Estudios Geológicos
enero-junio 2020, 76(1), e127
ISSN-L: 0367-0449
https://doi.org/10.3989/egeol.43542.536

Fossil suids from Bolt's Farm Palaeokarst System, South Africa: implications for the taxonomy of *Potamochoeroides* and *Notochoerus* and for biochronology

Suidos fósiles del Sistema paleokárstico de Bolt's Farm, Sudáfrica: implicaciones para la taxonomía y biocronología de Potamochoeroides *y los* Notochoerus

M. Pickford[1,*], D. Gommery[2,3,4]

[1] CR2P/UMR 7207, MNHN-CNRS-SU, Muséum national d'Histoire naturelle, CP 38, 8 rue Buffon, 75231 Paris Cedex 05, France. Email: martin.pickford@mnhn.fr; ORCID ID: http://orcid.org/0000-0002-9017-1107
[2] CR2P/UMR 7207, CNRS-MNHN-SU, Sorbonne Université, Campus Pierre et Marie Curie, T.46-56, E.5, case 104, 4 Place Jussieu, 75252 Paris cedex 05, France (e-mail dominique.gommery@sorbonne-universite.fr). ORCID ID: https://orcid.org/0000-0002-6288-1937
[3] Palaeo-Research Institute, University of Johannesburg, P.O. Box 524, Auckland Park 2006, South Africa.
[4] HRU, Plio-Pleistocene Palaeontology Section, Ditsong National Museum of Natural History, P.O. Box 413, Pretoria, 0001, South Africa.
* Corresponding author

ABSTRACT

Recent excavations at Aves Cave I (AC), Brad Pit 'A' (BPA), Milo 'A' (MA), Bridge Cave (BC) and Alcelaphine Cave (AL), in the Cradle of Humankind, Gauteng, South Africa, have yielded fossil suid remains which provide biostratigraphic information about the periods of deposition in the Bolt's Farm Palaeokarst System. At Aves Cave I there are Late Pliocene deposits which have yielded the extinct suid *Potamochoeroides hypsodon*, including skeletal elements that were poorly represented in previous collections from Bolt's Farm as well as rare remains of *Notochoerus capensis*. At Brad Pit 'A' remains of *Gerontochoerus koobiforaensis* occur. Milo 'A' and other deposits have yielded remains of the suid *Metridiochoerus andrewsi* that indicate a later phase of endokarst sedimentation (Early Pleistocene). The *Panthera* Spot at Bridge Cave has yielded articulated foot bones of a suid, provisionally identified as *Phacochoerus modestus* and which suggest an Early Pleistocene age for this infilling. The augmented samples of suids from Bolt's Farm invite detailed comparisons with the Suidae from Makapansgat which permits a review of the taxonomy of *Notochoerus* and *Potamochoeroides*. It is shown that both genera are Suinae, and could be synonyms. Comparisons are also made with Plio-Pleistocene suids from Malawi and Namibia.

Keywords: South Africa; Suidae; Taxonomy; Comparative anatomy; Plio-Pleistocene.

RESUMEN

Las recientes excavaciones en Aves Cave I (AC), Brad Pit 'A' (BPA), Milo 'A' (MA), Bridge Cave (BC) y Alcelaphine Cave (AL), en la Cuna de la Humanidad, Gauteng (Sudáfrica), han proporcionado restos fósiles de suidos que

---

Recibido el 18 de marzo de 2019; Aceptado el 2 de septiembre de 2019; Publicado online el 15 de junio de 2020

Citation / Cómo citar este artículo: Pickford, M. & Gommery, D. (2020). Fossil suids from Bolt's Farm Palaeokarst System, South Africa: implications for the taxonomy of *Potamochoeroides* and *Notochoerus* and for biochronology. Estudios Geológicos 76(1): e127. https://doi.org/10.3989/egeol.43542.536

aportan información bioestratigráfica sobre los intervalos de sedimentación del Sistema Paleokárstico de Bolt's Farm. En Aves Cave I, Plioceno superior, se han encontrado restos del suido extinto *Potamochoeroides hypsodon*, incluyendo elementos esqueléticos que estaban poco representados en las colecciones previas de Bolt's Farm, así como escasos restos de *Notochoerus capensis*. En Brad Pit 'A' se encontraron restos de *Gerontochoerus koobiforaensis*. En Milo 'A' y en otros depósitos se han hallado restos del suido *Metridiochoerus andrewsi* que indican la existencia de una fase posterior de sedimentación endokárstica (Pleistoceno inferior). En Panthera Spot en Bridge Cave se han encontrado huesos articulados del pie de un suido, determinados provisionalmente como *Phacochoerus modestus*, que indican una edad Pleistoceno inferior para este relleno. El aumento de la muestra de suidos de Bolt's Farm invita a realizar comparaciones detalladas con los de Makapansgat lo que permite una revisión de la taxonomía de *Notochoerus* y *Potamochoeroides*. Se demuestra que ambos géneros son Suina y podrían ser sinónimos. También se han podido realizar comparaciones con los suidos del Plio-Pleistoceno de Malawi y Namibia.

Palabras clave: Sudáfrica; Suidae; Taxonomía; Anatomía comparada; Plio-Pleistoceno.

Introduction

Fossil suids were first found at Bolt's Farm in the 1930's (Broom, 1937, 1948; Shaw, 1938) and have been collected sporadically since then (Cooke, 1993; Pickford & Gommery, 2016). Four suid species have been recorded from the Bolt's Farm Palaeokarst System (Table 1) comprising two assemblages separated in time: a Late Pliocene fauna with *Notochoerus capensis* and *Potamochoeroides hypsodon* (ca 3.0-2.7 Ma) and an Early Pleistocene one with *Metridiochoerus andrewsi* and *Phacochoerus modestus* (ca 1.8 Ma).

Recent excavations at Aves Cave I have yielded additional suid specimens, several of juvenile individuals, all of which can be attributed to *Potamochoeroides hypsodon*. Older deposits at Brad Pit 'A' have yielded specimens of *Gerontochoerus koobiforaensis* and younger deposits at Milo 'A', Bridge Cave and Alcelaphine Cave (Pickford & Gommery, 2016) have yielded remains of the large suid with hypsodont molars, *Metridiochoerus andrewsi*.

The aim of this contribution is to describe and interpret the new suid fossils from the Bolt's Farm Palaeokarst System, to document the juvenile dentition and to refine the biostratigraphic implications of the fossils. Detailed morphometric comparisons are made with the Makapansgat Suidae. A discussion on the systematic status of the genus *Notochoerus* is extended (adding to the recent work of Pickford, 2013), which indicate that it is a suine rather than a tetraconodont as thought by most authors since the late 1950's (Leakey, 1958; Ewer, 1958a; Cooke, 1976; Harris & White, 1979; Geraads & Bobe, 2017; Lazagabaster *et al*. 2018). The new analysis indicates that *Potamochoeroides* and *Notochoerus* are potentially synonymous.

Geological and Biochronological Context

The Bolt's Farm Palaeokarst System (Pickford & Gommery, 2016) is part of a regional karst network developed in dolomitic country rock, outcrops of which are widespread in Gauteng, South Africa (Sénégas *et al*., 2002; Thackeray *et al*., 2008). The Gauteng karst infillings are known for the diverse palaeoanthropological discoveries which have been made in them (Herries *et al*. 2013), and for other mammals found alongside the hominids (Sénégas & Avery, 1998). Fossil suids are reasonably well

Table 1.—Fossil suids from the Bolt's Farm Palaeokarst System, Gauteng, South Africa (Localites in bold letters represent new material described herein).

Taxon	Age	Localities	Reference
Phacochoerus modestus	ca 1.8 Ma	Bolt's Pit 3, **Bridge Cave (*Panthera* Spot)**	Cooke, 1993; Pickford & Gommery, 2016, This paper
Metridiochoerus andrewsi	ca 1.8 Ma	Bolt's Workings, **Milo 'A', Bridge Cave, Alcelaphine Cave**	Shaw, 1938; Broom, 1948; Ewer, 1956, 1958a, 1958b; Cooke, 1993; Pickford & Gommery, 2016; This paper
Notochoerus capensis	ca 3.0-2.6 Ma	Aves Cave I	Pickford & Gommery, 2016
Potamochoeroides hypsodon	ca 3.0-2.6 Ma	Bolt's Pit 14, **Aves Cave I**	Cooke, 1993; Pickford & Gommery, 2016; This paper
Gerontochoerus koobiforaensis	ca 3.7 Ma	Brad Pit 'A'	Forthcoming paper

represented, and have proven to be useful in two domains: biochronology and palaeoenvironmental studies (Pickford & Gommery, 2016).

The Bolt's Farm fossil record, and that of Gauteng in general, indicates that karst processes were not uniform in intensity or locale through geological time, but were more intense during some periods, less active during others, and, as is usual in karst systems, the zones undergoing karst processes shifted laterally and vertically as well as partly reworking deposits in the pre-existing networks (Fig. 1). In the last case, deposits may contain composite faunas from two time periods, as for example at Brad Pit. The fossiliferous deposits that accumulated in the karst network can thus be highly complex, with cut-and-fill structures, decalcification of breccias, re-cementing of decalcified breccias, and the juxtaposition of young and old breccias is common. Differences of opinion in the literature reveal that sorting out the sequence of events has been arduous and often controversial, but biochronology has provided valuable constraints, and among the fossil groups that have yielded important sequence and age data are the Suidae (Cooke, 1993, 1994, 2005; Pickford, 2006, 2012, 2013a, 2013b; Pickford & Gommery, 2016).

The oldest recognised endokarst deposits in the Bolt's Farm Palaeokarst System occur at Waypoint 160, aged ca 4.5 Ma (Sénégas, 2000, 2004; Sénégas & Avery, 1998) followed by Brad Pit 'A' aged ca 3.7 Ma, followed by Aves Cave I and related deposits (Pit 14) aged ca 2.6 Ma - 3 Ma, followed, after a break in deposition, by deposits aged ca 1.8 Ma (Pit 1, Pit 3, Milo 'A', Bridge Cave *Panthera* Spot). There are younger deposits in the same region such as the Rising Star Cave infillings (ca 0.25 Ma) (Dirks *et al*. 2017) close to Bolt's Farm, but over most of the karst system, there is little depositional activity occurring today (an exception comprises the deeper parts of Baboon Cave where karst sedimentation processes are still active). A summary of the chronology of the sites is provided in Figure 1.

Abbreviations and dental nomenclature

AC - Aves Cave I; AL - Alcelaphine Cave; BC - Bridge Cave; BPA - Brad Pit 'A'; BPI - Bernard Price Institute, University of the Witwatersrand, Johannesburg (Now ESI); DNMNHP- Ditsong National Museum of Natural History, Pretoria; ESI - Evolution Studies Institute, University of the Witwatersrand, Johannesburg; MA - Milo 'A'; NHMUK - Natural History Museum of the United Kingdom, London; PEM - Port Elizabeth Museum; TM - Transvaal Museum, Pretoria (Now DNMNHP).

The dental nomenclature employed in this paper is based on Hünermann (1968) modified by Pickford (1988) and Pickford (2013a).

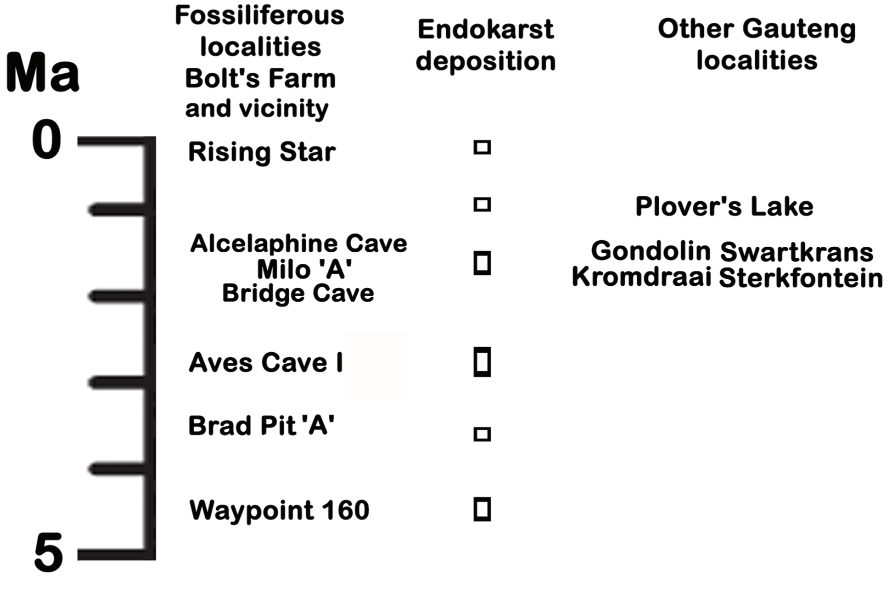

Figure 1.—Succession of endokarst deposits at Bolt's Farm Palaeokarst System and nearby areas in Gauteng. Suid fossils are common in the Late Pliocene and Early Pleistocene deposits, but are rare to absent in other time slots.

Systematic descriptions

Family Suidae Gray, 1821

Genus *Potamochoeroides* Dale, 1948

Type species.- *Potamochoeroides hypsodon* Dale, 1948

Species *Potamochoeroides hypsodon* Dale, 1948

Holotype.- ESI (BPI) M 303, right maxilla containing P3/-M3/.

Type locality and age.- Makapansgat, South Africa, Late Pliocene.

New material.- Excavations at Aves Cave I between 2015, 2017 and 2018, yielded a number of suid fossils, dominated by isolated teeth and postcranial bones, but also an adult maxilla containing three cheek teeth. Among this material, there are several deciduous teeth, especially incisors (9 specimens: Table 2), a canine, a D2/ two D3/s and a D4/, which provide precious information concerning the deciduous dentition in *Potamochoeroides*, revealing that it was similar to *Potamochoerus* Gray, 1854, and *Dasychoerus* Gray, 1873, in retaining the full complement of deciduous incisors and canines, and rather different from *Phacochoerus* in which the upper deciduous and permanent dentition lacks the lateral incisors (Fig. 2). The deciduous incisor battery of *Metridiochoerus* has not been reported, but the adults possess lower incisors like those of *Phacochoerus* (which often shed the permanent teeth (Pickford, 2013a).

Descriptions

The list of referred material is provided in Table 2.

Deciduous dentition

AC 431 is a right DI1/ with light wear along the distal crest (Fig. 2). The crown is weakly bilobate, mesiodistally elongated, labio-lingually compressed and low crowned. The crown axis is oblique to the root. AC 420 is a left DI1/, also bilobate, and with an enamel extension on the labial side of the distal lobe. These teeth look similar to their counterparts in the extant Bush Pig (*Potamochoerus*). AC 210 is a right DI2/ with a clear wear facet along the distal crest. It is mesio-distally more elongate than the DI1/s with greater curvature between the crown and the root. AC 320 is a left deciduous upper canine similar to its counterpart in the Bush Pig. It is basically a simple peg-like tooth with a labio-lingually compressed crown set on a long root. The wear is apical.

The left D2/ is in a maxilla fragment (AC 536). Anteriorly there is part of an alveolus for the P1/. The crown of the D2/ has a prominent main cusp on the buccal side of the tooth accompanied by a low disto-lingual cusplet. The precrista of the main cusp terminates at a low anterior accessory cusplet from which two brief cingular elements extend buccally and lingually. The post-crista of the main cusp extends to the distal cingulum which curves a short way onto the buccal side of the crown, and lingually it blends into the disto-lingual cusplet. There is a deep fovea between the mesial edge of the disto-lingual cusplet and a crest that descends from the apex of the main cusp towards the lingual side of the crown. The latter crest is separated from the anterior part of the main cusp by a vertical groove. There are two roots and the enamel is thin.

An unworn D3/ in the collection (AC 512) is informative about the crown morphology of this tooth, the other specimens being deeply worn (Fig. 2). It possesses three main cusps arranged in a triangle, one cusp anteriorly and two posteriorly. The anterior cusp (paracone) has a prominent lingual ridge in the place of the protocone, which curves round to join the mesial cingulum, thereby closing off a small mesial fovea. There is a swollen parastyle on the mesio-buccal corner of the tooth. It has swollen pre- and post-cristae on the buccal edge of the cusp, and a prominent groove (Furche) posteriorly. The posterior loph of the tooth is comprised of the metacone and hypocone as in permanent teeth, and there are pre- and post-cristae on the metacone forming a mesostyle and metastyle respectively. In the centre of the crown there is a median accessory cusplet close to the endo-crista of the hypocone. The distal cingulum extends from the metastyle to the base of the hypocone, via a small posterior accessory cusplet. Between the posterior accessory cusplet and the hypocone, there is a small, shallow distal fovea.The pre-hypocrista blends into a short lingual cingulum which walls off a small but deep fovea between the median accessory cusplet and the lingual cingulum. There is a small fovea on the buccal side of the median accessory cusplet, but it is open to the buccal side. Where it is unworn, the enamel surface of this tooth is coarsely wrinkled.

AC 415 is a deeply worn left D3/, with three roots (one anteriorly, two posteriorly) (Fig. 2). The only structures remaining in the occlusal surface are the depths of the foveae either side of the median accessory cusplet, and the basal remnants of the parastyle and metastyle.

The D4/ (AC 537) is moderately worn and is missing some chips of the crown mesially. The enamel is thin and the roots have been partly resorbed. The rear lobe of the tooth is slighly broader than the mesial lobe. There are four main cusps, with deep Furchen, and well-developed

Table 2.—List of fossils attributed to *Potamochoeroides hypsodon* collected at Aves Cave I, Bolt's Farm Palaeokarst System between 2015 and 2018 curated at the DNMNHP.

Dento-gnathic remains		Post-cranial skeleton	
Catalogue	Specimen	Catalogue	Specimen
AC 210	Left DI2/	AC 112	Abaxial 2nd phalanx
AC 320	Left DC1/	AC 187	Axial 1st phalanx
AC 361	Left c/1 fragment	AC 343	Abaxial metapodial
AC 370	Right c/1 fragment	AC 360	Left Mt III
AC 371	Left C1/	AC 363	Right Mc III (two fragments)
AC 415	Left D3/	AC 364	Axial 1st phalanx
AC 420	Left DI1/	AC 365	Radius distal epiphysis
AC 431	Right DI1/	AC 367	Abaxial 1st phalanx
AC 467	Left I1/	AC 407	Axial 1st phalanx
AC 490	Left C1/ fragment	AC 414	Axial 3rd phalanx
AC 500	Left c/1 fragment	AC 425	Distal left humerus
AC 502	Right C1/ fragment	AC 430	Axial 3rd phalanx
AC 506	Right c/1 fragment	AC 448	Axial distal metapodial
AC 512	Left D3/	AC 460	Proximal radius epiphysis
AC 515	Left maxilla with P4/-M2/	AC 462	Left talus fragment
AC 529	Right M2/	AC 480	Left navicular
AC 526	Right i/2	AC 482	Axial 3rd phalanx
AC 531	Left m/2	AC 484	Right distal ulna epiphysis
AC 532	Left m/1	AC 495	Left talus fragment
AC 533	Right M1/ fragment	AC 521	Conjoined abaxial phalanges 1 and 2
AC 534	2 fragments d/4	AC 542	Left calcaneum
AC 535	Right I1/	AC 543	Right Mc IV
AC 536	Left D2/ in maxilla fragment	AC 544	Metapodial
AC 537	Left D4/	AC 545	Axial ungual phalanx
AC 538	Left M1/	AC 559	Distal end metapodial
AC 539	Left P3/ rear half	AC 562	Left proximal end MC IV
AC 540	Left M2/	AC 578	Axial 2nd phalanx
AC 541	Tooth fragments	AC 610	Left talus
AC 542	Left M3/ fragment		
AC 548	Left d/4		
AC 560	Left m/2		
AC 564	Left m/2		
AC 565	Left M1/		
AC 570	Right i/1		
AC 589	Right m/1		
AC 597	Right M3/		
AC 598	Upper incisor		
AC 602	Left m/2		

median and posterior accessory cusplets. The anterior accessory cusplet is damaged. There is a tall prominent pillar in the lingual end of the median transverse valley.

AC 548 is a left d/4 just entering wear (Fig. 3). It is constructed of three lophids, each of two cusps, as is usual in suids, and there are accessory cusplets in the mid-line of the tooth between each of the lophids, and there is in addition a posterior accessory cusplet with a distinct distal cingulum behind it. The accessory cusplets are almost as tall as the main cusps. An interesting feature of this

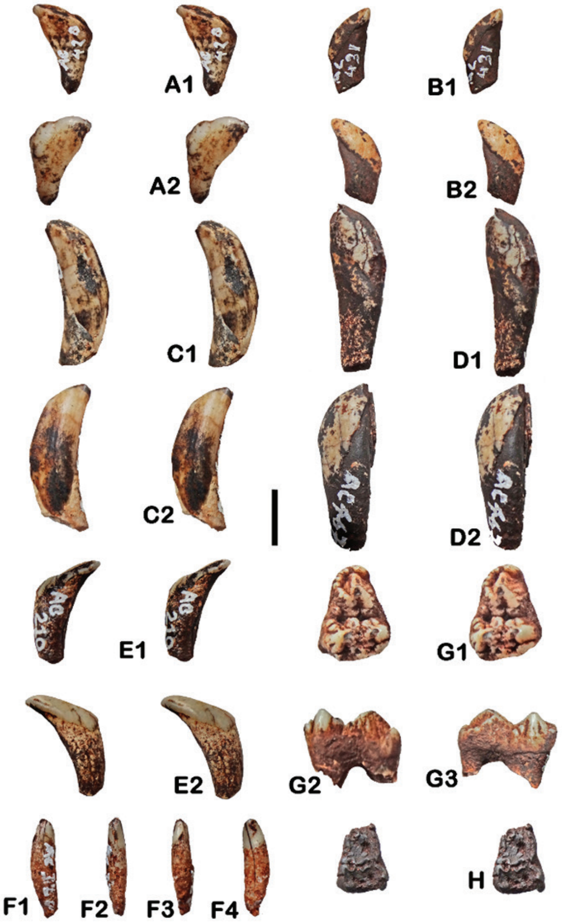

Figure 2.—Isolated teeth of *Potamochoeroides hypsodon* from Aves Cave I, Bolt's Farm Palaeokarst System. A) AC 420, left DI1/ (A1 - stereo lingual view, A2 - stereo labial view), B) AC 431, right DI1/ (B1 - stereo lingual view, B2 - stereo labial view), C) AC 526, right i/2 (C1 - stereo lingual view, C2 - stereo labial view), D) AC 467, left I1/ (D1 - stereo lingual view, D2 - stereo labial view), E) AC 210, right DI2/ (E1 - stereo lingual view, E2 - stereo labial view), F) AC 320, left DCI/, (F1 - lingual, F2 - mesial, F3 - distal, F4 - buccal views), G) AC 512, left D3/ (G1 - stereo occlusal view, G2 - buccal, G3 - lingual views), H) AC 415, left D3/ (stereo occlusal view) (scale: 10 mm).

tooth is that the pre- and post-cristids of the main cusps are beaded, as is the distal cingulum.The Furchen are relatively shallow and the enamel is lightly wrinkled.

Permanent dentition

AC 467 is a moderately worn left I1/ missing small chips of enamel mesially and distally (Fig. 2). The mesial half of the crown is labio-lingually broad, but the posterior half is compressed, the two halves being defined lingually by a longitudinal groove. Wear is apical and along the distal crest.

AC 535 is a lightly worn right I1/. The tooth has an incision apically dividing the crown into mesial and distal moieties. The distal part has a finely beaded apical edge. There is a discontinuous lingual cingulum, with prominent denticles in the middle and the distal part.The buccal surface has a broad, shallow furrow descending from the apical incision towards the root which gives the tooth a gently concave labial surface. In mesial view the crown is distinctly curved from root to apex. The root is small compared with the dimensions of the crown.

AC 371 is an almost complete, but unworn upper left canine (Fig. 11). The mesial profile is evenly curved, slightly more than a semi-circle. The distal side, in contrast, and unusual in a suid context, is comprised of a curved apical part adjoining an almost straight intermediate part between the apex and the root. There is a postero-dorsal groove extending from the root towards the crown but fading out in the apical third of the tooth. The palatal aspect of the crown shows coarse longitudinal wrinkles.

AC 539 is the rear half of the germ of the left P3/. Preserved is the rear half of the main cusp which is tall and the low disto-lingual cusp. The post-crista of the main cusp is beaded, and is interposed between the main cusp and the distal cingulum. There is a deep fovea between the disto-lingual cusp and the beaded post-crista of the main cusp.

AC 515, a left maxilla of a fully adult individual, retains the P4/ in light wear, the deeply worn M1/ and

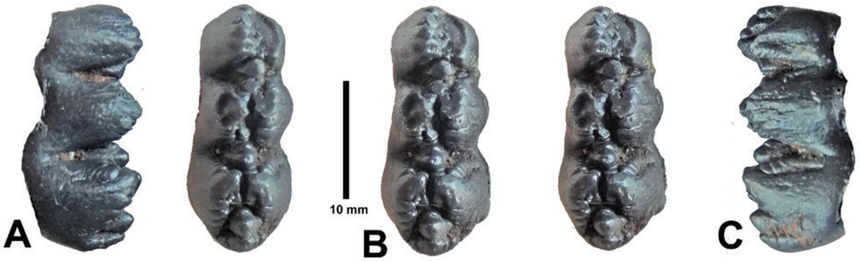

Figure 3.—AC 548, left d/4 from Aves Cave I, Bolt's Farm (cast) attributed to *Potamochoeroides hypsodon*. A) buccal view, B) stereo occlual views, C) lingual view (scale: 10 mm).

the moderately worn M2/ (Fig. 4). This stage of development corresponds to a two-year-old Wild Boar (*Sus scrofa* Linnaeus, 1758; Ide et al. 2013).

The P4/ has two main cusps supported on four roots, two buccal roots that are separated from each other at cervix, and two lingual ones which are fused beneath cervix, but which bifurcate about half the height of the root. The mesio-buccal root has a slight central extension hinting at the development of a fifth root anteriorly, poorly evident in this tooth, but present in the upper molars. The buccal roots are taller than the lingual ones, and their apices bend slightly distally. The paracone is larger than the protocone from which it is separated by a deep longitudinal central valley. There is a low parastyle at the mesial end of the pre-paracrista, which blends into the mesial cingulum. The post-paracrista is swollen. There are two vertical enamel ridges (sagittal cusplets) on the lingual aspect of the paracone, descending into the central valley, not blocking it, but imparting a zig-zag outline to the valley. The protocone is lower than the paracone, and is about half its area. Its pre- and post-cristae are swollen and blend into the mesial and distal cingula, thereby forming a wall to the central valley. Lingually, the protocone has a well-formed, swollen lingual cingulum.

The M1/ in this maxilla is deeply worn, to the stage that only the deepest parts of the foveae and Furchen are preserved. In lateral view, the roots are observed to curve distally. The M2/ is moderately worn, but the main cusps and accessory cusplets can be discerned. The mesio-lingual part of the protocone is missing, but the distal part is preserved and shows the post-protocrista and endo-protocrista well separated from each other by Furche N° 3 (Pickford & Gommery, 2016). The paracone is mesio-distally shorter than the protocone and Furchen N° 4 and N° 6 are deep and N° 5 is very shallow as is usual in suids. The anterior accessory cusplet is damaged; its mesial surface has risen upwards above the occlusal surface. Its distal part which is in the correct position, but slightly damaged, separates the mesial parts of the protocone and paracone. The median accessory cusplet is irregularly oval and does not separate the protocone from the paracone, although its distal half separates the mesial parts of the metacone and hypocone from each other. The metacone and hypocone lean distally such that there is a distinct overhang of the

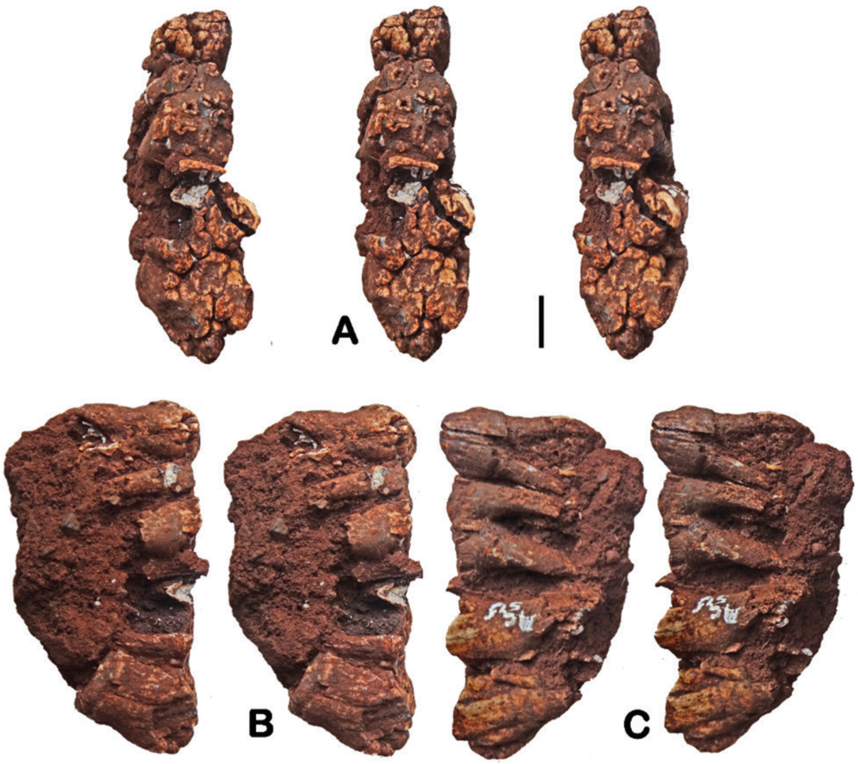

Figure 4.—*Potamochoeroides hypsodon* from Aves Cave I, Bolt's Farm Palaeokarst System. AC 515, left maxilla with P4/-M2/ (A - stereo occlusal triplet, B - stereo lingual view, C - stereo buccal view (scale: 10 mm).

distal part of the occlusal surface of the crown above the cervical part. Measurement of the length of the occlusal surface gives 25 mm, whereas at cervix the length of the tooth is 21.5 mm, a difference of 5.3%. The metacone and hypocone are ovoid in occlusal plan, with deep mesial and distal Furchen (N°s 7, 9, 10 and 12) and weaker inner Furchen (N°s 8 and 11). The posterior accessory cusplet is large and leans distally to a marked degree, contributing largely to the distal overhang of the crown. There are pillars of enamel in the lingual and buccal ends of the transverse valley, and the distal cingulum also forms low pillars on both sides of the posterior accessory cusplet.

AC 529 is a heavily worn right M2/ with only the deepest parts of the foveae and Furchen remaining (Fig. 5). The foveae are filled with cementum and the buccal and lingual walls of the crown are intensely wrinkled with fine enamel ridges (resembling the wrinked enamel of giraffid molars). In mesial view there are three roots, two main roots beneath the protocone and paracone respectively, and a short root slightly to the buccal side of the midline. In medial and lateral views the roots sweep slightly distally. In lingual view, the cervix of the protocone is horizontal and then takes a step rootwards beneath the hypocone where the cervix is still horizontal. In buccal view, in contrast, the cervix is straight, but is angled with respect to the occlusal surface, descending rootwards from mesial to distal. Similar « stepped » cervical profiles occur in other hypsodont suid teeth, such as those of *Metridiochoerus* and *Notochoerus*, for example (Pickford, 2013b). This tooth could well represent the same individual as AC 257, a right M1/ described by Pickford & Gommery (2016). The stage of wear and the interstitial contact are compatible with each other.

AC 531 is a lightly worn left M2/ lacking parts of the enamel walls on the two buccal cusps. The tooth shows strongly overhanging anterior and posterior accessory cusplets, the maximum length of the crown being 30.7 mm versus a length of only 18.4 mm at cervix. The enamel is lightly wrinkled, somewhat in the style of giraffid molars.

AC 597 is a right M3/ with light wear on the anterior loph. The height of the crown is about 29 mm, the basal length is 46 mm and the breadth of the anterior loph is 28.4 mm. The tooth is as tall as it is broad, and thus can be considered moderately hyposodont (Fig. 6). The crown is comprised of four main cusps as is usual in suids, and it has a tall and capacious, beaded anterior cingulum and a short talon comprised of pillar-like cingular structures. The latter is comprised of three pillars that fuse together well above the cervix of the tooth. The posterior accessory cusp is subdivided apically into three pillars. The lingual basal pillar between the protocone and hypocone is comprised of two separate tall pillars, the anterior one applied closely to the protocone, the posterior one adhering to the hypocone.

AC 532 is a left m/1 germ. It had four main cusps and prominent, tall anterior, median and posterior accessory cusplets, a beaded mesial cingulum in front of the anterior accessory cusplet and a distal cingulum behind the posterior accessory cusplet. The Furchen are deep and the pre- and post-cristids of the main cusps are beaded, being subdivided into one or two low pillar-like structures with light grooves on the sides of the tooth, fading out towards the cervix. The

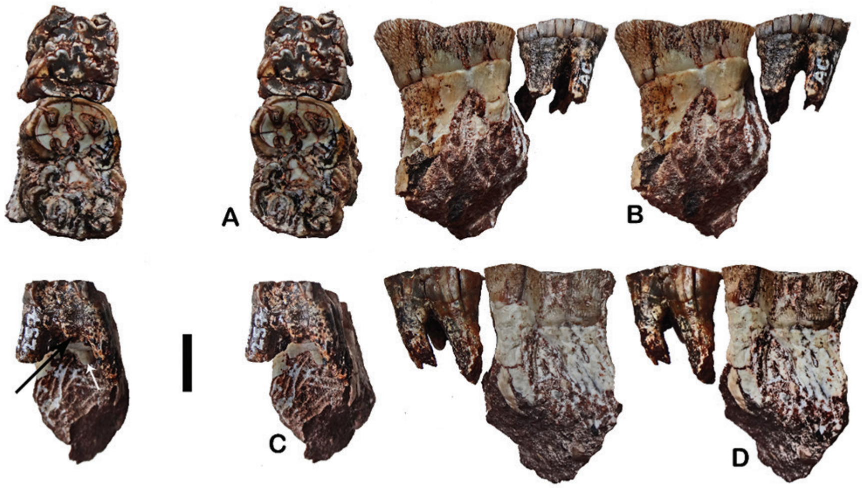

Figure 5.—AC 271, right M1/, and AC 529, right M2/ from Aves Cave I, Bolt's Farm Palaeokarst System, possibly representing a single individual. A) stereo occlusal view, B) stereo buccal view, C) stereo anterior view, arrows show small fifth root (black arrow for M1/, white arrow for M2/), D) stereo lingual view (scale: 10 mm).

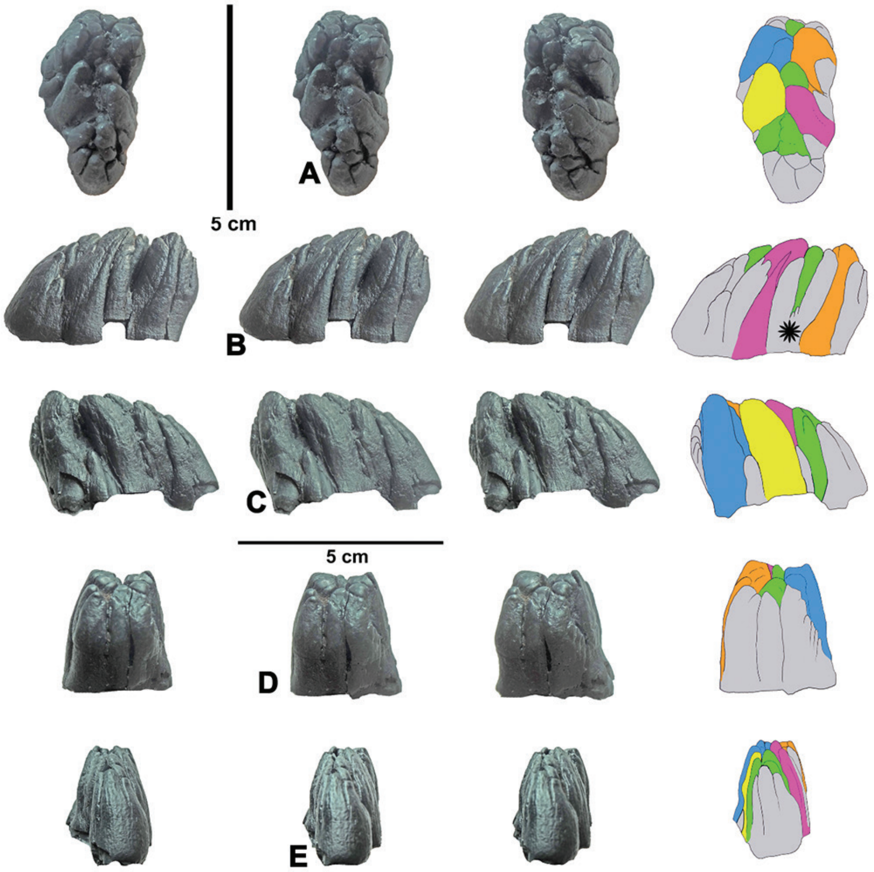

Figure 6.—AC 597, cast of right M3/ from Aves Cave I, Bolt's Farm, attributed to *Potamochoeroides hypsodon*. Stereo triplet views and interpretive drawing, illustrating the height of the cingular structures. A) occlusal, B) lingual, C) buccal, D) mesial, E) distal. Grey - cingulum and cingular pillars, Green - anterior, median and posterior accessory cusplets, Brown - protocone, Blue - paracone, Yellow - metacone, Red – hypocone. The star symbol in (B) shows two tall basal pillars on the lingual side of the tooth adhering to the protocone and hypocone respectively (scale: 5 cm).

anterior accessory and posterior accessory cusplets and their associated cingulids overhang the cervix, such that the occlusal surface is appreciably longer than the cervical part of the tooth. The enamel is lighty wrinkled, and in this specimen there are signs of cementum in the foveae.

Discussion

Pickford & Gommery (2016) described a juvenile maxilla (AC 231) with the milk teeth and first permanent molar in occlusion and the M2/ incompletely formed within its crypt, indicating an individual of about 8 months of age (using an extant *Sus scrofa* developmental clock (miniature pig) Ide *et al.*, 2013). They also described a lower milk incisor (AC 359) and fourth deciduous molar (AC 1) of an individual aged ca 5 months when it died.

The new fossils from Aves Cave I include several deciduous upper incisors and a canine as well as two examples of D3/ (Table 3) one of which is lightly worn at the cusp apices suggesting an individual of ca 3 months age, the other is deeply worn, indicating an older subject ca 11 months of age. There are also several fragments of upper and lower canines, some of which were incompletely formed at the time of death. An adult maxilla in the new collections (AC 515) is from an individual about 2 years old, and a heavily worn M2/ belongs to an even older individual, probably 2.5 to 3 years of age.

Post-cranial skeletal elements

Several additional suid post-cranial skeletal elements have been collected from Aves Cave I, all of them attributable to *Potamochoeroides hypsodon*

Table 3.—Measurements (in mm) of teeth of *Potamochoeroides hypsodon* from Aves Cave I, Bolt's Farm Palaeokarst System (measurements are taken at the cervix except those in brackets which are taken at the occlusal surface) (e – estimated measurement).

Catalogue	Tooth	Mesio-distal length	Bucco-lingual bredth
AC 431	DI1/ right	13.1	4.1
AC 420	DI1/ left	11.7	3.9
AC 210	DI2/ right	14.0	4.5
AC 320	DC1/ left	4.4	3.7
AC 536	D2/ left	9.5	6.0
AC 415	D3/ left	12.1	8.8
AC 512	D3/ left	13.1	9.5
AC 537	D4/ left	15.4	12.7
AC 467	I1/ left	10.2	7.1
AC 535	I1/ right	11.0	6.7
AC 598	I2/ or I3/	12.1	4.4
AC 371	C1/ left	22.0	18.1
AC 539	P3/ left	--	9.7
AC 515	P4/ left	13.1	15.7
AC 538	M1/ left	15.0 (21.5)	16e
AC 515	M1/ left	18.8	17.1
AC 515	M2/ left	22.3 (32.6)	21.8
AC 529	M2/ right	21.5 (25.0)	19.7
AC 540	M2/ left	--	21.6
AC 531	M2/ left	21.4 (30.4)	--
AC 565	M1/ left	18.0	14.0
AC 597	M3/ right	46.0	28.4
AC 533	di/2 right	4.3	5.2
AC 534a	d/4	--	10.5
AC 534b	d/4	--	12.7
AC 548	d/4 left	21.8	9.8
AC 570	i/1 right	6.0	6.4
AC 526	i/2 right	8.2	7.0
AC 532	m/1 left	25.0 (28.9)	14.7
AC 589	m/1 right	20	12.4
AC560	m/2 left	29	18
AC 602	m/2 left	28.0	16
AC 564	m/2 left	28.4	18.3

on the basis of the dimensions (Table 4; Figs 7-10). Most of them are similar to specimens already dealt with by Pickford & Gommery (2016) but a distal radius and ulna provide new information which is relevant to understanding some aspects of locomotion in this suid. A distal radius described by Pickford & Gommery (2016) is damaged and abraded which made it difficult to interpret its functional morphology correctly. The new specimens are in relatively good condition, although the peri-ulnar part of the radius is missing. There are also two partial tali and a navicular in the new collections, but these are typically suid in morphology and do not yield any surprises about locomotion in *Potamochoeroides*.

The fragment of distal radius AC 365, has a deep fossa for the cranial aspect of the first radial carpal bone, as in *Phacochoerus* and *Metridiochoerus* (Pickford, 2013b) unlike the shallower fossa that occurs in *Potamochoerus* (Fig. 7) The articular facet for the first radial carpal bone is damaged, but the

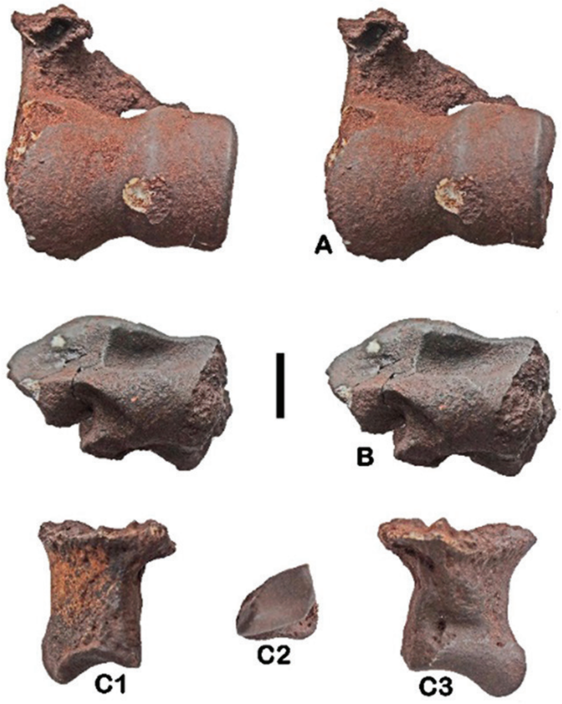

Figure 7.—Forelimb elements of *Potamochoeroides hypsodon* from Aves Cave I, Bolt's Farm Palaeokarst System. A) AC 425, distal end of left humerus, stereo cranial view, B) AC 365, distal end of right radius, stereo distal view, C) AC 484, distal epiphysis of right ulna (C1 - cranial view, C2 - distal view, C3 - caudal view) (scale: 10 mm).

articular facet for the second radial carpal extends well onto the posterior aspect of the epiphysis, indicating the possibility of hyperflexion of the carpal complex as in *Phacochoerus* and *Metridiochoerus*. The distal ulnar articulation also indicates that hyperflexion of the ulnar carpal joint was possible. From this it is deduced that *Potamochoeroides hypsodon* could practice carpogrady, in opposition to the suggestion by Pickford & Gommery (2016) that it probably could not.

The only other postcranial elements that warrant mention are conjoined abaxial first and second phalanges AC 521, which are strongly fused together (Fig. 10). Whether the fusion of these bones was a usual feature in the species, or whether it represents a pathological condition is not known, but is probably the latter.

Reproduction

The observation that there are almost as many juvenile as adult suid fossils at Aves Cave I suggests that *Potamochoeroides hypsodon* could have been breeding close to the caves and either lived within the cavities or may have been carried into the caves as prey items by carnivores. Some of the individuals

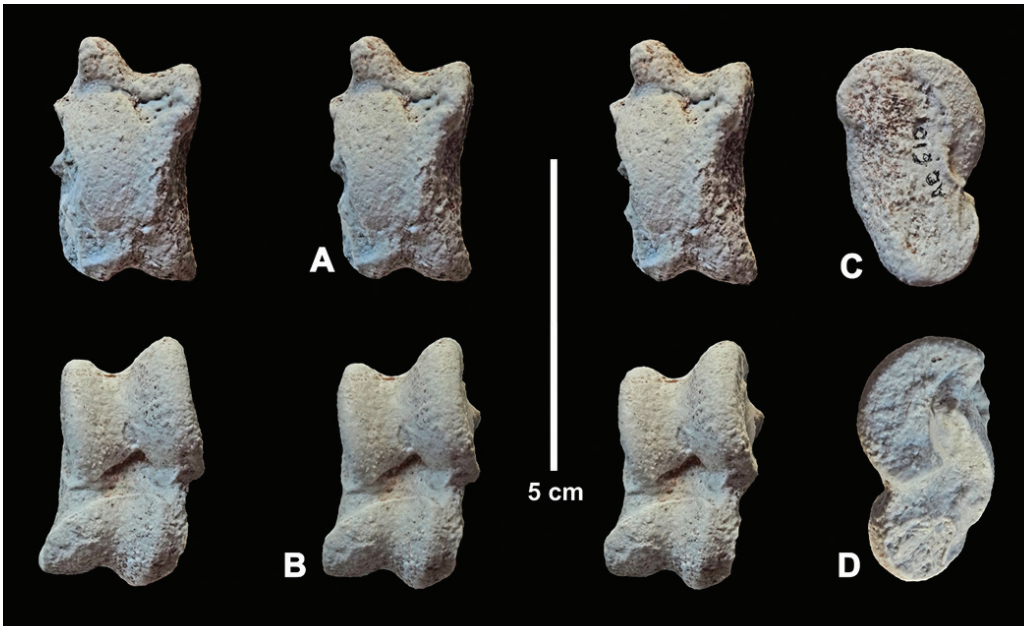

Figure 8.—AC 610, left talus from Aves Cave I, Bolt's Farm, attributed to *Potamochoeroides hypsodon* (cast). A) stereo caudal views, B) stereo cranial views, C) internal view, D) external view (scale: 5 cm).

Figure 9.—Metapodials and phalanges of *Potamochoeroides hypsodon* from Bolt's Farm Palaeokarst System, Aves Cave I. A) AC 360, left Mt III (A1 - lateral, A2 - dorsal, A3 - proximal, A4 - distal, A5 - medial, A6 - plantar views), B) AC 363, broken Mc III (B1 - stereo dorsal view, B2 - proximal, B3 - distal views), C) AC 364, stereo dorsal view of axial first phalanx, D) AC 414, axial third phalanx, dorsal view (scale: 10 mm).

Figure 10.—AC 521, fused abaxial first and second phalanges, *Potamochoeroides hypsodon*, from Aves Cave I, Bolt's Farm Karst System, lateral, medial and distal views (scale: 10 mm).

were extremely young (pre-weaning) when they died (D3/ unworn and without roots), others were slightly older (about to shed the D3/, canines almost fully formed but not yet erupted) whereas yet others were young adults (m/2 in wear but m/3 still in its crypt). There are also a few fully adult individuals with well-worn molars and canines.

Genus *Notochoerus* Broom, 1925

Type species.- Notochoerus capensis Broom, 1925

Species *Notochoerus capensis* Broom, 1925

Holotype.- PEM 1436/3, right M3/ lacking the anterior loph.

Type locality and age.- Longlands, South Africa, Middle Pliocene.

Description and Comments

Pickford & Gommery (2016) attributed a complete upper canine (AC 96) to *Potamochoeroides hypsodon*. Several other upper canines have been collected from the Aves Cave deposits including a complete specimen and several fragments (Fig. 11). Apart from specimen AC 96, all the other canines from the Aves Cave complex are compatible with each other in dimensions and morphology and clearly represent a single species. These specimens are morphometrically close to abundant material from Makapansgat, the type locality of *Potamochoeroides hypsodon*, and we accordingly attribute them to this species. The Makapansgat sample of this species is comprehensive and even though there is a significant range of metric variation, best interpreted in terms of sexual bimodality and individual variation within a single species, none of the specimens is as large as AC 96 which has twice the height of the other complete canine from Aves Cave I (AC 371) (Fig. 11) as do specimens from Makapansgat attributed to *Notochoerus capensis* (Ewer, 1958). Furthermore, the upper canines attributed to *Potamochoeroides* have an almost straight medial part in the distal profile of the tooth, whereas the canine AC 96 is evenly curved thoughout its distal profile (Fig. 11). We therefore incline to the view that AC 96 probably belongs to *Notochoerus capensis* rather than to an abnormally large male of *Potamochoeroides hypsodon*. In metric terms this re-attribution is compatible with the other dental specimens of *Notochoerus capensis* from the site, which are somewhat larger than specimens of *Potamochoeroides hypsodon*, and smaller than specimens of *Metridiochoerus andrewsi* (Pickford & Gommery, 2016). The ventral part of the canine (AC 96) is covered in enamel which is patterned by coarse longitudinal ridges as in *Potamochoerus* and *Potamochoeroides*.

A second specimen from Aves Cave I, AC 530 from Block N° AC 11-15, confirms the presence of *Notochoerus* at the site. It is the radicular part of a right upper canine, rather poorly preserved but showing the shallow but broad posterior groove, while the anterior surface is covered in coarsely ridged enamel as in specimens from Makapansgat. The section of the tooth measures 27.7 mm antero-posterior diameter x ca 37 mm dorso-ventral diameter which is considerably larger than canines of *Potamochoeroides hypsodon* (Table 3).

Genus *Metridiochoerus* Hopwood, 1926

Type species.- Metridiochoerus andrewsi Hopwood, 1926

Species *Metridiochoerus andrewsi* Hopwood, 1926

Holotype.- NHMUK M 12805, upper third molar.

Type locality and age.- Homa Mountain (Kanjera) Kenya, Middle Pleistocene.

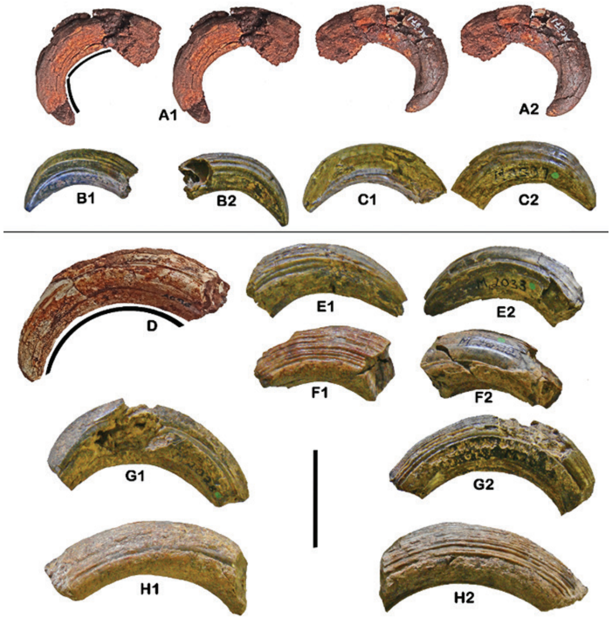

Figure 11.—A-C) Upper canines of *Potamochoeroides hypsodon*, D-H) upper canines of *Notochoerus capensis*, the curved black lines show the different profiles of the distal side of the teeth. A) AC 371, left upper canine from Aves Cave I (A1: stereo dorsal view, A2: stereo ventral view), B) M 372, left upper canine from Makapansgat, C) M 2037, left upper canine from Makapansgat (B1, C1 – ventral views, B2, C2- dorsal views); D) AC 96, left upper canine from Aves Cave I, dorsal view. E-H) upper canines fom Makapansgat, E) M 2033, left upper canine, (E1 - ventral, E2 - dorsal views) F) M 2032, right upper canine, (F1 - ventral, F2 - dorsal views), G) M 2028, left upper canine, (G1 - dorsal, G2 - ventral views) H) M 8994, left upper canine (H1 - dorsal, H2 - ventral views) (scale: 5 cm).

Bridge Cave (entrance dump): A left upper canine of a large suid (in a block labelled BC 09-18) was found in stratified red breccia at Bridge Cave (Fig. 12). The antero-posterior diameter at the open radicular end is 34 mm and the total height of the tooth from root to apex is 20 cm (measured in a straight line). The distal profile of the tooth is uniformly curved as in canines of *Metridiochoerus* and *Notochoerus*, unlike the interrupted curvature of canines of *Potamochoeroides*. The specimen is somewhat smaller than upper canines of *Metridiochoerus andrewsi* from Gondolin (Pickford, 2013b) (antero-posterior diameter at radicular end: 50 mm, height from root to apex ca 25 cm), but it probably belongs to this species.

Milo 'A': An upper canine of a large suid was found at Milo 'A'. The fossil is still in breccia, so cannot be measured, but its overall dimensions indicate that it represents *Metridiochoerus andrewsi*. This site also yielded a few molar fragments, one of which is probably an m/2 (MA 3) with a bucco-lingual diameter of 19.5 mm, compatible with *Metridiochoerus andrewsi*. A left i/2 from Milo 'A' (MA 44) measures 7.0 mm mesio-distal diameter by 6.8 mm labio-lingual diameter. It has an elongated wear facet along the distal margin of the crown which has removed most of the surface morphology which renders identification difficult.

Alcelaphine Cave on Bolt's Farm yielded a moderately worn, incomplete right m/2 (AL 4). Of the anterior lophid, only the distal parts of the protoconid and metaconid are preserved, along with the median accessory cusplet. The entoconid and hypoconid are almost vertical, but the hypoconulid (posterior accessory cusplet) leans distally, producing a prominent overhang in the distal part of the crown. The bucco-lingual diameter is 16.0 mm

Figure 12.—BC 09-18, left upper canine attributed to *Metridiochoerus andrewsi* from Bridge Cave, Bolt's Farm Palaeokarst System, stereo dorsal view (scale: 8 cm).

and the occlusal diameter is estimated to have been about 35 mm, similar to a specimen from Kromdraai 'A' (KA 2857 + KA 95-4 (m/2 length x breadth: 36.0 x 15.0 mm) Pickford, 2013a). The tooth is much bigger than m/2s of *Potamochoeroides hypsodon* (length x breadth: 26.1 x 15.4 mm; Pickford & Gommery, 2016) its crown is taller and the distal overhang is more exaggerated than in the latter species. AL 4 is much larger than corresponding teeth of *Phacochoerus modestus* (m/2 length ca 25 mm; Pickford, 2013a).

Genus *Phacochoerus* Cuvier 1826

Type species.- Aper aethiopicus Pallas 1767

Species *Phacochoerus modestus* (Van Hoepen & Van Hoepen, 1932)

Bridge Cave *Panthera* Spot yielded associated right talus and cuboid, and an associated set of left metatarsals and pedal phalanges (Tables 5-6; Figs 13-16). The material is well-preserved and warrants close examination. The Mt III is similar in dimensions and overall aspect to AC 360 from Aves Cave I, the main difference being its slightly more slender appearance, partly due to the fact that the proximal end is missing a sliver of bone from the medial side. It is also close in dimensions and morphology to extant *Potamochoerus porcus* and *Phacochoerus aethiopicus*. Detailed comparisons of the fossils were made with the corresponding bones of *Potamochoeroides hypsodon*, *Phacochoerus aethiopicus* and *Potamochoerus porcus*. All three of these taxa are approximately the same size, but the detailed layout of the articular facets is different. The comparisons revealed closer morphological similarities between the fossils and bones of the Desert Wart Hog rather than with the other two taxa. The specimens are therefore attributed to *Phacochoerus modestus*.

The talus (BC 985) is slightly smaller than the corresponding bone in *Potamochoeroides hypsodon* from Aves Cave I, and the internal ridge on the margin of the calcanear facet has a greater offset from the sustentacular surface. The angulation between the cuboid and navicular facets is sharper than in *Potamochoeroides* and the angulation between the proximal and distal articulations is less marked. All these features indicate that the Bridge Cave suid was more cursorially adapted than the suid from Aves Cave, in much the same way that the Wart Hog is a faster runner than the Bush Pig (personal observations MP).

The right cuboid from Bridge Cave *Panthera* Spot (BC 884) is robust with a well-developed calcanear facet. The proximal processes on the cranial and caudal ends of the talar facet are strong, the cranial one in particular, translating into a well-stabilised ankle joint. It fits well with the talus described immediately above, and probably represents the same individual.

The Mt II has a medio-laterally slender diaphysis which is dorso-plantarly shallow at the proximal end, deepening distally and curving gently medially towards the distal epiphysis. The proximal epiphysis is small with a clear facet for the Mt III, a minute proximal facet, and a lateral facet for the middle cuneiform (Flower, 1876; Plug, 2014).

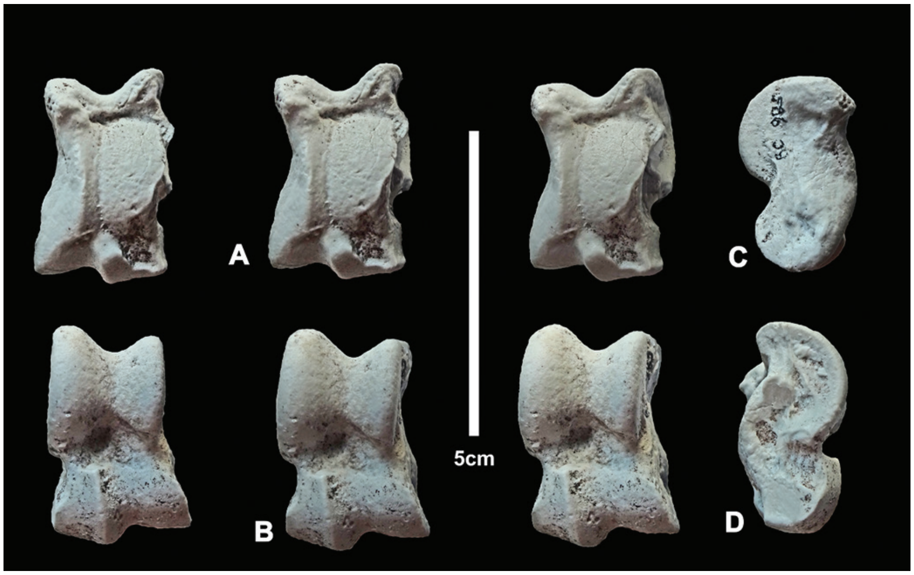

Figure 13.—BC 985, right talus from Bridge Cave *Panthera* Spot, Bolt's Farm attributed to *Phacochoerus modestus* (cast). A) stereo caudal views, B) stereo cranial views, C) internal view, D) external view (scale: 5 cm).

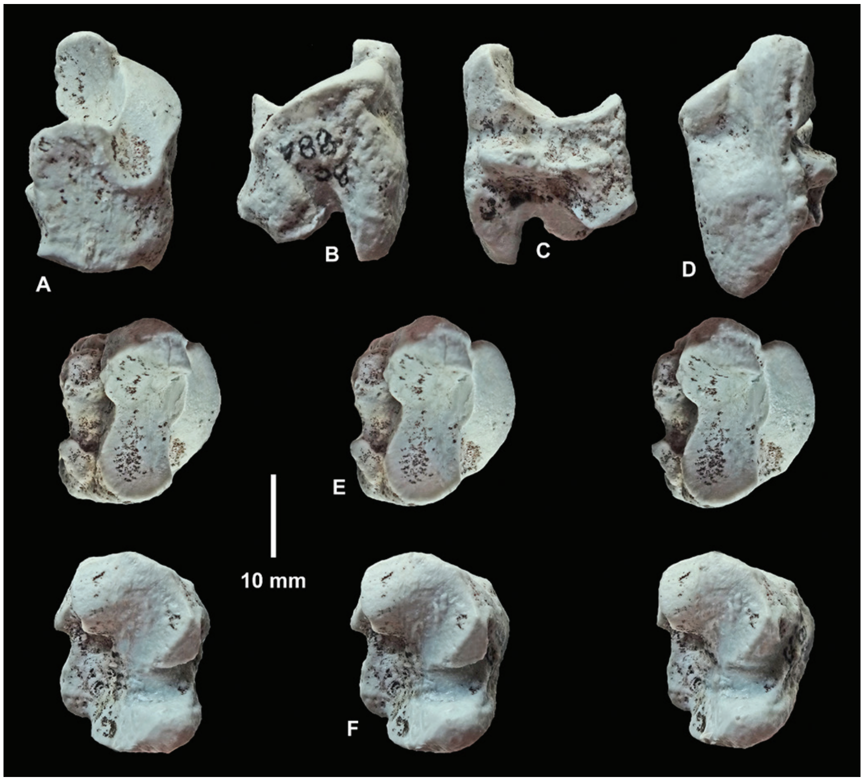

Figure 14.—BC 884, right cuboid from Bridge Cave *Panthera* Spot, Bolt's Farm, attributed to *Phacochoerus modestus* (cast) A) caudal view, B) lateral view, C) medial view, D) cranial view, E) stereo triplet proximal views, F) stereo triplet distal views (scale: 10 mm).

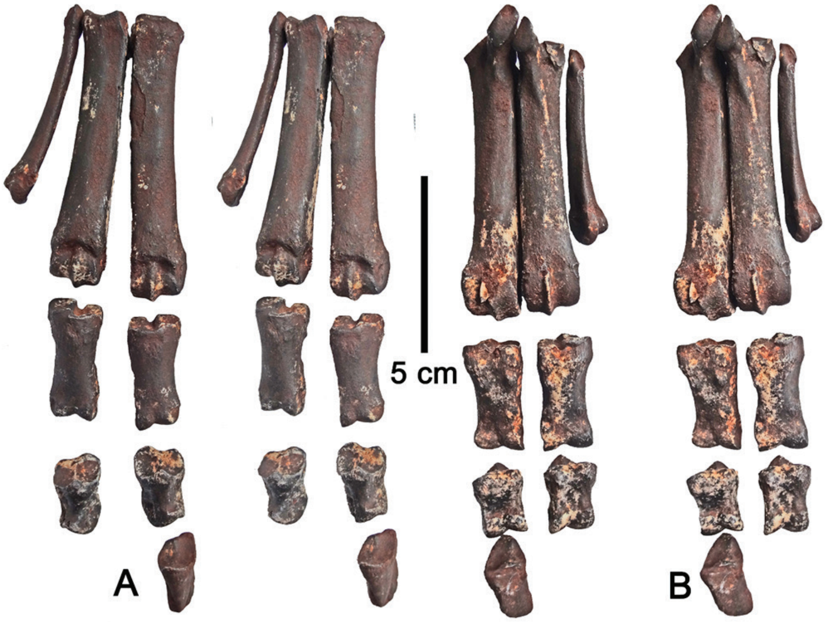

Figure 15.—Stereo images of BC 854, associated left foot bones from Bridge Cave *Panthera* Spot, attributed to *Phacochoerus modestus* (A) dorsal view, (B) plantar view. Elements preserved are the Mt II (BC 854a), Mt III (854b), Mt IV (854c) and the axial first (854d, e), second phalanges of digits III and IV (854f, g), and the ungual phalanx of digit IV (854h) (scale: 5 cm).

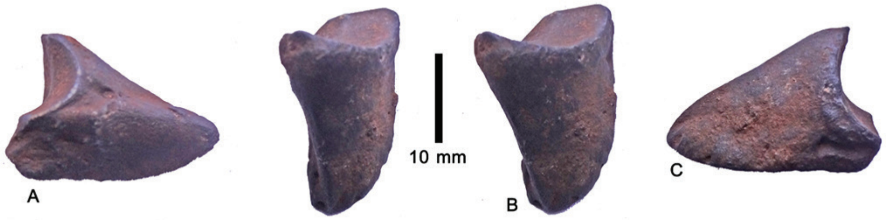

Figure 16.—BC 855, axial ungual phalanx from Bridge Cave *Panthera* Spot, attributed to *Phacochoerus modestus* (A) oblique plantar view, (B) stereo dorsal view, (C) abaxial view (scale: 10 mm).

The distal epiphysis is swollen, with a prominent internal ridge on the plantar side which blends into the dorsal surface of the articulation for the first phalanx. The medial part of the articular surface flares medially but is low dorsally.

The Mt III has a large concavo-convex facet for the external cuneiform, and a sloping medial facet which contacts the middle cuneiform. The medial part which articulates with the Mt IV is broken off which gives the impression that the bone is more slender than AC 360. There is a clear facet for the Mt II which is contiguous with the medial facet but is oriented vertically to it. The plantar process is prominent and has a facet where it contacts the plantar process of the Mt IV. The diaphysis is robust, flattened internally where it lies against the Mt IV, rounded medially and generally broadening gently towards the distal epiphysis. The distal articular surface has a prominent central ridge which extends from the plantar to the dorsal sides of the bone, but not extending onto the diaphysis. The part of the distal articulation close to the Mt IV is more distally positioned than the part which is close to the Mt II, as is usual in suoid metatarsals.

The morphology of the Mt IV is typically suid, with an almost flat proximal facet for the cuboid, and a well-developed plantar process which articulates with the plantar process of the Mt III (Flower, 1876, fig. 120). At the proximal end of the diaphysis on the internal side (which contacts the Mt III) there is a low ridge-like process which slots into a depression in the diaphysis of the Mt III. There is also a small facet laterally for the Mt V. The diaphysis and distal epiphysis are basically mirror images of those of the Mt III. The Mt IV is slightly longer than the Mt III as is usual in suids.

Metric comparison of fossil suid teeth from Bolt's Farm, Makapansgat, Malawi and Namibia

The augmented sample of suids from the Bolt's Farm Palaeokarst System, improves the basis for understanding the range of metric variation in the species and thereby permits a more informed comparison between the suids from this site and those from Makapansgat, which is the type locality of *Potamochoeroides hypsodon* (Fig. 17). *Potamochoeroides shawi*, also defined at Makapansgat, is considered to be a synonym of *Potamochoeroides hypsodon* (Pickford & Gommery, 2016). One of the outcomes of this comparison is that an upper canine (AC 96) from Aves Cave I previously attributed to *Potamochoeroides* is transferred to *Notochoerus capensis* and a lower p/3 (AC 258) previously identified as *Notochoerus capensis* is transferred to *Potamochoeroides hypsodon*. A second outcome of this revision is that a talus from Makapansgat previously interpreted to belong to *Notochoerus capensis* by Pickford & Gommery (2016) is far too large to belong to it, but is more likely to represent the huge tetraconodont suid *Gerontochoerus scotti*.

Three species of suids are present at Makapansgat: *Potamochoeroides hypsodon*, *Notochoerus capensis* and *Gerontochoerus scotti*. There are four species of suid at Bolt's Farm, but not all from the same time span: *Potamochoeroides hypsodon* and *Notochoerus capensis* from Aves Cave I, and *Metridiochoerus andrewsi* and *Phacochoerus modestus* from younger deposits on the farm. The lower third molar of *Potamochoeroides hypsodon* from Bolt's Farm (Cooke, 1993) appears to be narrower than the equivalent teeth from Makapansgat, but this is undoubtedly due to the fact that the unerupted m/3 in the mandible is incompletely formed, and would have been 4-5 mm broader if growth had been complete.

From this data it is inferred that the fossiliferous breccias at Makapansgat and Aves Cave I are close to each other in terms of geological age, but are older than the deposits that yield *Metridiochoerus andrewsi*, a species which is not reliably recorded from Makapansgat.

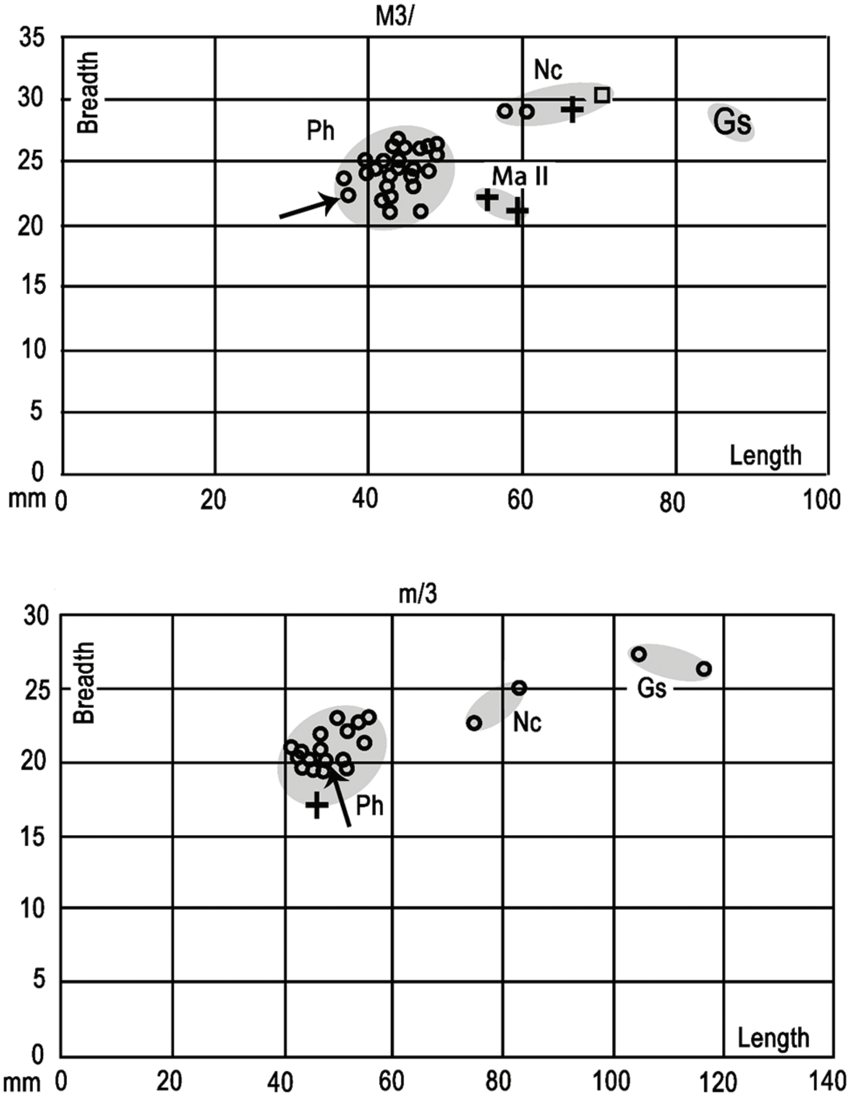

Figure 17.—Bivariate (length x breadth) plots of upper (top frame) and lower (bottom frame) third molars from Bolt’s Farm and Makapansgat, South Africa. Gs - *Gerontochoerus scotti*, Ma II - *Metridiochoerus andrewsi* stage II, Nc - *Notochoerus capensis*, Ph - *Potamochoeroides hypsodon*. **o** - Makapansgat, **+** - Bolt’s Farm. Arrows show holotypes of *Potamochoeroides hypsodon* (M3/) and *Potamochoeroides shawi* (m/3). Square: holotype of *Notochoerus capensis*; Gs in grey oval: holotype *Gerontochoerus scotti* from Omo, Ethiopia.

Kullmer (2008) described fossil suids from Malawi attributing them to six taxa - *Notochoerus jaegeri, Notochoerus euilus, Notochoerus scotti, Metridiochoerus andrewsi/compactus, Potamochoerus porcus* and *Phacochoerus aethiopicus*, the first four of which would be called « giant » according to the criteria of Broom (1925) and are thus of interest to compare with the large fossils from Bolt’s Farm.

The data presented in Fig. 17 suggests that *Notochoerus capensis* may be present in Malawi, along with *Gerontochoerus scotti* and a species of *Metridiochoerus*, probably large specimens of *Metridiochoerus andrewsi* as inferred by Kullmer (2008). In addition, some incomplete specimens (not plotted) can be attributed to *Potamochoeroides hypsodon*. The upper third molar from Malawi attributed to *Nyanzachoerus jaegeri* plots close to the range of variation of *Notochoerus capensis* (black line). The data suggests that the Bolt's Farm succession of breccias spans a similar time period to that in the Lake Malawi Basin (Fig. 18).

The sole suid specimen from « Rhino Site » at Ekuma, in the Etosha National Park, Namibia (Pickford *et al*. 2016) indicates the presence of *Gerontochoerus scotti,* on the basis of which a Middle Pliocene correlation is proposed for the deposits. The tooth is too long to be attributed to *Notochoerus capensis* (Fig. 18).

Brad Pit 'A': Parts of an upper canine of a large suid (BPA 152, BPA 79+13) were collected at Brad Pit 'A'. The dorso-ventral diameter measured some distance from the radicular end is 29 mm and the antero-posterior diameter is 45.1 mm. This specimen is compatible in cross-sectional shape and

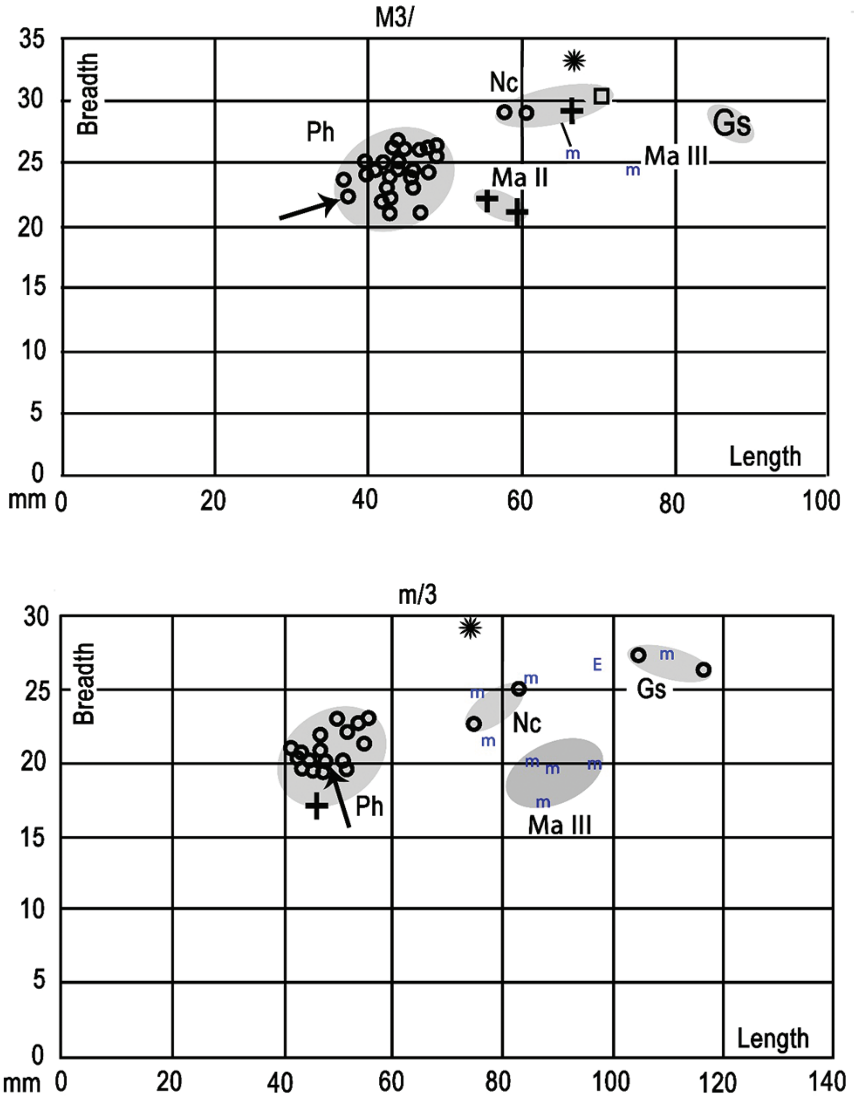

Figure 18.—Bivariate (length x breadth) plots of suid third molars from South Africa, Namibia, Malawi and Tunisia. The symbols and letters for South African specimens are as in Fig. 17, with the addition of « E » for a specimen from Ekuma, Namibia (Pickford *et al*. 2016) and « m » for specimens from Malawi (Kullmer, 2008). MA II - *Metridiochoerus andrewsi* stage II, Ma III - *Metridiochoerus andrewsi* stage III. Starburst symbol - holotype of *Nyanzachoerus jaegeri* Coppens, 1971, from Hamada Damous, Tunisia, for comparison.

dimensions to material of *Gerontochoerus koobiforaensis*. This specimen and other suid fossils from the site will be published in a separate paper.

Giant suids from the African Plio-Pleistocene

The word « giant » applied to the holotype of *Notochoerus capensis* Broom, 1925, has proven over the long term to be a source of confusion. When first described, the specimen from the Vaal River Gravels at Longlands, South Africa, was the largest known fossil suid tooth from the continent (indeed the World) with a length of ca 72-81 mm (minimum and maximum estimates made by Van der Made, 1998, depending on how the broken fossil is reconstructed) being much longer than upper third molars of the extant Giant Forest Hog (*Hylochoerus meinertzhageni* Thomas, 1904) which range in length from 38-48 mm (Figs 19-20). As such the adjective was appropriate when first applied to the species, but discoveries of much bigger material rapidly followed with teeth over 100 mm long reported in the literature (Hopwood, 1926; Broom, 1928; Van Hoepen & Van Hoepen, 1932; Shaw, 1938; Dietrich, 1942; Arambourg, 1943, 1947; Leakey 1943, 1958; Ewer, 1958a; Harris, 1983; Harris & White, 1979; Harris *et al*. 1988; Bender, 1990, 1992; Cooke, 1993; Van der Made, 1998; Kulmer, 2008). These reports soon rendered the word 'giant' somewhat inappropriate when applied to the specimen from Longlands. The writings of several authors, starting with Shaw (1938) reveal that they were so influenced by Broom's (1925) usage of the word « giant » that they erroneously attributed much larger teeth to the species *capensis* which adversely influenced their systematic and taxonomic interpretations. In the full panoply of suids now known from the continent, the Longlands tooth would today qualify for the word « large » rather than « giant ». This confusion is ongoing, partly because the very large suid specimens from Makapansgat which belong to *Gerontochoerus scotti* have usually been attributed to *Notochoerus capensis* (cf Cooke & Wilkinson, 1978; Harris & White, 1979, fig. 48, 49; Bender, 1990, 1992) which in turn has influenced identifications of very large teeth from sites in Malawi (Kullmer, 2008) and Namibia (Pickford *et al*. 2016).

The suid tooth from Longlands described by Broom (1925) would have had an original length of ca 72 mm (see Van der Made, 1998, for a discussion about the

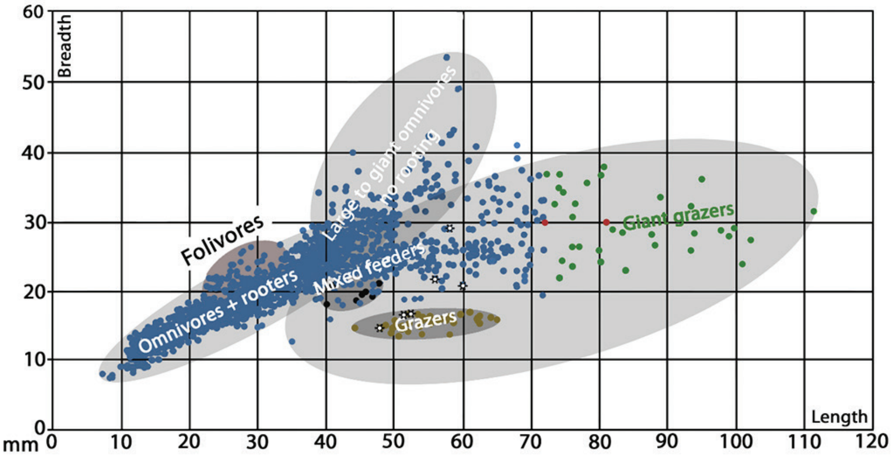

Figure 19.—Bivariate (length x breadth) plot of 2,826 fossil Old World suoid upper third molars to illustrate the currently known range of metric variation. Red dots are two estimates of the dimensions of the holotype M3/ of *Notochoerus capensis*. For comparison the teeth of the largest extant suid, the Giant Forest Hog, *Hylochoerus meinertzhageni*, are shown by black dots within a grey oval, and the elongated teeth of extant Wart Hogs, *Phacochoerus aethiopicus* and *Phacochoerus africanus*, are represented by beige dots enclosed by a dark grey oval. Teeth larger than those of the *Notochoerus capensis* type specimen are coloured green – all were found after the description of the species by Broom (1925). Also shown are inferred feeding categories, with most suids being omnivorous (incuding rooting) (left hand steeply inclined narrow oval), some with relatively broad molars are folivores and gigantic omnivores, some are mixed feeders, and others with elongated but narrow molars are predominantly grazers (right hand less inclined broad oval). All the suid specimens from Bolt's Farm (stars with white centres) fall within the grazing category although mixed feeding is not excluded for *Notochoerus capensis*.

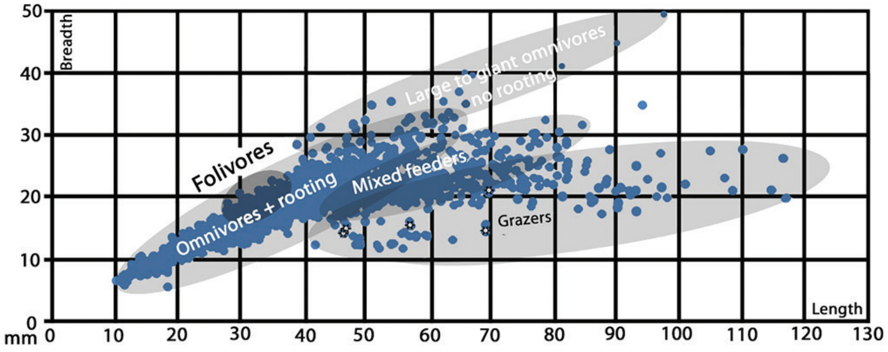

Figure 20.—Bivariate (length x breadth) plots of 3,227 fossil Old World suoid lower third molars. The lower teeth from Bolt's Farm (black star symbols) like the upper teeth, plot within the grazing category, but note that *Notochoerus capensis* is close to the mixed feeder category. Note also the sub-categories with relatively broad molars comprising folivores and gigantic omnivores some of which are as big as gomphotherian proboscideans.

possible original dimensions of the tooth) which pales when it is compared with the dimensions of teeth of the species *Gerontochoerus scotti* which has lower third molars nearly 72% longer (114.8 mm long for the holotype of *Notochoerus harrisi* Van der Made, 1998, a synonym of *Gerontochoerus scotti*, Leakey, 1958) and 116.5 mm long for a specimen from Makapansgat (ESI M 2077). A tooth from Malawi is 110.2 mm long (Kullmer, 2008) and one from Namibia is over 97 mm long (Pickford *et al*. 2016).

Over the years since the initial description of *Notochoerus capensis*, more than 230 suid third molars have been found in African Plio-Pleistocene deposits which are equal in length and/or breadth to, or are longer or broader than, the type specimen, attributed by their describers to a bewildering variety of taxa, many of which are synonyms (Harris & White, 1979) (*Nyanzachoerus jaegeri* Coppens 1971, *Nyanzachoerus pattersoni* Cooke & Ewer 1972, *Gerontochoerus eulius* (Hopwood, 1926), *Gerontochoerus koobiforaensis* Pickford 2013c, *Gerontochoerus scotti* Leakey 1943, *Gerontochoerus harrisi* (Van der Made, 1998), *Kolpochoerus heseloni* (Leakey, 1943), *Notochoerus paiceae* Broom, 1931, *Kolpochoerus sinuosus* Van Hoepen & Van Hoepen, 1932, *Kolpochoerus olduvaiensis* (Leakey, 1942), *Metridiochoerus andrewsi* (Hopwood, 1926), *Metridiochoerus hopwoodi* Leakey, 1958, *Metridiochoerus meadowsi* (Broom, 1928), *Stylochoerus compactus* Van Hoepen & Van Hoepen, 1932, *Synaptochoerus hieroglyphicus* Van Hoepen & Van Hoepen, 1932, *Afrochoerus nicoli* Leakey, 1958, *Notochoerus serengetensis* Dietrich 1942, *Pronotochoerus nyanzae* Leakey, 1958, *Orthostonyx brachyops* Leakey, 1958, among others (Cooke, 1949)). Bivariate plots of the length and breadth of these teeth suggest that significant numbers of specimens identified in the literature as lower third molars are likely to be upper third molars, but because few of the specimens have been illustrated it is not possible to make informed revisions without access to the original fossils. It is also likely that different ways of measuring teeth may be contributing to the uncertainty.

Taxonomic problems arising from convergence and parallelism in suid molar morphology

The mental gymnastics associated with the discussion of large African hypsodont suids, is evident in their taxonomic history, as shown by frequent name changes, shuffling of specimens between taxa, problems with determining the side or whether the teeth were upper or lower and so on (Pickford, 2013c; Geraads & Bobe, 2017). This uncertainty influences down-line analyses which flow from the basic data, such as biochronology, meaning that a thorough and general revision of these suids is required.

Ewer (1958a) listed 18 fossils from Makapansgat (plus 8 doubtful specimens) which she attributed to *Notochoerus* (*Gerontochoerus*) *euilus* and wrote «The specimens about to be described so closely resemble the Omo material that there can be little doubt that they belong to the same species. A comparison with the type

Table 4.—Measurements (in mm) of post-cranial bones of *Potamochoeroides hypsodon* from Aves Cave I, Bolt's Farm Palaeokarst System.

Catalogue	Anatomy	Measurement
AC 425	Humerus distal functional breadth	31.0
AC 425	Humerus minimum trochlea diameter	21.4
AC 484	Ulna distal epiphysis maximum diameter	18.2
AC 365	Distal radius antero-posterior height	21.0
AC 363	Metacarpal III proximal breadth	22.3
AC 363	Metacarpal III proximal height	18.4
AC 363	Metacarpal III distal breadth	17.9
AC 363	Metacarpal III distal height	16.4
AC 543	Metacarpal IV total length	70.0
AC 543	Metacarpal IV proximal height	16e
AC 543	Metacarpal IV distal breadth	17.0
AC 543	Metacarpal IV distal height	18.8
AC 562	Metacarpal IV proximal breadth	19.2
AC 562	Metacarpal IV proximal height	17.6
AC 542	Calcaneum total length	80.0
AC 542	Calcaneum height	32.2
AC 462	Talus distal breadth	26.6
AC 462	Talus distal height	19.8
AC 610	Talus internal length	36.0
AC 610	Talus external length	40.0
AC 610	Talus proxial breadth	21.0
AC 480	Navicular breadth	17.2
AC 480	Navicular antero-posterior diameter	23.0
AC 360	Metatarsal III length	76.6
AC 360	Metatarsal III proximal breadth	19.0
AC 360	Metatarsal III proximal height	22.3
AC 360	Metatarsal III distal breadth	15.8
AC 360	Metatarsal III distal height	18.4
AC 343	Abaxial metapodial length	51.6
AC 559	Abaxial metapodial distal height	13.3
AC 559	Abaxial metapodial distal breadth	11.3
AC 559	Distal abaxial metapodial breadth	13.3
AC 559	Distal abaxial metapodial height	11.7
AC 364	Axial 1st phalanx length	31.0
AC 364	Axial 1st phalanx proximal breadth	16.2
AC 364	Axial 1st phalanx proximal height	15.8
AC 364	Axial 1st phalanx distal breadth	13.0
AC 364	Axial 1st phalanx distal height	9.5
AC 187	Axial 1st phalanx length	24.2
AC 521	Abaxial Ist+2nd phalanx length	27.0
AC 578	Axial 2nd phalanx length	23.0
AC 578	Axial 2nd phalanx proximal breadth	16.3
AC 578	Axial 2nd phalanx proximal height	17.4
AC 578	Axial 2nd phalanx distal breadth	14.0
AC 578	Axial 2nd phalanx distal height	11.5
AC 414	Axial 3rd phalanx length	25.7
AC 545	Axial 3rd phalanx length	20.8
AC 545	Axial 3rd phalanx proximal breadth	9.8
AC 545	Axial 3rd phalanx proximal height	12.9

Table 5.—Measurements (in mm) of the suid right talus (BC985) and cuboid (BC 884), and the left foot bones (BC 854) from Bridge Cave *Panthera* Spot**.** In rounded brackets are measurements of Mt III (AC 360) and an axial first phalanx (AC 364) from Aves Cave I attributed to *Potamochoeroides hypsodon* and in square brackets are measurements of the corresponding bones in *Potamochoerus porcus* from East Africa (Walker, 1985) (e – estimated measurement).

Bone	Total length	Distal breadth	Distal height	Proximal breadth	Proximal height
Talus	34.0 (int.): 36.5 (ext.)	23.0	16.3	19.4	22.9
Cuboid	30.0	15.0	22.2	17.0	22.0
MT II	56.5 [55]	8.0	11.7	4.9	7.4
MT III	76.3 (76.6) [75.5]	16.0 (15.8)	16.7 (18.4)	18e (19.0)	20.8 (22.3)
MT IV	79.2 [81]	15.0	16.0	14.5	22.4
1st phalanx III	34.3 (31.0)	14.3 (13.0)	10.5 (9.5)	15.5 (16.2)	16.0 (15.8)
1st phalanx IV	32.9	13.4	10.1	15.9	16.0
2nd phalanx III	21.7	12.4	12.5	14.5	15.0
2nd phalanx IV	21.5	12.1	13.0	13.7	14.7
3rd phalanx IV	24.5	--	--	11.4	12.6
Axial 3rd phalanx	24.7	--	--	11.7	12.7

Table 6—Measurements (in mm) of the pedal bones of extant South African suids (TM AZ 1271, *Phacochoerus aethiopicus* female) and [TM AZ 1617, *Potamochoerus porcus* female] for comparison with the corresponding bones in *Phacochoerus modestus* (Table 5).

Bone	Total length	Distal breadth	Distal height	Proximal breadth	Proximal height
MT II	(52.5) [47.7]	(6.9) [7.9]	(10.4) [11.7]	(4.0) [3.2]	(6.1) [6.5]
MT III	(69.9) [68.7]	(12.5) [12.6]	(13.5) [14.7]	(15.7) [14.5]	(19.4) [21.4]
MT IV	(70.5) [69.8]	(12.1) [13.0]	(13.9) [15.0]	(12.5) [13.4]	(20.0) [23.0]
1st phalanx III	(33.5) [31.6]	(11.4) [12.0]	(8.4) [8.0]	(12.9) [13.4]	(13.0) [13.7]
1st phalanx IV	(32.3) [31.4]	(11.6) [11.3]	(8.6) [8.7]	(13.0) [13.9]	(12.8) [13.2]
2nd phalanx III	(19.0) [18.0]	(10.0) [11.2]	(10.0) [11.0]	(12.2) [13.4]	(13.0) [13.6]
2nd phalanx IV	(19.5) [19.5]	(10.0) [11.0]	(10.2) [10.6]	(12.2) [12.4]	(13.0) [13.0]
3rd phalanx IV	(22.5) [23.5]	(--) [--]	(--) [--]	(9.0) [10.3]	(10.7) [11.5]
Axial 3rd phalanx	(22.0) [22.0]	(--) [--]	(--) [--]	(8.9) [10.2]	(10.2) [11.0]

specimen of *Notochoerus capensis* shows that the differences are considerable - so great indeed that they appear to warrant more than specific separation. The Makapan material is therefore referred to *Notochoerus euilus*, and the name *Gerontochoerus* has been revived as a subgenus of *Notochoerus* to emphasise the differences». In fact, the 26 fossils from Makapansgat attributed to this species by Ewer (1958a) comprise two taxa, one a suine (*Notochoerus capensis*), the other a tetraconodont (*Gerontochoerus scotti*). Despite the observations made by Ewer (1958) concerning the major differences between fossils attributed by her to *Notochoerus* (*Gerontochoerus*) euilus and the holotype of *Notochoerus capensis*, subsequent authors (Cooke & Wilkinson 1978; Harris & White, 1979; Cooke, 2005) have amalgamated them into a single taxon, *Notochoerus capensis*, thereby producing a chimaera.

Bender (1990) did not enter into details concerning problems related to convergence and parallelism in the Makapansgat giant suids when he wrote «Notochoerus *from the Limeworks had previously been classified as* Notochoerus capensis *by a number of researchers (Cooke and Wilkinson 1978; Harris and White 1979). The classification was based on the twenty one specimens studied in the B.P.I. collections. Due to its fragmentary nature, it is not possible to revise the taxonomic position of the* Notochoerus *collection, the few comparisons made with East African specimens indicated a similarity with* Notochoerus capensis*. On the basis of the antero-posterior length of the lateral wall of the lingual face in M3/, it appears that* Notochoerus capensis *is distinct from*

Notochoerus euilus *and* Notochoerus scotti *(Cooke and Wilkinson 1978)*. Despite the difference in the M3/s of *Notochoerus capensis* on the one hand and of *Notochoerus euilus* and *Notochoerus scotti*, on the other, he continued «*Cooke and Wilkinson (1978) and Harris and White (1979) constructed very similar phylogenies for* Notochoerus*, in which it is derived from* Nyanzachoerus*.* Notochoerus euilus *is considered generally more primitive and ancestral to* Notochoerus capensis*, which in turn is regarded as ancestral to* Notochoerus scotti».

Dietary considerations of suids from Bolt's Farm

All the suid upper third molars from Bolt's Farm with the exception of that of *Notochoerus capensis*, plot within the « grazers » oval (Fig. 19) well away from the « omnivores » oval. From this it is inferred that the vegetation in the Gauteng region during the Plio-Pleistocene was not suitable for omnivores (*Potamochoerus porcus* for example) but that grass supplies were sufficiently reliable for « grazers » to survive and thrive. From the dental morphology (hypsodonty, strongly infolded enamel outlines, presence of cementum on the molars) it is inferred that all four suid taxa known from Bolt's Farm (*Potamochoeroides hypsodon*, *Notochoerus capensis*, *Phacochoerus modestus* and *Metridiochoerus andrewsi*) were grazers, a possibility borne out by stable isotope studies (Harris & Cerling, 2002) but in addition, it seems clear that the geologically younger taxa (Early Pleistocene *Phacochoerus modestus* and *Metridiochoerus andrewsi*) were dentally better adapted to grazing than were the earlier taxa (Pliocene *Potamochoeroides hypsodon* and *Notochoerus capensis*) which could have been « mixed feeders » at least on a seasonal basis. Examination of the lower third molars reveals a similar pattern (Fig. 20).

General Discussion and Conclusions

In African Plio-Pleistocene strata, suids are well-represented, and have proven to be useful for coarse-focus biostratigraphy, not only in East Africa where many records have been calibrated by radio-isotopic dating of subjacent volcanic deposits (Cooke & Maglio, 1972) but also in Southern African karst-related deposits (Harris & White, 1979) where there are no volcanic deposits associated with the strata.

Fossil suids are represented in many of the karstic infillings in the Gauteng Cradle of Humankind, including the Bolt's Farm Palaeokarst System. This paper documents the fossil suids from several karst deposits in the latter system. There were three phases of deposition in which suids have been found, the earliest one corresponding to the Middle Pliocene at Brad Pit 'A' (ca 3.7 Ma), a second late Pliocene assemblage aged ca 2.6-3.0 Ma (Aves Cave I, Bolt's Pit 14) and a third one correlating to the Pleistocene, ca 1.8-2.0 Ma (Milo 'A', Alcelaphine Cave and Bridge Cave). Older deposits at Waypoint 160 (ca 4.5 Ma) have not yet yielded suids.

New fossil suid material from Aves Cave I comprises several juvenile individuals, which collectively reveal that the deciduous and permanent dental formula of *Potamochoeroides hypsodon* was close to those of *Dasychoerus verrucosus* (Müller & Schlegel, 1845) (the extant Warty Pig) and *Potamochoerus porcus* (Linnaeus, 1758) (the extant Bush Pig), but different from that of *Phacochoerus aethiopicus* (Pallas, 1767) (the Wart Hog) which has suppressed two of the upper incisors. Unfortunately, the deciduous dentition of derived species of *Metridiochoerus* such as *M. andrewsi*, is poorly represented in the fossil record so it is not possible to make detailed comparisons. Recall that Harris & White (1979) considered that the species here referred to as *Potamochoeroides hypsodon*, was an early form of *Metridiochoerus andrewsi* lineage (in their scheme, Phase I of a 3-phase evolutionary sequence), but Pickford (2013a) showed that, even though they are possibly related forms, the skull morphology, the form and penetration of the lower canine within the mandible and other features indicated that *Potamochoeroides* and *Metridiochoerus* are better classified in distinct genera (see below).

The prevalence of juveniles at Aves Cave I, even of unweaned infants suggest that *Potamochoeroides* may have been breeding near the sites, perhaps even sheltering within the cave entrances, but they could also represent the remains of prey items carried into the caves by predators.

A well preserved distal radius and ulna from Aves Cave I indicates that *Potamochoeroides hypsodon* was probably a carpograde suid, like the Wart Hog and *Metridiochoerus andrewsi* (Pickford, 2013b). In a previous study (Pickford & Gommery, 2016) the only available distal ulna was crushed and its bone surface was flakey, which obscured details of the functional features related to carpogrady, on which basis it was erroneously deduced that the genus probably did not practice this particular form of locomotion. That can now be rectified, and it would appear that carpogrady was a feature of the Middle Pliocene suid *Potamochoeroides hypsodon*. Two distal radii from Makapansgat (BPI M 10883, M 4804) indicate the same thing.

It was hypothesised by White & Harris (1977) that *Potamochoeroides hypsodon* was a basal member (stage I) of a tripartite *Metridiochoerus andrewsi* lineage but Pickford (2012) resurrected the genus *Potamochoeroides* because of significant differences in cranio-dental anatomy between these suids. The distinction between these genera is underlined by the new discoveries at Aves Cave I and by study of the Gondolin suids (Pickford, 2013b). A major difference between these genera concerns the lower canines: in *Potamochoeroides*, the radicular part of the tooth extends beneath the premolars, well into the horizontal ramus, as in *Dasychoerus*, for example, whereas in *Metridiochoerus* the lower canine root terminates in the symphyseal area, and does not extend distally into the horizontal ramus. Furthermore, the canines in advanced species of *Metridiochoerus* such as *M. andrewsi* are considerably larger than those of *Potamochoeroides hypsodon* and they extend only a short way into the mandible, their radicular ends not extending beyond the symphysis. As a consequence, the mandibular canal in *Metridiochoerus* is voluminous and extends as far anteriorly as the rear of the symphysis, differing from the condition in *Potamochoeroides* in which the mandibular canal is narrow in the zone of the premolars and diastemata. In addition, the lower canines of *Metridiochoerus compactus* are endowed with a core of osteodentine (Harris & White, 1979), whereas those of *Potamochoeroides hypsodon* are not. Nevertheless, these two extinct genera appear to be related to each other (Pickford, 2013b) as well as to the Wart Hog (*Phacochoerus*).

The presence of *Notochoerus capensis* at Aves Cave I seems to be assured on the basis of the M3/ and a p/4 described by Pickford & Gommery (2016). The attribution to *Notochoerus capensis* of a large upper canine from Aves Cave I, that was previously identified as *Potamochoerides hypsodon* is done on the basis that there appear to be only two taxa of suids at the site, the smaller *Potamochoeroides hypsodon*, and the larger *Notochoerus capensis*. If this reattribution is correct, then it suggests that *Notochoerus* may be closely related to *Potamochoeroides* than to Tetraconodontinae. However, until more complete remains of *Notochoerus capensis* are recovered it will be difficult to explore the possibility that *Notochoerus* and *Potamochoeroides* could be synonyms. As it stands, the morphology of the Aves Cave I suid canine, the M3/ and the p/4 and attributed to *Notochoerus capensis* recall those of *Potamochoeroides hypsodon* in several respects, in its known parts the former being an upscaled version of the latter, and both taxa differing in similar ways from *Metridiochoerus andrewsi*.

ACKNOWLEDGEMENTS

We would like to thank Lazarus Kgasi, Nonhlanhla Vilakazi, Mirriam Tawane, Heidi Fourie and Frank Sénégas for their help during this study. The CNRS and NRF (LIA HOMEN (Hominids and Environments: Evolution of Plio-Pleistocene Biodiversity (Cradle of Humankind, South Africa), the CNRS (CR2P-UMR7207) and the French Ministry of Europe and Foreign Affairs (Sous-direction de l'Enseignement supérieur et de la Recherche - Pôle Sciences Humaines et Sociales, Archéologie et Patrimoine) funded this study.

References

Arambourg, C. (1943). Observations sur les Suidés fossiles du Pléistocène d'Afrique. Bulletin du Muséum d'Histoire Naturelle, Paris, 15: 471–476.

Arambourg, C. (1947). Mission Scientifique de l'Omo 1932–1933. Tome 1: Géologie-Anthropologie. Fascicule 3. Contribution à l'étude géologique et Paléontologique du bassin du lac Rodolphe et de la basse vallée de l'Omo. Deuxième partie: paléontologie. Editions du Muséum, Paris, pp. 231–562.

Bender, P.A. (1990). A Reconsideration of the Fossil Suid, *Potamochoeroides shawi*, from the Makapansgat Limeworks, Potgietersrus, Northern Transvaal. MSc Thesis, University of the Witwatersrand, Johannesburg, 82 pp, 33 figures, Appendix.

Bender, P.A. (1992). A reconsideration of the fossil suid, *Potamochoeroides shawi*, from the Makapansgat Limeworks, Potgietersrus, Northern Transvaal. Navorsinge van die Nasionale Museum Bloemfontein, 8 (1): 1-66.

Broom, R. (1925). On evidence of a giant pig from the late Tertiaries of South Africa. Records of the Albany Museum, Grahamstown, 3: 307–308.

Broom, R. (1928). On some new mammals from the Diamond Gravels of the Kimberley District. Annals of the South African Museum, 22: 439–444.

Broom, R. (1931). A new extinct giant pig from the diamond gravels of Windsorton, South Africa. Records of the Albany Museum, Grahamstown, 4: 167–168.

Broom R. (1937). Notices of a few more new fossil mammals from the caves of the Transvaal. Annals and Magazine of Natural History, 20: 509–514.

Broom R. (1948). Some South African Pliocene and Pleistocene mammals. Annals of the Transvaal Museum, 21: 1–38.

Cooke, H.B.S. (1949). The fossil Suina of South Africa. Transactions of the Royal Society of South Africa, 32: 1–44.

Cooke, H.B.S. (1993). Undescribed suid remains from Bolt's Farm and other Transvaal cave deposits. Palaeontologia africana, 30: 7–23.

Cooke, H.B.S. (1994). *Phacochoerus modestus* from Sterkfontein Member 5. South African Journal of Science, 90: 99–100.

Cooke, H.B.S. (2005). Makapansgat suids and *Metridiochoerus*. Palaeontologia africana, 41: 131–140.

Cooke, H.B.S. & Ewer, R.F. (1972). Fossil Suidae from Kanapoi and Lothagam, Kenya. Bulletin of the Museum of Comparative Zoology Harvard, 143: 149–295.

Cooke, H.B.S. & Maglio, V.J. (1972). Plio-Pleistocene stratigraphy in East Africa in relation to proboscidean and suid evolution. In: Calibration of Hominoid Evolution, (Bishop W.W. & Miller J.A. Eds) Scottish Academic Press, Edinburgh, pp. 303–329.

Cooke, H.B.S. & Wilkinson, A. (1978). Suidae and Tayassuidae. In: Evolution of African Mammals (Maglio V.J. & Cooke H.B.S. Eds), Harvard University Press, Cambridge, pp. 435–482.

Coppens, Y. (1971). Une nouvelle espèce de Suidé du Villafranchien du Tunisie, *Nyanzachoerus jaegeri* nov. sp. Comptes rendus de l'Académie des Sciences de Paris, Série D, 272: 3264–3267.

Cuvier, F, (1826). Dictionnaire des Sciences Naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les arts, Suivis d'une biographie des plus célèbres naturalistes. F.G. Levrault, Editeur, Strasbourg, vol. 39: 1–559.

Dale, M. (1948). New fossil Suidae from the Limeworks Quarry, Makapansgat, Potgietersrust. South African Science, 2: 114–117.

Dietrich, W.O. (1942). Altestquartäre Säugetiere aus der südlichen Serengeti, Deutsch-Ostafrika. Palaeontographica, Abteilung A, 94 (3–6): 43–133.

Dirks, P.; Roberts, E.M.; Hilbert-Wolf, H.; Kramers, J.; Dosseto, A.; Duval, M.; Elliott, M.; Evans, M.; Grün, R.; Hellstrom, J.; Herries, A.; Joannes-Boyau, R.; Makhubela, T.V.; Placzek, C.J.; Robbins, J.; Spandler, C.; Wiersma, J.; Woodhead, J. & Berger, L.R. (2017). The age of *Homo naledi* and associated sediments in the Rising Star Cave, South Africa". *eLife, 6: e24231*. https://doi.org/10.7554/eLife.24231

Ewer, R.F. (1956). The fossil suids of the Transvaal caves. Proceedings of the Zoological Society of London, 127: 527–544.

Ewer, R.F. (1958a). The fossil Suidae of Makapansgat. Proceedings of the Zoological Society of London, 130: 329–372.

Ewer, R.F. (1958b). Adaptive features in the skulls of African Suidae. Proceedings of the Zoological Society of London, 131: 135–155.

Flower, W.H. (1876). An Introduction to the Osteology of the Mammalia : Being the Substance of Lectures Delivered at the Royal College of Surgeons of England in 1870. 2nd Edition, MacMillan and Co. London, 344 pp.

Geraads, D. & Bobe, R. (2017). Suidae from Kanapoi. Journal of Human Evolution. https://dx.doi.org/10.1016/j.jhevol.2017.05.004. 6 pp.

Gray, J.E. (1821). On the natural arrangement of vertebrose animals. London Medical Repository, 15 (1): 296–310.

Gray, J.E. (1854). On the painted pig of the Cameroons (*Potamochoerus penicillatus*). Proceedings of the Zoological Society of London, 1854: 129–131.

Gray, J.E. (1873). Handlist of the Edentate, Thick-skinned and Ruminant Mammals in the British Museum. British Museum Trustees, London. 174 pp. 41 pls.

Harris, J.M. (1983). Family Suidae. In: Koobi Fora Research Project: Volume II: The Fossil Ungulates, Proboscidea, Perissodactyla, and Suidae (Harris, J.M. Ed.), Oxford University Press, Oxford, pp. 215–300.

Harris, J.M. & Cerling, T.E. (2002). Dietary adaptations of extant and Neogene African suids. Journal of Zoology, 256: 45–54.

Harris, J.M. & White, T.D. (1979). Evolution of Plio-Pleistocene African Suidae. Transactions of the American Philosophical Society, New Series, 69: 1–128.

Harris, J.M.; Brown, F.H. & Leakey, M.G. (1988). Stratigraphy and Paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. Contributions in Science, 399: 1–128.

Herries, A.I.R.; Pickering, R.; Adams, J.W.; Curnoe, D.; Warr, G.; Latham, A.G. & Shaw, J. (2013). A multidisciplinary perspective on the age of *Australopithecus* in Southern Africa. In: The Paleobiology of *Australopithecus*. (Reed, K., Fleagle, J. & Leakey, R., Eds) Springer Science+Business Media, Dordrecht, pp. 21–40.

Hopwood, A.T. (1926). Some Mammalia from the Pliocene of Homa Mountain, Victoria Nyanza. Annals and Magazine of Natural History, 9th Ser. 18: 267–280.

Hünermann, K.A. (1968). Die Suidae (Mammalia, Artiodactyla) aus den Dinotheriensanden (Unterpliozän = Pont) Rheinhessens (Südwestdeutschland). Schweizerische Paläontologische Abhandlungen, 86: 1–96.

Ide, Y.; Nakahara, T.; Nasu, M.; Matsunaga, S.; Iwanaga, T.; Tominaga N. & Tamaki Y. (2013). Postnatal mandibular cheek tooth development in the Miniature Pig based on two-dimensional and three-dimensonal X-Ray analyses. The Anatomical Record, 296: 1247–1254.

Kullmer, O. (2008). The fossil Suidae from the Plio-Pleistocene Chiwondo Beds of Northern Malawi, Africa. Journal of Vertebrate Paleontology, 28: 208–216.

Lazagabaster, I.A.; Souron, A.; Rowan, J.; Robinson, J.R.; Campisano, C.J. & Reed, K.E. (2018). Fossil Suidae (Mammalia, Artiodactyla) from Lee Adoyta, Ledi-Geraru, lower Awash Valley, Ethiopia : Implications for the late Pliocene turnover and paleoecology. Palaeogeography, Palaeoclimatology, Palaeoecology, 504: 186–200.

Leakey, L.S.B. (1942). New fossil Suidae from Olduvai. Journal of the East Africa and Uganda Natural History Society, 16: 178–196.

Leakey, L.S.B. (1943). New fossil Suidae from Shungura, Omo. Journal of the East Africa and Uganda Natural History Society, 17: 45–61.

Leakey, L.S.B. (1958). Some East African Pleistocene Suidae. Fossil Mammals of Africa, 14: 1–69.

Linnaeus, C. (1758). Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, Editio decima, reformata, Laurentii Salvii, Holmiae (Stockholm) 823 pp.

Müller, S. & Schlegel, H. (1845). Over die wilde zwijnen van den Indische Archipel, In: Temminck, C.J. (Ed.) Verhandelingen over de natuurlijke geschiedenis der Nederlandsche Overzeesche Bezittingen, door de leden der Natuurkundige Commissie in OostIndië en andere schrijvers. Luchtmans & Van den Hoek, Leiden, pp. 169–182, pls 28–32.

Pallas, P.S. (1767). Elenchus Zoophytorum Sistens Generum Adumbrationes Generaliores et Speciorum Cognitarum Succinctas Descriptiones cum Selectis Auctorum Synonymis. Hagae, 451 pp.

Pickford, M. (1988). Revision of the Miocene Suidae of the Indian Subcontinent. Münchner Geowissenschaftliche Abhandlungen, 12: 1–91.

Pickford, M. (2006). Synopsis of the biochronology of African Neogene and Quaternary Suiformes. Transactions of the Royal Society of South Africa, 61 (2): 51–62.

Pickford, M. (2012). Ancestors of Broom's Pigs. Transactions of the Royal Society of South Africa, 67: 17–35.

Pickford, M. (2013a). The diversity, age, biogeographic and phylogenetic relationships of Plio-Pleistocene suids from Kromdraai, South Africa. Annals of the Ditsong National Museum of Natural History, 3: 1–32.

Pickford, M. (2013b). Locomotion, diet, body weight, origin and geochronology of *Metridiochoerus andrewsi* from the Gondolin karst deposits, Gauteng, South Africa. Annals of the Ditsong National Museum of Natural History, 3: 33–47.

Pickford, M. (2013c). Reappraisal of *Hylochoerus euilus* Hopwood, 1926 (Suidae, Mammalia) from the Albertine Rift (Pliocene) Uganda. Geo-Pal Uganda, 6: 1–26.

Pickford, M. & Gommery, D. (2016). Fossil Suidae (Artiodactyla, Mammalia) from Aves Cave I and nearby sites in Bolt's Farm Palaeokarst System, South Africa. Estudios Geologicos, 72 (2): 24 pp.

Pickford, M.; Mocke, H.; Ségalen, L. & Senut, B. (2016). Update of the Pliocene fauna of the Ekuma Valley, Etosha, Namibia. Communications of the Geological Survey of Namibia, 17: 115–144.

Plug, I. (2014). What Bone is that? A Guide to the Identification of Southern African Mammal Bones. Rosslyn Press, Pretoria, 514 pp.

Sénégas F. (2000). Les faunes de rongeurs (Mammalia) plio-pléistocènes de la province du Gauteng (Afrique du Sud) : mises au point et apports systématiques, biochronologiques et precisions paléoenvironnementales. PhD Thesis, University of Montpellier II, Montpellier, France. Volume 1, 232 pp, Volume 2, 227 pp.

Sénégas F. (2004). A new species of *Petromus* (Rodentia, Hystricognatha, Petromuridae) from the early Pliocene of South Africa and its paleoenvironmental implications. Journal of Vertebrate Paleontology, 24: 757–763.

Sénégas F. & Avery M. (1998). New evidence for the murine origins of the Otomyinae (Mammalia, Rodentia) and the age of Bolt's Farm (South Africa). South African Journal of Science, 94: 503–507.

Sénégas F., Thackeray J.F., Gommery D. & Braga J. (2002). Palaeontological sites on 'Bolt's Farm', Sterkfontein Valley, South Africa. Annals of the Transvaal Museum, 39: 65–67.

Shaw, J.C.M. (1938). The teeth of the South African fossil pig (*Notochoerus capensis*, syn. *meadowsi*) and their geological significance. Transactions of the Royal Society of South Africa, 26: 25–37.

Thackeray J.F.; Gommery D.; Sénégas F.; Potze S.; Kgasi L.; McCrae C. & Prat S. (2008). A survey of past and present work on Plio-Pleistocene deposits on Bolt's Farm, Cradle of Humankind, South Africa. Annals of the Transvaal Museum, 45: 83–89.

Thomas, O. (1904). On *Hylochoerus*, the forest pig of Central Africa. Proceedings of the Zoological Society of London, 1904: 193–199.

Van der Made, J. (1998). Biometrical trends in the Tetraconodontinae, a subfamily of pigs. Transactions of the Royal Society of Edinburgh: Earth Sciences, 89: 199–225.

Van Hoepen, E. & Van Hoepen, H. (1932). Vrijstaatse Wilde Varke. Paleontologiese Navorsing van die Nasionale Museum, Bloemfontein, 2 (4): 1–23, 39–62.

Walker, R. (1985). A Guide to the Post-cranial Bones of East African Animals. Hylochoerus Press (F. Crowe & Sons Ltd), Norwich, England, 285 pp + 7 annex pp.

White, T. & Harris, J. (1977). Suid evolution and correlation of African hominid localities. Science, 198: 13–21.