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

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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.

Within Elephantoïd, 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; Hendey, 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; pcpoc, posterior central posttrite conule.

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teeth and does not permit us to study the individual variation. Recently, the Mission Paléoanthropologique 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 mesoconelet. 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); Laetolil 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 – Hendey, 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