

A fossil aardvark (Mammalia, Tubulidentata) from the lower Pliocene of Chad

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Received 25 February 2004; received in revised form 27 December 2004; accepted 7 January 2005

Abstract

The Mission Paléanthropologique Franco-Tchadienne (MPFT) found a new species of Orycteropodidae (Mammalia, Tubulidentata) in the Kollé fossiliferous sector, northern Chad. After *Orycteropus abundulafus* [Journal of Vertebrate Paleontology 20 (1) (2000) 205–209; Lehmann, T., Vignaud, P., Likius A., Brunet M., in press. A new Orycteropodidae (Mammalia, Tubulidentata) in the Mio-Pliocene of Northern Chad. Zool. J. Linnean Soc.], this specimen is the second complete skeleton of fossil aardvark found in the Djurab desert. It is the first complete representative of an *Orycteropus* species found in the Pliocene of Africa. In regard to the Miocene fossil aardvarks, this new taxon, *Orycteropus djourabensis* nov. sp., shows more affinities with the extant *O. afer*. The main differences are the larger teeth and the shorter hand in the fossil form. Kossom Bougoudi and Kollé represent a chronological series that gives a unique opportunity for studying the evolution of the African Tubulidentata around the Mio-Pliocene boundary (5.5–4 My). The new species is distinct from the older Chadian Orycteropodid from KB and it embodies the taxonomic turnover that took place within the order Tubulidentata around this boundary in Africa. Moreover, this new species is the oldest known *Orycteropus* species that clearly belongs to the modern forms including the extant aardvark.

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Keywords: Africa; *Orycteropus*; Pliocene; Systematics; Turnover

1. Introduction

The Mission Paléanthropologique Franco-Tchadienne (MPFT) found the first Chadian fossil aardvark during the 1997 fieldwork in the fossiliferous area of Kossom Bougoudi (KB; northern Chad) (Brunet and MPFT, 2000; Lehmann et al., 2005). One year later, farther west, the younger Kollé (KL) fossiliferous area yielded a large sub-complete skeleton of fossil Tubulidentata. This is the best-preserved fossil aardvark found in the Pliocene of Africa. KL sector is situated

30 km NNE from the Hominid sites of Koro Toro in the Djurab desert (Brunet et al., 1995, 1996). Brunet et al. (1998) estimated a biochronological age of 5 to 4 Ma for KL.

The order Tubulidentata is represented by a single extant species: the aardvark, *Orycteropus afer* (Pallas, 1766). It lives in sub-Saharan Africa. Little is known about the origin of Tubulidentata but the classically accepted oldest forms are known from the Early Miocene of Kenya. During the Miocene, fossil aardvarks were widespread in Africa, and also Eurasia where they disappeared before the end of Pliocene. More derived forms replaced these aardvarks during the Plio-Pleistocene in Africa but they are very poorly known.

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This paper describes a new fossil aardvark species from Chad and it discusses the phylogeny and the biogeography of aardvarks around the Mio-Pliocene.

2. The Orycteropodinae

Following the classical and cautious description made by Patterson (1975), the Tubulidentata Huxley, 1872 consists of a single family (Orycteropodidae Gray 1821) and two sub-families (Orycteropodinae Gray, 1821 and Plesiorycteropodinae Patterson, 1975). Four genera, among which three are fossil, have been described so far, but their validity and affinities are still debated (Pickford, 1975; Made, 2003).

Among Orycteropodinae, *Leptorycteropus* Patterson, 1975 has been found in the Upper Miocene of Lothagam (Kenya). The genus *Orycteropus* Geoffroy, 1791 is known from Early Miocene to the Recent in Africa and Eurasia. The only living species of the order Tubulidentata belongs to this genus: *Orycteropus afer*. This nocturnal mammal eats ants and termites but also insect larva. Aardvarks live in burrows and are very efficient diggers that can break open termite mounts. At least 18 doubtful sub-species have been described from South Africa to sub-Saharan regions (Shoshani et al., 1988).

From Late Miocene to Recent, all fossil Orycteropodinae species belong to the genus *Orycteropus* except *Leptorycteropus guilielmi* Patterson, 1975. Among these fossils, there are Eurasian forms like *Orycteropus gaudryi* Major, 1888 from the Turolian of Greece (Colbert, 1941), Italy (Rook and Masini, 1994), Turkey (Sen, 1994), Moldavia (Pavlova, 1915), and Iran (Major, 1893), and *Orycteropus depereti* Helbing, 1933 from the Pliocene of France. In Africa, *Orycteropus* is represented by *O. abundulafus* from the close to the Mio-Pliocene boundary site of KB (Chad); *O. crassidens* MacInnes, 1956 from the Pleistocene of Kenya; and *O. afer*, the extant and type species, recognised since the Late Pleistocene of Algeria (Romer, 1938) (Fig. 1).

Indeterminate fossil Tubulidentata from Upper Miocene and Pliocene sites have also been unearthed. *Orycteropus* sp. is present in the Upper Miocene of Greece (Bonis et al., 1994), East Africa (Patterson, 1975; Milledge, 2003). Pliocene specimens have been found in East Africa (Dietrich, 1942; Butzer, 1971; Leakey, 1987) and South Africa (Kitching, 1963; Hendey, 1973; Lehmann, 2004).

3. Materials and methods

All measurements are taken directly on the material and are in millimetres, unless otherwise stated. In order to define large populations and allow reliable comparison with the biometry of single specimens, the Confidence

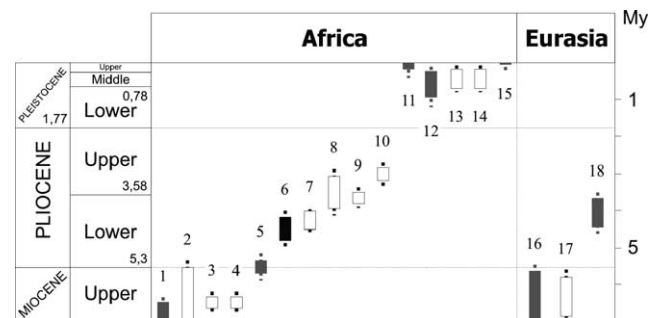


Fig. 1. Biochronological repartition of fossil Tubulidentata from Upper Late Miocene to present time (based on Colbert, 1933; Helbing, 1933; Dietrich, 1942; MacInnes, 1956; Arambourg, 1959; Kitching, 1963; Ozansoy, 1965; Hendey, 1973; Pickford, 1975; Leakey, 1987; Bonis et al., 1994; Rook and Masini, 1994; Sen, 1994; Milledge, 2003). 1 = *Leptorycteropus guilielmi* (Lothagam); 2 = *Orycteropus* sp. (Lothagam); 3 = *O. sp.* large form (Lukeino); 4 = *O. sp.* tiny form (Lukeino); 5 = *O. abundulafus* (Chad); 6 = *O. djourabensis* nov. sp. (Chad); 7 = *O. cf. afer* (Langebaanweg); 8 = *O. sp.* (Shungura); 9 = *O. sp.* (Laetoli); 10 = *O. cf. afer* (Makapansgat); 11 = *O. afer* (Africa); 12 = *Orycteropus crassidens* (Kenya); 13 = *O. sp.* (Olduvai and Vogel River); 14 = *O. sp.* (Gambles Cave II); 15 = *Plesiorycteropus madagascariensis* (Madagascar); 16 = *O. gaudryi* (Greece, Turkey); 17 = *O. cf. gaudryi* (Monticino); 18 = *O. depereti* (France). Filled bars for determined species and blank bars for indeterminate forms (*O. sp.* or *O. cf.*).

Interval for Individual Observation around the mean (CIIO) will be used. The limits of this interval are calculated with mean $\pm 1.96 \times$ standard deviation. They give the range in which the dimensions of 95% of the individuals of a population are expected to be located.

The material from Chad is compared to fossil material from other localities from Africa and Europe. The original extant aardvark database developed in this study consists of over 100 specimens studied in different institutions: the American Museum for Natural History, New York (AMNH); the Archeozoological Collection, Transvaal Museum, Pretoria; the Bernard Price Institute, Witwatersrand University, Johannesburg; the Staatliches Naturhistorisches Museum, Stuttgart; and the Museum für Naturkunde, Berlin. The following abbreviations will be used for reference in text and tables.

KNM = Kenya National Museum (ER = East Rudolf; LAET = Laetoli; LT = Lothagam)
 MNHN = Muséum National d'Histoire Naturelle, Paris
 Rss = Naturhistorisches Museum, Basel

4. Systematic palaeontology

Order: Tubulidentata Huxley, 1872
 Family: Orycteropodidae Gray, 1821
 Genus: *Orycteropus* Geoffroy, 1791
 Species: *Orycteropus djourabensis* nov. sp.

4.1. Holotype

KL09-98-001 (Fig. 2 and 3). A sub-complete skeleton discovered in anatomical connection. It includes: cranium and mandible with teeth (right P^2-M^3 , left M^1-M^3 and right P_3-M_3 , left P_4-M_3); right pectoral girdle (in part); vertebrate spine elements and ribs in anatomical connection; complete right and left forelimbs (except left stylopode and some carpals); pelvic girdle: both acetabular regions and part of the ilium, ischium and pubis; right femur, tibia, fibula, tarsals, metatarsals, and phalanges (including sesamoids); complete left femur, tibia, tarsals, metatarsals, and phalanges (including sesamoids). After study, the specimen will be held in the Centre National d'Appui à la Recherche (C.N.A.R.) from N'Djaména, Chad.

- *Hypodigm*: Type only.
- *Type locality*: KL09 site, Kollé, Djurab desert (Chad).
- *Age*: Pliocene (5 to 4 Ma) (Brunet et al., 1998).

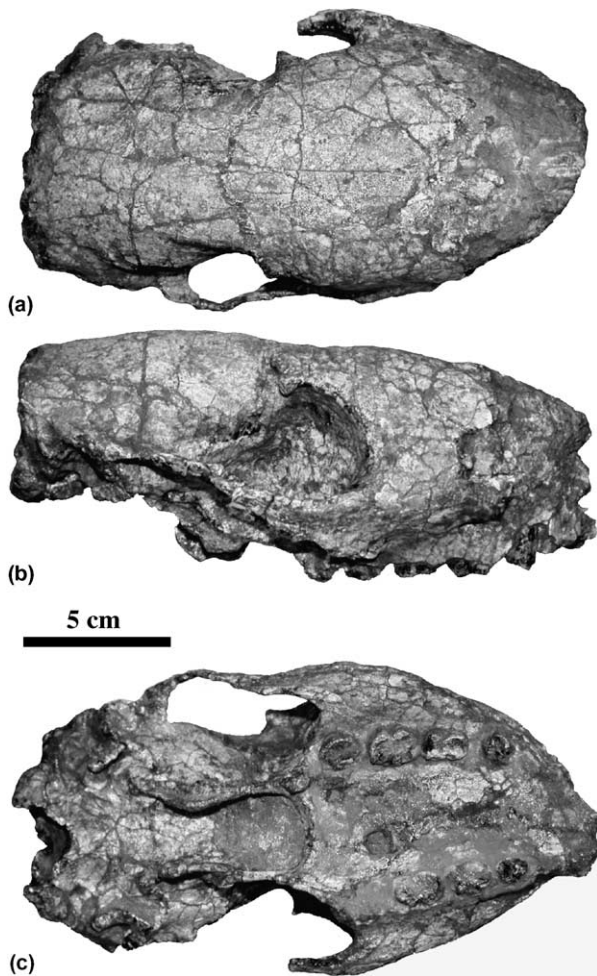


Fig. 2. Cranium of *Orycteropus djourabensis* nov. sp.: (a) in dorsal view; (b) in lateral view; (c) in ventral view.

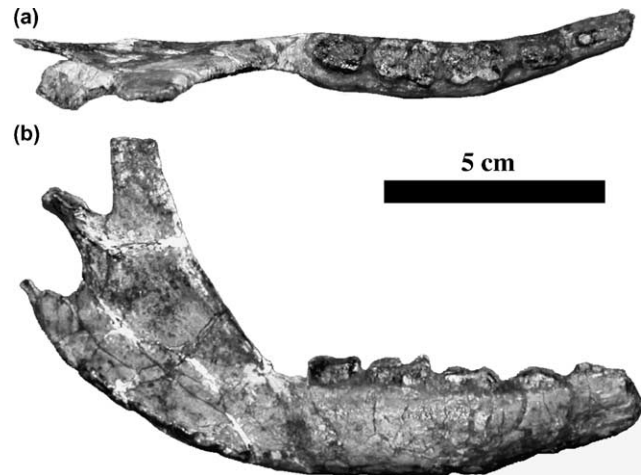


Fig. 3. Right hemi-mandible of *Orycteropus djourabensis* nov. sp.: (a) in occlusal view; (b) in lateral view.

- *Etymology*: The new species name refers to the Djurab desert (Djourab in French) where the specimen has been found.
- *Diagnosis*: Species of *Orycteropus* very close to *Orycteropus afer* in size but different by its longer pre-molars, longer lower molars, its shorter and more slender hands, and the articulation axis of the semi-lunar notch oblique to the diaphysis on the ulna.

5. Description

The skeleton belongs to a fully mature individual as all epiphysis are fused and no traces of their suture lines remain visible. All bones were found in a consolidated sandstone.

5.1. Cranium

It is well preserved but lacks the front part of the snout (cf. Fig. 2). The right side of the cranium is slightly compressed laterally and the cerebral cavity suffered from a coronal torsion. The left zygomatic arch is broken but the pterygoids and the ectotympanics are preserved.

The general size of the cranium is much closer to that found for the extant aardvark than that observed for the Late Miocene fossils from our set of comparison (Table 1) or the much smaller *Myorycteropus africanus* MacInnes, 1956 and *Orycteropus minutus* Pickford, 1975. When compared to specimens of *O. afer*, the Chadian fossil shows affinities with the largest extant sub-species that were collected in regions south from Chad.

The lambdoid crest (in dorsal view) is straight like in *O. afer* and not V-shaped like in *O. depereti*, *O. gaudryi*, and *O. abundulafus*.

Table 1

Cranium measurements (in mm) of *Orycteropus djourabensis* nov. sp. (KL09-98-001, holotype) compared to other Tubulidentata

| Species | Lf | Lfo | Lpar | Bio | Bpop | Bfps | Lutr | Hoccip | Hpter |
|-------------------------------|-------------------|---------------------|--------------------|--------------------|--------------------|--------------------|-----------------|--------------------|-------------------|
| <i>O. afer</i> | 57.3 ± 6 (80) | 117.6 ± 9.3 (80) | 51.9 ± 5.1 (77) | 57.3 ± 3.7 (84) | 64 ± 4.5 (86) | 47 ± 3.2 (88) | 51.7 ± 6.4 (79) | 47.2 ± 3.3 (62) | 62 ± 4.9 (65) |
| <i>O. depereti</i> (Holotype) | 53.6 | 105.4 | 48 | 52.3 | 59.6 | 42.9 | 45.6 | 40 | 50.6 |
| <i>O. gaudryi</i> | 48.5 ± 4.7 (7) | 86.2; 101.7 (2) | 43 ± 3.5 (6) | 56.8 ± 19.8 (7) | 66.8 ± 19.8 (5) | 47.5 ± 21.8 (8) | 43.4 ± 4 (7) | 35.6 (1) | 45.3 ± 2.5 (6) |
| <i>O. abundulafus</i> | 45.7 | 100.1 | 44.4 | 48.6 | 59 | 42.8 | 43.2 | | |
| <i>O. djourabensis</i> | 58.7 | 116 ^a | 55.6 | 62 | 65 ^a | 49.5 | 61.5 | 45 | 65.4 |

Lf = frontal length; Lfo = dorsal length from naso-frontal suture to occipital; Lpar = parietal length; Bio = interorbital breadth; Bpop = breadth taken between the tips of the postorbital processes; Bfps = breadth of the cranium at the frontoparietal suture; Lutr = upper tooth row length (P³ to M³); Hoccip = height of the cranium from the occipital condyle to the lambdoid crest; Hpter = height of the cranium from tip of the pterygoid to cranial roof. Descriptive statistics: mean ± standard deviation; number of observations indicated in brackets.

^a For estimated measurements.

The position of the anterior rim of the orbit relative to the upper tooth row is above M³ in the Chadian fossil as well as in all studied specimens of *O. afer*. In *O. abundulafus*, *O. gaudryi* and *O. depereti*, this rim is situated above M². The ventral-most point of the maxillo-jugal suture is, like in *O. afer* and *O. depereti*, behind M³, unlike in the two other fossil forms where it is above. From the figure of the skull presented by MacInnes (1956, plate 3), *O. crassidens* shows the same configuration that in *O. afer* and *O. djourabensis* nov. sp.

The estimated palatine breadth of KL09-98-001 is 29 mm. This value is in the CHIO range obtained from the measurements of 89 extant aardvarks (31.5 mm ± 3.8). The same measurement gives 23.9 mm for *O. depereti* (Rss 55), has a mean of 19.8 mm ± 1.2 for seven *O. gaudryi* from AMNH, and is 18 mm for *O. abundulafus*. The snout of the Kollé fossil is thus much wider than the one of the older Chadian species. The postpalatine torus is straight and far behind the level of M³ in the new species and in the extant form. Conversely, in *O. depereti*, *O. gaudryi*, and the specimen from KB, the torus is curved and tangent to the M³. It is not possible to say if KL09-98-001 has a palatine groove or not because the snout is broken in front of P³.

Many authors (MacInnes, 1956; Made, 2003; Lehmann et al., 2005) have noticed the general increase in size and the elongation of the snout from fossil forms to the extant aardvark. The elongation of the snout is a convergent character among anteaters (Redford, 1987). Lehmann et al. (2005) propose that the tooth-row was shifted forward by the maxilla during the evolution of the aardvark with the elongation as well as the widening of the snout as a result. The comparative set used in this study shows that all Late Miocene forms are about 25% smaller than *O. afer* and have a slender palatine. In *Leptorycteropus* the maxillary is not extending forward into an elongated snout. All aardvarks found in younger sites (except *O. depereti*) are not significantly smaller than the living aardvark and they possess a large and elongated snout.

The suture point between palatine, pterygoid and alisphenoid is swollen on the lateral side. This is also the case in some *O. afer*. It differs from the configuration observed in *O. abundulafus* and in some *O. gaudryi* specimens where an oblique crest extends on the lateral side of the pterygoid and alisphenoid bone. The glenoid cavity is large and flat as in *O. afer*. The lateral tubercle present in *O. depereti* and *O. gaudryi*, and *O. abundulafus* is absent. The zygomatic arch is whether broken or distorted.

5.2. Mandible

Both hemi-mandibles have been preserved (cf. Fig. 3). The right one is abnormally curved medially whereas the left one is not deformed. The symphyseal part is broken and the tips of some of the processes are missing.

The articular condyle shows a flat surface like in *O. afer*, in contrast to the concave surface found in *O. gaudryi* and *O. abundulafus*. This is correlated with the flat glenoid cavity on the cranium. This shape precludes a large opening of the mouth but enables lateromedial and/or anteroposterior movements of the mandible. Moreover, the large glenoid cavities allow some amplitude in these movements. Interestingly, the dental microwear signal in the extant species consists mostly of mesiodistal scratches. The angle formed by the anterior border of the vertical branch and the tooth row is about 61° in KL09-98-001 (angle measured on a picture of the left hemi-mandible). This measurement is within the CHIO found for *O. afer* and is distinct from the angle found in *O. abundulafus* and *O. gaudryi* (Table 2). Nonetheless, this value is among the lowest of the extant species. The angle measured in *M. africanus* is very different, with a value of about 45°.

5.3. Dentition

The observable dental formula is: 3/2 P 3/3 M. The teeth of *O. djourabensis* nov. sp. show the classical shape

Table 2

Mandible measurements (in mm) of *Orycteropus djourabensis* nov. sp. (KL09-98-001, holotype) compared to other Tubulidentata

| Species | Lltr | LM _{1–3} | BM ₂ | HM _{2–3} | Hac | Bac | Hcp | Hap | Angle |
|--|--------------------|--------------------|--------------------|--------------------|--------------------|-----------------------|-----------------------|--------------------|---------------------|
| <i>O. afer</i> | 52.9 ± 3.7 (66) | 37.4 ± 3.9 (63) | 12.7 ± 1.6 (78) | 20 ± 2.5 (78) | 67.5 ± 7.2 (77) | 9.7 ± 1.7 (76) | 87.9 ± 9.4 (82) | 44.1 ± 7.2 (78) | 66.2° ± 5.1 (67) |
| <i>O. crassidens</i> ^a (Holotype) | | 43 | | 23 | | | | | 71.1° |
| <i>O. gaudryi</i> | 48.4 ± 3.8 (13) | 33.5 ± 2.7 (15) | 11.1 ± 0.7 (15) | 17.5 ± 0.9 (17) | 56.4 ± 2.9 (7) | 10; 10.5; 11.3 (3) | 70; 70.3; 73.6 (3) | 34.1 (1) | 76.1° ± 3.7 (7) |
| <i>O. pottieri</i> (Holotype) | 48.1 | 32.1 | 10.5 | 16 | 48.3 | 11.9 | | 29.2 | 67° |
| <i>O. abundulafus</i> | 44.8 | 32.7 | 12.8 | 17.9 | 55 | 11 | | 35.3 | 76.6° |
| <i>O. djourabensis</i> | 57.9 | 44.7 | 13.6 | 21.6 | 68.3 | 10.1 | 82 ^b | 44.5 | 61° |

Lltr = lower tooth row length (P₃ to M₃); LM_{1–3} = length of the molar row; BM₂ = ramus breadth at the M₂ level; HM_{2–3} = ramus height at the M_{2–3} level; Hac = articular condyle height; Bac = articular condyle breadth; Hcp = coronoid process height; Hap = angular process height; Angle = angle between the tooth row and the coronoid process measured on pictures (in degree). Other conventions as in Table 1.

^a After measurements and drawings in MacInnes (1956).

^b For estimated measurements.

for Orycteropodidae: the premolars are peg-like and the molars are 8-shaped (cf. Fig. 2, 3). Noticeably, the lower M3 are bilobed whereas the upper ones are rounded. The occlusal surface of the molars shows advanced dental wear. The intracuspals rims (ir; see Lehmann et al., 2005) are transverse like in *O. afer* and unlike *O. depereti*.

The upper teeth of the Orycteropodidae are slightly convex on their vestibular side, and their alveoli are oblique in regard to the palatine plane. Thus, the teeth are not vertical but follow this general orientation in the maxilla. In *O. crassidens* however, “the socket is practically perpendicular to the plane of the palate” (MacInnes, 1956: 30). This feature is clearly visible in caudal view on the M³ because its socket is situated in the orbit region. Noticeably, in *O. gaudryi* or in *O. abundulafus*, the socket of M³ and of M² are visible. This results from the forward shifting of the tooth row in modern forms. The orientation of the sockets of the upper tooth row can be considered as a diagnostic character for *O. crassidens*. The Kollé specimen presents the standard condition of the Tubulidentata and differs from the Kenyan form for this feature.

The M2 is the largest teeth of the upper tooth row, whereas M1 and M2 have equal length in the lower tooth row. In a large majority of the observed *O. afer* specimens, lower and upper M2 are the largest teeth. Conversely, in *O. mauritanicus*, the largest teeth are always the M1.

The teeth of KL09-98-001 are similar to the large teeth of *O. afer* but are somewhat more elongated (Table 3). The premolars, for instance, are among the largest in the sample studied here. The dental robustness index, of very high value for the Chadian *O. abundulafus*, is not significantly different in *O. afer*, *O. crassidens* and *O. djourabensis* nov. sp., except for the M₃. This indicates that the proportions of their teeth are quite similar. Nonetheless, the molar's lengths of the new species are not included in the CIIO of *O. afer*. On one hand, taken separately, only the M₁, M₃, and M³ of the Kollé spec-

imen are significantly longer than the same teeth in *O. afer*, but they are not distinguishable from the teeth of *O. crassidens* (Table 3). Taken as a whole, the cumulative length of the upper and lower molars (mathematical addition of their length; Table 3: CL^M and CL_M) of *O. djourabensis* nov. sp. is, by far, the longest of the data set (Fig. 4). On the other hand, whereas the upper molar row length (Table 1: Lutr) does not differ significantly in *O. djourabensis* nov. sp., *O. afer* and *O. crassidens*, the lower one (Table 2: Lltr) is longer in the Kollé fossil. The length of the diastema between the molars can explain these differences. In fact, they are short between the lower molars in KL09-98-001 like in *O. gaudryi*, but in the upper molar row, the diastema are of comparable length with those in *O. afer*.

The indeterminate Tubulidentate specimens available from the Pliocene of Kenya, Tanzania, South Africa and

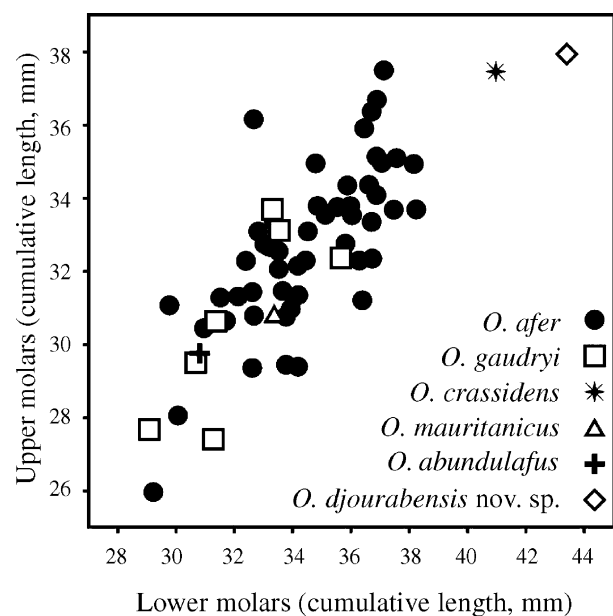


Fig. 4. Diagram of cumulative length of lower molars vs. upper molars in some *Orycteropus* species.

Table 3
Dental measurements (in mm) of *Orycteropus djourabensis* nov. sp. (KL09-98-001, holotype) compared to other Tubulidentata

| Lower teeth | P ₃ | | P ₄ | | M ₁ | | | M ₂ | | | M ₃ | | | CL _M |
|--|-------------------|-------------------|-------------------|-------------------|--------------------|-------------------|--------------------|--------------------|-------------------|--------------------|-------------------|-------------------|--------------------|--------------------|
| | L | B | L | B | L | B | R | L | B | R | L | B | R | |
| <i>O. afer</i> | 4.2 ± 0.9 (49) | 2 ± 0.5 (49) | 6.1 ± 1.2 (67) | 3.7 ± 0.8 (67) | 11.5 ± 1.1 (71) | 7.6 ± 1.3 (71) | 66.2 ± 8 (71) | 12.4 ± 1.3 (69) | 9 ± 1.2 (69) | 72.1 ± 5.6 (69) | 10 ± 1.2 (67) | 7.7 ± 1 (67) | 77.2 ± 7.9 (67) | 34 ± 3 (64) |
| <i>O. crassidens</i> ^a (Holotype) | | | 8 | 5.5 | 13.8 | 9.5 | 69.1 | 15 | 11.3 | 75 | 12.3 | 9.8 | 79.6 | 41 |
| <i>O. gaudryi</i> | 5.7 ± 0.6 (11) | 2.9 ± 0.3 (11) | 7.3 ± 0.7 (17) | 4.1 ± 0.5 (17) | 11 ± 0.8 (19) | 7.1 ± 0.6 (19) | 64.4 ± 3.5 (19) | 11.5 ± 0.6 (17) | 7.8 ± 0.5 (17) | 68.1 ± 3.8 (17) | 9.4 ± 0.8 (18) | 4.2 ± 0.5 (18) | 70.5 ± 5.1 (18) | 31.7 ± 2.2 (15) |
| <i>Leptorycteropus guilielmi</i> (Holotype) | 4.8 | 1.8 | 4.9 | 2.7 | | | | | | | | | | |
| <i>O. sp.</i> ^b (KNM-LAET 1418) | | | | | | | | 13.2 | 8 | 60.6 | | | | |
| <i>O. sp.</i> ^b (KNM-LAET 4937) | | | | | | | | 12.2 | 8 | 65.6 | | | | |
| <i>O. abundulafus</i> | 5.2 | 2.5 | 5.7 | 4.5 | 10.5 | 8.7 | 82.9 | 10.8 | 9.6 | 88.9 | 9.6 | 8 | 83.3 | 29.8 |
| <i>O. djourabensis</i> | 7 | 2.9 | 9.3 | 5.5 | 14.7 | 9 | 61.2 | 14.7 | 10 | 68 | 14.1 | 8.9 | 63.1 | 43.5 |
| Upper teeth | P ³ | | P ⁴ | | M ¹ | | | M ² | | | M ³ | | | CL ^M |
| | L | B | L | B | L | B | R | L | B | R | L | B | R | |
| <i>O. afer</i> | 4.7 ± 0.8 (65) | 2.8 ± 0.6 (65) | 6.9 ± 1 (68) | 5.3 ± 0.9 (67) | 11.1 ± 1.2 (69) | 7.4 ± 1.3 (69) | 66.3 ± 9 (69) | 11.9 ± 1.2 (66) | 8.6 ± 1 (65) | 71.7 ± 6 (65) | 9.3 ± 1.2 (64) | 7.3 ± 0.9 (64) | 78.5 ± 7.8 (64) | 32.4 ± 2.6 (64) |
| <i>O. crassidens</i> ^a (Holotype) | 6.3 | 4 | 8.8 | 7.3 | 12 | 9.3 | 77.1 | 14 | 10.8 | 76.8 | 11.5 | 9 | 78.3 | 37.5 |
| <i>O. depereti</i> (Holotype) | | | 6.9 | 5.5 | 11.6 | 7.7 | 66.4 | 11.7 | 7.8 | 66.7 | 9 | 7.3 | 81.1 | 32.3 |
| <i>O. gaudryi</i> | 5.2 ± 0.2 (5) | 3.3 ± 0.3 (5) | 7.3 ± 0.7 (9) | 5.1 ± 0.3 (9) | 11.2 ± 0.8 (12) | 7.2 ± 0.4 (13) | 63.9 ± 3.5 (12) | 12.1 ± 1.1 (12) | 7.9 0.5 (13) | 65.6 ± 3.9 (12) | 7.9 ± 0.8 (13) | 6.5 ± 0.5 (14) | 82.4 ± 4.4 (13) | 31.5 ± 2.5 (10) |
| <i>Leptorycteropus guilielmi</i> (Holotype) | | | | | | | | 11.1 | 7 | 63.1 | 7.4 | 6.9 | 93.2 | |
| <i>O. abundulafus</i> | 4.4 | 2.7 | 6.7 | 5 | 10.7 | 8 | 74.8 | 11.1 | 8.6 | 77.5 | 8 | 8 | 100 | 29.8 |
| <i>O. djourabensis</i> | 7.1 | 5.3 | 8.6 | 6.4 | 12.8 | 8.5 | 66.4 | 13.6 | 9.9 | 72.8 | 11.6 | 9.5 | 81.9 | 38 |

L = mesio-distal length; B = maximum vestibulo-lingual breadth; R = robustness index (B/L × 100); CL_M = cumulative length of the lower molars; CL^M = cumulative length of the upper molars. Other conventions as in Table 1.

^a After MacInnes (1956).

^b After Leakey (1987).

Ethiopia (unpublished material) show the same tendency for large teeth. However, *O. djourabensis* nov. sp. has developed the longest lower molar row and the length of the lower teeth remains from Laetoli and Makapansgat are included in the CIIO of *O. afer* (Table 3).

Longer molars, or molar tooth row, can be considered as a diagnostic feature for the new species from Kollé because the skull of *O. djourabensis* nov. sp. has the same general size that *O. afer* and *O. crassidens*. As suggested by Made for *O. crassidens* (2003: 140): “larger teeth in a skull of the same size is a morphological difference”. *O. djourabensis* nov. sp. and *O. crassidens* show similarities about the size of their teeth. But they differ in the orientation of the sockets of the upper tooth row relative to the palatine plate.

The elongation of the snout also affected the mandible: maxilla and mandible are longer in the aardvarks from the Pliocene to Quaternary than in the Miocene ones. The lengthening of the upper and lower molars could be a consequence of jaw elongation. This elongation could have been responsible for the broadening of the diastema, although these modifications do not affect upper and lower tooth rows in the same proportion. The diagnostic features of *O. djourabensis* nov. sp. are mostly found on the lower tooth row. In one stem lineage of Tubulidentata, a shortening of the lower molars must have taken place between the Pleistocene and the Recent, leading to the configuration of *O. afer*. Correlatively, length of the diastema within upper and lower molar rows increased. Thus, in *O. djourabensis* nov. sp., the active surface available for chewing on the mandible is significantly longer than in *O. afer*. Noticeably, extant aardvarks rarely chew their food (Taylor et al., 2002). Moreover, and like many other extant anteaters, the aardvark possesses a gizzard-like organ for grinding up the insects (Melton, 1976). Unfortunately, it is not possible to know if the earliest aardvark did possess a gizzard.

5.4. Humerus

Both humeri are preserved, but their distal epiphysis are damaged and parts of the deltoid crests are broken. The general shape of the bone is so similar to the extant form that no detailed description is necessary. Nevertheless, the proximal epiphysis has small dimensions and a poorly developed lateral tuberosity. Some measurements of the humerus are similar with those found for the juvenile specimens of *O. afer*. The length (142.7 mm) and the Hildebrand index (distal breadth/length, estimated at 35.5%) of the humerus of *O. djourabensis* nov. sp. are not significantly different from those obtained for 48 humeri of *O. afer* (154.7 mm \pm 13.9 and 37.4% \pm 2.3 respectively). A high Hildebrand index value, like in *O. afer* or *M. africanus* (47.6%), is corre-

lated with a fossorial mode of life. Thus, the humerus of the fossil aardvark from Kollé is not less adapted for digging than that of the extant form. Noticeably, the distal articulation surface for the ulna (the trochlea) presents different orientations of its medio-lateral axis. In *O. afer*, the trochlea extends more distally in reference to the capitulum than in *O. djourabensis* nov. sp. The articulation axis is thus more oblique in the extant form.

The data published for *O. crassidens* are confusing. In fact, the distal fragment of humerus from the holotype described by MacInnes (RI 1811'50; 1956) shows a very large distal breadth (64.5 mm) that matches the CIIO found for 51 specimens of *O. afer* (58 mm \pm 5.2). The material referred by Pickford (1975) to “*O. afer crassidens*” (KNM ER 876 and KNM ER 877) contains humeri that have much smaller dimensions: (published measurements) 133 mm long for a distal breadth of 41.4 mm and another distal breadth of 32.5 mm (juvenile individual). These measurements are significantly different from the extant species data. It is not clear, from the published values and description, what is the phylogenetic position of these specimens. For the purpose of this article, only the holotype of *O. crassidens* is considered. The humerus of *O. afer*, *O. crassidens* and *O. djourabensis* nov. sp. cannot be distinguished by their dimensions.

The humerus from KL clearly differs from that of the older Chadian species. For instance, in Kollé, the deltoid crest is well developed (also in opposition with *L. guilielmi*) and the olecranon fossa is bounded proximally (also in contrast with *O. gaudryi*). The size of both fossils is very different as *O. abundulafus* is about 75% as large as *O. djourabensis* nov. sp. Moreover, the humerus of the Pliocene Chadian fossil is more specialised for digging than that of the Miocene one.

5.5. Ulna

Only the right one is complete. The left ulna is known by a small part of the semi-lunar notch. Again, the similitude with the extant form is striking. For instance, the length of the cubitus, is within the CIIO found for *O. afer* (Table 4). The olecranon of KL09-98-001 is upright dorsoventrally (more than in common *O. afer*) but this situation has also been observed in some extant specimens. This configuration can be linked to the degree of development of the *Musculus anconeus*, strong extensor of the forearm, which is inserted on the lateral side of the ulna, behind the semi-lunar notch.

The articulation surfaces of the semi-lunar notch are slightly wider, and the articulation axis is more perpendicular to the diaphysis, in *O. afer* than in *O. djourabensis* nov. sp. But the breadth of the notch is similar: 28 mm for the Kollé aardvark versus 32 mm \pm 3.3 for $n = 35$ specimens of *O. afer*. This is correlated with the orientation of the distal articulation of the humerus.

Table 4

Ulna and radius measurements (in mm) of *Orycteropus djourabensis* nov. sp. (KL09-98-001, holotype) compared to other Tubulidentata

| Species | MUL | MRL | MHD | TBd |
|--|-------------------|------------------|-----------------|-----------------|
| <i>O. afer</i> | 157.8 ± 13.4 (37) | 108.8 ± 8.7 (38) | 18.7 ± 2.1 (35) | 32.8 ± 2.7 (37) |
| <i>O. gaudryi</i> (AMNH 22762) | 120 | 83.2 | | 23.8 |
| <i>O. pottieri</i> ^a | 90 | | | |
| <i>O. sp.</i> ^b (KNM-LAET 1813) | | 85 | 14.4 | 25 |
| <i>O. abundulafus</i> | 110.8 | 76.1 | 11.9 | 19 |
| <i>O. djourabensis</i> | 152.1 | 102.3 | 18.5 | 29.5 |

MUL = maximum ulna length; MRL = maximum radius length; MHD = radius maximum head diameter; TBd = radius distal transversal breadth. Other conventions as in Table 1.

^a After Bonis et al. (1994).

^b After Leakey (1987).

In the new species, the two facets are facing each other and the articulation axis is oblique in respect to the diaphysis. In *O. afer* the facets do not face each other and are perpendicular to the diaphysis. The pitch of these surfaces enlarges the contact with the distal epiphysis of the humerus and prevents uncontrolled movement or dislocation. Such mechanisms are common among digging mammals. Therefore, the aardvark is suited with an elbow system adapted for scratch digging (see Hildebrand, 1985) whereas its Kollé relative is more generalised for this feature.

5.6. Radius

Only the right radius is preserved and is still in connection with the carpals. The dimensions of the bone match those of the extant form and are larger than those of *O. abundulafus*, *O. gaudryi* or *M. africanus* (Table 4). The proximal epiphysis is oval in shape, but is limited laterally by a thick and continuous articular facet for the ulna. This facet is not continuous and less developed in *O. afer*. The proximal contact surface between the two bones is thus narrower in *O. djourabensis* nov. sp. than in *O. afer*. Moreover, the configuration described for the Chadian fossil interlocks, in a firmer manner, radius and cubitus and inhibits any movement of pro- or supination. This arrangement can be advantageous for specialised scratch diggers and for digitigrade tetrapods. The radial tuberosity (or bicipital tuberosity) is button-like as in *O. afer* but unlike the one in *O. abundulafus*.

The general outline of the diaphysis is slender like in *O. afer*, but it is more curved dorsoventrally. The distal epiphysis is also similar. Triangle-shaped, it shows the same grooves for ligaments. Noticeably, an early late Pliocene radius found in Laetoli (KNM-LAET 1813; Leakey, 1987) has a narrower dorsoventral distal epiphysis. The radius is shorter than the humerus in *O. djourabensis* nov. sp.: the brachial index (maximum radius length on maximum humerus length) equals 0.72, a value similar to *O. abundulafus* (0.72) or *O. afer* (0.71 ± 2.8; $n = 34$), suggesting a fossorial mode of life according to MacPhee (1994).

5.7. Hand

Both hands are very well preserved. They have been found in anatomical connection with even the ungual phalanges and sesamoids bones. All carpals were preserved except the pisiform bone. The shapes of the carpals of KL09-98-001 are similar to their counterparts in *O. afer*. The contact surfaces are identical so that the carpals are interlocking in both forms. The only difference with *O. afer* is the smaller dimensions of the carpals of *O. djourabensis* nov. sp. In fact, the medial and lateral components of the wrist show a significant reduction of their medio-lateral breadth (scaphoid, unciform, pyramidal and trapezoid; see Table 5). The general shape of the basipode is more slender in *O. djourabensis* nov. sp. than in *O. afer*.

The metacarpals (Mc) are very similar in *O. djourabensis* nov. sp. and in *O. afer*. The proximal epiphyses present the same articulation surfaces, which promote a firm interlocking. The distal epiphyses show the same median keel that prevents lateromedial movements of the digits. These configurations are common among the Tubulidentates studied in this work. However, the Mc III and Mc IV of *O. afer* are significantly different from all other comparable fossil Orycteropodidae in the medio-lateral breadth of their proximal epiphyses (Table 5). In fact, the index “proximal breadth on length” for the Mc III is 0.32 ± 0.01 ($n = 19$) in *O. afer* versus 0.24, 0.24, and 0.29 for *O. abundulafus*, *O. pottieri*, and *O. djourabensis* nov. sp. respectively. The same index for Mc IV has a value of 0.37 ± 0.02 ($n = 19$) in *O. afer* versus 0.22, 0.28, and 0.32 for *O. abundulafus*, *O. pottieri*, and *O. djourabensis* nov. sp. respectively. The wrist of the extant form has a relatively larger surface of articulation than in other Orycteropodidae. The contact is reinforced between Mc III and Mc IV and enhances the cohesion with the carpals. As noticed before, the mediolateral breadth of the trapezoid (articulated with the Mc III) and the unciform (articulated with the Mc IV in a large extant) are also larger in the extant form. Likewise, the length of Mc II and Mc III are significantly shorter in the new species than in the extant

Table 5
Hand measurements (in mm) of *Orycteropus djourabensis* nov. sp. (KL09-98-001, holotype) compared to other Tubulidentata

| Carpals | Species | L ₁ | | L ₂ | | L ₃ | | | | | | | | | | | |
|---|------------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|---------------------|--------------------|---------------------|----------------|--------------------|--------------------|--------------------|--------------------|--|
| Scaphoid | <i>O. djourabensis</i> | 12.5 | | 22.3 | | | | | | | | | | | | | |
| | <i>O. afer</i> | 12.6 ± 1.4 (21) | | 27.3 ± 1.8 (21) | | | | | | | | | | | | | |
| Pyramidal | <i>O. djourabensis</i> | 13.5 | | 13.5 | | | | | | | | | | | | | |
| | <i>O. afer</i> | 14.7 ± 1.5 (19) | | 19 ± 1.5 (19) | | | | | | | | | | | | | |
| Trapezium | <i>O. djourabensis</i> | 8.3 | | 11.7 | | 11.2 | | | | | | | | | | | |
| | <i>O. afer</i> | 10.4 ± 1 (19) | | 13 ± 1.2 (19) | | 12.4 ± 1.1 (19) | | | | | | | | | | | |
| Trapezoid | <i>O. djourabensis</i> | 11 | | 14.5 | | 7.5 | | | | | | | | | | | |
| | <i>O. afer</i> | 14 ± 1.3 (20) | | 17 ± 0.9 (20) | | 8.3 ± 0.6 (20) | | | | | | | | | | | |
| Magnum | <i>O. djourabensis</i> | 14.9 | | 14.4 | | 7.6 | | | | | | | | | | | |
| | <i>O. afer</i> | 17 ± 1.5 (21) | | 17.3 ± 1.3 (21) | | 8.1 ± 1.2 (21) | | | | | | | | | | | |
| Unciform | <i>O. djourabensis</i> | 17.5 | | 15 | | 11.8 | | | | | | | | | | | |
| | <i>O. afer</i> | 21.6 ± 2 (20) | | 21 ± 2.3 (20) | | 13.2 ± 1.3 (20) | | | | | | | | | | | |
| Species | Mc _{II} | | Mc _{III} | | Mc _{IV} | | Mc _V | | Php _{II} | | Php _{III} | | Php _{IV} | | Php _V | | |
| | L | B | L | B | L | B | L | B | L | B | L | B | L | B | L | B | |
| <i>O. afer</i> | 62.7 ± 3.2 (20) | 14.1 ± 1.3 (19) | 62.5 ± 3.9 (22) | 19.9 ± 1.3 (19) | 44.6 ± 2.4 (19) | 16.5 ± 1.5 (19) | 25.2 ± 1.5 (21) | 13 ± 1.3 (21) | 44.3 ± 2 (15) | 13.1 ± 1.2 (15) | 40.5 ± 3 (18) | 13 ± 2 (16) | 34.6 ± 2.3 (18) | 12.7 ± 1.4 (18) | 24.9 ± 1.7 (21) | 12.1 ± 1.1 (21) | |
| <i>O. crassidens</i> ^a (Holotype) | 68 | | 69 | | 51 | | 29 | | 45 | | 41 | | 35 | | 24 | | |
| <i>O. gaudryi</i> (AMNH 22762) | | | 46.5 | | | | | | 32.5 | 8.7 | 35.1 | 9.7 | 28.6 | 8 | 19.8 | 8.3 | |
| <i>O. pottieri</i> ^b (PNT 61,62,63) | 39.1 | 8.8 | 39.1 | 9.5 | 30.5 | 8.5 | | | | | | | | | | | |
| <i>O. abundulafus</i> | 44.7 | 11 ^c | 44.6 | 10.5 | 33.5 | 7.3 ^c | 20.6 | 7.4 | 33.2 | 8.6 | 30.2 | 8 | 25.3 | 7.5 | 19.7 | 6.2 | |
| <i>O. djourabensis</i> | 55 | 11.1 | 54.7 | 15.7 | 41.1 | 13 | 23.6 | 11.4 | 39.1 | 12.5 | 35.5 | 11.5 | 32.7 | 10.6 | 22.9 | 10.8 | |
| | Phm _{II} | | Phm _{III} | | Phm _{IV} | | Phm _V | | Finger II length | | Finger III length | | | | | | |
| | L | B | L | B | L | B | L | B | (Mc + Php + Phm) | | (Mc + Php + Phm) | | | | | | |
| <i>O. afer</i> | 21.9 ± 1.3 (12) | 12 ± 1.1 (12) | 21.6 ± 2.1 (14) | 11.9 ± 1 (12) | 20.9 ± 1.3 (12) | 12.3 ± 0.9 (12) | 17.1 ± 1.3 (12) | 11.6 ± 0.8 (12) | 128.6 ± 6.3 (11) | | 123.5 ± 8.3 (13) | | | | | | |
| <i>O. crassidens</i> ^a (Holotype) | 21 | | 21 | | 22 | | 17 | | 134 | | 131 | | | | | | |
| <i>O. gaudryi</i> (AMNH 22762) | 14.3 | 8 | 15 | 8.4 | 15.2 | 8 | 12 | 7.9 | | | 96.6 | | | | | | |
| <i>O. abundulafus</i> | 14 | 7.5 | 14.4 | 7.5 | 13.6 | 7.4 | 10.8 | 6.6 | 91.9 | | 89.2 | | | | | | |
| <i>O. djourabensis</i> | 20.7 | 11.3 | 20.5 | 11.2 | 19.7 | 10 | 17 | 10.7 | 114.8 | | 110.7 | | | | | | |

L₁ = dorsoventral length; L₂ = mediolateral length; L₃ = proximodistal length; Mc = metacarpal; Php = proximal phalange; Phm = middle phalange; L = length, B = proximal breadth. Other conventions as in Table 1.

^a After MacInnes (1956).

^b After Bonis et al. (1994).

^c For estimated measurements.

aardvark (Table 5). Noticeably, the Mc III and IV of *O. crassidens* are either among the largest or are significantly longer than those of *O. afer*. The other data obtained from the metacarpals of the Kollé species are not significantly different from the extant form.

The phalanges of *O. djourabensis* nov. sp. are, like in *O. afer*, strongly built with broad diaphyses contrasting with the slender phalanges of *O. abundulafus*, or *O. gaudryi*. The proximal ones (Php) possess a proximal epiphysis that fits the median keel of the Mc. The distal articulations of the proximal and median phalanges (Phm) are more cylindrical. The distal phalanges (Phd), very delicate, are more altered than the other bone of the hand. The proximal epiphyses of the Phd of the Kollé specimen are not different in shape but in size from their extant relative.

The second finger of the hand (Mc to Phm) is the longest as in *O. afer*. Its length (114.8 mm) is, however, significantly shorter than for the extant form ($128.6 \text{ mm} \pm 6.3$; $n = 11$). Thus, the manus of the Chadian fossil aardvark is more slender and shorter (about 11%) than in *O. afer* and *O. crassidens*. A shorter and more slender hand reduces the efficiency of the power stroke as it displaces less sediment at a time. Conversely, a longer forelimb enlarges the range of action and paves the way far in front of the delicate head and large trunk.

5.8. Pelvic girdle and vertebrae

The sacrum, the lumbar vertebrae and the pelvis are still in connection. On the left side, a great part of the ilium, the pubis and the root of the ischium are preserved. On the right side, only the acetabular region is preserved with the pubis (cf. Fig. 5).

Like in the extant aardvark, the ilium of *O. djourabensis* nov. sp. presents a dorsal extension of its blade (oriented dorsoposteriorly) that delimits the sciatic notch. This feature is one of the differences that exist be-

tween the Orycteropodinae and *Plesiorycteropus* Filhol, 1895, some Xenarthra, and the “Condylarthra” (MacPhee, 1994). The iliopectineal eminence and the insertion for the *Musculus rectus femoris* in front of the acetabulum, although broken, are well developed as in *O. afer*. The pubis is stick-like and oriented caudally in the same manner as in the extant species, which indicates a fossorial animal (MacPhee, 1994).

The dimensions of the pelvis of *O. djourabensis* nov. sp., like for *O. crassidens*, are within the CIIO found for *O. afer* (Table 6). The Miocene aardvarks (for which an innominate was found) have all significantly smaller pelvises than these latter three species. Noticeably, the value obtained for *O. djourabensis* nov. sp. and *O. crassidens* are among the smallest extant individuals.

Like in *O. afer*, 6 vertebrae are fused to form the sacrum. It also presents the same shape and contact with the ilium. The area for sacro-iliac articulation is as developed as in *O. afer* and not smaller like in *M. africanus*. The vertebrae are still in connection and are stuck in the sediment by their dorsal surface: the specimen was found lying on its back (Fig. 5). The vertebral spine is broken into three blocks: the axis and five cervical vertebrae are preserved separated from (but in continuity with) a series of 12 costal vertebrae themselves apart from five lumbar vertebrae in connection with the sacrum and innominate block. By comparison with the ex-

Table 6

Pelvis measurements (in mm) of *Orycteropus djourabensis* nov. sp. (KL09-98-001, holotype) compared to other Tubulidentata

| Species | AW | AH |
|---|---------------------|---------------------|
| <i>O. afer</i> | 38.1 ± 3.1 (31) | 31.5 ± 3.1 (31) |
| <i>Leptorycteropus guilielmi</i> (Holotype) | 19 | 16.2 |
| <i>O. abundulafus</i> | 17.9 | 10.3 |
| <i>O. djourabensis</i> | 32.7 | 27 |

AW = acetabulum proximodistal length; AH = acetabulum dorsoventral length. Other conventions as in Table 1.

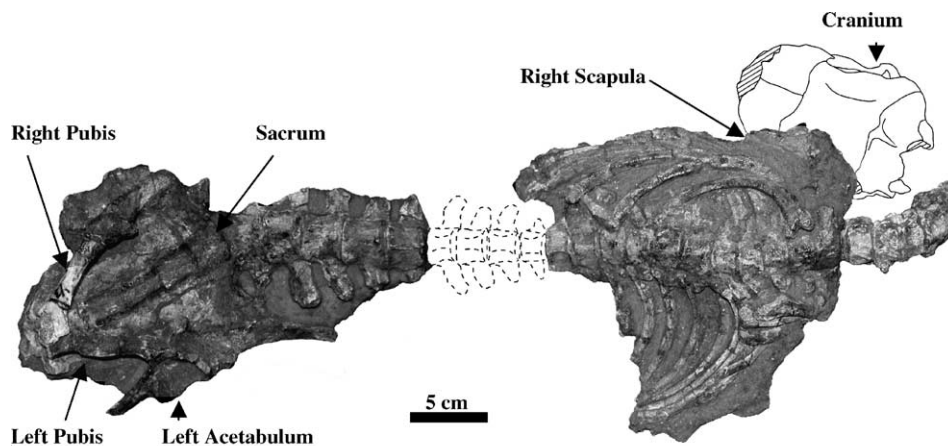


Fig. 5. Axial skeleton of *Orycteropus djourabensis* nov. sp. (ventral view) and repositioned cranium. Missing vertebrae drawn in dotted lines.

tant form, one costal and three lumbar vertebrae are lacking. About ten ribs are in anatomical connection on each side. The curvature of the spine is concave dorsally (from lumbar to cervical vertebrae). This must be due to a post-mortem retraction of the interspinous ligaments because the normal stance of the aardvark is an arched back. Thus, the body of the animal must have dried up in open air for some time (Weigelt, 1989). In this perspective, it should be noticed that no sign of predation have been observed on the KL skeleton.

5.9. Femur

Both femurs are preserved. The left one is complete but somehow weathered at its distal end. The right femur lacks the proximal epiphysis. Both third trochanters are broken at their tip.

The proximal epiphysis of KL09-98-001 is very similar to the one in *O. afer*. In the extant form, the top of the great trochanter (insertion for the *Mm. gluteus minimus* and *piriformis*) is above the level of the head of the femur. It is also the case in Kollé, but in a lesser extent, whereas it is the opposite in *Myorycteropus*. A true neck cannot be observed like in all Tubulidentata except *Myorycteropus* and *Plesiorhycteropus*. The lesser trochanter is more massive in *O. djourabensis* nov. sp. and it shows a more pronounced dorsomedial expansion than in *O. afer*.

The third trochanter, projecting laterally, is well developed like in all known Tubulidentata. The fourth trochanter (or pectineal tubercle), one of the diagnostic features of the Tubulidentata (except *Plesiorhycteropus*), is developed. It is the insertion point for the *Musculus pectineus*, one of the muscles responsible for the adduction of the femur, and its outward rotation.

The distal epiphysis is large and similar to the one in *O. afer*. The patellar surface is grooved like in all Tubulidentata except in the genus *Plesiorhycteropus*. The articular facet for the sesamoid bone dedicated to the *Musculus gastrocnemius*, situated above the lateral con-

dyle of the femur, is positioned at the diaphysis level like in *O. afer* and unlike in *O. gaudryi* and *O. abundulafus* (see Lehmann et al., 2005).

The dimensions of the femur of *O. djourabensis* nov. sp. are fully comparable with the data found in *O. afer* and *O. crassidens* (Table 7). These three species are significantly distinct from all other Miocene species. The size of the femur of the aardvark from Kollé is comparable to that of small specimens of extant *O. afer*.

5.10. Tibia and Fibula

The right tibio-fibula is complete whereas the left one is only known by the tibia. The diaphysis and the proximal epiphysis of the right fibula are damaged and distorted. Tibia and fibula are fused proximally but not distally like in all Tubulidentata except the genus *Plesiorhycteropus*. The dimensions of the tibio-fibula of *O. djourabensis* nov. sp. are included in the CHIO obtained for *O. afer* and *O. crassidens* (Table 8). The measurements also show that the tibio-fibula of these three species are significantly larger than in the Miocene aardvarks. Noticeably, *O. gaudryi* and *O. mauritanicus* present tibio-fibula that are as long as in some small specimens of *O. afer*. This can be correlated to a specific character of *O. gaudryi*: its tibia is longer than its femur.

On the proximal epiphysis, the tibial tuberosity is a flat and oblique surface continuous with the proximal articulation surface like in *O. afer*. This tuberosity is slender like in *O. mauritanicus* (Arambourg, 1959). Moreover, in *O. abundulafus* and *O. gaudryi*, this surface is concave. Arambourg tried to distinguish *O. afer*, *O. gaudryi* and *O. mauritanicus* by features on their proximal epiphysis. On the basis of a cast of AMNH 22976 (MNHN-1957-17-5), he found that *O. gaudryi* has a trilobed proximal epiphysis due to the reduction of the medial articular surface for the femur relative to the lateral one. He also mentioned that the lateral articular surface is separated from the tibial crest by a deep notch. In fact, the fossil has a broken medial surface and it is

Table 7

Femur measurements (in mm) of *Orycteropus djourabensis* nov. sp. (KL09-98-001, holotype) compared to other Tubulidentata

| Species | MFL | PMB | DMB | DAB |
|--|-------------------|-----------------|-----------------|-----------------|
| <i>O. afer</i> | 193.9 ± 17.1 (43) | 67.7 ± 7.4 (43) | 58.3 ± 4.7 (43) | 58.1 ± 4.3 (40) |
| <i>O. gaudryi</i> (AMNH 22762; AMNH 22888) | 142.2; 136.6 | 44.5; 43 | 41.4; 37.5 | 39.9; 35.2 |
| <i>O. pottieri</i> (PNT 130) ^a | 137 | 45.5 | 41 | 37 |
| <i>Leptorycteropus guillemi</i> (Holotype) | | | 28.3 | 26.2 |
| <i>Myorycteropus africanus</i> (Holotype) ^b | 108 | 21 | 35 | 33 |
| <i>O. abundulafus</i> | | 44.6 | 35 ^c | 37 ^c |
| <i>O. djourabensis</i> | 177.4 | 63.3 | 52.9 | 54.2 |

MFL = maximum femur length; PMB = proximal mediolateral breadth; DMB = distal mediolateral breadth; DAB = distal anteroposterior breadth. Other conventions as in Table 1.

^a After Bonis et al. (1994).

^b After MacInnes (1956).

^c For estimated measurements.

Table 8

Tibio-fibula measurements (in mm) of *Orycteropus djourabensis* nov. sp. (KL09-98-001, holotype) compared to other Tubulidentata

| Species | MTFL | TFPW | DAB | DMB |
|---|-------------------|-----------------|-----------------|-----------------|
| <i>O. afer</i> | 181.8 ± 12.9 (40) | 56.3 ± 4.2 (39) | 28.6 ± 3.4 (28) | 38.5 ± 4.3 (16) |
| <i>O. gaudryi</i> (AMNH 22762; AMNH 22976) | 156.7; 152.1 | 40.6 | 19; 20.6 | 24 |
| <i>O. mauritanicus</i> ^a | 164.5 | 39 | 22 | 29.7 |
| <i>Leptorycteropus guilielmi</i> (Holotype) | 111 ^b | 30 | 14.2 | 19.1 |
| <i>O. abundulafus</i> | 140 ^b | | 19 | 22.8 |
| <i>O. djourabensis</i> | 168.5 | 52.8 | 24.7 | 35.6 |

MTFL = maximum tibio-fibula length; TFPW = tibio-fibula proximal mediolateral width, malleolus to malleolus; DAB = distal anteroposterior breadth of tibia; DMB = distal mediolateral breadth of tibia. Other conventions as in Table 1.

^a After Arambourg (1959).

^b For estimated measurements.

damaged where Arambourg (1959) described a notch. These fractures are not clearly visible on the cast. A complete epiphysis is preserved in another specimen of *O. gaudryi* (mounted skeleton AMNH 22762). On this specimen, the medial part of the epiphysis is more developed than thought by Arambourg. Unfortunately, the bone is damaged between the lateral articulation surface and the tibial crest. Finally, Arambourg's (1959) conclusion about the trilobed shape of the epiphysis in *O. gaudryi* is correct, but it is due to the absence of a falciform process. This process, projecting from the dorsolateral side of the epiphysis in *O. afer*, is also absent in *L. guilielmi* and *Plesiorycteropus* (MacPhee, 1994). *O. djourabensis* nov. sp. shares some of these features with *O. gaudryi* and *O. mauritanicus*, and others with *O. afer*. For instance, though the dorsolateral side of the epiphysis is broken in both tibio-fibula, a massive root is still visible in the new species, contrasting with the thin border in *O. gaudryi* and *O. mauritanicus*. Thus, the falciform process present in the extant species is also likely to have been present in the aardvark from Kollé. The study of the proximal epiphysis of KL09-98-001, *O. gaudryi* and *L. guilielmi* shows that they all have a slender tibial tuberosity. Moreover, they all show a continuous border, running from the tibial tuberosity to the junction with the fibula, and projecting dorsally over the insertion fossa for the *Musculus tibialis anterior*. As noticed by Patterson (1975), a deep notch replaces this border and opens the fossa on the proximal surface in *O. afer*.

Like in *O. afer*, the tibial crest is developed and presents no cnemial tuberosity that is only present in *Plesiorycteropus* and *Myorycteropus*. The crest ends more distally and less abruptly than in *O. abundulafus* or *O. gaudryi*. The diaphysis of the fibula being damaged in KL09-98-001, the distal epiphysis of the fibula is not aligned on the anatomical axis. The fibula is very similar in the two species.

5.11. Foot

The two feet were found in anatomical connection with their sesamoids. They are well preserved, but the left calcaneum and the talus, as well as some ungual

phalanges, are broken. The dimensions of the talus of *O. djourabensis* nov. sp. are within the CIIO found for specimens of *O. afer*, except for the smaller dorsoventral breadth (Table 9). The head of the talus is not round. The ratio mediolateral breadth on dorsoventral breadth for the condyle shows that the value obtained for the Kollé aardvark (1.25) is significantly higher than for *O. abundulafus* (1.04), *O. afer* (1.1 ± 0.1 ; $n = 19$), *O. sp.* from Laetoli (in Milledge, 2003, 1.14), and *O. sp.* from Lothagam (KNM-LT 28641, in Milledge, 2003, 1.21). The indices found with the published measurements of *M. africanus* and *O. minutus* are particularly higher (1.51 and 1.41 respectively). The latter configuration privileges one direction of articulation. When the ankle joint is dorsoflexed, the entire foot is brought close to the tibia. With a developed dorsoventral articulation surface of its head, the talus enables the metapodials to dorsoflex further, to a position quite parallel to the tibia in *O. afer*. Such a flexion is of a smaller amplitude for species like *O. djourabensis* nov. sp., that shows a smaller dorsoventral breadth of the talus condyle. The talus of KL09-98-001 is not elongated like in *O. abundulafus*, *O. gaudryi*, and *O. mauritanicus*. It is quadrate and has a posteromedial process like in *O. afer*. The other articular surfaces are similar to those in the extant form. MacInnes (1956, 34) observed that the talus of *O. crassidens* "closely resembles that of *O. afer*". He also underlined that "the inner flange of the tibia facet appears to merge gradually with the neck, whereas in the Recent species the anterior part of the facet ends abruptly in a sharp edge". *O. djourabensis* nov. sp. is similar to *O. afer* for this feature.

The fragments of calcaneum from KL09-98-001 are very comparable to the calcaneum of *O. afer* (Table 9), although a difference exists on the medial development of the *sustentaculum tali*. In fact, in *O. afer*, the medial articulation facet for the talus is larger than the one in *O. djourabensis* nov. sp., and in *O. abundulafus*. The articular surface for the cuboid has a median ridge in the KL form merging from the last millimetres on its dorsal border. The navicular from *O. djourabensis* nov. sp. is also comparable to those in *O. afer* and its dimensions are included in their CIIO at 95% (Table 9). The

Table 9

Foot measurements (in mm) of *Orycteropus djourabensis* nov. sp. (KL09-98-001, holotype) compared to other Tubulidentata

| Species | Talus | | | | | | | | | | | | Calcaneum | | | | | | | | | | | | | |
|--|-------------------|--|-----------------|------------------|----------------|-------------------|------------------|--------------------|------------------|-------------------|-----------------|------------------|-----------------|-------------------|-----------------|--------------------|--|-----------------|-----------------|--|-----------------|-----------------|-----------------|-----------------|--|--|
| | L ₁ | | L ₂ | | L ₃ | | NfL ₁ | | NfL ₂ | | | | L ₁ | | L ₂ | | | | | | | | | | | |
| <i>O. afer</i> | 26.6 ± 2.3 (18) | | 38.3 ± 3.2 (20) | | 38.2 ± 3 (21) | | 15.8 ± 1.5 (19) | | 17.1 ± 1.2 (19) | | | | 40.3 ± 3.3 (25) | | 41.7 ± 4 (25) | | | | | | | | | | | |
| <i>O. gaudryi</i> (AMNH 22762; AMNH 22976) | 17.6 | | | | 27.8 | | | | | | | | 25.7 | | 29.9 | | | | | | | | | | | |
| <i>O. mauritanicus</i> ^a | | | 27.5 | | 30.4 | | | | | | | | | | 30 | | | | | | | | | | | |
| <i>O. abundulafus</i> | 17.1 | | 21.5 | | 25.6 | | 11 | | 11.4 | | | | 22.3 | | 28 | | | | | | | | | | | |
| <i>O. djourabensis</i> | 21.6 | | 33 | | 34.4 | | 12.2 | | 15.3 | | | | 38.3 | | 35 | | | | | | | | | | | |
| | Navicular | | | Cuboid | | | Cuneiform I | | | Cuneiform II | | | Cuneiform III | | | | | | | | | | | | | |
| | L ₁ | | L ₂ | L ₃ | | L ₁ | | L ₂ | L ₃ | | L ₁ | | L ₂ | L ₃ | | L ₁ | | L ₂ | L ₃ | | | | | | | |
| <i>O. afer</i> | 24.4 ± 2.1 (22) | | 23.8 ± 1.6 (22) | 18.2 ± 1.6 (22) | | 22.5 ± 2 (22) | | 23.8 ± 2.9 (22) | 17 ± 2.2 (22) | | 22.9 ± 2.1 (21) | | 10.5 ± 0.7 (21) | 27.1 ± 2.1 (21) | | 18.8 ± 1.7 (20) | | 10.3 ± 1.4 (20) | 8.3 ± 0.8 (20) | | 24.6 ± 3.7 (22) | 12.7 ± 1.6 (22) | 13.5 ± 1.2 (22) | | | |
| <i>O. gaudryi</i> (AMNH 22762; AMNH 22976) | 16.2; 16.4 | | | 12.5 | | 15; 14.2 | | 18.4 | 11.6 | | | | 7.5 | | | 17 | | | 7.8 | | | | | | | |
| <i>O. abundulafus</i> | 15.2 | | 13.9 | 13.9 | | 13.7 | | 17.4 | 10.6 | | 18.5 | | 8.2 | 22.9 | | 11.3 | | 7.2 | 6 | | 16.2 | | 8.2 | 8.5 | | |
| <i>O. djourabensis</i> | 21.6 | | 22 | 16.7 | | 19.7 | | 22.2 | 14.3 | | 19.2 | | 10 | 25 | | 16.2 | | 9.4 | 7 | | 22.8 | | 10.5 | 12.3 | | |
| | Mt _I | | | Mt _{II} | | Mt _{III} | | Mt _{IV} | | Mt _V | | Php _I | | Php _{II} | | Php _{III} | | | | | | | | | | |
| | L | | B | L | | B | L | | B | L | | B | L | | B | L | | B | L | | B | L | | B | | |
| <i>O. afer</i> | 38.7 ± 2.9 (22) | | 11.1 ± 0.9 (22) | 76 ± 3.2 (22) | | 12.4 ± 1.1 (21) | 79 ± 3.6 (24) | | 15.6 ± 1.1 (22) | 64.3 ± 2.8 (22) | | 17 ± 1.4 (22) | 36.6 ± 2 (22) | | 15 ± 2.3 (22) | 34.1 ± 2.1 (15) | | 12.7 ± 0.9 (15) | 42.7 ± 2.2 (18) | | 16.7 ± 1.4 (18) | 40.1 ± 2.2 (20) | | 16.3 ± 1.6 (18) | | |
| <i>O. crassidens</i> ^b (Holotype) | 38.5 | | 11.5 | | | | | | | | | | | | | | | | | | | | | | | |
| <i>O. gaudryi</i> (AMNH 22762; AMNH 22976) | 37.4 | | 9.6 | 65; 67.5 | | 9.3 | | | | 35; 36.8 | | | 33.3 | | 9.7 | 37.2; 37.8 | | | 11.9 | | | 39.3; 36.8 | | 12.5; 10.8 | | |
| <i>O. abundulafus</i> | 38.6 | | 9 | 62.9 | | 9 | 63.1 | | 9.7 | 53.7 | | 10.5 | 36.6 | | 7.8 | 31.9 | | 9 | 35 | | 11.1 | | 36.9 | 11.5 | | |
| <i>O. djourabensis</i> | 36.6 | | 10.9 | 70.1 | | 10.9 | 73.1 | | 13.6 | 61.3 | | 16 | 35.4 | | 12.4 | 28.4 | | 11.1 | 38.2 | | 16.3 | | 38.3 | 15.6 | | |
| | Php _{IV} | | | Php _V | | Phm _{II} | | Phm _{III} | | Phm _{IV} | | Phm _V | | Finger II | | Finger III | | | | | | | | | | |
| | L | | B | L | | B | L | | B | L | | B | L | | B | length | | length | | | | | | | | |
| <i>O. afer</i> | 37.4 ± 1.9 (18) | | 15.2 ± 1.1 (18) | 24.8 ± 1.5 (15) | | 12.1 ± 0.8 (15) | 21.8 ± 0.9 (12) | | 13.8 ± 0.7 (12) | 21.3 ± 1.6 (14) | | 13.5 ± 0.8 (12) | 19.8 ± 0.8 (12) | | 12.2 ± 0.7 (12) | 14.4 ± 1.1 (10) | | 9.7 ± 0.8 (10) | 139 ± 4.8 (11) | | 139 ± 5.4 (13) | | | | | |
| <i>O. gaudryi</i> (AMNH 22762; AMNH 22976) | 34.4 | | 10.3 | 25.6; 26.2 | | 8.9; 8.7 | 19.1; 18 | | 10.9; 9.7 | 19.8; 18.8 | | 9.9; 9.9 | 16.4 | | 8.7 | 11.8 | | 6.6 | 121.3; 123.3 | | | | | | | |
| <i>O. abundulafus</i> | 33.9 | | 9.5 | 25.7 | | 7.9 | 19.4 | | 10.1 | 19.4 | | 9.4 | 17.6 | | 7.9 | 12.9 | | 6.3 | 117.3 | | | | 119.4 | | | |
| <i>O. djourabensis</i> | 34.8 | | 14.3 | 23.4 | | 11.1 | 20.9 | | 14.1 | 20.1 | | 13.7 | 19 | | 12.1 | 13.9 | | 9.2 | 129.2 | | | | 131.5 | | | |

L₁ = dorsoventral length; L₂ = mediolateral length; L₃ = proximodistal length; Nf = navicular facet; Mt = metacarpal; Php = proximal phalange; Phm = middle phalange; L = length, B = proximal breadth. Other conventions as in Table 1.

^a After Arambourg (1959).

^b After MacInnes (1956).

articulation surface for the calcaneum is smaller in the fossil and the articular facet for the talus is rounder. The ventral border of the latter facet is also more mediolaterally oriented in the extant form. The dimensions of the cuboid match those found for *O. afer* (CHIO). Its articulation surface with the calcaneum presents a little depression on its dorsal border that is the counterpart of the median ridge observed on the calcaneum. This interlocking configuration inhibits mediolateral movements between the two bones. Limited dorsoventral movements are possible. Such a character is not present in *O. afer* or in *O. gaudryi* but can be seen in a lesser extent in *O. abundulafus*.

The peculiar first cuneiform of the Tubulidentata plays on a medial condyle of the navicular and can extend the hallux apart from the rest of the foot. This capacity increases the stability of the feet when the animal is digging, standing uniquely on its hind limbs. The bone shows no significant differences in size or shape between *O. afer* and *O. djourabensis* nov. sp. (Table 9). The two other cuneiforms of the Kollé aardvark are similar to their homologues in *O. afer*, although the second cuneiform lacks a ventral excrescence present in *O. afer*.

The metatarsals (Mt) closely resemble those of *O. afer* and have the same proportions. Nonetheless, the proximolateral cuneiform protuberance of the first metatarsal is developed ventrally. The dimensions of the metatarsals of *O. djourabensis* nov. sp. are included in the CHIO found for *O. afer* (Table 9). However, the second and third metatarsals are in the size range of the smallest specimens of extant aardvark. The metatarsals in *O. abundulafus* or *O. gaudryi* are more slender. The proximal phalanges (Php) are very similar to those of *O. afer*. Remarkably, the Php I is not as long as in *O. afer* but its shape is identical. In fact, there is a pinching of the dorsal part of the diaphyses in KL09-98-001 close to the proximal epiphysis. In the same way, Php II is significantly shorter than its counterpart in *O. afer*. Thus, Php II and Php III are sub equal in length in *O. djourabensis* nov. sp., whereas, in *O. afer*, Php II is longer than Php III. The median phalanges (Phm) and fragments of distal phalanges (Phd) show no significant difference in size and shape with those of *O. afer*. The dimensions are generally larger than in *O. abundulafus* or *O. gaudryi*.

The second and third toes (Mt to Phm) of *O. djourabensis* nov. sp. have sub equal length like in the extant aardvark and in *O. abundulafus*. The length of the longest finger of the pes is within the CHIO found for *O. afer*. The ratio length of the longest finger of the hand on length of the longest toe is 0.77 for *O. abundulafus*, 0.79 for *O. gaudryi*, 0.87 for the KL aardvark, and 0.90 ± 0.01 ($n = 10$) for *O. afer*. The size of the foot and the hand are well characterized by the length of their longest finger. The foot is always longer than the hand in the fossil species and in the extant form, but, as noted by Colbert (1941), there is a relative increase

in size for the manus between Early Pliocene and Recent times. The forelimb is thus a major locus of evolutive trend in Tubulidentata, along with the body size and the length of the snout (nasal bone). The new species from Chad has not reached the degree of development of the hand shown in *O. afer*. According to Colbert (1941, p. 327) this lengthening of the hand in *Orycteropus* is “a result of the accentuation of its fossorial habits”.

6. Comparison

Orycteropus djourabensis nov. sp. differs from *O. afer* (type species) by: longer premolar, longer M_1 , M_3 , and M^3 , longer cumulative length of the upper and lower molars; semi-lunar notch oblique in respect to the diaphysis of the ulna; slenderer wrist, smaller hand; slender tibial tuberosity, continuous border from tibial tuberosity to the junction with the fibula; head of the talus larger medio-laterally than dorsoventrally; smaller proximal phalanges I and II; hand proportionally shorter in respect to the foot.

Orycteropus djourabensis nov. sp. differs from *O. crassidens* by: oblique sockets for the upper teeth; longer cumulative length of the upper and lower molars; smaller hand.

Orycteropus djourabensis nov. sp. differs from *O. gaudryi* by: larger size; straight lambdoid crest; anterior border of the orbit above M^3 ; larger snout and basicranium; straight postpalatine torus; no crests on pterygoid wall; flat glenoid cavity; flat articular condyle on the mandible, lower mandibular angle; longer premolars and molars, longer cumulative length of the upper and lower molars; oval and bounded proximally olecranon fossa; button like bicipital tuberosity on the radius; broader metacarpals and finger of the hand; facet for the *M. gastrocnemius* sesamoid bone situated at the diaphysis level on the femur, femur longer than tibia; falciform process present on the tibia, longer tibial crest ending less abruptly; quadrate talus, broader metatarsals and toes.

Orycteropus djourabensis nov. sp. differs from *O. abundulafus* by: larger size; straight lambdoid crest; anterior border of the orbit above M^3 ; larger snout and basicranium; straight postpalatine torus; no crests on pterygoid wall; flat glenoid cavity; flat articular condyle on the mandible; lower angular angle; longer premolars and molars, lower robustness index, longer cumulative length of the upper and lower molars; well developed deltoid crest on the humerus, oval and bounded proximally olecranon fossa; button like bicipital tuberosity on the radius; broader metacarpals and finger of the hand; facet for the *M. gastrocnemius* sesamoid bone situated at the diaphysis level on the femur; falciform process present on the tibia, longer tibial crest ending less

abruptly; quadrate talus, head of the talus larger medio-laterally, broader metatarsals and toes.

Orycteropus djourabensis nov. sp. differs from *O. mauritanicus* by: larger size; straight lambdoid crest; larger snout and basicranium; transverse intracuspal rims; M^2 and M_1 and M_2 largest teeth, longer premolars and molars, longer cumulative length of the upper and lower molars; falciform process present on the tibia; quadrate talus.

Orycteropus djourabensis nov. sp. differs from *O. depereti* by: larger size; straight lambdoid crest; anterior border of the orbit above M^3 ; larger snout and basicranium; straight postpalatine torus; flat glenoid cavity; transverse intracuspal rims; longer premolars and molars; longer cumulative length of the upper molars.

7. Discussion and conclusion

The new species from Chad opens a window in the history of the order Tubulidentata because it fills a gap in the fossil record. It is represented by the most complete skeleton known to date from Plio-Pleistocene deposits. The holotype KL09-98-001 gives information on the degree of development of some of the supposed evolutionary trends in Tubulidentata proposed by previous authors (Colbert, 1941; Patterson, 1975; Pickford, 1975; Made, 2003). This study shows that the dimensions of the animal did rise from the Miocene to the Recent. Nonetheless, the size of the forelimb and the length of the nasal have increased relatively faster. The latter features are specialisations linked to fossorial habits and to a myrmecophagous diet. Comparison of *O. djourabensis* nov. sp. with *O. afer*, *O. crassidens*, and various *O. sp.* specimens from the Pliocene of Africa shows that the breadth of the teeth remained constant during the Plio-Pleistocene but the length was variable. Noticeably, Lower Pliocene and Pleistocene specimens can have longer teeth (*O. djourabensis* nov. sp. and *O. crassidens* respectively) than in *O. afer*, while Upper Pliocene specimens show teeth of the same size (*O. cf. afer* from Makapansgat). Thus, the determination of Plio-Pleistocene Tubulidentate species can only be pertinent with relatively good preserved remains with at least parts of the forelimbs and teeth.

The Late Miocene is the interval during which the Tubulidentata had their widest geographical range and their greatest diversity. In Pliocene times, the aardvarks became rarer in Eurasia until the Pleistocene, when the order became restricted to Africa.

Upper Miocene species are smaller than the extant *O. afer*, by about 25%. Moreover, in the Upper Miocene of Lothagam, *Orycteropus sp.* specimens have been found associated with *Leptorycteropus*. Although larger than the latter genus, they are “one fifth smaller than the extant aardvark” (Milledge, 2003). Correlatively, in the

Upper Miocene site of Lukeino, Pickford (1975) found a “tiny” and a “large” *O. sp.* The two specimens are different, according to the author, but the largest is still smaller than *O. afer*. Thus, it seems that different species of Tubulidentata coexisted in the same environment during the Miocene. The Pliocene and Pleistocene species are similar in size and share more characters with the living taxon. It is also true for the indeterminate specimens of this period. Unfortunately, *O. cf. afer* from Langebaanweg (Pliocene) is only known by an isolated tooth. Thus, the oldest known fossil aardvark comparable in size and anatomy with *O. afer* is the new species from the Pliocene of Kollé.

The youngest fossil aardvark found in Eurasia is *O. depereti* (France). The skull and teeth of this taxon are smaller than those of *O. djourabensis* nov. sp. but are not significantly smaller than those of the studied specimens of *O. afer*. In contrast to these two taxa, *O. depereti* shows oblique ir on the molars and a V-shaped lambdoid crest. Moreover, the anterior border of the orbit is situated above M^2 in the French aardvark. In this respect, *O. depereti* displays features that are shared with Miocene Tubulidentata, but it has a larger size. Still, this taxon cannot be seen as an intermediate form between Miocene aardvarks and *O. afer* because, in Africa, a penecontemporary species (*O. djourabensis* nov. sp.) already had a size and an anatomy closer to the extant form. *O. depereti* is likely to be a late descendant of the last Tubulidentate lineage in Eurasia. The increase in size would thus be a convergence.

The MPFT has been working since 1994 in the Djourab desert, Northern Chad. The team found fossiliferous sectors that are chronologically distinct. Study of the Chadian faunal change through time is therefore possible. Fossil aardvarks are rare in the fossil record of the Old World and consist mainly of limb fragments. In Chad, several complete skeletons have been found in anatomical connection in different sectors. The KB species is very close to the specimens of *O. gaudryi* from Samos. It is a form 25% smaller than *O. afer* or than the Kollé aardvark, and has a less specialised forelimb. The snout is not elongated and the teeth are broad. This species is representative of the Late Miocene small aardvarks. The new species from Kollé is slightly younger. As described here, the differences with the living species concern mainly the proportions of the teeth and forelimbs. It is a characteristic Plio-Pleistocene large aardvark of Africa. The two Chadian forms are too different to be direct relatives. Furthermore, they are closer to other non-Chadian species than to each other. In fact, in Chad, the Late Miocene aardvark is replaced by a more modern form, larger and more specialised for digging like *O. afer*. This phenomenon is also recognizable in East Africa (Kenya and Tanzania) and in Ethiopia where a large aardvark appeared around 4 My (unpublished material). At the exception of some

fragmentary material from Langebaanweg, the first known aardvarks from South Africa (Makapansgat and Swartkrans) are also large specimens. This suggests that a faunal turnover took place for the Tubulidentata in Africa. The fossiliferous area KB is aged around the Mio-Pliocene boundary whereas the age of KL is closer to 4 My like the site that yielded large aardvarks in Ethiopia. Thus, this turnover must have taken place in the Early Pliocene. The *Orycteropodidae* succession in Chad can reflect what happened on the continent, during this period.

It shall be recalled that the majority of the Eurasian forms disappeared at the Mio-Pliocene boundary. Concomitant events, like the Messinian salinity crisis, affected both continents and must have had an incidence on the widespread distribution of the modern forms. These large *Orycteropus* must have appeared prior to the event. Made (2003) suggested that several dispersal events from Eurasia into Africa, involving different taxa, may have happened around 11, 10.4, 7.7 and 6.3 Ma ago. However, there is no evidence for the presence of such modern aardvarks during the Late Miocene, neither in Africa nor in Eurasia. The geographical origin of these modern forms is still unknown.

Acknowledgement

We thank the Chadian authorities (Ministre de l'Education Nationale de l'Enseignement supérieur et de la Recherche, Université de N'Djaména, and CNAR). We extend gratitude for their support to the Ministère français de l'Education Nationale (Faculté des Sciences, Université de Poitiers), de la Recherche (Département SDV et Programme ECLIPSE du CNRS) and des Affaires Etrangères (DCSUR, Paris, and SCAC, N'Djaména), to the Région Poitou-Charentes, the RHOI project (F.C. Howell and T.D. White) funded by the NSF, and also to the Armée française (MAM and Epervier) for logistic support. T.L. acknowledges financial support from a DAAD Kurzstipendium für ausländische Nachwuchswissenschaftler and an AMNH, Collection Study Grant, New York. We also thank M. Novacek of the American Museum of Natural History (New York), J. D. Skinner of the University of Pretoria, P. Tassy of the Muséum National d'Histoire Naturelle (Paris), F. Thackeray of the Transvaal Museum of Pretoria, and T. White of the University of California (Berkeley) for support. We express our gratitude to the Museum für Naturkunde Berlin, the Naturhistorisches Museum Basel, the Staatliches Museum für Naturkunde Stuttgart, and the American Museum of Natural History, New York, for giving us the opportunity to work in their collection. We especially thank Emmanuel Fara for his help for spelling and his comments on the manuscript. We thank F. Lihoreau, S. Sen, and J. Van der

Made for discussion and advice. We are most grateful to Ghislaine Florent and Carine Noël for MPFT administrative guidance. None of the work could have been possible without the field and technical work of all the MPFT participants.

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