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## New material of *Anancus kenyensis* (proboscidea, mammalia) from Toros-Menalla (Late Miocene, Chad): Contribution to the systematics of African anancines

Lionel Hautier<sup>a,b,\*</sup>, Hassane Taisso Mackaye<sup>c</sup>, Fabrice Lihoreau<sup>b,c</sup>, Pascal Tassy<sup>d</sup>, Patrick Vignaud<sup>a</sup>, Michel Brunet<sup>a,b,c,d,e</sup>

<sup>a</sup>Institut International de Paléoprimatologie, Paléontologie Humaine, Evolution et Paléoenvironnements (IPHEP), UMR CNRS 6046, Université de Poitiers, UFR-SFA, 40 Avenue du Recteur Pineau, 86022 Poitiers Cedex, France

<sup>b</sup>Laboratoire de Paléontologie, Institut des Sciences de l'Evolution de Montpellier, Université Montpellier 2, UMR CNRS 5554, 2 Place Eugène Bataillon, Cc 064, F-34095 Montpellier Cedex 5, France

<sup>c</sup>Laboratoire de Paléontologie, Université de N'Djamena, Faculté des Sciences Exactes et Appliquées (FSEA), BP1117, N'Djamena, Chad

<sup>d</sup>Muséum National d'Histoire Naturelle et CNRS UMR 8569, Rue Cuvier, 75005 Paris, France

<sup>e</sup>Collège de France, Chaire de Paléontologie humaine, 3 Rue d'Ulm, 75231 PARIS Cedex 05, France

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### ABSTRACT

New fossil remains of the proboscidean genus *Anancus* are described. Among them, a complete skull allows us to revisit for the first time the entire Chadian *Anancus* fossil record. This genus occurred in the Old World from the late Miocene up to the early Pleistocene. The analysis of dental and cranial characters was allowed individual variations from specific characters to be distinguished. In this study we show that *Anancus kenyensis* and *Anancus osiris* are very likely synonym taxa which leads us to emend the diagnosis of *A. kenyensis*. In addition, this study shows that dental characters in anancines lineage are of little significance for biostratigraphical inference, by contrast to previous works. This study brings new data about the phylogenetical and palaeobiogeographical history of the African anancines.

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Within Elephantoid, Anancines can be distinguished by the peculiar arrangement of the cuspid of their molar, an autapomorphic dental morphology named anancoidy. This term refers to the establishment of an alternating arrangement of the pretrite and posttrite half-loph(id)s (Tassy, 1986). Anancines have an exclusive Old World distribution. The genus *Anancus* was very diversified during the Mio-Pliocene. From African deposits, three species have been recognized according to the molars morphology: *Anancus kenyensis* MacInnes, 1942 from East and Central Africa (Cooke

and Coryndon, 1970; Hendeby, 1978; Coppens et al., 1978; Mebrate and Kalb, 1985; Tassy, 1986, 1994; Cooke, 1993; Kalb and Mebrate, 1993 and Mackaye, 2001); *Anancus osiris* Arambourg 1945 from North Africa (Arambourg, 1970; Coppens et al., 1978 and Geraads and Metz-Muller, 1999); *Anancus petrocchii* Coppens 1965 from North and Central Africa (Coppens, 1965; Mackaye, 2001). These species are mostly differentiated by the number of cone pairs on intermediate molars and the complexity of the third molar. However, the intra-specific variations of molar morphology in anancines are due to variable growth of these conules. Tassy (1986) considered *A. petrocchii* as a non-valid taxa and included it in *A. kenyensis* proposing it as a complex morph characterized by pentalophodont intermediate molars. In addition, Metz-Muller (1995, 2000) described in European species of *Anancus* a marked individual variation of specific characters. Finally, Mackaye (2001) indicated great similarities between the molars of *A. kenyensis* and *A. osiris*.

Consequently, it appears that the systematics of anancines largely depends on the completeness of the available fossil remains. In Africa, most of the fossil material of *Anancus* consists of isolated

**Abbreviations:** M1/, first upper molar; M/1, first lower molar; acprc, anterior central pretrite conule; pcprc, posterior central pretrite conule; pcpc, posterior central posttrite conule.

\* Corresponding author. Address: Institut International de Paléoprimatologie, Paléontologie Humaine, Evolution et Paléoenvironnements (IPHEP), UMR CNRS 6046, Université de Poitiers, UFR-SFA, 40 Avenue du Recteur Pineau, 86022 Poitiers Cedex, France. Fax: +33 4 6714 3610.

E-mail addresses: [Lionel.Hautier@univ-montp2.fr](mailto:Lionel.Hautier@univ-montp2.fr) (L. Hautier), [mhtaisso@gmail.com](mailto:mhtaisso@gmail.com) (H.T. Mackaye), [Fabrice.lihoreau@univ-montp2.fr](mailto:Fabrice.lihoreau@univ-montp2.fr) (F. Lihoreau), [ptassy@mnhn.fr](mailto:ptassy@mnhn.fr) (P. Tassy), [patrick.vignaud@univ-poitiers.fr](mailto:patrick.vignaud@univ-poitiers.fr) (P. Vignaud), [michel.brunet@univ-poitiers.fr](mailto:michel.brunet@univ-poitiers.fr) (M. Brunet).

teeth and does not permit us to study the individual variation. Recently, the Mission Paléanthropologique Franco-Tchadienne (MPFT) discovered numerous Late Miocene localities included in the Anthracotheriid Unit (A.U.) at Toros-Menalla (Northern Chad – Fig. 1) which have yielded, together with the earliest known Hominid *Sahelanthropus tchadensis* (Brunet et al., 2002), a rich and well-preserved vertebrate fauna (Vignaud et al., 2002). Within this abundant material, complete remains of proboscidean give us the opportunity to assess the range of intra-specific morphological variation of molars. In this study, we described one of the most complete *Anancus* skull and mandible belonging to one individual. We will therefore be able to discuss the individual variability on molars and to reconsider the validity of the specific characters. The systematics of African species of the genus *Anancus* will therefore be revisited and an emended diagnosis of *A. kenyensis* is proposed.

### 1. Systematic palaeontology

Order. Proboscidea Illiger, 1811

Superfamily. Elephantoidea Gray, 1821

Family. Gomphotheriidae Hay, 1922

Subfamily. Anancinae Hay, 1922

Genus. *Anancus* Aymard In Dorlhac, 1855

**Diagnosis** (following Tassy, 1986). Tetralophodont gomphotheres with a high and short skull. Elevated dome. Enlarged tympanic bulla. Short mandible without tusks. Straight upper tusks without enamel. Loss of premolars. Tetralophodont intermediate molars (occasionally pentalophodont M2/ in *A. kenyensis*, *A. petrocchii* and *Anancus sivalensis*). Posterior central pretrite conule reduced on upper molars. Reduction of the anterior central pretrite conule on the lower molars and fusion with the mesoconule. Alternation of the pretrite and posttrite half-loph(id)s which allows the establishment of an alternative contact of successive loph(id)s.



Fig. 1. Map of Chad, with the position of Toros-Menalla sector discussed in this paper.

Type species. *Anancus arvernensis* Croizet and Jobert (1828) Including valid species. *A. kenyensis* MacInnes, 1942, *A. petrocchii* Coppens, 1965, *A. sivalensis* Cautley (1836), *A. perimensis* Falconer and Cautley (1847), *Anancus sinensis* Hopwood (1935) and *Anancus kazachstanensis* Aubekerova (1974).

#### *Anancus kenyensis* MacInnes, 1942

*Anancus kenyensis* MacInnes, 1942 Figs. 2–4

1942 *Pentalophodon sivalensis kenyensis* MacInnes, p. 82

1943 *Anancus arvernensis* subsp. Dietrich (1943, p. 46)

1945 *Anancus arvernensis* subsp. Dietrich: Arambourg, p. 487

1945 *Anancus osiris* Arambourg, p. 487

1945 *Pentalophodon sivalensis kenyensis* MacInnes: Arambourg, p. 490

1947 *Anancus kenyensis* (MacInnes): Arambourg (1947, p. 305)

1967 *Anancus kenyensis* (MacInnes): Leakey (1967, p. 20)

1970 *Anancus kenyensis* (MacInnes): Cooke and Coryndon, p. 119

1970 *Anancus osiris* (Arambourg): Arambourg, pp. 1–126

1976 Anancinae (a primitive form): Smart (1976, p. 363)

1978 *Anancus kenyensis* (MacInnes): Coppens et al., p. 348

1978 *Anancus osiris* (Arambourg): Coppens et al., p. 348

1979 *Anancus kenyensis* (MacInnes): Tassy (1979, p. 266)

1982 *Anancus kenyensis* (MacInnes): Kalb et al. (1982, p. 246)

1985 *Anancus kenyensis* (MacInnes): Mebrate and Kalb, p. 96

1986 *Anancus kenyensis* (MacInnes): Tassy, p. 87

1993 *Anancus kenyensis* (MacInnes): Kalb and Mebrate, p. 32

1993 *Anancus kenyensis* (MacInnes): Cooke, p. 27

1998 *Anancus kenyensis* (MacInnes): Brunet et al., p. 155

1999 *Anancus osiris* (Arambourg): Geraads and Metz-Muller, p. 52

2000 *Anancus kenyensis* “kenyensis morph”: Brunet et al., p. 207

2001 *Anancus kenyensis* (MacInnes): Mackaye, p. 54

2001 *Anancus osiris* (Arambourg): Mackaye, p. 64

**Holotype**: left M2/, M15400 housed at the Natural History Museum of London (NHML); [MacInnes \(1942, pl. 7, Fig. 5 = KE20\)](#).

**Age**: Late Miocene to Late Pliocene.

**Distribution**: Lower Kaiso Formation and Nkondo Fm (Uganda – Cooke and Coryndon, 1970 and Tassy, 1994); Laetoli beds, Olduvai I, Wembere Manonga (Tanzania – Coppens et al., 1978 and Tassy, 1986); Mursi Fm, Adu-Asa Fm, Kuseralee (Ethiopia – Coppens et al., 1978; Mebrate and Kalb, 1985 and Kalb and Mebrate, 1993); Lower Kanam beds, the Ekora, Aterir, Lothagam-1 beds, Chemeron, Kanapoi and Lukeino Fm (Kenya – Coppens et al., 1978 and Tassy, 1986); Langebaanweg and Bolt’s Farm Transvaal (South Africa – Hendeby, 1978 and Cooke, 1993), Kollé (Brunet et al., 1998), Kossom Bougoudi (Brunet et al., 2000) and Toros Menalla (Chad – Mackaye, 2001 and Vignaud et al., 2002); Aïn Boucherit (Algeria – Coppens et al., 1978); Hamada Damous, Grombalia and Lac Ichkeul (Tunisia – Arambourg, 1970 and Coppens et al., 1978); Oued el Akrech and Ahl al Oughlam (Morocco – Coppens et al., 1978 and Geraads and Metz-Muller, 1999); Wadi Natrun (Egypt – Coppens et al., 1978).

**New material from the Anthracotheriid Unit of Toros-Menalla, Chad**. TM 90-01-71: mandible with right and left M/3; TM 146-01-07: left hemi-mandible with M/2; TM 158-01-01: skull with mandible; TM 160-01-21: complete mandible with right and left M/3; TM 242-01-42: left hemi-mandible with D/4. All of these specimens are housed in the Centre National d’Appui à la Recherche at N’Djamena (Chad).

**Emended diagnosis**: Exo-occipital and supra-occipital are laterally stretched; the occipital face is semi-rectangular; the dislocation of the half-lophids are more or less stressed with a variable development of the central posttrite conules; the tubercles of some

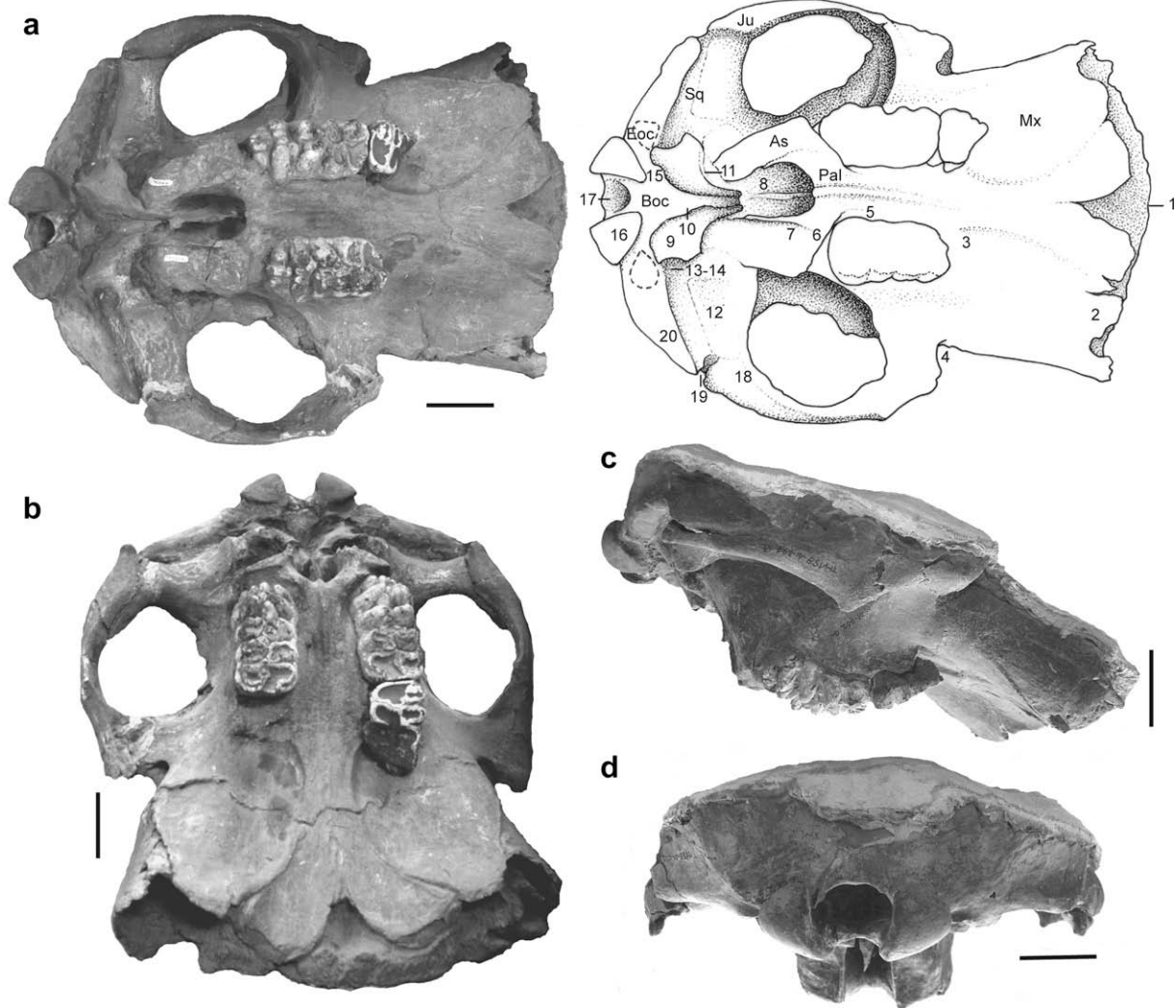
lower molars are slightly tilted forward, and convergent toward the sagittal plane in occlusal view.

### 1.1. Description

**Skull (Fig. 2, Table 1).** TM 158-01-01 has most of its brain case broken but the basicranium, zygomatic arch, rostrum and the palate are complete without any *post-mortem* distortion. The specimen can be considered as fully adult due to the functional M3/s associated to a worn right M2/. The premaxillae and maxillae are laterally extended constituting an hourglass-like rostrum (Fig. 2). The orbits are advanced with regard to dental rows. The basicranium is slanted. The alisphenoid has lateral pillar-like processes. Tympanic bullae are enlarged. Therefore, it presents all the characters of the specimen KNM LU 795 from Lukeino considered as autapomorphic characters of *A. kenyensis* (Tassy, 1986). It also shows characters considered as primitive in *Anancus* lineage by Tassy (1986), like the absence of the latero-ventral process of the auditory canal, the lack of post-glenoid fossa and a stylo-mastoid foramen opposite to the contact of the post-tympanic and post-glenoid parts of the squamosal.

The posterior margin of the maxillary zygomatic process is situated in front of the M2/ distal loph on TM 158-01-01 at the level of M3/ mesial side on KNM LU 795. This difference is certainly relative to different individual ages. At the exoccipital-squamosal joint, the paroccipital process forms a “moss bulge” less individualized than on Kenyan skull (Tassy, 1986). The occipital face is one of the most complete known for an African *Anancus* skull. Compared to the European *A. arvernensis* semi-circular occipital face, the Chadian skull shows exo-occipital and supra-occipital laterally stretched. Thus the occipital face appears to be semi-rectangular.

**Upper dentition (Figs. 2 and 4a, Table 2).** The right M2/ is tetralophodont and worn. The third molars are wide and low-crowned. The dislocation of the half-lophs is slight. The crown structure is complex on the proximal side and simple on the distal side. The two first pretrite half-lophs are complex with extended anterior central pretrite conule (acprc) 1–2 and posterior central pretrite conule (pcprc) 2 bulge-like. The third and fourth half-lophs are simplified with the lack of pcprc and the presence of a reduced mesoconelet partly jointed to the principal tubercle. The acprc 3 and 4 are rounded and well developed. On the posttrite side, the



**Fig. 2.** Basicranium of TM 158-01-01 in ventral view (a). 1. *fissura incisiva*; 2. Anterior part of the maxillare; 3. *crista interalveolaris*; 4. *foramen infraorbitale*; 5. palatin foramen; 6. *processus pterygoideus palatinus*; 7. *crista* of the pterygoidean part of the sphenoid; 8. choanes; 9. tympanic bulla; 10. *foramen caroticum*; 11. *foramen lacerum orale*; 12. *fossa mandibularis*; 13. insertion fossa of the tympanohyal ligament; 14. stylomastoid foramen; 15. *foramen metoticum*; 16. occipital condyle; 17. *foramen magnum*; 18. *pars temporalis* of the jugal; 19. *meatus acusticus spurius*; 20. *processus post-tympanicus squamosalis*. Cranium TM 158-01-01 with right M2/ and M3/s in palatine view (b). Cranium TM 158-01-01 in lateral view (c) Cranium TM 158-01-01 in occipital view (d). (Scale bar: 10 cm).



**Table 1**

Cranium measurement of TM 158-01-01 compared to the specimen KNM LU 795 of *A. kenyensis* from Lukeino (Tassy, 1986). Measurement to nearest mm. C1: length between anterior extremity of the maxillary median suture and foramen magnum; C2: length between anterior extremity of the choanes and anterior extremity of the rostrum; C3: length of the orbito-temporal fossa; C4: length of the basicranium between *foramen magnum* and anterior tip of the basisphenoid; C5: length at *foramen infraorbitale* level; C6: maximal anterior width of rostrum; C7: width of palate between the second loph of the M3; C8: maximal width of cranium between zygomatic arches; C9: width of basicranium between the *meatus acusticus spurius*; C10: maximal width of the choanes; C11: width of the *foramen magnum*; C12: height of the *foramen magnum*.

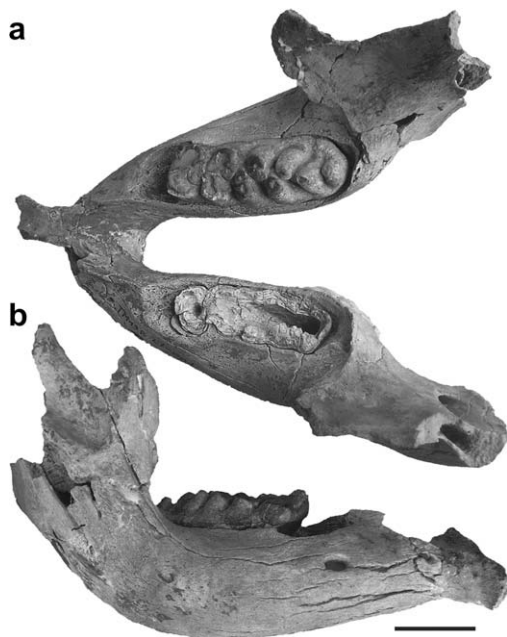
Specimen	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12
TM 158-01-001	860	52	192	153	425	51	76.7	620	513	68.9	71.4	64.7
KNM LU 795	780	570	210	140	330	380	90	600	520	60	77	48

**Table 2**

Comparative dimensions of molars for *Anancus* sp. from Toros-Menalla compared to the specimen KNM LU 795 of *A. kenyensis* from Lukeino (Tassy, 1986). Measurement to nearest mm. N: number of loph(id); L: greatest anteroposterior length; W1: greatest buccolingual width of the first loph(id), W2: second loph(id), W3: third loph(id), W4: fourth loph(id), W5: fifth loph(id), W6: sixth loph(id); H: greatest height; E: enamel thickness.

Specimen	N	L	W1	W2	W3	W4	W5	W6	H	E
<i>Upper molars</i>										
M3/ l. TM 158-01-01	5	155	76	78	78	86	66	–	56	6
M3/ r. TM 158-01-001	5	155	76	78	78	82	62	–	58	6
M3/ l. KNM LU 795	5	170	–	78	78	75	67	–	55.6	–
M3/ r. KNM LU 795	5	170	74	76.5	77	75.5	72	–	–	–
<i>Lower molars</i>										
D/4 l. TM 242-01-42	4	312	–	–	–	–	–	–	30.9	2.4
M/2 l. TM 146-01-07	4	136.5	–	59.8	–	56.5	–	–	45.7	4.6
M/3 l. TM 90-01-71	5	268	89.8	–	100.5	107	–	–	–	10.3
M/3 r. TM 158-01-01	5	186	63.2	71.5	74.8	65.7	39.9	–	60.7	5.5
M/3 l. TM 160-01-21	6	220	–	80.1	77.3	77.1	68.9	59.4	–	5.5
M/3 r. TM 160-01-21	6	219.5	–	80	78.8	77.6	70.6	61.9	–	6.3
M/3 l. KNM LU 795	6	184	64	15	79	77.5	70	57.5	–	–
M/3 r. KNM LU 795	6	185	–	78	81	79	74	59	–	–

structure is similar. Indeed, the anterior half-lophs are also complex with a triple posterior central posttrite conule (pcpoc) 1 and a large pcpoc 2 united to a little bulge. The mesoconelets, separated from principal tubercles by folds, are slightly compressed. Their size decreases on the distal lophs. The pcpoc 3 is reduced to a bulge and the pcpoc 4 and 5 are absent. The last loph is very simplified with the anancoid contact that is not established with the fourth loph. The tubercles do not converge to the sagittal plane. The distal cingulum lacks.



**Fig. 3.** Mandible TM158-01-001 with right M/3 in dorsal view (a). Right hemimandible TM158-01-001 with M/3 in lingual view (b). (Scale bar: 10 cm).

*Mandibles* (Fig. 3, Table 3). The mandibles are more abundant than the skull remains in the Chadian localities. All characters described by Tassy (1986) on KLM LU 795, like the brevirostry have been found on the mandibles of Toros-Menalla. The beak is prominent with a large gutter on the symphysis. The ascending ramus is high with subvertical anterior and posterior margins. The masseteric fossa is slightly vertical. The condyles are distantly positioned and stretched laterally. The coronoid apophyse is high above the dental row compared to the primitive gomphotheres. The mandibular corpus is laterally dilated.

With regard to the Kenyan anancines material, the Chadian mandibles show an association of primitive and derived characters (Tassy, 1986). The long horizontal ramus and the strong symphysis are more primitive characters. On the contrary the re-erected lower part of the posterior side and the relative high position of the angular region can be considered as more derived. Nevertheless, taking in mind the limited material and the important individual variation observed on *Loxodonta africana* (Beden, 1979), it is difficult to attribute to these characters any evolutive value.

*Lower dentition* (Figs. 3 and 4b, Table 2). The third molar of TM 158-01-01 is long and narrow. The third mesial lophids are functional. The alternation of the half-lophids is important. Except for the first lophid, the mesoconelets are reduced. On the mesial lophids, the anancoid contact is established between the pcpoc and the mesoconelet of the following lophid. The crown structure is extremely simplified distally and the fifth lophid is reduced to a single principal posttrite tubercle. On the posttrite side, the tubercles are tilted forward, and they are convergent toward the sagittal plane in occlusal view.

## 2. Discussion

*A. osiris* was described for the first time by Arambourg (1945), but recently Metz-Muller (2000) emended and completed the diagnosis. This species is defined by a simple and a sub-hypsodont crown with a large valley, tubercles strongly tilted forward and

**Table 3**

Measurements of the mandibles for *Anancus* sp. from Toros-Menalla. Measurement to nearest mm. M1: length of interalveolar crista; M2: length between tip of beak and anterior extremity of tooth row; M3: length between anterior extremity of tooth row and anterior extremity of ascending ramus; M4: length back of anterior extremity of ascending ramus; M5: height of ramus at anterior extremity of tooth row; M6: height of ramus at anterior extremity of ascending ramus; M7: height between mandibular condyle and ventral side of the ramus; M8: length of ascending ramus back of the condyle; M9: maximal width of ascending ramus; M10: height between ventral extremity of the mandibular foramen and tip of the condyle; M11: inter-condylar width; M12: width of condyle; M13: length of condyle; M14: width at coronoid process; M15: width at anterior extremity of ascending ramus; M16: length of symphysis; M17: maximal width of beak.

	TM 90-01-71	TM 146-01-07	TM 158-01-01	TM 160-01-21(r)	TM 160-01-21(l)	TM 242-01-42
M1	–	–	177	–	–	–
M2	–	–	154.5	–	–	–
M3	268	209	236	212	209	116.2
M4	315	250	152	248.5	248	–
M5	190	133.8	128	–	157	–
M6	207	124	127	142	142.5	72.9
M7	510	–	–	470	473	–
M8	73.8	–	–	66.4	68.5	–
M9	–	–	239.5	283	296	–
M10	228	–	–	228	223.5	–
M11	–	–	375	–	–	–
M12	106.3	–	–	–	–	–
M13	58.8	–	–	48.3	49.7	–
M14	–	–	387	–	–	–
M15	–	–	407.5	–	–	–
M16	–	–	155	–	–	–
M17	62	–	41.7	–	–	–

slightly curved, posttrite elements formed by two cones, pretrite elements slightly compressed mesio-distally, a great alternation of the half-lophids, pretrite mesoconelets reduced on the mesial lophids of the M/3 with a variable development of the acprc, and an ananoid contact established between the pcprc and the mesoconelet of the following lophid on the molars. The molar of TM 158-01-01 (Fig. 4b) presents an association of characters very close to *A. osiris*. The simplified structure of the third and fourth lophid is very characteristic. The unusual arrangement of the last lophid, with its isolated tubercle, might be considered as an individual variation. Indeed, this type of extreme simplification for the last lophid has always been observed on gomphotheres M/3 (Tassy, pers. observ. 2005).

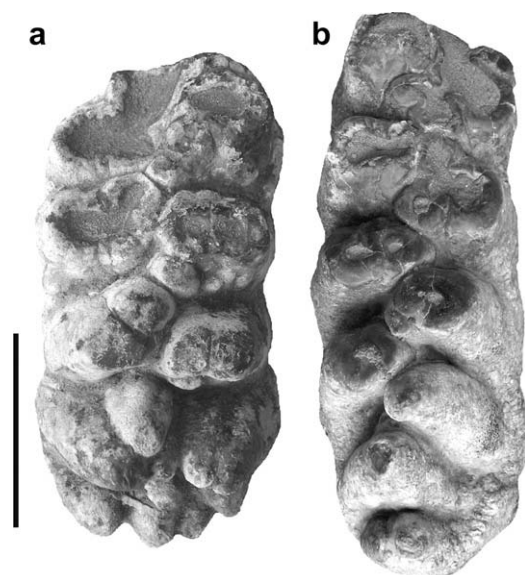
The molars of *A. kenyensis* present an association of characters very different from those of *A. osiris*. Indeed, the molars of this species are characterized by a slight alternation of the half-lophs, five or six lophs on M3/ with pcprc always developed on the mesial

lophs, narrow interloph valleys occasionally full of cement, parallel tubercles, and an ananoid contact established between the acprc and the pcprc of the previous loph. All these characters have been found associated on the M3/ of the specimen TM 158-01-01 (Fig. 4a). The relative simplicity of their distal portion induced by the lack of ananoid contact and the absence of the posterior cingulum allow their attribution to *A. kenyensis*. The complex structure of the mesial lophs does not allow us to assign these molars to *A. osiris*.

Consequently, the same specimen exhibits upper molars with *A. kenyensis* characters and lower molars with *A. osiris* ones. As a result, *A. kenyensis* [MacInnes \(1942\)](#) and *A. osiris* [Arambourg \(1945\)](#) are very likely synonyms as already suggested by [Cooke and Coryndon \(1970\)](#) and [Mackaye \(2001\)](#). This suggestion leads to an emended diagnosis of *A. kenyensis*. According to the International Code of Zoological Nomenclature, the species *A. kenyensis* must be used for this species, as it has the priority.

In Europe, *Anancus* have a widespread distribution. The study of Bulgarian locality of Dorkovo ([Metz-Muller, 2000](#)), which yielded numerous specimens allocated to *A. arvernensis*, allowed us to distinguish individual variations from specific characters and to clarify the phylogenetic relationships between European *Anancus* species. [Schlesinger \(1917\)](#) suggested to include all European forms in one species, *A. arvernensis*. The precise morphological study, [Metz-Muller \(1995, 2000\)](#) validated this hypothesis and suggested that *A. arvernensis* presented a tendency towards a shortening of the molars, an increase of the hypsodonty and a simplification of the crown. Up to now, the African fossil record is scarce, and the systematic position of the African species has been largely discussed. The new material from Toros-Menalla shows an important morphological variability of the molars of *A. kenyensis*. Similar morphological tendencies observed in the European anancines, also seems to occur in the African stock.

This work sheds new light on the biodiversity of the Mio-Pliocene African proboscidean in general and the African anancines paleobiogeographic history in particular. It was suggested that *A. osiris* evolved from an European anancines stock ([Metz-Muller, 2000](#)). This species was described with few specimens or just cited in the faunal lists (e.g. Wadi Natrun, Egypt, Late Miocene; [Coppens et al., 1978](#)). [Mackaye \(2001\)](#) indicates great similarities between the molars of *A. kenyensis* and *A. osiris*. In this context, the new remains of Chadian anancines provide arguments for phylogenetic



**Fig. 4.** Left M3/ (TM 158-01-01) in occlusal view (a). Right M3/ (TM 158-01-001) in occlusal view (b). (Scale bar: 10 cm).

systematics and paleogeographic reconstructions. Until now, two antagonist hypotheses implicated lines of dispersal between Europe and Africa in the lower Pliocene. Metz-Muller (1995) considers that *A. osiris* evolved from the European species *A. arvernensis* while Mackaye (2001) proposed that *A. osiris* was the stem group of *A. arvernensis*. These hypotheses were based on similarities of the dental morphology between the two species. At this time, the fossil record cannot attest dispersal between the two continents during the Lower Pliocene.

### 3. Conclusion

These preliminary results indicate the importance of the intra-specific morphological variations and the limits of using dental characters to resolve Neogene proboscidean phylogeny. It is important to reconsider the informative value of the characters used by Metz-Muller (2000) in *Anancus* phylogeny. The upper and lower molar morphology is strongly different and it is not pertinent to describe species with only a few remains. Always the number of specimens is important for morphology and dimensions. It will be also necessary to revise the type material of *A. petrocchii*, the third African species. This material is only represented by lower molars and the species was defined on the pentalophodonty of the M/2. An interpretation of these variations in an evolutionary perspective must take the intra-specific component into account. Therefore, the use of these dental characters in biostratigraphy is here challenged.

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