned in the original description made by MacInnes (1956), but does belong to the skeleton. The specimen NHM M 21517 does not apparently exist.

Paratype: Fragment of right mandible (NHM M 21539); fragment of right mandible (NHM M 21540); fragment of mandible (field number MW 61′52); right M_3 or P_4 (?) (field number 369′52); metacarpal V (KNM RU 5968) (the latter specimen is housed at the NMK).

Type locality and age: Rusinga Island (R.2–4 Series, Kulu-Waregi), Lake Victoria (GPS: 0°25′S, 34°11′E) (Kenya). This site is dated to around 17.8 Mya (Drake *et al.*, 1988).

Main occurrences: Rusinga Island and Mfwangano (Kenya).

Additional material: Several isolated basipode elements from Mfwangano, and elements of the hindlimb from Rusinga, described by Pickford (1975), or yet unpublished, housed at the NMK, Nairobi (KNM MW 183; KNM MW 480; KNM RU 8263; KNM RU 8269; KNM RU 8307–8308; field numbers MFW 566′55, MFW 781′55, MFW 64′52).

Remarks: Specimen KNM MW 183 (relabelled) corresponds to the published specimen KNM MW 83 of Pickford (1975). The phalanx KNM RU 3059 described by Pickford (1975) is not a Tubulidentata.

Discussion: In his original description, MacInnes (1956: 2) suggested that the infraorbital foramen was situated ‘very nearly in the middle of the total vertical height of the skull’, and thus that the skull was less elevated than in the modern aardvark. However, the dorsal deformation of the specimen and the absence of data concerning the development of the frontal and nasal bones hinder such conclusions. MacInnes (1956: plate 1, figs 1, 4) represented the mandible of the holotype with a complete articular condyle in connection with the rest of the mandible. The current condition of that specimen is different. Indeed, the articulation surface itself is damaged now, and the articular condyle is separated from the rest of the mandible, without a perfect contact surface. Thus, it is not possible to reconstruct or to confirm the restoration of the mandible made by MacInnes. Likewise, MacInnes (1956: 6) proposed a reconstruction of the length of the mandible based on an index joining the ‘distance from the posterior border of the M_3 to the anterior tip of the horizontal ramus’ in the modern aardvark. This index is 28.5% according to MacInnes (1956), and has been confirmed by the analysis of a large sample of *O. afer* (mean = 28.3% ± 2.3; $n = 61$). Nonetheless, the same index is 31.6% for *O. crassidens* (holotype), 37.6% for aff. *A. pottieri* (holotype), and 34.6% for *A. abundulafus* (holotype). These results show first that the index is not constant for all Orycteropodidae, and second, that the antemolar part of the mandible is relatively longer in the extant aardvark than in the fossil ones. Therefore, the calculated length of the mandible of *M. africanus* is not confirmed in this study.

On the scapula of *M. africanus*, the anterior border of the acromion, the edge directly opposite to the metacromion, is slightly expanded. MacInnes (1956: 13) interpreted this structure as suggestive of a ‘strong trapezius in direct opposition to the powerful deltoid’. However, this edge is the insertion surface of the subclavius muscle (Thewissen & Badoux, 1986), which is a muscle involved in the digging process, and is not an antagonist to the deltoid. This feature strengthens the idea of a powerful digging animal. The two humeri of the holotype have been preserved. However, the diaphysis of the left one is broken and glued together above the deltoid crest. This reconstruction is contested here, as the right humerus has an intact diaphysis and is distinctly longer. I propose that the left humerus, used by MacInnes (1956) throughout his description, is distorted, and is missing a portion of its shaft. The ‘sharp curvature of the shaft’ described by MacInnes (1956: 15), and followed by (Patterson, 1975: 207), was probably based on this distorted left humerus. The shaft of the right humerus is more similar to those of the other Orycteropodidae. Note that the distal mediolateral breadth to length ratio for *M. africanus* has been accordingly calculated using the length of the right humerus and the distal breadth of the left humerus (the right distal epiphysis being damaged). Another point about the humeri of the holotype concerns the proportion of the proximal epiphysis. Indeed, the left humerus shows subequal dorsoventral and mediolateral breadths, whereas the right humerus shows a longer dorsoventral breadth. This intraindividual variation probably results again from post-mortem deformations, but no indication of such alteration can be seen on the proximal epiphysis of the humeri. Although we know that the left humerus suffered from distortions (see above), it is the configuration of the right humerus that is out of the ordinary among Orycteropidinae. In consequence, the peculiarities of the proximal humerus of *M. africanus* will not be taken into account for the diagnosis until further material is discovered.

A specificity that is unique among Orycteropodidae is the important distal development of the medial distal condyle of the femur in *M. africanus*. In fact, this condyle is the distalmost point of the femur, whereas in all other aardvarks, it is the lateral condyle. This feature has never been highlighted before, and is probably related to another peculiarity displayed by the proximal epiphysis of the tibio-fibula. Indeed, in dorsal view, the proximal articulation surface of the tibio-fibula is tilted approximately 45° relative to the diaphysis, which is sharply curved. Patterson (1975: 207) already brought attention to the fact that MacInnes (1956) reconstructed the tibio-fibula with such an oblique proximal epiphysis. He concluded that such a tibia would fit a femur with an outward inclination (45°) that is 'surely an impossible position'. The left hindlimb of the holotype is the only known specimen of *M. africanus* where the articulation of the knee can be completely observed. Thus, the present configuration could be an isolated pathologic knee joint. Nonetheless, no fracture or gap, suggesting a reconsolidated injury or a post-mortem deformation, can be seen on the tibia and femur. Besides, the left tarsus of the holotype shows no unusual structure that would compensate for such an oblique orientation of the tibia. The distal epiphysis of the tibia is missing in all specimens, so that the ankle joint configuration remains totally unknown for *M. africanus*. Considering the unique orientation of the caput femoris in *M. africanus*, and thus the peculiar pelvis/femur articulation, it may not be surprising to also have a remarkable knee, and perhaps also ankle, joint. Although very unlikely, the hypothesis of a 45° angle between femur and tibia must not be rejected until new material has been discovered. These characters must be integrated in the diagnosis of the genus if confirmed.

SPECIES *MYORYCTEROPUS* CF. *AFRICANUS* KENYA

Material: Various cranial and post-cranial elements, usually found isolated, described by MacInnes (1956) and Pickford (1975), or yet unpublished (NHM M 21542, housed at the NHM, London; KNM MW 184–KNM MW 189; KNM MW 484; KNM MW 537; KNM MW 649; KNM RU 3048–3061; KNM RU 3590; KNM RU 5767, housed at the NMK, Nairobi).

Remarks: The Specimen NHM M 21542 might correspond to the left talus quoted by MacInnes (1956) as 'unnumbered from R.1 series of Rusinga'. Specimens KNM MW 184–KNM MW 189 (relabelled) correspond to the published specimens KNM MW 84–KNM MW 89 of Pickford (1975). This author also attributed some of these specimens to '*O. minutus*' (but see discussion below).

Locality and age: Rusinga Island and Mfwangano (Kenya), dated to around 17.8-Mya (Drake *et al.*, 1988).

Discussion: The material considered here has been exclusively found at Rusinga Island and Mfwangano, where the holotype and paratype of *M. africanus* were also discovered. These skeletal elements have, however, no counterparts in the hypodigm of the aforementioned species, or are too weathered to display any diagnostic features to help with their determination. Their size and shape are nonetheless close enough to *M. africanus* to place the material close to that species.

SPECIES *MYORYCTEROPUS* SP. ARRISDRIFT

Material (the specimens have not been directly seen by the author): Isolated teeth, maxilla, and mandible fragments, as well as isolated autopodes (PQAD 2356; PQAD 2575; AD 330′94; AD 587′94; AD 159′96; AD 160′96; AD 408′96; AD 342′98; AD 94′00; AD 640′00) previously attributed to '*O.* cf. *minutus*' (Pickford, 1996) and later to '*O. minutus*' (Pickford, 2003). They are tentatively referred to *Myorycteropus* in that work. The material is housed at the National Earth Science Museum, Windhoek, Namibia (Namibia).

Locality and age: These specimens have been found at Arrisdrift (GPS: 28°28′30″S, 16°42′20″E) (Namibia), which is dated to between 17.5 and 17 Mya (Pickford, 2003).

Discussion: The small size of the material found at Arrisdrift is distinct from all other Orycteropodidae, except for the *Myorycteropus* and aff. *M. minutus* forms. The right M^2 found enclosed in a fragment of maxilla is similar in size to that of the holotype of *M. africanus*. However, it presents a deep lingual groove and a trapezoidal outline that is unlike those in the holotype of *M. africanus*. Note that there is no M^2 known for aff. *M. minutus*. The size of the lower molars is also very close to those found in the holotype of *M. africanus*, and the M_1 and M_2 (?) of aff. *M. minutus*. However, according to the figures presented by Pickford (2003), the lower molars have a rectangular outline as in *M. africanus*, and are unlike those in aff. *M. minutus*. Moreover, the angle between the two mandibular rami (character 17) can be measured on two of the three mandible fragments from Arrisdrift (AD 242′98 and AD 94′00). From the figures provided by Pickford (2003), the angles are between 55° and 60° (AD 242′98), and close to 75° (AD 94′00) (but see remarks). This is confusing, as a high angle (> 73°) is diagnostic of *Amphiorycteropus*, whereas a low angle (< 60°) is the plesiomorphic state shown by *Myorycteropus*. The determination of the genus for this material is thus very delicate until direct observation can be made. Nonetheless, the small size of all elements, as well as the shallow angle of at least one of the mandibles, suggests a relationship with the genus *Myorycteropus*. Therefore, I recommend 'faute de mieux' a cautious determination of *Myorycteropus* sp. for the Arrisdrift specimens. The species level is not assessable with the available material. The determination made by Pickford (2003) is thus not followed here.

Remarks: The two mandibular fragments present fractures on the bases of their vertical ramus. Direct observations might confirm whether the mandibular angles measured are distorted by post-mortem deformation or not.

GENUS AFF. *MYORYCTEROPUS* MACINNES, 1956

SPECIES AFF. *MYORYCTEROPUS CHEMELDOI* (PICKFORD, 1975)

Emended diagnosis: Orycteropodidae species of medium size. It can be distinguished from all other Tubulidentata for the low robustness of its M_1 and M_2 (ratio of breadth to length < 50%). Additionally, this species displays rectangular lower molars with subequal grooves on the lingual and vestibular sides, as in *Orycteropus* and *Myorycteropus* species, as well as in aff. *A. pottieri*. Aff. *M. chemeldoi* can be distinguished from *M. africanus* and aff. *M. minutus* by its longer teeth, its larger mandible, and by the larger elements of its hand.

Remarks: The size of this species was estimated 'about 66% of the size of *O. afer lademanni* Grote' by Pickford (1975: 70). The elements of the hand of aff. *M. chemeldoi* (paratype) indeed show a length that is between 66 and 72% of that of the extant species (between the mean of each elements). However, the length of the lower molar tooth row is about 90% of that of the length in *O. afer* (mean).

Holotype: KNM BN 544, a left hemimandible with P_2–M_3, housed at the NMK, Nairobi.

Remarks: the specimen KNM BN 1256 (a fragment of left hemimandible with P_2) was previously considered as a separate specimen. It is now recognized as a fragment of the holotype, and the two elements have been glued together.

Paratype: Associated elements of a left hand (KNM BN 269; KNM BN 834; KNM BN 835; KNM BN 870) housed at the NMK, Nairobi.

Hypodigm: Upper premolars (?) (KNM BN 422; KNM BN 546) and lower molars (KNM BN 492; KNM BN 545), housed at the NMK, Nairobi.

Remarks: The isolated right M_2 (KNM BN 545) is so similar to the right M_2 of the holotype, that one might wonder whether they are not the antimere of one another (both specimens come from locality 2/1).

Type locality: Northwest of the Baringo lac, Tugen Hills Formation (locality 2/1) (Kenya).

Main occurrences: Type locality and locality 2/56 from the Tugen Hills Formation (northwest of the Baringo lac, Kenya).

Remarks: Further excavations lead by D. Pilbeam and A. Hill renamed and dated the sites more precisely. For instance, locality 2/1 is now locality BPRP#38 (see Hill *et al.*, 2002).

Age: The Tugen Hills material comes from the Middle Miocene Ngorora Formation (member B). Hill (2002) dated the Ngorora Formation to between 13 and 8.5 Mya, and the site BPRP#38 more precisely dated to about 12.5 Mya.

Discussion: Hill *et al.* (2002) reported the presence of '*Orycteropus*' *chemeldoi* [*sic*] from locality BPRP#38 and Fort Ternan. Without more indications, the use of quotation marks by those authors certainly signifies their doubts about the generic attribution of these specimens. I concur with Hill *et al.* (2002), and 'faute de mieux' place this species in *affinis Myorycteropus* until further material is discovered. For more details, see the section 'S*pecies excluded from the cladistic analysis*'.

SPECIES AFF. *MYORYCTEROPUS MINUTUS* (PICKFORD, 1975)

Emended diagnosis: Orycteropodinae species that is different from all other known Tubulidentata for its small size (about 50% of the general size of the extant aardvark). In particular, its metacarpals and tarsals are about 80% of the length of their homologues in *M. africanus*. The species aff. *M. minutus* also differs from all other Orycteropodidae, except *M. africanus*, for its talus displaying a drop-shaped sustentacular facet, a crescent-shaped, medioventrally to laterodorsally oriented, condyle for the navicular, as well as a derived vertical and negligible cotyloid facet. Moreover, the lower molars exhibit a trapezoidal outline.

Remarks: The general size of the animal is based on its small talus and metacarpals (holotype), which are 50% smaller than their extant counterpart. According to Pickford (1975: 62) 'the carpals, tarsals, metacarpals, metatarsals and phalanges are about 80% of the length of their homologues in [*M.*] *africanus*

MacInnes'. However, only the metacarpals II and V, as well as a talus and a navicular, can be compared between aff. *M. minutus* and *M. africanus*. That is why the diagnosis has been modified in the present work. The same author considered these bones to be 60–70% slimmer in aff. *M. minutus* than in *M. africanus*. However, only the holotype (metacarpal II) shows such proportions, not the other comparable specimens, which are more or less isometrically smaller.

Holotype: KNM SO 1231, articulated right metacarpals II and III, housed at the NMK, Nairobi.

Remarks: The taxonomic identity of the species aff. *M. minutus* cannot be determined from the existing name-bearing type, which does not possess any of the diagnostic features of the species except the small size. According to the ICZN (Glossary and Art. 75.5), the species aff. *M. minutus* should be considered a *nomen dubium*. Nonetheless, even if the talus could be proposed as a good neotype, it would eventually only be distinguishable from *M. africanus* for its smaller size. Additional material is thus required before suggesting a reliable neotype.

Paratype: Isolated teeth, a pelvic fragment, and basipode elements found at Songhor (KNM SO 963; KNM SO 1225–KNM SO 1228; KNM SO 1230; KNM SO 1232–KNM SO 1236; KNM SO 1976; housed at the NMK, Nairobi).

Remarks: The specimen KNM SO 1976 corresponds to the right acetabulum, Sgr 2269′66, described by Pickford (1975). The specimen KNM SO 1229 initially described by Pickford (1975) as Tubulidentata has been relabelled KNM SO 3853, and is actually a Suid. This author also included in the hypodigm specimens from Rusinga Island and Mfwangano (KNM MW 86–KNM MW 88; KNM RU 3055–KNM RU 3056) on the basis of their small size (but see below).

Type locality and age: Songhor, Redbeds Member (GPS: 0°02′S, 35°13′E) (Kenya) dated to around 19.6 Mya (Pickford, 1981).

Main occurrences: Type locality.

Additional material: A fragment of molar (KNM SO 4734), an intermediate phalanx of the foot (KNM SO 978), as well as one right and one left tali (KNM SO 13292 and KNM SO 8325, respectively) from Songhor have been found in the collection of the NMK, Nairobi (S. Cote, pers. comm.).

Remarks: These specimens are added to the aff. *M. minutus* material on the basis of their size, and also provenance, like the majority of the hypodigm, that were already found during different excavation seasons. Note that the two additional tali lack a developed concave cotyloid facet, and have a crescent-shaped, medioventrally to laterodorsally oriented, condyle for the navicular, like *M. africanus* and aff. *M. minutus*.

Discussion: The aardvark material found at Songhor is fragmentary and difficult to identify. Nonetheless, it is the oldest unquestionable fossil aardvark taxon so far, and its status is thus very important for the order Tubulidentata. Pickford (1975) suggested that it represents a new species on the basis of its very small size, and did not provide any discrete character to support this. This analysis shows that the original hypodigm actually bears no diagnostic features, except for its small size. Conversely, the additional tali found in the collection bring new elements that suggest a close relationship with *Myorycteropus*, but these might be convergent features. This is why it is difficult to use modern phylogenetic methods to confirm that the Songhor aardvark is even a singular species. Nonetheless, this analysis shows that aff. *M. minutus* is distinct from the species of the genera *Amphiorycteropus* and *Orycteropus*. Unfortunately, the known material of *L. guilielmi* cannot be compared with the Songhor specimens. Therefore, it seems that *M. africanus* is the closest taxon known so far. On the other hand, aff. *M. minutus* is smaller than any other Tubulidentata species, and, above all, displays trapezoidal lower molars unlike those in *M. africanus*. The latter character is only shared by the species of the genus *Amphiorycteropus* and aff. *A. seni*, but these taxa are dissimilar for their shallow lingual groove. The different outline displayed by the lower molars in *M. africanus* and aff. *M. minutus* could thus justify the species distinction. Given the phylogenetic importance of the Songhor aardvark, and this difference between the molars, I recommend keeping the species status, and bringing this form close to the genus *Myorycteropus*.

Relying on the small size of '*O. minutus*', Pickford (1975) added material from Rusinga Island and Mfwangano (type localities of *M. africanus*) to the present taxon. However, no study of the intraspecific variation of the species *M. africanus* was yet possible. Furthermore, these five specimens show a size that is intermediate between that of aff. *M. minutus* and *M. africanus*, save for KNM MW 187 (a and b), which is very similar to KNM SO 1234 and KNM SO 1235 (aff. *M. minutus*). It is doubtful to assume the presence of another species in a site solely on the basis of a few smaller specimens, especially when the size variation of the first species is not known. Besides, the difference in size between the smallest individual of extant *O. afer* and the largest is similar to the difference found between these autopode elements in aff. *M. minutus* and *M. africanus*. So far, I recommend referring only the specimens found at Songhor to aff. *M. minutus*, and to consider these five elements found at Rusinga Island and Mfwangano as *M.* cf. *africanus* until more material is discovered.

SPECIES AFF. *MYORYCTEROPUS* SP. NAPAK

Material (the specimens have not been directly seen by the author): A talus (Nap I′61) and a distal foot phalanx (Nap IV′65) described by Pickford (1975) as '*O. africanus*'. The material could not be found at the Uganda Museum, Kampala.

Locality and age: Napak I and IV (Uganda) dated to around 19 Mya (Bishop, Miller & Fitch, 1969).

Discussion: Pickford (1975: 69) gives the following description for Nap I′65: 'An isolated terminal phalanx from the pes is represented in the collection from Napak IV in Uganda. It is typical of *Orycteropus* and is probably representative of [*M.*] *africanus* judging from its size'. According to Pickford (1975: 69–70), 'Nap I′61 [is] a left talus lacking the head. [It differs] from those of *O. afer* in that the mesial tibial surface possesses a poorly developed facet for the tibia'. The later feature described by this author corresponds to the cotyloid facet of the talus (character 38). In this specimen, the character is in the derived state shown only by *M. africanus* and aff. *M. minutus*. On the basis of this single character, an accurate determination cannot be given. But it suggests, along with its small size, a possible affinity with the genus *Myorycteropus*.

GENUS *ORYCTEROPUS* GEOFFROY ST HILAIRE, 1796

Diagnosis: Large-sized Orycteropodidae displaying the following apomorphic characters on the cranium: low temporal lines, and a post-palatine foramina positioned caudally to the M^3. On the post-cranium: six sacral vertebrae, the presence of a falciform process on the proximal epiphysis of the tibio-fibula, and a femur longer than the tibia. Moreover, this genus distinctively has a flat (or button-like) radial (or bicipital) tuberosity on the radius, possesses a deep dorsal notch between the tibial tuberosity and the fibula on the proximal epiphysis of the tibio-fibula, and shows a quadrate talus (subequal breadth and length). Additionally, all *Orycteropus* species are characterized by the combination of the following features: a rectilinear nuchal line; an anterior border of the orbit situated above the M^3; a ventralmost point of the maxillojugal suture caudal to M^3; a rectilinear post-palatine torus caudal to the M^3; a broad palate; the presence of a palatine groove; the absence of crests on the pterygoid; an interorbital constriction formed strictly by the frontal, orbitosphenoid, and the alisphenoid; the absence of canines; a rectangular outline of the upper and lower molars; a mandibular angle ranging from 60° to 73°; flat (or slightly convex on the mandible) craniomandibular articulation surfaces; a strong and projected laterally deltoid crest on the humerus; an oval and bounded proximally olecranon fossa on the humerus; a broad distal epiphysis of the humerus; a sharp oblique rim on the radius; a caput femoris oriented mediolaterally; an articular facet for the sesamoid bone of the gastrocnemius muscle on the femur positioned at the level of the diaphysis; a long tibial crest merging in a gentle slope close to the middle of the diaphysis of the tibia; and a concave and developed cotyloid facet on the talus.

Remarks: The original diagnosis of the genus given by Geoffroy St Hilaire (1796: 1) is very concise: 'Orycterope. *Orycteropus*. Dents molaires (six), à couronne plate; corps recouvert de poils'. To the best of my knowledge, no other author has proposed another diagnosis for this genus.

Type species: Orycteropus afer (Pallas, 1766).

Other forms: Orycteropus crassidens MacInnes, 1956; *Orycteropus djourabensis* Lehmann *et al.*, 2004; *Orycteropus* cf. *afer* Langebaanweg (Hendey, 1973; Pickford, 2005; Lehmann, 2006b); *Orycteropus* cf. *afer* Makapansgat (Kitching, 1963; Lehmann, 2004); *Orycteropus* cf. *afer* Swartkrans (Lehmann, 2004); *Orycteropus* aff. *djourabensis* Lothagam Lower Nawata (Milledge, 2003); *Orycteropus* aff. *djourabensis* Lothagam Upper Nawata (Milledge, 2003); *Orycteropus* aff. *djourabensis* Lukeino (Pickford, 1975); *Orycteropus* sp. Asa Koma (Lehmann, 2008a); *Orycteropus* sp. Laetoli (Dietrich, 1942, Leakey, 1987); *Orycteropus* sp. Swartkrans (Lehmann, 2004).

Etymology: The genus name is a latinized form based on the Greek όρυκτήρ ('orukter', a burier), which is a variation of όρύκτης ('oryctes'), and πούς ('pous', foot). It means litteraly: 'digging foot'.

Geographic distribution: Africa.

Temporal distribution: Late Miocene to present day. The oldest record (*O.* sp.) is from the Lower Nawata Formation of Lothagam, dated to between 7.4 and 6.5 Mya (Leakey & Harris, 2003).

SPECIES *ORYCTEROPUS AFER* (PALLAS, 1766)

Emended diagnosis: Same as for the genus. *Orycteropus afer* also shares the following unique characters with *O. crassidens*: the presence of an incisura mandibulae on the mandible, and the articulation axis of the semilunar notch on the ulna perpendicular to the diaphysis. Moreover, the extant aardvark can be distinguished from other Orycteropodidae by the deep lingual groove on the upper molars (like *O. crassidens*, aff. *A. pottieri* and aff. *A. seni*), and by the long and broad tibial tuberosity on the proximal epiphysis of the tibia (as in *A. mauritanicus*).

Holotype: Pallas (1766: 64) made his description of '*Myrmecophaga afra*' (i.e. *O. afer*) on a foetus, which could not be localized.

Type locality: Cape of Good Hope (South Africa).

Main occurrences: Aardvarks are currently distributed all over Africa, south of the Sahara desert. They are absent from the desert, but not from the forest (see Pagès, 1970). To the best of my knowledge, fossil specimens identified as *O. afer* have been found from: Tanezrouft (Algeria); Lukenya Hill (Kenya); Matupi I and II (République démocratique du Congo); Elands bay cave, Equus Cave, Glen Elliott, Kasteelberg, Riversmead, Saldanha Bay, and Tienfontein 2 (South Africa) (see Romer, 1938; Klein, 1979, 1986; Van Neer, 1984; Klein *et al.*, 1991, 2007; Marean, 1992; Grine & Klein, 1993).

Age: From the Palaeolithic (from 3 Mya to 12 Kya) to recent times.

Discussion: The aardvark ('earth-pig' in Dutch) is the last living member of the order Tubulidentata. Historically, besides *O. afer*, seven extant species had been described until Rothschild (1907) distinguished them as subspecies (or 'races') of the sole species *O. afer*. There are currently 18 subspecies of aardvark, but their validity is doubtful: *Orycteropus afer adametzi* Grote, 1921, *Orycteropus afer aethiopicus* Sundevall, 1843, *Orycteropus afer afer* (Pallas, 1766), *Orycteropus afer albicaudus* Rothschild, 1907, *Orycteropus afer angolensis* Zukowsky & Haltenorth, 1957, *Orycteropus afer erikssoni* Lönnberg, 1906, *Orycteropus afer faradjius* Hatt, 1932, *Orycteropus afer haussanus* Matschie, 1900, *Orycteropus afer kordofanicus* Rothschild, 1927, *Orycteropus afer lademanni* Grote, 1921, *Orycteropus afer leptodon* Hirst, 1906, *Orycteropus afer matschiei* Grote, 1921, *Orycteropus afer observandus* Grote, 1921, *Orycteropus afer ruvanensis* Grote, 1921, *Orycteropus afer senegalensis* Lesson, 1840, *Orycteropus afer somalicus* Lydekker, 1908, *Orycteropus afer wardi* Lydekker, 1908, *Orycteropus afer wertheri* Matschie, 1898.

As discussed previously, and following Lehmann (2006b), the specimens from Langebaanweg (South Africa) are cautiously referred to *O.* cf. *afer* in this study (see below). Therefore, the oldest ascertained specimens of *O. afer* so far are the ones discovered in Tanezrouft (Algeria). Unfortunately, the age of that material (Palaeolithic, from 3 Mya to 12 Kya.) cannot be specified.

SPECIES *ORYCTEROPUS* CF. *AFER* LANGEBAANWEG

Material: Two hemimandibles (SAM-PQL-050197; SAM-PQL-050461); isolated teeth (SAM-PQL-012027; SAM-PQL-050199; SAM-PQL-058087; SAM-PQL-058088; SAM-PQL-058089; SAM-PQL-058090; SAM-PQL-058091; SAM-PQL-058092; SAM-PQL-058093); a fragment of humerus (SAM-PQL-033454); a right ulna (SAM-PQL-048627); a right coxal bone (SAM-PQL-047909); two left tali (SAM-PQL-50117; SAM-PQM-69579); a right calcaneum (SAM-PQL-51072); a left cuboid (SAM-PQL-052989); and isolated metapodes and phalanges (SAM-PQL-000908; SAM-PQL-030068; SAM-PQL-030477; SAM-PQL-031702; SAM-PQL-041459; SAM-PQL-048510; SAM-PQL-050196; SAM-PQL-050198; SAM-PQL-050273; SAM-PQL-052098; SAM-PQL-053083; SAM-PQL-053083B; SAM-PQL-058073; SAM-PQL-058074; SAM-PQL-058075; SAM-PQL-058076; SAM-PQL-058077; SAM-PQL-058078; SAM-PQL-058079; SAM-PQL-058080; SAM-PQL-058081; SAM-PQL-058082; SAM-PQL-058083; SAM-PQL-058084; SAM-PQL-058085; SAM-PQL-058086; SAM-PQL-063467; SAM-PQL-063814), housed at the IZIKO, South African Museum, Cape Town (South Africa). This material has been discussed and described by Hendey (1973), Pickford (2005), and Lehmann (2006b).

Locality and age: Langebaanweg (South Africa), dated to around 5 Mya, and Baard's Quarry (South Africa) dated around 1.8 Mya.

Discussion: See section 'S*pecies excluded from the cladistic analysis*' for more details.

SPECIES *ORYCTEROPUS* CF. *AFER* MAKAPANSGAT

Material: A right M^1 (M8271), and a fragment of right hemimandible with broken M_1 and complete M_2 (M8272), described by Kitching (1963) as *O.* cf. *afer*. The material is housed at the Bernard Price Institute, University of the Witwatersrand, Johannesburg (South Africa).

Locality and age: Makapansgat (South Africa), dated to between 3.06 and 3.32 Mya (MacFadden, Brock & Partridge, 1979).

Discussion: Lehmann (2004) revised the anatomical position of the different elements as given above. The upper and lower molars are rectangular in shape, and present deep lingual and vestibular grooves. Therefore, the attribution to the redefined genus *Orycteropus* is confirmed. The revised dimensions of the teeth 'are not significantly different from corresponding data obtained from extant aardvark' (Lehmann, 2004: 313), but are large. These teeth are closer to *O. afer* than to *O. crassidens* in their size, and do not belong to *O. djourabensis* because they show a deep lingual groove on the upper molar. However, until further material is discovered, I recommend keeping the cautious determination made by Kitching (1963).

SPECIES *ORYCTEROPUS* CF. *AFER* SWARTKRANS

Material: Distal part of a right humerus (SKX 14261), housed at the Transvaal Museum, Pretoria. Lehmann (2004) revised this specimen and identified it as *O.* cf. *afer*.

Locality and age: Swartkrans, Member 1 (South Africa), dated to around 1.8 Mya (Brain, 1993).

Discussion: As described by Lehmann (2004: 312), the data collected on this distal humerus shows '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 the data obtained for *O. afer*, and is strictly larger than all other Tubulidentata except *O. crassidens*'. Moreover, the olecranon fossa of that specimen is oval and bounded proximally. This information confirms the generic attribution of that specimen to *Orycteropus*. The species level cannot be accurately identified. Therefore, I recommend following the cautious determination given by Lehmann (2004).

SPECIES *ORYCTEROPUS CRASSIDENS*
MACINNES, 1956

Emended diagnosis: Large-sized species of *Orycteropus* (general dimensions equivalent to or larger than the largest specimens of *O. afer*), which can be distinguished from the other species of the genus by the perpendicular orientation of the upper molars alveoli with respect to the palatine plan (as in *M. africanus*), as well as the association of a large general body size (especially the post-cranial elements) with large molars. *Orycteropus crassidens* also shares the following unique characters with *O. afer*: the presence of an incisura mandibulae on the mandible, and the articulation axis of the semilunar notch on the ulna perpendicular to the diaphysis. Moreover, *O. crassidens* presents a deep lingual groove on the upper molars (like *O. afer*, aff. *A. pottieri*, and aff. *A. seni*).

Holotype: NHM M 21543–NHM M 21569 (former field number 1811′50), partial skeleton, housed at the NHM, London.

Paratype: NHM M 15412 and associated elements (former field number Kanjera 1-1955), partial skeleton housed at the NHM, London.

Remarks: The reference number NHM M 15412 corresponds uniquely to the complete right and left humeri of that specimen. The other elements are not labelled. MacInnes (1956: 28) did not clearly designate this specimen as the paratype of the species, but only as a 'referred specimen'. The author described the material from Kanjera at the same time as the holotype, and clearly attributed it to *O. crassidens*. Consequently, in accordance with the ICZN (Art. 72.4.5), this specimen represents, with the holotype, the type series of *O. crassidens*, and therefore it is the paratype.

Type locality: Rusinga Island (Kiahera-Sienga area; Nyamwita), Lake Victoria (GPS: 0°26′S, 34°9′E) (Kenya).

Main occurrences: Type locality and Kanjera (GPS: 0°20′S, 34°36′E) (Kenya).

Age: Pleistocene. MacInnes (1956) stated that the holotype was found in a pocket of Pleistocene gravel and alluvium. Moreover, according to Behrensmeyer *et al.* (1995), Kanjera is dated to between 1.5 and 0.5 Mya.

Discussion: As explained previously, Pickford (1975, 2005) relegated *O. crassidens* from its species level. This author also described new specimens from East Rudolf sites (KNM ER 875; KNM ER 876; KNM ER 877) that he referred to '*O. a. crassidens*' (Pickford, 1975). In regard to these new specimens and the types of *O. crassidens*, Pickford (1975: 81) suggested that: 'These specimens form a group of *Orycteropus* close to *O. afer* both in size and postcranial morphology and are here classified as a subspecies of *O. afer*. [. . .] If *O. a. crassidens* were classified as a separate species from *O. afer*, the three lower Pleistocene partial skeletons from Rusinga [the holotype of *O. crassidens*, n.d.], Kanjera [the paratype of *O.*

crassidens, n.d.], and East Rudolf [the additional material described by Pickford (1975), n.d.] would all have to be specifically separated, a view which seems to be extreme for deposits of closely comparable age'. First, I concur with this author: the specimens of *O. crassidens* form a group of *Orycteropus* close to *O. afer*. In the present analysis, these relationships resulted in the redefinition of the genus *Orycteropus*. Then, the three lower Pleistocene partial skeletons might actually be specifically separated. On the one hand, the fossil aardvarks from Rusinga and Kanjera belong to *O. crassidens*, whereas on the other hand the specimens from East Rudolf could belong to *O. djourabensis*, as suggested by Lehmann (2008b). The species *O. crassidens* would hence be known exclusively by its holotype and paratype.

Finally, MacInnes (1956: 35) provisionally referred an ungual phalanx (field number 1218′50, now labelled NHM M 21570) to *O. crassidens*. Patterson (1975: 205) also reported this specimen, but expressed some doubts: 'This bone differs from the unguals of *O. afer* and of the Kanjera specimen of *O. crassidens* in characters that suggest less proficiency in digging. It may not be referable to the genus'. The revision of this specimen shows that, on its palmar aspects, this ungual phalanx lacks the typical heel of the Tubulidentata. Moreover, its distal extremity is broad, its proximal articular surface is oblique, and most of all, shows traces of a median crest. These characters, far from being less specialized, are very different from those normally present in the ungual phalanx of Orycteropodidae. Therefore, I recommend withdrawing this specimen from the hypodigm, as this specimen might not be a Tubulidentata at all.

SPECIES *ORYCTEROPUS DJOURABENSIS* LEHMANN *ET AL.*, 2004

Emended diagnosis: Species of *Orycteropus* showing small- to medium-sized post-cranial elements, but a large skull. *Orycteropus djourabensis* differs from the other species of the genus by the long premolars and lower molars, the continuous border between the tibial tuberosity and the fibula on the proximal epiphysis of the tibio-fibula, as in *Amphiorycteropus*, as well as the proportionally short and slender hands. This species can also be distinguished from the other *Orycteropus* by the following features: the absence of incisura mandibulae; the shallow lingual groove on the upper molars; the oblique orientation of the articulation axis of the semilunar notch, with respect to the ulnar diaphysis; and the short and slender tibial tuberosity.

Remarks: The longer length of the lower molars in *O. djourabensis* is best seen when comparing the cumulative length (arithmetical addition) of the three lower molars. The talus of *O. djourabensis* is quadrate, as in the other *Orycteropus* species, but the shape of the condyle for the navicular is different. Indeed, it is compressed ventrodorsally, and thus limits the movement of the ankle in the Chadian aardvark. This character has only been observed on the holotype, so far, and additional specimens are thus required before considering it a diagnostic feature.

Holotype: KL09-98-001, a subcomplete skeleton found in anatomical connection, housed at the CNAR, N'Djaména.

Type locality: Kollé (GPS: 16°20′N, 19°00′E) (Chad).

Main occurrences: Type locality, as well as possibly Ileret and Koobi Fora (Area 103) from the Koobi Fora region, east of the lake Turkana (Kenya) (see Lehmann, 2008b).

Age: Early Pliocene to Early Pleistocene, from between 4 and 1.52 Mya (Lehmann, 2008b).

Additional material: A subcomplete ulna (KNM ER 875); elements of the skeleton of an adult individual (KNM ER 876); elements of the skeleton of a juvenile individual found in association with the preceding adult (KNM ER 877).

Remarks: Lehmann (2008b) demonstrated that these specimens belong to *O. djourabensis*.

Discussion: Orycteropus djourabensis is the oldest known species of the genus *Orycteropus* so far. It possesses characters that are less derived than in the other members of the genus, as well as unique features. Moreover, this taxon confirms but also questions some of the hypotheses on the evolutionary trends of the Orycteropodidae suggested by numerous authors (e.g. Colbert, 1941; Patterson, 1975; Pickford, 1975; van der Made, 2003). For instance, the length of the forelimb of *O. djourabensis*, intermediate between that of the Miocene *Amphiorycteropus* and the Plio–Pleistocene *Orycteropus*, compared with the large size of its skull, shows that the evolution of the Tubulidentata is more complex than has been assumed. The trend towards a general increase in size over time for the Orycteropodidae thus varies according to the element of the skeleton used to assess the size of the animal. On the other hand, the hand of *O. djourabensis* is significantly shorter than in the other *Orycteropus* species, whereas the length of the foot is comparable among these taxa. This would confirm the observation made by Colbert (1941) that there is a relative increase in size for the manus between the Early Pliocene and recent times. Accordingly, allometric evolution over time should be considered for Tubulidentata. Finally, *O. djourabensis* shows the difficulties in identifiying Plio–Pleistocene species on the basis of post-cranial elements or cranial remains only. These difficulties are best illustrated in the identification of the aardvark specimens from South Africa (see Lehmann, 2004, 2006b) and from East Africa (Lehmann, 2008b).

SPECIES *ORYCTEROPUS* AFF. *DJOURABENSIS* LOTHAGAM LOWER NAWATA

Material: Elements of the hindlimb (KNM LT 28641) described by Milledge (2003) as *Orycteropus* sp. and housed at the NMK, Nairobi.

Locality and age: Lothagam, Lower Nawata Formation (Kenya). This formation is dated to between 7.4 and 6.5 Mya (Late Miocene) (Leakey & Harris, 2003).

Discussion: These specimens are the oldest-known representatives of the genus *Orycteropus* to date. The tibia of the Lothagam aardvark lacks a cnemial tuberosity typical of *Myorycteropus*, and its dimensions are larger than those in *Leptorycteropus*. The talus is quadrate, as in *Orycteropus*, but is dissimilar to *Amphiorycteropus*. The cotyloid facet for the medial malleolus of the tibia is concave and developed, unlike in *Myorycteropus*. The dimensions of the talus are significantly smaller than those in *O. afer*, whereas they are close, but still smaller, to those of *O. djourabensis*. Noticeably, the articular condyle for the navicular is compressed dorsoventrally, as in *O. djourabensis*. One can be assured that the Lothagam Lower Nawata aardvarks belong to the genus *Orycteropus*. However, the absence of cranial and dental remains makes it difficult to accurately identify the species. If the diagnostic status of the dorsoventrally compressed articular condyle for the navicular on the talus were confirmed, these specimens would be brought closer to *O. djourabensis*. Therefore, I recommend referring this material to *Orycteropus* aff. *djourabensis* until new material is discovered.

SPECIES *ORYCTEROPUS* AFF. *DJOURABENSIS* LOTHAGAM UPPER NAWATA

Material: A partial right calcaneum (KNM LT 25136) and the proximal part of a right ulna (KNM LT 32873) described by Milledge (2003) as *Orycteropus* sp., housed at the NMK, Nairobi.

Locality and age: Lothagam, Upper Nawata Formation (Kenya). This formation is dated to between 6.5 and 5.5 Mya (Late Miocene) (Leakey & Harris, 2003).

Discussion: The ulna presents an oblique articulation axis of the semilunar notch, as in *O. djourabensis* and *Amphiorycteropus*. However, the dimensions of this fragment are larger than those in any of the other Miocene species, and are closer to *O. djourabensis*. Conversely, the calcaneum is distinctively small, with a size close to that of *A. mauritanicus* and the largest *A. gaudryi*. One could consider that the two specimens belong to two different taxa, or that the calcaneum belongs to a juvenile individual. There is no direct comparison possible between the aardvarks from the Lower and Upper Nawata Formation in Lothagam. Nonetheless, I also tentatively refer the latter specimens to *O.* aff. *djourabensis*. These fossil aardvarks, along with the specimens from Asa Koma, Lothagam Lower Nawata, and Lukeino, are then the oldest specimens of *Orycteropus*.

SPECIES *ORYCTEROPUS* AFF. *DJOURABENSIS* LUKEINO

Material: A left talus (KNM LU 668) and the proximal epiphysis of a left proximal phalanx IV of the hand (KNM LU 750), described by Pickford (1975) as '*Orycteropus* sp. indet.', housed at the NMK, Nairobi.

Locality and age: Lukeino (Kenya). The Lukeino Formation is dated to between 6.2 and 5.6 Mya (Hill, 2002).

Discussion: In his description, Pickford (1975) reported two isolated specimens from the Lukeino Formation that he characterized as belonging to a tiny and a large orycteropodid, respectively. The phalanx is very small, and is only comparable with the smallest Orycteropodidae, such as *M. africanus* and aff. *M. chemeldoi*. No homologous phalanx is known for aff. *M. minutus* at this time. The possibility that this specimen belongs to a very juvenile individual cannot be excluded. Conversely, the talus is very large, similar in size to the talus of the type of *O. djourabensis*, but distinctly smaller than those of *O. afer* and a fortiori of *O. crassidens*. Although damaged, the Lukeino talus seems quadrate, as in *Myorycteropus* and *Orycteropus* taxa, and is thus distinct from the genus *Amphiorycteropus*. Moreover, the cotyloid facet for the medial malleolus of the tibia appears concave and developed, unlike in *Myorycteropus*. This talus, considered alone, would thus be very close to *O. djourabensis*. It is not yet clear if the two specimens were found in the same stratigraphic level, and if KNM LU 750 belongs to a juvenile individual of the same form as the talus. Therefore, until new material is found, I suggest placing the aardvarks from Lukeino in *affinis* with *O. djourabensis*.

SPECIES *ORYCTEROPUS* SP. ASA KOMA

Material: Two fifth metacarpals (ASK-VP-1/23; ASK-VP-3/247), described by Lehmann (2008a) as *Orycteropus* sp. The material is housed at the National Museum of Ethiopia, Addis Ababa.

Locality and age: Asa Koma (Middle Awash, Ethiopia) from the Asa Koma Member (Adu-Asa Formation) dated from the Late Miocene, between 5.54 and 5.77 Mya (WoldeGabriel *et al.*, 2001).

Discussion: Lehmann (2008a) suggested that the material from Asa Koma was closer in size and showed more affinities with the 'Plio-Pleistocene forms than [with] other Miocene species. In particular, their lengths are close to the largest individuals of *O. afer* and *O. crassidens*'. I therefore recommend refering these Ethiopian specimens to the genus *Orycteropus*. The material is too fragmentary to allow identification at the species level. Along with the specimens from Lothagam, and Lukeino, these fossil aardvarks are the sole known representatives of the genus in the Miocene.

SPECIES *ORYCTEROPUS* SP. LAETOLI

Material: Fragment of a right hemimandible (KNM LAET 1418), isolated M^2 (KNM LAET 4937), left radius (KNM LAET 1813), proximal fragment of ulna (KNM LAET 3625), distal fragment of tibia (KNM LAET 4891), distal fragment of fibula (KNM LAET 3010), left talus (KNM LAET 3234), and isolated phalanx of the foot (KNM LAET 1812; KNM LAET 2711; KNM LAET 2737; KNM LAET 3469), housed at the NMK, Nairobi; as well as a fragment of a right hemimandible (MB 30867) and isolated right metacarpals V (MB 30868; MB 30869), housed at the Museum für Naturkunde, Berlin. The MB specimens have been described by Dietrich (1942), and were identified as '*Orycteropus* sp. cf. *aethiopicus*'. Leakey (1987) referred the NMK specimens to *Orycteropus* sp.

Locality and age: Laetoli (Tanzania): localities 3, 5, 9, 10w, 11, and 22; as well as Garusi, 'Grey Tuffs from the Vogelriver', and north-western bay of the Njarasa lac. Localities 3, 5, 9, 10w, 11, and 22 come from the Upper Laetolil Beds, dated from the Pliocene, more precisely between 3.8 and 3.5 Mya (Drake & Curtis, 1987).

Remarks: Leakey (1987: 297) pointed out that the specimens described by Dietrich (1942); Garusi, Grey Tuffs, and Njarasa lac) are of uncertain provenance.

Discussion: The specimens discovered by Dietrich (1942) are added to the material found by Leakey (1987) because they also come from the Laetoli area. However, there are no comparable metacarpals in the fossils collected by the latter author.

The molars found in Laetoli show a rectangular outline and a deep lingual groove, as in *O. afer* and *O. crassidens*. However, the teeth of *O. crassidens* and of *O. djourabensis* are significantly larger. Additionally, the M^2 is more slender than any other upper molars of *Orycteropus*. The articulation axis of the semilunar notch is perpendicular to the diaphysis of the ulna, unlike in *Amphiorycteropus* and *O. djourabensis*. The talus is quadrate, as in *Orycteropus*, and the condyle for the navicular is round in shape, unlike in *O. djourabensis*. However, this talus is significantly smaller than those in any other taxa from the genus *Orycteropus*. Finally, the fossil aardvarks from Laetoli are very close to *O. afer* in their morphology, and clearly belong to the genus *Orycteropus*. Nonetheless, they are significantly smaller than any of the known *Orycteropus* species. Therefore, I propose keeping the uncertainty at the species level until new material is discovered.

SPECIES *ORYCTEROPUS* SP. LAINYAMOK

Material: A right coxal bone (KNM WM 16318) and a subcomplete left tibia (KNM WM 16319) reported in the faunal list as *O. afer*, but never described (Shipman, Potts & Pickford, 1983; Potts, Shipman & Ingall, 1988; Potts & Deino, 1995). These specimens are housed at the NMK, Nairobi.

Locality and age: Lainyamok (Kenya). The horizon Khaki 2 where the specimens were found is dated from the Late Pleistocene, and more precisely from between 392 and 330 Kya (Potts & Deino, 1995).

Discussion: The coxal bone shows dimensions comparable with those of *O. afer*, and that are larger than those in *O. djourabensis*. No coxal bone is known for *O. crassidens* so far. The tibia presents the deep dorsal notch between the tibial tuberosity and the fibula on the proximal epiphysis of the tibio-fibula, as well as a large and developed tibial tuberosity, typical of *O. afer* and *O. crassidens*, but different from *O. djourabensis* and the *Amphiorycteropus*. Moreover, the dimensions of this tibia match those of the larger specimens of *O. afer*. No tibia is known for *O. crassidens* at this time. Therefore, the aardvarks from Lainyamok clearly belong to the genus *Orycteropus*, and can even be distinguished from *O. djourabensis*. Nonetheless, as no comparable elements exist for *O. crassidens*, it is not yet possible to assign them to a species. Noticeably, Potts & Deino (1995) counted 32 aardvark specimens (the maximum number of individuals). However, only two specimens have been found at the present time in the collections of the NMK, Nairobi. The analysis of the remaining material might allow a more precise identification.

SPECIES *ORYCTEROPUS* SP. SWARTKRANS

Material: Several isolated phalanges of the foot (SKX 75; SKX 498; SKX 1199; SKX 37832), housed at the Transvaal Museum, Pretoria. Lehmann (2004) identified these specimens as *Orycteropus* sp.

Locality and age: Swartkrans, Member 2 and Member 3 (South Africa). Member 2 is dated to around 1.5 Mya, and Member 3 is at least 1-Myr old (Brain, 1993).

Discussion: The very fragmentary aardvark material from Members 2 and 3 can only be compared by size with other Tubulidentata. Indeed, these phalanges are similar to their counterparts in *O. afer* in their morphology. The dimensions are also comparable with those in *O. afer*, but the phalanges are more slender. Therefore, I consider that these specimens belong to the genus *Orycteropus*, but are too fragmentary to enable a specific identification.

INCERTAE SEDIS

SPECIES ORYCTEROPODINAE SP. CHINJI

Material: Fragment of left hemimandible with P_3–M_2 (AMNH 101259), housed at the AMNH, New York; fragment of hemimandible with P_3–M_1 (GSI K13/448), probably housed at the Geological Survey India, Calcutta; proximal and intermediate phalanges of the hand (GSP 4346) and a terminal phalanx (GSP 767), probably housed at the Geological Survey Pakistan, Islamabad; and elements of a post-cranial skeleton (GSP S 234), housed at the Harvard Peabody Museum, Cambridge, USA. Pickford (1978) reported these specimens as '*Orycteropus* sp. indet. small'.

Remarks: The specimens GSP 767, GSP 4346, and GSI K13/448 have not been directly seen by the author.

Locality and age: Dhok Talian, Chinji, and Chinji Bungalow in the Potwar Plateau, as well as Sind (Pakistan). The Potwar Plateau specimens come from the Middle Miocene Chinji Formation, dated to between 14.2 and 11.2 Mya (Barry *et al.*, 2002). The Sind material also comes from the Chinji Formation, according to Pickford (1978).

Discussion: In his revision of the fossil aardvark from Pakistan, Pickford (1978) reported the presence in the Siwaliks of another species (undetermined), smaller than *A. browni*, but too fragmentary to warrant the erection of a new name yet. From the available material, one can observe that the lower molars are rectangular and present subequal lingual and vestibular grooves, as in *Orycteropus* and *Myorycteropus* species, as well as in aff. *A. pottieri*. However, the dimensions of these teeth are significantly shorter than in any of the known species of *Orycteropus*. Indeed, the teeth are intermediate in size between those of *M. africanus* and aff. *M. minutus*, on the one hand, and *Amphiorycteropus*, on the other hand. The teeth are also very slender, as in *M. africanus*, and are almost as slender as those in aff. *M. chemeldoi*. The post-cranial elements are also very small. The acetabular fragment of GSP S 234, for instance, is equivalent in size to that of aff. *M. minutus* and *Leptorycteropus*. The fragment of metacarpal (GSP S 234) is close in size to aff. *M. chemeldoi* and *A. abundulafus*. The calcaneum (GSP S 234) is slightly smaller than in *M. africanus*. Conversely, the metatarsals and the intermediate phalanges of the foot show a larger size than in the Kenyan taxon, and are closer to *A. abundulafus*. The contradictory results obtained by the biometrical analysis hinder an accurate identification. There are no discrete characters to really point towards a particular species, or even to a genus. Until further material is discovered, I therefore suggest placing these specimens in generic and species indetermination.

SPECIES ORYCTEROPODINAE SP. FORT TERNAN

Material: Two phalanges of the foot (KNM FT 3326; KNM FT 3327) described by Pickford (1975) as part of the hypodigm of '*Orycteropus chemeldoi*'. The specimens are housed at the NMK, Nairobi.

Remarks: These specimens were identified as phalanges of the hand by Pickford (1975).

Locality and age: Fort Ternan, level IV (Kenya), dated to around 14 Mya (see Hill *et al.*, 2002).

Discussion: The type series of aff. *M. chemeldoi* has been found in the Tugen Hills. Nonetheless, Pickford (1975) added these two specimens from Fort Ternan to the hypodigm of his new species. Even with their misidentification as medial and proximal phalanges of the hand, there is no comparable counterpart for the Fort Ternan specimens in the material of aff. *M. chemeldoi* from the Tugen Hills. Therefore, I withdraw this material from the hypodigm. Moreover, this material is too fragmentary to allow any precise identification at the genus and species level: more material is needed.

SPECIES ORYCTEROPODINAE SP. KAKARA

Material (the specimen has not been directly seen by the author): Isolated proximal phalanx of the foot (KI 79′92), previously attributed to '*O.* cf. *chemeldoi*' (Pickford, 1994). The specimen might be housed at the Uganda Museum, Kampala.

Locality and age: Specimens found at locality KI6 from the Kakara Formation (Uganda), dated to around 10 Mya (Pickford, 1994).

Discussion: Typical orycteropodid proximal phalanx, with dimensions only matching those of the second proximal phalanx of the holotype of *M. africanus* (no homologous element is known for aff. *M. minutus* and aff. *M. chemeldoi*). However, the material is too fragmentary to give an accurate determination, and is thus placed in generic and specific indetermination.

SPECIES ORYCTEROPODINAE SP. KORU

Material: a left M^1 (?) (M 14265), housed at the NHM, London; a fragment of mandible with M_2 and an isolated M_3 (KNM-KO-84), housed at the NMK, Nairobi.

Remarks: The specimen M 14265 has not been directly seen by the author.

Locality and age: Koru (GPS: 0°10′S, 35°15′E, according to MacInnes 1956) and locality 31 (Koiyabi) (Kenya) from the Koru Formation. The Koru Formation is dated to between 19.6 and 19.5 Mya (Pickford & Andrews, 1981).

Discussion: Pickford & Andrews (1981) reported one aardvark specimen found at Koru between 1977 and 1979. They considered it to be '*Orycteropus minutus*' in their faunal list, but gave no description. This specimen, a left hemimandible fragment (KNM KO 84) is of small size, but is larger than the mandibles of any of the *Myorycteropus* species. The lower molars show a trapezoidal outline, and a lingual groove slightly shallower than the vestibular one. This configuration is different from the lower molars of *M. africanus*, but can be compared with that in aff. *M. minutus*, the species from the genus *Amphiorycteropus*, and, more particularly, with aff. *A. seni*. However, the dimensions of the teeth are larger than in aff. *M. minutus*, and are close to those of *Amphiorycteropus* taxa.

The size of this isolated left M^1 (?) (M 14265), described by MacInnes (1956) as '*Orycteropus* sp. indet', is not incompatible with the size of KNM KO 84. Therefore, I associate the two specimens in this description. The dimensions of the upper molar are again closer to those in *Amphiorycteropus* and the smallest *Orycteropus* specimens than to *Myorycteropus*. No description of the lingual groove and of the outline of the tooth are given, but based on its size, MacInnes (1956: 27) was confident that this specimen 'is certainly not another example of *Myorycteropus*'. The material found at Koru is too fragmentary to give an accurate identification. Thus, I recommend keeping these specimens in species and genus indetermination until more material is found. The specimens from Koru potentially represent one of the oldest remains of fossil Tubulidentata ascertained so far. Nonetheless, it is possible that these specimens were found in pockets of younger sediments (M. Pickford, pers. comm.), which would explain their relatively large size.

SPECIES ORYCTEROPODINAE SP. PROCHOMA

Material (the specimens have not been directly seen by the author): Two phalanges (PXM 259; PXM 260) described by de Bonis *et al.* (1994) as '*Orycteropus* sp.'.

Locality and age: Prochoma 1 (Macedonia, Greece), dated from the Late Miocene (MN11).

Discussion: As stated by de Bonis *et al.* (1994: 356): 'these remains are too fragmentary for a specific identification'. Therefore, and in regard to the delicate generic determination of specimens geographically and chronologically close to these specimens, I recommend keeping this aardvark material from Prochoma in generic and specific indetermination, until new material is discovered.

BIOCHRONOLOGY AND PALAEOBIOGEOGRAPHY

The revision of the order Tubulidentata, as well as the creation of a new genus, allows us to propose biochronological and palaeobiogeographical patterns of the order for the last 20 million years (Fig. 7).

At the present time, only the regions of Kenya, Namibia, and Uganda are known for yielding fossil aardvarks from the Early Miocene. The oldest unequivocal fossil Tubulidentata is African, and comes from Koru (Kenya). Unfortunately, this specimen is too fragmentary to be accurately identified. Therefore, the oldest species of Tubulidentata is aff. *M. minutus*, from Songhor (Kenya). This species already displays the diagnostic tubulidentate tooth

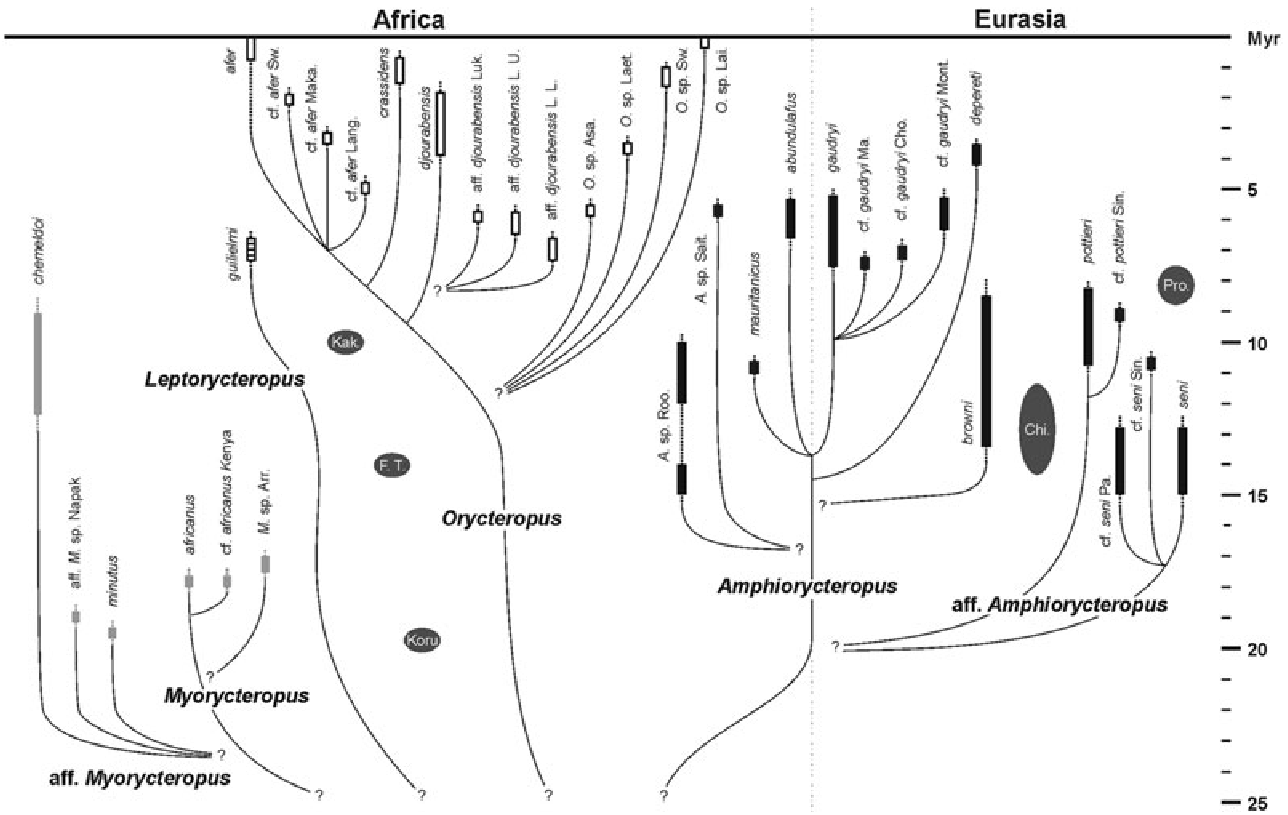


Figure 7. Phylogeny of the order Tubulidentata. Legend: Arr., Arrisdrift; Asa., Asa Koma; Laet., Laetoli; Lai., Lainyamok; Lang., Langebaanweg; L. L., Lothagam Lower Nawata; L. U., Lothagam Upper Nawata; Luk., Lukeino; Ma., Maragheh; Maka., Makapansgat; Mont., Monticino; Pa., Paşalar; Roo., Rooilepel; Sait., Saitune Dora; Sin., Sinap; Sw., Swartkrans. Undetermined taxa referred to Orycteropodinae sp. are represented by balloons: Chi., Chinji; F. T., Fort Ternan; Kak., Karara; Koru; Pro., Prochoma. See text for details.

structure, which suggests that the ancestry of the order Tubulidentata is deeply nested in the Paleogene (or perhaps even in the Cretaceous), as has been proposed by some authors (e.g. Colbert, 1941; Springer *et al.*, 2003; Bininda-Emonds *et al.*, 2007; for further references see Holroyd & Mussel, 2005). According to the present study, all of the species discovered in the Early Miocene belong to (or are *affinis* to) the genus *Myorycteropus*. Nonetheless, this taxon is morphologically too specialized to be a form close to the morphotype expected for the common ancestor of the other genera (also see the section '*Intergeneric relationships*'). This result suggests that other Early Miocene fossil Tubulidentata most probably exist, but have not been found yet. The biodiversity of the order is thus certainly higher than previously thought.

The first ascertained fossil Tubulidentata to reach Eurasia were found in the Middle Miocene of Pakistan (Chinji) and Turkey (Çandir, Inönü, and Paşalar). According to these fossils, Orycteropodidae arrived on this continent around 15 Mya. This dispersion from Africa to Eurasia is consistent with a large dispersal event for Mammalia that occurred between 15 and 13 Mya. For instance, this event was marked by the appearance of *Griphopithecus* in Anatolia (Çandir and Paşalar; see Rögl, 1999). In parallel, there is a gap in the tubulidentate fossil record between 17 and 15 Mya in Africa. The species aff. *M. chemeldoi* is therefore the only fossil Tubulidentata species from the Middle Miocene of Africa that is known to date. Along with the undetermined specimen from Fort Ternan and the *Amphiorycteropus* sp. specimens from Rooilepel (Namibia), they also represent the only fossil record for the order on the continent during that period.

Conversely, in Eurasia, a radiation took place in Pakistan and Turkey during the Middle Miocene, as shown by the number of sites that yielded fossil aardvarks there. Tubulidentata also reached their easternmost locality (Pakistan) by the end of the Middle Miocene. Unfortunately, the relationships between the Middle Miocene aardvarks (from Africa and Eurasia) and the Early Miocene ones are not very clear. Only aff. *M. chemeldoi* is tentatively related to the Early Miocene genus *Myorycteropus*, but this hypothesis must be confirmed with more complete material. Likewise, the link between these first Eurasian aardvarks and their counterparts in Africa remains unclear. For instance, *Amphiorycteropus* and aff. *Amphiorycteropus* seem to appear at the same time on both continents, and are possibly related, but their relationships with the other genera could not be resolved in this study.

The Late Miocene is the period during which the Tubulidentata experienced their largest geographical distribution (from Italy to Pakistan, and throughout Africa) and their maximum diversity, with at least seven species. It is also the period when *Amphiorycteropus* prevailed in Africa, and especially in Eurasia. The close relationship between *A. abundulafus*, *A. gaudryi*, and *A. mauritanicus* suggests that intercontinental exchanges occurred during the Late Miocene for that genus. By the end of that period, and except for the specimens from Ethiopia (Saitune Dora), *Amphiorycteropus* was pushed back in circum-Mediterranean regions. This might be linked to the increase of dryness observed over the Mediterranean basin during that period (Griffin, 2002).

The genus *Leptorycteropus* is only known from the Late Miocene of Lothagam (Kenya) at this time. During this interval, and in particular around 10 Mya, another major dispersal event enabled Eurasian mammals to enter Africa, such as, for instance, Hipparions (see Rögl, 1999). In this respect, Leakey *et al.* (1996) observed that the fauna discovered in the Lower Nawata Formation of Lothagam (7.5–6.5 Mya) showed a large number of Eurasian taxa. Therefore, it cannot be excluded that the genus *Leptorycteropus* shared a Eurasian origin. The Late Miocene is also characterized by the first appearance data of the genus *Orycteropus* in East Africa, also found in the Lower Nawata Formation of Lothagam (Kenya). These fragmentary specimens are placed in aff. *O. djourabensis* in this study, which would be in accordance with the basal position of the Chadian species in the genus *Orycteropus*. The relationships with the other genera cannot be resolved in the present study, so that the geographical origin of *Orycteropus* is not yet known. However, as for the genus *Leptorycteropus*, a Eurasian origin cannot be excluded. Finally, fossil aardvarks are totally absent from the Late Miocene in several areas of Africa (e.g. South Africa), or have only been recently discovered, as in Central Africa (Chad). Therefore, the relatively patchy distribution of the Tubulidentata in Africa during this period certainly does not represent a dispersal pattern, but is rather caused by the scarcity of Late Miocene sites in these regions.

The Pliocene was marked by the extinction of the genus *Amphiorycteropus* in Africa, and the progressive disappearance of the order Tubulidentata from Eurasia. The last aardvark known from this continent was *A. depereti* from the Early Pliocene of France. Consequently, Tubulidentata were restricted to Africa since the Late Pliocene, and intercontinental exchanges no longer occurred. During the Plio–Pleistocene, the genus *Orycteropus* spread all over Africa. Eventually, the extant *O. afer* appeared and colonized all of Africa, replacing the other forms until it became the last survivor of the order Tubulidentata. The discovery of Palaeolithic aardvarks in the south of Algeria (Romer, 1938), the presence of living aardvarks in the Ennedi massif in Chad (Capot-Rey, 1965), and several archaeological clues, such as paintings and the possible association between the Egyptian god Seth and the aardvark (Keimer, 1944; Frechkop, 1946; Manlius, 2002), all suggest that the current sub-Saharan distribution of the extant aardvark is probably only a recent phenomenon.

CONCLUSION

Since the first description of a living aardvark, the phylogeny of the order Tubulidentata has never been comprehensively established. Moreover, after the thorough conspectus made by Patterson (1975), and despite the numerous new fossil discoveries, the systematics and the taxonomy of this mammalian order have never been updated. In this paper, the first complete revision of the order Tubulidentata in over 30 years is proposed. For the first time, a thorough cladistic analysis was conducted on the Orycteropodidae. This analysis notably: (1) shows that the 'Plio-Pleistocene *Orycteropus*' species and the 'Miocene *Orycteropus*' species belong to two separate lineages; (2) confirms the close relationships between Middle Miocene African and Eurasian species, now regrouped in a specific new genus; (3) confirms the synonymy of '*O. pilgrimi*' with *A. browni*; and (4) substantiates the higher than suspected biodiversity of the fossil Tubulidentata with the validation of 14 species. The present study also suggests some affinities for the species from Songhor and Ngorora with the genus *Myorycteropus* on the one hand, and for the Turkish species with the new genus on the other hand. The genera *Leptorycteropus* and *Myorycteropus* have been validated, and the new genus *Amphiorycteropus* has been created for the 'Miocene *Orycteropus*' aardvarks. The genus *Orycteropus* has been restricted to the African continent.

Furthermore, the present work moderates the Mio–Pliocene turnover for Tubulidentata proposed by Lehmann *et al.* (2004), inasmuch as *Orycteropus* specimens (large modern aardvarks *sensu* Lehmann *et al.*, 2004) coexisted for some time during the Late Miocene with *Amphiorycteropus* (Late Miocene small aardvarks *sensu* Lehmann *et al.*, 2004) and *Leptorycteropus*. Nonetheless, this study shows that the genus *Amphiorycteropus* disappeared from Africa at the Mio–Pliocene boundary, wheareas the genus *Orycteropus* experienced a radiation after that period, until eventually prevailing in Africa. Concomitantly, the aardvarks completely disappeared from Eurasia, save for one last species in France. The Late Miocene–Early Pliocene period has thus witnessed a kind of biodiversity crisis for the Tubulidentata.

The creation of the new genus *Amphiorycteropus*, the redefinition of *Orycteropus*, and the validation of *Myorycteropus* and *Leptorycteropus* give structure for the phylogeny of the order Tubulidentata consisting of four lineages, the relationships of which are still unclear. In two of these lineages (genera *Amphiorycteropus* and *Orycteropus*), later species can be smaller in their general size than earlier ones (e.g. *A. mauritanicus* is larger than *A. gaudryi*; *O. crassidens* is larger than *O. afer*). Nonetheless, Plio–Pleistocene aardvarks are generally larger than their Miocene relatives. Thus, the order Tubulidentata as a whole experienced an increase in the body size of its members over time. However, no general trend can be clearly defined, because this increase in size varied in speed and process (allometry or isometry) according to the lineage and the body part. The traditionally accepted gradual increase in aardvark body size over time (e.g. Patterson, 1975; Pickford, 1975; van der Made, 2003) must thus be moderated. The evolutionary history of the morphology of the aardvarks is more complex than previously thought.

The grouping of the whole order into a single genus *Orycteropus sensu* Pickford (1975, 2004, 2005) minimizes the apparent biodiversity of the order Tubulidentata, and leads to poorly justified taxonomic attribution. Conversely, the definition of more distinct genera, based on cranial and post-cranial features, as in the present article, illustrates more accurately the range of morphological variations existing in the order, and encourages us to be more cautious in attributing isolated dental and post-cranial remains.

This revision is of course not complete, and several problems remain. Further investigations are called for in order to determine the relationships between the genera of Tubulidentata. This work should also include the specimens that could not be directly observed for the present paper (e.g. those from Turkey, Namibia, and Uganda). Moreover, the discussion of the origin of the order Tubulidentata should be pursued. Comparison of the known Tubulidentata with Paleogene mammals like the Condylarthra, as suggested by Le Gros Clark & Sonntag (1926), the Ptolemaiida (see Tabuce *et al.*, 2008), as well as with the fossil Paenungulata, Macroscelidae, and Tenrecidae, with respect to the Afrotheria clade, should be performed. Nonetheless, the present study has already made some progress towards the recognition and resolution of significant phylogenetic problems. Moreover, the proposed palaeobiogeographical patterns for the Tubulidentata are congruent with the large-scale Mammalian dispersal event during the Neogene. Finally, and above all, this phylogenetic revision provides a consistent framework for future discoveries and studies related to the order Tubulidentata.

ACKNOWLEDGEMENTS

This study was conducted with the support of the Mission Paléoanthropologique Franco-Tchadienne (MPFT), directed by M. Brunet (UMR CNRS 6046, Institut International de Paléoprimatologie, Paléontologie Humaine: Evolution et Paléoenvironnement (IPHEP), Université de Poitiers). The first stage of this work was funded by a PhD study grant from the French Ministère de l'Education Nationale, de la Recherche et des Technologies. The NRF provided additional support for a postdoctoral fellowship at the Transvaal Museum, Pretoria. The last stage of this work was funded by a Humboldt Research Fellowship for postdoctoral research at the Museum für Naturkunde, Berlin. The author would also like to acknowledge financial support from a DAAD Kurzstipendium für ausländische Nachwuchswissenschaftler, an AMNH, New York Collection Study Grant, and the RHOI project (Late F. C. Howell and T. D. White), funded by the NSF. I gratefully thank the heads and other workers of the following institutions: American Museum of Natural History, New York; Bernard Price Institut, Johannesburg; Centre National d'Appui à la Recheche, N'Djaména; National Earth Science Museum, Windhoek; IZIKO South African Museum, Cape Town; National Museum of Ethiopia, Addis Ababa; National Museums of Kenya, Nairobi; Natural History Museum, London; Naturhistorisches Museum, Basel; Museum für Naturkunde, Berlin; Muséum National d'Histoire Naturelle, Paris; Staatliches Museum für Naturkunde in Stuttgart; and Transvaal Museum, Pretoria, South Africa. I express my gratitude to L. Foley-Ducrocq, J. Müller, S. Sen, P. Vignaud, my colleagues at the University of Poitiers and the Transvaal Museum, and two anonymous reviewers for discussion and feedback on the manuscript. Finally, none of this work could have been initiated without the efforts of all of the members of the MPFT.

REFERENCES

Alferez F, Molero G, Maldonado E, Inigo C. 1988. Los restos fósiles más antiguos de Orycteropodidae (Tubulidentata, Mammalia) hallados en Eurasia, Coll. Homen. A. R. Adrover, Sabadell, 14–16 Dec. 1988, Bioeventos y sucesiones faunisticas en el terciario continental ibérico.

Amaghino F. 1905. Les édentés fossiles de France et d'Allemagne. *Annales du Muséum National de Buenos Aires* **13:** 175–250.

Andrews CW. 1896. On a skull of *Orycteropus gaudryi* from Samos. *Proceedings of the Zoological Society, London*, **1896:** 196–199.

Anthony R. 1934. La dentition de l'oryctérope, morphologie, développement, structure, interprétation. *Annales des Sciences Naturelles, Zoologie* **17**, 10ème série: 289–322.

Arambourg C. 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. *Publications du Service de Carte Géologique, Algérie, n. s., Paléontologie* **4:** 42–53.

Asher RJ. 2007. A web-database of mammalian morphology and a reanalysis of placental phylogeny. *BMC Evolutionary Biology* **7:** 108.

Asher RJ, Lehmann T. 2008. Dental eruption in afrotherian mammals. *BMC Biology* **6:** 14.

Barry JC, Morgan ME, Flynn LJ, Pilbeam D, Behrensmeyer AK, Raza SM, Khan IA, Bagley C, Hicks J, Kelley J. 2002. Faunal and environmental change in the late Miocene Siwaliks of Northern Pakistan. *Paleobiology Memoirs* **28:** 1–72.

de Beaumont G. 1970. Observations sur un *Orycteropus gaudryi* Major (Mammalia, Tubulidentata). *Bulletin de la Société vaudienne de Sciences Naturelles* **70:** 327–336.

Behrensmeyer AK, Potts R, Plummer T, Tauxe L, Opdyke N, Jorstad T. 1995. The Pleistocene locality of Kanjera, Western Kenya: stratigraphy, chronology and paleoenvironments. *Journal of Human Evolution* **29:** 247–274.

Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck DMD, Grenyer F, Price SA, Vos RA, Gittlenman JL, Purvis A. 2007. The delayed rise of present-day mammals. *Nature* **446:** 507–512.

Bishop WW, Miller JA, Fitch FJ. 1969. New Potassium-Argon age determinations relevant to the Miocene fossil mammal sequence in East Africa. *American Journal of Science* **267:** 669–699.

de Bonis L, Bouvrain G, Geraads D, Koufos GD, Sen S. 1994. The first aardvarks (Mammalia) from the late Miocene of Macedonia, Greece. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **194:** 343–360.

Brain CK. 1993. Structure and stratigraphy of the Swartkrans Cave in light of the new excavations. In: Brain CK, ed. *SWARTKRANS – a caves chronicle of early man*. Pretoria: Transvaal Museum, 35–73.

Broom R. 1909a. On the milk dentition of *Orycteropus*. *Annals of the South African Museum* **5:** 381–384.

Broom R. 1909b. On the organ of Jacobson in *Orycteropus*. *Proceedings of the Zoological Society, London* **1909:** 680–683.

Brunet M, MPFT. 2000. Chad: discovery of a vertebrate Fauna close to Mio-Pliocene Boundary. *Journal of Vertebrate Paleontology*, **20:** 205–209.

Capot-Rey P. 1965. La bordure meridionale de l'Ennedi *Travaux de l'institut de recherches sahariennes* [Alger], tome **XXIV:** 47–64.

Le Gros Clark WE, Sonntag CF. 1926. A monograph of *Orycteropus afer*. – III. The skull. The skeleton of the trunk and limbs. *Proceedings of the Zoological Society, London* **30:** 445–485.

Colbert EH. 1933. The presence of tubulidentates in the Middle Siwalik Beds of northern India. *American Museum Novitates* **604:** 1–10.

Colbert EH. 1941. A study of *Orycteropus gaudryi* from the island of Samos. *Bulletin of the American Museum of Natural History* **78:** 305–351.

Coupin F. 1926. Recherches sur les fosses nasales de l'Oryctérope. *Nouvelles Archives du Muséum d'Histoire Naturelle, Paris* **1:** 151–171.

Cox PG. 2006. Character evolution in the orbital region of the Afrotheria. *Journal of Zoology* **269:** 514–526.

Cuvier G. 1798. *Tableau élémentaire de l'histoire naturelle des animaux*. Paris: Baudouin.

Cuvier G. 1817. *Le règne animal distribué d'après son organisation*, Tome 1, p. 221.

Cuvier G. 1823. Sur l'Ostéologie des Tatous et de l'Oryctérope. In: Cuvier G, ed. *Recherches sur les Ossements fossiles*, Tome V, 1ère partie, 132–141.

Cuvier G. 1835. *Leçons d'Anatomie comparée*, Tome IV, 2ème partie, p. 461.

Dietrich WO. 1942. Ältestquartäre Säugetiere aus der südlichen Serengeti, Deutsch-Ostafrika. *Palaeontographica* **94** (Abt. A): 43–133.

Drake R, Curtis GH. 1987. K-Ar Geochronology of the Laetoli fossil localities. In: Leakey MD, Harris JM, eds. *Laetoli, A Pliocene site in northern Tanzania*, Oxford: Clarendon Press, 48–51.

Drake RE, van Couvering JA, Pickford M, Curtis GH, Harris JA. 1988. New chronology for the early Miocene mammalian faunas of Kisingiri, Western Kenya. *Journal of the Geological Society, London* **145:** 479–491.

Edgeworth FH. 1924. On the masticatory, intermandibular, and hyoid muscles of *Orycteropus capensis*. *Journal of Anatomy* **58:** 134–139.

Filhol H. 1894. Observations concernant quelques mammifères fossiles nouveaux du Quercy. *Annales de Sciences Naturelles Zoologie* **16:** 129–150.

Filhol MH. 1895. Observations concernant les mammifères contemporains à *Aepyomis* à Madagascar. *Bulletin du Museum d'Histoire Naturelle, Paris* **1:** 12–14.

Fortelius M. 1990. Less common ungulate species from Pasalar, middle Miocene of Anatolia (Turkey). *Journal of Human Evolution* **19:** 479–487.

Fortelius M, Nummela S, Sen S. 2003. Fossil Aardvaks of the Miocene Sinap Formation, Turkey. In: Fortelius M, Kappelman J, Sen S, Bernor R, eds. *Geology and paleontology of the Miocene Sinap formation, Turkey*. Columbia: Columbia University Press, 194–201.

Franz F. 1908. Das Auge von *Orycteropus afer*. *Zoologischer Anzeiger* **32:** 148–150.

Frechkop S. 1946. L'Oryctérope, ne serait-t-il pas le prototype de l'incarnation de Seth-Typhon? *Chroniques d'Egypte* **41:** 91–92.

Gabunia L. 1956. An extinct Tubulidentate (*Orycteropus* sp.)

from the Middle Miocene deposits of Belomechetskaya (North Caucase). *Dok. AN Azerbaidzhanskoi SSR* **12:** 203–206. [In Russian]

Galton JC. 1869. The myology of the upper and lower extremities of *Orycteropus capensis*. *Transactions of the Linnean Society of London* **26:** 567–608.

Gazin CL. 1952. The Lower Eocene Knight Formation of western Wyoming and its mammlian faunas. *Smithsonian Institution, Miscellaneous Collections, Washington, D.C* **117:** 1–98.

Geoffroy St Hilaire E. 1796. Extrait d'un mémoire sur le *Myrmecophaga capensis* Gmelin, 1788. *Bulletin de la Société Philomatique, Paris* **50:** 1–2.

Gray JE. 1821. On the natural arrangement of vertebrose animals. *London Medical Repository* **XV:** 296–310.

Griffin DL. 2002. Aridity and humidity: two aspects of the late Miocene climate of North Africa and the Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology* **182:** 65–91.

Grine FE, Klein RG. 1993. Late Pleistocene human remains from the Sea Harvest site, Sadanha Bay, South Africa. *South African Journal of Science* **89:** 145–152.

Grote H. 1921. Neue Erdferkel (*Orycteropus*) aus Deutsch-Ostafrika und Kamerun. *Archiv für Naturgesellschaft. Sect. A, pt. 7* **87:** 121–127.

Hatt RT. 1932. The aardvark of the Haut-Uele. *American Museum Novitates* **535:** 1–2.

Heissig K. 1999. Order Tubulidentata. In: Rössner G, Heissig K, eds. *Land Mammals of Europe*. München: Friedrich Pfeil Verlag, 155–156.

Helbing H. 1933. Ein *Orycteropus*-Fund aus dem Unteren Pliocaen des Roussillon. *Eclogae Geologicae Helvetiae* **26:** 256–267.

Hendey QB. 1973. Fossil occurrences at Langebaanweg, Cape Province. *Nature* **244:** 13–14.

Heuvelmans B. 1939. Le problème de la dentition de l'oryctérope. *Bulletin du Musée royal d'Histoire naturelle de Belgique, Bruxelles* Tome **XV:** 1–30.

Hildebrand M. 1985. Digging of quadrupeds. In: Hildebrand M, Bramble DM, Liem KL, Wate DB, eds. *Functional vertebrate morphology*. Cambridge: Harvard University Press, 89–109.

Hill A. 2002. Paleoanthropological researh in the Tugen Hills, Kenya. *Journal of Human Evolution* **42:** 1–10.

Hill A, Leakey M, Kingston JD, Ward S. 2002. New cercopithecoids and a hominoid from 12.5 Ma in the Tugen Hills succession, Kenya. *Journal of Human Evolution* **42:** 75–93.

Hirst AS. 1906. A new species of *Orycteropus*. *Annales and Magazine of Natural History ser. 7* **17:** 383–384.

Holroyd PA, Mussel JC. 2005. Macroscelidae and Tubulidentata. In: Rose KD, Archibald JD, eds. *Placental Mammals: origins and relationships of the major clades*. Baltimore: JohnHopkins University Press, 71–83.

Howell AB. 1941. The femoral trochanters. *Field Museum for Natural History, Zoological Series* **27:** 279–291.

Humphey GM. 1869. On the myology of *Orycteropus capensis* and *Phoca communis*. *Journal of Anatomy and Physiology* **2:** 290–322.

Huxley TH. 1872. *A manual of the anatomy of vertebrated animals*. New York: D. Appleton and Company.

International Commission on Zoological Nomenclature. 1999. *International code of zoological nomenclature*, 4th edn, adopted by the International Union of Biological Sciences. London, United Kingdom: International Trust of Zoological Nomenclature in association with the British Natural History Museum, (in English and French).

Jepsen GL. 1932. *Tubulodon taylori*, a Wind River Eocene tubulidentate. *Proceedings of the American Philosophy Society* **71:** 255–274.

Jäger KF. 1837. Anatomische Untersuchung des *Orycteropus capensis*. Inaugural-Dissertation, Stuttgart; Carl Erhard, pp. 1–22.

Kappelman J, Maas MC, Sen S, Alpagut B, Fortelius M, Lunkka J-P. 1996. A new early Tertiary mammalian fauna from Turkey and its paleobiogeographic significance. *Journal of Vertebrate Paleontology* **16:** 592–595.

Kappelman J, Rasmussen DT, Sanders WJ, Feseha M, Bown T, Copeland P, Crabaugh J, Fleagle J, Glantz M, Gordon A, Jacobs B, Maga M, Muldoon K, Pan A, Pyne L, Richmond B, Ryan T, Seiffert E, Sen S, Todd L, Wiemann MC, Winkler A. 2003. Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. *Nature* **426:** 549–552.

Keimer L. 1944. L'oryctérope dans l'Egypte Ancienne. *Etude d'Egyptologie* **6:** 1–20.

Kitching JW. 1963. A fossil *Orycteropus* from the limeworks quarry, Makapansgat, Potgietersrus. *Paleontologica Africana* **8:** 119–121.

Kjer KM, Honeycutt RL. 2007. Site specific rates of mitochondrial genomes and the phylogeny of Eutheria. *BMC Evolutionnary Biology* **7:** 8.

Klein RG. 1979. Paleoenvironmental and cultural implications of late Holocene archaeological faunas from the Orange Free State and North Central Cape Province, South Africa. *South African Archaeological Bulletin* **34:** 34–49.

Klein RG. 1986. The prehistory of stone age herders in the Cape province of South Africa. *South African Archaeological Society Goodwin Series* **5:** 5–12.

Klein RG, Avery G, Cruz-Uribe K, Steele TE. 2007. The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artefacts at Elandsfontein, Western Cape Province, South Africa. *Journal of Human Evolution* **54:** 164–186.

Klein RG, Cruz-Uribe K, Beaumont PB. 1991. Environmental, ecological, and paleoanthropological implications of the late Pleistocene mammalian fauna from Equus Cave, Northern Cape Province, South Africa. *Quaternary Research* **36:** 94–119.

Kostopoulos DS, Sen S, Koufos GD. 2003. Magnetostratigraphy and revised chronology of the late Miocene mammal localisites of Samos, Greece. *International Journal of Earth Sciences* **92:** 779–794.

Lamberton C. 1946. Contribution à la connaissance de la faune subfossile de Madagascar – Note XV – Le *Plesiorycteropus madagascariensis* Filhol. *Bulletin de l'Académie Malgache* **25:** 25–53.

Lavocat R. 1958. Tubulidentata. In: Piveteau J, ed. *Traité de Paléontologie*, Vol. 6(2). Paris: Masson et Cie, 139–144.

Leakey MG. 1987. Fossil aardvarks from the Laetolil Beds. In: Leakey MD, Harris JM, eds. *Laetoli, a Pliocene site in Northern Tanzania*. Oxford: Clarendon Press, 297–300.

Leakey MG, Harris JM, eds. 2003. *Lothagam – the dawn of humanity in Eastern Africa*. New York: Columbia University Press.

Leakey MG, Feibel C, Bernor RL, Harris JM, Cerling TE, Stewart KM, Storrs GW, Walker A, Werdelin L, Winkler A. 1996. Lothagam: a record of faunal change in the Late Miocene of East Africa. *Journal of Vertebrate Paleontology* **16:** 556–570.

Lehmann T. 2004. Fossil aardvark (*Orycteropus*) from Swartkrans Cave, South Africa. *South African Journal of Science* **100:** 311–314.

Lehmann T. 2006a. The biodiversity of the Tubulidentata over Geological time. *Afrotherian Conservation* **4:** 6–11.

Lehmann T. 2006b. Langebaanweg aardvarks: phylogenetic and palaeobiogeographical implications. *African Natural History* **2:** 187–188.

Lehmann T. 2007. Amended taxonomy of the order Tubulidentata (Mammalia, Eutheria). *Annals of the Transvaal Museum* **44:** 179–196.

Lehmann T. 2008a. Tubulidentata. In: Haile-Selassier Y, Woldegabriel G, eds. *Ardipithecus kadabba*. Berkeley: University of California Press, 517–520.

Lehmann T. 2008b. Plio-Pleistocene aardvarks (Mammalia, Tubulidentata) from East Africa. *Fossil Records* **11:** 67–81.

Lehmann T, Vignaud P, Likius A, Brunet M. 2004. A fossil aardvark (Mammalia, Tubulidentata) from the lower Pliocene of Chad. *African Journal of Earth Science* **40:** 201–217.

Lehmann T, Vignaud P, Mackaye HT, Brunet M. 2005. A new species of Orycteropodidae (Mammalia, Tubulidentata) in the Mio-Pliocene of Northern Chad. *Zoological Journal of the Linnean Society* **143:** 109–131.

Lehmann T, Vignaud P, Likius A, Mackaye HT, Brunet M. 2006. A sub-complete fossil aardvark (Mammalia, Tubulidentata) from the Upper Miocene of Chad. *Comptes Rendus Palévol* **5:** 693–703.

Lesson RP. 1840. Observations zoologiques. *Revue Zoologique par la Société Cuvierienne* **3:** 225–227.

Lewis GE. 1938. A skull of *Orycteropus pilgrimi*. *American Journal of Science* **36:** 401–405.

Lydekker R. 1908. *The game animals of Africa*. London: Rowlond Ward, Limited.

Lönnberg E. 1906. On a new *Orycteropus* from Northern Congo and some remarks on the dentition of the Tubulidentata. *Akiv für Zoologi* **3:** 1–35.

MacFadden PL, Brock A, Partridge TC. 1979. Palaeomagnetism and the age of the Makapansgat hominid site. *Earth and Planetary Science Letters* **44:** 373–382.

MacInnes DG. 1956. Fossil Tubulidentata from East Africa. *Fossil Mammals of Africa*, British Museum (Natural History), London **10:** 1–38.

MacPhee RDE. 1994. Morphology, adaptations, and relationships of Plesiorycteropus, and a diagnosis of a new order of eutherian Mammals. *Bulletin of the American Museum of Natural History* **220:** 1–214.

van der Made J. 2003. The aardvark from the Miocene hominoid locality Çandir, Turkey. Courier Forschungs-Institut Senckenberg. *Frankfurt* **240:** 133–147.

Major F. 1888. Sur un gisement d'ossements fossiles dans l'île de Samos, contemporains de l'âge de Pikermi. *Compte Rendu de l'Académie des Sciences de Paris* **117:** 1178–1181.

Major F. 1893. On the tooth of an ant bear. *Proceedings of the Zoological Society of London*, **1893:** 239–240.

Manlius N. 2002. Aardvarks to otters: ancient Egypt's unusual fauna. *Ancient Egypt* **3:** 24–31.

Marean CW. 1992. Implications of late quaternary mammalian fauna from Lukenya Hill (South-Central Kenya) for paleoenvironmental change and faunal extinctions. *Quaternary Research* **37:** 239–255.

Matschie P. 1898. Aus der Säugetierwelt der mittleren Hochländer Deutsch-Ost-Afrikas. In: Werther CW, ed. *Die mittleren Hochländer des Nördlichen Deutsch-Ost-Afrikas*. Berlin: Hermann Patel Verlag, 205–267.

Matschie P. 1900. Einige Säugetiere aus dem Hinterlande von Kamerun. *Gesellschaft naturforschender Freunde, Berlin* **3:** 87–138.

Melton DA. 1976. The biology of aardvark (Tubulidentata-Orycteropodidae). *Mammal Revue* **6:** 75–88.

Milledge SAH. 2003. Fossil aardvarks from the Lothagam Beds. In: Harris JM, Leakey MG, eds. *Lothagam – the down of humanity in Eastern Africa*. New York: Columbia University Press, 303–308.

Murphy WJ, Pringle TH, Crider TA, Springer MS, Miller W. 2007. Using genomic data to unravel the root of the placental phylogeny. *Genome Research* **17:** 413–421.

Ozansoy F. 1965. Etude des Gisements Continentaux et des Mammifères du Cénozoique de Turquie. *Mémoires de la Société Géologique de France* **102:** 1–92.

Pagès E. 1970. Sur l'écologie et les adaptations de l'oryctérope et des pangolins sympatriques d'Afrique. *Biologia Gabonica* **6:** 27–92.

Pallas PS. 1766. *Miscellanea zoologica*. La Haye: AP Van Cleef.

Pallas PS. 1780. Observationes circa *Myrmecophagam africanam* et *Didelphidis novam speciem orientalem*, e litteris celeberrimi Petri Camper excerplae et illustratae. *Acta Academiae scientiarum imperialis Petropolitanae pro anno 1777*, p. 225, pars posterior, Petropoli.

Patterson B. 1975. The fossil Aardvarks (Mammalia: Tubulidentata). *Bulletin of the Museum of Comparative Zoology, Cambridge* **147:** 185–237.

Patterson B. 1978. Pholidota and Tubulidentata. In: Maglio VJ, Cooke HBS, eds. *Evolution of African Mammals*. Cambridge: Harvard University Press, 268–278.

Pavlova MV. 1915. Mammifères tertiaires de la Nouvelle Russie. *Nouveaux Mémoires de la Société des Naturalistes, Moscou* **XVII:** 45–46.

Pickford M. 1975. New fossil Orycteropodidae (Mammalia, Tubulidentata) from East Africa. *Netherlands Journal of Zoology* **25:** 57–88.

Pickford M. 1978. New evidence concerning the fossil Aardvarks (Mammalia, Tubulidentata) of Pakistan. *Tertiary Research* **2:** 39–44.

Pickford M. 1981. Preliminary Miocene mammalian biostratigraphy for Western Kenya. *Journal of Human Evolution* **10:** 73–97.

Pickford M. 1994. Tubulidentata of the Albertine Rift Valley, Uganda. In: Senut B, Pickford M, eds. *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. II: Palaeobiology*. CIFEG 29 Occasional Publications, 261–262.

Pickford M. 1996. Tubulidentata (Mammalia) from the Middle and Upper Miocene of southern Namibia. *Comptes Rendus de l'Académie des Sciences, série IIa* **322:** 805–810.

Pickford M. 2003. Minute species of *Orycteropus* from the early Middle Miocene at Arrisdrift, Namibia. *Memoir of the Geological Survey of Namibia* **19:** 195–198.

Pickford M. 2004. Southern Africa: a cradle of evolution. *South African Journal of Science* **100:** 205–214.

Pickford M. 2005. *Orycteropus* (Tubulidentata, Mammalia) from Langebaanweg and Baard's Quarry, Early Pliocene of South Africa. *Comptes Rendus Palevol* **4:** 715–726.

Pickford M, Andrews P. 1981. The Tinderet Miocene sequence in Kenya. *Journal of Human Evolution* **10:** 1–33.

Pickford M, Morales J. 1998. Une lignée de suiformes de type tubulidenté (Tayassuidae, Mammalia) du Miocène inférieur d'Espagne. *Comptes Rendus de l'Académie des Sciences – Séries IIA – Earth and Planetary Science* **327:** 285–290.

Pocock RI. 1924. Some external characters of *Orycteropus afer*. *Proceedings of the Zoological Society, London* **46:** 697–706.

Potts R, Deino A. 1995. Mid-Pleistocene change in large Mammal faunas of East Africa. *Quaternary Research* **43:** 106–113.

Potts R, Shipman P, Ingall E. 1988. Taphonomy, paleoecology, and hominids of Lainyamok, Kenya. *Journal of Human Evolution* **17:** 597–614.

Robinson RJ, Seiffert ER. 2004. Afrotherian origins and interrelationships: new views and future prospects. *Current Topics in Developmental Biology* **63:** 37–60.

Romer AS. 1938. Mammalian remains from some Paleolithic stations in Algeria. *Logan Museum Bulletin* **5:** 165–184.

Rook L, Masini F. 1994. Orycteropus cf. gaudryi (Mammalia, Tubulidentata) from the late Messinian of the Monticino Quarry (Faenza, Italy). *Bullettino dellà Società Paleontologica Italiana* **33:** 369–374.

Rothschild W. 1907. On a new race of *Orycteropus*. *Novitates Zoologicae* Tring. **14:** 506.

Rothschild W. 1927. Description of a new race of Aardvarks (*Orycteropus afer kordofanicus*). *Annals and Magazine of Natural History, ser. 9* **19:** 512.

Rögl F. 1999. Circum-Mediterranean Miocene palaeogeography. In: Rössner G, Heissig K, eds. *The Miocene Land Mammals of Europe*. München: Friedrich Pfeil Verlag, 39–48.

Sen S. 1986. *Contribution à la magnétostratigraphie et à la paléontologie des formations continentales néogènes du pourtour méditerranéen. Implications biochronologiques et paléobiologiques*. Unpublished D. Phil. Thesis, Université Paris VI.

Sen S. 1990. *Hipparion datum* and its chronologic evidence in the mediterranean area. *NATO ASI Series, Serie A; Life Science 'European Neogene Mammal Chronology'* **180:** 495–595.

Sen S. 1994. Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie: 5. Rongeurs, Tubulidentés et Chalicothères. *Bulletin du Museum National d'Histoire Naturelle de Paris* **16**; 4ème série; section C: 97–111.

Sen S, Valet JP. 1986. Magnetostratigraphy of late Miocene continental deposits in Samos, Greece. *Earth and Planetary Science Letter* **80:** 167–174.

Shipman P, Potts R, Pickford M. 1983. Lainyamok, a new middle Pleistocene hominid site. *Nature* **306:** 365–368.

Shoshani J, Goldman CA, Thewissen JGM. 1988. *Orycteropus afer*. *Mammalian Species* **300:** 1–8.

Simpson GG. 1959. A new Middle Eocene edentate from Wyoming. *American Museum Novitates* **1950:** 1–12.

Sondaar PY. 1971. The samos *Hipparion*. *Proceeding of the Koninklijke Nederlandse Akademie van Wetenschappen, series B* **74:** 417–441.

Sonntag CF. 1925. A monograph of *Orycteropus afer*. – I. Anatomy except the nervous system, skin, and skeleton. *Proceedings of the Zoological Society, London* **23:** 331–437.

Sonntag CF, Woolard HH. 1925. A monograph of *Orycteropus afer*. – II. Nervous system, sense organs and hairs. *Proceedings of the Zoological Society, London* **1925:** 1185–1235.

Springer MS, Cleven GC, Madsen O, de Jong WW, Waddell VG, Amrine HM, Stanhope MJ. 1997. Endemic African mammals shake the phylogenetic tree. *Nature* **388:** 61–64.

Springer MS, Murphy WJ, Eizirik E, O'Brien SJ. 2003. Placental mammal diversification and the Cretaceous-Tertiary boundary. *Proceedings of the National Academy of Sciences of the United States of America* **100:** 1056–1061.

Springer MS, Stanhope MJ, Madsen O, de Jong WW. 2004. Molecules consolidate the placental mammal tree. *Trends in Ecology and Evolution* **19:** 430–438.

Stanhope MJ, Waddell VG, Madsen O, de Jong WW, Hedges SB, Cleven GC, Kao D, Springer MS. 1998. Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. *Proceeding of the National Academy of Science USA* **95:** 9967–9972.

Sundevall CJ. 1843. *Orycteropus aethiopicus*. *Kongliga Svenska Vetenskaps-Akademeins Handlingar Stockholm* **1842:** 236–242.

Swofford DL. 1998. *PAUP – Phylogenetic Analysis Using Parcimony*. Massachussets, Sunderland: Sinauer Associates.

Tabuce R, Marivaux L, Adaci M, Bensalah M, Hartenberger J-L, Mahboubi M, Mebrouk F, Tafforeau P, Jaeger J-J. 2007. Early Tertiary mammals from North Africa reinforce the molecular Afrotheria clade. *Proceedings of the Royal Society, B* **274:** 1159–1166.

Tabuce R, Asher RJ, Lehmann T. 2008. Afrotherian Mammals: a review of current data. *Mammalia* **72:** 2–14.

Taylor WA, Skinner JD. 2003. Activity patterns, home ranges and burrow use of aardvarks (*Orycteropus afer*) in the Karoo. *Journal of Zoology, London* **261:** 291–297.

Taylor WA, Lindsey PA, Skinner JD. 2002. The feeding ecology of the aardvark *Orycteropus afer*. *Journal of Arid Environments* **50:** 135–152.

Tekkaya I. 1993. Türkiye fosil Orycteropodidae'leri. *T. C. Kültür Bakanligi Anitlar ve Müzeler Genel* Müdürlügü. VIII Arkeometri Sonuçlari Toplantisi 1992, Ankara, 275–289.

Thewissen JGM. 1985. Cephalic evidence for the affinities of Tubulidentata. *Mammalia* **49:** 257–284.

Thewissen JGM, Badoux DM. 1986. The Descriptive and Functional Myology of the Fore-Limb of the Aardvark (*Orycteropus afer*, Pallas 1766). *Anatomische Anzeiger, Jena* **162:** 109–123.

Thomas O. 1890. A milk dentition in *Orycteropus*. *Proceedings of the Royal Society, London* **47:** 246–248.

Urbain A. 1954. Biologie de l'Oryctérope. *Annales du Muséum Royal du Congo Belge (NS), Sciences Zoologiques* **1:** 101–105.

Van Neer W. 1984. Faunal remains form Matupi cave, an iron age and late stone age site in norhteastern Zaïre. *Academia Analecta* **46:** 58–76.

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

Waddell PJ, Kishino H, Ota R. 2001. A phylogenetic foundation for comparative mammalian genomics. *Genome Informatics Series* **12:** 141–154.

Willis CK, Skinner JD, Robertson HG. 1992. Abundance of ants and termites in the False Karoo and their importance in the diet of the aardvark, *Orycteropus afer*. *African Journal of Ecology* **20:** 322–334.

WoldeGabriel G, Haile-Selassie Y, Renne PR, Hart WK, Ambrose SH, Asfaw B, Heiken G, White T. 2001. Geology and palaeontology of the late Miocene Middle Awash valley, Afar Rift, Ethiopia. *Nature* **412:** 175–177.

Woodward AS. 1901. On the bone-beds of Pikermi, Attica, and on similar deposits in Northern Euboea. *The Geological Magazine, New Series* decade IV, **III:** 481–486

Yang F, Alkalaeva EZ, Perelman PL, Pardini AT, Harrison WR, O'Brien PCM, Fu B, Graphodatsky AS, Ferguson-Smith MA, Robinson TJ. 2003. Reciprocal chromosome painting among human, aardvark, and elephant (superorder Afrotheria) reveals the likely eutherian ancestral karyotype. *Proceedings of the National Academy of Sciences of the United States of America* **100:** 1062–1066.

von Zimmermann EAW. 1778. *Geographische Geschichte der vierfüßigen Tiere*. Band I, Leipzig, *P*. 305 and Band II, p. 407.

Zukowsky L, Haltenorth T. 1957. Das Erdferkel (*Orycteropus afer*) aus Angola, eine eigene Unterart? *Säugetierkundliche Mitteilungen* Band **V:** 124–126.

APPENDIX

Description and comments on the characters chosen for the cladistic analysis

Cranium (Figs S1, S2)

1. *Facial surface of lacrimal:* absent or slight (0); distinct (1).
   For further details and illustration, see Cox (2006: character 2).
2. *Lacrimal foramen:* facial (0); orbital (1).
   For further details and illustration, see Cox (2006: character 4).
3. *Caudal tympanic process of the petrosal:* reduced (0); shields posterior bulla (1).
   For further details and illustration, see Asher (2007: character 22).
4. *Mastoid exposure in ventral basicranium and occipital region:* moderate to extensive (0); reduced to absent (1).
   For further details, see MacPhee (1994: character 12).
5. *Position of the temporal line:* high (0); low (1); absence of temporal line (2).
   On the cranium, a slightly projecting line marks the dorsal limit of the insertion surface for the temporal muscle. This almost horizontal line can be situated somewhat above the squamoso–parietal suture (1), or closer to the sagittal plan, and thus higher on the cerebral cap, featuring a constriction towards the nuchal line (0).
6. *Nuchal line (lambdoid crest) (in dorsal view):* rectilinear (0); V-shaped (1).
   In all Tubulidentata, the occipital, and sometimes the parietal, participate in the nuchal line. The lambdoid suture (between these two bones) fits the shape of this line, and in some taxa (such as *O. gaudryi*) the suture is situated on the line itself, thus forming a lambdoid crest. Remarkably, the V-shaped indentation of the nuchal line observed in some fossil taxa evokes the triangular shape of the interparietal bone present in juvenile specimens of *O. afer*.
7. *Relative position of the anterior border of the orbit (in lateral view):* anterior to M^2 (0); above M^3 (1); above M^2 (2).
   Taking the upper tooth row as the horizontal, the character refers to the position of the perpendicular through the anterior border of the orbit with regard to the upper tooth row. This position can reflect the lengthening of the snout (Colbert, 1941; Lehmann *et al.*, 2005). Contra MacInnes (1956), it is impossible to determine the state of this character for *M. africanus* because the anterior border of the orbit is not preserved. Moreover, the study of the holotype of *O. crassidens* led to a

different interpretation for the state of this character, formerly described by Arambourg (1959).

8. *Ventralmost point of the maxillo–jugal suture (in lateral view):* caudal to M^3 (0); above M^3 (1).
   As for character 3, the upper tooth row must be taken as the horizontal in order to determine the state of this character. The suture between maxilla and jugal bones extends obliquely from the lacrimal bone to the ventral part of the jugal process. This character refers to the position of the ventralmost point of the suture with regard to the upper tooth row. Lehmann *et al.* (2005) suggested that the position of this point can also denote the lengthening of the snout.
9. *Palatine groove:* absent (0); present (1).
   In the extant *O. afer*, the rostral region of the palate shows a more or less deep median groove (1). However, in other Orycteropodidae, this groove is absent and the entire rostral part of their palate takes, in ventral view, a concave shape (0). Both states of character are present in specimens of *O. gaudryi* found in Samos (Greece). Note that a very distinct groove can already be observed in the juveniles of *O. abundulafus* and *O. afer*.
10. *Palate breadth:* broad (0); slender (1).
    This character refers to the proportion of the palate expressed with a palate index (breadth of the palate at the maxillo–palatine suture/length of the palate, from the post-palatine torus to the tip of the maxilla). Broad palates show a palate index superior to 21% (0), and slender ones show an index inferior to 21% (1). The 21% limit corresponds to the minimum palate index found for the extant *O. afer* ($n = 79$, mean = 25.1% ± 2.1). Correlatively, Orycteropodidae with a broad palate (0) often show parallel upper tooth rows, whereas Tubulidentata with a slender palate (1) show rather rostrally converging upper tooth rows. Remarkably, the juvenile specimens of *O. afer* (not taken into consideration here) show an index that is usually higher than their adult relatives. This character has been estimated for the species *O. browni*, because it could only be observed on a cast of specimen YPM 13901 as the original fossil is apparently lost.
11. *Relative position of the post-palatine foramina:* at the level of the M^2 (0); at the level of M^3 (1); caudal to M^3 (2).
    Orycteropus browni is the only Tubulidentata known so far to present the character state (0). However, and as for the previous feature, this character could only been observed on a cast of specimen YPM 13901.
12. *Shape of the post-palatine torus:* rectilinear (0); curved (1).
    This character is probably linked to the general breadth of the cranium. It is not possible to determine the state of this character in *O. crassidens* (contra MacInnes, 1956) because this part of the palatine is broken.
13. *Relative position of the post-palatine torus:* caudal to M^3 (0); at the level of M^3 (1).
14. *Lateral wall of the pterygoid:* smooth (0); with ridges (1).
    On the lateral wall of the pterygoid, oblique ridges can extend towards the alisphenoid in some Tubulidentata. These crests edge a basin situated in front of the oval foramen. This depression is not similar to a *fossa pterygoidea* (seen for instance in rabbits, hedgehogs, and humans), because it does stretch on the alisphenoid and is strictly limited to the lateral part of the pterygoid, not its dorsal part. The surface enclosed by those ridges is probably the insertion surface for the pterygoideus lateralis and medialis muscles. A bulging of the suture between palatine, pterygoid, and alisphenoid bones can occasionally be observed in some taxa, such as *O. afer*, but it never develops into a real crest. Conversely, when distinct crests are present (1), the rostral crest can sometimes be surmounted by a small tubercle (see Lehmann *et al.*, 2006).
15. *Extension of the interorbital constriction:* also including the palatine (0); formed strictly by the frontal, orbitosphenoid, and alisphenoid (1); no orbital constriction (2).
    The two orbital cavities are deep in all Tubulidentata. However, this constriction is stronger at the orbitosphenoid/alisphenoid level in some taxa (1), whereas it is stronger rostrally to the orbitosphenoid, and thus involves the palatine as well, in others (0).
16. *Configuration of the cranio-mandibular articulation:* flat or slightly convex on the mandible (0); with a tubercle on the glenoid cavity, and a concave surface on the mandible (1).
    For the character state (0), both articular surfaces (on the mandible and the glenoid cavity) are broad and flat, or are slightly convex. Conversely in some Orycteropodidae, for the character state (1), the articular surface on the mandible is concave and the glenoid cavity presents a lateral tubercle that fits the mandibular concavity. Therefore, the character state has been assessed even if one part of the cranio-mandibular articulation is missing (e.g. *O. depereti* is known by its sole cranium that displays a lateral tubercle).

Mandible (Fig. S2)

17. *Angle between the mandibular rami (in lateral view):* inferior to 60° (0); between 60° and 73° (1); superior to 73° (2).
    This character refers to the measurement of the supplement of the angle formed by the anterior border of the vertical branch and the lower tooth row (as measured by MacInnes, 1956). It is always an acute angle. The 60° limit corresponds with the minimum angle measured for the extant species ($n = 63$, mean = 66° ± 5.2), whereas the 73° limit corresponds with the minimum angle found in *O. abundulafus* and *O. gaudryi* ($n = 4$, mean = 77.4° ± 5.2 and $n = 9$, mean = 77.8° ± 3.1, respectively).
18. *Position of the articular condyle of the mandible with respect to the coronoid process:* separated by a mandibular notch (0); in contact (1).
    This character refers to the absence (1) or presence (0) of an incisura mandibulae. This notch enables the passage of the massetericus nerve in order to inerve the masseter pars superficialis muscle (Edgeworth, 1924). In state (1), the passage for the nerve is probably limited, or is even blocked.

Dentition (Fig. S2)

The dentition usually plays a very important role when inferring the phylogeny of mammalian taxa. The teeth of the Tubulidentata are unique among mammals: their minute structure was even used to name their order. However, from the oldest known *O. minutus* to the extant *O. afer*, the teeth of the aardvarks are very similar, so that it is very difficult to use these elements for diagnosis and cladistic analysis. In fact, the shape, size, and number of teeth in an individual all show minor variations, and these variations can be found in several species. For instance, the bilobation of the upper and lower M3 has often been put forward as a specific and even generic diagnostic feature (e.g. Colbert, 1941; MacInnes, 1956). However, in the extant species, the M3 can present all of the different stages of bilobation, from the total absence to the presence of very deep lingual and vestibular grooves. Therefore, only five characters of the 39 are related to the dentition in this analysis.

19. *Dental microstructure:* not tubulidentate (0); tubulidentate (1).
20. *Shape of the upper molar outline (in occlusal view):* rectangular (0); trapezoid (1).
    In Tubulidentata, the outline of the upper and lower molars is usually similar, except for *O. pottieri* and perhaps *O. seni*, according to published data. Besides being bilobed, the lingual and vestibular borders of the molars are more or less parallel. Conversely, the mesial and distal borders are not always parallel with each other. In character state (0), the borders are parallel two by two, and adjacent sides are perpendicular to each other, whereas in state (1), at least the distal border is not perpendicular to the lingual and vestibular border, so that the outline of the tooth is rather trapezoid.
21. *Lingual groove on the upper molars (in occlusal view):* shallow (0); deep (1); shallow only on the M^2 (2).
    The upper molars of all Tubulidentata are bilobed, but the two grooves that cut their lingual and vestibular borders are not always similar. In character state (0), the lingual groove is almost absent on the M^1 and M^2. In state (1), the lingual and vestibular grooves are subequal and deep. Finally, in state (2) (only seen in *M. africanus* so far), the M^1 shows subequal and deep grooves, whereas only the vestibular groove is deep on the M^2. The condition of the M^3, more variable, is not taken into account for this character. Remarks: the lower molars of all Orycteropodidae present two deep grooves, except in *O. seni* for which the lingual groove is shallow.
22. *Orientation of the upper molars alveoli with respect to the palatine plan (in caudal view):* perpendicular (0); oblique (1).
23. *Canines:* present (0); absent (1).
    As noticed by Lehmann *et al.* (2005), the canines of *L. guilielmi* and *O. pottieri* (not included in the cladistic analysis, see Material and methods) are large, significantly larger than the premolars. Helbing (1933), Arambourg (1959), and Patterson (1975) described *O. depereti* and *O. mauritanicus* as possessing canines. Those maxillary teeth are in fact the fifth ones in front of the molars, and are smaller than the premolars. In the extant *O. afer*, supernumerary teeth are sometimes visible, especially in the immature stages, and are always smaller than the teeth posterior to them. Therefore, I consider here that *O. depereti* and *O. mauritanicus* display supernumerary premolars, and not real canines.

Post-cranium (Figs S3, S4)

24. *Development of the deltoid crest on the humerus:* weak and not projected laterally (0); strong and projected laterally (1).
    The dorsal side of the humerus of an aardvark usually bears two more or less developed crests: the pectoral crest and the deltoid crest. The latter is summed up to a faint line along the diaphysis in some taxa (0). However, the deltoid crest is usually strongly developed and laterally projected (1). *Leptorycteropus guilielmi* and *O. abundulafus*

share the absence of a well-developed deltoid crest. However, as in all other Tubulidentata, the deltoid and pectoral crests form a flat part on the diaphysis of *O. abundulafus*, whereas this part is round and bears a central pectoral crest in *L. guilielmi*.

25. *Shape of the olecranon fossa on the humerus:* oval and bounded proximally (0); triangular, ascending in the middle (1).
26. *Breadth of the distal epiphysis of the humerus:* slender (0); broad (1).
    This character refers to the proportion of the distal epiphysis of the humerus expressed with an index (distal mediolateral breadth/length of the humerus). Broad epiphyses show an index superior to 35% (1), whereas slender ones show an index inferior to 35% (0). The 35% limit corresponds with the minimum index found for the extant *O. afer* ($n = 43$, mean = 39% ± 2). However, this index is always superior to 30% in all known Tubulidentata. According to Hildebrand (1985), a high index (30–70%) suggests fossorial habits. Remarkably, the juvenile specimens of *O. afer* (not taken into consideration here) show an index that is usually higher than their adult relatives. Note that the humerus of *L. guilielmi* is not complete. However, its length can be roughly estimated between 80 and 90 mm. Thus, its breadth to length ratio ranges between 33.1 and 29.4%, and can be confidently characterized as slender (state 0).
27. *Relative orientation of the articulation axis of the trochlear notch on the ulna (in ventral view):* perpendicular to the diaphysis (0); oblique to the diaphysis (1).
    When the articulation axis of the trochlear notch is oblique to the diaphysis (0), the proximal and distal articulation surfaces of the notch face each other. Conversely, when the articulation axis is perpendicular to the diaphysis (1), the articulation surfaces do not face each other, but are instead set aside. According to Lehmann *et al.* (2004: 208), in the later configuration, 'The pitch of these surfaces enlarges the contact with the distal epiphysis of the humerus and prevents uncontrolled movement and dislocation. Such mechanisms are common among digging mammals'.
28. *Shape of the oblique rim on the radius (dorsal view):* sharp (0); blunt, with muscular insertion marks (1).
    In Tubulidentata, the oblique rim of the radius starts as a sharp crest close to the distal epiphysis. It extends proximally until it broadens, approximately at the proximal third of the bone, and shows muscular insertion marks (of the supinator muscle) (0). However, as in *O. abundulafus*, this rim can begin to broaden more distally, under the midline of the diaphysis, and supports a bony flat part where the insertion marks are visible (1).
29. *Number of sacral vertebrae:* five (0); six (1); between five and seven (2); three (3).
    In *O. afer*, the number of vertebrae involved in the sacrum varies as a function of the age of the individual. In the early stages of ontogeny, the sacrum consists of five vertebrae. Before the animal reaches adolescence, however, the first caudal vertebra fuses completely with the sacrum. Only adult specimens have thus been taken into account for assessing the state of this character.
30. *Relative orientation of the caput femoris (in proximal view):* mediodorsal to lateroventral (0); mediolateral (1); ball-like caput femoris, no orientation (2).
    Taking the dorsal wall of the trochanteric fossa as the mediolateral mark, this character refers to the orientation of the longest axis of the caput femoris. In *Chrysochloris*, the caput femoris is ball-like, so that no longest axis can be defined.
31. *Pectineal tubercle:* absent (0); present (1).
    In the Tubulidentata, a distinct tubercle is present distally from the second trochanter. Quoting Howell (1941), MacPhee (1994) refers to it as the 'fourth trochanter'. However, Howell's fourth trochanter is situated more distally on the femur, and is the insertion point for the caudofemoralis muscle (in some mammals, several reptiles, and birds, in general), and the presemimembranosus muscle (present in all vertebrates, but situated more distally). Moreover, Le Gros Clark & Sonntag (1926) showed that the tubercle present in the Orycteropodidae is the insertion point for the pectineus muscle. Howell's fourth trochanter and the pectineal tubercle of the Tubulidentata are thus not homologous structures.
32. *Relative position of the articular facet for the sesamoid bone of the gastrocnemius muscle on the femur (in lateral view):* at the level of the diaphysis (0); recessed, ventral to the diaphysis line (1).
    This sesamoid bone articulates with the lateral condyle of the distal epiphysis of the femur. The ventral line of the diaphysis, aligned on the third trochanter, is taken as the reference line for the diaphysis. In Tubulidentata, the gastrocnemius muscle keeps the foot extended while displacing the soil, and, according to Lehmann *et al.* (2005: 122), 'a more anterior position of the sesamoid bone [character state (0); n.d.], involving a moment arm axis closer to the lateromedial diameter of the diaphysis, reduces energy expenditure'.

33. *Development of the tibial tuberosity on the tibia (in dorsal view):* concave and slender (0); flat and broad (1); flat and slender (2).
34. *Falciform process on the proximal epiphysis of the tibio-fibula (in proximal view):* absent (0); present (1).

    Arambourg (1959) tried to distinguish *O. afer*, *O. gaudryi*, and *O. mauritanicus* according to the shape of the proximal epiphysis of their tibio-fibula. However, as shown by Lehmann *et al.* (2004), Arambourg was deceived by a bad cast of *O. gaudryi*, and his conclusion must thus be taken with reserve. Nevertheless, his description of the epiphysis in *O. gaudryi* as trilobed is correct, but is rather a result of the absence of a falciform process (0). Indeed, the presence of this process projecting from the dorsolateral side of the epiphysis (1), as in *O. afer*, adds a fourth lobe in proximal view. The morphological function of this process is unknown (MacPhee, 1994).
35. *Relative length of the tibia and the femur:* subequal length (0); tibia longer than the femur (1); femur longer than the tibia (2).

    This character refers to the comparison between the maximum lengths of the tibia and the femur. Remarkably, the juvenile specimens of *O. afer* show a tibia that is longer than the femur (1), whereas their adult relatives show a femur that is longer than the tibia (2). Therefore, only adult specimens have been taken into account for assessing the state of this character.
36. *Relative development of the tibial crest:* short and merging abruptly with the diaphysis (0); long and merging in a gentle slope, close to the middle of the diaphysis (1).
37. *Mediolateral shape of the tibial diaphysis (in dorsal view):* straight (0); curved (1).
38. *Cotyloid facet of the talus:* concave and developed (0); vertical and negligible (1).

    The cotyloid facet articulates with the medial malleolus of the tibia. Taxa like *M. africanus* presenting the character state (1) also display a water-drop shaped sustentacular articulation facet for the calcaneum. The presence of a concave cotyloid facet was described as a probable synapomorphy of the Afrotheria ('cotylar fossa'; Tabuce *et al.*, 2007).
39. *Astragalar posteromedial process:* small or absent (0); prominent (1).

    For further details and illustration, see Asher (2007: character 172).

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Cranial character states. A, dorsal view of the cerebral capsules of *Orycteropus afer* (left; AMNH 51374) and *Orycteropus gaudryi* (right; AMNH 20562). B, caudal view of crania of *O. afer* (left; Collection of the University of Poitiers) and *Orycteropus crassidens* (right; NHM M21543). C, detail of a lateral view of the pterygoid region of crania of *O. afer* (top; Collection of the University of Poitiers) and *Orycteropus abundulafus* (bottom; TM255-03-01). D, lateral view of crania of *O. afer* (left; AMNH 150398) and *O. gaudryi* (right; AMNH 20561). Scale bars: 1 cm.

Figure S2. Craniomandibular and dentition character states. A, ventral view of crania of *Orycteropus gaudryi* (left; AMNH 20694) and *Orycteropus afer* (right; AMNH 51372). Note that the tip of the snout of AMNH 20694 is reconstructed in plaster. B, vestibular view of the left hemimandibles of *O. gaudryi* (top; AMNH 20694) and *O. afer* (bottom; AMNH 51372). C, dorsal view of the mandibles (focused on the articular condyle) of *O. afer* (top; Collection of the University of Poitiers) and *O. gaudryi* (bottom; AMNH 20694). Scale bars: 1 cm.

Figure S3. Post-cranial character states. A, dorsal view of the right humerus of *Orycteropus abundulafus* (left; TM255-03-01) and of the left humerus *Orycteropus afer* (right; AMNH 51374). B, ventral view of the right ulnae (focused on the proximal epiphysis) of *Orycteropus djourabensis* (left; KL09-98-001) and *Orycteropus crassidens* (right; NHM Kanjera 1-1955). C, dorsal view of the right radius of *O. abundulafus* (left; KB03-97-214) and of the left radius of *O. afer* (right; ZMB 84710). Scale bars: 1 cm.

Figure S4. Post-cranial character states. A, proximal view of the right femurs of *Myorycteropus africanus* (left; NHM M21509) and *Orycteropus abundulafus* (right; KB03-97-214); not to scale. B, lateral view of the right femur of *Orycteropus afer* (top; AMNH 51374) and of the left femur of *Orycteropus gaudryi* (bottom; AMNH 22888). C, dorsal–oblique view of the left tali of *M. africanus* (left; NHM M21512) and *O. afer* (right; ZMB 84695). D, dorsal view of the right tibio-fibulae of *O. gaudryi* (left; AMNH 22762) and *O. afer* (right; Collection of the University of Poitiers). Scale bars: 1 cm.