Suidae and Sanitheriidae from Wadi Moghra, early Miocene, Egypt

MARTIN PICKFORD, ELLEN R. MILLER, and AHMED N. EL-BARKOOKY

Pickford, M., Miller, E.R., and El-Barkooky, A.N. 2010. Suidae and Sanitheriidae from Wadi Moghra, early Miocene, Egypt. *Acta Palaeontologica Polonica* 55 (1): 1–11.

New suid and sanithere material from Wadi Moghra, early Miocene, Egypt, is described and discussed. The new material greatly improves the sample size and diversity of suoids known from North Africa, and includes one species of Sanitheriidae and three species of Kubanochoerinae. The Moghra suoid assemblage most closely resembles that from Gebel Zelten, Libya, suggesting that at least part of the Moghra deposits may overlap in time with part of Zelten, i.e., is equivalent in age to MN 4–5 of the European mammal zonation, or PIII of the East African one. Information from suids and sanitheres is consistent with previous interpretations, that the Moghra deposits were formed under swampy and littoral paleoenvironmental conditions.

Key words: Mammalia, Suidae, Sanitheriidae, biochronology, Miocene, Egypt, Africa.

Martin Pickford [pickford@mnhn.fr], Département Histoire de la Terre, Muséum National d'Histoire Naturelle, 8, rue Buffon, 75005, Paris, France;
Ellen R. Miller [millerer@wfu.edu], Department of Anthropology, Wake Forest University, Winston Salem, NC 27103, USA;
Ahmed N. El-Barkooky [ahmed.el-Barkooky@shell.com], Geology Department, Faculty of Sciences, Cairo University, Egypt.

Received 29 January 2009, accepted 03 August 2009, available online 17 August 2009.

Introduction

Wadi Moghra [= Moghara] Qattara Depression, Egypt, is an early Miocene fossil locality preserving a rich array of fossil mammals, including 27 species in 12 families. The first systematic work on the Moghra fauna was that of Fourtau (1918, 1920), who recorded the presence of anthracotheres but no other artiodactyls. The first mention of suoids at Moghra was that of Miller and Simons (Miller 1996; Miller and Simons 1996; Miller 1999), who documented the occurrence of *Nguruwe kijivium* (3 specimens) and *Diamantohyus* (= *Xenochoerus) africanus* (5 specimens) based on isolated teeth and gnathic fragments.

In recent years, however, work at Moghra has substantially enhanced the collection of suoids known from North Africa, including: the recovery of an exceptionally well-preserved palate, several partial mandibles and isolated teeth of the sanithere *Diamantohyus africanus*; additional dental material of the small suid *Nguruwe kijivium*; possibly the first Egyptian records of the suids *Libycochoerus anchidens* or *Libycochoerus* cf. *jeanneli* and two specimens of *Libycochoerus* cf. *massai*. This contribution describes and discusses new fossil suoid material from Wadi Moghra, including what the presence of this assemblage indicates about the biochronology and paleoenvironment of Moghra.

Institutional abbreviations.—AD, Arrisdrift, Geological Survey of Namibia; ATH, field number, Gebel Zelten, Libya; BAR, Baringo (Kipsaraman), Kenya; BG, Nachola (Aka Aiteputh, Baragoi), Kenya; bpv, fossils in the Beijing Natural History Museum, China; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; BU, Bristol University, UK; BUK, Bukwa, Uganda Museum; CGM, Cairo Geological Museum, Egypt; CU, Chianda Uyoma, Kenya; DPC, Duke University Division of Fossil Primates, Carolina, USA; EF, Elisabethfeld, Geological Survey of Namibia; F followed by a number, old numbering system of the Kenya National Museum, Kenya; FS, Fiskus, Geological Survey of Namibia; GSI, Geological Survey of India; GT, Grillental, Geological Survey of Namibia; HGSP, Harvard-Geological Survey of Pakistan collection, Massachusetts, USA; KA, Karungu, Kenya; KNM, Kenya National Museum; LBE, Muséum National d'Histoire Naturelle, Libye collection, Paris, France; LC, Locherangan (National Museum of Kenya); LT Langental (Geological Survey of Namibia); M followed by a number, Natural History Museum, London, UK; MB, Maboko, Kenya; MNHN, Muséum National d'Histoire Naturelle, Paris; MO, Moruorot, Kenya; MW, Mfwangano, Kenya; NAP, Uganda Museum, Napak collection, Uganda; OM, Ombo, Kenya; PQN, Iziko South African Museum, Cape Town; RK, Ryskop, South Africa; RU, Rusinga, Kenya; SO, Songhor, Kenya; THB, Thymiana B, Chios; UBC, University of Cali-

doi:10.4202/app.2009.0015

fornia, Berkeley, USA; UM, Uganda Museum Kampala, Uganda; V, fossils in the Institute for Vertebrate Palaeontology and Palaeoanthropology, Academica Sinica, Beijing, China; WK, Kalodirr, National Museum of Kenya; WM, Cairo University, Egypt (WM numbers are field numbers, the material has no accession numbers). Locality abbreviations at Moghra have differed over the years depending on the collecting party. Some localities are designated by "MGL" (Moghra Locality), others by "L" (Locality) by the year the specimen was collected (e.g., 97–22), some combination of the year the material was collected and its locality (e.g., 83-E), or simply by "WM"; WS, West Stephanie (Buluk), Kenya; X, locality unknown, Kenya National Museum.

Other abbreviations.—An uppercase letter denotes a tooth in the maxillary series, and a lowercase letter a tooth in the mandibular series. For example, M1 is a first upper molar, m2 a second lower molar, and dp4 a fourth deciduous lower premolar.

Conventions.—Measurements were taken with calipers to the nearest 0.1 mm. Dental nomenclature is based on Pickford 1986 and Van der Made 1996.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Artiodactyla Owen, 1848

Family Sanitheriidae Simpson, 1945

Genus *Diamantohyus* Stromer, 1922

Diamantohyus africanus Stromer, 1922

Figs. 1–4.

Holotype: BSPG 1926 X, right maxilla with P3, M1–2, currently lost (Gertrude Rößner, personal communication 2009). Figured in Stromer 1926: pl. 40: 17; also figured in Pickford 1984: fig. 1.

Type locality and horizon: Langental, Namibia, Early Miocene.

Material.—CGM 82975, right mandible fragment with p4–m2; WM 97-697, right mandible fragment with m2–m3; WM 05-50, palate with left and right P2–M3 (Fig. 1A); WM 06-49, left mandible with p4–m3 (Fig. 4A); WM 06-14, left mandible with dp4–m2 (Fig. 4F); WM 05-21, right M2 (Fig. 4B); WM 05-48, right m3 (Fig. 4C); WM 06-55, right mandible with worn m3 (Fig. 4G); WM DEC06-11, right m1 (Fig. 4D); WM DEC06-025, m3 (Fig. 4C); DPC 17688, palate with roots of left and right P2–M3 (Fig. 2); DPC 12599, left mandible, i1–m1 (Fig. 3A); DPC 14581, mandible with symphysis, roots of right i1–p2, left i1–p4 (Fig. 3B); DPC 8997, right mandible, m1–2, p4 erupting (Fig. 1C); DPC 6469, juvenile mandible with dp4, m1–2 (Fig. 1D); DPC 6618, mandible with m2–m3 (Fig. 1B); DPC 12942, left maxilla containing P4–M2.

Diagnosis.—Differs from *Sanitherium* in having less molarized premolars, and in having anterior and posterolingual cusps less developed; P4 with two main cusps and two subsidiary ones; metastylid prominent on unworn specimens; m1–m3 ca. 40 mm (range 37.5 to 42.5 mm) (after Pickford 1984).

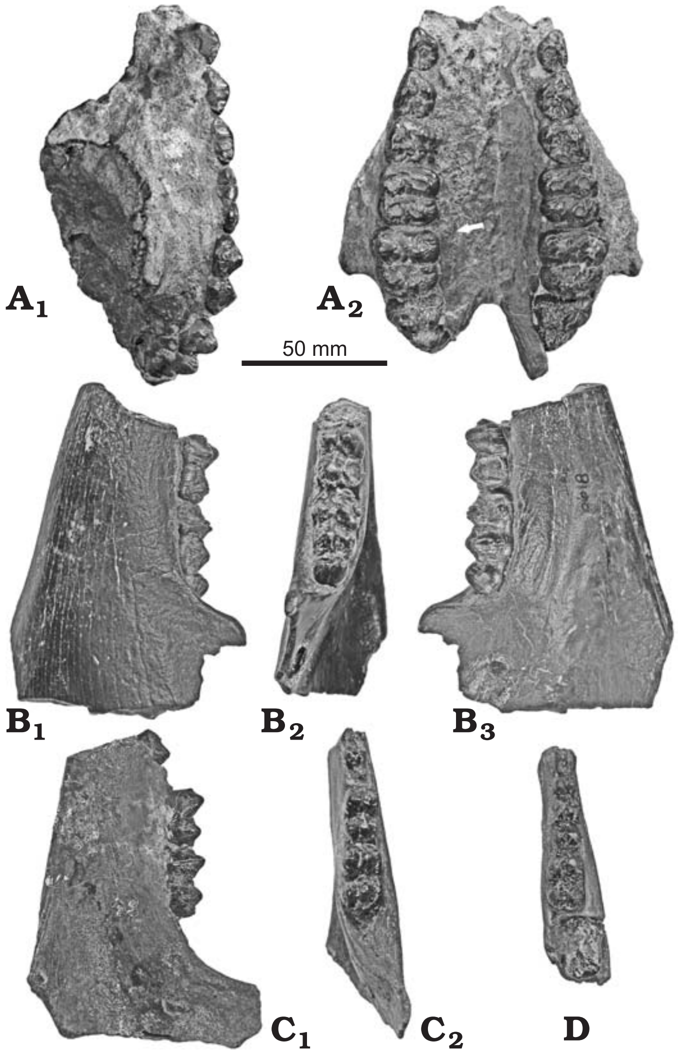

Fig. 1. Sanitheriid mammal *Diamantohyus africanus* Stromer, 1922 from early Miocene of Wadi Moghra, Egypt. **A**. Palate of a young adult (WM 05-50) in buccal (A_1) and occlusal (A_2) views (arrow points to the palatine foramen opposite front of M2). **B**. Left mandible (DPC 6618), m2–3 in buccal (B_1), occlusal (B_2), and lingual (B_3) views. **C**. Juvenile left mandible (DPC 8997), m1–2, p4 erupting in lingual (C_1) and occlusal (C_2) views. **D**. Juvenile right mandible (DPC 6469) with part of dp3, complete dp4 and m1, m2 in crypt in occlusal view.

Description.—Palate and upper dentition: WM 05-50 is the most complete sanithere palate known, all other material being distorted or broken (Fig. 1). The specimen is of a young adult, with the M3s beginning to erupt, and M1s in medium wear. Lingually the cheek tooth rows are parallel to each other (distance between the P2s and the M2s is 17 mm). In this young individual the palatine foramen is opposite the rear of M1 (Fig. $1A_2$) and the posterior choanae invaginate the palate as far forwards as the front of the M3. However, this position would probably have changed had the individual lived to maturity, as revealed by the position of the palatine foramen in DPC 17688, which lie opposite the middle of M2 (Fig. 2B). The rear of the zygomatic process of the maxilla is located above the rear of M2, and anteriorly it rises from the facial surface at about the level of P4–M1. In lateral view, the occlusal surface of the cheek teeth in WM 05-50 appears convex from front to back, a condition that is commonly observed in sanitheres but which is unlike that observed among suids, in which the tooth row is concave (Pickford 1986, 2004). A second specimen, DPC 17688, preserves the snout but with much worn cheek teeth, and also shows a convex tooth row (Fig. 2C). In this latter specimen, the infraorbital foramen opens above P3 and is preceded by a large depression, which extends anteriorly as a broad groove that rises and narrows above the canine jugum, as in a sanithere specimen KNM-BG 41925A from Aka Aiteputh, Kenya (Pickford and Tsujikawa 2005). Although a P1 crown is not represented in the collection, the roots of this tooth are present in DPC 17688, and reveal a biradicular condition. On WM 05-50 (Fig. 1A), P2 has a prominent paracone and metacone, forming a continuous buccal wall. Lingually, the protocone is close to the paracone and is followed distally by a depression that is full of wrinkled enamel. This depression is bordered lingually by a prominent puffy cingulum. P3 is constructed along the same lines as the P2, but the cusps are more isolated from each other. In particular, the protocone is separated from the paracone and is oriented more obliquely. P4 is essentially a larger version of P3, but with a better developed, broader, distal part, and the paracone and metacone are separated from each other by a shallow valley. M1 is comprised of four sub-equal cusps, and anterior and buccal cingula. The protocone sends a strong crest antero-buccally where it joins the pre-crista of the paracone, the junction lying distal to the anterior cingulum. The protocone is broader than the paracone. The hypocone has a sloping lingual surface, so that its apex is close to the midline of the crown. The metacone has an almost circular enamel outline. There is a low cingular remnant at the lingual end of the median transverse valley. M2 differs from M1 in being slightly larger in size, and in having a more prominent cingular cusplet at the lingual end of the transverse valley. Because the M2 crown is less worn than that of M1, the wrinkling in the enamel is more in evidence, and the grooves on the buccal cusps can be discerned. The orientation of these grooves is typical of Sanitheriidae, and quite different from that seen in suids. The buccal cingulum is narrow with a beaded edge, it is continuous from front to back, and it extends onto the distal surface of the metacone and hypocone. There is a posterior accessory cusplet in the midline of the tooth, between the metacone and hypocone, which joins the distal cingulum. M3 is similar to M2, save that it sports a small talon cusp in the disto-lingual extremity of the crown, imparting a trapezoidal occlusal outline to the tooth. Measurements of the upper and lower teeth from Moghra are presented in Table 1. Tables S1 and S2 (see Supplementary Online Material at http://app.pan.pl/SOM/app55-Pickford_etal_SOM.pdf) provide measurements for the Moghra sanitheres compared with a large sample of other African and Eurasian sanitheres.

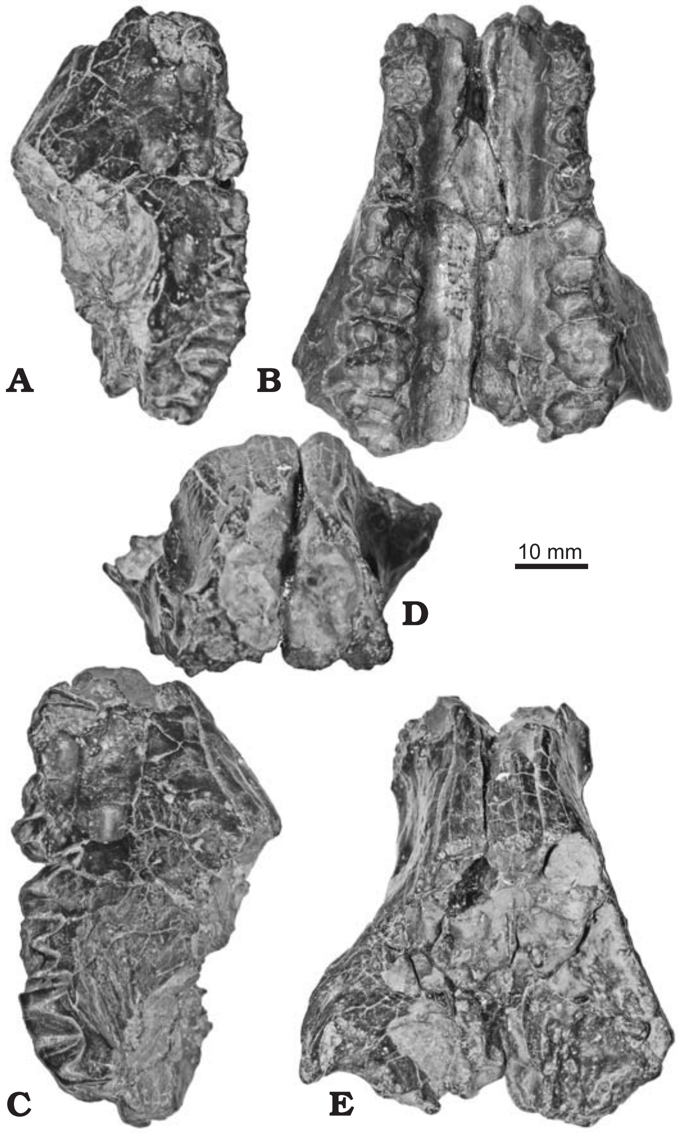

Fig. 2. Sanitheriid mammal *Diamantohyus africanus* Stromer, 1922 from early Miocene of Wadi Moghra, Egypt, snout (DPC 17688) in right lateral (**A**), occlusal (**B**), left lateral (**C**), anterior (**D**), and superior (**E**) views (note palatine foramina opposite middle of M2).

Mandible and lower dentition: DPC 12599 is a left mandible with the two central incisors, the left i2–p2 and p4 as well as the roots of p3 and anterior root of m1 (Fig. 3A). The individual was very old when it died, the crowns of the teeth being deeply worn. The central and second incisors in particular show secondary dentine associated with the pulp canal, leaving little of the crown to describe. What remains are oval occlusal surfaces worn almost flat. The i1 and i2 are subequal in dimensions, whereas the i3 is appreciably smaller than the i2. There are extremely short gaps anterior and distal to the i3. The canine is small with two fused roots, and is in contact with the p1, which also has fused roots. The i3 is slightly compressed labio-lingually, and shows a blunt distal crest. The canine is oval with a posterior crest bordered by shallow grooves. Its morphology and dimensions indicate that the individual was a female (Pickford 2006). The p1 is deeply worn, but shows evidence of a distal cusplet separated from the main cusp by shallow buccal and lingual grooves. The p2 is in medium wear and reveals that the crown is comprised of a main cusp positioned above the gap between the two roots.

doi:10.4202/app.2009.0015

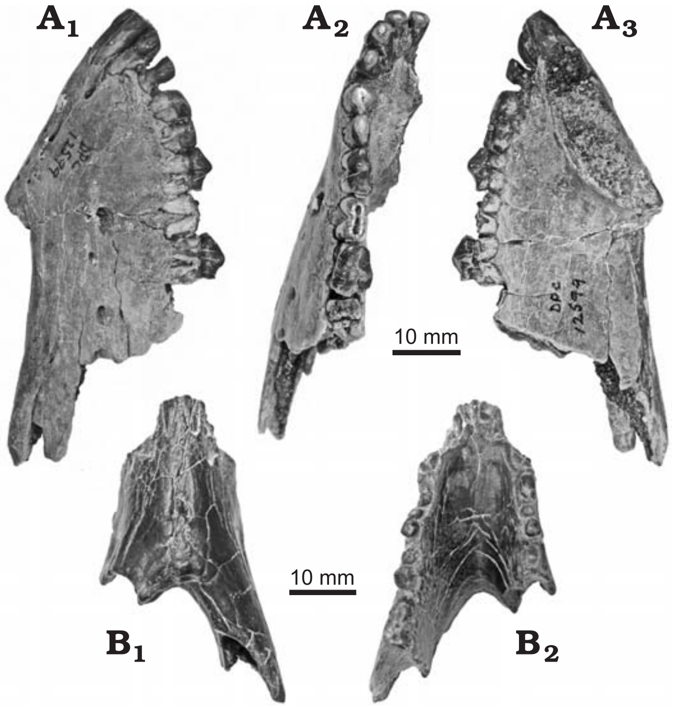

Fig. 3. Sanitheriid mammal *Diamantohyus africanus* Stromer, 1922 from early Miocene of Wadi Moghra, *Egypt*. **A**. Left mandible (DPC 12599) preserving both central incisors, and left i2–p2, roots of p3, p4 and anterior root of m1 in buccal (A_1), occlusal (A_2), and lingual (A_3) views. **B**. Edentulous symphysis (DPC 14581) in inferior (B_1) and superior (B_2) views.

From the apex of this cusp there is an anterior crest that curves lingually near the anterior end of the tooth, and there is a stronger posterior crest and postero-lingual cusplet. The p3 crown is missing. The p4 is damaged distally, but it has a main cusp above the gap between the two roots. There is a prominent lingual cuspid attached to the main cusp which broadens the centre of the tooth. An anterior crest curves lingually close to the anterior margin of the crown. Distally, there is a broad crest descending from the apex of the tooth towards the distal edge but the cusplet at its disto-lingual margin is damaged. In lateral view, the most striking aspect of this mandible is the curvature of the occlusal surface of the incisor battery. This curvature is enhanced by the advanced wear stage of the teeth, but nevertheless, there can be little doubt that the occlusal surface of the incisors curves strongly ventrally starting at the level of the canines. There are four mental foramina, three large ones at mid-height of the jaw, respectively beneath the anterior root of the p3 and the two roots of the m1, and a smaller one slightly lower down, beneath the anterior root of p4. There are also two prominent nutritive foramina in the anterior part of the symphysis in line with the root of i2. In lingual view the symphysis is long and robust, terminating distally beneath the level of the p3. The same applies to an edentulous mandibular symphysis (DPC 14581) (Fig. 3B), in which the two halves of the jaw are solidly fused to each other, a condition that may be age-related, although it seems to be observed more often in sanitheres and other suoids than in anthracotheres.

WM 06-14 and WM 06-49 are two mandible fragments (Fig. 4A, F). The former specimen is a juvenile with the rear two thirds of the dp4 preserved, distal to which m1 is fully erupted and m2 is in its crypt. The latter specimen is fully adult, with p4–m3 fully erupted. The rear of the symphysis in WM 06-49 lies opposite the middle of p3, and a break in the specimen anterior to the p3 alveolus reveals no sign of an enlarged canine alveolus, indicating that this individual was probably a female. There are mental foramina beneath the junction between p2–p3 and p4–m1, at about half the depth of the jaw. The mandible is slender and the tooth row is straight except where the m3 curves slightly buccally. The rear two pairs of cusps of the dp4 in WM 06-14 are in medium wear and have lost most details of crown morphology. What remains looks like a small version of the m1. The p4 in WM 06-49 has a large protoconid and a prominent metaconid almost as tall as the protoconid, but is separated from it apically. Distally there is a low hypoconid from which a distal cingulum descends lingually. Buccally there is a low cingulum between the hypo-

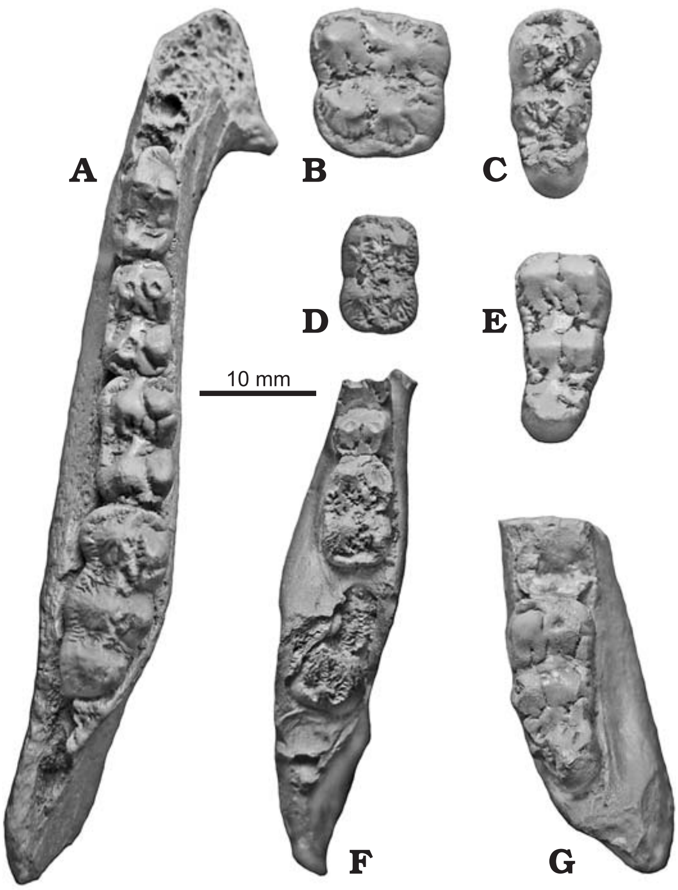

Fig. 4. Sanitheriid mammal *Diamantohyus africanus* Stromer, 1922 from early Miocene of Wadi Moghra, Egypt (occlusal views of casts). **A**. Left mandible with p4–m3 (WM 06-49). **B**. Right M2 (WM 05-21). **C**. Right m3 (WM 05-48). **D**. Right m1(WM DEC06-11). **E**. Left m3 (WM 06-25). **F**. Left mandible with dp4–m2 (WM 06-14). **G**. Right mandible with m3 (WM 06-55).

Table 1. Dental measurements (mm) of *Diamantohyus africanus* Stromer, 1922 from early Miocene of Wadi Moghra, Egypt. Abbreviations: MD, mesiodistal length; BL, buccolingual breadth.

Tooth	P2	P2	P3	P3	P4	P4	M1	M1	M2	M2	M3	M3
Specimen/measurement	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
WM-05-50L	7.0	5.1	8.4	6.9	7.9	8.3	10.6	10.6	12.5	12.3	–	10.7e
WM-05-50R	7.1	5.3	8.2	7.1	8.1	8.3	10.4	10.4	12.4	12.0	15e	10.8e
WM-05-21									12.2	11.9		
Tooth	i1	i1	i2	i2	i3	i3	c	c	p1	p1	p2	p2
Specimen/measurement	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
DPC 12599	4.8	3.1	4.9	3.2	5.2	3.4	3.5	3.6	6.0	4.1	5.5	3.1
Tooth			p3	p3	p4	p4	m1	m1	m2	m2	m3	m3
Specimen/measurement			MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
DPC 12599			7.2	3.9								
WM-06-49					10.6	5.8	10.6	6.3	11.5	7.5	17.9	8.3
CGM 82975					9.3	5.6	9.7	7.2				
WM-06-14							9.3	6.1				
WM-06-11							10.6	7.0				
DPC 8997							10.9	7.4				
97-697									11.8	8.6	18.0	8.6
WM Dec 06-25											16.5	8.2
WM Dec 06-48											16.7	8.2
WM 06-55											17.5	8.4
DPC 6618											16.3	7.6

conid and the protoconid and at the antero-buccal corner of the crown. The protoconid has prominent pre- and postcristids oriented antero-posteriorly, the pre-cristid curving lingually as it descends towards the cervix. There are two roots. The m1 in the adult mandible is in light wear with dentine exposed on three cusps (not on the entoconid). There is a well developed, beaded, buccal cingulum which curves anteriorly and posteriorly at the ends of the tooth. The lingual cusps are transversely compressed and are thus narrower than the buccal cusps. The small cuspid immediately distal to the metaconid is just visible, although heavily worn. The protoconid has pre- and post-cristids that curve lingually, but not so far as to enclose the metaconid. Between the rear parts of the protoconid and metaconid there is a small but tall cuspid. The hypoconid also has pre- and postcristids that curve lingually, but only reach the midline of the tooth, the precristid blocking the median transverse valley.

The m2 is a larger version of the m1, but being less worn, it shows the structures of the crown better. In particular, the small cuspid just distal to the metaconid is clearly distinguishable, its apex being separated from that of the metaconid. The m3 is like the m2 save for the presence of a large, almost centrally positioned hypoconulid distal to the second lophid of the tooth. Measurements of the upper and lower teeth from Moghra are presented in Table 1, and Tables S1 and S2 (see Supplementary Online Material at http://app.pan.pl/SOM/app55-Pickford_etal_SOM.pdf) provide dental measurements for the Moghra specimens compared with a large sample of other African and Eurasian sanitheres.

Remarks.—New sanithere specimens from Wadi Moghra increase our knowledge about the family Sanitheriidae, most notably concerning the form of the palate and lower incisors, which were absent or poorly preserved in previously available samples. The palate is remarkably uniform in breadth from P2 to M3, the inner margins of the upper cheek teeth being almost parallel. The posterior choanae invaginate anteriorly to the level of distal M2, but this may have changed had the individual lived to maturity. The morphology and dimensions of the mandible and upper and lower cheek teeth fall within the range of variation for *Diamantohyus africanus* (Stromer 1922, 1926; Pickford 1984). The upper premolars of the more derived species *Diamantohyus nadirus* are more complex, with better developed cutting edges in the anterior cusps (Pickford and Tsujikawa 2005; Pickford 2006). The Moghra material differs from Eurasian *Sanitherium leobense* (de Bonis et al. 1997) and *Sanitherium schlagintweiti* (Koufos 2007) in its narrower molars and simpler premolar morphology.

Geographic and stratigraphic range.—Namibia (Langental, Fiskus, Bogenfels); Kenya (Rusinga (Hiwegi, R1a, R1, R3, R45, RVII, R91, Kaswanga, Kulu, Gumba), Locherangan, Kalodirr, Karungu, Kajong, Majiwa, Chianda Uyoma); Uganda (Bukwa, Napak); Egypt (Wadi Moghra); Libya (Gebel Zelten), early Miocene.

Family Suidae Gray, 1821

Subfamily Kubanochoerinae Gabunia, 1960

Genus *Nguruwe* Pickford, 1978

Type species: *Nguruwe kijivium* (Wilkinson, 1976), early Miocene, Uganda.

doi:10.4202/app.2009.0015

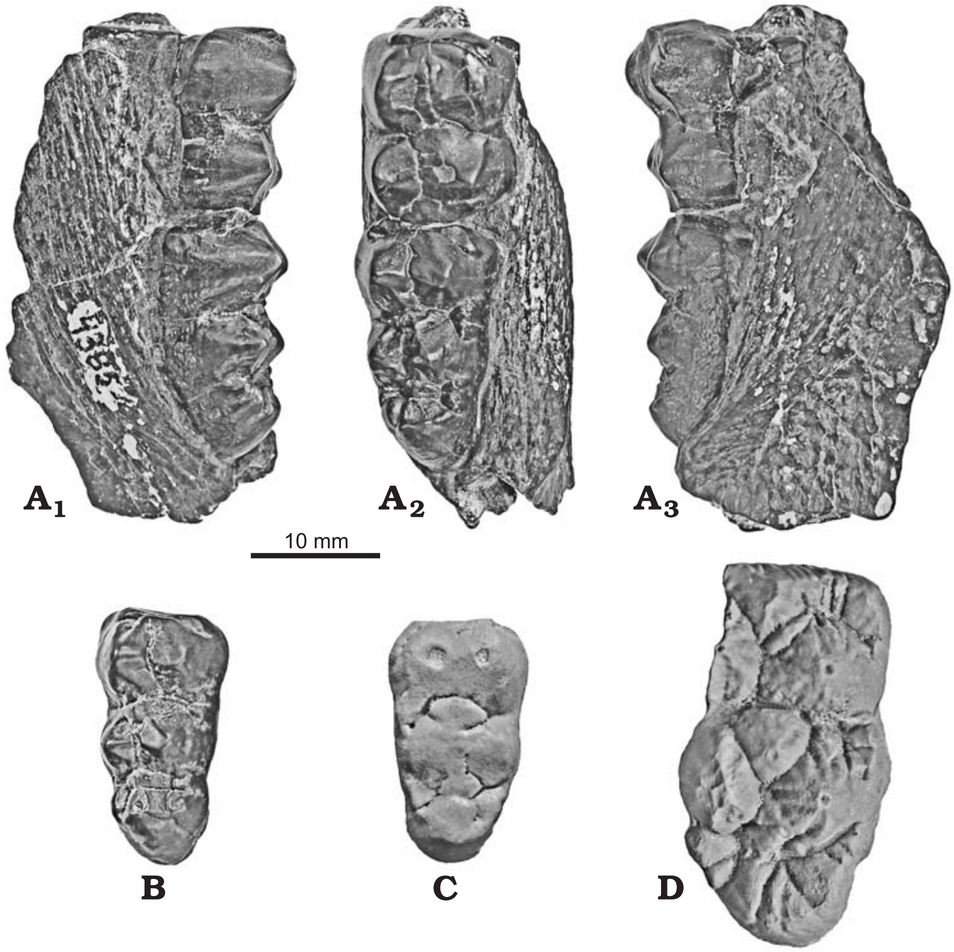

Fig. 5. Kubanochoerin suids from early Miocene of Wadi Moghra, Egypt. **A**–C. *Nguruwe kijivium* (Wilkinson, 1976). **A**. Right mandible with m2–3 (DPC 4385) in lingual (A_1), occlusal (A_2), and buccal (A_3) views. **B**. Right m/3 (DPC 14564) in occlusal view. **C**. Left m3 (WM Dec 06-10) in occlusal view. **D**. *Libycochoerus massai* Arambourg, 1961 partial, right M3 (WM Dec 09) in occlusal view.

Nguruwe kijivium (Wilkinson, 1976)

Fig. 5A–C.

Holotype: NAP I'64, left maxilla fragment with M1–3, figured in Wilkinson 1976: pl. 2: g; Pickford 1986: fig. 6.

Type locality and horizon: Early Miocene, Napak I, Uganda.

Material.—WM 97-715, left m3; WM DEC06-10, worn left m3 (Fig. 5C); DPC 4385, right mandible fragment with m2–3 (Fig. 5A); DPC 14564, right m3 (Fig. 5B).

Diagnosis.—A small genus of Kubanochoerinae in which I1 is labiolingually compressed, not meeting interproximally; P4 with two main cusps and complete cingulum; molars with thick enamel, inflated main cusps, closed lingual notches; simple talon/id in upper and lower third molars; occlusal outline of m3 symmetrical; p3 with wide distal lingual cingular cusp or platform; p4 with metaconid almost completely suppressed; dm4 buccolingually inflated; lower canine scrofic; upper canine with dorsal cement cover (Pickford 1986).

Description.—DPC 4385, a right mandible fragment, retains m2 and m3 in medium wear (Fig. 5A). The m2 has four main cusps arranged in two lophids and there are small anterior, median and posterior cusplets in the center line of the crown. The median accessory cusplet is antero-posteriorly compressed, transversely elongated, and at the wear stage in which the dentine lake extends over about half the width of the crown. The median transverse valley is extremely narrow from just above cervix level to the occlusal surface of the tooth, as in other specimens of *Nguruwe*. The m3 is similar to the m2 save for the presence of a large talonid cusp positioned slightly buccal to the mid-line of the tooth. The posterior transverse valley of this tooth possesses low tubercles buccally and lingually and there is a low tubercle at the buccal extremity of the median transverse valley.

Lower third molars of *N. kijivium* from Wadi Moghra are simple, bunodont teeth with a small almost centrally positioned talonid (Fig. 5C). WM DEC06-55 shows a medium amount of wear, with dentine showing at the apices of the two anterior cusps, and all evidence of the furchen abraded away. The enamel is thick as in specimens of this genus from East Africa and Namibia (Pickford 1986, 1987, 1995, 1997, 2003, 2004). The hypoconulid is located slightly to the buccal side of the central line, and it has cingular crests running antero-buccally and antero-lingually. The anterior cingulum is narrow and extends slightly onto the buccal

Table 2. Dimensions (mm) of m3 and M3 of Kubanochoerinae from early Miocene of Wadi Moghra, Egypt. Abbreviations: e, estimated; MD, mesiodistal length; BL, buccolingual breadth.

Tooth	Taxon	m3	m3	M3	M3
Specimen/ Measurement		MD	BL	MD	BL
97-715	*Nguruwe kijivium*	18.9	10.3		
WM Dec 06-10	*Nguruwe kijivium*	19.0	10.9		
DPC 4385	*Nguruwe kijivium*	18.8	11.3		
WM Dec 06-09	*Libycochoerus massai*			33.4	26e

side of the protoconid. The anterior accessory cusplet is deeply worn, being barely perceptible. The median accessory cusplet is heavily worn showing a transversely elongated wear facet occupying about half the extent of the transverse valley. This is similar to the situation observed in East African and Namibian specimens of the species that are worn to a comparable stage. The posterior accessory cusplet lies anterior to the hypoconulid in the midline of the tooth. Cingular remnants block the buccal ends of the median and posterior transverse valleys, but there is no cingulum at the lingual end of the median transverse valley. The dimensions of these teeth are close to those of *Nguruwe kijivium* from Eastern and Southern Africa (Table 2). In addition, Tables S3 and S4 (see Supplementary Online Material at http://app.pan.pl/SOM/app55-Pickford_etal_SOM.pdf) compare M3 and m3 dimensions of Kubanochoerinae from Moghra with a large sample of other African and Eurasian kubanochoerines.

Remarks.—Fossils from Moghra attributed to *Nguruwe kijivium* are similar to specimens of this taxon from East Africa and Namibia. This species ranges in age from about 20–18 Ma in East Africa, and up to about 17.5 Ma in Namibia. It is thus a useful marker for the upper part of the early Miocene, and possibly the base of the middle Miocene. The deposits where this species has been found are usually correlated to MN 3 and MN 4 of the European mammal zones.

Geographic and stratigraphic range.—Uganda (Napak, I, IV, V); Kenya (Songhor, Koru, Mteitei, Mfwangano, Rusinga (Hiwegi)); Egypt (Wadi Moghra); Namibia (Arrisdrift), early to ?middle Miocene.

Genus *Libycochoerus* Arambourg, 1961

Type species: *Libycochoerus massai* Arambourg, 1961, early to middle Miocene, Libya.

Libycochoerus massai Arambourg, 1961

Fig. 5D.

Holotype: Left mandible with p2–m3, No. 1961-5-8 MNHN Paris.

Type locality and horizon: Terminal early Miocene to basal middle Miocene, Gebel Zelten, Libya.

Material.—WM DEC06-09, partial right M3 (Fig. 5D); CGM 30791, right talus; DPC 17744 canine and DPC 14565 canine are provisionally referred to this species.

Diagnosis.—Large kubanochoere, about 10–20% smaller than *Kubanochoerus robustus*; upper molar series about 100 mm long (Pickford 1986).

Description.—WM DEC06-09, a partial upper third molar is unworn but is missing part of the paracone and the buccal edge of the metacone (Fig. 5D). However, enough remains of the tooth to reveal its main characters. The protocone, metacone and hypocone are well preserved conical bunodont cusps with coarse but shallow furchen and wrinkles. The anterior and median accessory cusplets are also conical and voluminous, being about 2/3rd the height of the main cusps. The anterior accessory cusplet is located well anterior to the line joining the apices of the paracone and protocone, and it is fused to the beaded anterior cingulum. The hypocone has a cingular remnant on its antero-lingual corner, partly blocking off the transverse valley. The median accessory cusp is relatively small and low. The hypoconule is located in line with the protocone and hypocone, and it sends a descending beaded cingulum antero-buccally. This tooth is remarkably similar to material of *Libycochoerus massai* from Gebel Zelten (see specimens illustrated by Van der Made 1996: pl. 10: 7, 8). In terms of size, WM DEC06-09 plots out at the small end of the range of variation of *L. massai* from Gebel Zelten (Fig. 7), but we have little hesitation in attributing this tooth to the species. Dental dimensions for the Moghra specimen are provided in Table 2 and Table S4 (see Supplementary Online Material at http://app.pan.pl/SOM/app55-Pickford_etal_SOM.pdf) provides comparative dental data from a large sample of other African and Eurasian kubanochoerines.

CGM 30791 is a right talus from a large suid the dimensions of which are close to those of LBE 505, a right talus from Gebel Zelten attributed to *L. massai* (Orliac 2007: fig. 66.2). Dimensions of the Moghra and Zelten tali are provided in Table S5 (see Supplementary Online Material at http://app.pan.pl/SOM/app55-Pickford_etal_SOM.pdf).

Geographic and stratigraphic range.—Wadi Moghra, Egypt; Gebel Zelten, Libya (Arambourg 1961, 1963), early to middle Miocene.

cf. *Libycochoerus* sp. sensu Drake et al. (1988)

Locality and horizon: Moruorot and Kalodirr are aged ca. 17.2 Ma, whereas Rusinga and Karungu are 17.8 Ma (Drake et al. 1988).

Material.—DPC 8947, left mandible fragment with wind-abraded m1 to m3.

Description.—DPC 8947, a sand-blasted left mandible with part of the right symphysis preserved, contains worn and damaged m1–m3 and roots of p4 (Fig. 6). The symphysis is solidly fused and very thick dorso-ventrally, its posterior extremity lying beneath about the p3, but the specimen is so damaged that little can be said about its morphology. It is possible to see however, that the junction between the two halves of the symphysis forms a raised ridge lingually, suggesting that the individual was aged when it died, a possibility supported by the heavy wear on the m3. The buccal surface of the jaw has been destroyed leaving nothing to be ob-

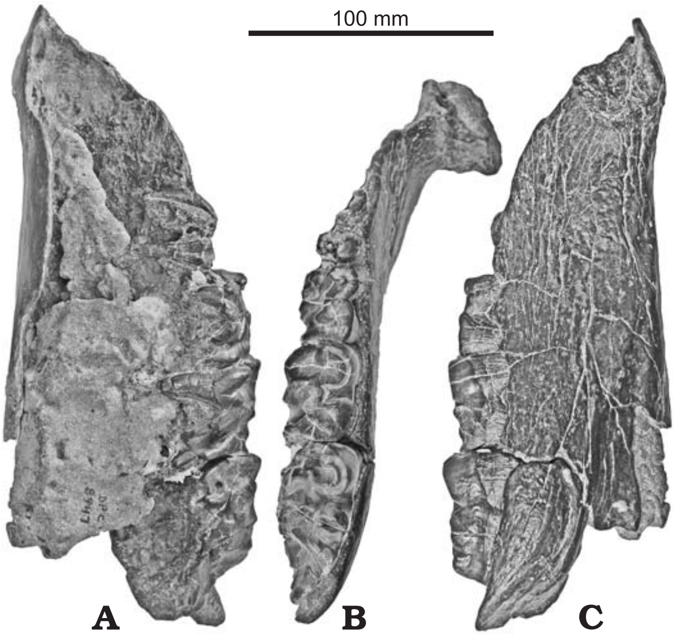

Fig. 6. Kubanochoerin suid cf. *Libycochoerus* sp. (size of *Libycochoerus jeanneli* and *Libycochoerus anchidens*) sensu Drake et al. (1988) from early Miocene of Wadi Moghra, Egypt, (DPC 8947), left mandible fragment with wind-abraded m1–m3 in buccal (**A**), occlusal (**B**), and lingual (**C**) views.

served concerning the position of the mental foramen or the dimensions of the canine. The sublingual fossa is large and extends anteriorly as far as the m1, forming a deep recess beneath m3. The teeth are deeply worn occlusally and on their buccal sides have suffered greatly from wind-driven sand. Lingually the teeth are better preserved, and they reveal that the median transverse valleys in the m2 and m3 were broad near the cervix, as in the genus *Libycochoerus* (Pickford 1986). The median accessory cusps extend across less than half the bucco-lingual breadth of the tooth. This is clearly visible in the m2, in which the remnant of this accessory cusplet shows an almost circular outline, markedly divergent from the bucco-lingually elongated and mesio-distally compressed outline that occurs in teeth of *Nguruwe* species. The ends of the median transverse valleys do not possess any tubercles or cingular remnants. Although accurate measurements are difficult to take on account of the abrasion of the specimen, DPC 8947 is clearly larger than known specimens of *Kenyasus rusingensis* (Fig. 7), and is about the same size as *Libycochoerus jeanneli* and *L. anchidens* (Table 3).

Discussion.—The restricted amount of morphology that is discernible in this wind-abraded fragment is not compatible with Listriodontinae or Hyotheriinae, but recalls Kubanochoerinae. The dimensions of DPC 8947 are comparable with both *Libycochoerus anchidens* and *Libycochoerus jeanneli*, and both species are known from East Africa in deposits dated to between ca. 17.8 and 17.2 Ma (Pickford 1986, 2007). Miocene suid taxa tend to be extremely widespread, so the presence of one or the other of these species at Moghra would not be surprising. The species *Nguruwe kijivium* is equally widespread, being reported from Namibia, East Africa and Moghra. The possible presence of *Libycochoerus anchidens* or *Libycochoerus jeanneli* at Moghra would provide additional support for the view that the stratigraphic succession in the region includes deposits spanning the end of the early Miocene.

Geographic and stratigraphic range.—*Libycochoerus jeanneli* is known from Moruorot (type locality) and Kalodirr, Kenya (Arambourg 1933; Pickford 1986; Orliac 2007): *Libycochoerus anchidens* is known from Rusinga (type locality) and Karungu, Kenya (Pickford 1986; Van der Made 1996), early Miocene.

Discussion

Biochronology.—At present, the age of Moghra can only be assessed through faunal correlation, although work is under-

Table 3. Dental measurements (mm) of the mandible DPC 8947, compared with those of *Libycochoerus jeanneli* and *Libycochoerus anchidens* (data from Pickford 1986; van der Made 1996; Orliac 2007) (e = estimated, + = measurement is greater than the figure given).

Specimen	Tooth	Species	Length	Breadth
DPC 8947	m1 left	*Libycochoerus* cf. *anchidens* or *jeanneli*	18e	14e
KNM RU 2785	m1 left	*Libycochoerus anchidens*	18.8	13.9
KNM RU 2721	m1	*Libycochoerus anchidens*	15.5	10.5
KNM RU 15076	m1	*Libycochoerus anchidens*	17.1	12.9
UBC	m1 right	*Libycochoerus jeanneli*	16.5	11.6
UBC	m1 right	*Libycochoerus jeanneli*	16.8	11.7
KNM MO 18127	m1 right	*Libycochoerus jeanneli*	20.4	14.2
DPC 8947	m2 left	*Libycochoerus* cf. *anchidens* or *jeanneli*	22e	18e
KNM RU 2785	m2 left	*Libycochoerus anchidens*	20.5	17.1
UBC	m2 right	*Libycochoerus jeanneli*	19.8	14+
DPC 8947	m3 left	*Libycochoerus* cf. *anchidens* or *jeanneli*	22e	18e
KNM RU 2785	m3 left	*Libycochoerus anchidens*	31.8	19.2
KNM RU 15164	m3	*Libycochoerus anchidens*	32.2	18.8
KNM MO 18127	m3 right	*Libycochoerus jeanneli*	24.7+	20.0

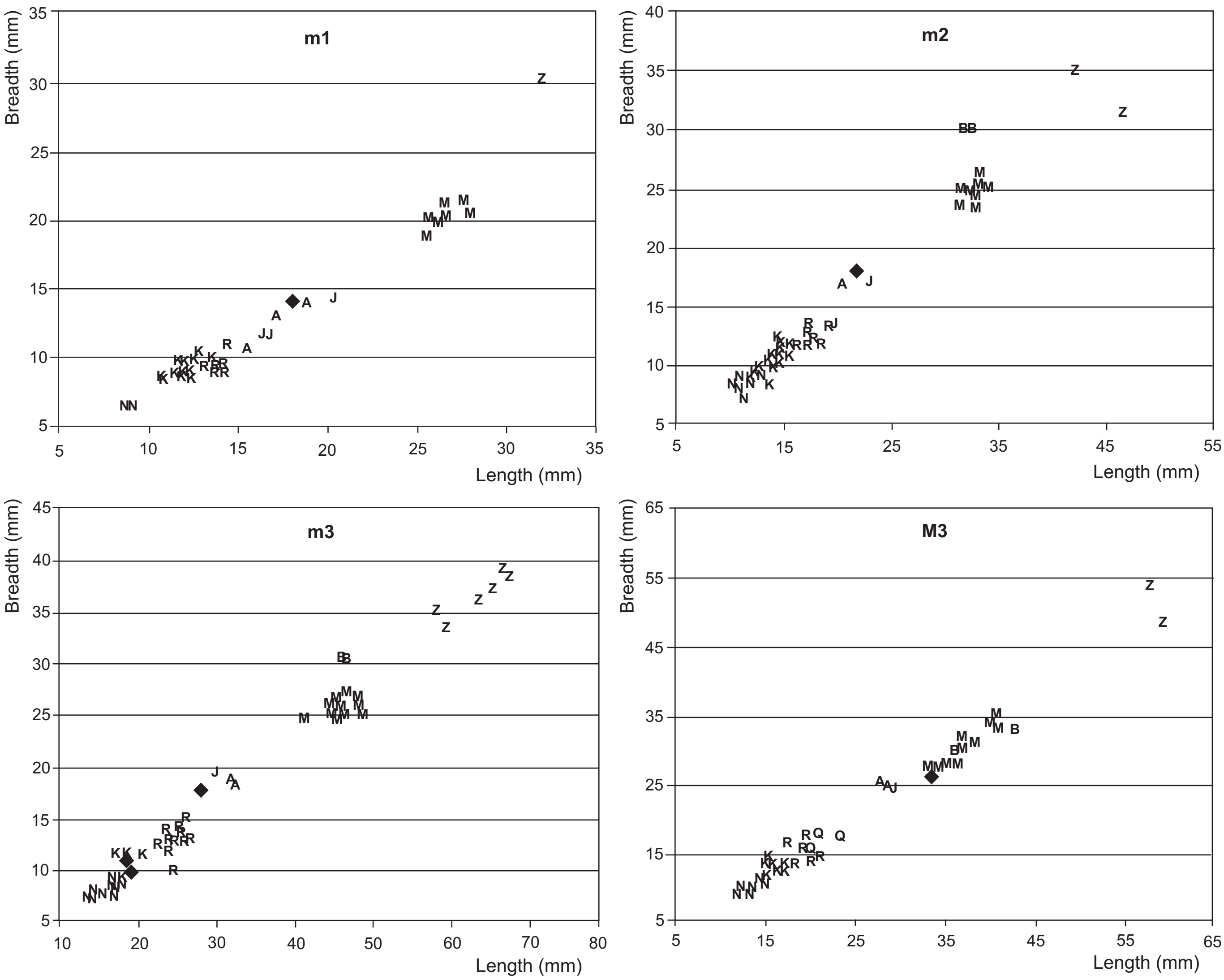

Fig. 7. Length versus breadth scatter plots of suid molars from early Miocene of Wadi Moghra (black diamond) compared with early and middle Miocene suids from other localities in Africa. Abbreviations: A, *Libycochoerus anchidens* (Van der Made, 1996); B, *Megalochoerus marymuunguae* (Van der Made, 1996); J, *Libycochoerus jeanneli* (Arambourg, 1933); K, *Nguruwe kijivium* (Wilkinson, 1976); M, *Libycochoerus massai* Arambourg, 1961; N, *Nguruwe namibensis* (Pickford, 1986); Q, *Kenyasus namaquensis* Pickford and Senut, 1997; R, *Kenyasus rusingensis* Pickford, 1986; Z, *Megalochoerus khinzikebirus* (Wilkinson, 1976).

way to obtain dates for the Moghra succession on the basis of strontium analyses (Safiya Hassan, personal communication 2008). Absolute dates cannot be obtained through potassium-argon dating because there are no volcanic deposits in the area. Paleomagnetic studies are also problematic, because the fossiliferous deposits at Moghra are highly ferruginous as a result of diagenetic processes.

Overall, information from the suids and sanitheres present at Moghra is largely compatible with other estimates for the age of Moghra, i.e., the deposits are broadly early Miocene (MN 4), and also perhaps partly early middle Miocene (MN 5) (Fig. 8). Miller (1996, 1999) estimated the age of Moghra to be early Miocene only, ca. 18 Ma, equivalent to the European MN 4, based primarily on the combined presence of the sanithere *D. africanus* (ca. 20–17 Ma) the suid *N. kijivium* (ca. 20–18 Ma) (MN 4), and the apparent absence of the large suid, *L. massai*. Sanders and Miller (2002) reached a similar conclusion (ca. 18 Ma), based on the proboscidean assemblage. In addition, the possible presence of *Libycochoerus* cf. *jeanneli* or *L.*cf. *anchidens* is compatible with an early Miocene age for the Moghra fauna, as these species have been reported from localities in Kenya ranging between ca. 17.8–17.2 Ma (Rusinga, Karungu, Moruorot, Kalodirr) (Pickford 1993). However, the occurrence of *Libycochoerus massai* at Moghra, documented here, may indicate that at least part of the Moghra stratigraphic succession extends into the base of the middle Miocene, equivalent to MN 5 in Europe. *Libycochoerus massai* is so far known from only one other locality, Gebel Zelten, Libya, part of which has been dated to ca. 17–16 Ma based on faunal correlation with East Africa and Europe (Pickford 1991a). This finding, that at least part of Moghra may extend into the early middle Mio-

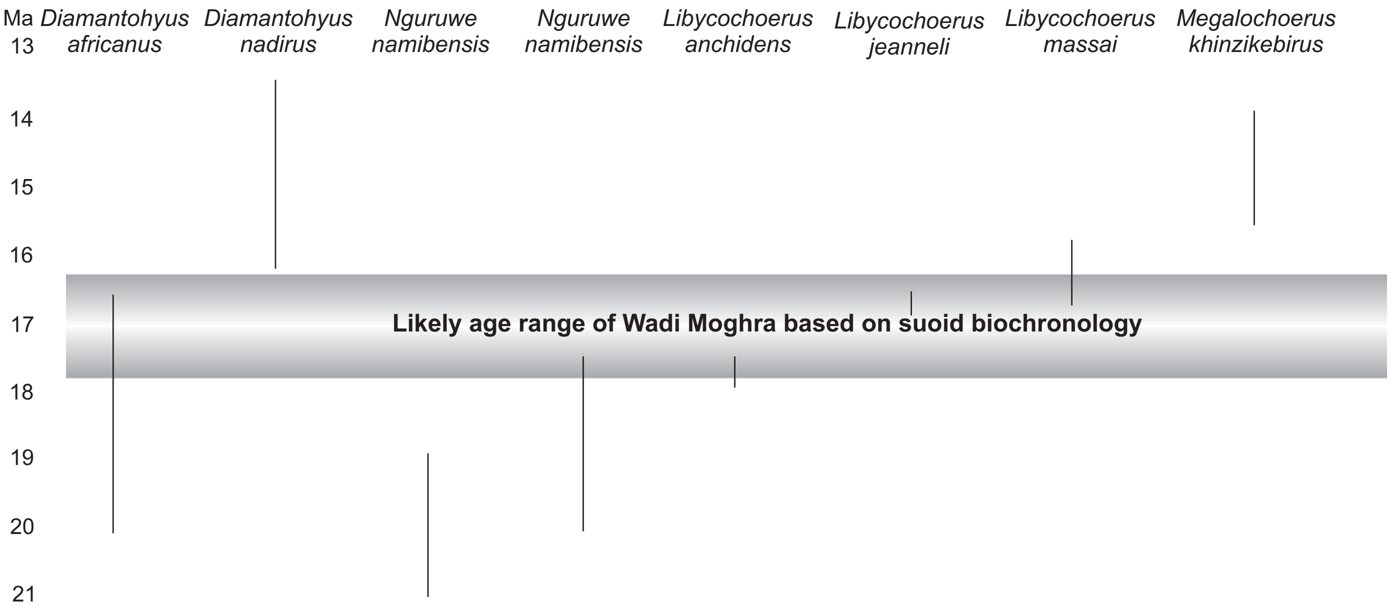

Fig. 8. Likely age range of Wadi Moghra, Egypt, based on suoid biochronology.

cene, was also the conclusion of a recent study based on the carnivores and creodonts from Moghra (Morlo et al. 2007).

Despite a general agreement of an age for the Moghra fauna of ca. 18–17 Ma, it is important to note that the Moghra deposits comprise a stratigraphic sequence of alternating near-shore continental and marine deposits that is about 230 m thick. The great thickness of the sequence at Moghra, coupled with the use of faunal correlation to date the deposits, means that estimates for the age of Moghra are probably heavily influenced by time averaging. Essentially, estimations of the age of Moghra based on biochronology rely on the assumption that the faunal elements present are contemporaneous, which is not necessarily true. The base of the Moghra deposits is not exposed, but the actual age range of the sediments could well span from the early Miocene up through the early middle Miocene (ca. 21–16 Ma), and this time range could be represented either fairly continuously or discontinuously. The same is also true for the sequence preserved at Gebel Zelten in Libya, that is, the Libyan deposits also likely represent an appreciable span of time. Pickford (1991a) has suggested that the base of the Gebel Zelten succession probably correlates with MN 3 in Europe and P II in East Africa, but there is also evidence of much younger strata (MN 5 and P III).

Paleoenvironment.—Recent work on the geology of Moghra (Miller 1999; Miller and Simons 1996; Miller et al. 2006) has documented that the deposits were formed as part of a large river system trending southeast-northwest, combined with episodic marine transgressions trending in the opposite direction. Mammal fossils at Moghra are recovered from estuarine channel deposits.

The interpretation of the Moghra paleoenvironment based on geological information is supported by paleontological evidence. The Moghra fauna has an aquatic component that includes a mix of saltwater elements (e.g., sharks, rays), and freshwater animals that can tolerate slow-moving water with a high sediment content (e.g., crocodiles, turtles, catfish). The land mammal fauna is dominated by a number of different anthracothere species, artiodactyls that were likely hydrophilic or preferred an aquatic-margin habitat, as they are found most commonly in fluviatile and lacustrine deposits (Pickford 1991b).

Recovery of a fair number of well-preserved sanithere fossils supports previous interpretations of the Moghra paleoenvironment (Miller 1996, 1999; Miller et al. 2006). Sanitheres are widely distributed across Eurasia and Africa, and in all cases where their depositional environment can be reconstructed, they appear to be preferentially preserved in swampy and littoral settings (Pickford 1984). Moreover, the fact that these animals are sometimes exceptionally well-preserved at Moghra, showing little if any evidence of post-mortem transport (e.g., fairly complete maxillae, a mandible with its peg-like incisors intact), supports the interpretation of them as autochthonous elements.

Nguruwe kijivium is widespread in East and Southern Africa and its bunodont dentition indicates an omnivorous diet. *Libycochoerus anchidens* and *L. jeanneli* possessed slightly more lophodont dentitions, but nothing like that developed in species of *Listriodon*. Both taxa were probably omnivores with minor folivorous tendencies. *Libycochoerus massai* is a large bunodont suid with extremely wide and robust upper central incisors, possibly adapted for removing edible bark from branches. The dental morphology of all these suids indicates the presence of relatively closed vegetation habitats.

Conclusions.—Four species of suoids occur at Wadi Moghra, the sanithere *Diamantohyus africanus*, and three suids: *Nguruwe kijivium*, cf. *Libycochoerus anchidens* or *L. jeanneli* and *Libycochoerus massai*. If this suoid assemblage is contemporaneous, it would indicate an age for Moghra equivalent to

Faunal Set III in East Africa, and Zone MN 4-5 in Europe, ca. 18–17 Ma. Alternatively the specimens could have been derived from a substantial thickness of strata, in which case an age ranging from ca 17.8 to about 16 Ma is possible for the Moghra succession (i.e., Faunal Sets P II to P III). As for palaeoenvironmental indications, the sanitheres are consistently found in deposits that accumulated in or near swamps and shallow lakes (Pickford 1984, 2002; Pickford and Senut 1997), and the suids suggest the presence of forest in the Moghra region at the time of deposition.

Acknowledgements

We thank Team Moghra: Mohamed Abdel Rahman Hamdan, Safiya Mohamed Ali, Mohamed Korany Ismail, Moustafa Aboud, Sayed Ahmed Nour El-Din, Khamis Farhoud, Sameh Ibrahim, Gregg F. Gunnell (University of Michigan, Ann Arbor, USA), Louise Blundell (University of Toronto, Toronto, Canada), and Courtney Nichols (Wake Forest University, Winston Salem, USA). Russell L. Ciochon (University of Iowa, Iowa City, USA) took many of the specimen photographs. Funding for this project was provided by the National Science Foundation, International Collaboration Grant (# 0403472 to E.R.M., A.N.E-B), and the Archie Fund of Wake Forest University (E.R.M.). Finally, we thank the referees Maeva Orliac (University of Montpellier, Montpellier, France) and Hiroshi Tsujikawa (Tohoku University, Sendai, Japan) for helping to improve the paper.

References

Arambourg, C. 1933. Mammifères miocènes du Turkana, Afrique orientale. *Annales de Paléontologie* 22: 121–148.

Arambourg, C. 1961. Note préliminaire sur quelques vertébrés nouveaux du Burdigalien de Libye. *Comptes Rendus Sommaires des Séances de la Société géologique de France* 1961: 107–109.

Arambourg, C. 1963. Le genre *Bunolistriodon* Arambourg, 1933. *Bulletin de la Société géologique de France* (7)5: 903–911.

Bonis, L. de, Koufos, G., and Sen, S. 1997. The sanitheres (Mammalia, Suoidea) from the Middle Miocene of Chios Island, Aegean Sea, Greece. *Revue de Paléobiologie* 16: 259–270.

Drake, R., Van Couvering, J.A., Pickford, M., Curtis, G., and Harris, J.A. 1988. New chronology for the early Miocene mammalian faunas of Kisingiri, Western Kenya. *Journal of the Geological Society of London* 145: 479–491. doi:10.1144/gsjgs.145.3.0479

Fourtau, R. 1918. *Contribution à l'Étude des Vertébrés miocènes de l'Égypte*. 121 pp. Survey Department, Ministry of Finance, Egypt Government Press, Cairo.

Fourtau, R. 1920. *Contribution à l'Étude des Vertébrés miocènes de l'Égypte. 2nd printing with additions*. 121 pp. Survey Department, Ministry of Finance, Egypt Government Press, Cairo.

Koufos, G. 2007. Suoids (Mammalia, Artiodactyla) from the Early / Middle Miocene locality of Antolios, Macedonia, Greece. *Senckenbergiana lethaea* 87: 171–186.

Miller, E.R. 1996. *Mammalian Paleontology of an Old World Monkey Locality, Wadi Moghara, Early Miocene, Egypt*. 372 pp. Unpublished Ph.D. thesis. Washington University, St. Louis.

Miller, E.R. 1999. Faunal correlation of Wadi Moghara, Egypt: implications for the age of *Prohylobates tandyi*. *Journal of Human Evolution* 36: 519–533. doi:10.1006/jhev.1998.0286

Miller, E.R and Simons, E.L. 1996. Relationships between the mammalian fauna from Wadi Moghara, Qattara Depression, Egypt, and the faunas of other African lower Miocene sites. *Proceedings of the Geological Survey of Egypt, Centennial Special Publication* 75: 547–580.

Miller, E.R., El-Barkooky, A.N., Korany, M., and Nichols, C. 2006. Paleoenvironmental reconstruction of the mammals from Wadi Moghra, Egypt. *Journal of Vertebrate Paleontology* 26: 100A.

Morlo, M., Miller, E.R., and El-Barkooky, A.N. 2007. Creodonta and Carnivora from Wadi Moghra, Egypt. *Journal of Vertebrate Paleontology* 27: 145–159. doi:10.1671/0272-4634(2007)27[145:CACFWM]2.0.CO;2

Orliac, M. 2007. *Le rôle des Listriodontinae dans la différenciation des Suidae (Mammalia): Paléoanatomie. Systématique. Phylogenie*. 705 pp. Unpublished Ph.D. thesis. L'Université Pierre et Marie Curie, Paris.

Pickford, M. 1984. A revision of the Sanitheriidae, a new family of Suiformes. (Mammalia). *Geobios* 17: 133–154. doi:10.1016/S0016-6995(84)80139-4

Pickford, M. 1986. A revision of the Miocene Suidae and Tayassuidae (Artiodactyla, Mammalia) of Africa. *Tertiary Research Special Papers* 7: 1–83.

Pickford, M. 1987. Miocene Suidae from Arrisdrift, South West Africa—Namibia. *Annals of the South African Museum* 97: 283–295.

Pickford, M. 1991a. Biostratigraphic correlation of the middle Miocene mammal locality of Jabal Zaltan, Libya. *In*: M.J. Salem, O.S. Hammuda, and B.A. Eliagoubi (eds.), *The Geology of Libya (Volume IV)*, 1483–1490. Elsevier, Amsterdam.

Pickford, M. 1991b. Revision of Neogene Anthracotheriidae of Africa. *In*: M.J. Salem, O.S. Hammuda, and M.T. Eliagoubi (eds.), *The Geology of Libya (Volume IV)*, 1491–1525. Elsevier, Amsterdam.

Pickford. M. 1993. Old World suoid systematics, phylogeny, biogeography and biostratigraphy. *Paleontologia i Evolucio* 26–27: 237–269.

Pickford, M.1995. Suidae (Mammalia, Artiodactyla) from the early Middle Miocene of Arrisdrift, Namibia: *Namachoerus* (gen. nov.) *moruoroti* and *Nguruwe kijivium*. *Comptes Rendus de l'Académie des Sciences de Paris* 320 IIa: 319–326.

Pickford. M. 1997. Lower Miocene Suiformes from the northern Sperrgebiet. Namibia. *Comptes Rendus de l'Académie des Sciences de Paris* 325 IIa: 285–292.

Pickford, M. 2002. Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda. *Comptes Rendus Palevol* 1: 213–219. doi:10.1016/S1631-0683(02)00029-5

Pickford, M. 2003. Suidae from the Middle Miocene of Arrisdrift, Namibia. *Memoirs of the Geological Survey of Namibia* 19: 291–303.

Pickford, M. 2004. Miocene Sanitheriidae (Suiformes. Mammalia) from Namibia and Kenya: systematic and phylogenetic implications. *Annales de Paléontologie* 90: 223–278.

Pickford, M. 2006. New suoid specimens from Gebel Zelten, Libya. *Estudios Geológicos* 62: 499–514.

Pickford, M. 2007. Suidae and Hippopotamidae from the Middle Miocene of Kipsaraman, Kenya, and other sites in East Africa. *Palaeontological Research* 11: 85–105. doi:10.2517/1342-8144(2007)11[85:SAHFTM]2.0.CO;2

Pickford, M. and Senut, B. 1997. Cainozoic mammals from coastal Namaqualand, South Africa. *Palaeontologica Africana* 34: 199–217.

Pickford, M. and Tsujikawa, H. 2005. A partial cranium of *Diamantohyus nadirus* (Sanitheriidae. Mammalia) from the Aka Aiteputh Formation (16–15 Ma). Kenya. *Palaeontological Research* 9: 319–328. doi:10.2517/prpsj.9.319

Sanders, W.J. and Miller, E.R. 2002. New proboscideans from the early Miocene of Wadi Moghara, Egypt. *Journal of Vertebrate Paleontology* 22: 388–404. doi:10.1671/0272-4634(2002)022[0388:NPFTEM]2.0.CO;2

Stromer, E. 1922. Erste Mitteilung über Tertiäre Wirbeltierreste aus Deutsch-SüdwestAfrika. *Sitzungsberichte der bayerischen Akademie der Wissenschaften Mathematik und Physikalische Klasse* 1921: 331–340.

Stromer, E. 1926. Reste Land- und Süsswasser Bewohnender Wirbeltiereteste aus dem Diamantefeldern Deutsch-SüdwestAfrikas. *In*: E. Kaiser (ed.), *Die DiamantenwüsteSüdwestAfrikas* 2: 107–153.

Van der Made, J. 1996. Listriodontinae (Suidae, Mammalia), their evolution, systematics, and distribution in time and space. *Contributions to Tertiary and Quaternary Geology* 33: 3–254.

Wilkinson, A. 1976. The lower Miocene Suidae of Africa. *Fossil Vertebrates of Africa* 4: 173–282.