Fossil Suidae (Artiodactyla, Mammalia) from Aves Cave I and nearby sites in Bolt's Farm Palaeokarst System, South Africa

Suidos fósiles (Artiodactyla, Mammalia) de Aves Cave I y yacimientos cercanos en el systema paleokárstico de Bolt's Farm, Sudáfrica

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ABSTRACT

Excavations carried out since 2011 at Bolt's Farm Palaeokarst System, South Africa, have led to the recovery of interesting remains of suids, notably from Aves Cave I. The taxa present are *Potamochoeroides hypsodon* and *Notochoerus capensis*, the same as those that occur at Makapansgat. The new *Notochoerus* material, which includes an upper third molar and a lower fourth premolar, strengthens the conclusion that this genus is a suine and not a tetraconodont as thought for the past half century. *Potamochoeroides* has thickened mandibular rami indicating that it descended from the genus *Dasychoerus* that dispersed into Africa from Eurasia about 5 million years ago. Other karst deposits at Bolt's Farm have yielded a younger suid fauna comprising *Metridiochoerus andrewsi* and *Phacochoerus modestus*, indicating that the Bolt's Farm Karst System was active for a considerable period of time (ca 4.5 Ma - 1.8 Ma). The fact that all the suid taxa from Bolt's Farm are hypsodont indicates that the palaeoenvironment contained abundant grass.

Keywords: Bolt's Farm Palaeokarst System; South Africa; Plio-Pleistocene; Suidae; Biochronology; Palaeoenvironment.

RESUMEN

Las excavaciones llevadas a cabo desde 2011 en el sistema paleokárstico de Bolt's Farm (Sudáfrica), han dado lugar a la recuperación de interesantes restos de suidos, sobre todo en Aves Cave I. Los taxones presentes son *Potamochoeroides hypsodon* y *Notochoerus capensis*, los mismos que aparecen en Makapansgat. El nuevo material de *Notochoerus*, que incluye un tercer molar superior y un cuarto premolar inferior, refuerza la conclusión de que este género es un suinae y no un tetraconodonto como se ha aceptado durante el último medio siglo.

Potamochoeroides tiene rmas mandibulares engrosadas lo que indica que descendió del género *Dasychoerus* que se extendió por África desde Eurasia hace unos 5 millones de años. Otros depósitos kársticos de Bolt's Farm han proporcionado una fauna de suidos más jóvenes, incluyendo *Metridiochoerus andrewsi* y *Phacochoerus modestus*, lo que sugiere que el sistema kárstico de Bolt's Farm estuvo activo durante un período de tiempo considerable (aproximadamente 4,5 Ma - 1,8 Ma). El hecho de que todos los taxones de suidos de Bolt's Farm sean hipsodontos indica que el paleoambiente contenía abundante hierba.

Palabras clave: Sistema Palaeokárstico de Bolt's Farm; Sudáfrica; Plio-Pleistoceno; suidos; biocronología; Paleoambiente.

Introduction

Robert Broom was the first palaeontologist to work at Bolt's Farm (Fig. 1, 2) starting in 1936 (Broom, 1937, 1948; Cooke, 1991; Thackeray et al., 2008). He described diverse suid remains from "Bolt's workings at Sterkfontein" (Broom, 1948) but the detailed provenance of the material is unknown. A large sample of suid remains from Bolt's Farm was collected between 1947 and 1948 by the University of California Africa Expedition

Southern Section (UCAE) led by C. Camp (Camp, 1948; Cooke, 1991; Larson, 2004). This expedition prospected Bolt's Farm and mapped 23 "Pits" which correspond to cavities left by lime miners (Cooke, 1991). Over several decades, the calcite from speleothems from the caves in the Sterkfontein Valley was used in gold extraction processes at the nearby gold mines at Kromdraai and Krugersdorp. F.E. Peabody, a member of the UCAE, carried out a plane table survey which was the basis for the first map of the area, on which the locations of some Pits were marked.

Fig. 1.—Relief Map of Africa showing the regional setting of the Cradle of Humankind, Gauteng, South Africa, and the detailed position of the Bolt's Farm Palaeokarst System (BF in the inset).
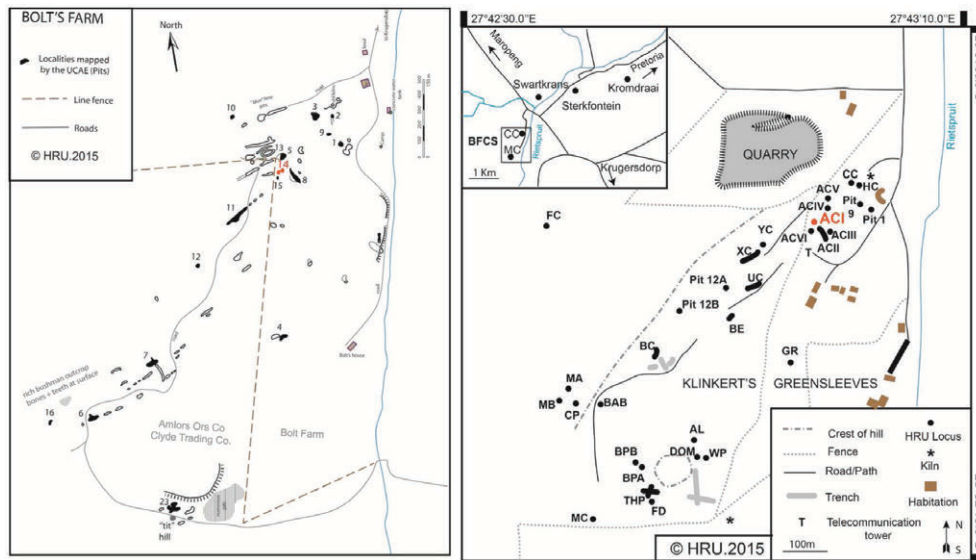
Fig. 2.—Positions of fossiliferous deposits in the Bolt's Farm Palaeokarst System. Left frame : Localities mapped by UCAE: 1, Pit 1 (Kraal Pit); 2, Pit 2 (no name); 3, Pit 3 (Kaffir Beer Cave); 4, Pit 4 (Garage Ravine Cave); 5, Pit 5 (Smithy Cave); 6, Pit 6 (Baboon Cave); 7, Pit 7 (Elephant Cave); 8, Pit 8 (no name); 9, Pit 9 (no name); 10, Pit 10 (Grey Bird Pit); 11, Pit 11 (no name); 12, Pit 12 (no name); 13, Pit 13 (no name); 14, Pit 14 (Bench Mark Pit); 15, Pit 15 (no name); 16, Pit 16 (Equine Pit); 23, Pit 23 (Tit Hill Pit). Right frame : Localities mapped by HRU: - **Greensleeves property**: Pit 1 (Kraal Pit); Pit 9 (no name); CC (Cobra Cave); HC (H Cave); GR (Garage Ravine Cave); ACI (Aves Cave I); ACII (Aves Cave II); ACIII (Aves Cave III); ACIV (Aves Cave IV); ACV (Aves Cave V); ACVI (Aves Cave VI); - **Klinkert's property**: AL (Alcelaphine); BAB (Baboon Cave); BC (Bridge Cave); BE (Bolt's Cave); BPA (Brad Pit A); BPB (Brad Pit B); CP (Carnivore Pit); DOM (Dom's Site); FC (Franky's Cave); FD (Femur Dump); MA (Milo A); MB (Milo B); MC (Machine Cave); Pit 12A (no name); Pit 12B (no name); THP (Tit Hill Pit); UC (U Cave); XC (X Cave); YC (Y Cave); WP (Waypoint 160).

Cooke (1991) redrew this map which, until recently, was used for locating Bolt's Farm sites (Sénégas et al., 2002; Thackeray et al., 2008; Gommery et al., 2012). Between October 1957 and June 1958, Cooke benefitted from discussions with Peabody and had access to his field notes. The UCAE discovered remains of suids at Pit 3 and Pit 14 (Cooke, 1993). With the exception of two specimens now in the collection of the Plio-Pleistocene Palaeontology Section of the Ditsong National Museum of Natural History (DNMNH, formerly the Transvaal Museum (TM)) in Pretoria, South Africa, the other specimens are in the collections of the University of California, Museum of Paleontology (UCMP) in the USA. For Pit 14, also called "Bench Mark Pit", the suid discovered *Potamochoeroides shawi* (now known as *Potamochoeroides hypsodon*) (Cooke, 1993; Pickford, 2013a), suggests an age for the deposit earlier than the bulk of the sites in the Gauteng region (Sterkfontein, Kromdraai, Swartkrans, Cooper's, Gondolin).

Until 2006, research at Bolt's Farm was intermittent (Thackeray et al., 2008). Since then, the HRU (Hope (Hominid Origins and Past Environments) Research Unit) has prospected the area of Klinkert's and Greensleeves Properties systematically and has excavated since 2011. The preliminary geological studies and the discovery of previously unrecognised deposits indicate that there is an extensive palaeokarst network on the farm and that it is better to call this area "Bolt's Farm Palaeokarst System" rather than Bolt's Farm on its own. The latter name has caused confusion in the past, misleading some authors to believe that there is a single deposit at a single site (Cooke, 1993). The fossiliferous deposits span a discontinuous chronological sequence from the Early Pliocene to the end of the Early Pleistocene (Sénégas, 2000; Sénégas & Avery, 1998; Sénégas et al., 2000, 2002; Thackeray et al., 2008; Gommery et al., 2012).

In order to locate the different Pits mapped by the UCAE, the HRU team used the map published by Cooke in 1991, but it was not always easy to correlate them with the cavities and the *in situ* breccia deposits that were observed on the ground. Subsequently, a copy of the original map drawn by

Peabody was obtained (Fig. 2) which shows some differences from the one published by Cooke (1991) and this eliminated some of the ambiguity, especially for the area of Pits 5, 8, 13, 14 and 15, now on the Greensleeves Property. The "Pits" represent cavities made by lime miners, so in order to avoid mixing the UCAE and HRU collections, a new nomenclature was devised for locating the material collected by the HRU.

The breccia deposits at Aves Cave are probably remnants of infillings of a fossil karst network, here called the Aves Cave Complex. The HRU has differentiated the remnant deposits in different places and has kept the fossils from each site separate from the others. For example, Pit 14 represents the lime miner's excavation inside Aves Cave I (ACI) deposit. The excavations done since 2011 show that the deposit is extensive and deep, probably continuous with the deposits inside Pit 8 (ACII) and in the southern entrance of Pit 13 (ACIV). It is too early to provide details about the geology of ACI, but it appears that the deposit comprises a huge detritic cone that accumulated inside a palaeo-cave during the Late Pliocene.

Material and Methods

The HRU fossil collection, including cranio-dental and post-cranial remains of suids, came not only from decalcified breccia and isolated blocks of breccia in the mining dumps but also from *in situ* breccia (for example specimen AC 231). The material enclosed in breccia was prepared with 6% acetic acid by L. Kgasi at the Ditsong Preparation Laboratory of the DNMNH. All the material is curated in the Plio-Pleistocene Palaeontology Section in the said Museum with the site abbreviation AC.

Fossils were measured with sliding calipers to the nearest tenth of a mm. Images were captured with a Sony Cybershot Camera, and treated with Photoshop Elements 03 in order to enhance the contrast and remove unwanted background. Scales were added manually in order to avoid distortions due to parallax and the frustrum effect (digital effects).

Dental nomenclature (Fig. 3) follows the scheme outlined by Hünermann, 1968, and Pickford, 1988. Upper teeth are represented by capital letters (I – Incisor, C – Canine, D – Deciduous upper molar, P – Premolar, M – Molar) followed by the meristic position and by a forward slash representing the occlusal surface (e.g. 1I/, C1/, D4/, P3/, M2/). Lower teeth are in lower case letters and the meristic position is below the forward slash (e.g. i/3, p/4, m/3). Experience has shown that omission of the forward slash makes it difficult to control misprints (if M1 is misprinted m1, it is not evident that there is an error, whereas if M1/ is misprinted as m1/ it is immediately clear that something is wrong).

Curation of suids from the Bolt's Farm Palaeokarst System:

Fossils from Bolt's Farm are curated at three separate museums, the Ditsong National Museum of Natural History, Pretoria (previously the Transvaal Museum), the Bernard Price Institute, University of the Witwatersrand, Johannesburg, and the Palaeontology Museum of the University of California, Berkeley. The Ditsong collections from Bolt's Farm have diverse register numbers : old collections are preceded by the abbreviation TM BF, the new ones just the site abbreviation (for example AC) followed by the number. The ESI (BPI) collections have register numbers preceded by the letter "M".

Abbreviations:

AC - Aves Cave
BF - Bolt's Farm
ESI – Evolutionary Studies Institute (previously known as BPI - Bernard Price Institute)
DNMNH - Ditsong National Museum of Natural History
PEM - Port Elizabeth Museum
SK - Swartkrans
TM - Transvaal Museum (previous name for the DNMNH)
UCMP - University of California, Museum of Paleontology

Geological Setting

The Bolt's Farm Palaeokarst System comprises a series of fissures and caves in dolomitic country rock in which a variety of sedimentary and speleothem infillings accumulated, as well as some epikarstic deposits. The system was intermittently active during the Pliocene and Pleistocene, with the result that infillings of diverse ages are found in close proximity to each other. The oldest recognised deposits in the area occur at Waypoint 160 aged ca 4.5 Ma (Sénégas, 2004; Sénégas & Avery, 1998), followed by Aves Cave I and related deposits (Pit 14) aged ca 2.7 Ma - 3 Ma, followed by other strata aged ca 1.8 Ma (Pit 1, Pit 3). Today, most of the karst network appears to be inactive, but some parts of the system, such as the depths of Baboon Cave, are still active.

Note on the Geological Time Scale

When Shaw (1938) and Broom (1948) were discussing the ages of the Vaal River Gravels and the Transvaal Cave Breccias, they worked within the preponderant chronological scheme of the time which was dominated by the concept of glacial-interglacial cycles and their supposed tropical equivalents, the pluvial-interpluvial periods (Cooke, 1958). With the application of radio-isotopic age determinations to deposits in East Africa and elsewhere during the late 1950's and subsequently (Evernden & Curtis, 1965), notions of the timing of stratigraphic events were radically modified, leading eventually to the abandonment of Pluvial-Interpluvial stratigraphy (Flint, 1959; Bishop, 1972). There followed a phase during which the terms Lower and Upper
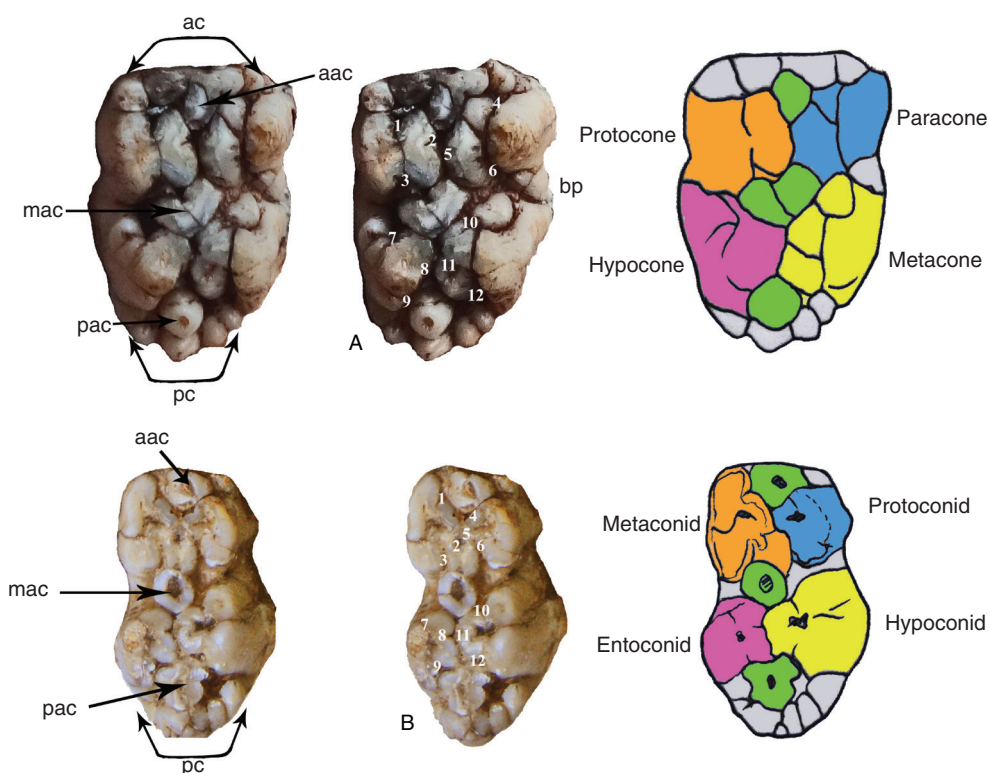
Fig. 3.—Nomenclature of molars of *Potamochoeroides hypsodon*. A) left M1/, AC 231 : stereo occlusal view and interpretive drawing, and B) right m/2, TM BF 3 14-342 : stereo pair and interpretive drawing, (ac - anterior cingulum, aac - anterior accessory cuslet, bp - basal pillar, mac - median accessory cusplet, pac - posterior accessory cusplet, pc - posterior cingulum; 1-12 - Furchen). Note how the main cusps of the M1/, especially the paracone, metacone and hypocone are becoming subdivided not only by the deepening of the Furchen but also by the incision of subsidiary grooves, and how the beads of the cingula are developing into low pillars.

Villafranchian were employed for correlating African faunas (Cooke & Coryndon, 1970), with Lower Villafranchian corresponding more or less to the Early Pleistocene, and the Upper Villafranchian to the Late Pleistocene as understood at the time. Recent changes have occurred to the chronostratigraphic scale which impact on the names applied to Plio-Pleistocene strata in particular, such that deposits which used to be correlated to the Late Pliocene on the basis of their radio-isotopic ages are now placed into the Early Pleistocene. This flows from the recommendation by the International Commission on Stratigraphy that the Pliocene/Pleistocene Boundary be placed at 2.588 Ma (Cohen et al., 2013) rather than at 1.8 Ma (Gradstein et al., 2004). Under the latest schema, Bolt's Farm Aves Cave I falls into the early part of the Late Pliocene.

Previous studies on suids from Bolt's Farm

Suids from Bolt's Farm have been described on several previous occasions. Shaw (1938, 1939) described some material from "Sterkfontein Lime Works" as *Notochoerus capensis* syn. *meadowsi*. On the basis of the matrix and colour of the fossils, some of these fossils probably came from Bolt's Farm (Cooke,

1993). Some unsourced cranial material, said to be from "Bolt's workings at Sterkfontein", was attributed by Broom (1948) to *Notochoerus meadowsi*, but was transferred to *Tapinochoerus meadowsi* by Ewer (1956) and then to *Metridiochoerus* cf *jacksoni* by Cooke (1993). A complete suid skull from Pit 3 at Bolt's Farm was classified as *Phacochoerus modestus* by Cooke (1993). The latter author also described fossils from Bolt's Farm Pit 14 which he identified as *Potamochoeroides shawi*.

Because of the complicated history of nomenclature of Plio-Pleistocene suids of Africa, a summary of the names given to specimens from Bolt's Farm in prior studies, and the names used in this paper is provided in Table 1.

The Suidae from Bolt's Farm Palaeokarst System

Systematic Descriptions

Family Suidae Gray, 1821
Genus *Potamochoeroides* Dale, 1948
Type species.- *Potamochoeroides hypsodon* Dale, 1948

Table 1.—**Summary of suid names applied to specimens from Bolt's Farm, and current usage. (sl – sensu lato)**

Published name	Locality	Author	Name in this paper
Notochoerus capensis syn. *meadowsi*	Sterkfontein (sl)	Shaw, 1938	*Metridiochoerus andrewsi*
Notochoerus meadowsi	Bolt's working	Broom, 1948	*Metridiochoerus andrewsi*
Tapinochoerus meadowsi	Bolt's	Ewer, 1958a	*Metridiochoerus andrewsi*
Metridiochoerus cf jacksoni	Bolt's	Cooke, 1993	*Metridiochoerus andrewsi*
Phacochoerus modestus	Bolt's Pit 3	Cooke, 1993	*Phacochoerus modestus*
Potamochoeroides shawi	Bolt's Pit 14	Cooke, 1993	*Potamochoeroides hypsodon*
Notochoerus capensis	Aves Cave I	This paper	*Notochoerus capensis*

Species *Potamochoeroides hypsodon* Dale, 1948
Holotype.- ESI (BPI) M 303, right maxilla containing P3/-M3/.
Type locality and age.- Makapansgat, South Africa, Late Pliocene.

Description of fossils from Aves Cave I

Dentition (Figs. 4, 5, 6; Table 2)
Upper Incisors:
    The upper central incisor has an elongated, slender crown, concave lingually with a central lingual pillar. The apical margin of the crown is comprised of two elongated cusps separated from each other by a shallow notch (which wears away but leaves a slight bend in the apical margin as in AC 334) Both apical cusps are lightly beaded (only visible in unworn or lightly worn specimens such as AC 144). Part of the lingual cingulum is present mesially, forming a low hook.
    The I3/ has a short crown (AC 134), but the only specimen available is deeply worn leaving little morphology to observe. Its root is short but markedly curved.

Lower incisors:
    First and second lower incisors from Aves Cave I have tall crowns and elongated roots and in lingual view, there is a distinct bend towards the mesial side at the crown-root margin, especially marked in the i/3. AC 283, a left i/1, shows a low central rib on the lingual side, but is otherwise almost peg-like with an almost square section with rounded corners. Viewed mesially or distally, the lingual profile of the tooth is almost straight, the buccal profile gently convex.
    The i/2 (AC 149) is more bent in lingual view than the i/1 is, and its central lingual rib leans distally more than in the i/1.
    The i/3 (AC 356) is considerably shorter than the i/1 and i/2, and is much more bent in lingual view. In contrast to the permanent incisors, the only deciduous incisor in the collection (AC 359) shows no bend in the profile of the tooth in lingual view. Indeed the tooth is remarkably straight, as is usual in suid deciduous incisors.

Upper Canine:
    The upper canines from Aves Cave I are in general poorly preserved, but there is an almost complete specimen (AC 96) which shows the morphology well. The tooth is robust, curved laterally and distally with an ovoid section interrupted on its dorsal aspect by a broad gutter. The apex of this specimen is worn to such an extent that no enamel is left, but a younger individual (AC 107) shows a ventral enamel cap which has a granular slightly ridged aspect. It also shows a distal crest which would soon disappear with wear. The upper canine is not preserved in AC 231, but there is a vast alveolus for it, only a short distance in front of the D2/. The diastemal ridge between the rear of the canine and the front of the D2/ is 11 mm long.

Lower Canines:
    The lower canines are hypselodont with a scrofic section (BF 3 14-342). None of the material from Aves Cave I is complete, but one specimen (AC 202) which has split from apex to root, shows an enamel-covered buccal surface and an enamel-free distal one. The canine *in situ* in specimen BF 3 14-342 shows a scrofic section of the canine, with a broader lingual surface (18.5 mm) than the buccal one (15.3 mm) and quite a broad distal surface (13 mm).

Upper deciduous cheek teeth:
    A juvenile left maxilla from Aves Cave I (AC 231) contains all three deciduous molars, as well as the M1/ erupted and in light wear, and the M2/ incompletely formed within its crypt. There is no alveolus for the P1/ between the canine alveolus and the D2/, the diastema between these teeth being formed of a low ridge. In occlusal view the D2/ has a narrow triangular occlusal outline, sharp mesially, blunt distally. It is posed on two roots and the main cusp is only slightly taller than the mesial and distal cusplets. The D3/ is also triangular in occlusal view, but is much broader distally than the D2/. It consists of three main cusps, one anteriorly and two posteriorly, bordering a large but shallow central fovea. The D4/ is quadricuspate with the mesial loph slightly narrower bucco-lingually than the distal loph. There are small anterior, median and posterior accessory cusplets in the midline of the crown, the median accessory cusplet blocking the median transverse valley. The

Fig. 4.—Suid incisors from Aves Cave I, Bolt's Farm Palaeokarst System, attributed to *Potamochoeroides hypsodon*. A) AC 334, left I1/, A1 - distal, A2 - labial, A3 - stereo occlusal view; B) AC 130, right I1/, B1 - labial view, B2 - stereo lingual view; C) AC 144, left I1/, C1 - lingual, C2 - labial, C3 - stereo occlusal view; D) AC 41, left i/1, D1 - distal, D2 - stereo lingual, D3 - labial, D4 - mesial view; E) AC 283, left i/1, E1 - labial, E2 - distal, E3 - stereo lingual view, E4 - distal view; F - AC 149, right i/2, F1 - labial, F2 - stereo lingual, F3 - mesial view; G) AC 359, right di/1, G1 - labial, G2 - distal, G3 - stereo lingual, G4 - distal view; H) AC 356, left i/3, H1 - stereo lingual, H2 - labial view (scale 10 mm).

paracone, metacone and hypocone show the development of slits apically which subdivide the cusps into low columns.

Lower deciduous cheek teeth:

The only deciduous lower cheek tooth from Aves Cave I is a left d/4 in light wear (AC 1). It consists of three lophids, each with two cusps, as is the case with suids (and artiodactyls) in general. It has two roots on the lingual side, and three on the buccal side, unlike Doliochoeridae and Hippopotamidae which have no medio-buccal root and thus show only two roots on the buccal side of the tooth. The main cusps are rounded with shallow Furchen, and the transverse valleys are mesio-distally broad and are barely blocked by the median accessory cusplet.

Permanent upper cheek dentition:

No upper premolars were found. The M1/ and M2/ are preserved in AC 231. The M1/ is comprised of four main cusps (paracone, protocone, metacone, hypocone) as is usual in suids, and there are anterior, median and posterior acessory cusplets

in the midline of the crown. The anterior and posterior cingula are beaded, and there is a remnant of a cingulum in the buccal end of the median transverse valley, forming a basal pillar. What distinguishes this M1/ from those of bunodont suines, is the fact that the main cusps are tall and have a distinct tendency to split into columns. The Furchen play an important role in this subdivision of the cusps, especially numbers 1 and 3 in the protocone, 4 and 6 in the paracone, 7 and 9 in the hypocone and 10 and 12 in the metacone. In addition, there are slits developed into the apices of the main cusps which extend cervically for some distance, and are more or less deeply incised into the surface of the cusps. For instance, the paracone shows a prominant pillar in its mesio-lingual part, the metacone has a pillar in its mesial part, the apex of the hypocone is subdivided into one cusplet distally and two cusplets anteriorly. The apex of the protocone has worn away, but it too probably possessed slits in its apical parts. The anterior and posterior accessory cusplets are simple pillars, but the median accessory cusplet is divided into two parts. To complete the picture, each of the beads in the anterior and posterior cingula shows a tendency to develop into a pillar.
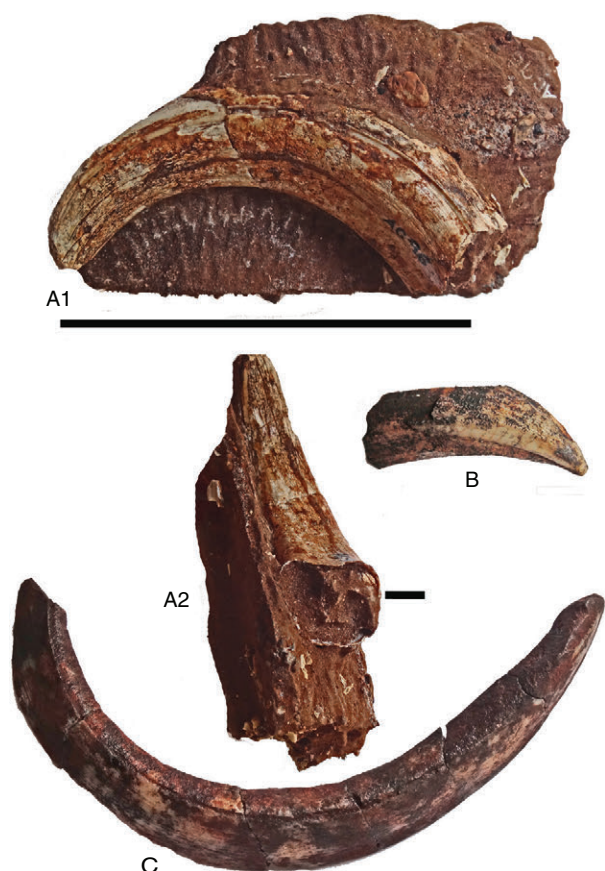
Fig. 5.—Suid canines from Aves Cave I, Bolt's Farm Palaeokarst System, attributed to *Potamochoeroides hypsodon*. A) AC 96, left C1/, A1 - dorsal view, A2 - view of radicular end; B) AC 107, left upper canine, ventral view; C) AC 202, left lower canine, lingual view (scale 10 cm and 10 mm).

A deeply worn M1/ from Aves Cave I (AC 257) shows only the remnants of the median transverse valley and the deepest parts of the foveae between the protocone and the paracone in the anterior loph, and between the hypocone and metacone in the posterior one. There are also remnants of the valleys between the lingual main cusps and the mesial and distal cingula. This tooth shows a short accessory rootlet on its mesial side.

The M2/ in AC 231 shows the same basic crown morphology as the M1/ but being completely unworn it is possible to determine that the apices of all the main cusps are scored by superficial slits, in addition to the Furchen. The same can be observed in AC 297, an unworn but slightly damaged right M2/.

Permanent lower cheek dentition:

The lower cheek teeth of suids are poorly represented at Aves Cave I, with only one premolar being attributable to *Potamochoeroides hypsodon* (AC 143). The crown is narrow, with low anterior and posterior accessory cusps. There is an Innenhügel just behind and slightly lingual to the main cusp and the two roots are close together.

Description of a mandible of *Potamochoeroides hypsodon* from Pit 14, Bolt's Farm (Figs. 7, 8)

Since the sample of lower cheek teeth from Aves Cave I is so restricted, a description of a much more complete specimen (TM BF 3 14-342) from the Old Collections (Bolt's Pit 14) is given (Table 3). Cooke (1993) already mentioned and illustrated this mandible, but a more detailed description and interpretation is warranted.

The place where p/2 would have been positioned is damaged, so it is not clear whether this tooth was present or not, although other samples from Makapansgat show that this tooth was usually present. The p/3 has a tall main cusp with low mesial and distal cusplets about half the height of the main cusp. The cingula are swollen such that shallow hollows are formed buccally and lingually. The distal crest is beaded. The main cusp is slightly mesially positioned with respect to the two roots. The p/4 has a tall main cusp with a distinctly offset Innenhügel. The posterior accessory cusplet is almost as tall as the main cusp (ca 4/5ths its height). The anterior accessory cusplet is lower, being only 2/3rds the height of the main cusp. The disto-buccal hollow has a small but tall pillar, and the distal crest is subdivided. The m/1 is deeply worn and is missing part of the anterior buccal cusp. The anterior and median accessory cusplets are clear, but the distal one has been worn away. The lingual part of the median transverse valley is broad, the buccal one is almost worn down to its base. The m/2 is lightly worn and shows classic suid lower molar morphology of four main cusps scored by Furchen, and anterior, median and posterior accessory cusplets in the midline of the crown. The tooth is however, appreciably more hypsodont than teeth of *Dasychoerus verrucosus*, for example. The lingual notch is broad, the buccal one narrower. The distal cingulum is beaded, forming the beginning of columns.

The m/3 was in its crypt, and has been developed out by removing the surrounding bone. The front part is similar in morphology and cusp layout to the m/2, save for the presence of a groove on the lingual side of the metaconid. It is much taller than the m/2. The anterior and posterior cristids of the main cusps (protoconid, metaconid, entoconid, hypoconid) have a tendency to form pillars separated from the central part of the cuspid by narrow but not very deep slits. The cervix is sub-parallel to the occlusal surface. The talonid is comprised of a tall beaded cingular complex behind the hypoconulid but slightly lower than it. The canine section in this specimen is intermediate between scrofic and verrucosic kinds and the jaw is markedly thickened laterally as in *Dasychoerus* and *Kolpochoerus*.

Postcranial skeleton

The suid postcranial skeletal remains found at Aves Cave I are typically suid-like in overall morphology (Figs. 9, 10, 11; Table 4). The distal humerus has well-formed trochlea and conoid parts separated by quite deep parallel grooves indicating that movements at the elbow joint were largely restricted to the parasagittal plane, with little if any pronation or supination movements possible at this joint. This is confirmed by the morphology of the proximal part of the ulna which shows a solid, well-constrained sigmoid articulation for the distal humerus.
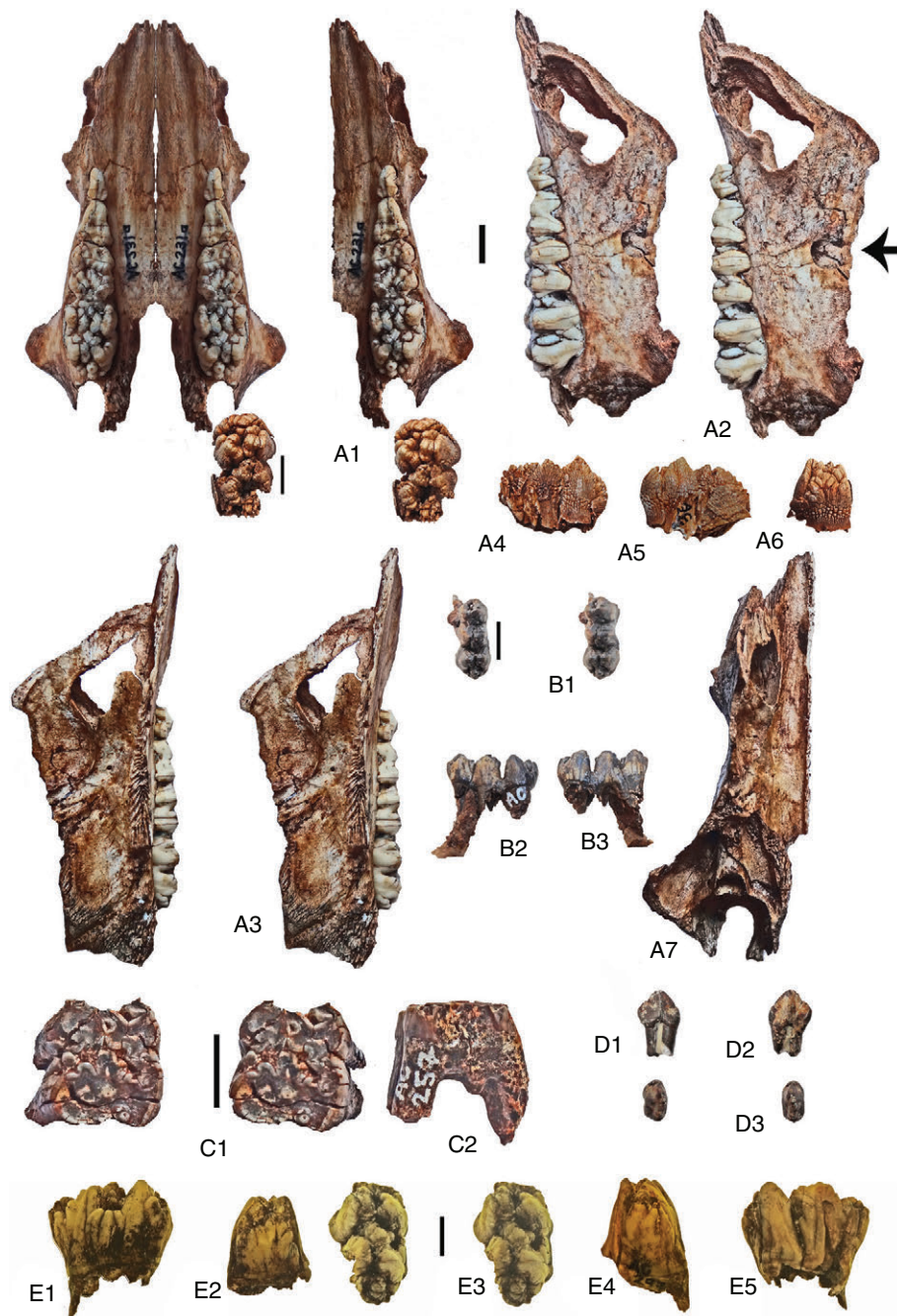
Fig. 6.—Suid cheek teeth from Aves Cave I, Bolt's Farm Palaeokarst System, attributed to *Potamochoeroides hypsodon*. A) AC 231, left maxilla containing erupted D2/-D4/ and M1/, and M2/ in crypt, A1) stereo occlusal view and mirror image reconstruction of palate, A2 - stereo buccal view, A3 - stereo lingual view, A4 - lingual view of M2/, A5 - buccal view of M2/, A6 - mesial view of M2/, A7 - dorsal view; B) AC 1, left d/4, B1 - stereo occlusal view, B2 - buccal, B3 - lingual view; C) AC 257, right M1/, C1 - stereo occlusal view, C2 - mesial view to show small additional rootlet; D) AC 143, right p/3, D1 - buccal, D2 - lingual, D3 - stereo occlusal view; E) AC 297, right M2/, E1 - lingual, E2 - mesial, E3 - stereo occlusal view, E4 - distal view, E5 – buccal view (scale : 10 mm).

Table 2.—**Measurements (in mm) of suid teeth from Aves Cave I, Bolt's Farm, South Africa. (Own are the author's measurements)**

Aves Cave I Suids	Tooth	Length	Breadth	Taxon	Data source
AC 359	di/1 rt	4.3	3.8	*Potamochoeroides hypsodon*	Own, 2015
AC 1	d/4 lt	21.2	9.7	*Potamochoeroides hypsodon*	Own, 2011
AC 283	i/1 lt	6.0	8.2	*Potamochoeroides hypsodon*	Own, 2015
AC 41	i/1 lt	6.5	7.4	*Potamochoeroides hypsodon*	Own, 2015
AC 149	i/2 rt	6.7	7.7	*Potamochoeroides hypsodon*	Own, 2015
AC 356	i/3 lt	--	5.4	*Potamochoeroides hypsodon*	Own, 2015
AC 258	p/3 rt	12.7	6.7	*Notochoerus capensis*	Own, 2015
AC 143	p/3 rt	10.8	6.0	*Potamochoeroides hypsodon*	Own, 2013
AC 372	p/4 lt	--	9.0	*Notochoerus capensis*	Own, 2015
AC 357	p/4 rt	16.0	10.6	*Notochoerus capensis*	Own, 2015
AC 100	m/2 lt	30.6	18.1	*Notochoerus capensis*	Own, 2013
AC 29	m/3 rt	--	18.5	*Notochoerus capensis*	Own, 2013
AC 231	D2/ lt	8.7	5.3	*Potamochoeroides hypsodon*	Own, 2015
AC 231	D3/ lt	12.5	9.4	*Potamochoeroides hypsodon*	Own, 2015
AC 231	D4/ lt	15.8	12.3	*Potamochoeroides hypsodon*	Own, 2015
AC 257	M1/ rt	18.0	16.4	*Potamochoeroides hypsodon*	Own, 2015
AC 144	I1/ lt	17.0	5.7	*Potamochoeroides hypsodon*	Own, 2015
AC 334	I1/ lt	16.0	7.4	*Potamochoeroides hypsodon*	Own, 2015
AC 134	I1/ rt	12.5	5.5	*Potamochoeroides hypsodon*	Own, 2015
AC 227	I2/ rt	18.3	5.7	*Potamochoeroides hypsodon*	Own, 2015
AC 96	CM/ lt	25.3	23.2	*Potamochoeroides hypsodon*	Own, 2015
AC 231	M1/ lt	20.8	14.3	*Potamochoeroides hypsodon*	Own, 2015
AC 18	M1/ rt	16.0	17.3	*Potamochoeroides hypsodon*	Own, 2015
AC 231	M2/ lt	--	16.6	*Potamochoeroides hypsodon*	Own, 2015
AC 123	M2/ rt	--	19.6	*Notochoerus capensis*	Own, 2013
AC 18	M2/ rt	27.0	--	*Potamochoeroides hypsodon*	Own, 2015
AC 297	M2/ rt	30.5	22.2	*Potamochoeroides hypsodon*	Own, 2015
AC 31	M2/ rt	--	22.7	*Potamochoeroides hypsodon*	Own, 2015
AC 165	M3/ rt	67.0	29.0	*Notochoerus capensis*	Own, 2013

The shaft of the ulna is remarkably curved. The distal radius is poorly preserved but does not appear to show any of the morphology associated with hyperflexion of the carpal complex that exists in the warthog (*Phacochoerus*) and *Metridiochoerus* (Pickford, 2013b).

From Aves Cave I, the calcaneum (AC 105) attributed to *Potamochoeroides hypsodon* on the basis of its dimensions and discovery locus, has a robust tuber calcis, and the lateral talar articulation shows a strong process which interlocks with the talus. The sustentaculum is thick. This morphology indicates that the ankle joint was highly stabilised and that movements at the joint were largely constrained to the parasagittal plane.

The only suid talus available from Aves Cave I is a fragment articulated with an ankle joint (AC 60) (Fig. 12) comprising the distal tibia, talus fragment, calcaneum fragment and several metatarsals, sesamoids and phalanges. The talus is compatible in dimensions with specimens of *Potamochoeroides hypsodon* from Makapansgat (Fig. 13), being slightly larger than tali of *Potamochoerus porcus* from South Africa (sometimes called *Potamochoerus larvatus*, but generally considered to belong to *Potamochoerus porcus* : Skinner & Smithers, 1990 (there exists some overlap in dimensions, but two out of three specimens of *Po. hypsodon* are larger than the talus of *Potamochoerus porcus*). These tali are larger than all specimens of southern African *Phacochoerus aethiopicus* measured (sometimes referred to *Phacochoerus africanus*, but most authorities refer the southern African warthog to *Phacochoerus aethiopicus* Roberts, 1951). In contrast, a talus from Swartkrans attributed to *Phacochoerus modestus*, fits into the range of variation of the extant warthog.

Since body weight and talar dimensions in suids (and in artiodactyls in general, Pickford, 2013b) appear to be closely correlated, it is inferred that *Potamochoerides hypsodon* would have been somewhat heavier and more massive than extant *Potamochoerus porcus* and *Phacochoerus aethiopicus*. In contrast, *Notochoerus capensis* with tali almost double the size of those of warthogs, would have been a huge animal, well over

Fig. 7.—TM BF 3 14-342, right mandible of *Potamochoeroides hypsodon from* Bolt's Pit 14, A) stereo buccal, B) stereo lingual view (scale : 5 cm).
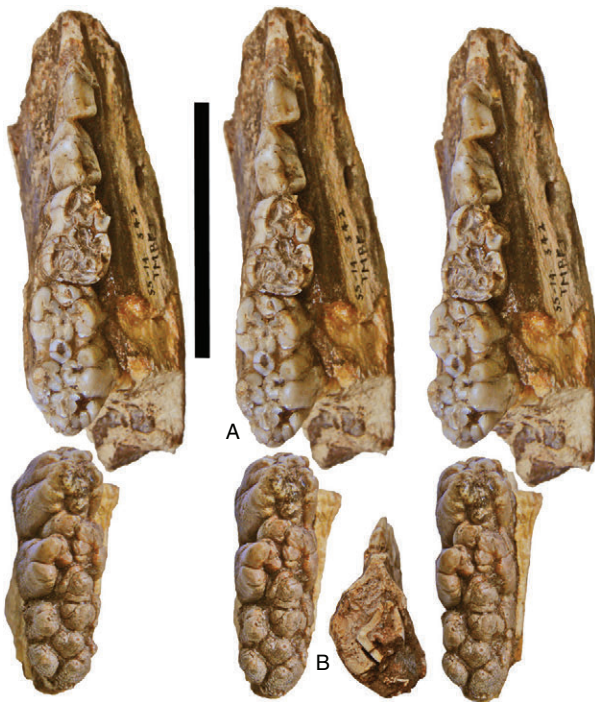

Fig. 8.—TM BF 3 14-342, right mandible of *Potamochoeroides hypsodon* from Bolt's Pit 14, A) stereo triplet of the occlusal view and B) anterior view showing the section of the canine (scale : 5 cm).

500 kg. Pickford (2013b) calculated a body weight of between 270 and 380 kg for *Metridiochoerus andrewsi* from Gondolin, based on body weights of extant suids from Southern Africa (Smithers, 1983). Somewhat greater body weights for the extinct taxa would result if MacDonald's (2001) data on the body weights of extant species are used.

The Aves Cave I metacarpals attributed to *Potamochoeroides hypsodon* are typical of suids in general, being close in overall morphology to those of *Potamochoerus porcus*. The distal flange in the lateral metapodial is not as salient as it is in specimens of *Metridiochoerus* (Pickford, 2013b). The presence of *Potamochoeroides hypsodon* in the Bolt's Farm Palaeokarst System is confirmed by the present study (Fig. 14).

Discussion

Cooke (1993) already identified this suid in the collection from Bolt's Farm Pit 14, which is likely the same deposit as the one at Aves Cave I, but he called it *Potamochoeroides shawi*. However, the type species of the genus is *Potamochoeroides hypsodon* Dale, 1948, whereas the name *shawi* Dale, 1948, was first attached to the genus *Pronotochoerus* Leakey, 1943. The nomenclatural issues were sorted out by Pickford (2013a). Pickford (2012) thought that there might be two species of *Potamochoeroides* at Makapansgat, an earlier species *Potamochoeroides hypsodon*, and a later, more hypsodont one, *Potamochoeroides shawi*, but the available fossils do not permit a clear indication to be reached. The specimens from Bolt's Farm Palaeokarst System do not help to resolve the issue, although the dimensions of the talus and the teeth support attribution to a species larger than the extant warthogs from southern Africa. Cranial material would settle the debate.

Potamochoeroides hypsodon has a thickened mandibular ramus, a feature that links it to the Eurasian genus *Dasychoerus*, which entered Africa during the Early Pliocene, whereupon it radiated, giving rise to the *Kolpochoerus* lineage, as well as to *Potamochoeroides* (Pickford, 2012).

The talus and other post-cranial bones of *Potamochoeroides hypsodon* reveal that it was on average somewhat larger than the bush pig, *Potamochoerus porcus*, and the warthog, *Phacochoerus africanus*. Its locomotion would have been close to that of *Potamochoerus*, as the distal radius appears not to show any of the carpograde adaptations that typify the warthog (*Phacochoerus*).

Table 3.—**Measurements (in mm) of suid teeth from Bolt's Farm, South Africa (old collections)**

Bolt's Farm Old Collections	Tooth	Length	Breadth	Taxon	Data source and comments
TM BF 3 14-342	c/1 rt	18.5	13	*Po. hypsodon*	Own, 2011
TM BF 3	p/3 rt	10.5	5.7	*Po. hypsodon*	Own, 2011; Cooke, 1993 as 11 x 5.5, BF 14-342
TM BF 3	p/4 rt	12.5	8.8	*Po. hypsodon*	Own, 2011; Cooke, 1993 as 13 x 9, BF 14-342
TM BF 1?	p/4 rt	11.4	7.8	*M. andrewsi*	Own, 2011; Cooke, 1993 as 11.1 x 7.8
TM BF 1?	m/1 lt	--	14.5	*M. andrewsi*	Own, 2011
TM BF 1?	m/1 rt	18.0	13.0	*M. andrewsi*	Own, 2011; Cooke, 1993 as 17.4 x 13
TM BF 3	m/1 rt	17.2	12.3	*Po. hypsodon*	Own, 2011; Cooke, 1993 as 17 x 12.5, BF 14-342
TM BF 1?	m/2 lt	32.0	15.2	*M. andrewsi*	Own, 2011
TM BF 1?	m/2 rt	31.5	16.0	*M. andrewsi*	Own, 2011; Cooke, 1993 as 22 x 16.7
TM BF 3	m/2 rt	26.1	15.4	*Po. hypsodon*	Own, 2011; Cooke, 1993 as 27 x 15.5, BF 14-342
TM BF 1?	m/3 lt	69.0	14.5	*M. andrewsi*	Own, 2011; Cooke, 1993 as 57 x 16
TM BF 2	m/3 lt	--	19.0	*M. andrewsi*	Own, 2011; Cooke, 1993 as 70 x 21
TM Bolt's 'A'	m/3 lt	--	--	*M. andrewsi*	Own, 2011
TM BF 3	m/3 rt	46.6	16.0	*Po. hypsodon*	Own, 2011; Cooke, 1993 as 47.5 x 17, BF 14-342
TM BF 3-335	m/3 lt	46.4	14.3	*Ph. modestus*	Own, 2011
ESI (BPI) Bolt's Farm	D3/ lt	11.0	7.5	*Po. hypsodon*	Own, 2011
TM BFW 14	D3/ lt	10.3	8.0	*Po. hypsodon*	Own, 2014
ESI (BPI) Bolt's Farm	D4/ lt	13.8	9.0	*Po. hypsodon*	Own, 2011
TM BFW 14	D4/ lt	13.6	10.0	*Po. hypsodon*	Own, 2014
UCMP 69515	P3/ lt	12.5	10.5	*Po. hypsodon*	Cooke, 1993
UCMP 69513	P3/ lt	11.1	9.5	*Po. hypsodon*	Cooke, 1993
UCMP 69512	P3/ lt	12.0	10.5	*Po. hypsodon*	Cooke, 1993
UCMP 69512	P4/ lt	11.0	13.0	*Po. hypsodon*	Cooke, 1993
ESI (BPI) Bolt's Farm	M1/ lt	18.3	12.0	*Po. hypsodon*	Own, 2011
TM BFW 14	M1/ lt	17.5	12.0	*Po. hypsodon*	Own, 2014
UCMP 69512	M1/ lt	18.5	17.0	*Po. hypsodon*	Cooke, 1993
UCMP 69514	M2/ rt	32.0	21.0	*Po. hypsodon*	Cooke, 1993
UCMP 69516	M2/ lt	31.0	22.0	*Po. hypsodon*	Cooke, 1993
TM BF 1?	M2/ lt	36.0	17.7	*M. andrewsi*	Own, 2011; Cooke, 1993 as 35.5 x 22.2
TM BF 1?	M2/ rt	36.0	17.7	*M. andrewsi*	Own, 2011; Cooke, 1993 as 35.1 x 20
TM BF 1?	M3/ lt	60.0	21.0	*M. andrewsi*	Own, 2011; Cooke, 1993 as 59 x 21
TM BF 1?	M3/ rt	56.0	22.0	*M. andrewsi*	Own, 2011; Cooke, 1993 as 58 x 21.5
TM BF 3-335	M3/ lt	51.5	16.8	*Ph. modestus*	Own, 2011; Cooke, 1993 as 52.5 x 17
TM BF 3-335	M3/ rt	47.8	14.7	*Ph. modestus*	Cooke, 1993

The fact that the cheek dentition of *Potamochoeroides hypsodon* is, as its name implies, hypsodont, indicates that this species was most likely to be a herbivore that included a significant fraction of grass in its diet (Ewer, 1958a). It was likely an opportunistic feeder, like the warthog is today (Ewer, 1958b), but for certain periods of the year it would have subsisted largely or solely on grass. It would be of interest to test this hypothesis using stable isotope markers or micro-wear analysis, but these approaches are beyond the scope of this paper. The lower incisors show a mesial bend between the root and the crown, which exposes the distal edge of the crown towards the front, much as the lower incisors of warthogs are bent mesially. In functional terms, this reorientation of the crown increases the length of the incisive cutting edge, but it requires the development of a spatulate mandibular symphysis to accommodate the teeth. Mandibles of *Potamochoeroides hypsodon* from Makapansgat show that the symphysis was indeed extremely short and spatulate.

The presence of *Potamochoeroides hypsodon* at Aves Cave I indicates that the deposits probably accumulated at about the same geological time span as the breccias at Makapansgat (3.0 Ma - 2.7 Ma, Pickford, 2006; or 3.03 Ma - 2.58 Ma, Herries et al., 2013).

Fig. 9.—Distal humerus and proximal ulna of *Potamochoeroides hypsodon*, from Aves Cave I, Bolt's Farm Palaeokarst System. A) AC 174, distal humerus, anterior stereo view; B) AC 131, left ulna, B1 - medial view, B2 - anterior view, B3 - lateral view; C) AC 263, left distal radius, C1 - stereo distal view, C2 - stereo volar view (scale : 5 cm).

Genus *Notochoerus* Broom, 1925

Type species- *Notochoerus capensis* Broom

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 of fossils from Aves Cave I and Makapansgat (Figs. 15, 16, 17, 18)

Premolars:

The right p/3 (AC 258) has a tall main cusp and low mesial and distal cusplets. The distal cusplet is swollen, and the low cingular swellings anteriorly and posteriorly border low depressions (foveae) in the crown. There are two strong roots.

The p/4 (AC 357) is unworn, and shows the morphology well. The main cusp is positioned above the gap beween the two roots, and it is accompanied by a small Innenhügel located

slightly behind and lingually to the main cusp. The anterior cusplet, which is an enlarged precristid, is almost as tall as the main cusp. The posterior cusplet is also tall, but not as much as the anterior cusplet, and it is accompanied by a distal cingulum which rises as high as it.

No upper premolars of *Notochoerus capensis* have been found at Aves Cave I, but there is a specimen from Makapansgat which is worth describing. ESI (BPI) M 6916, is triangular in occlusal outline with rounded corners. The main cusp is robust, occupying almost half the volume of the crown. It is accompanied by a swollen anterior cingular cusplet which forms a tall mesial hook. There is a large bucco-distal cusp behind the main cusp which is accompanied by a small low cingular bead buccally, and by a beaded cingulum lingually. The lingual cingulum encloses a shallow distal fovea.

Molars:

A left m/2 from Aves Cave I (AC 100) is unworn, and shows the crown morphology clearly. The roots had started to form at the time of death. The tooth is comprised of four main cusps arranged in two lophids, with anterior, median and posterior accessory cusplets in the mid-line of the crown, and there are mesial and distal cingula. The lingual and buccal notches (i.e. the ends of the median transverse valley) between the two lophids are broad apically and narrow gently towards cervix. They stop short well above the cervix, about one third of the height of the crown on the lingual side. There are no basal pillars in either end of the median transverse valley. The cervix is only slightly shorter mesio-distally than the longest part of the tooth which is at the level of the anterior and posterior accessory cusplets. This is a major difference from *Metridiochoerus*, in which the mesio-distal dimension at the cervix is considerably smaller that at the level of the accessory cusplets. The Furchen are not deeply incised into the cusps, although there are slight incisions into the apices of the cusps.

The upper third molar from Aves Cave I (AC 165) lacks the anterior loph. It is moderately worn anteriorly, but the most distal part of the talon is unworn. The hypocone and metacone have shallow Furchen and the cusps are not flattened buccally except near cervix. The median accessory cusplet has a distal extension which invades the space between the metacone and hypocone. In buccal and lingual views, the cervix is seen to be oriented at a marked angle to the occlusal surface. In radicular view, the apices of the foveae (capsules) are clearly formed and terminate close to cervix level.

The lower third molar of *Notochoerus capensis* from Aves Cave I (AC 29) is broken anteriorly and the remaining fragment comprises essentially the talonid. It is moderately worn right to the distal end. The tooth is extremely hypsodont and the posterior part of the cervix is subparallel to the occlusal surface, as is usually the case in lower third molars.

Post-cranial skeleton

On the basis of dimensions and discovery locale, the only post-cranial bone from Aves Cave I that can be attributed to *Notochoerus capensis* is a distal metapodial epiphysis and a short part of the diaphysis (AC 307). The breadth of the distal

Fig. 10.—Metapodials of *Potamochoeroides hypsodon* from Aves Cave I, Bolt's Farm Palaeokarst System A) AC 195, left MC IV, A1 - proximal view, A2 - distal view, A3 - axial view, A4 - stereo dorsal view, A5 - abaxial view, A6 - volar view; B) AC 360, right MT IV, B1 - proximal view, B2 - distal view, B3 - axial view, B4 - stereo dorsal view, B5 - abaxial view, B6 - volar view; (scale : 10 mm).

articulation is 22 mm, compared with breadths of ca 16 - 18 mm in *Potamochoeroides hypsodon* from Aves Cave I.

Discussion

Even though *Notochoerus capensis* is rare at Aves Cave I, the sample is valuable in that it supports the recent view (Pickford, 2013c) that the genus belongs to the Suinae rather than to the Tetraconodontinae as thought by most researchers for the past half century since Leakey (1958) put the genus into the latter subfamily. The Aves Cave I specimens provide new evidence that confirms the subfamily status of the genus, because the sample contains the first known p/3 and p/4 of the species which clearly demonstrate that it is not a tetraconodont, all of which have enlarged p/3 and

p/4. The morphology of the lower premolars from Aves Cave I accord with those of suines, in particular those which have an offset Innenhügel in the p/4. An upper third premolar from Makapansgat strengthens this conclusion, as it too shows suine rather than tetraconodontine morphology (Fig. 15D).

The hypsodont molars of *Notochoerus* suggest that it was including a substantial proportion of grass in its diet, yet the m/2 from Aves Cave I is not excessively hypsodont, much less so that the teeth of *Metridiochoerus*.

Notochoerus was a huge suine, the tali from Makapansgat suggesting a body weight in excess of 500 kg.

Fig. 11.—AC 105, right calcaneum of *Potamochoeroides hypsodon* from Aves Cave I, Bolt's Farm Palaeokarst System, A) caudal view, B) stereo medial view, C) lateral, D) cranial view (scale 10 mm).

Distinguishing *Potamochoeroides* from *Metridiochoerus*

There has been debate about the status of the genus *Potamochoeroides* Dale, 1948. Ewer (1958a) accepted its validity and declared *Pronotochoerus shawi* to belong to it. Cooke & Wilkinson (1978) proposed that there were three species: *Potamochoeroides shawi*, *Metridiochoerus jacksoni* and *Metridiochoerus andrewsi*. Harris & White (1979) considered that all the material attributed to *Potamochoeroides* represented an early stage (Stage 1) of the *Metridiochoerus andrewsi* lineage, which they envisaged as having three stages, with *M. jacksoni* representing Stage 2 and the type species representing Stage 3. Cooke (1993) discussed the issue and adhered to his previous views on the matter, but without providing any new evidence. Bender (1992) resurrected the genus *Potamochoeroides* on

the basis of cranial and mandibular differences from *Metridiochoerus*. Cooke (2005) entered into great detail about the question, providing a convincing demonstration of the existence of significant differences between the crania and mandibles of the genera, but, despite the differences, he maintained his view that the two "genera" could be subsumed under *Metridiochoerus*. Pickford (2006) accepted the opinion of Harris & White (1979) that the two genera were synonymous, but noted that this made the chronological range of the species much longer than that of most other suid lineages in Africa.

Undescribed fossils from Swartkrans and Makapansgat and the specimens from Aves Cave I described herein, provide additional evidence that the genera are distinct. In particular, the evidence from the deciduous cheek dentition is important, as it reveals that *Potamochoeroides* has rather typical suine deciduous molars not very different from the ancestral condition seen in *Dasychoerus arvernensis*, whereas *Metridiochoerus* has d/4 morphology that is well outside the "norm" for suines, having a greatly elongated and much more hypsodont third lophid than "normal" suids do, while there is a proliferation of small cuspules along the midline of the crown, and the buccal and lingual cuspids are flattened and heightened as in the permanent molars. Furthermore, the specimens are complete enough to reveal that *Metridiochoerus* has lost the two anterior premolars (p/1 and d/2) whereas *Potamochoeroides* has lost only the anteriormost one (p/1) although some individuals retain it, (Cooke, 2005). *Dasychoerus*, the likely ancestor of *Potamochoeroides*, retains a full complement of premolars. The trend towards shortening the post-canine diastema of the mandible that is observed in *Potamochoeroides* is taken to extreme in *Metridiochoerus*. It is also interesting to note that the mandibular ramus is greatly thickened in *Potamochoeroides*, even in the juveniles, and this character links the genus to *Dasychoerus*, one of the defining characters of which is the pachygnathic lower jaw, a feature that also links *Dasychoerus* to the genus *Kolpochoerus* (Pickford & Obada, 2016).

Given the magnitude of the dental and dentary differences between the Swartkrans jaws on the one hand and those from Aves Cave I and Makapansgat on the other, it is realistic to

Table 4.—**Measurements (in mm) of suid postcranial bones from Aves Cave I, Bolt's Farm, South Africa. (MC - Metacarpal; MT - Metatarsal; Pb - Proximal breadth; Ph - Proximal height; Db - Distal breadth; Dh - Distal height)**

| Catalogue : Bone	Taxon	Length	Pb	Ph	Db	Dh
AC 307 : axial metacarpal	*N. capensis*	--	--	--	22.0	15+
AC 249 : left MC III	*Po. hypsodon*	75.0	17.0	16.8	16.5	18.2
AC 24+236 : right MC IV	*Po. hypsodon*	67.2	17.0	13.4	16.6	17.2
AC 250 : left MC IV	*Po. hypsodon*	72.0	19.2	17.7	18.4	17.8
AC 195 : left MC IV	*Po. hypsodon*	69.0	18.0	16.8	16.8	17.8
AC 289 : right tibia	*Po. hypsodon*	--	--	--	27.2	27.3
AC 105 : right calcaneum	*Po. hypsodon*	70.0	--	31.5	--	--
AC 60 : right talus	*Po. hypsodon*	--	22.3	--	--	--
AC 60 : right MT III	*Po. hypsodon*	80.2	16.4	23.0	16.0	--
AC 360 : right MT IV	*Po. hypsodon*	76.4	18.5	22.4	15.8	18.6
AC 60 : right MT V	*Po. hypsodon*	56.6	--	--	--	--
AC 60 : right Ist phalanx III	*Po. hypsodon*	36.0	18.5	--	--	--
AC 60 : right Ist phalanx IV	*Po. hypsodon*	23.3	--	--	14.0	--
AC 364 : axial phalanx	*Po. hypsodon*	31.0	16.5	15.8	13.0	9.6
AC 174 : distal humerus	*Po. hypsodon*	--	--	--	33.0	--
AC 131 : proximal ulna	*Po. hypsodon*	--	--	45.8	--	--
AC 264 : distal radius	*Po. hypsodon*	--	--	--	42.3	25.0
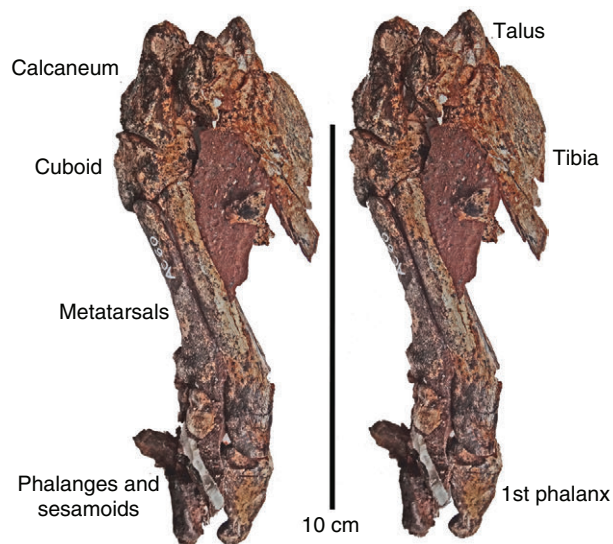
Fig. 12.—AC 60, stereo lateral view of articulated ankle joint and foot of *Potamochoeroides hypsodon* from Aves Cave I, Bolt's Farm Palaeokarst System (scale : 10 cm).

recognise that the Makapansgat suids belong to a genus distinct from *Metridiochoerus*, as was already realised by Bender (1992). The species should be called *Potamochoeroides hypsodon* and not *Potamochoeroides shawi* because the type species of the genus is *Po. hypsodon*. This point was already discussed by Pickford (2013a).

The maxillary deciduous and permanent teeth confirm the inferences made on the basis of the mandible. The D4/ of SK R 14131 (*Metridiochoerus andrewsi*) is so deeply worn that most crown details have been eradicated. The unerupted second upper molar, however, shows a much expanded hypoconule (posterior accessory cusplet) which overhangs the distal edge of the cervix by a large margin, and a more hypsodont crown than that of *Potamochoeroides*.

General Discussion on Suidae from Bolt's Farm Palaeokarst System

The fossil suids from Aves Cave I, Bolt's Farm Palaeokarst System, South Africa, belong to two taxa, *Potamochoeroides hypsodon* and *Notochoerus capensis* (Table 1). It should be noted that *Notochoerus capensis* is not a tetraconodont as was thought by most researchers for the past half century after it was transferred to this subfamily by Leakey (1958) but is a suine (Pickford, 2013c). The Aves Cave I specimens provide confirmation of the subfamily status of the genus, because the sample contains the first known premolars of the species from South Africa, revealing its affinities with suines rather than with tetraconodonts. Most of the East African fossils previously called *Notochoerus*
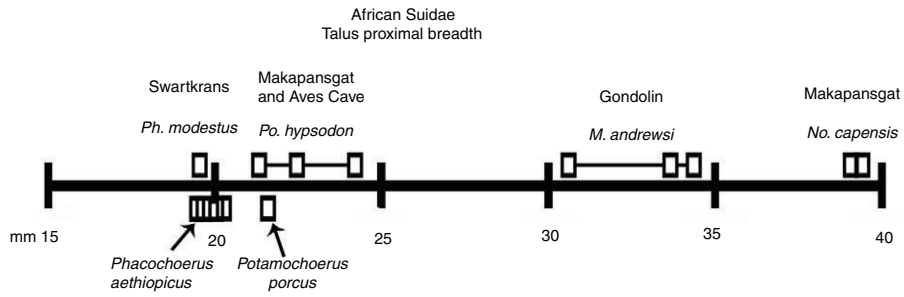
Fig. 13.—Proximal talar breadth of extant and fossil African Suidae. Below the line are specimens of extant *Phacochoerus aethiopicus* and *Potamochoerus porcus* from Southern Africa, while above the line are fossils from karst infillings at Swartkrans (*Phacochoerus modestus*) Makapansgat (*Potamochoeroides hypsodon* and *Notochoerus capensis*) Aves Cave I (*Potamochoeroides hypsodon*) and Gondolin (*Metridiochoerus andrewsi*).

Fig. 14.—Pedal bones from Aves Cave I, Bolt's Farm Palaeokarst System, attributed to *Potamochoeroides hypsodon* (A-D) and *Notochoerus capensis* (E). A) AC 289, right distal tibia, A1 - anterior view, A2 - stereo distal view; B) AC 24+236, right MT IV, B1 - axial view, B2 - stereo dorsal view, B3 - stereo volar view, B4 - abaxial view; C) AC 235, lateral metapodial, C1 - axial view, C2 - distal view, C3 - stereo dorsal views, C4 - abaxial view, C5 - plantar view; D) AC 364, axial 1st phalanx, D1 - proximal view, D2 - distal view, D3 - abaxial view, D4 - dorsal view, D5 - axial view, D6 - volar view; E) AC 307, distal end of axial metacarpal, stereo dorsal view (scale : 10 mm).

Fig. 15.—Dental specimens of *Notochoerus capensis* from Aves Cave I, Bolt's Farm Palaeokarst System (A-C) and from Makapansgat (D). A) AC 258, right mandible fragment containing right p/3, A1 - buccal, A2 - stereo occlusal, A3 - lingual view; B) AC 357, right p/4, B1 - buccal, B2 - stereo triplet of the occlusal view, B3 - lingual view; C) AC 100, left m/2, C1 - lingual, C2 - stereo occlusal, C3 - buccal view, C4 - mesial view, C5 - distal view; D) ESI (BPI) M 6916, right P3/, D1 - buccal view, D2 - stereo occlusal view, D3 - lingual view (scale : 10 mm).

belong instead to Tetraconodontinae, as shown by their premolar morphology, and should be called *Gerontochoerus* Leakey, 1943, the senior name for these suids.

Once the admixture of fossils from Bolt's Farm and Sterkfontein has been taken into account, the old collections of suids genuinely from Bolt's Farm contain three taxa, *Metridiochoerus andrewsi* Hopwood 1926, *Potamochoeroides hypsodon* Dale 1948, and *Phacochoerus modestus* (Van Hoepen & Van Hoepen, 1932) (Table 1) (Cooke, 1993). From this it is concluded that the karst infillings at Bolt's Farm Palaeokarst System span a considerable period of time, with an older assemblage yielding *Potamochoeroides hypsodon* and *Notochoerus capensis* Broom, 1925, and

younger assemblages yielding *Metridiochoerus andrewsi* and *Phacochoerus modestus*.

The Aves Cave I assemblage belongs to the older series of karst infillings, probably co-eval with Makapansgat, or at least not very different in age from it. The Aves Cave I fauna is older than those from the nearby cave fills at Kromdraai, Sterkfontein, Swartkrans and Gondolin (Pickford, 2012, 2013a, b).

As its species name implies, *Potamochoeroides hypsodon* shows a distinct tendency towards cheek tooth hypsodonty, a process that reached its culmination in the extremely hypsodont suids such as *Notochoerus capensis* and *Metridiochoerus andrewsi*. *Phacochoerus modestus* is also a very hypsodont taxon. From this it is concluded that there
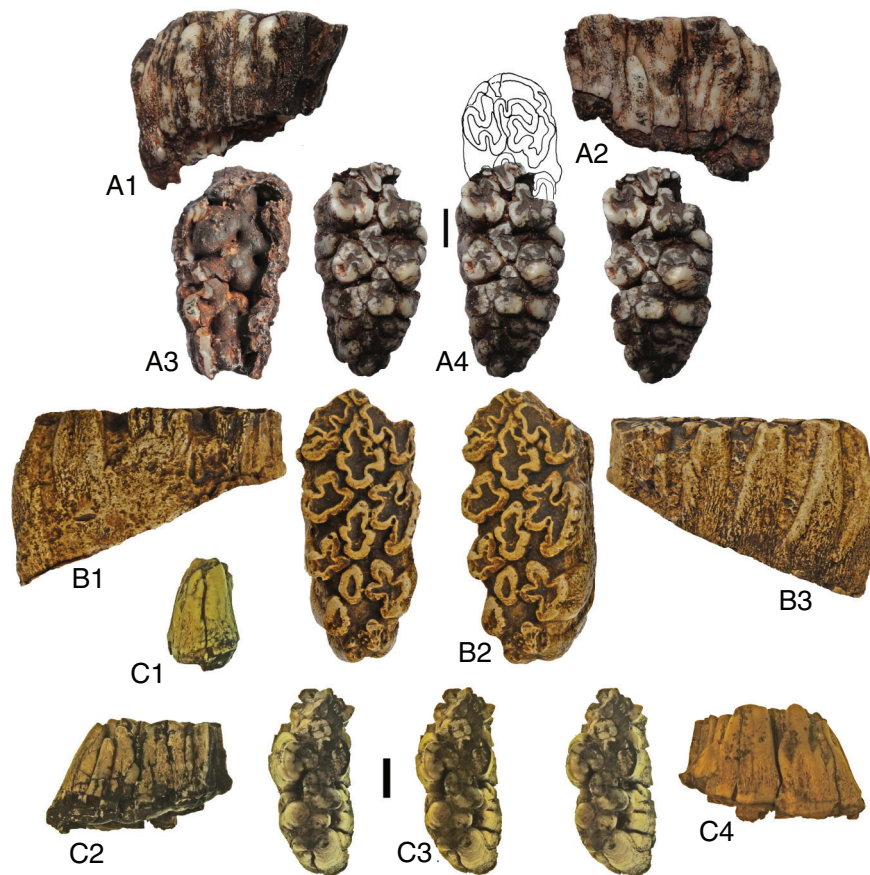
Fig. 16.—Third molars of *Notochoerus capensis* from Aves Cave I (A, C) and Makapansgat (B). A) AC 165, right M3/ lacking the anterior loph, A1 - lingual, A2 - buccal, A3 - radicular, A4 - stereo triplet occlusal view; B) PEM 1436/3, cast of holotype right M3/ from Longlands, B1 - lingual, B2 - stereo occlusal view, B3 - buccal view; C) AC 29, right m/3 fragment, C1 - distal, C2 - buccal, C3 - stereo triplet view of the occlusal surface, C4 - lingual view (scales : 10 mm).

was abundant grass in the Bolt's Farm area, not only during the early phase of karst infilling, but also during the later phases during which the grass cover may have comprised a greater fraction of the vegetation than during the earlier phase. Future research on stable isotopes in enamel and studies of dental microwear would perhaps throw light on the hypothesis.

Biochronology

Shaw (1938) thought that *Notochoerus capensis* syn. *meadowsi* at Sterkfontein (the fossils he studied were probably from Bolt's Farm) indicated an age similar to the Vaal River Gravels at Longlands, in sharp contrast to Broom's (1925, 1928) opinion that the Transvaal Cave deposits were Upper

Pleistocene and the Vaal Gravels Lower Pleistocene or even Pliocene. Ewer (1956) commented upon the value of fossil suids from Bolt's Farm for determining the age of the deposits. She concluded that *Tapinochoerus meadowsi* is a typically middle Pleistocene species, probably correlating to the Upper Villafranchian. Cooke (1993) wrote that various pockets of sediment at Bolt's Farm were of diverse ages. He recorded *Potamochoeroides shawi*, *Phacochoerus modestus* and *Metridiochoerus* cf *jacksoni* from Bolt's Farm, but did not enter into great detail about the biochronological significance of the fossils. He mentioned that the *Metridiochoerus* specimens would fit with an age of ca 2 Ma. He wrote that at Olduvai Gorge, Tanzania, *Phacochoerus modestus* ranges in age from Bed I to
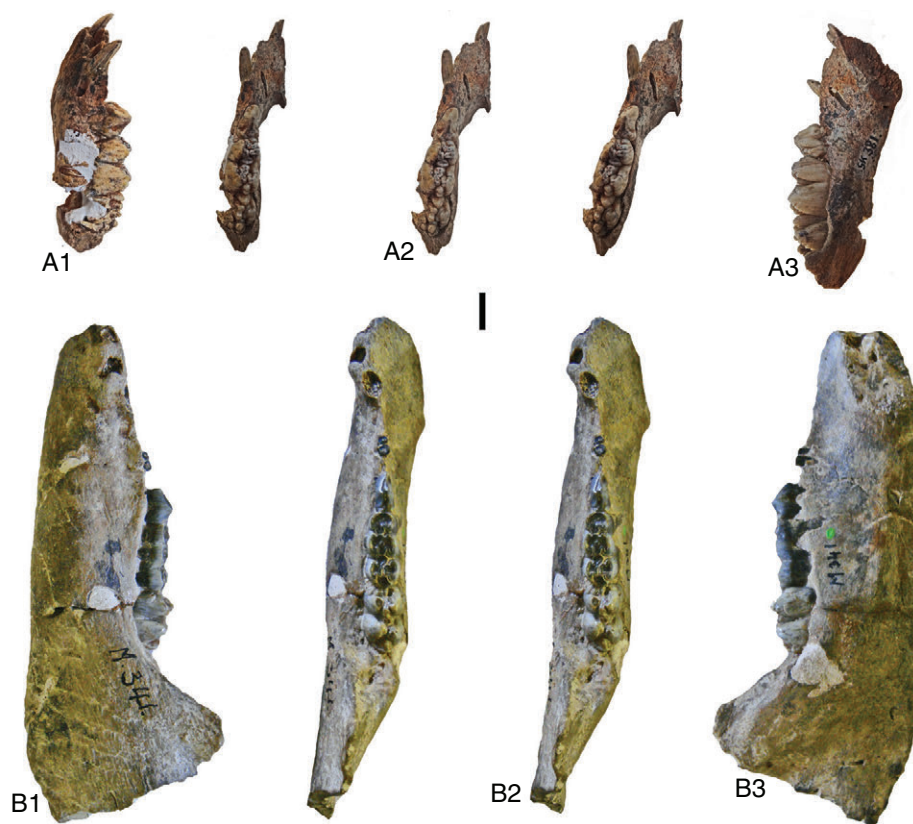
Fig. 17.—Juvenile mandibles of *Metridiochoerus andrewsi* (A) and *Potamochoeroides hypsodon* (B). A) TM SK 381, left mandible from Swartkrans containing di/1, dc/1, d/3 and d/4, A1 - buccal, A2 - stereo triplet of the occlusal view, A3 - lingual view; B) ESI (BPI) M 341, left mandible from Makapansgat containing alveoli of i/2-i/3, c/1, roots of d/3 and complete d/3-d/4 and m/1, B1 - buccal, B2 - stereo occlusal and, B3 - lingual views (scale : 10 mm).

Bed IV, and that as such it was not a very sensitive species for biochronology, although it is inferred that an age prior to 2.3 Ma (Shungura Member G3, Ethiopia) would be unlikely (Cooke, 1994). As for *Potamochoeroides shawi*, he wrote that the Bolt's Farm specimen was remarkably similar to some individuals from Makapansgat, which would imply a middle Pliocene age.

The new samples of suids from Aves Cave I not only add grist to the biochronological mill, but they also confirm that there are indeed deposits of widely divergent ages represented in the Bolt's Farm Palaeokarst System (Harris & White, 1979). The association of *Notochoerus capensis* and *Potamochoeroides hypsodon* at Aves Cave I, indicate that late Pliocene deposits are present (ca 2.7 Ma - 3.0 Ma) (Pickford, 2006). Herries et al., (2013) recently refined the age estimates of the Makapansgat deposits, placing Makapansgat

Members 3 and 4 between 3.03 Ma and 2.58 Ma. In contrast, the records of *Metridiochoerus andrewsi* and *Phacochoerus modestus* at other Bolt's Farm sites suggest that some of the breccias must be about 2.3 Ma - 1.8 Ma. If we add to this the deposits at Waypoint 160, which have not yet yielded suid fossils, the age span of the Bolt's Farm Palaeokarst System reaches down well into the Early Pliocene (ca 4.5 Ma - 5 Ma) (Sénégas, 2004).

Phylogeny and Taxonomy

The new data about *Potamochoeroides hypsodon* and *Notochoerus capensis* from Aves Cave I (and Makapansgat) modify previously published hypotheses of their phylogenetic relationships.

The pachygnathic mandibular ramus of *Potamochoeroides hypsodon* allies it to the genus *Dasychoerus*, which is widespread in
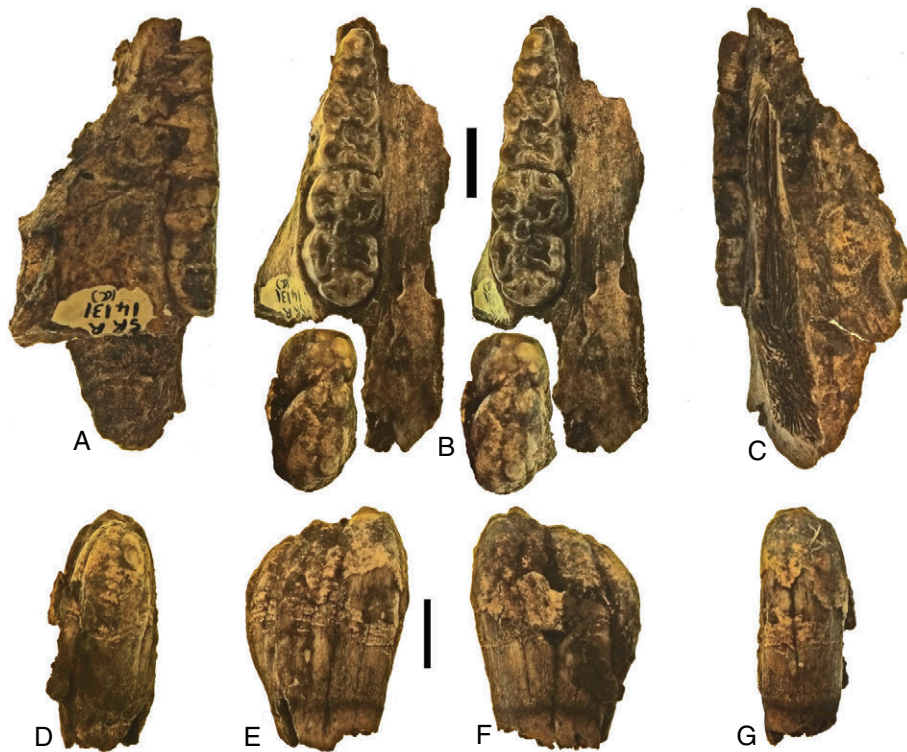
Fig. 18.—TM SK R 14131, right maxilla of a juvenile *Metridiochoerus andrewsi* from Swartkrans, South Africa, containing the erupted D3/-D4/, and M1/, and the M2/ in crypt. A - buccal, B - stereo occlusal view, C - lingual view, D-G) various views of the M2/, D – distal, E - lingual, F - buccal, and G - mesial (scale : 10 mm).

Plio-Pleistocene deposits of Eurasia (Pickford & Obada, 2016). This genus, known colloquially as the warty pig, survives in the Far East (*Dasychoerus verrucosus*). The extinct African genus *Kolpochoerus* also displays a thickened mandibular ramus, and it too is hypothesised to have descended from *Dasychoerus* (Pickford, 2012, 2013c; Pickford & Obada, 2016).

On the basis of its premolar morphology, *Notochoerus capensis* is a typical Suinae and appears to have descended from a different suine lineage, possibly "*Sus*" *provincialis*. Until recently, the genus was attributed to the subfamily Tetraconodontinae, but re-examination of the fossil material from East Africa and South Africa, reveals that the southern African fossils differ in premolar and molar morphology from tetraconodonts, whereas most of the East African fossils are indeed tetraconodonts (Pickford, 2013c). The East African tetraconodont fossils formerly attributed to *Notochoerus* should be called *Gerontochoerus* Leakey, 1943, the oldest available name for them (Pickford, 2013).

Conclusions

Aves Cave I, part of the Bolt's Farm Palaeokarst System, contains breccia which accumulated during the middle Pliocene, ca 2.7 Ma - 3 Ma. This age estimate is made on the basis of the presence in the breccias of two suid taxa, *Potamochoeroides hypsodon* and *Notochoerus capensis*. These two suids are known to occur together at Makapansgat, South Africa, but they are poorly represented in other fossil sites in the subcontinent. A suite of younger breccia infillings in the Bolt's Farm Palaeokarst System has yielded different suid taxa, *Metriodiochoerus andrewsi* and *Phacochoerus modestus*, probably aged ca 2 Ma - 1.8 Ma. There was thus a radical change in the suid fauna at Bolt's Farm over geological time.

All the suids known from Bolt's Farm have hypsodont cheek teeth, which indicates that the species from both periods appear to have been dependent upon a substantial supply of grass in their diets. The earlier assemblage, comprising *Potamochoeroides*

and *Notochoerus* are less hypsodont than the suids of the younger assemblage (*Metridiochoerus* and *Phacochoerus*) which might indicate that the former were more opportunistic feeders which included grass in their diet when necessary and available (on a seasonal basis?), whereas the younger assemblage seem to have been obligate grazers, even if they too were occasionally opportunistic feeders, just as the extant warthog is today.

The post-cranial bones of *Potamochoeroides* do not appear to show any adaptations to carpogrady, but both *Metridiochoerus* and *Phacochoerus* show clear evidence that they practiced this form of loco-motion (Pickford, 2013b). The postcranial skeleton of *Notochoerus* is too poorly known to throw much light on its locomotor affinities.

On the basis of the dimensions of the talus, *Potamochoeroides* was a large suid, somewhat heavier than the extant bush pig, *Potamochoerus porcus*, which ranges in weight from ca 50 kg to 120 kg and the warthog *Phacochoerus aethiopicus* which ranges in weight from 50 to 100 kg (MacDonald, 2001). A body weight of ca 120-200 kg would be acceptable for *Potamochoeroides hypsodon*. This brings it into the range of body weight of the extant giant forest hog, *Hylochoerus meinertzhageni* (130-275 kg). *Notochoerus capensis*, in contrast, was a huge pig, probably weighing in excess of 500 kg.

ACKNOWLEDGEMENTS

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