

A new species of Orycteropodidae (Mammalia, Tubulidentata) in the Mio-Pliocene of northern Chad

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A new species of fossil Tubulidentata has been found by the Mission Paléoanthropologique Franco-Tchadienne in Northern Chad. It is the first fossil Orycteropodidae (aardvark) from the Mio-Pliocene of Central Africa. The new taxon, *Orycteropus abundulafus* sp. nov., is considered in the framework of the available Orycteropodidae fossil record. The Chadian specimen is characterized by the highest dental robustness index among all Tubulidentata, the presence of crests on the pterygoid, the triangular-shaped olecranon fossa and the reduction of the deltoid crest. All of these characters are linked to a less fossorial animal that had a tougher diet. This new African species is closer to the Eurasian *O. gaudryi* than to any other Tubulidentata. Together they form a clade distinct from that which includes *O. afer*. This is the first evidence of a relationship for aardvarks between Africa and Eurasia. An initial step is made towards revision of the phylogeny of the order. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, 143, 109–131.

ADDITIONAL KEYWORDS: Africa – Eurasia – palaeogeographical relationships – phylogeny – systematics.

INTRODUCTION

During palaeontological fieldwork in 1997 at Kossom Bougoudi (Chad), the Mission Paléoanthropologique Franco-Tchadienne (MPFT) discovered a partial aardvark skeleton. This is the first fossil of Tubulidentata discovered in Chad. The site is situated west of Koro Toro and east of Toros-Menalla (B.E.T. Province, northern Chad), two fossiliferous areas that yielded hominids (Brunet *et al.*, 1995, 1996, 2002). On the basis of biostratigraphy, Brunet & MPFT (2000) estimate an age close to the Mio-Pliocene boundary for the site.

Currently, the order Tubulidentata is only represented by a single species, *Orycteropus afer*. Geographically, this aardvark lives in sub-Saharan Africa.

Fossil Tubulidentata are not numerous but their record can be followed from the Miocene onwards to present times. Moreover, the fossil forms are widespread from France to Pakistan and in Africa, where

they are found in numerous early hominid sites (Koobi Fora, Laetoli, Lukeino, Makapansgat, Olduvai, Toros-Menalla, etc.).

The discovery of the Chadian fossil is important for at least two reasons. First, although fossil Tubulidentata are known from North, South and East Africa as well as Eurasia, this is the first Central African fossil aardvark found. Secondly, very few complete skeletons of fossil aardvarks have been found until now, and a detailed description of the major part of this new form is possible, regarding the cranium, teeth and postcranial skeleton. This facilitates comparison with other fossils, which are often fragmentary, and permits the development of the first data matrix for the order, relevant for assessing relationships between taxa.

ORDER TUBULIDENTATA

The order Tubulidentata Huxley, 1872 consists of a single family: the Orycteropodidae Gray, 1821. Following Patterson (1975, 1978), this family contains two subfamilies (Orycteropodinae Gray, 1821; Plesio-orycteropodinae Patterson, 1975) and four genera

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(three fossil), the affinities and validity of which are still debated (Pickford, 1975).

The genus *Plesiorycteropus* Filhol, 1895, from the Pleistocene of Madagascar, is the single member of the Plesiorycteropodinae. MacPhee (1994) shows evidence that this taxon does not belong to the Tubulidentata but represents a new order: Bibymalagasias. However, other authors continue to refer to the genus as a member of the Tubulidentata (Milledge, 2003). It is not the purpose of this paper to debate this issue. Two species of *Plesiorycteropus* are recognized: *Plesiorycteropus madagascariensis* Filhol, 1895 and *Plesiorycteropus germainepetterae* MacPhee, 1994, both subfossils from different localities on Madagascar.

Among Orycteropodinae, two genera from Kenya have been described: *Myorycteropus* MacInnes, 1956 from the Lower Miocene and *Leptorycteropus* Patterson, 1975 from the Upper Miocene. Both are monospecific: *Myorycteropus africanus* MacInnes, 1956 from Rusinga and Mfwangano, and *Leptorycteropus guilielmi* Patterson, 1975 from Lothagam.

The fourth genus is *Orycteropus* Geoffroy, 1791. The only living species of the order Tubulidentata, *Orycteropus afer* (Pallas, 1766) (the armadillo), belongs to this genus. It is a nocturnal animal that burrows relatively deeply in the ground for shelter. The armadillo shows a very low degree of sexual dimorphism, such that zoo specimens are often 'resexed' after their death (M. Damen, pers. comm.). Its diet consists of ants, termites and larvae of some insects. The armadillo is easily able to break open termite mounds. From South Africa to sub-Saharan regions, 18 subspecies have been described since 1766 (Shoshani, Goldman & Thewissen, 1988), but their taxonomic validity is uncertain.

Fossils representing this genus are found from the Lower Miocene until the present. Traditionally, it includes six Eurasian species: *O. seni* Tekkaya, 1993 from the Middle Miocene of Çandir (Turkey); *O. browni* and *O. pilgrimi* Colbert, 1933 from the Middle and Upper Miocene of Nagri, Dhok Pathan and Chinji (Pakistan) (Pickford, 1978); *O. pottieri* Ozansoy, 1965 from the Vallesian of Sinap (Turkey) and Pentalophos (Greece) (Bonis *et al.*, 1994); *Orycteropus gaudryi* Major, 1888 from the Turolian of Samos (Colbert, 1941), Italy (Rook & Masini, 1994), Turkey (Sen, 1994), Moldavia (Pavlova, 1915) and Iran (Major, 1893); and *O. depereti* (Helbing, 1933) from the Pliocene of Perpignan (France). In Africa, the genus comprises five species: *O. minutus* Pickford, 1975 from the Lower Miocene of Songhor, Mfwangano, Rusinga (Kenya); *O. chemeldoi* Pickford, 1975 from the Middle and Upper Miocene of Ngorora and Fort Ternan (Kenya); *O. mauritanicus* Arambourg, 1959 from the Upper Miocene of Bou Hanifia (Algeria); *O. crassidens* MacInnes, 1956 from the Pleistocene of Rusinga and

Kanjera (Kenya); and *O. afer*, the extant and type species, recognized from the Late Pleistocene of Algeria (Romer, 1938) onwards. Pickford (1975) considers *Myorycteropus* and *Leptorycteropus* as synonyms of *Orycteropus*.

Many *Orycteropus* fossils have not been attributed to any species in particular. An *Orycteropus* sp. is present in Lower Miocene deposits from East Africa (MacInnes, 1956). Other specimens have been discovered in Middle Miocene deposits in Asia, notably in Pakistan (Pickford, 1978), Georgia (Gabunia, 1956) and Turkey (Fortelius, 1990; Tekkaya, 1993; Sen, 1994). Upper Miocene specimens have been excavated in Greece (Bonis *et al.*, 1994), East Africa (Patterson, 1975; Milledge, 2003) and South Africa (Hendey, 1973). Pliocene specimens have been found in East Africa (Dietrich, 1942; Pickford, 1975; Leakey, 1987) and South Africa (Kitching, 1963; Lehmann, 2004). Pleistocene specimens are represented throughout Africa (Leakey, 1931–1951; Clark, 1942; Lehmann, 2004).

The Upper Miocene is the period during which the Tubulidentata show their widest distribution and greatest diversity. Later, in the Pliocene, armadillos are found mostly in Africa. The Pleistocene is the real beginning of the isolation of the order in Africa.

SYSTEMATIC PALAEONTOLOGY

ORDER TUBULIDENTATA HUXLEY, 1872

FAMILY ORYCTEROPODIDAE GRAY, 1821

GENUS *ORYCTEROPUS* GEOFFROY, 1791

SPECIES ***ORYCTEROPUS ABUNDULAFUS* SP. NOV.**

Holotype: KB03-97–214 (Figs 1–9, 11). It is a subcomplete skeleton discovered in anatomical connection (assigned to *Orycteropus* sp. nov. in Brunet & MPFT, 2000). It includes cranium and mandible with teeth; pectoral girdle (left and right glenoid part); vertebrate spine in articulation (cervical vertebrae to sacrum); some rib fragments; complete right and left forelimbs (including ungual phalanges and sesamoids); pelvic girdle including the right acetabular region; right femur (proximal end), tibia, fibula, tarsal, metatarsals, right phalanges (including ungual phalanges and sesamoids); left femur (distal epiphysis), left tibia (distal end), tarsal, metatarsals and left phalanges (including ungual phalanges and sesamoids). After study, the specimen will be permanently curated in the Centre National d'Appui à la Recherche (CNAR) in N'Djaména, Chad.

Hypodigm: Type only.

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

Age: Mio-Pliocene boundary (around 5 Mya) (Brunet & MPFT, 2000).

Etymology: Specific name, *abundulafus* (Latin), derived from Abundoulaf meaning 'the one who digs' and also aardvark in Chadian Arabic language.

Diagnosis: General size around 75% that of the extant form, *Orycteropus afer*.

Skull: Glenoid cavity with well-developed lateral tubercle, lateral crests on pterygoid wall.

Mandible: Long symphysis (21% of total length), concave condyle.

Dentition: Very robust molars with transversal intracanal rim.

Forelimb: Deltoid ridge of the humerus not projecting laterally, olecranon fossa triangular in shape.

Hind limb: Sesamoid bone for the M. gastrocnemius situated backwards.

DESCRIPTION AND COMPARISON

The teeth have an advanced dental wear and some limb bones (femur) do not have fused epiphyses. In the extant form, the adult size is reached at 1 year of age (Jacobi, 1972) but sexual maturity is reached at 2 years (Haltenorth & Diller, 1977). The anatomical stages of development in aardvark have not been well studied, but KB03-97-214 is estimated to be a late subadult in terms of development, having reached adult size at time of death.

CRANIAL

Cranium (Table 1; Figs 1–3)

The skull is remarkably well preserved and despite *post mortem* deformation of the preorbital region, the right side is complete. The infra-orbital foramina are not visible and the left orbital region is weathered.

A depression on the frontal, above and in front of the orbit, is present. Although the fossil has been slightly compressed laterally during fossilization, the cranial roof is flatter in *O. abundulafus*, *O. gaudryi* or *O. depereti* than in *O. afer*. The temporal lines (representing the dorsal limit of the temporal muscle) are positioned closer to the sagittal plane (as in *O. depereti* or *O. gaudryi*) than is the case in *O. afer*. The suture between squamosal and parietal (squamosal scale) is very distinct. Its position can be related to the weak lateral extension of the parietal. The lambdoid crest (in dorsal view) has a clear V-shaped outline as in *O. gaudryi*, *O. depereti* and *O. pottieri* but not in the living aardvark. The frontal is slightly longer sagittally than the parietal in *O. abundulafus*,

O. depereti and *O. afer*, whereas in *O. gaudryi* it is the opposite.

The angle between tooth row and zygomatic arch is about 30° in *O. abundulafus*, which matches the range of variation measured in 16 skulls of *O. afer* (26–38°) from the Transvaal Museum (Pretoria) collections, hereafter referred to as the TMP sample. Conversely, the same angle measured from Colbert's (1941) diagram of *O. gaudryi* is c. 25°.

As suggested by Colbert (1941), there is a constant and significant difference in the position of the anterior rim of the orbit relative to the dentition in the Orycteropodinae. It is always situated above M² in *O. abundulafus*, in *O. gaudryi* and in *O. depereti* whereas it is always above M³ for all *O. afer* ($n = 57$) from the TMP sample, as well as in the zoological collection of the Museum für Naturkunde in Berlin (ZMB sample) and in the collection of the Staatliches Museum für Naturkunde Stuttgart (SNMS sample), and in *O. mauritanicus* (Colbert, 1941; Arambourg, 1959). The ventral most point of the zygomatic arch (at the maxillojugal suture) also has a variable position. In *O. abundulafus* it is above M³ as in *O. gaudryi*, whereas it is behind M³ in *O. depereti*, as well as in all the *O. afer* ($n = 57$) specimens from the TMP, ZMB and SNMS samples.

The palatine of KB03-97-214 (Fig. 2) is slender with a low breadth-to-length index of 0.197 (Bpal/Lpal; Table 1). The palatine region is wider in *Orycteropus afer* in the TMP, ZMB and SNMS samples ($n = 65$) with an index of 0.25 ± 0.02 . Noticeably, in *O. gaudryi* (AM 20562) this ratio is 0.19 and in *O. depereti*, it is estimated to be c. 0.25. There are two palatine foramina at the M³ level, which are not developed backwards in this tooth. They are circular as in *O. depereti* and *O. gaudryi* but not elongated as in *O. afer* and lead into the orbit solely. The posterior rim of the palatine is straight and posterior to the M³ in the extant species. In the specimen from Chad, and in *O. gaudryi* as well as in *O. depereti*, the rim is curved and is at the level of, or tangential to, the M³. A well-marked palatine groove occurs in front of the palatine in KB03-97-214, similar to the condition in *O. afer*. In *Orycteropus gaudryi*, *O. depereti*, and *Leptorycteropus guilielmi*, however, the palatine is not grooved but displays a concave outline (Patterson, 1975). The palatine bones are depressed in front of the palatine foramina, but not bulged as in *O. afer* or *O. depereti*.

Many features show elongation and widening of the snout in the living aardvark as well as in *O. mauritanicus* or *O. depereti*. In fact, it seems that there is a shifting forward of the tooth-row in some species. As proposed by MacInnes (1956), taking the tooth row as the horizontal, we measured the distance between perpendiculars through the posterior border of the infra-orbital foramina and the anterior rim of

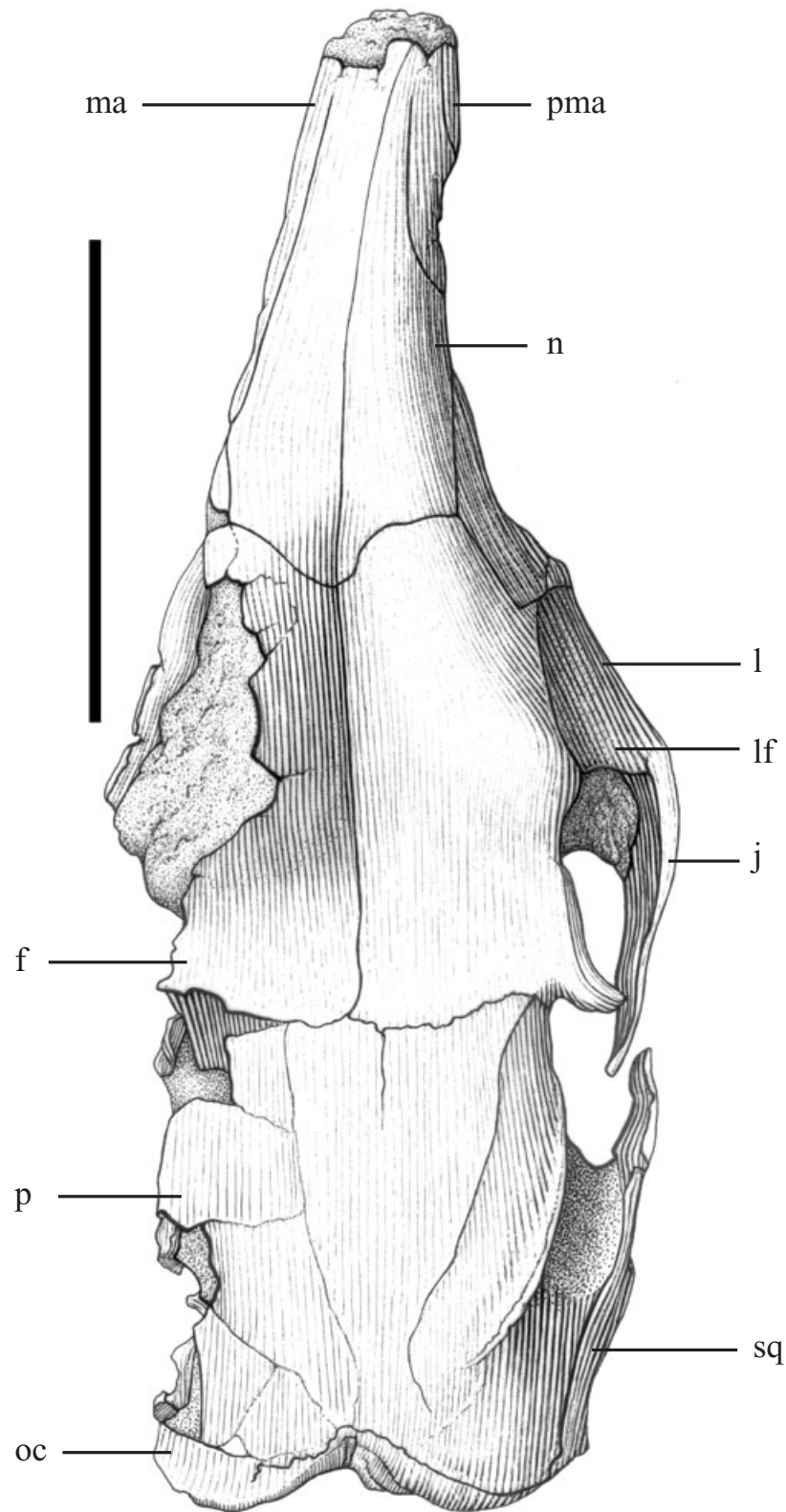


Figure 1. Cranium of *Orycteropus abundulafus* sp. nov. in dorsal view. f, frontal; j, jugal; l, lacrymal; lf, lacrymal foramen; ma, maxillary; n, nasal; oc, occipital; p, parietal; pma, premaxillary; sq, squamosal. Scale bar = 5 cm.

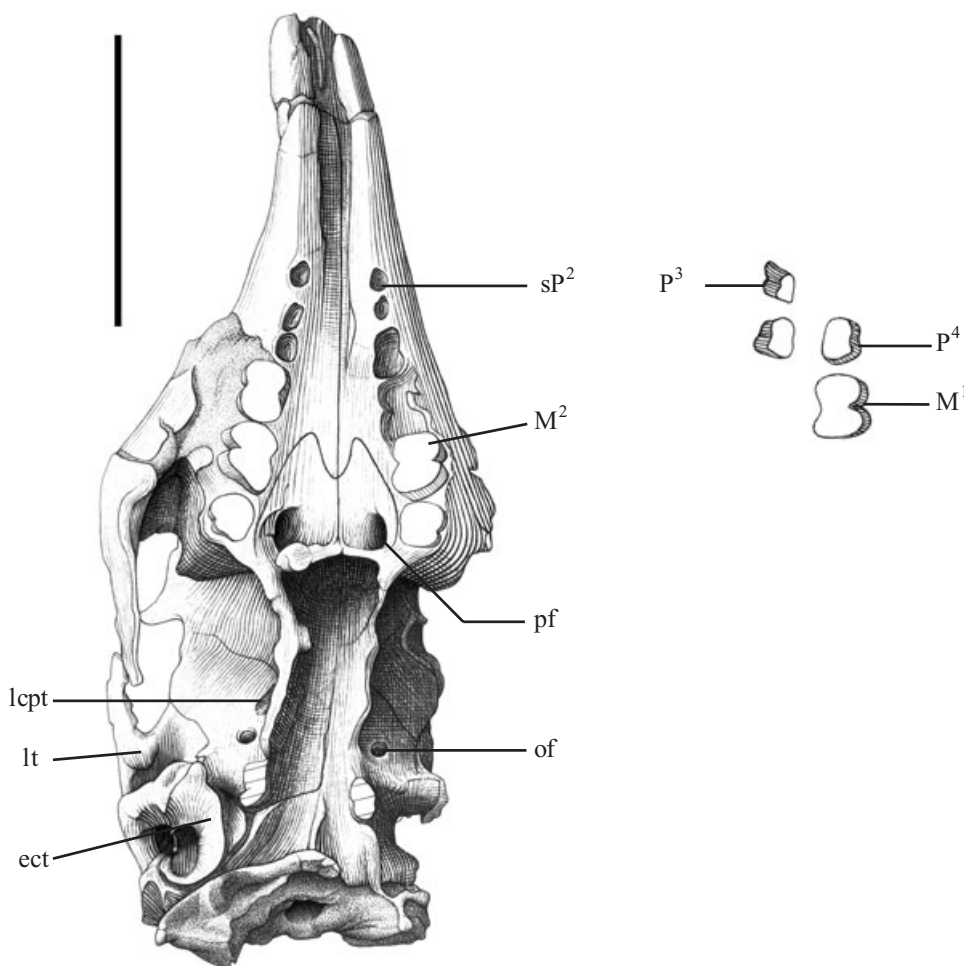


Figure 2. Cranium and upper teeth of *Orycteropus abundulafus* sp. nov. in ventral view. ect, ectotympanic; lcpt, lateral crest on the pterygoid wall; lt, lateral tubercle of the glenoid cavity; of, oval foramen; pf, palatine foramen; sP², socket for P². Scale bar = 5 cm.

the orbit (L1) and the distance between perpendiculars through the posterior border of the infra-orbital foramina and the M³ (L2) in *O. afer* and *O. gaudryi*. The ratio L1/L2 gives 0.55 for Colbert's figure (1941) of *O. gaudryi* used by MacInnes, whereas the ratio ranges from 1 to 0.73 for the TMP sample of *O. afer* ($n = 11$). In contradiction to MacInnes, we found a different ratio for the two species. Given the different position of the anterior border of the orbit and the variable position of the infra-orbital foramina relative to the dentition in the two species (more posterior in *O. afer*), the distance L2 tends to get shorter from Lower Pliocene to more recent samples. This is interpreted as growing and moving forward of the maxillary, dragging the M³ and the complete tooth-row. Further evidence of this is that the distance from M³ to the posterior rim of the palatine is greater in *O. afer* and *O. mauritanicus* than it is in *O. abundulafus* and

O. gaudryi. Moreover, this border is rectilinear for the two former species whereas it is bowed in *O. abundulafus* and *O. gaudryi*. The maxillary is in contact with the lateral edges of the rim and can, while moving forward, drag the wings of the rim to fall into line forwards. This movement results in the widening of the snout in *O. afer* and *O. mauritanicus*. *O. depereti* has a wide palatine and the transversal rim is flatter than it is in *O. gaudryi*. However, the position of the M³ relative to the orbit is closer to that of *O. gaudryi*. *O. depereti* appears to be intermediate in terms of this feature.

On the pterygoid lateral wall and on part of the alisphenoid is an oblique crest bordering anteriorly a shallow basin in front of the oval foramen (Fig. 3). Another crest, on the pterygoid, closes the basin posteriorly. This depression is different from a fossa pterygoidea because it extends on the alisphenoid. It

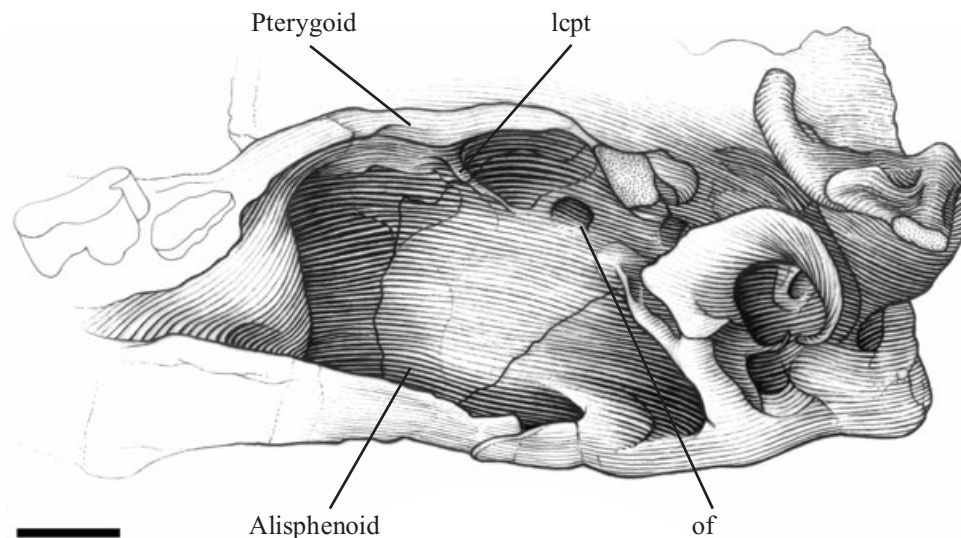


Figure 3. Cranium of *Orycteropus abundulafus* sp. nov. in lateral view (right side) showing detail of the infratemporal region. lcpt, lateral crest on the pterygoid wall; of, oval foramen. Scale bar = 1 cm.

is clearly visible on the right side of the skull whereas it is somewhat damaged but still distinct on the left side (not visible on Fig. 2 because of perspective). Apart from *O. abundulafus* and *O. depereti*, no Tubulidentata present this feature, previously unrecognized. Andrew (1896) and Colbert (1941) did not notice any peculiarity on the pterygoid of *O. gaudryi*. The basin does not enclose the oval foramen, but in *O. depereti* the crests are thicker. This is part of the insertion surface of Mm. pterygoideus medialis and lateralis. Those muscles participate in the occlusion and anteroposterior movement of the mandible. This feature shows that *O. abundulafus* had a more powerful chewing potential than *O. afer*. Unfortunately, the insertion of the M. masseter on the jugal has been distorted during fossilization, so the importance of that muscle cannot be assessed. A strong constriction is observed under the orbitosphenoid, in front of the optical and sphenorbital foramina. This constriction continues forwards to the frontal and palatal components of the orbit, beneath the ethmoidal foramen. The same can be seen in *O. depereti* and in *O. gaudryi*, whereas in *O. afer*, linked to the widening of the snout, it is wider.

The oval foramina are orientated anterolaterally/posteromedially and are round in shape. By contrast, in *O. afer*, they are more oval and the orientation of the aperture is anteroposterior.

The glenoid cavity is slender, much deeper in comparison with that of the extant form, and shows a well-developed lateral tubercle (Fig. 2). The glenoid cavities of *O. depereti* (broader) and *O. gaudryi* are similar.

The post glenoid process is strong and more vertically raised in *O. abundulafus* than in *O. afer*. The

lengthening of the skull in the extant form extends the lateral components of the cerebral cavity posteriorly, such that the caudal part of the process projects over the tympanic rim. Adjacent to the squamosal, the ectotympanic of *O. abundulafus* is more erect on the petrosal than in its extant relative. The principal axis of the tympanic rim is anteroposterior and displays an oval shape.

The breadth of the cranium at the level of the hypoglossal foramen (Bh, Table 1) in *O. abundulafus* and *O. gaudryi* represents approximately 75% of that in *O. afer*. The widening of the snout is correlated with a widening of the whole cranium from Lower Pliocene to present times.

Mandible (Table 2; Fig. 4)

The mandible is complete from the symphysis to the angular apophyse. On the left side, the vertical branch is truncated. The articular condyle and coronoid process are missing. On the right side, only the coronoid process is incomplete. The symphysis was still fused, which is rare.

The mandible swells at the level of the molars in all Tubulidentata. However, Table 3 shows that *O. abundulafus* has the greatest mandible buccolingual broadening with the doubling of the breadth from the P₃ to the M₂. Two mental foramina can be observed on the vestibular side, adjacent to the P₂. The symphysis remains fused, which is rare for Tubulidentata, extant and extinct. It is longer than in the extant aardvark. The length of the symphysis compared with the total mandible length (Ls and L, Table 2) gives an index of 20.8 compared with 17 ± 0.2 for the TMP,

Table 1. Biometry (measurements in mm) of the cranium of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

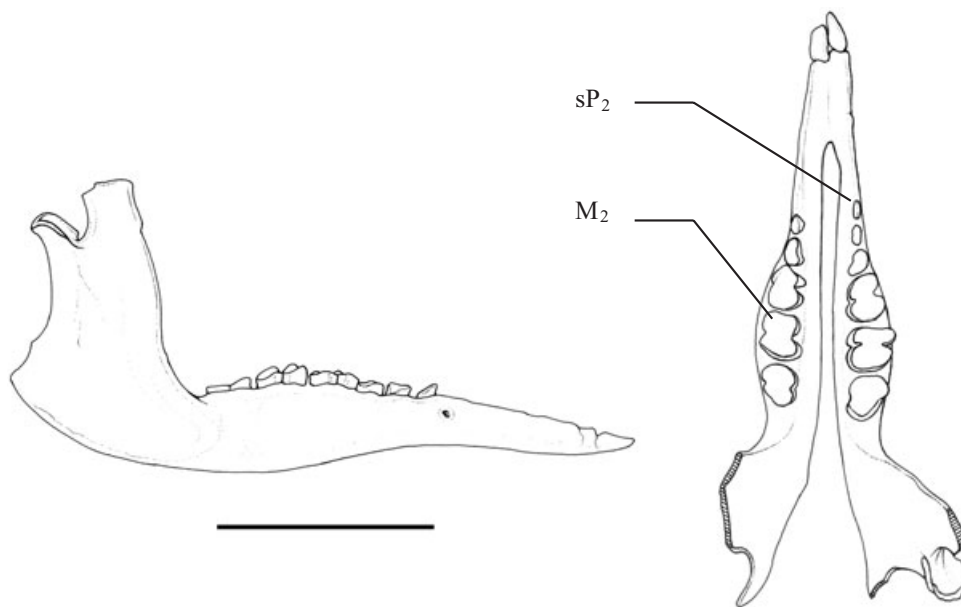
MSL	L _{no}	L _n	L _f	L _{fo}	L _{par}	B _{mjs}	B _{io}	B _{pop}	B _{fps}	B _c	B _h	L _{pal}	B _{pal}	Lutr (P ³ to M ³)	Lutr (P ² to M ³)
165*	154*	60*	45.7	100.1	44.4	74.2*	48.6*	59*	42.8*	46*	49*	91.2	18	43.2	49.5

MSL, maximum cranium length; L_{no}, nasal to occipital dorsal length; L_n, nasal length; L_f, frontal length; L_{fo}, frontal to occipital dorsal length; L_{par}, parietal length; B_{mjs}, breadth of the cranium at the maxillojugal suture; B_{io}, interorbital breadth; B_{pop}, breadth taken between the tips of the postorbital processes; B_{fps}, breadth of the cranium at the frontoparietal suture; B_c, cerebral cavity breadth; B_h, breadth of the cranium at the hypoglossal foramen level; L_{pal}, palatine length, from posterior rim to tip of the maxilla; B_{pal}, palatine breadth at the M² level; Lutr, upper tooth row length. *Estimated measurements.

Table 2. Biometry (measurements in mm) of the mandible of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

L	Ls	L _{ltr} (M ₃ to P ₄)	L _{ltr} (M ₃ to P ₃)	L _{ltr} (M ₃ to P ₂)	H _{ac}	B _{ac}	H _{ap}	BM ₂	HM ₂₋₃	LM ₁₋₃
132.5	27.6	38.7	44.8	50	55	11	35.3	12.8	17.9	32.7

L, length from anterior-most point to tip of the angular process; Ls, length of symphysis; L_{ltr}, lower tooth row length; H_{ac}, articular condyle height; B_{ac}, articular condyle breadth; H_{ap}, angular process height; BM₂, ramus breadth at the M₂ level; HM₂₋₃, ramus height at the M₂₋₃ level; LM₁₋₃, length of the molar row.

**Figure 4.** Mandible of *Orycteropus abundulafus* sp. nov. in lateral (left) and dorsal (right) view. M₂, second lower molar; sP₂, socket for P₂. Scale bar = 5 cm.

ZMB and SNMS samples ($n = 51$). The connection between the two parts of the mandible is then greatly strengthened. The lingual side of the symphysis is strongly concave buccolingually.

The angular apophyse, on the left side, is well defined. The dorsal notch is deep and the apophyse is stretched dorsally and posteriorly. This slender, sharp, curved and dorsally projected apophyse could be seen

as an angular spine. The articular condyle shows a concave surface in *O. abundulafus* instead of the flat shape in *O. afer*. In caudal view, it tends to be flared and its medial component is wider. The mandibular articulation configuration precludes any disconnection of the joint. However, limited lateromedial and/or anteroposterior movements of the mandible are possible. The anteroposterior movement of mastication has

Table 3. Comparative breadth (measurements in mm) of the *ramus horizontalis* in some *Orycteropodinae*

Species	B P ₃	B M ₂	Index
<i>O. pottieri</i> (type specimen MNHN-TRQ1003)	6.8	11	56.7%
<i>O. gaudryi</i> AM 20562 (cast)	7.1	11.2	63.5%
<i>O. afer</i> (MNHN-1923–398)	6.9	10.7	64.5%
<i>O. abundulafus</i> sp. nov. (KB3-97–214)	6.5	12.8	50.8%

B P₃, vestibulolingual breadth of the ramus at P₃ level;
B M₂, vestibulolingual breadth of the ramus at M₂ level;
Index: B P₃/B M₂.

low amplitude due to the strong postglenoid process and the developed glenoid lateral tubercle, but is powerful. Although the two flat articulation surfaces in the recent form enable wider movements, there are apparently no differences between the dental microwear signal. Major mesiodistal scratches are found in both species.

A commonly used character is the angle formed by the anterior border of the vertical branch and the tooth row. *Orycteropus abundulafus* sp. nov. shows an angle of c. 74°. The TMP sample ($n = 13$) presented an angle ranging from 64.9 to 75.5°. This angle is c. 45° in *Myorycteropus africanus* and is close to 80° in *O. gaudryi* (MacInnes, 1956).

Dentition (Table 4; Figs 2, 4)

The dental formula is I $\frac{0}{0}$ C $\frac{0}{0}$ P $\frac{3}{3}$ M $\frac{3}{3}$. Upper right M¹, P⁴ as well as left P⁴ and P³ were found out of their socket. Both P² and the right P³ are missing. All teeth show advanced dental wear with sloping occlusal surfaces, accentuated on the lower teeth.

The teeth show minute internal structures characteristic of the Tubulidentata. The upper and lower P₄ are bilobed as in *O. depereti*, some *O. gaudryi* and *O. pottieri* and, in a more symmetric manner, in *O. mauritanicus*. This feature is variable in *O. afer*. Conversely, the upper and lower P₃ are never bilobed in the Tubulidentata except perhaps for the P³ of *Myorycteropus africanus* described by MacInnes (1956: 3) as having 'a slight constriction on either side'. A distinct vertical groove on the medial aspect of both the upper and lower P₃ is clearly detectable in *O. abundulafus*. This tooth is bilobed. Because the alveoli of the premolars do not show exactly the same shape as the tooth, it is not possible to assess the general outline of P².

Table 4. Biometry (measurements in mm) of the dentition of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

Tooth	Anteroposterior length	Breadth of the anterior lobe	Breadth of the posterior lobe
P/2	4.2	—	1.7
P/3	5.2	2.1	2.5
P/4	5.7	3.5	4.5
M/1	10.5	7.6	8.7
M/2	10.8	9.5	9.6
M/3	9.6	8	6.5
P3/	4.4	2.7	3.1
P4/	6.7	4.3	5
M1/	10.7	7.2	8
M2/	11.1	8.3	8.6
M3/	8	8	6.2

Molars are the only teeth displaying grooves on the lingual and vestibular side. Upper and lower M₁ and M₂ of the Chadian fossil aardvark, as well as M₃ are distinctly bilobed, whereas on M³, only the vestibular wall is grooved. The unworn molars present two cusps, one on each lobe. In the adult, the upper molars are uniformly worn so that the occlusal surface is almost flat. However, as the occlusion with the lower molars is largely alternating, the occlusal surface shows wear facets on the mesial and distal side of the cusps. Thus, an intracuspal rim, usually smooth, is visible between those facets. Sen (1994) termed this a loph. In *O. abundulafus* the intracuspal rim has a transversal orientation with regard to the mesiodistal length of the tooth. The lower molars of an adult aardvark are not as flat as the upper molars. Instead, they are strongly concave in the vestibulolingual direction. The lingual wall is higher than the vestibular one. However, an intracuspal rim is still visible, transversal in the Chadian form. The lobes of the molars, as well as the intracuspal rim, have a transversal orientation in *O. gaudryi* (Sen, 1994) and *O. afer* as in *O. abundulafus*, whereas in *O. depereti* and *O. mauritanicus* the intracuspal rim is oblique. Diastema are found between the premolars and between the molars as well as between premolars and molars, but this can change from one hemimandible to another. The distance between the right M² and M³ is probably the result of deformation during fossilization as the right M₃ does not occlude with the right M³. Lower and upper M₂ are the largest teeth (Table 4). *O. gaudryi*, *O. depereti*, *Leptorycteropus guilielmi* and a large majority of *O. afer* (TMP, ZMB, and SNMS samples) show a similar pattern. In *O. mauritanicus* it is the M₁, which is the largest molar. In *O. pottieri* and *Myorycteropus africanus*, the largest teeth are M₂ and M¹.

Table 5. Dental Robustness Index calculated for some Orycteropodinae

Species	M ₁	M ₂	M ₃	M ¹	M ²	M ³
<i>O. afer</i> (n = 60)*	67.8 ± 6	72.4 ± 5	65.7 ± 8.9	67.2 ± 8.3	70.7 ± 7	67.4 ± 8.2
<i>O. chemeldoi</i> †	38.9	42.3	68.4	—	—	—
<i>O. crassidens</i> ‡	69.1	75	79.6	77.1	76.8	78.3
<i>O. depereti</i>	—	—	—	64.3	60.5	71.8
<i>O. gaudryi</i> (n = 18)§	64.5 ± 5.6	68.4 ± 4.9	69.1 ± 5.6	63.0 ± 2.9	65.2 ± 4.5	80.6 ± 6.7
<i>O. mauritanicus</i> ¶	54.9	64.4	64.0	59.1	70.4	95.4
<i>O. pottieri</i> (n = 10)**	59.3 ± 3.9	60.6 ± 2.6	70.0 ± 1.8	63.3	72	81
<i>O. abundulafus</i> sp. nov.	82.9	88.9	83.3	74.8	77.5	100

Dental Robustness index = maximum breadth/length × 100. *Data from the TMP, ZMB and SNMS samples for comparison.

†After Pickford (1975). ‡After MacInnes (1956), §After Colbert (1941), Tekkaya (1993) and Sen (1994). ¶After Arambourg (1959). **After Tekkaya (1993) and Bonis *et al.* (1994).

Dental size of the new Chadian fossil is similar to that of the other Miocene Orycteropodinae. However, the cheek teeth are broader than in every other Tubulidentata. The dental robustness index (Table 5) is significantly higher in *O. abundulafus*. This implies that the occlusal surface is relatively large, vestibulolingual, in each molar.

POST-CRANIAL SKELETON

Scapula (Table 6)

Both left and right glenoid parts and the right acromion are preserved. The acromial process projects a caudal apophysis. The spinous curves steeply relative to the glenoid cavity. Thus, the neck of the scapula is shorter in *O. abundulafus* and *O. gaudryi* than in *O. afer*.

Humerus (Table 7; Fig. 5)

Both left and right humeri are intact, but the distal epiphyses are incomplete.

Having fused, the two tuberosities of the proximal epiphysis are well developed. The proximal epiphysis is as wide anteroposteriorly as it is mediolaterally (HMD and HAD, Table 7), as seen in *O. afer*. In *Myorycteropus africanus*, the anteroposterior diameter is more developed (MacInnes, 1956).

The pectoral crest merges under the proximal epiphyses, in continuity with the bicapital groove. It is not continuous with the deltoid tuberosity, but the pectoral crest is as developed in *O. abundulafus* as it is in *O. afer* or *O. gaudryi*, as shown in the drawings of Colbert (1941: 327). This crest is the surface of insertion for the pectoral muscles. Those muscles are responsible for the adduction of the arm, help in the flexion of the shoulder joint, rotate the humerus inward and participate in the pull-off of the limb. A V-shaped deltoid tuberosity is present in KB03-97-214 (Fig. 5D). Its position is low on the bone, below the mid line. An important and diagnostic feature on the humerus that

Table 6. Biometry (measurements in mm) of the scapula of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

Scapula	SGV	SGT	La	Ba
Right side	17.9	10.3	26.8	11.6*
Left side	18.2	10.8	—	—

SGV, transverse diameter of glenoid cavity; SGT, vertical diameter of glenoid cavity; La, acromion length; Ba, acromion breadth. *Estimated measurement.

distinguishes *O. abundulafus* from *O. afer* and *O. gaudryi* is the absence of a well-developed deltoid crest. It is prominent and laterally projected in the extant aardvark, whereas in the Chadian aardvark fossil the shaft shows only a very small crest. This can be compared with the situation described by Patterson (1975: 192) in *Leptorycteropus guilielmi*: 'The deltoid crest is unique in being rather feebly developed, nearly straight and merging imperceptibly at its distal end into the body of the shaft'. The morphology in *O. depereti* is unknown as there are no post-cranial elements for comparison. This crest serves as insertion surface for the two deltoid muscles. They are the main abductors of the member, and rotate the humerus outward. The reduction of the lateral projection of the deltoid crest reduces the moment arm of those muscles as well as the available attachment area. The brachial crest has a very strong development, as suggested by its remaining bases. According to MacInnes (1956), this reflects a digging adaptation. The brachial crest is the insertion area for the M. triceps brachii, extensor of the elbow, which presses the lower arm against the substrate during its retraction (Thewissen & Badoux, 1986).

The general shape of the olecranon fossa is triangular, ascending in the middle, with well-marked rims

Table 7. Biometry (measurements in mm) of the humerus of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

Humerus	MHL	GTCL	HMD	HAD	Bd	Lef	HI
Right side	105.5	101.9	26.5	24.5	32.2–37*	–	0.30–0.35*
Left side	105.2	100.3	25.9	24.3	32.7–37*	5.4	0.31–0.35*

MHL, maximum humerus length; GTCL, length from greater tuberosity to capitulum; HMD, mediolateral diameter of the head; HAD, anteroposterior diameter of the head; Bd, distal mediolateral breadth; Lef, entepicondylar foramen length; HI, Hildebrand Index (Bd/MHL). *Estimated measurements.

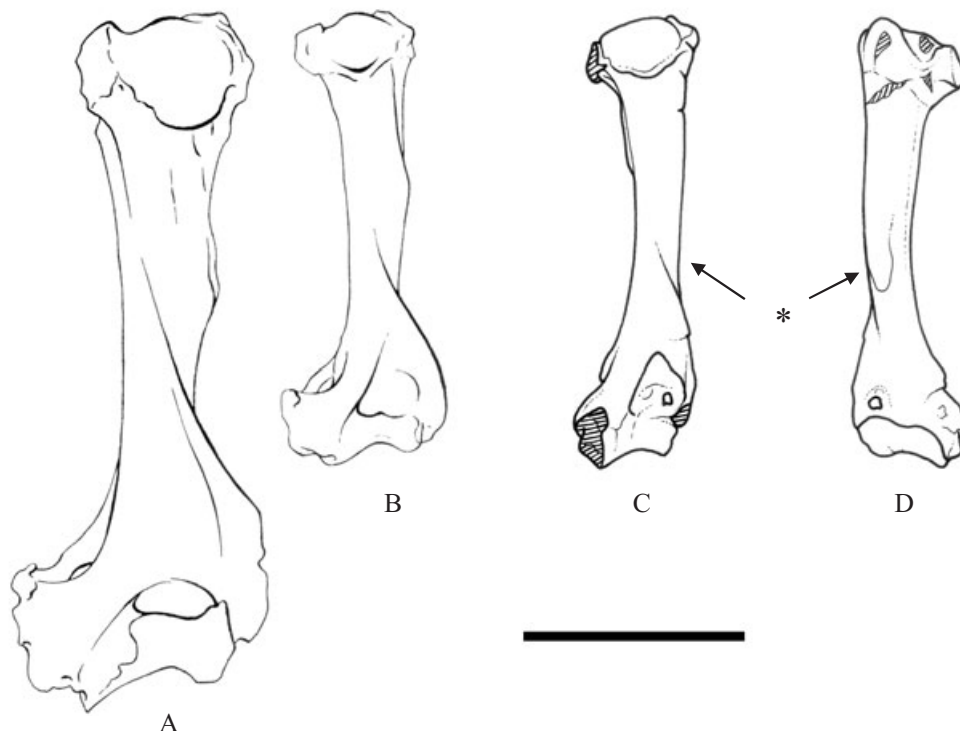


Figure 5. Comparative set of humeri. A, B and C in dorsal view; D in ventral view. A, *Orycteropus afer* (after Colbert, 1941); B, *Orycteropus gaudryi* (after Colbert, 1941); C, D, *Orycteropus abundulafus* sp. nov. *No projection of the deltoid crest. Note that A and B are scaled approximately relative to C and D. Scale bar = 5 cm.

(Fig. 5C). A cylindrical pillar can be observed bordering the fossa medially as in *O. gaudryi*. Proximally, the border of the fossa continues in a steep gradient but is still distinct. By contrast, in *O. afer*, the fossa is oval and bound proximally. Colbert (1941: 326) states: 'The principal qualitative difference (in respect to *O. afer*; n.d.) is that in the fossil (*O. gaudryi*; n.d.) the olecranon fossa is not bounded proximally by a rim as it is in the recent species'. In the Chadian specimen, this fossa is also slender in comparison with the extant form. Thus, when reconstructed, the elbow of *O. abundulafus* shows limited mediolateral movements for the sigmoid notch in the olecranon fossa. Triangular and slender in shape, sloping steeply proximally, the olecranon fossa of the new species is simi-

lar to that of *O. gaudryi*. The distal epiphysis would have been broad, but preservation is unfortunately poor. The estimated Hildebrand index (Bd/MHL, Table 7) is between 0.30 and 0.35, suggesting fossorial abilities (Hildebrand, 1985). The index is 0.37 ± 0.028 in the combined TMP, ZMB and SNMS samples of *O. afer* ($n = 37$). Noticeably, in a badger (*Meles meles*, MO2-5-040, Collection of the University of Poitiers) a value of 0.30 is found.

Ulna (Table 8; Fig. 6)

Both left and right cubitus are well preserved, but the left olecranon is missing. The olecranon is straight, with little medial expansion. The diaphysis is curved

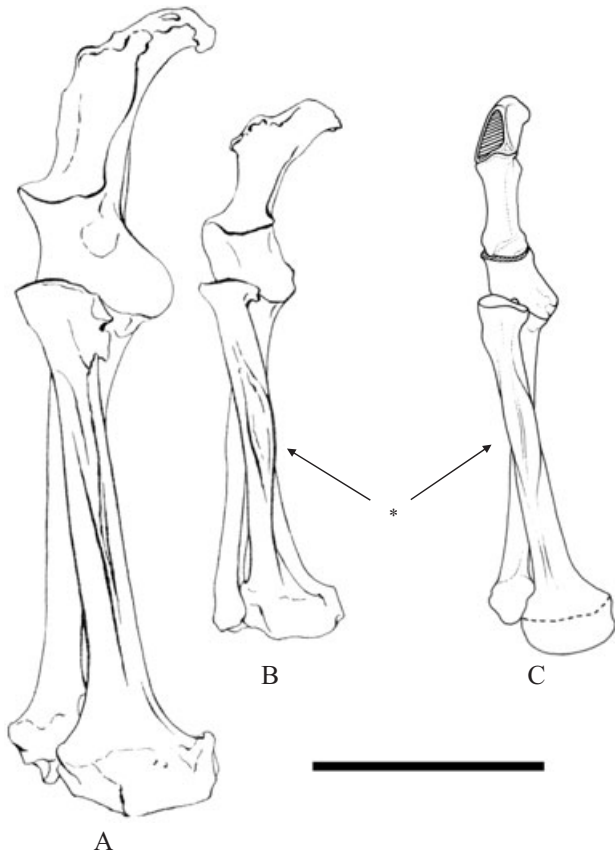


Figure 6. Comparative set of radio-ulna. A, *Orycteropus afer* (after Colbert, 1941); B, *Orycteropus gaudryi* (after Colbert, 1941); C, *Orycteropus abundulafus* sp. nov. *Blunt oblique rim. Note that A and B are scaled approximately relative to C. Scale bar = 5 cm.

Table 8. Biometry (measurements in mm) of the cubitus of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

MUL	Bd	Bsn	LOC	LSN	Busn
110.8	15.8	15	29.1	18	6.1

MUL, maximum ulna length; Bd, distal breadth; Bsn, sigmoid notch breadth; LOC, olecranon process length; LSN, sigmoid notch length; Busn, mediolateral breadth of the shaft under the sigmoid notch.

and slender. It is also marked with very strong muscular insertions.

Radius (Table 9; Fig. 6)

Both left and right radii are preserved and complete. Minor morphological differences reflect post-depositional effects.

Table 9. Biometry (measurements in mm) of the radius of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

MRL	Lro	MHD	TBd	APBd	Lbt	Bbt
76.1	75.7	11.9	19	14.1	7.2	3.2

MRL, maximum radius length; Lro, radius length along the oblique rim; MHD, maximum head diameter; TBd, distal transverse breadth; APBd, distal anteroposterior breadth; Lbt, bicipital tuberosity length; Bbt, bicipital tuberosity breadth.

The proximal epiphysis is oval in shape. The general outline of the diaphysis is slender. The distal epiphysis is slender and mediolaterally elongated but broader anteroposteriorly, and thus more triangular-shaped in *O. afer*. The radius is shorter than the humerus (Tables 7, 9). The brachial index (MRL/MHL) is 0.72, a value suggesting a fossorial way of life (MacPhee, 1994). The radial tuberosity (or bicipital tuberosity), which acts as insertion point for the M. biceps brachialis, forms an anteromedial prominent process in *O. abundulafus* instead of being flat and button-like as in *O. afer*. The diaphysis is strongly keeled. In particular, the oblique rim is blunt and longer than in *O. afer*, showing some significant ridges along the proximal two-thirds of the length of the bone (Fig. 6C). These rugosities serve as insertions for M. supinator. In the extant species, the pro- and supinator muscles are either reduced or have aberrant functions because any rotations of the radius are mechanically inhibited (Thewissen & Badoux, 1986). Thus, the M. biceps brachialis becomes an accessory flexor of the elbow joint and the M. supinator would fuse with the extensor of the fingers (see Thewissen & Badoux, 1986). In the Chadian species, the strong insertions of such muscles show that they were well developed. Nonetheless, the morphology of the radius suggests that no rotation would have been possible. In *O. gaudryi*, the oblique rim is marked, according to the drawing of Colbert (1941: 328), and also possesses some ridges (Fig. 6B). In this respect, *O. abundulafus* is close to *O. gaudryi*. The pro- and supinator seem to have lost their function before the Late Miocene and continued a reductional trend until recent times.

Hand (Table 10; Fig. 7)

Both hands are remarkably well preserved, having being found articulated, with ungual phalanges as well as sesamoid bones.

Most of the carpals are not disjoint and have been weathered. The unciform and the pyramidal bone are similar in shape to those of *O. afer*, but differ by being of smaller size. The metacarpals are all characterized by their slenderness, especially the narrow epiphysis.

Table 10. Biometry (measurements in mm) of the hand of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

Carpals	Dorsoventral length		Mediolateral length		Proximodistal length
Unciform	11		11.3		8.3
Pyramidal bone	6.2		9.6		6*

Metacarpals and phalanges	L	Bp	Hp	Bd	Hd
Mc II	44.7*	11.1*	10.5*	7.7	8.2
Mc III	44.6	10.5	10.3	7.1	8.6
Mc IV	33.5	7.3*	8.6	7	7.9
Mc V	20.6	7.4	7.6	7.2	8
Php II	33.2	8.6	8.8	6.9	5.6
Php III	30.2	8	8.9	7.3	5.7
Php IV	25.3	7.5	8.4	6.9	5.7
Php V	19.7	6.2	9.3	6	5.5
Phm II	14	7.5	7.4	6	5.6
Phm III	14.4	7.5	7.9	5.9	6.1
Phm IV	13.6	7.4	8.3	5.7	6.4
Phm V	10.8	6.6	7.6	5	5.2
Phu II	19*	6.7*	10*	—	—
Phu III	19.5*	5.9	10.1	—	—
Phu IV	19.6	5.4	11.8	—	—
Phu V	17.8	4.9	10.6	—	—

Mc, metacarpal; Php, proximal phalange; Phm, middle phalange; Phu, ungual phalange; L, length; Bp, proximal breadth; Hp, proximal height; Bd, distal breadth; Hd, distal height. *Estimated measurements.

Table 11. Biometry (measurements in mm) of the pelvis of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

Acetabulum antero-posterior width	Acetabulum vertical height	Preacetabular surface length
17.9	10.3	26.8

This is a similarity with *O. gaudryi*. Moreover, the plantar surface is straighter in both fossils whereas it is curved in the extant form. On the fifth metacarpal, the proximal articular facet for the metacarpal IV is developed until the middle of the diaphysis in *O. afer* whereas it is shorter (only until the proximal quarter of the diaphysis) in *O. abundulafus*. Similarly, the phalanges are slender in *O. abundulafus* but are more bulged and broad in *O. afer*. The dorsal aspect is distinct proximally in *O. gaudryi* and in *O. abundulafus*. Finally, the second finger (metacarpal to medial phalange) is the longest in *O. abundulafus* and in *O. afer*.

Pelvis (Table 11)

The only preserved part of the pelvis is the right acetabular region. The pubis is stick-like and orientated

Table 12. Biometry (measurements in mm) of the femur of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

PMB	CAD	MB	AB	DMB	DAB
44.6	18.1	18.4	14*	35*	37*

PMB, proximal mediolateral breadth; CAD, anteroposterior diameter of the condyle; MB, mediolateral breadth under the fourth trochanter; AB, anteroposterior breadth at the level of the third trochanter; DMB, distal mediolateral breadth; DAB, distal anteroposterior breadth. *Estimated measurements.

caudally, another feature indicating a fossorial animal (MacPhee, 1994). The femoral spine (the insertion for the M. rectus femoris) is large and straight. The iliopectineal eminence is well developed.

Femur (Table 12; Fig. 8)

The proximal half of the right femur, broken at the level of the third trochanter, is preserved. On the left side, only the distal epiphysis (unfused) remains.

The femoral head is almost globular in shape and orientated at 80° to the axis of the diaphysis. However,

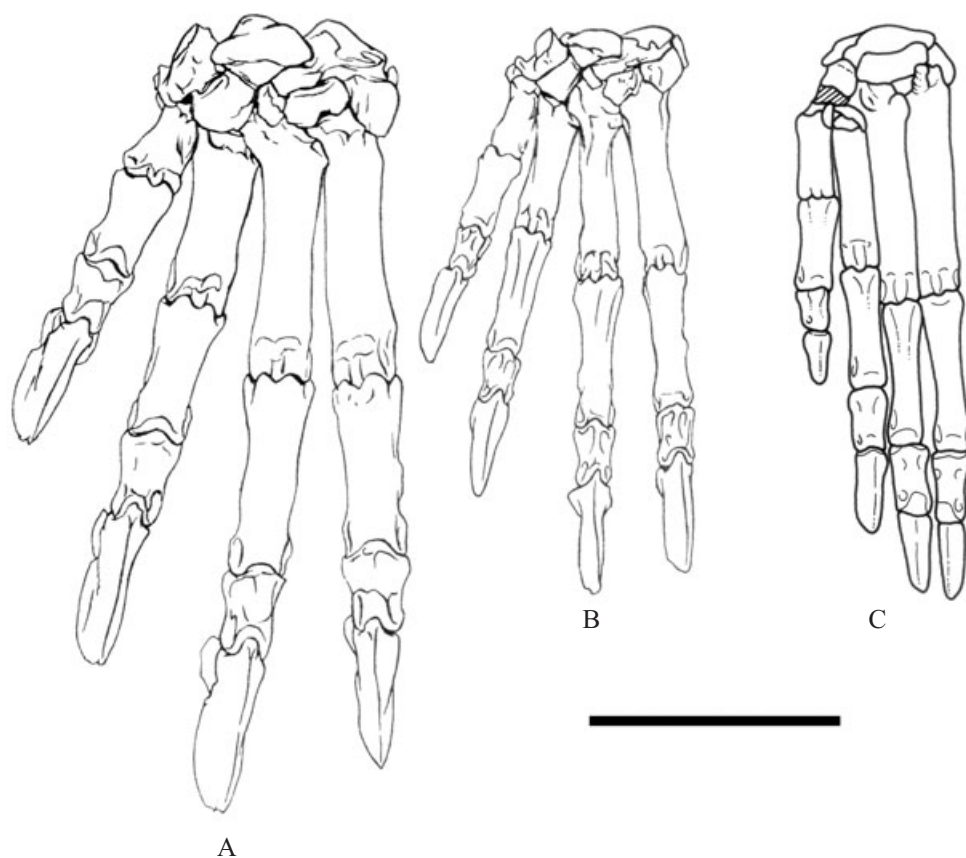


Figure 7. Comparative set of hands. A, *Orycteropus afer* (after Colbert, 1941); B, *Orycteropus gaudryi* (after Colbert, 1941); C, *Orycteropus abundulafus* sp. nov. Note that A and B are scaled approximately relative to C. Scale bar = 5 cm.

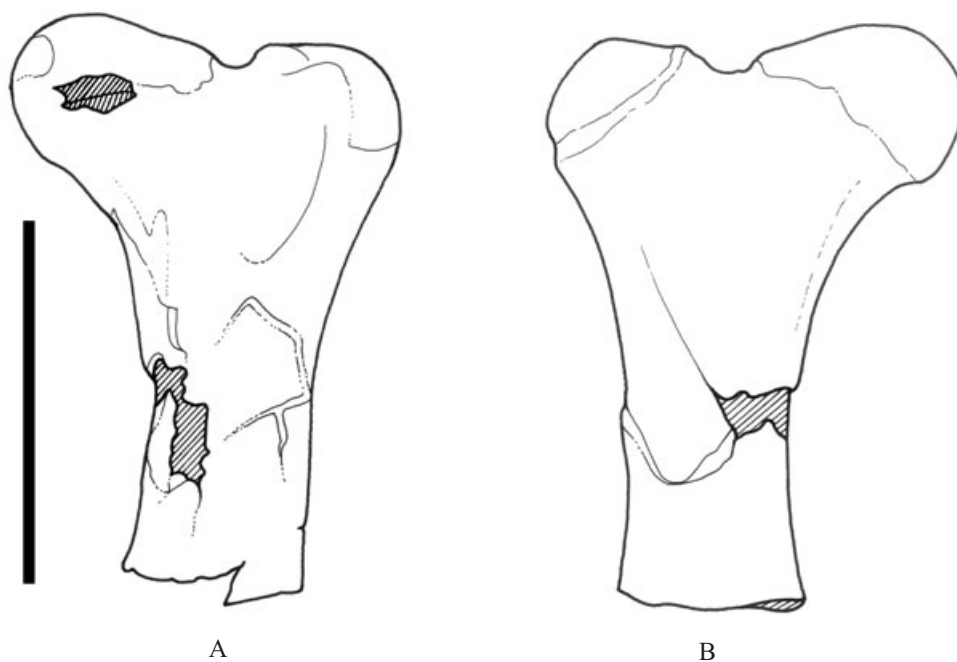


Figure 8. Proximal epiphysis of the right femur of *Orycteropus abundulafus* sp. nov. in ventral (A) and dorsal (B) view. Scale bar = 5 cm.

the proximolateral part of the articular condyle is rather flat and its extension to the great trochanter ends laterally in a depression. A true neck cannot be outlined. According to Reed (1951), animals with fossorial habits show an indistinct neck, close to the axes of the diaphysis. The head of the femur is separated from the great trochanter (insertion for the Mm. gluteus profundus and pyriformis) by the anterior wall of the trochanteric fossa. In *O. abundulafus* and *O. gaudryi*, this side is narrower (anteroposteriorly) than it is in *O. afer*. In addition, the great trochanter is slender, semilunar in shape and extends backwards. Thus, the trochanteric fossa (insertion for the Mm. obturator externus, obturator internus and gemelli) is deep and distinct.

Below the femoral head, the lesser trochanter (insertion for the Mm. psoas and iliacus) is broken. However, its base suggests that it was prominent. Distally, the most diagnostic trait of the Orycteropodinae, the fourth trochanter (or pectineal tubercle) (MacPhee, 1994) is present but broken too. It is the insertion point of the M. pectineus, one of the muscles responsible for the adduction of the femur, and its outward rotation. Only the beginning of a slender third trochanter remains. The third trochanter of *O. gaudryi* is thin and not swollen in the middle like in *O. afer*.

Distally, the patellar surface is grooved as in all Tubulidentata except the genus *Plesiorycteropus*. The distal epiphysis of the femur as a whole is large. The lateral origin of the M. gastrocnemius arises from the sus-condyloid cavity and contains a large sesamoid bone, which acts on the femur just below the tendon. The facet for this sesamoid bone, above the lateral condyle of the femur, is situated behind the diaphysis level in *O. abundulafus*, posteriorly to that in *O. afer*. This feature is important because the M. gastrocne-

mius goes back to the calcaneum with its strong Achilles tendon and, with the whole triceps, it can extend, adduct and rotate the foot inward. While digging, the aardvark uses its hindlimbs for displacing the soil. The M. gastrocnemius is one of the muscles that can keep the foot extended. A more anterior position of the sesamoid bone, involving a moment arm axis closer to the lateromedial diameter of the diaphysis, reduces energy expenditure.

Tibia and fibula (Table 13)

The right tibio-fibula is complete except for the proximal epiphysis. On the left side, tibia and fibula are represented by distal components.

It is not certain whether the tibia and fibula were fused proximally. They are not fused distally, as is the case in all Tubulidentata except the genus *Plesiorycteropus*.

The tibia is slender and curved. On the proximal epiphysis, the tibial tuberosity (or patellar tuberosity, for the insertion of the patellar ligaments) is a well-defined concave and oblique surface continuous with the proximal articulation surface as in *O. afer* or *O. mauritanicus* (Arambourg, 1959). In *O. gaudryi*, an angular border limits the surface posteriorly. In *Lep- torycteropus guilielmi* and *O. gaudryi*, Patterson (1975: 198) found that 'there is an uninterrupted rim of bone running from the patellar tuberosity to the junction with the fibula, a contrast to the living species in which a deep notch is present in this area'. In *O. abundulafus*, the rim is broken. The tibial crest is developed and runs on the proximal third of the diaphysis. It is rectilinear and there is no real cnemial tuberosity that is present in only *Plesiorycteropus* or *Myorycteropus*. The crest terminates higher on the shaft of *O. abundulafus* than in *O. afer*.

Table 13. Comparative biometry (measurements in mm) of the tibio-fibula of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype) and other Tubulidentata

Species	MTFL	TFDW	TSD	FSW	FSD	DAB	DMB
<i>O. afer</i> ($n = 29$)†	180.4 ± 23.3	59 ± 5	27.1 ± 2.7	8.1 ± 0.8	8.8 ± 1	36.2 ± 6.1	29.2 ± 3.9
<i>Myorycteropus africanus</i> ‡	103	—	—	6	6	—	—
<i>O. mauritanicus</i> ‡	164.5	—	—	—	—	29.7	22
' <i>O. capensis</i> '‡	180	—	—	—	—	24.6	19.5
<i>O. gaudryi</i>	151.5	—	26.7	—	—	20.7	25.3
AM 22976 (cast)							
<i>O. abundulafus</i> sp. nov.	140*	36.3	25*	7.3	5.7	19	22.8

MTFL, maximum tibio-fibula length; TFDW, tibio-fibula distal mediolateral width, malleolus to malleolus; TSD, antero-posterior depth of tibial shaft, at end of the tibial crest; FSW, minimum mediolateral breadth of fibula (taken at same level as TSD); FSD, anteroposterior breadth of fibula (at 90° to FSW); DAB, distal anteroposterior breadth of tibia; DMB, distal mediolateral breadth of tibia. *Estimated measurements. †Data from the TMP, ZMB and SNMS samples for comparison. ‡After Arambourg (1959).

The tibia is longer in *O. gaudryi* than in *O. abundulafus* (Table 13). However, the crest and the proximal epiphysis are of same size. The tibial diaphysis appears proportionally longer in *O. gaudryi*. This is of importance because *O. gaudryi* is the only known species of Orycteropodidae that has a tibia longer than the femur (although *Leptorycteropus* may also display this feature; Patterson, 1975). The total length of the femur of *O. abundulafus* is not known, but it seems that the tibia would not have been longer. The distal epiphysis shows a small but deep trochlea and is broader in *O. afer* than in *O. gaudryi*, itself broader than in *O. abundulafus* (Table 13). The fossa for the medial lip of the talus is not as broad as in *O. gaudryi* but is deeper as in *Leptorycteropus*. The medial malleolus, for articulation with the astragalus, is convex.

Tibia and fibula are curved and close to one another. The fibula is not distinct from that of *O. afer* except for the smaller size.

Foot (Tables 14–16; Fig. 9)

The two feet were found articulated, with sesamoids. They are very well preserved.

The talus is very similar to that of *O. gaudryi* except for the smaller breadth (Table 14). This bone is long relative to width in *O. abundulafus*, *O. gaudryi*, *O. crassidens* and *O. mauritanicus* but not in *O. afer* (Arambourg, 1959). The neck of the talus, short but less distinct than in *O. mauritanicus*, supports a nearly round condyle. An astragalar foramen is

present as in all Tubulidentata except *Plesiorycteropus*. The posteromedial process, on the medial aspect of the proximal articulation of the talus, is absent as in *O. mauritanicus*, contrary to all other comparable Tubulidentata. Apart from size, the calcaneum shows no other significant differences with *O. afer*. It is slender and has all articular facets found in *O. afer*. The navicular is smaller than in the extant form. The articular facet for the talus is rounder than in *O. afer*. It is oval in *Myorycteropus africanus* (MacInnes, 1956). The cuboid is also smaller than in the extant form and has a more triangular proximal surface. The cuneiform shows no significant differences from that of *O. afer* except in terms of smaller size.

The general outline of the metatarsals of *O. abundulafus* is identical to that of *O. gaudryi* and *O. afer*. Nonetheless, metatarsals II, III and IV are c. 20% shorter than in the extant species, whereas metatarsals I and V are almost equal (Table 15). The metatarsals, especially metatarsal V, are relatively broader in *O. afer* than in *O. abundulafus* (Table 15).

The phalanges are slender in *O. abundulafus*, and their length is close to that of *O. gaudryi* and *O. afer*. The extant form is distinct from the two fossil forms by the relative broader size of the phalanges (Table 16). The dorsal surface is convex, without the pinching found on the hand (Fig. 9A). This condition is also present in *O. gaudryi*. The phalanges of the fifth finger are longer in the Chadian specimen than in the extant form. Fingers II and III are of similar length. The foot size in the three species shows a degree of overlap (Tables 15, 16). Colbert (1941: 329) noted: 'In

Table 14. Biometry (measurements in mm) of the tarsals of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype)

Segment	Dorsoventral length		Mediolateral length		Proximodistal length	
Navicular	15.2		13.9		13.9	
Cuboid	13.7		17.4		10.6	
Cuneiform I	12.9		8.2		18.5	
Cuneiform II	11.3		7.2		6*	
Cuneiform III	16.2		8.2		8.5*	

Segment	Dorsoventral length			Mediolateral length			Lm	
Calcaneum	22.3			28			48.4	

Segment	MW	ML	TW	NL	HH	HW	MH	EcF	EnF
Talus	21.5*	25.6	10	11.8	11	11.4	17.1	12.2	13.5*

MW, maximum mediolateral width; ML, maximum anteroposterior length; TW, mediolateral width of trochlea; NL, length of head and neck; HH, dorsoplantar head height; HW, mediolateral head width; MH, maximum height; EcF, ectal facet anteroposterior length; EnF, ental facet anteroposterior length; Lm, length along manubrium. *Estimated measurements.

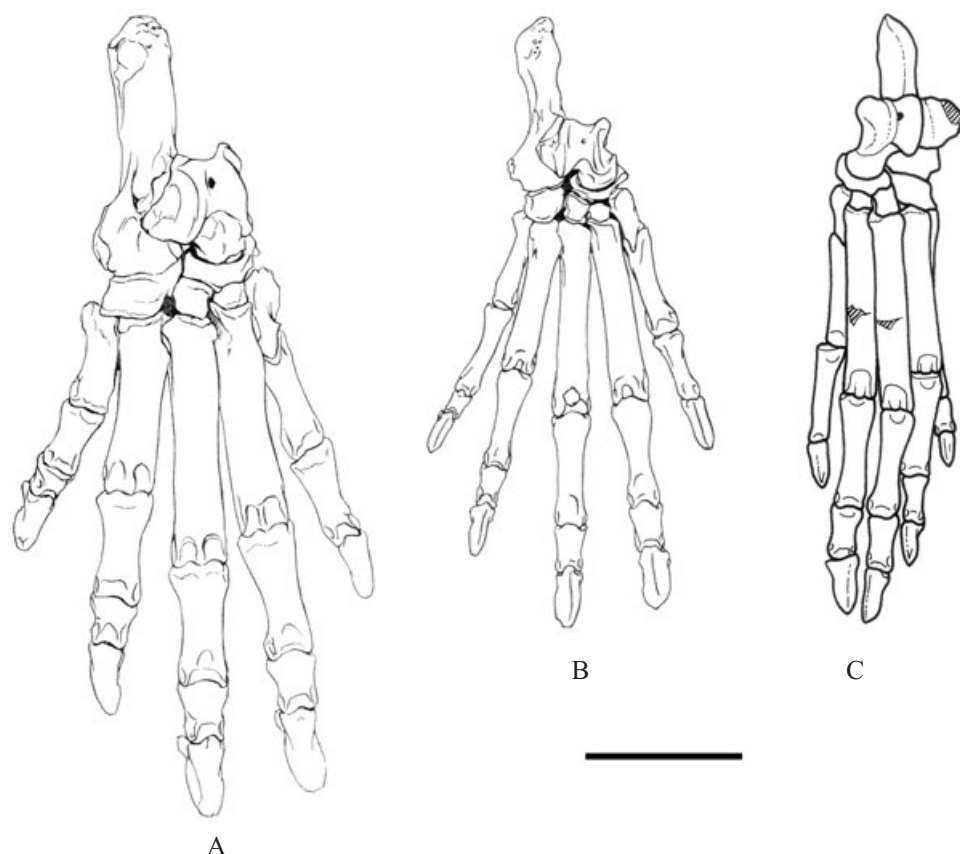


Figure 9. Comparative set of feet. A, *Orycteropus afer* (after Colbert, 1941); B, *Orycteropus gaudryi* (after Colbert, 1941); C, *Orycteropus abundulafus* sp. nov. Note that A and B are scaled approximately relative to C. Scale bar = 5 cm.

contrast to the development of the manus, there has been no relative increase in the size of the pes in *Orycteropus* between Lower Pliocene and Recent times'. The third finger of the pes is longer than the third finger of the hand (119.4 mm vs. 89.2 mm, from metapodial to the medial phalange) in *O. abundulafus* and *O. gaudryi*, whereas they are almost equal in *O. afer*. According to Colbert (1941: 327) this lengthening of the hand in *Orycteropus* is 'a result of the accentuation of its fossorial habits'.

PHYLOGENY

At the Miocene–Pliocene boundary, three forms coexisted, including *O. cf. afer* from Langebaanweg and *O. sp.* from Lothagam in Africa (Hendey, 1973; Milledge, 2003), and *O. gaudryi* in Europe. Similarities between *O. abundulafus* sp. nov. and *O. gaudryi* can be observed, and are discussed below. The material referred to the genus *Orycteropus* in the Upper Nawata Formation of Lothagam differs from the Chadian Tubulidentata mostly by its larger size, although smaller than the living aardvark. No description of the single tooth attributed to *O. cf. afer*

from Langebaanweg is currently available. This example illustrates how scarcity of fossil aardvark material has tended to limit comparisons of features in terms of phylogenetic relationships. Only Patterson (1975: fig. 16) and Van Der Made (2003: fig. 4) suggested possible relationships among the known tubulidentate genera and species, respectively. A data matrix that compares characters and taxa is not yet available for Tubulidentata species, although MacPhee (1994) published a matrix at a higher taxonomic level.

The anatomical description and comparison performed in this study highlight the affinities between *O. abundulafus* and *O. gaudryi*, the penecontemporary European form. It also shows that the Chadian fossil aardvark displays fewer affinities with *O. depereti*, *O. mauritanicus* and *O. pottieri* (which had canines). Moreover, *O. afer*, *O. crassidens* and *O. chemeldoi* are closer to each other than to *O. abundulafus* in terms of size, and also in terms of limb bone and hand proportions.

This overview shows that the discovery of the new, almost complete, material from Chad constitutes a great opportunity for studying the relationships within the genus *Orycteropus*. A cladistic analysis has

Table 15. Comparative biometry (measurements in mm) of the metatarsals of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype), *O. gaudryi* (AM22762, cast) and *O. afer*

Measurements	<i>O. abundulafus</i>	<i>O. gaudryi</i> AMNH 22976 (cast)	<i>O. afer</i> (<i>n</i> = 21)†	Index <i>O. abundulafus</i> / <i>O. afer</i>
L Mt _I	38.6	34*	38.6 ± 2.9	1.00
L Mt _{II}	62.9	66*	75.8 ± 3	0.83
L Mt _{III}	63.1	69	78.7 ± 3.3	0.80
L Mt _{IV}	53.7	—	64.1 ± 2.6	0.84
L Mt _V	36.6	37*	36.5 ± 2	1.00

Measurements	<i>O. abundulafus</i>	<i>O. afer</i> (<i>n</i> = 21)†	Index B/L <i>O. abundulafus</i>	Index B/L <i>O. afer</i>
Bp Mt _I	9	11 ± 0.8	0.23	0.29 ± 0.02
Bp Mt _{II}	8.7	12.4 ± 1.1	0.14	0.16 ± 0.01
Bp Mt _{III}	9.7	15.6 ± 1.1	0.15	0.20 ± 0.01
Bp Mt _{IV}	10.5	17 ± 1.5	0.20	0.27 ± 0.02
Bp Mt _V	7.8	15 ± 2.3	0.21	0.41 ± 0.06
Bd Mt _I	8.2	12 ± 1	0.21	0.31 ± 0.02
Bd Mt _{II}	10.7	15.6 ± 1	0.17	0.21 ± 0.01
Bd Mt _{III}	10.1	15.6 ± 1.2	0.16	0.20 ± 0.01
Bd Mt _{IV}	8.8	14 ± 1.1	0.16	0.22 ± 0.01
Bd Mt _V	7.4	10.9 ± 0.9	0.20	0.30 ± 0.02

L, maximum length; Bp, proximal mediolateral breadth; Bd, distal mediolateral breadth. *Estimated measurements. †Data from the TMP, ZMB and SNMS samples for comparison.

Table 16. Comparative biometry (measurements in mm) of the posterior phalanges of *Orycteropus abundulafus* sp. nov. (KB03-97-214, holotype) and *O. afer*

Segment	Species	L	Bp	Bd	I ₁	I ₂
Php _I	<i>O. abundulafus</i>	31.9	9	6.3	0.28	0.2
	<i>O. afer</i> †	33.5 ± 3.6	12.7 ± 0.9	9.4 ± 0.8	0.38 ± 0.04	0.28 ± 0.03
Php _{II}	<i>O. abundulafus</i>	35	11.1	9.6	0.32	0.27
	<i>O. afer</i> †	42.7 ± 2.2	16.6 ± 1.4	14 ± 1.3	0.39 ± 0.02	0.33 ± 0.02
Php _{III}	<i>O. abundulafus</i>	36.9	11.5	10	0.31	0.27
	<i>O. afer</i> †	40 ± 2.3	16.6 ± 1.6	13.9 ± 1.5	0.41 ± 0.03	0.35 ± 0.03
Php _{IV}	<i>O. abundulafus</i>	33.9	9.5	7.9	0.28	0.23
	<i>O. afer</i> †	37.3 ± 2	15.1 ± 1.2	12.9 ± 1.2	0.41 ± 0.02	0.35 ± 0.02
Php _V	<i>O. abundulafus</i>	25.7	7.9	6.2	0.31	0.24
	<i>O. afer</i> †	24.9 ± 1.5	12.7 ± 0.9	9.7 ± 0.7	0.49 ± 0.03	0.39 ± 0.03
Phm _{II}	<i>O. abundulafus</i>	19.4	10.1	8.5	0.52	0.44
	<i>O. afer</i> †	21.7 ± 0.8	13.6 ± 0.5	11.3 ± 0.4	0.63 ± 0.02	0.52 ± 0.02
Phm _{III}	<i>O. abundulafus</i>	19.4	9.4	7.7	0.48	0.4
	<i>O. afer</i> †	21.7 ± 0.8	13.3 ± 0.6	11.6 ± 1.2	0.61 ± 0.03	0.53 ± 0.05
Phm _{VI}	<i>O. abundulafus</i>	17.6	7.9	6.2	0.45	0.35
	<i>O. afer</i> †	19.7 ± 0.8	12.1 ± 0.5	9.9 ± 0.4	0.61 ± 0.03	0.5 ± 0.02
Phm _V	<i>O. abundulafus</i>	12.9	6.3	5	0.49	0.39
	<i>O. afer</i> †	14.2 ± 1.1	9.5 ± 0.5	8.2 ± 0.6	0.67 ± 0.03	0.58 ± 0.04

L, maximum length; Bp, proximal mediolateral breadth; Bd, distal mediolateral breadth; I₁, index Bp on L; I₂, index Bd on L. *Estimated measurements. †(*n* = 18) Data from the TMP, ZMB and SNMS samples for comparison.

thus been conducted at the species level with the best represented forms of the genus. Most of their descriptions are based on the literature (Colbert, 1941; MacInnes, 1956; Arambourg, 1959; Patterson, 1975; Bonis *et al.*, 1994; MacPhee, 1994). The developed data matrix (Table 17) shows the states of 29 cranial and post-cranial characters among seven species of *Orycteropus* and the three species *Myorycteropus africanus*, *Leptorycteropus guilielmi* and *Plesiorhycteropus madagascariensis*. The last of these has been chosen as an outgroup because it is close to *Orycteropodinae* for some morphological features, but is also set apart for others, as shown by MacPhee (1994). The matrix has been analysed using the program PAUP, version 4 (Swofford, 1998), in a heuristic search for most-parsimonious arrangements of taxa.

Characters were used with the presumed plesiomorphic state denoted by a '0' and derived states by integers. Question marks indicate unavailable features or characters not described in the literature. All characters are of equal weight and of type 'unord' in this analysis. Comments are included in the list given below, where relevant.

SKULL

1. Temporal line position: low (0); high (1).
In *O. afer*, the temporal lines are situated on the middle of the cerebral cavity whereas in other forms, like *O. gaudryi*, they are closer to the sagittal plane, and thus higher on the cerebral cavity.
2. Lambdoid crest: rectilinear (0); V-shaped (1).
3. Anterior border of the orbit: above M² (0); above M³ (1).
Taking the upper tooth-row as the horizontal, the character refers to the position of the perpendicular through the anterior border of the orbit.
4. Ventral-most point of the maxillo-jugal suture: above M³ (0); behind M³ (1).
5. Zygomatic arch thickness: thin (0); thick (1).
6. Zygomatic arch angle with the upper tooth-row: low (< 25°) (0); high (> 25°) (1).
7. Palatines breadth: slender (index Bpal/Lpal < 20) (0); broad (index > 20) (1).
8. Palatine groove: absent (0); present (1).
9. Palatine posterior rim shape: curved (0); rectilinear (1).
When curved, this rim is U-shaped with the concave part in the caudal direction.
10. Palatine posterior rim position: at the M³ level (0); behind M³ (1).
11. Pterygoid lateral wall: smooth (0); with ridges (1).
12. Glenoid cavity: with a lateral tubercle (0); flat (1).

This feature is redundant with the shape of the mandibular articulation.

13. Intracuspal rims orientation: transversal (0); oblique (1).
The orientation is relative to the mesiodistal axis of the tooth.
14. Canine: present (0); absent (1).
The canines of *L. guilielmi* and *O. pottieri* are large, significantly larger than the premolars. Helbing (1933), Arambourg (1959) and Patterson (1975) described *O. depereti* and *O. mauritanicus* as possessing canines. Those maxillary teeth are in fact the fifth ones in front of the molars and are smaller than the premolars. In the extant form, supernumerary teeth are sometimes visible, especially in the immature stages, and are always smaller than the teeth posterior to them. It is suggested that *O. depereti* and *O. mauritanicus* display supernumerary premolars and not canines.
15. Longest tooth (mesiodistal): M₂ and M² (0); M₁ and M¹ (1); M₂ and M¹ (2).

POST-CRANIUM

16. Radius oblique rim: sharp (0); blunt (1).
17. Deltoid crest: developed (0); weak (1).
18. Humeral proximal epiphysis: anteroposterior > mediolateral diameter (0); subequal diameters (1).
19. Humeral diaphysis: curved (0); straight (1).
20. Olecranon fossa: oval and bounded proximally (0); triangular (1).
21. Hildebrand Index: low (< 0.35) (0); high (> 0.35) (1).
22. Femoral neck: distinct from the diaphysis (0); indistinct (1).
23. Tibial proximal epiphysis: trilobed (0); quadrilobed (1).
As suggested by Arambourg (1959), in proximal view the tibial proximal epiphysis of *O. gaudryi* and *L. guilielmi* lacks the anterolateral development. This trait is unavailable in *O. abundulafus* sp. nov.
24. Tibio-fibula diaphysis: straight (0); curved (1).
25. Cnemial tuberosity: present (0); absent (1).
26. Anterior tuberosity of the tibial plate: modestly developed (0); well elongated (1).
As suggested by Arambourg (1959), the proximal surface of the tibial crest, or anterior tuberosity of the tibia, displays a sloping surface. In *O. gaudryi* and *M. africanus*, this surface is modestly developed.
27. Astragalus neck: short (0); long (1).

Table 17. Data matrix (see text for description of characters)

Characters	<i>Plesiorycteropus madagascariensis</i> [†]	<i>Leptorycteropus guilielmi</i> [‡]	<i>Myorycteropus africanus</i> [§]	<i>Orycteropus abundulafus</i> sp. nov.	<i>O. afer</i>	<i>O. crassidens</i> [§]	<i>O. depereti</i>	<i>O. gaudryi</i> [¶]	<i>O. mauritanicus</i> ^{††}	<i>O. pottieri</i> ^{‡‡}
1 TEMPORAL LINE	0	?	?	1	0	0	1	1	?	1
2 LAMBDROID CREST	0	?	?	1	0	0	1	1	?	1
3 ANT BORDER ORBIT	?	?	0	0	1	1	0	0	1	?
4 VM MAX-JUG SUTURE	?	1	?	0	1	1	1	0	0	?
5 ZYGO ARCH THICKNESS	?	?	?	0	0	0	1	0	1	?
6 ZYGO ARCH ANGLE	?	?	?	1	1	0	0	0	?	?
7 PALATINE BREATH	?	?	?	0	1	?	1	0	1	?
8 PALATINE GROOVE	?	0	?	1	1	?	0	0	0	?
9 PAL POST RIM SHAPE	?	?	?	0	1	?	0	0	1	?
10 PAL POST RIM POSITION	?	?	?	0	1	1	1	0	?	?
11 PTERYGOID LAT WALL	0	?	?	1	0	0	1	0	?	?
12 GLENOID CAVITY	?	?	?	0	1	1	0	0	?	0
13 IR ORIENTATION	?	0	0	0	0	0	1	0	1	1
14 CANINE	?	0	?	1	1	1	1	1	1	0
15 LONGEST TOOTH	?	0	2	0	0	0	0	0	1	2
16 RADIUS OBLIQUE RIM	0	0	?	1	0	?	?	1	?	?
17 DELTOID CREST	0	1	0	1	0	?	?	0	?	?
18 HUM PROX EPIPHYSIS	0	?	0	1	1	?	?	1	?	?
19 HUMERAL DIAPHYSIS	0	1	0	1	1	?	?	1	?	?
20 OLECRANON FOSSA	0	0	0	1	0	0	?	1	?	?
21 HILDEBRAND INDEX	0	1	1	0	1	1	?	1	?	?
22 FEMORAL NECK	0	1	0	1	1	?	?	1	?	?
23 PROX TIB EPIPHYSIS	0	0	?	?	1	?	?	0	1	?
24 TIB FIB DIAPHYSIS	0	0	1	1	1	?	?	1	1	?
25 CNEMIAL TUBEROSITY	0	1	0	1	1	?	?	1	1	?
26 ANT TUBEROSITY TIBIA	0	0	0	1	1	?	?	0	1	?
27 ASTRAGAL NECK	0	?	1	0	0	0	?	0	1	0
28 ASTR POST MED PROC	0	?	?	1	0	0	?	?	1	0
29 ASTRAG PROPORTION	1	?	0	0	2	2	?	0	0	0

[†]After the description made by MacPhee (1994). [‡]After the description made by Patterson (1975). [§]After the description made by MacInnes (1956). [¶]In part after the description made by Colbert (1941). ^{††}After the description made by Arambourg (1959). ^{‡‡}In part after the description made by Bonis *et al.* (1994).

28. Astragalus posteromedial process: present (0); absent (1)

29. Astragalus proportions: length > breadth (0); breadth > length (1); length = breadth (2)

Eight equally most parsimonious trees (MPTs) have been found. For all trees, the length is 45, the consistency index (CI) is 0.69 and the retention index (RI) is 0.60. The strict consensus tree (Fig. 10) shows all unambiguous diagnostic characters (characters with a CI = 1 that support clades) and the selected ones that will be discussed hereafter. This tree shows that the disagreement among the MPTs

concerns the relationships between *Myorycteropus* and clade A (*Leptorycteropus* + all *Orycteropus* species) as well as the relationships within the clade A. However, four clusters are identical in all eight MPTs. A bootstrap proportion, based on 1000 replicates, obtained with the heuristic search option in PAUP version 4, supports this analysis. The bootstrap index for clade A is 64%; for the clade B (*O. abundulafus* + *O. gaudryi*) it is 59%; and for the clade D (*O. afer* + *O. crassidens*) it is 76%. Clade C, containing *O. mauritanicus* as sister group of clade D, is not well supported, with a bootstrap index of only 39%.

M. africanus is separated from other genera in all MPTs. This analysis provides new evidence for *Myorycteropus* as a valid genus of the order Tubulidentata. The species included in clade A are united by four well-defined synapomorphies (characters 18, 19, 22 and 25). Those characters are well represented in the data matrix and their assumed polarity seems to be confirmed. These traits should be taken into consideration, as no real diagnosis for the genus *Orycteropus* is currently available. However, this group also includes the genus *Leptorycteropus*.

Clade A presents a polytomy at its base. The position of *L. guilielmi* is not resolved in the eight MPTs. In three instances it is a sister group of *O. pottieri*, and only once is it a sister group of all *Orycteropus* species. The relationships of the two outlying species, *O. depereti* and *O. pottieri*, are also ambiguous. This is mostly due to the lack of comparative material. No post-cranial elements are known for *O. depereti* and some character state assessments are absent from the published descriptions of *O. pottieri*. However, they both share characters with *O. abundulafus* and *O. gaudryi*, for example in terms of trait 1 (high temporal lines) and trait 2 (lambdoid crest V-shaped). This helps to explain why, in all MPTs, these four *Orycteropus* species are regrouped into the sister group of clade C. The strict consensus tree does not present this topology because the position of the two outlying species in reference to clade B is variable. Moreover, the state of characters 1 and 2 is unknown for *L. guilielmi*. This taxon is basal to the group or within this group.

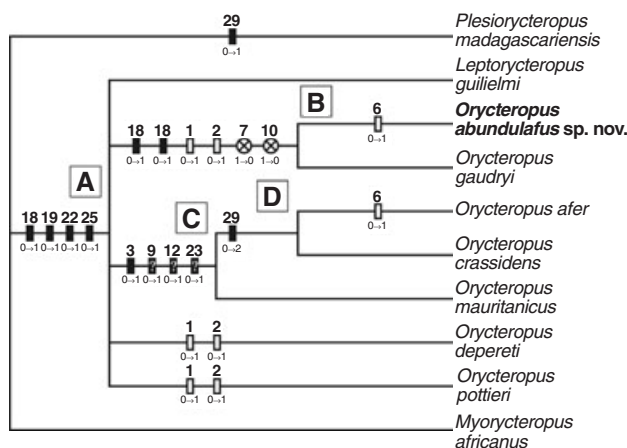


Figure 10. Strict consensus three of eight most parsimonious trees resulting from a heuristic search, PAUP version 4. Tree length = 45, CI = 0.69 and RI = 0.60. Apomorphies are marked with black bars, convergences are marked with white bars, reversions are marked with crossed circles, and apomorphies discussed in the text are marked with black bars and question marks. The character number and direction of state change are given next to the bar.

The unresolved position of *L. guilielmi* causes the polytomy within clade A. This relates to the problem of monophylogeny of the genera *Orycteropus* and *Leptorycteropus*.

Clades B and C are placed in polytomy with the other clade A taxa, but they are both well supported as monophyletic groups. Clade B (*O. abundulafus* + *O. gaudryi*) has at least two uniquely derived synapomorphies (16 and 20). The developed oblique rim of the radius (16) and the triangular and not bounded proximally olecranon fossa (20) can be viewed as the strongest defining traits of this clade. Beyond these two diagnostic features, and traits 1 and 2 in *O. depereti* and *O. pottieri*, two further characters seem to be uniquely reversed in clade B: features 7 (slender palatine) and 10 (posterior rim of the palatine at the M^3 level). However, these reversions are in contradiction with our description of the evolutionary trend toward an elongation of the snout. In fact, these characters are not observable in the other genera or in *O. crassidens*, *O. mauritanicus* and *O. pottieri*. Nonetheless, some species (*O. pottieri* or *L. guilielmi* for instance) show indirect clues that their palatines were short and slender. Thus, the assumed polarity for characters 7 and 10 is maintained here. Trait 11 (ridges on the lateral pterygoid wall), only shared by *O. abundulafus* and *O. depereti*, appears to be a convergent character. Clade B, supported by the strict consensus tree and the bootstrap proportion, is considered valid.

In the three species of clade C, the anterior border of the orbit lies above M^3 (3), whereas it is above M^2 in clade B, in *L. guilielmi* and in *O. depereti*. Thus, character 3 is a diagnostic apomorphy of the group containing the aardvark. Three other synapomorphies (9, 12 and 23) are uniquely shared by two species included in clade C, while in the third, *O. mauritanicus*, their state is unknown. That explains why the bootstrap proportion is low. Clade D, included in the former, is better supported because *O. afer* and *O. crassidens* actually share the following synapomorphies: (12) flat glenoid cavity and (29) talus as long as wide. Character 12 could thus be a diagnostic character of clade D not shared by *O. mauritanicus* that would not change the relationship among clade C.

Although it is not the aim of this paper to discuss the validity of *O. crassidens* as a distinct species (see Pickford, 1975), it is noted that the strict consensus tree shows that *O. afer* and *O. crassidens* are very close, but at least one character distinguishes both: the angle of the zygomatic arch (6). Moreover, as described by MacInnes (1956), *O. crassidens* differs from *O. afer* by the orientation of the socket of the upper tooth row. This feature was not included in the matrix because its state is generally unknown in most species.

DISCUSSION AND CONCLUSION

The specimen was found in foetal position, lying on its right side (Fig. 11). The left side has been more damaged by erosion. In this position, even sesamoids have been preserved. There is evidence against any *post mortem* displacement of the body. In association with this specimen, other articulated fossils have been found, including an incomplete skeleton of a gazelle (at KB03) and two gazelle limbs (at KB07, a nearby site). Despite the lack of sedimentological evidence (there is no heterogeneity in the sediments surrounding the skeleton), it is possible that the specimen died in its burrow.

Orycteropus abundulafus sp. nov. shows peculiar features that are morphofunctionally different from the extant species, *O. afer*. The chewing apparatus is more compact and more powerful in *O. abundulafus* and the amplitude of movement of the mandible was probably reduced. Demand for a higher pressure on a more focused area could be a sign of a tougher diet. In this perspective, it should be noted that there is considerable evidence of dung beetles at KB (Düringer *et al.*, 2000). With reference to mastication, the greater vestibulolingual expansion of the occlusal molar surface in the Chadian fossil is important. The digging ability of this form is also different. The absence of projecting deltoid crest probably indicates a less developed deltoid muscle. However, the Hildebrand index and the large brachial crest show that the animal was probably able to burrow. Moreover, the pectoral muscles are likely to have been as developed as in the extant aardvark. Less dedicated to the digging effort, those muscles could have been associated with the animal's locomotion. Correlatively, the elbow

joint, because of the slender olecranon fossa and slender distal epiphysis as a whole (Hildebrand index, Table 7) restrain the ad- or abduction of the lower arm's with respect to the upper arm. This can be compared with the situation in many digitigrad animals. Additionally, the shorter hand further reduces the efficiency of the power stroke. Thus, *O. abundulafus* was a less specialized fossorial animal with smarter gait, like the badger.

A mosaic palaeoenvironment existed at Kossom Bougoudi, with an aquatic habitat, a forested area and a more open landscape (Brunet & MPFT, 2000). The presence of fishes, crocodilians, aquatic birds, hippos and liana-like plants indicate the vicinity of a stream or lake. Elephants, pigs, giraffes and rhinos identified in KB indicate a wooded savannah. However, hare, squirrel and hipparions reflect a nearby more open environment. Some bovids also indicate a humid grassland. Pagès (1970) is the only author to have observed and reported aardvark from a wooded environment. It is not possible to infer whether *O. abundulafus* lived in forest. During the Turolian, Samos had a forest-woodland environment (Solounias & Dawson-Saunders, 1988). Morphological convergence between *O. abundulafus* and *O. gaudryi* may be suggested.

The cladistic analysis shows that *O. abundulafus* and *O. gaudryi* form a clade. The relationships with the other species of the genus are still unresolved, *O. depereti* and *O. pottieri* being the closest taxa. Noticeably, this clade is distinct from a group including the extant aardvark, *O. crassidens* and *O. mauritanicus*. The genus *Leptorycteropus* is not clearly separated from the *Orycteropus* species. As a whole, these results show that the monophylogeny of the genus *Orycteropus* should be re-examined. At

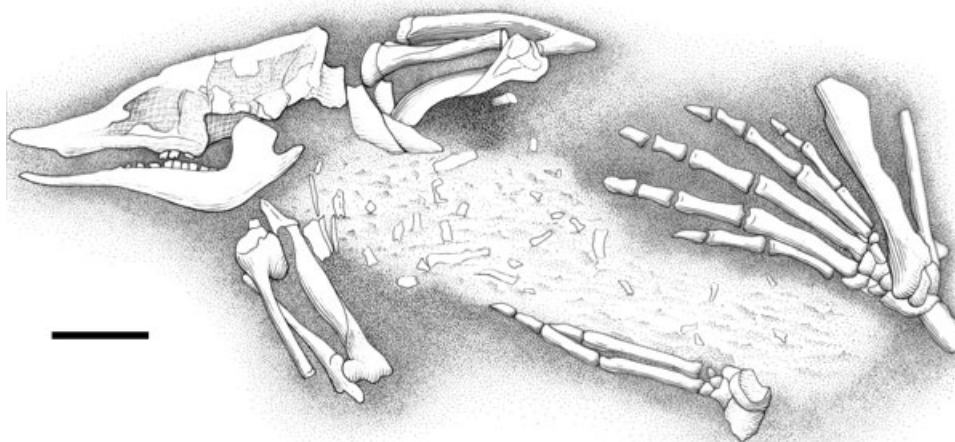


Figure 11. Skeleton *in situ* of *Orycteropus abundulafus* sp. nov. Scale bar = 5 cm.

present, we cannot suggest appropriate generic distinctions, but reconsideration of previously reported fossil material and description of new specimens will likely lead to a revision of the order Tubulidentata.

The discovery of an Orycteropodidae in Chad extends the knowledge of aardvark distribution in Africa. The less specialized features of this new taxon are unique for the genus in Africa and suggest a rather isolated palaeobiogeographical history from the rest of the continent at the Mio-Pliocene boundary. Some of these features can also be found in Eurasian fossil aardvarks. No species of Tubulidentata were known to have representatives in both Africa and Eurasia, but the present phylogenetic reconstruction gives us new evidence for such relationships. For the moment, *O. abundulafus* is the only Orycteropodidae known from Africa that shows clear affinities with a Eurasian form. The relationships suggested here imply that intercontinental dispersions of Tubulidentata occurred during the Late Miocene.

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