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C. R. Palevol 5 (2006) 693–703
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Systematic Palaeontology (Vertebrate Palaeontology) / Paléontologie systématique

A sub-complete fossil aardvark (Mammalia, Tubulidentata) from the Upper Miocene of Chad

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Received 12 July 2005; accepted after revision 21 November 2005
Available online 11 April 2006
Presented by Philippe Taquet

Abstract

A new sub-complete specimen of fossil Tubulidentata has been found by the 'Mission paléoanthropologique franco-tchadienne' (MPFT) in Chad. After *O. abundulafus* Lehmann et al., 2005 from Kossom Bougoudi, *O. djourabensis* Lehmann et al., 2004 from Kollé, it is the first described aardvark from the fossiliferous sector Toros-Menalla. This specimen belongs to *O. abundulafus*. This discovery extends the stratigraphic range of that species, enables to validate and supplement its diagnosis, and confirms that a relationship exists between *O. abundulafus* from Chad and *O. gaudryi* from Greece/Turkey. The recent studies undertaken on the Chadian specimens will become the cornerstone for the revision of the Tubulidentata. ***To cite this article: T. Lehmann et al., C. R. Palevol 5 (2006)***.
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Résumé

Découverte d'un oryctérope fossile sub-complet (Mammalia, Tubulidentata) dans le Miocène supérieur du Tchad. Un nouveau spécimen sub-complet de Tubulidentata a été mis au jour au Tchad par la Mission paléoanthropologique franco-tchadienne (MPFT). Après *O. abundulafus* Lehmann et al., 2005 de Kossom Bougoudi, *O. djourabensis* Lehmann et al., 2004 de Kollé, c'est le premier oryctérope du secteur fossilifère de Toros-Menalla décrit. Ce spécimen appartient à l'espèce *O. abundulafus*. Sa découverte prolonge la répartition stratigraphique de cette espèce, permet de valider et de compléter sa diagnose, et confirme que des relations de parenté entre *O. abundulafus* du Tchad et *O. gaudryi* de Grèce/Turquie existent. Les récentes études entreprises sur les spécimens tchadiens vont servir de base à une révision des Tubulidentata. ***Pour citer cet article : T. Lehmann et al., C. R. Palevol 5 (2006)***.
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Keywords: Central Africa; Chad; Systematics; Tubulidentata; Upper Miocene

Mots clés : Afrique centrale ; Miocène supérieur ; Systématique ; Tchad ; Tubulidentata

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doi:10.1016/j.crpv.2005.12.016

Version française abrégée

Introduction

Les Tubulidentata sont des taxons fossiles rares dans les dépôts néogènes. De plus, le matériel mis au jour est souvent très fragmentaire. Des spécimens de cet ordre sont néanmoins connus dans tout l'Ancien Monde (voir [10]). Depuis 1994, la Mission paléoanthropologique franco-tchadienne (MPFT) poursuit des recherches paléontologiques dans le désert du Djourab (Nord Tchad). Quatre secteurs fossilifères ont ainsi été mis au jour : Koro Toro [3,4], Kollé [5], Kossom Bougoudi [6] et Toros-Menalla [7,16]. Deux nouvelles espèces d'oryctérope fossile ont été décrites. La première, *Orycteropus abundulafus*, une espèce de taille moyenne, a été mise au jour à Kossom Bougoudi et datée à près de 5 Ma [6,10]. La seconde, *O. djourabensis*, une espèce de grande taille, provient de Kollé et est âgée de près de 4 Ma [11]. Les deux espèces n'ont pas de relations de parenté directe et illustrent le remplacement partout en Afrique de petites formes par des taxons de taille plus grande, proches de l'espèce actuelle. Récemment, des spécimens d'oryctéropes fossiles, dont un squelette subcomplet, ont été mis au jour dans le secteur fossilifère de Toros-Menalla, daté biochronologiquement à environ 7 Ma. Ces restes sont les plus anciens connus pour l'ordre des Tubulidentata en Afrique centrale. Cet article porte sur l'étude de ce nouveau spécimen subcomplet.

Systématique

Ordre : Tubulidentata Huxley, 1872
Famille : Orycteropodidae Gray, 1821
Sous-famille : Orycteropodinae Gray, 1821
Genre : *Orycteropus* Geoffroy, 1791
Espèce : *O. abundulafus* Lehmann et al., 2005

Holotype : KB03-97-214, squelette sub-complet d'un individu sub-adulte (voir [10]).

Localité type : KB03, Kossom Bougoudi (Tchad).

Nouveau matériel : TM255-03-01, squelette subcomplet d'un individu adulte découvert en connexion anatomique (Fig. 1). Il comprend : le crâne et la mandibule (Fig. 2), la cavité glénoïde de la scapula droite, des fragments de l'humérus gauche et la totalité de l'humérus droit (Fig. 3), les radius et ulna droits et gauches, des phalanges de la main gauche et une grande partie de la main droite, des vertèbres, dont certaines en connexion, les régions acétabulaires des os coxaux gauche et droit, ainsi que des fragments du sacrum ; les membres postérieurs sont complets (Fig. 4). Après étude, ce spécimen sera conservé au Centre national d'appui à la recherche (CNAR) de N'Djaména, Tchad.

Âge : Le secteur fossilifère Kossom Bougoudi est daté biochronologiquement à proximité de la limite Mio-Pliocène [6], environ 5–5,5 Ma, tandis que le site TM255 est proche de 7 Ma. En effet, le degré évolutif de la faune mammalienne de ce site (bovidae, anthracotheriidae, etc.) est comparable à celui de la « anthracotheriid unit » (AU) définie par Vignaud et al. [16].

Diagnose émendée : Espèce d'*Orycteropus* fossile plus petite que *O. afer* (près de 25% plus petite d'après les os des membres) ; présence d'une crête latérale sur le ptérygoïde ; longue symphyse mandibulaire (21% de la longueur totale) ; surface dorsale du condyle articulaire de la mandibule concave ; molaires très larges (rapport largeur maximum sur longueur de la M_2 > 80%) ; crête deltoïde de l'humérus réduite et ne se projetant pas latéralement ; épiphyse distale de l'humérus réduite (indice largeur distale/longueur < 35%) et fosse olécrânienne triangulaire ; tibio-fibula plus long que le fémur.

Diagnose différentielle : *O. abundulafus* se distingue de *O. afer* (Pallas, 1766) par sa plus petite taille, la position du bord antérieur de son orbite (au-dessus de la M^2), son museau et basicrâne plus étroits, la présence d'un tubercule latérale dans la cavité glénoïde du crâne, la présence d'une crête sur le ptérygoïde, la forme en « V » de sa crête lambdoïde, son condyle articulaire de la mandibule concave, l'angle entre les branches de sa mandibule plus élevé (Tableau 1), le plus grand rapport largeur maximum sur longueur (*B*/*L*) de ses molaires (Tableau 2), le plus court col de la scapula, sa crête deltoïde sur l'humérus non projetée latéralement et sa fosse olécrânienne triangulaire, un indice largeur distale sur longueur de l'humérus plus faible (Tableau 3), la forme pincée de la tubérosité bicipitale et le plus long bord oblique du radius, l'axe articulaire de l'échancrure sigmoïde oblique à la diaphyse de l'ulna, son fémur plus court que le tibio-fibula (Tableau 4), la crête tibiale plus courte, l'astragale plus long proximo-distalement que médio-latéralement, les éléments des autopodes plus fins, les doigts I et V proportionnellement plus longs et les pieds plus longs que les mains. *O. abundulafus* diffère de *O. crassidens* MacInnes, 1956 par sa plus petite taille, la position du bord antérieur de son orbite (au-dessus de la M^2), l'angle entre les branches de sa mandibule plus élevé, le plus grand rapport (*B*/*L*) de ses molaires (sauf la M^1), l'orientation des alvéoles dentaires supérieures oblique au plan du palais, sa crête deltoïde non projetée latéralement et sa fosse olécrânienne triangulaire, un indice largeur distale sur longueur

de l'humérus plus faible, la forme pincée de la tubérosité bicipitale du radius, l'axe articulaire de l'échancrure sigmoïde oblique à la diaphyse de l'ulna. *O. abundulafus* se distingue de *O. depereti* Helbing, 1933 par un museau et un basicrâne plus étroits, la présence d'un sillon palatin, la position de la suture maxillo-jugale (au-dessus de la M^3), une arcade zygomatique plus fine, le frontal aussi long que le pariétal, le plus grand rapport (*B*/*L*) de ses molaires et la crête intra-cuspide transversale sur sa M^1. *O. abundulafus* peut être différencié de *O. djourabensis* Lehmann et al., 2004 par sa plus petite taille, la position du bord antérieur de son orbite (au-dessus de la M^2), son museau et basicrâne plus étroits, la présence d'un tubercule latérale dans la cavité glénoïde du crâne, la présence d'une crête sur le ptérygoïde, la forme en « V » de sa crête lambdoïde, son condyle articulaire de la mandibule concave, l'angle entre les branches de sa mandibule plus élevé, le plus grand rapport (*B*/*L*) de ses molaires, sa crête deltoïde sur l'humérus non projetée latéralement et sa fosse olécrânienne triangulaire, un indice largeur distale sur longueur de l'humérus plus faible, la forme pincée de la tubérosité bicipitale et le plus long bord oblique du radius, son fémur plus court que le tibio-fibula, la crête tibiale plus courte, l'astragale plus long proximo-distalement que médio-latéralement, les éléments des autopodes plus fins. *O. abundulafus* diffère de *O. gaudryi* Major, 1888 par un frontal aussi long que le pariétal, le plus grand rapport (*B*/*L*) de ses molaires, sa crête deltoïde non projetée latéralement, un indice largeur distale sur longueur de l'humérus plus faible, des doigts II, III et IV plus courts, mais un doigt V plus long, la présence d'une crête dorsale sur la diaphyse des phalanges de la main. *O. abundulafus* se distingue de *O. mauritanicus* Arambourg, 1959 par le plus grand rapport (*B*/*L*) de ses molaires, un sillon vestibulaire moins profond sur les molaires supérieures, des M2 plus longues que les M1 correspondantes, les os des membres plus courts et moins robustes, la présence d'une crête dorsale sur la diaphyse des phalanges. *O. abundulafus* diffère de *O. pottieri* Ozansoy, 1965 par la présence d'une crête sur le ptérygoïde, l'angle entre les branches de sa mandibule plus important, le plus grand rapport (*B*/*L*) de ses molaires et l'absence de canines.

Description (voir la version anglaise)

Le spécimen TM255-03-01 partage les caractères diagnosiques de l'espèce décrite à Kossom Bougoudi. De plus, certains os ou structures non conservés chez l'holotype sont présents sur ce spécimen. En particulier, la crête visible sur le ptérygoïde est très développée et porte un tubercule saillant. La crête brachiale de l'humérus droit est large, comme chez les autres *Orycteropus*. D'après MacInnes [12], cette configuration serait liée à un mode de vie fouisseur. L'épiphyse distale de l'humérus est moins large que chez les autres *Orycteropus* : l'indice représentant le rapport de la largeur distale à la longueur de l'humérus (Tableau 3) est faible. Selon Hildebrand [9], un rapport important (30 à 70%) traduit une aptitude au fouissage. Comme pour *O. gaudryi* et à la différence d'*O. afer*, le tibio-fibula d'*O. abundulafus* est plus long que le fémur (Tableau 4). Enfin, l'épiphyse proximale du tibio-fibula ne porte pas de processus falciforme présent chez *O. afer* et *O. djourabensis*. En vue proximale, cette configuration donne à l'épiphyse une forme trilobée comme pour *O. gaudryi* et *O. mauritanicus* (contra [1], mais voir [11]).

Discussions et conclusion

Le nouveau spécimen de Tubulidentata découvert dans le secteur fossilifère de Toros-Menalla est un individu adulte appartenant à la même espèce que l'oryctérope de Kossom Bougoudi. La comparaison entre ces deux spécimens confirme l'estimation faite par Lehmann et al. [10], à savoir que l'holotype est un individu sub-adulte ayant atteint la taille adulte. Ainsi, la diagnose d'*O. abundulafus* a été complétée et les caractères diagnosiques, proposés pour l'holotype de cette espèce, ont été confirmés.

La précédente étude morphologique et phylogénétique [10] montrait de fortes relations de parenté entre *O. abundulafus* et *O. gaudryi*. Le nouveau matériel mis au jour à Toros-Menalla confirme ces relations de parenté (par exemple, le tibio-fibula plus long que le fémur). *O. gaudryi* est un taxon de taille moyenne connu dans le Turolien (7,65–5,3 Ma) de Grèce et de Turquie (voir [2,8,15]). *O. abundulafus* n'était connu que dans un seul site (Kossom Bougoudi), daté à près de 5 Ma, mais la découverte faite à Toros-Menalla étend la répartition stratigraphique de l'espèce jusqu'à environ 7 Ma. Ces deux espèces, plus petites qu'*O. afer*, sont donc pénécontemporaines et disparaissent toutes les deux à la limite Mio-Pliocène. À partir du Pliocène, *O. depereti*, une espèce proche d'*O. gaudryi* est le seul représentant des Tubulidentata en Europe. En Afrique en revanche, ce sont de grands oryctéropes comparables à *O. afer* qui émergent à cette époque et remplacent les plus petites formes. Par exemple, au Tchad, *O. djoura-*

bensis succède à *O. abundulafus* : ces deux espèces sont ainsi des marqueurs biochronologiques à l'échelle locale.

Une tendance évolutive traditionnellement admise au sein des Tubulidentata est l'augmentation progressive de la taille (voir [8,13,14]). Néanmoins, cette tendance ne semble pas confirmée entre 15 et 5 Ma. En effet, l'espèce *O. mauritanicus* du Vallésien d'Algérie est plus grande que les espèces *O. abundulafus* et *O. gaudryi* du Turolien. De plus, au cours du Turolien, *Leptorycteropus guilielmi* Patterson, 1975, une espèce encore plus petite, apparaît au Kenya. En outre, au Tchad, l'augmentation de taille entre *O. abundulafus* et *O. djourabensis* est soudaine. La tendance évolutive très linéaire envisagée par de nombreux auteurs devrait donc être reconsidérée à la lumière de ces nouvelles découvertes. La phylogénie des Tubulidentata est aussi très probablement plus complexe que proposée jusque là par les auteurs.

1. Introduction

Fossil Tubulidentata are among the less common taxa found in Neogene deposits. Only dental remains and isolated bones, and rarely skulls or few incomplete skeletons (Lothagam, Rusinga Island, Samos) are mainly found. Fossil Orycteropodidae are still widely known from Africa and Eurasia (for a review, see [10]).

Since 1994, the Djurab desert (northern Chad) is the premise of long-term palaeontological excavations undertaken by the 'Mission paléoanthropologique franco-tchadienne' (MPFT). This research program led to the discovery of four fossiliferous sectors: Koro Toro [3,4], Kollé [5], Kossom Bougoudi [6], and Toros-Menalla [7,16]. The first fossil aardvark from Chad was found in 1997 in the Mio-Pliocene boundary sector Kossom Bougoudi [6,10]. It consists of an articulated skeleton that is the holotype and single specimen of a new medium-sized species: *Orycteropus abundulafus* Lehmann et al., 2005. Another much larger species, *O. djourabensis*, has later been discovered in the Early Pliocene sector Kollé [11]. However, both species are not closely related. This chronological substitution in Chad is an illustration of the replacement of small aardvarks (close to *O. gaudryi*) by modern, larger, and more specialised forms like the extant *O. afer* that takes place all over Africa (see [11]). More recently, several fragmentary remains of aardvarks have been found in the Upper Miocene sector Toros-Menalla. They represent the oldest Tubulidentata known from Central Africa. One of these specimens is a nearly complete and well-preserved articulated skeleton.

The aim of this paper is to describe this specimen and to determine its relationships with the Kossom Bougoudi and Kollé aardvarks as well as with the other fossil Tubulidentata. This discovery allows us to complete the description and diagnosis of the Chadian material and to extend our knowledge of Tubulidentata evolution between the Upper Miocene and the Pliocene.

2. Systematics

Order: Tubulidentata Huxley, 1872
Family: Orycteropodidae Gray, 1821
Sub-family: Orycteropodinae Gray, 1821
Genus: *Orycteropus* Geoffroy, 1791
Species: *O. abundulafus* Lehmann et al., 2005

Holotype: KB03–97–214, sub-complete skeleton of a sub-adult specimen (see [10]).

Type locality: KB03 site, Kossom Bougoudi (Chad).

New material: TM255-03-01, sub-complete skeleton of an adult specimen discovered in anatomical connection (Fig. 1), including: cranium and mandible with teeth; glenoid cavity of right scapula; distal part of left humerus; left radius and ulna; phalanges of left hand; right humerus; right radius and ulna; articulated right hand (with sesamoids but without carpals); fragments of atlas and axis, and caudal vertebrae (some are in connection); fragments of pelvic girdle including both acetabular regions; fragment of the sacrum; complete hindlimbs (including ungueal phalanges and sesamoids). After study, the specimen will be housed in the 'Centre national d'appui à la recherche' (CNAR) in N'Djaména, Chad.

Age: The fossiliferous sector Kossom Bougoudi is dated around the Mio-Pliocene boundary [6], ca. 5–5.5 Myr. The evolutionary degree of the mammal assemblage from TM255 (bovid, anthracotheriid, etc.) is similar to that of the 'anthracotheriid unit' (AU) defined by Vignaud et al. [16], and is thus ca. 7 Myr old.

Emended diagnosis: Extinct species of *Orycteropus* smaller than the extant *O. afer* (by about 25% according to the limb bones); lateral crests on the pterygoid wall on the cranium; long mandibular symphysis (21% of total length); concave dorsal surface of the articular condyle of the mandible; very broad molars (maximum breadth on length index for $M_2 > 80\%$); deltoid ridge of the humerus reduced and not projecting laterally; slender distal epiphysis of the humerus (index distal

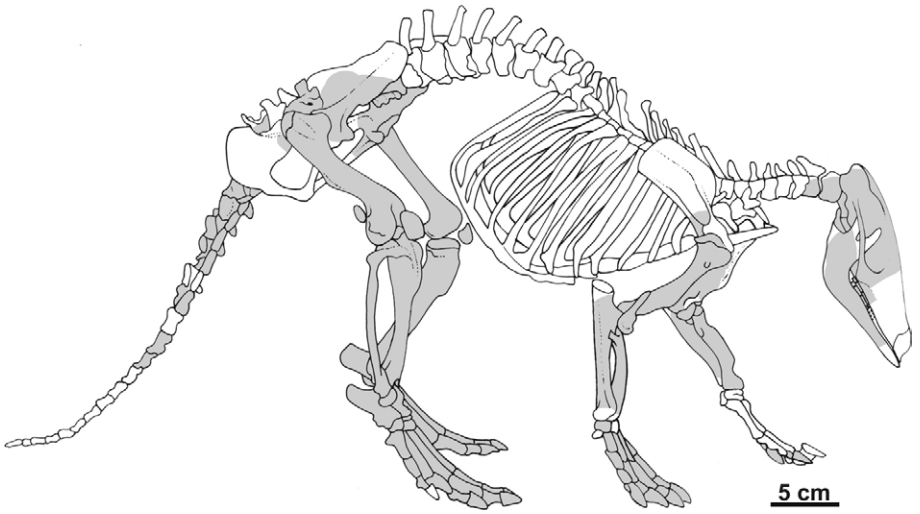

Fig. 1. Reconstruction of the skeleton of *Orycteropus abundulafus* after the specimen TM255-03-01. In grey, preserved bones in this specimen. Drawing by Sabine Riffaut.
Fig. 1. Reconstitution du squelette d'*Orycteropus abundulafus* à partir du spécimen TM255-03-01. En gris, os conservés sur ce spécimen. Dessin de Sabine Riffaut.

breadth/length < 35%) and olecranon fossa triangular in shape; tibio-fibula longer than the femur.

Emended differential diagnosis: *O. abundulafus* differs from *O. afer* (Pallas, 1766) by its overall smaller size, the position of the anterior border of the orbit (above M^2), its slenderer snout and basicranium, the presence of a lateral tubercle in the glenoid cavity on the cranium, the presence of a crest on the pterygoid, its V-shaped lambdoid crest, the concave articular condyle of the mandible, a higher angle between the branches of the mandible (Table 1), the greater maximum breadth on length (*B*/*L*) index of the molars (Table 2), the shorter neck of the scapula, its non projecting deltoid crest and triangular olecranon fossa on the humerus, a lower distal breadth on length index for the humerus (Table 3), the prominent bicipital tuberosity and the longer oblique rim on the radius, the oblique articulation axis of the trochlear notch on the ulna, its femur shorter than the tibio-fibula (Table 4), the shorter tibial crest, the talus longer proximo-distally than medio-laterally, the slenderer elements of the autopodes, the proportionally longer digit I and V and its foot longer than its hand. *O. abundulafus* differs from *O. crassidens* MacInnes, 1956 by its smaller size, the position of the anterior rim of the orbit (above M^2), a higher angle between the branches of the mandible, the greater (*B*/*L*) index of the molars (except M^1), the oblique orientation of the socket of the upper tooth-row in respect to the palatine plane, its non-projecting deltoid crest and triangular olecranon fossa on the humerus, a lower distal breadth on length index for the humerus, the prominent bicipital tuberosity on the radius, the oblique articulation axis of the trochlear notch on the ulna. *O. abundulafus* differs from *O. depereti* Helbing, 1933 in having a slenderer snout and basicranium, the palatine groove, a maxillo-jugal suture situated above M^3, a slenderer zygomatic arch, a frontal as long as the parietal, a greater (*B*/*L*) index of the molars and a transversal intracuspal rim on the M^1. *O. abundulafus* differs from *O. djourabensis* Lehmann et al, 2004 by its overall smaller size, the position of the anterior border of the orbit (above M^2), its slenderer snout and basicranium, the presence of a lateral tubercle in the glenoid cavity on the cranium, the presence of a crest on the pterygoid, its V-shaped lambdoid crest, the concave articular condyle of the mandible, a higher angle between the branches of

Table 1
Compared angles (in degree) between the horizontal and vertical branches of the mandibles (gingival level and anterior border respectively) of some Orycteropodinae
Tableau 1. Mesures angulaires comparées (en degré) entre les branches horizontale et verticale des mandibules (ligne gingivale et bord antérieur respectivement) de quelques Orycteropodinae.

Species	***O. afer*** **(*n* = 63)**	***O. crassidens*** **(Holotype)**	***O. djourabensis*** **(Holotype)**	***O. gaudryi*** **(*n* = 9)**	***O. abundulafus***	
					Holotype	**TM255-03-01**
Mandibular angle	66° ± 5.2°	66°	61°	77.8° ± 3.1°	76.6°	74°

Table 2
Compared measurements (in mm) of the lower molars of some Orycteropodinae. Legend: *L*, length; *B*, maximum breadth; *R*, maximum breadth on length (*B*/*L*) index of the molars
Tableau 2. Mesures comparées (en mm) des molaires inférieures de quelques Orycteropodinae. Légende : *L*, longueur ; *B*, largeur maximale ; *R*, rapport largeur maximum sur longueur (*B*/*L*) des molaires.

Lower molars	M_1			M_2			M_3		
	L	***B***	***R***	***L***	***B***	***R***	***L***	***B***	***R***
O. afer	11.6 ± 1 (n = 71)	7.9 ± 0.9 (n = 71)	67.5% ± 6 (n = 71)	12.6 ± 1 (n = 71)	9.1 ± 0.9 (n = 71)	72.7% ± 4.8 (n = 71)	10.1 ± 1 (n = 70)	7.8 ± 1 (n = 70)	78% ± 6.7 (n = 70)
O. crassidens **(Holotype)**	13.1	8.8	67.2%	14.3	10.6	74.1%	12	8.9	74.2%
O. djourabensis **(Holotype)**	14.7	9	61.2%	14.7	10	68%	14.1	8.9	63.1%
O. gaudryi	11.1 ± 0.8 (n = 22)	7.1 ± 0.5 (n = 21)	64% ± 3.6 (n = 21)	11.5 ± 0.6 (n = 19)	7.8 ± 0.5 (n = 19)	67.8% ± 3.9 (n = 18)	9.4 ± 1 (n = 20)	6.5 ± 0.6 (n = 19)	70.8% ± 5.1 (n = 19)
O. abundulafus **(Holotype)**	10.5	8.7	82.9%	10.8	9.6	88.9%	9.6	8	83.3%
(TM255-03-01)	9.4	6.6	70.2%	9.5	8	84.2%	9	6.3	70%

Table 3
Compared index (distal breadth/length) of the humeri of some Orycteropodinae
Tableau 3. Comparaison des indices (largeur distale/longueur) des humérus de quelques Orycteropodinae.

Humerus	***O. afer*** **(*n* = 43)**	***O. crassidens*** **(Paratype)**	***O. djourabensis*** **(Holotype)**	***O. gaudryi*** **(AMNH 22762)**	***O. abundulafus***	
					Holotype	**TM255-03-01**
Distal breadth/length	39% ± 2%	37%	36.8%	36.2%	30–35%	32.5%

Table 4
Compared measurements (in mm) of the femurs and tibio-fibula of some Orycteropodinae. Legend: F, femur; TF, tibio-fibula; L, length; Bp, proximal medio-lateral breadth; Bd, distal medio-lateral breadth; e, estimated measurements
Tableau 4. Mesures comparées (en mm) des fémurs et tibio-fibula de quelques Orycteropodinae. Légende : F, fémur ; TF, tibio-fibula ; L, longueur ; Bp, largeur médio-latérale proximale ; Bd, largeur médio-latérale distale ; e, mesure estimée.

Species	***O. afer***	***O. djourabensis*** **(Holotype)**	***O. mauritanicus*** **(Paratype)**	***O. gaudryi*** **(AMNH 22762)**	***O. abundulafus***	
					Holotype	**TM255-03-01**
FL	194 ± 13.5 (n = 39)	174		137.9		138.3
FBp	68.5 ± 6.5 (n = 41)	63.3		44.5	44.6	44
FBd	58.7 ± 4.5 (n = 42)	52.9		41.4	35e	37.7
TFL	183.8 ± 10.8 (n = 36)	168.5	164.4	156.7	140e	143.1
TFBd	58.4 ± 4.7 (n = 35)			37.4	36.3	35.8

the mandible, the greater (*B*/*L*) index of the molars, its non-projecting deltoid crest and triangular olecranon fossa on the humerus, a lower distal breadth on length index for the humerus, the prominent bicipital tuberosity and the longer oblique rim on the radius, its femur shorter than the tibio-fibula, the shorter tibial crest, the talus longer proximo-distally than medio-laterally, the slenderer elements of the autopodes. *O. abundulafus* differs from *O. gaudryi* Major, 1888 in having a frontal as long as the parietal, a greater (*B*/*L*) index of the molars, a non projecting deltoid crest on the humerus, a lower distal breadth on length index for the humerus, shorter digit II, III and IV but longer V, a pinching on the shaft of the anterior phalanges. *O. abundulafus* differs from *O. mauritanicus* Arambourg, 1959 by the greater (*B*/*L*) index of the molars, the shallower vestibular groove on the upper molars, its upper and lower M2 being longer than the corresponding M1, the shorter and less robust limb bones, the presence of a pinching on the shaft of the phalanges. *O. abundulafus* differs from *O. pottieri* Ozansoy, 1965 by the presence of a crest on the pterygoid, a higher angle between the branches of the mandible, the greater (*B*/*L*) index of the molars, the absence of canines.

3. Description

3.1. Skull

The cranium of TM255-03-01 has been damaged during the fossilization process (Fig. 2). The snout is completely gone on the left side, whereas on the right

side, orbit and tooth row are preserved. The supra-occipital part of the occipital bone has disappeared and the parietal is somewhat crushed along the sagittal plane. The atlas and axis are still in connection with the occipital condyles. The basioccipital region is the only part of the cranium that did not suffer deformations.

The anterior border of the orbit is situated above the M^2 and the ventral-most point of the fronto-jugal suture is above the M^3 like in *O. gaudryi* and *O. mauritanicus*. In *O. afer*, *O. crassidens* and *O. djourabensis*, those characters are situated above M^3 and behind M^3 respectively. On the cerebral capsule, the temporal lines (dorsal limit of the temporal muscle) are located close to the sagittal plane like in the Kossom Bougoudi holotype. In the Kollé and in the extant aardvarks, these lines are more remote from one another on each side of the cranium. Like all Upper Miocene Tubulidentata, this specimen shows a V-shaped lambdoid crest. The basicranium shows a well-developed crest on the lateral wall of the pterygoid (PtC, Fig. 2). This crest, also present in *O. abundulafus*, but not in *O. afer* and *O. djourabensis*, delimits the insertion surface for *Mm pterygoideus medialis* and *lateralis*. Moreover, the crest is less damaged in this specimen than in the holotype and shows a tubercle pointing laterally from the middle of the crest. The oval foramens are round dislike in the Kollé and extant species and are oriented anterolaterally/posteromedially not anteroposteriorly.

On the mandible, the horizontal ramus broadens progressively at the molar level. This ramus is broken before the symphysis. The articular condyle of the mandible shows a concave surface like in *O. abundulafus*, *O. gaudryi* and *O. pottieri* but unlike in *O. afer* and *O. djourabensis* for which the articulation surface is flat. This feature infers the presence on the cranium of a lateral tubercle on the glenoid cavity like in the Kossom Bougoudi holotype. This configuration precludes any disconnection of the mandibular joint. The angle formed by the two branches of the mandible (as taken by MacInnes [12]) displays an angle close to 75° like in *O. gaudryi* and it is different from that of *O. afer*, *O. crassidens* and *O. djourabensis* (Table 1). A smaller angle may be linked to the relatively longer mandible and snout of the Plio-Pleistocene taxa (Lehmann, in prep.).

The teeth of this Upper Miocene aardvark show the tubulidentate minute structure that characterizes the order Tubulidentata. Moreover, the molars are bilobed and very broad: the maximum breadth on length (*B*/*L*) index of the molar is very high (Table 2), especially for the M_2, which is diagnostic for *O. abundulafus*. The intracuspal rims of the molars (see [10]) are transversal in respect to the maximum length of the tooth like in *O. abundulafus*, *O. afer*, *O. gaudryi* and *O. djourabensis*. Conversely, the M^1 of *O. depereti* and the M_1 and M_2 of *O. pottieri* show oblique rims. The upper molars of the Toros-Menalla and Kossom Bougoudi aardvarks are trapezoidal like in *O. gaudryi* and *O. mauritanicus* but unlike in *O. afer* and *O. djourabensis* for which they are rectangular. Two grooves give the bilobed outline of the molars. However, in *O. abundulafus* from Kossom Bougoudi and Toros-Menalla, the lingual groove is superficial and not as deep as the vestibular one. This feature is also displayed by *O. gaudryi*, *O. mauritanicus* (the vestibular groove being deeper) and by *O. djourabensis*, but not by *O. afer*, whose grooves are sub-equal. The premolars are peg-like and show no informative character. Though, the upper and lower P3 are not bilobed on the new specimen so that the feature observed on the holotype (see [10]) has no

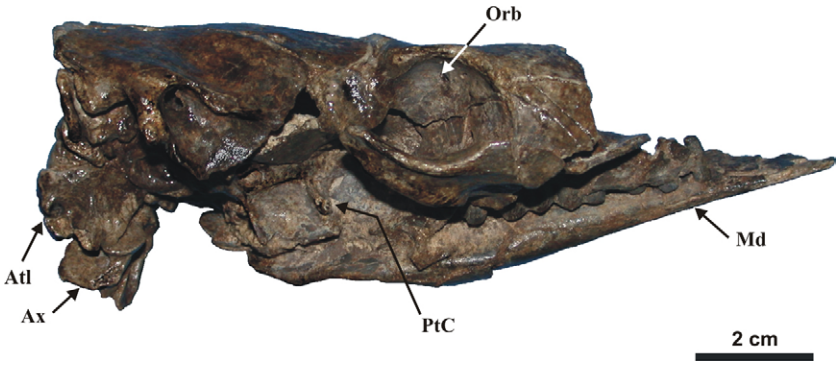

Fig. 2. Cranium of *Orycteropus abundulafus* TM255-03-01 in lateral view. Right hemi-mandible has been removed for description. Legend: Atl, atlas; Ax, axis; Md, left hemi-mandible; Orb, orbite; PtC, pterygoid crest.

Fig. 2. Crâne d'*Orycteropus abundulafus* TM255-03-01 en vue latérale. L'hémi-mandibule droite a été détachée pour la description. Légende : Atl, atlas ; Ax, axis ; Md, hémi-mandibule gauche ; Orb, orbite ; PtC, crête ptérygoïde.

diagnostic significance for the species. The upper and lower M3 are distinctly bilobed but this is a variable feature among Tubulidentata. The teeth of the Toros-Menalla specimen are slightly shorter than in the holotype of *O. abundulafus*.

3.2. Postcranium

The right humerus of TM255-03-01 is complete and well preserved, whereas the left one is more fractured (Fig. 3). The dimensions of the humerus are similar to those of the holotype of *O. abundulafus* (when comparable) and smaller than those of *O. gaudryi*. The deltoid ridge is absent in the Toros-Menalla specimen, whereas it is well developed and projects laterally in all *Orycteropus* species except *O. abundulafus*. Like in the Kossom Bougoudi holotype, this ridge is replaced by a smooth line that follows the shaft of the bone and do not project laterally. On that line, a tubercle is observed directly under the proximal epiphysis of the humerus, on the lateral side of the shaft. Such blunt tubercle is present at the same level in the holotype of *O. abundulafus*. The absence of projecting deltoid crest is a diagnostic feature of *O. abundulafus*. The pectoral crest and the deltoid tuberosity are well developed as in all *Orycteropus*. However, the pectoral crest is interrupted above the deltoid tuberosity like in *O. abundulafus*, but unlike in *O. afer*, *O. gaudyi* and *O. djourabensis*, whose crests are continuous with the tuberosity. This tuberosity has a low position on the bone, below the mid line of the shaft. The brachial crest has a strong development from the deltoid tuberosity level to the lateral side of the distal epiphysis. According to MacInnes [12], a developed brachial crest reflects a digging adaptation. The distal epiphysis is intact in the Toros-Menalla specimen, but not in the Kossom Bougoudi holotype. The former specimen shows a slender distal epiphysis in comparison with other *Orycteropus* species. In particular, the index bringing together the distal breadth and the length of the humerus is close to 30%. Only *O. abundulafus* (estimated measurement for the type) shows an index as low for the humerus (Table 3). According to Hildebrand [9], a high index (30 to 70%) suggests fossorial habits. The olecranon fossa is triangular in shape like in *O. abundulafus* from Kossom Bougoudi and *O. gaudryi*, but in *O. afer* and *O. djourabensis*, it is oval.

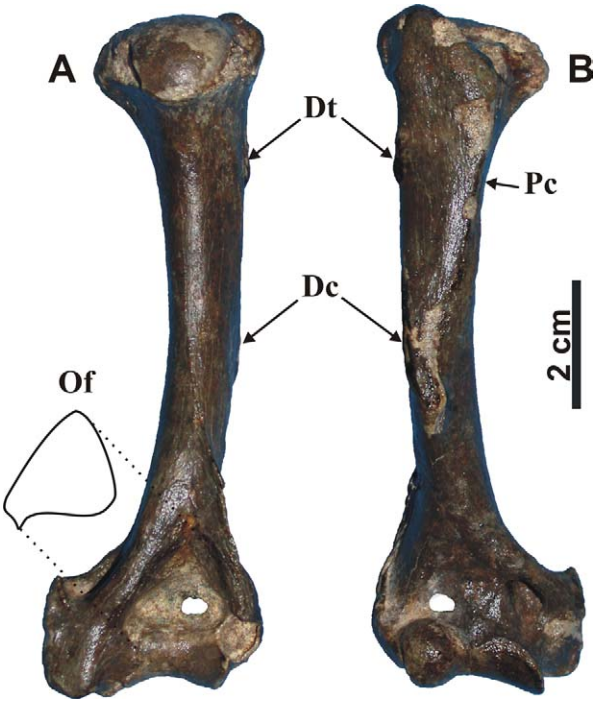

Fig. 3. Right humerus of *Orycteropus abundulafus* Toros-Menalla 255-03-01 (**A**) in dorsal view; (**B**) in ventral view. Legend: Dc, absence of deltoid crest; Dt, tubercle on the deltoid line; Of, olecranon fossa triangular; Pc, pectoral crest.
Fig. 3. Humérus droit d'*Orycteropus abundulafus* TM255-03-01 (**A**) en vue dorsale ; (**B**) en vue ventrale. Légende : Dc, absence de crête deltoïde ; Dt, tubercule présent sur la ligne deltoïde ; Of, fosse olécrânienne triangulaire ; Pc, crête pectorale.

Both radii are preserved; only the distal epiphysis of the right one is broken. The radius of the Toros-Menalla specimen is similar in size to those in *O. abundulafus* and *O. gaudryi*. The proximal epiphysis is oval-shaped. The distal epiphysis is less triangular than in *O. afer* and *O. djourabensis*. The bicipital tuberosity (or radial tuberosity) forms a prominent process, like in *O. abundulafus* and *O. gaudryi*, which is distinctly different from the button-like tuberosity in *O. afer* and *O. djourabensis*. Moreover, the oblique rim of the Toros-Menalla specimen, which serves as insertion surface for *M. supinator*, is as long as in *O. abundulafus* from Kossom Bougoudi.

The ulnas of the Toros-Menalla specimen lack their distal epiphysis and show signs of weathering and rodent gnawing. The dimensions of these ulnas are similar to those of *O. abundulafus* and *O. gaudryi*. Moreover, the articulation surfaces of the trochlear notch are facing each other so that the articulation axis is oblique in respect to the diaphysis of the ulna. This situation is also observed in *O. abundulafus* and *O. djourabensis*, but not in *O. afer*, for which the articulation axis is transversal. The latter configuration enlarges and stabilises the contact with the distal epiphysis of the humerus in the extant form.

The right hand of TM255-03-01 is well preserved, but the carpals are missing. Like in all Orycteropodinae, the metacarpals show a medial keel on their distal epiphysis that fits in the groove on the proximal epiphysis of the proximal phalanges. This configuration restricts the movement of these bones and prevents dislocations. The metacarpals and phalanges of this specimen and those of the Kossom Bougoudi one show similar dimensions. Moreover, the medial phalanges of TM255-03-01 show a pinching on the dorsal surface of the shaft like in *O. abundulafus* but dislike in *O. gaudryi*. In *O. afer* and *O. djourabensis*, the elements of the hand are larger and proportionally broader.

The acetabular regions of both coxal bones as well as parts of the sacrum and left ilium are preserved. The size of the Toros-Menalla pelvis is comparable with that of the Kossom Bougoudi holotype. The pubis is stick-like and oriented caudally at the difference from *Leptorycteropus guilielmi* Patterson, 1975, whose pubis is oriented more ventrally. The ilium of all Tubulidentata shows a dorso-caudal extension. This wing is the support of the sciatic notch. In lateral view, this notch is positioned at the level of the acetabulum in the Toros-Menalla specimen like in *O. abundulafus* and *L. guilielmi*. In *O. afer*, *Myorycteropus africanus* MacInnes, 1956 and in *O. djourabensis*, however, this notch is located more rostrally, at the level of the femoral spine (the insertion for the *M. rectus femoris*).

In the holotype of *O. abundulafus* from Kossom Bougoudi, head and distal epiphysis are the only femur fragments known (Fig. 4). Conversely, both femurs of TM255-03-01 are in a very good state of preservation: the patellas are still in connection with their distal epiphysis (Fig. 4A). Like in all *Orycteropus* species, the femur of the Toros-Menalla specimen does not show a distinct neck. The lesser trochanter is well developed and oriented ventrally, like in the extant aardvark. It extends along the shaft to the pectineal tubercle (fourth trochanter): the presence of this tubercle is a diagnostic character of the Orycteropodinae. The third trochanter, on the lateral side of the shaft, is thin, but widens in its middle. On the lateral condyle of the distal epiphysis, the facet for the sesamoid bone for *M. gastrocnemius* is situated behind the diaphysis level, like in the holotype

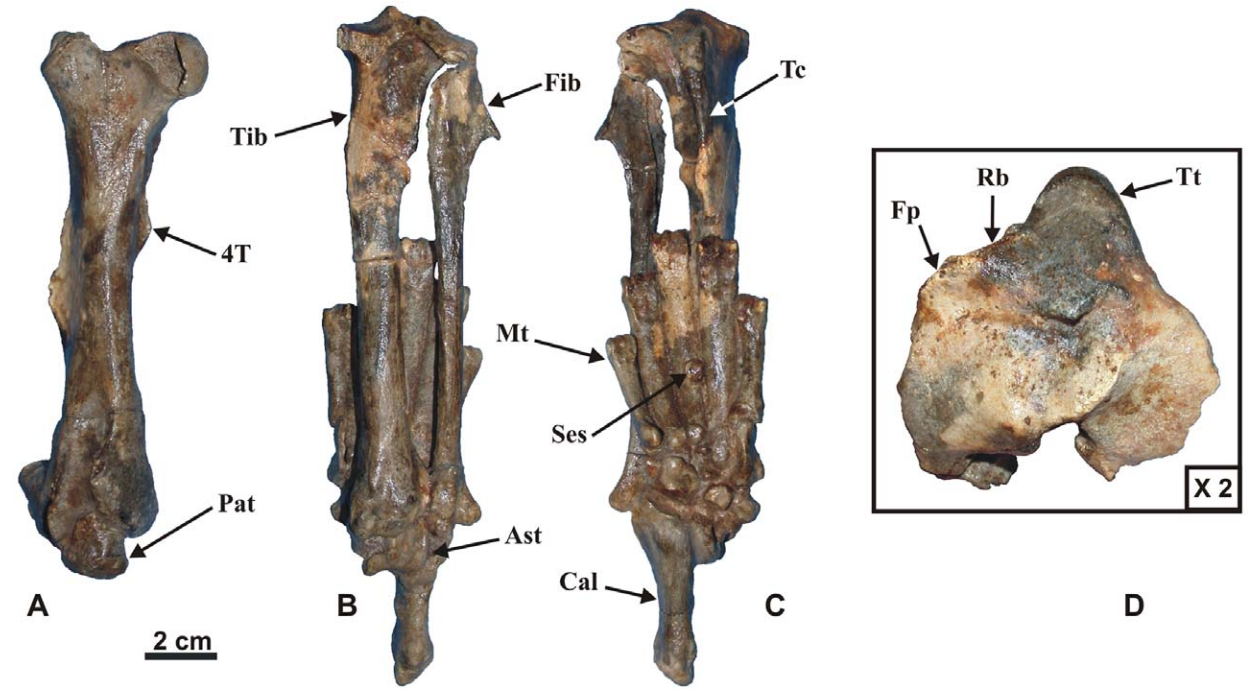

Fig. 4. Right hind limb of *Orycteropus abundulafus* TM255-03-01: (**A**) femur in dorsal view; (**B**) tibio-fibula in ventral view; (**C**) tibio-fibula in dorsal view; (**D**) detail of the proximal epiphysis of the left tibio-fibula in proximal view. Legend: 4T, fourth trochanter; Ast, talus; Cal, calcaneum; Fib, fibula; Fp, absence of falciform process; Mt, metatarsal; Pat, patella; Rb, rim of bone between tibia and fibula; Ses, sesamoid bone; Tc, tibial crest; Tib, tibia; Tt, tibial tuberosity.

Fig. 4. Membre postérieur droit d'*Orycteropus abundulafus* TM255-03-01 : (**A**) fémur en vue dorsale ; (**B**) tibio-fibula en vue ventrale ; (**C**) tibio-fibula en vue dorsale ; (**D**) détail de l'épiphyse proximale du tibio-fibula gauche en vue proximale. Légende : 4T, quatrième trochanter ; Ast, astragale ; Cal, calcanéum ; Fib, fibula ; Fp, absence de processus falciforme ; Mt, métatarsiens ; Pat, patella ; Rb, bord osseux entre tibia et fibula ; Ses, os sésamoïde ; Tc, crête tibiale ; Tib, tibia ; Tt, tubérosité tibiale.

of *O. abundulafus* and more posteriorly than the one in *O. afer* (see [10]). The dimensions of the femur of the Toros-Menalla aardvark are similar to those found in the Kossom Bougoudi specimen (when comparable) and in *O. gaudryi* (Table 4). Moreover, the hypothesis proposed by Lehmann et al. [10] can be tested: the femur of *O. abundulafus* is shorter than the tibio-fibula like in *O. gaudryi* (see [8]) but unlike in *O. afer* and *O. djourabensis*. Noticeably, the juvenile specimens of the extant aardvark present also shorter femur than tibio-fibula, whereas it is reversed when they reach maturity. From a biomechanical point of view, the length of the tibio-fibula has direct repercussion on the length of *M. gastrocnemius*, which extends from the distal part of the femur to the calcaneum. The efficiency of the power stroke at the ankle is not altered. However, during the flexion of the leg, a longer tibio-fibula enables the foot to cover a longer distance at a time or cover the same distance faster.

Both tibio-fibulae are well preserved. In fact, they are still in connection with the tarsus and the metatarsus (as well as some sesamoid bones) (Fig. 4). Only fragments from the epiphysis of the tibio-fibula of the holotype were previously documented. Tibia and fibula of the Toros-Menalla specimen are fused proximally, but not distally, like in all Orycteropodinae. The diaphysis of the tibia is slender and curved. The tibial tuberosity (for the insertion of the patellar ligaments) is concave, oblique and continuous with the proximal articulation surface, like in the extant species and *O. abundulafus* from Kossom Bougoudi. In TM255-03-01, an uninterrupted rim of bone extends from the tibial tuberosity to the junction with the fibula instead of the deep notch present in *O. afer*. No falciform process is present on the dorso-lateral side of the proximal epiphysis like in *O. gaudryi*, but unlike in *O. afer* and *O. djourabensis*. Thus, in proximal view, the proximal epiphysis of the tibio-fibula of the Toros-Menalla aardvark adopts a trilobed configuration (Fig. 4D), like in *O. gaudryi* and *O. mauritanicus* (contra [1] but see [11]). The tibial crest is proportionally shorter and ends more abruptly in the Toros-Menalla specimen than in the extant and Kollé species. No cnemial tuberosity is present as in all *Orycteropus* species. The dimensions of the tibio-fibula of the Toros-Menalla specimen are similar to those in the holotype of *O. abundulafus* (when comparable) and in *O. gaudryi* (Table 4). The tibio-fibula of *O. mauritanicus* is longer.

Both feet are preserved and tarsus and metatarsus are still in connection (with sesamoids). The talus is difficult to study as the tibia and the calcaneum concealed it. An astragalar foramen and a distinct neck are still visible. Whereas no posteromedial process is present on the talus of the holotype, the Toros-Menalla specimen shows a distinct one. Thus, this feature is variable in this species. The other tarsal bones are comparable in dimensions and features to those of *O. abundulafus* from Kossom Bougoudi. The metatarsal and phalange are proportionally slender as in the Kossom Bougoudi species in contrast to those of *O. afer* and *O. djourabensis*. However, these bones are shorter and slenderer than in the holotype of *O. abundulafus* and the proximal phalanges show a small dorsal depression on the distal epiphysis. This depression has also been observed in a few extant specimens. It represents the insertion surface for ligaments of the extensor muscles of the digits. Digit II and III have sub-equal length. In *O. abundulafus*, the foot is longer than the hand. In practice (especially for fossil specimens), this is best estimated by comparing the length of the longest finger (metapode to medial phalanx) and longest toe, which are ca. 90 and 110 mm (ratio close to 82%) respectively in the Chadian specimen. Conversely, in *O. afer* foot and hand have subequal length: the ratio length of the longest finger on longest toe is 0.90 ± 0.01 ($n = 10$), whereas *O. djourabensis* shows an intermediate configuration with a ratio of 0.87 (see [11]).

4. Discussions and conclusion

The new aardvark from the fossiliferous sector Toros-Menalla belongs to *O. abundulafus* previously described from Kossom Bougoudi [10]. Moreover, the Toros-Menalla specimen shows elements missing in the holotype from Kossom Bougoudi and represents the skeleton of an adult individual. The comparison between the Kossom Bougoudi and Toros-Menalla specimens confirms the estimation made by Lehmann et al. [10] that the holotype is a sub-adult having reached adult size at time of death. Thus the diagnosis of *O. abundulafus* has been supplemented.

O. abundulafus was formerly known from a single locality (Kossom Bougoudi) aged from about 5 Myr. Previous anatomical comparison and phylogenetic study [10] showed that *O. abundulafus* is closely related to *O. gaudryi*, a middle-sized form known from the Turolian (7.65–5.3 Myr) of Greece and Turkey (see [2,8,15]). The new material from Toros-Menalla displays features (e.g., tibio-fibula longer than femur; see description) that confirm this relationship and it extends the stratigraphic range of *O. abundulafus* back to about 7 Myr. Both species are thus smaller than *O. afer*, are

penecontemporary, and disappear at the same time around the Mio-Pliocene boundary in Africa and Europe. In Europe, *O. depereti* is the last tubulidentate that occurs in the Pliocene and it is closely related to *O. gaudryi*. On the other hand, in Africa, all forms are replaced in the Pliocene by new, larger species, close to the extant *O. afer*. In that context, *O. djourabensis* from Chad succeeds to *O. abundulafus*, and we can tentatively consider both species as local biochronological markers.

The progressive increase in size is a classically admitted evolutive trend within Tubulidentata (see [8,13, 14]). However, this trend is not confirmed between 15 and 5 Myr. *O. mauritanicus* from the Vallesian of Algeria is larger than the Turolian *O. abundulafus* and *O. gaudryi*, and than *Leptorycteropus guilielmi* from Kenya. Finally, in Chad, the size increase between *O. abundulafus* and *O. djourabensis* around the Mio-Pliocene boundary is fast. Thus the linear evolutive trend proposed by several authors should be reconsidered in the frame of the new discoveries in Chad. The phylogeny of the Tubulidentata is also more complex than previously thought. The relationships within Tubulidentata can only be clarified by a revision and study of all fossil aardvark material based on the sub-complete Chadian specimens (Lehmann, in prep.).

Acknowledgements

We thank the Chadian authorities and extend gratitude for their support to the 'Ministère de l'Éducation nationale, de la Recherche et de l'Enseignement supérieur', and the 'Ministère des Affaires étrangères' (France). This study benefited from the support of the NSF RHOI project. T.L. thanks the NRF Postdoctoral Fellowship Grant for funding. We acknowledge S. Ducrocq for the improvement of the manuscript. None of the work could have been possible without the field and technical work of all the MPFT participants.

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