

Southern African Tetraconodontinae : Recent discoveries

Martin PICKFORD¹, Dominique GOMMERY^{2,3,4}, Lazarus KGASI³, Nonhlanhla VILAKAZI⁴,
Brigitte SENUT¹ & Helke MOCKE⁵

1. CR2P/UMR 7207, MNHN-CNRS-SU, Muséum national d'Histoire naturelle, CP 38, 8 rue Buffon, 75231 Paris Cedex 05, France (e-mail : martin.pickford@mnhn.fr, brigitte.senut@mnhn.fr).
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).
3. HRU, Plio-Pleistocene Palaeontology Section, Ditsong National Museum of Natural History, P.O. Box 413, Pretoria, 0001, South Africa (e-mail : chocky.kgasi@gmail.com).
4. Palaeo-Research Institute, University of Johannesburg, P.O. Box 524, Auckland Park 2006, South Africa (e-mail : nonny.vilakazi@gmail.com).
5. Geological Survey of Namibia, Aviation Road, Windhoek, Namibia (e-mail : helke.mockke@gmail.com).

Abstract: Tetraconodont suids are in general rather poorly represented in Southern Africa, except at Langebaanweg, Cape Province and the Chiwondo Beds, Malawi. We here describe material from two localities in Namibia and one in South Africa in order to fill out the fossil record of this subfamily of artiodactyls in the subcontinent. The oldest specimens (*Nyanzachoerus* sp. cf. *jaegeri*) are from Kaukausib Fontein, Namibia (ca 4-6 Ma), the next oldest (*Gerontochoerus koobiforaensis*) are from Brad Pit 'A', Bolt's Farm, South Africa (ca 3.7 Ma) and the youngest (*Gerontochoerus scotti*) are from Ekuma Rhino Site, northern Namibia (ca 3.2 Ma).

Key words: Suidae, Pliocene, Pleistocene, Southern Africa, Biochronology

To cite this paper: Pickford, M., Gommery, D., Kgasi, L., Vilakazi, N., Senut, B. & Mocke, H. 2019. Southern African Tetraconodontinae : Recent discoveries. *Communications of the Geological Survey of Namibia*, **21**, 59-81.

Introduction

Ongoing palaeontological field surveys in Southern Africa have resulted in the discovery of abundant fossil plants and animals of Late Miocene to Pleistocene age. This report deals with fossil suids (pigs) found in Namibia and South Africa, which belong to the subfamily Tetraconodontinae. The fossils belong to three different species and they throw light on the ages of the strata from which they were extracted as well as yielding information about their diet. The species were collected from three localities : 1) Kaukausib Fontein, Sperrgebiet, Namibia, 2) Brad Pit 'A', Gauteng, South Africa and 3) Ekuma Rhino Site, Etosha Basin, Namibia.

The aim of this paper is to describe and interpret the new suid fossils from Southern Africa within the framework of what is known about Tetraconodontinae in the equatorial and septentrional latitudes of the continent. The fossils belong to well-established taxa, the ages of which are reasonably well-constrained in other parts of Africa and on this basis, the ages of the localities from which the fossils were collected are estimated.

An additional value in the fossils is that they throw light on the long-standing debate about the affinities of the genus *Notochoerus*, supporting the hypothesis that this genus is a Suinae rather than a Tetracondontinae.

Background and discovery context

Kaukausib Fontein

Two suid specimens from indurated grits at Kaukausib Fontein, Sperrgebiet, Namibia, belong to the *Nyanzachoerus kanamensis/jaegeri/australis* group, all three species of which are relatively brachyodont Tetraconodontinae. The fossils indicate that

deposition of the Kaukausib Fontein travertines and grits likely took place sometime between 6 and 4 Ma. This period is more or less coeval with the deposition of the so-called 50 metre littoral marine package along the western coast of South Africa and Namibia (Pether, 1986).

The biochronology provides constraints on the timing of deposition of the grits in the Tsirub and Kaukausib drainages and of the tectonic activity which affected these sediments. The fossils attest to a somewhat more humid and possibly cooler palaeoclimate than occurs in the region today. Travertine activity could be related to higher rainfall in the interior of Namibia than occurs today, or it could be linked to the fact that sea-level was 50 metres higher during the period of deposition than it is today, leading to a concomitant rise in the altitude of the water table, which thereby increased flow at the Kaukausib spring and in the Tsirub and Kaukausib drainage networks in general.

Fossils were first recorded in the grits exposed in the Kaukausib Valley in 1996. An extract from the field report of the Namibia Palaeontology Expedition compiled by Pickford & Senut (1996) reads « *Kaukausib Fountain lies well inland from Grillental in the upper reaches of the same valley. Fossils were found by R. SPAGGIARI and D. WARD during geological mapping, and a follow-up study was carried out by the authors. The site consists of several steeply dipping travertine layers intercalated with grits. The strata appear to have originally formed a tufa dome which has since been incised, revealing the various strata*

Brad Pit ‘A’

Excavations at Brad Pit ‘A’, a karst infilling in the Bolt’s Farm Karst System (Pickford & Gommery, 2016, in press) have yielded several teeth of a large suid, including premolars of typical tetraconodont morphology and a moderately hypsodont, elongated m/3. The specimens differ markedly from suid remains from the nearby site of Aves Cave I attributed to *Notochoerus capensis* by Pickford & Gommery (2016). The presence of these two taxa in neighbouring sites (of roughly similar

Ekuma River Rhino Site

At the main Ekuma Site 1 in the Etosha Basin, the fossils which are in the Ekuma Delta Member in the upper part of the Andoni Formation are estimated by Miller *et al.* (2010) to be about 4 Ma, but the strata at the Ekuma Rhino Site are somewhat younger (ca 3.2 Ma) (Pickford *et al.* 2016). The Ekuma Main Site 1 (ca 4.5 Ma) yielded a large suid talus and a calcaneum, but so far no cheek teeth (only a fragment of tusk) and the underlying Etosha Pan Clay Member which is ca 6 Ma yielded a large

dipping away from a central "eye" area which probably represents the site of a former hard-water spring. Abundant vertebrate fossils were observed in several of the grit layers, but only plant fossils were seen in the travertine, which is onyx-like. The mammal assemblage, although restricted, appears to be of Late Pliocene to Pleistocene affinities, but collection and preparation of fossils is needed to confirm this estimate. The grit is extremely indurated, which is why the bulk of fossils was left in situ for careful extraction in the future. Some of the fossils occur as partly articulated skeletons, and it was decided to leave this material in place as a possible tourist attraction. Indeed, several of the bone patches would be of great interest to the public, as the bones are easily visible, and the occurrence is spectacular, as is the surrounding countryside ».

In 2019, the suid fossils were extracted from the outcrop using rock cutters and drills (Pickford & Senut, 2019) and a new specimen was collected in a loose block of grit lying on the surface (Fig. 3, 4). In the laboratory, the fossils were extracted from the grit by a combination of formic acid attack and airtube techniques and then consolidated with plexigum dissolved in acetone.

ages) is of interest, and adds fuel to the long-lasting debate about the subfamilial status of *Notochoerus capensis* (is it a suine or is it a tetraconodont?). The Brad Pit ‘A’ fossils are described and compared with East African members of the Tetraconodontinae and it is concluded that they represent the species *Gerontochoerus koobiforaensis*, a mid-Pliocene species. From this we deduce that the Brad Pit ‘A’ deposits are about 3.7 Ma, but could be as old as 4 Ma or as young as 3.2 Ma.

suid patella. Pending the discovery of suid teeth in these older levels, we refrain from naming the taxa to which these postcranial bones belong, merely observing that they belong to huge suids calculated to have weighed between 360 and 960 kg (Pickford *et al.* 2013).

The fossil suid m/3 from Ekuma Rhino Site was mentioned briefly by Pickford *et al.* (2016) who attributed it to *Gerontochoerus koobiforaensis*. However, the specimen has five

pairs of cusps, and thus accords better with the more derived species *Gerontochoerus scotti*.

Locations and geological context of fossiliferous sites

The tetraconodont fossils described herein came from three localities - in chronological order Kaukausib Fontein (Namibia), Brad Pit 'A' (South Africa) and Ekuma Rhino Site

(Namibia). The locations of these sites is given in Figs 1 and 2, along with the positions of other African localities discussed in the text.

Kaukausib Fontein, Sperrgebiet, Namibia

The superficial geology of the Kaukausib Fontein and surrounding areas was described by Pickford (2018) who built on pioneer mapping by Bennett & Kalbskopf (1978). The suid fossils described herein were enclosed in

coarse, poorly sorted grit cemented by calcium carbonate. The grit layers are intercalated between pure onyx-like travertine deposits (Fig. 3).



Figure 1. Location of African sites discussed in the text which have yielded remains of tetraconodont suids (*Nyanzachoerus* and *Gerontochoerus*) and suines *Notochoerus* (BF - Bolt's Farm (with Brad Pit 'A'), KF - Kaukausib Fontein).

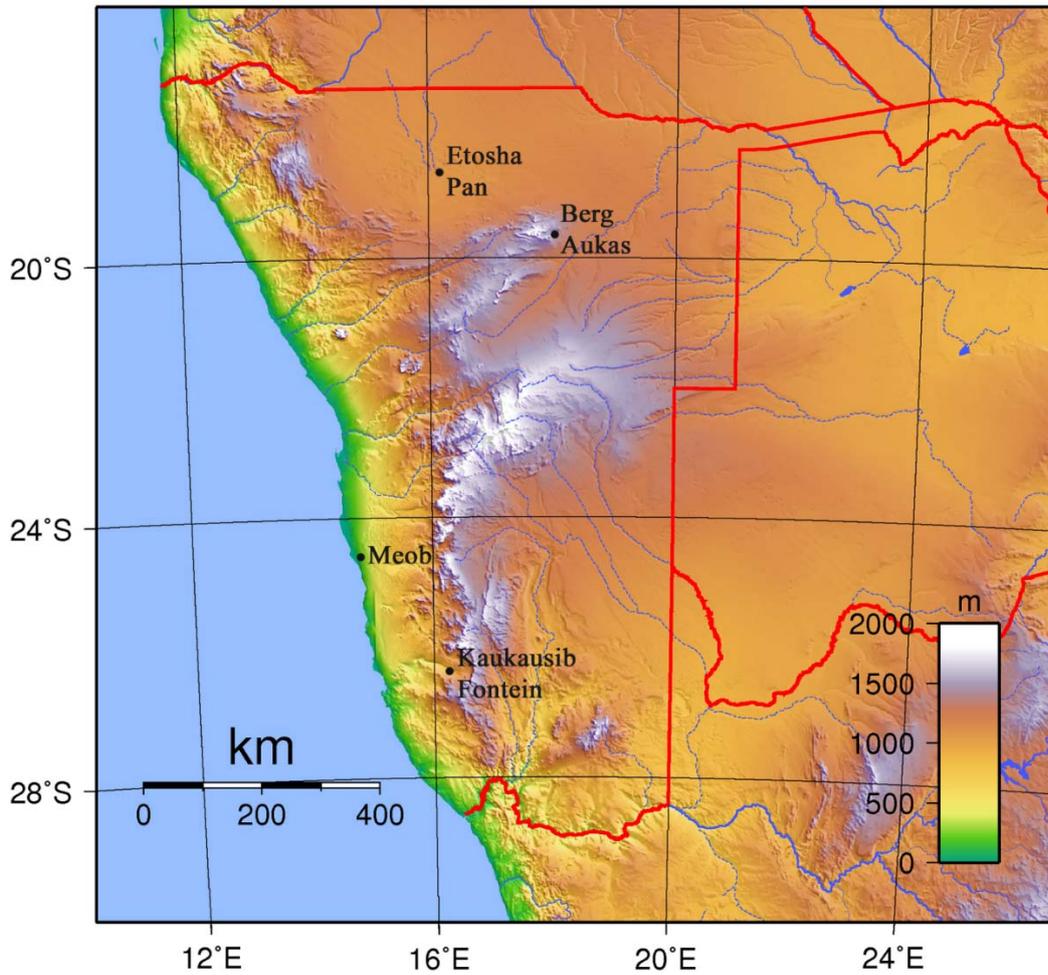


Figure 2. Digital Elevation Map of Namibia showing the distribution of Late Miocene to Basal Pliocene sedimentary deposits that have yielded fossil mammals (not shown are aeolianites spanning the same period that have yielded eggshells of struthious birds).

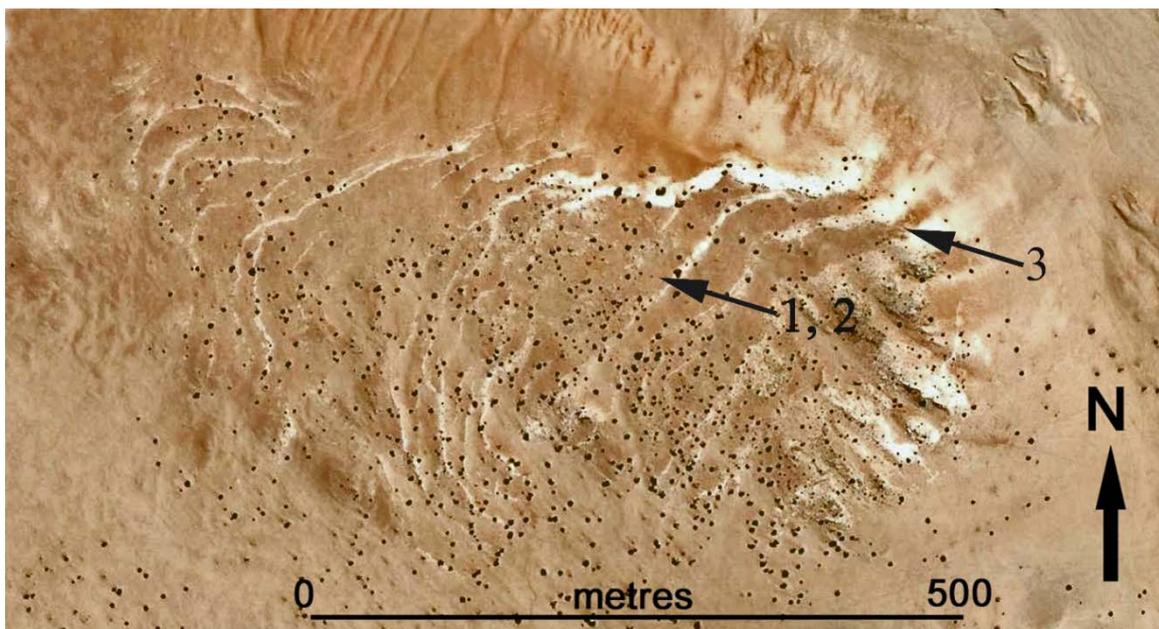


Figure 3. The Kaukausib Fontein Travertine - Grit complex. The precise positions of specimens GSN KF 1'19 to GSN KF 3'19 are shown (1, 2, 3) (Base map is from Google Earth).

Brad Pit 'A', Bolt's Farm Karst System

The geological context and age of the Bolt's Farm Karst System (Figs 1, 4) has been discussed on several occasions (Sénégas, 2000, 2004; Sénégas & Avery, 1998; Sénégas *et al.* 2002; Thackeray *et al.* 2008; Gommery *et al.* 2012; Pickford & Gommery, 2016). On the

basis of the presence of a late form of *Euryotomys* older than the Aves Cave I form, but younger than the species from Waypoint 160, the episode of karst infilling at Brad Pit 'A' is estimated to have occurred about 3.7 Ma (Fig. 4) (range 4-3.2 Ma).

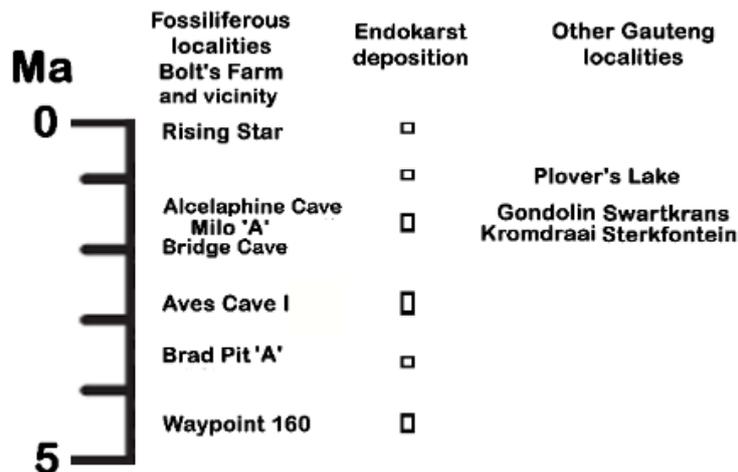


Figure 4. Estimated ages of karst infillings in the Cradle of Humankind, Gauteng, South Africa. The suid teeth described herein were collected from the Brad Pit 'A' infilling (from Pickford & Gommery, in press).

Ekuma Rhino Site, Etosha, Namibia

The geological context of the Ekuma Rhino Site was published by Miller *et al.* (2010) and Pickford *et al.* (2013, 2016). The specimens are from the Ekuma Delta Clay Member, which

spans the period ca 4.5 to 3.2 Ma, the Rhino Site being in the younger levels of the unit for which we estimate an age of ca 3.2 Ma.

Material and methods

The fossils described herein comprise suid specimens from Kaukausib Fontein (GSN KF) and Ekuma Rhino Site (GSN EKR), curated at the National Earth Science Museum, Geological Survey of Namibia, Windhoek, and three teeth curated at the Ditsong National Museum of Natural History, Pretoria (DNMNH where fossils from Brad Pit 'A' are catalogued under the abbreviation BPA). Other fossils are curated at the Natural History

Museum, London (abbreviations NHMUK and NHML) and the Kenya National Museum (KNM including its previous name CM (Coryndon Museum)). Images were taken with a Sony Cybershot camera and treated with Photoshop Elements15 to improve contrast and to remove unwanted background. Scales were added manually. Measurements were taken with sliding calipers to the nearest tenth of a mm.

Dental nomenclature

Figure 5 shows the nomenclature utilised in this paper. There are many terms used for hypsodont suid teeth which do not conform to classic dental nomenclature, and this has given rise to a certain degree of confusion as was pointed out by Pickford (2013). For example,

many authors (Cooke, 1976, 2007; Kullmer, 1999, 2008) have used the term 'laterals' (or 'lateral pillars') for the transversely arranged cusp pairs in such teeth, but only the buccal cusp of each pair can legitimately be called lateral, the lingual one by definition being medial.

Cooke (1976) for example, described the third molars of *Notochoerus euilus* as having « only four or five pairs of lateral pillars » by which he meant four or five pairs of pillars, each ‘pair’ of cusps being called a ‘lateral’ despite the fact that each such ‘pair’ comprises a buccal (lateral) and a lingual (medial) cusp. Other informal names such as skirts, pillars and columns have been used to describe hypsodont cingular structures, tall basal pillars, and tall anterior, median and posterior accessory cusplets. These non-conformant terms have in a way distanced hypsodont suids from their brachyodont and bunodont ancestors to such an extent that most authors failed to realise that all the structures in hypsodont suid teeth have corresponding structures in their bunodont ancestors and this has obscured the evolutionary relationships between the brachyodont (and bunodont) ancestral lineages and their highly derived hypsodont descendants (Pickford, 2013).

Hypsodonty in suids has been achieved independently by at least five different lineages,

each of which emphasised different parts of the tooth crowns at different ontogenetic stages, and in different ways along the tooth row (White, 1959). Whereas some lineages such as *Gerontochoerus* (Tetraconodontinae), *Kolpochoerus* and *Hylochoerus* (Suinae) added cusp pairs to the third molars, thereby increasing the length of the teeth, others emphasised the distal cingular complex (*Potamochoeroides*, *Metridiochoerus*, *Stylochoerus*, *Phacochoerus*) to produce a complicated multicusped complex of pillars at the rear of the tooth.

Some suid lineages emphasised the hypsodonty of the apical parts of the crown, others the mid-crown parts of the tooth, and yet others the crown base. The results are quite different in detail, yet all can be described as hypsodont. Furthermore, the upper and lower molars may achieve hypsodonty in slightly different ways, so it is not always obvious to identify isolated upper molars on the basis of what the lowers look like and vice versa.

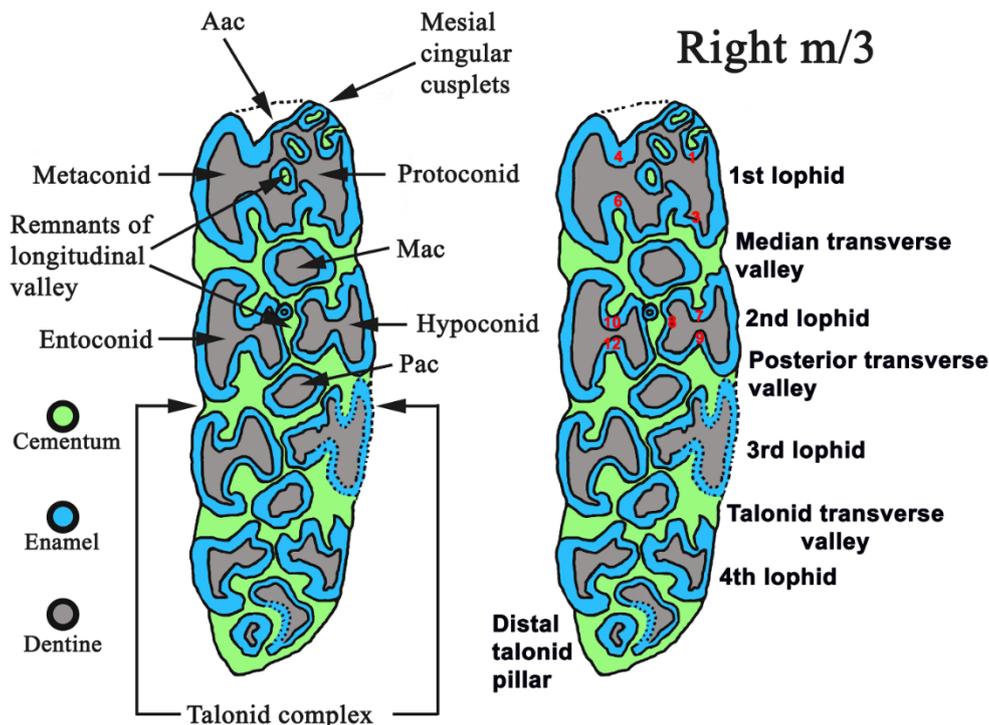


Figure 5. Nomenclature of the lower third molar of *Gerontochoerus koobiforaensis* from Brad Pit ‘A’, South Africa (Aac - anterior accessory cusplet, Mac - median accessory cusplet, Pac - posterior accessory cusplet). 1-12 (in red figures) are Furchen (some have been obliterated by wear) which impart the characteristic ‘H’-shape to the occlusal outline of each cusp.

Systematic Palaeontology

Family Suidae Gray, 1821

Genus *Nyanzachoerus* Leakey, 1958

Diagnosis: A genus of the family Suidae that possesses large posterior (third and fourth) premolars in relation to the anterior premolars and in general, simple bunodont molars similar to those of *Potamochoerus* Gray, 1854, but taller and with thicker enamel; molars have cusps that, when worn, show dentine islands forming a star shape; more derived specimens show a trend towards increased elaboration of the third molars and reduced premolars; incisors wide and large; upper canines oval to flattened

oval in transverse section; lower canines verrucose with thin, weakly grooved enamel on two lateral faces; strong sexual dimorphism characterized by larger size, robustness, massiveness of skull, and the presence of large zygomatic knobs in males; robust mandibles, with thick corpus that contrast with the unusually thin bone forming the angle (after Cooke & Ewer, 1972; Harris & White, 1979; Bishop, 2010; Reda *et al.* 2017).

Species *Nyanzachoerus cf jaegeri* Coppens, 1971

Diagnosis: A progressive species of the genus *Nyanzachoerus* with dental attributes that are intermediate in morphology and size between a more typical *Nyanzachoerus* condition and a more derived tetraconodont condition (genus *Notochoerus*) skull morphology, number of premolars, number, morphology and size of

incisors and enamel thickness as in *Nyanzachoerus*. Derived dental characteristics include longer third molars, molars with more enamel folding and smaller premolars; otherwise general teeth architecture as in *Nyanzachoerus kanamensis* (from Reda *et al.* 2017).

Material :

GSN KF 1'19, left maxilla fragment containing base of M3/ (length x breadth : -- x 33 mm).

GSN KF 2'19, upper molar base (length x breadth : 37 x -- mm).

GSN KF 3'19, juvenile right mandible fragment with broken m/1 and m/2 germs (length x breadth x lingual height - m/1 : 29.5 x 18 x 14.0 mm; m/2 : 32 x -- x 17.5 mm).

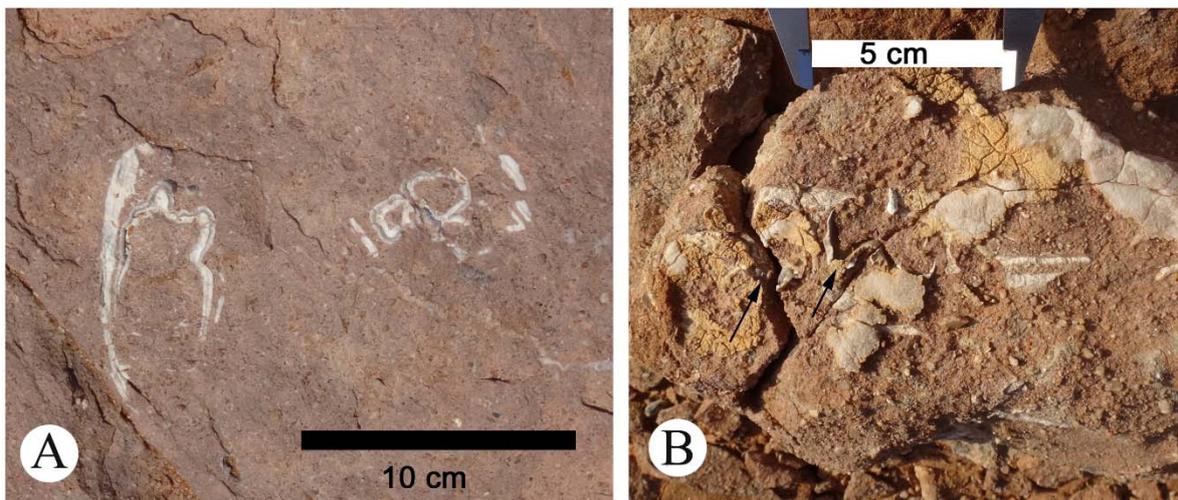


Figure 6. The suid fossils from Kaukausib Fontein prior to extraction from their enclosing grit. A) GSN KF 1'19 and GSN KF 2'19, B) GSN KF 3'19 (Black arrows in B show the teeth).

Description

The best preserved suid tooth from Kaukausib Fontein is the right m/1 germ, GSN KF 3'19 (Fig. 6b, 7). Part of the buccal side was eroded away prior to collection, but extraction using an aircscribe has revealed much of the distal lophid and the rear half of the anterior lophid with well-preserved median and posterior accessory cusplets. The lingual notch is antero-posteriorly broad with a U-shaped base and no basal cusplets. The Furchen are shallow and the postmetacristid, preentocristid and postentocristid are well-defined, as are the prehypocristid and posthypocristid. The

endocristids of the entoconid and hypoconid are directed towards the median transverse valley and slightly anteriorly. The median and posterior accessory cusplets are about 2/3 the height of the main cusps. The distal cingulum is low and distinct from the posterior accessory cusplet. The poorly preserved lingual side of the m/2 is preserved in its crypt. The enamel surface reveals that the crown was incompletely formed at the time of death, but crown height can be estimated. In general what remains of the morphology of this tooth is like that of the m/1.

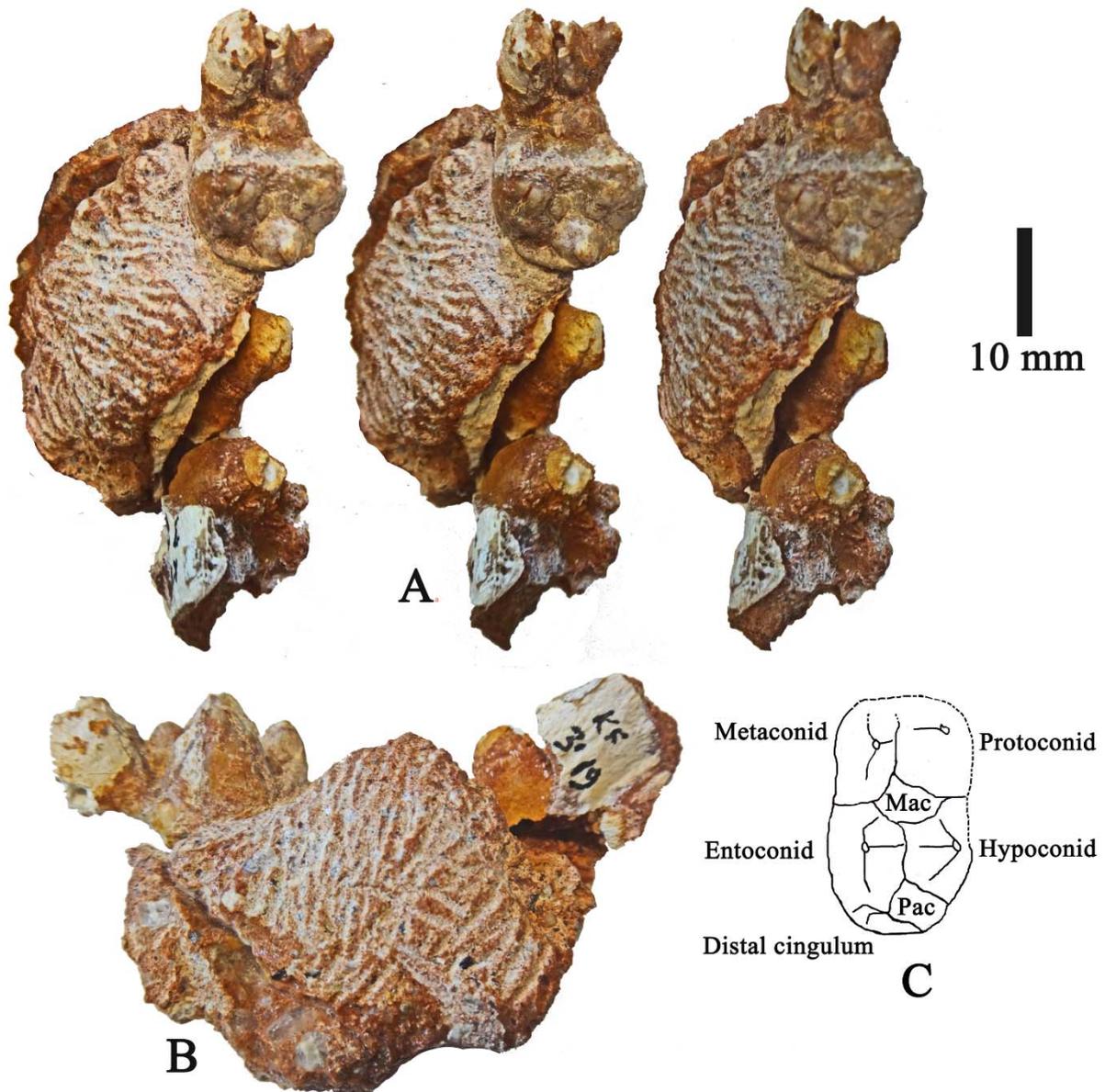


Figure 7. GSN KF 3'19, right m/1 and m/2 germs in a fragmentary mandible. A) stereo occlusal views, B) buccal view, C) interpretive drawing of m/1 (Mac - median accessory cusplet, Pac - posterior accessory cusplet) (scale : 10 mm).

The left M3/, GSN KF 1'19, is missing most of the crown which was eroded off prior to collection (Fig. 6a). Parts of the maxilla and palatine bone are preserved, but are in poor condition. What remains of the tooth has been exposed using an airscribe. The anterior cingular complex is reasonably well-preserved on the buccal half, and reveals that it is low in comparison with the dimensions of the tooth. The base of the anterior accessory cusplet is preserved and it is distinct from the mesial cingulum. The cervix is well-defined, and overhangs the roots to a small extent. The base

Discussion

The two molar germs in GSN KF 3'19 are brachyodont (crown height is less than the breadth : 14/18 mm), whereas lower molars of species of *Potamochoeroides*, *Metridiochoerus*, *Notochoerus*, *Phacochoerus* and *Hylochoerus* are hypsodont (crown height is greater than the breadth). Some species of *Kolpochoerus* are relatively weakly hypsodont, but unlike the Kaukausib specimens, they generally have tall mesial cingular complexes and tall anterior, median and posterior accessory cusplets (Pickford, 1994). The anterior cingular complex in the M3/ (GSN KF 1'19) is low, and the cervix is clearly defined between the crown and the roots. The brachyodonty of the Kaukausib Fontein suid teeth indicate that the specimens are unlikely to belong to large species of *Libychochoerus* or *Kubwachoerus* (Pickford & Tsujikawa, 2019) which have bunodont molars with marked lingual and buccal flare. The same observations apply to species of *Sivachoerus*.

The dimensions of the Kaukausib Fontein suid teeth excludes the possibility that they might pertain to *Potamochoerus* which is a much smaller genus.

The only known African taxon which accords with the morphology and dimensions of the Kaukausib Fontein teeth is *Nyanzachoerus*. Several species of this genus have been defined (Fig. 8). Some, such as *Nyanzachoerus waylandi*, are small whereas there are several

of the median transverse valley is preserved, and it appears to have been mesio-distally broad with a U-shaped profile and there are no signs of cusplets in its base.

The other specimen from Kaukausib Fontein (GSN KF 2'19) is so deeply eroded that no useful details can be obtained, other than an estimate of its dimensions and proportions which reveal that it is likely to be an upper molar, possibly an M2/. The base of the crown is comprised of coarsely wrinkled enamel as in some specimens of *Nyanzachoerus*.

which are large including species with rather bunodont molars (*cookei*, *syrticus*, *khinzir*) which are sometimes classified in the genus *Sivachoerus*. The dimensions and brachyodont morphology of the Kaukausib Fontein suid teeth accord with three species of the genus *Nyanzachoerus* (*N. kanamensis*, *N. jaegeri*, *N. australis*).

Even though a definitive species identification of the Kaukausib suid teeth is not possible, given the limited nature of the sample, the best morphometric fit is with the small subgroup of *Nyanzachoerus jaegeri* described from the Western Rift, Uganda (Pickford, 1994) and with the fossils from Kanam, Kenya (the type locality of *Nyanzachoerus kanamensis* Leakey, 1958).

If this identification is valid, then it suggests that the fossils correlate to the latest Miocene or basalmost Pliocene (between 6 and 4.5 Ma) but given the uncertainty they could be as young as 4 Ma. There is a possibility that the specimens could pertain to the well-known Langebaanweg, South Africa, taxon *Nyanzachoerus australis* Cooke & Hendey, 1992, which has also been recovered from the 50 metre littoral marine package at Hondeklip Bay in Namaqualand (Pickford & Senut, 1997). This littoral marine package is considered to date from ca 6 Ma (Pether, 1986; Pickford, 1998).

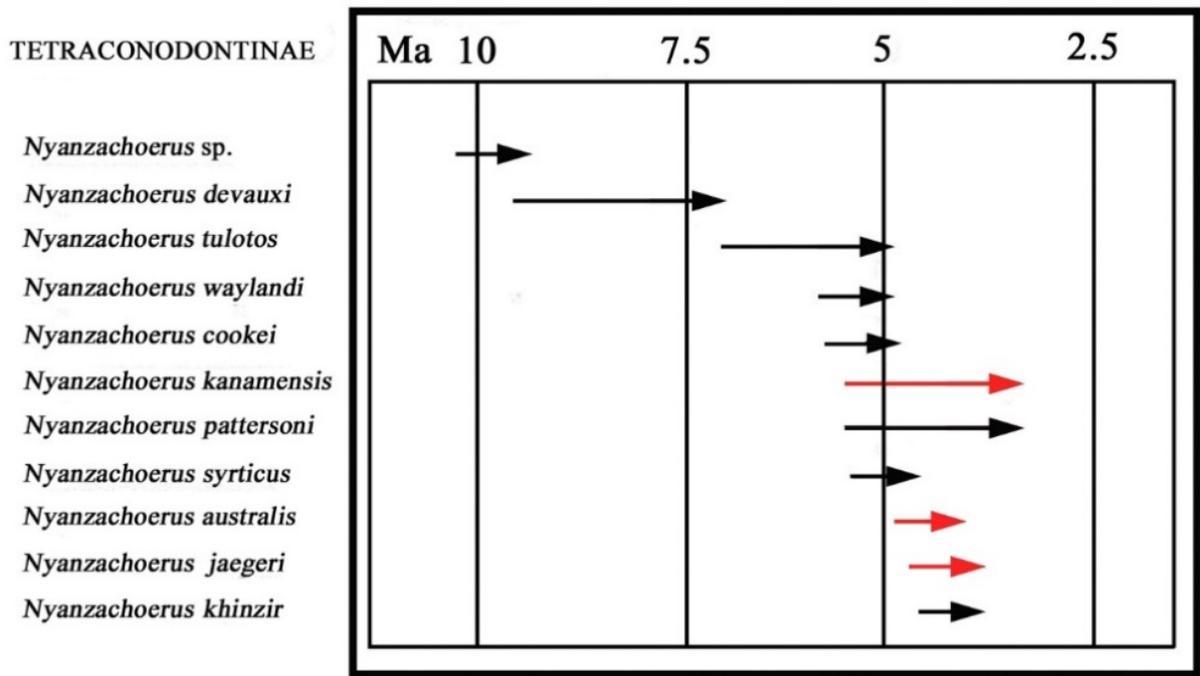


Figure 8. Biochronology of African brachyodont and bunodont tetraconodonts. Some authors classify the more bunodont species such as *devauxi*, *tulotos*, *cookei*, *syrticus* and *khinzir* in the genus *Sivachoerus*, and the brachyodont forms in *Nyanzachoerus*. The Kaukausib Fontein suid teeth are closest in dimensions and crown morphology to the taxa represented by red arrows (*Nyanzachoerus jaegeri*, *N. australis* and early forms of *N. kanamensis*) (Figure modified and extended from Pickford, 2006).

Conclusion

Three suid teeth from coarse grits interbedded with onyx-like travertine at Kaukausib Fontein in the Sperrgebiet, Namibia, are closest in morphometric details to large, brachyodont species of *Nyanzachoerus*. Given the limitations of the material, it is not possible to provide a secure species identification, but comparisons with 1639 fossil and extant African suid molars (779 M3/s, 343 m/1s and 517 m/2s) of all ages (20 Ma to Present day) reveals that the specimens accord best with basal Pliocene specimens of *Nyanzachoerus jaegeri*, late Miocene specimens of *Nyanzachoerus kanamensis* and basal Pliocene specimens of *Nyanzachoerus australis*.

If the identification is valid, then travertine deposition at Kaukausib Fontein likely occurred at the Miocene-Pliocene transition, at the same time as deposition of the 50 metre littoral marine package defined by Pether (1986) a possibility that invites scenarios of cause and effect. In brief, an eustatic rise in sea level would likely cause a concomitant rise in groundwater levels in the vicinity of the coast, meaning that the water table would rise, likely

leading to increased flow at springs such as Kaukausib Fontein, which today flow at reduced rates or at other springs in the region that have dried up altogether as a result of subsequent lowering of the water table.

Mapping of the travertines exposed in the Kaukausib and Tsirub drainages has not been completed (Pickford, 2018) but it is clear that spring flow was orders of magnitude greater during the late Miocene and basal Pliocene than it is today. An alternative scenario is that regional climate may have been cooler and somewhat more humid than it is today resulting in greater volumes of groundwater.

If the biochronology proposed on the basis of the suid teeth from Kaukausib Fontein is valid, then this record extends the geographic representation of the late Miocene to basal Pliocene fossil register of Namibia into the Sperrgebiet. Previously, the only known deposits of this period of time in the country were reported from the Otavi Mountains (Pickford, 2002) from Etosha Pan (Miller *et al.* 2010; Pickford *et al.* 2016) and from Meob (Morales *et al.* 2011) (Fig. 2).

Genus *Gerontochoerus* Leakey, 1943

Type species: *Gerontochoerus scotti* Leakey, 1943

Original genus diagnosis: Suidae with high-crowned and long-rooted third molars composed of four or more pairs of pillars and a small talon. The line of demarcation between

crowns and roots very clearly differentiated. Upper third molars more complex than lowers (from Leakey, 1943).

Emendation to diagnosis: Tetraconodont Suidae in which the upper and lower third molars possess additional cusp pairs resembling the first two pairs, plus more or less complex talon(id)s. Anterior, median and posterior accessory cusplets distinct and tall and not intervening between the main cusps. Third and fourth premolars significantly larger than the second premolars (which are often absent) but with a tendency for them to be smaller than those of other tetraconodonts such as

Nyanzachoerus, *Sivachoerus* and *Tetraconodon* in which the second premolars are always present. Cementum present on molars, molar enamel finely and intensely wrinkled. Tendency for the main cusps to produce 'H'-shaped (or mushroom shaped) enamel outlines at the occlusal surface due to the presence of deeply indented Furchen and tall basal cusplets which, with wear coalesce with the anterior and posterior ends of the pre- and postcristids of the main cusps.

Species *Gerontochoerus koobiforaensis* Pickford, 2013

Holotype: KNM ER 3541, a skull and mandible (Harris & White, 1979, Plates 1-3).

Type locality and age: Unit 2 of the Koobi Fora Formation, East Turkana, Kenya (ca 4 Ma).

Diagnosis: A species of *Gerontochoerus* intermediate in dimensions between *Gerontochoerus euilus*, which is smaller, and *Gerontochoerus scotti*, which is larger (from

Pickford, 2013). The species has four pairs of cusps in the third molars, as opposed to five or more in the other species.

Descriptions of the fossils from Brad Pit 'A'

DNMNHP BPA 852, right m/3 (Fig. 9).

This tooth is deeply worn; even the terminal pillars at the distal end of the crown are in light wear, signifying a fully adult individual but not a senile one. The crown as preserved is ca 19 mm tall at the entoconid and 21.5 mm tall at the distal end on the lingual side (unworn the distal cusps would have been ca 23 mm tall). This tooth, even though hypsodont, is not nearly as hypsodont as teeth of *Potamochoeroides*, *Metridiochoerus*, *Stylochoerus*, *Phacochoerus* and *Notochoerus*, in all of which the talonid cusps are considerably taller than in *Gerontochoerus*.

The cervix is clearly expressed and is almost rectilinear, and there are remnants of root beneath all the cusps as well as the talonid.

Distal to the third lophid, the cervix rises at a gentle angle beneath the talonid indicating that this is a lower molar. This is confirmed by the fact that the occlusal surface and the cervix are sub-parallel to each other (Pickford, 2013). The slope of the root beneath the talonid indicates that this is a right lower third molar, as do the positions of the median and posterior accessory cusplets, the mesial cingular cusplets and the slightly greater buccal flare of the crown on the right aspect of the talonid, the left side being almost vertical. The crown is slightly distorted by damage such that in occlusal view it bends gently to the left rather than being straight or gently curved to the right.

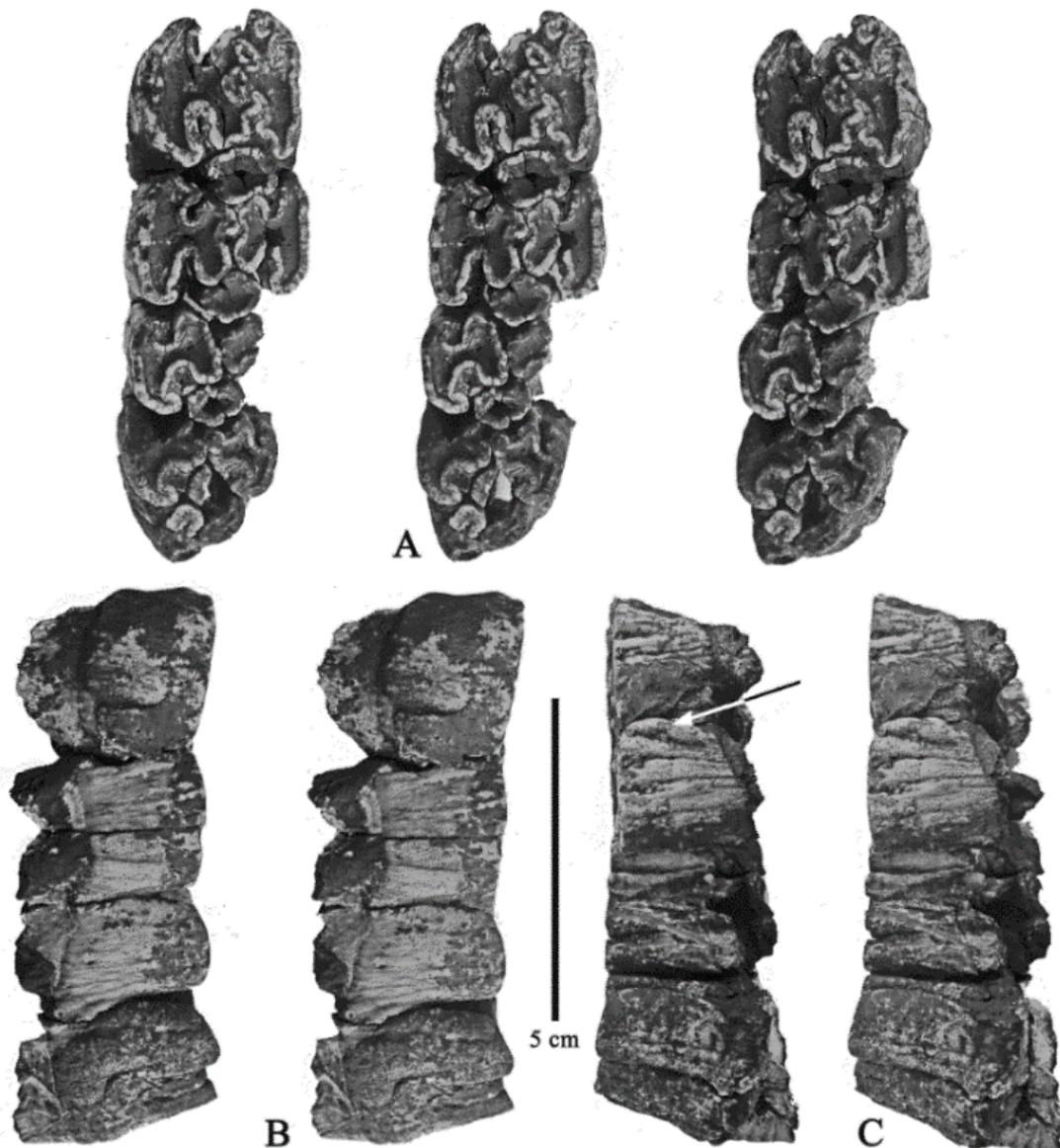


Figure 9. DNMNHP BPA 852, right m/3 of *Gerontochoerus koobiforaensis* from Brad Pit ‘A’, Bolt’s Farm Karst System, South Africa. A) stereo occlusal views, B) stereo lingual view, C) stereo buccal view. Arrow shows a tall basal pillar coalescent with the prehypocristid which contributes to the ‘H’-shaped outline of the occlusal surface. Note the remnant of cementum filling the median transverse valley between the metaconid and entoconid on the lingual side and on the buccal side of the protoconid (scale : 5 cm).

The crown is composed of four bicuspid lophids (‘pairs of pillars’ in the terminology of Leakey, 1943; ‘laterals’ in the terminology of Cooke, 1976, 2007) and a short distal cingular complex. Each lophid is comprised of two main cusps with deep indentations anteriorly and posteriorly, which impart an ‘H’ shaped occlusal outline to each cusp (sometimes called a mushroom shape). These indentations correspond to Furchen (Fig. 5 right image) (N°s 1, 3, 4, 6, 7, 9, 10, 12) (see Hünemann, 1968; Pickford, 2013, for definitions of the groove system or Furchenmuster of suid molars). There are

accessory pillars close to the mesial and distal ends of the buccal sides of the protoconid and hypoconid and the lingual sides of the metaconid and entoconid, which with wear coalesce with the main cusps, thereby lengthening the mesio-distal length of the ‘H’ outline on the outer edges of the tooth and thereby narrowing the exits of the transverse valleys. These accessory pillars impart shallow, narrow vertical grooves to the buccal surface of the crown. They represent hypsodont basal pillars that often occur in bunodont and brachyodont suid teeth at the buccal end of the median transverse valley.

The four anterior cusps are the protoconid, metaconid, hypoconid and entoconid, as in suids in general. The anterior accessory cusplet has broken off but part of the anterior cingular complex and the deep foveae (cement-filled pits) are preserved. The median accessory cusplet and the posterior accessory cusplet are present near the midline of the crown blocking the median transverse valley and the posterior transverse valley respectively. Behind the posterior accessory cusplet lies the talonid complex which is comprised of two pairs of large cusps, with a central pillar between them

(much like the posterior accessory cusplet). The morphology of the cusps in each talonid cusp pair resembles those in the anterior lophids but the cusps are shorter mesio-distally with less indented Furchen. Behind the 4th lophid there is another central pillar, and a lingual cingular pillar on the disto-lingual end of the crown.

The surface of the enamel is partly hidden by a cover of cementum, but where this has spalled away it is possible to observe that the surface of the enamel is lightly but intensively wrinkled, like shagreen.

DNMNHP BPA 1356, right P3/ (Fig. 10).

This tooth is typical of Tetraconodontinae, comprising a large, inflated paracone closely fused to the smaller protocone. In occlusal view, the crown is an equilateral triangle, with one apex pointing mesially. The preparacrista extends in the midline of the tooth towards a tall prominent mesial cingular cusplet, the accompanying cingulum extending slightly buccally and lingually as it descends towards cervix. The postparacrista extends disto-

buccally to join the distal cingulum which is tall, forming a depression on the buccal side of the lateral surface of the tooth. The hypocone is coalescent with the distal cingulum, forming a low cusp on the disto-lingual corner of the tooth. There are three robust roots, one anteriorly and two posteriorly which are partly fused together beneath cervix but separated from each other apically.

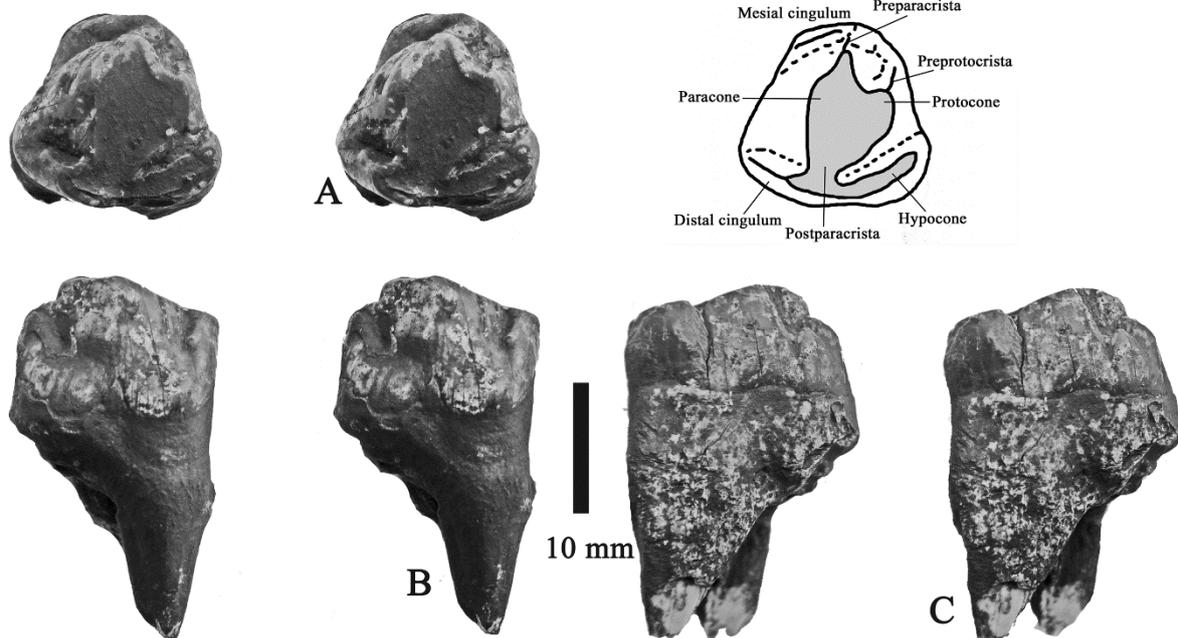


Figure 10. DNMNHP BPA 1356, right P3/ of *Gerontochoerus koobiforaensis* from Brad Pit ‘A’, Bolt’s Farm Karst System, South Africa. A) stereo occlusal view and interpretive drawing (grey is dentine), B) stereo buccal view, C) stereo lingual view (scale : 10 mm).

DNMNHP BPA 1481, right p/3 (Fig. 11).

Only the distal half of this moderately worn tooth is preserved. It shows the inflated morphology of the main cusp that is typical of Tetraconodontinae, accompanied distally by a

tall distal cusplet and weak distal cingulum forming a small but distinct cingular cusplet close behind and to the buccal side of the distal cusplet. There is a strong interstitial wear facet

caused by contact with the p/4 behind, which has worn a hollow into the disto-lingual side of the tooth near cervix. The root is transversely

broad and mesio-distally compressed with a deep mesial re-entrant groove, as is usual in tetracondont teeth (and suid teeth in general).

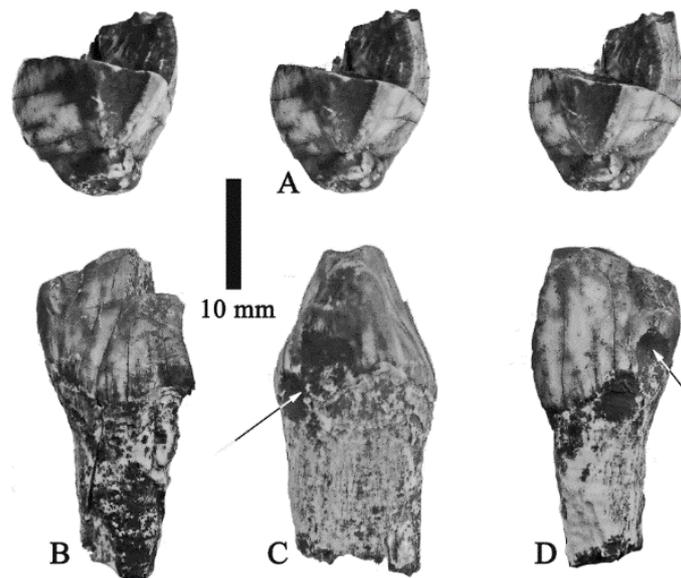


Figure 11. DNMNHP BPA 1481, distal half of right p/3 of *Gerontochoerus koobiforaensis* from Brad Pit ‘A’, Bolt’s Farm Karst System, South Africa. A) stereo occlusal views, B) buccal view, C) distal view, D) lingual view. Arrows show the interstitial wear facet caused by contact with the p/4 (scale : 10 mm).

DNMNHP BPA 152, upper canine fragment (Fig. 12).

Brad Pit ‘A’ yielded a fragment of suid upper canine which is remarkable for its large dimensions and for the presence of a broad but shallow dorsal gutter. Although such a fragment would generally be considered unidentifiable at

the genus level, it accords with upper canines of *Gerontochoerus koobiforaensis* which possess large upper canines with broad, shallow dorsal gutters. The holotype of the species shows this feature well (Harris & White, 1979).

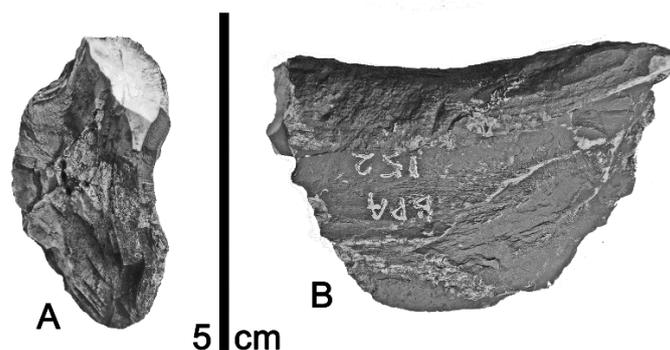


Figure 12. DNMNHP BPA 152, fragment of upper canine of a large suid attributed to *Gerontochoerus koobiforaensis*. A) cross section, B) dorsal surface. Note the broad but shallow dorsal gutter (scale : 5 cm).

Table 1. Measurements (in mm) of the teeth of *Gerontochoerus koobiforaensis* from Brad Pit A, Bolt’s Farm Karst System, South Africa.

Tooth	Mesio-distal Length	Breadth 1st lophid	Breadth 2nd lophid	Breadth 3rd lophid	Breadth 4th lophid
BPA 852 right m/3	91.0	28.8	30.7	--	28.8
BPA 1356 right P3/	18.0	16.0			
BPA 1481 right p/3	--	14.7+			
BPA 152 upper canine	40.7	--			

Discussion

The large suid teeth from Brad Pit 'A' are clearly tetraconodont, the enlarged and inflated P3/ and p/3 being characteristic of this subfamily of suids. The m/3 is moderately hypsodont and mesio-distally elongated by the addition of two extra pairs of cusps which are basically similar in morphology to the two anterior pairs of cusps and there is a small but tall distal cingular pillar. The tooth has a clearly defined cervix below which there are remnants of roots. The fragment of upper canine from Brad Pit 'A', even though undiagnostic, reveals that the suid it came from was of huge dimensions, the section being over 4 cm across. The dimensions of the BPA teeth, plus the

length/breadth proportions of the m/3 and the ratio of the dimensions of the P3/ to the m/3 (Fig. 13) all coincide with the species *Gerontochoerus koobiforaensis*, a taxon which is well-known in East Africa, generally under the name *Notochoerus euilus* (Cooke, 1976; Harris & White, 1979 and references therein; Harris, 1983). The m/3 of this species typically has a total of four pairs of cusps accompanied by a simple posterior talonid pillar, but some authors include specimens with three or five pairs of cusps.

The canine of East African specimens possess a broad, shallow dorsal gutter (Harris & White, 1979) like that observed in BPA 152.

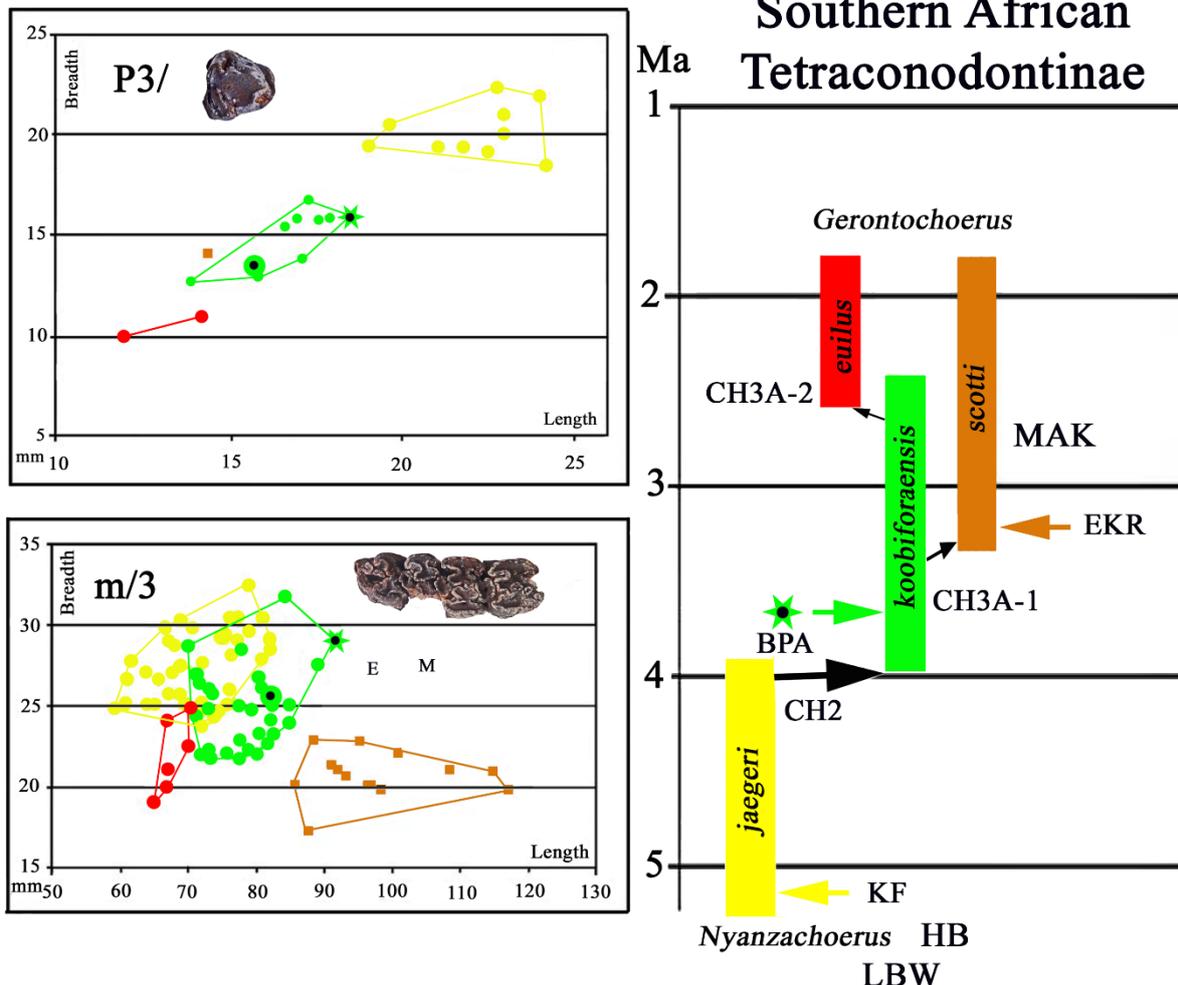


Figure 13. Bivariate length : breadth plots of the P3/ and m/3 of *Nyanzachoerus jaegeri* (yellow) and three species of *Gerontochoerus* (green, brown, red) and a phylogeny and biostratigraphy of these African tetraconodonts. BPA (green star with black centre) represents the fossils from Brad Pit 'A'. Figure modified from Pickford (2013) with additions (CH : Chiwondo (with different stratigraphic levels 2, 3A-1, 3A-2, Kullmer, 2008), E (EKR) : Ekuma Rhino Site (Pickford *et al.* 2016), HB : Hondeklip Bay (Pickford & Senut, 1997), KF : Kaukausib Fontein, LBW : Langebaanweg, M (MAK) : Makapansgat). Large green dots with black centres represent the holotype of *Gerontochoerus koobiforaensis*.

Harris & White (1979) and Cooke (2007) provided summary statistics of dental metrics of teeth attributed to *Nyanzachoerus kanamensis*, *Notochoerus capensis*, *Notochoerus euilus* (equivalent to *koobiforaensis* in this paper), *Notochoerus scotti* and *Notochoerus clarki* (declared to be a synonym of *euilus* by Pickford, 2013), the sorting of the third molars being based on the number of ‘laterals’ or pairs of pillars in them and the degree of hypsodonty. The ranges of variation calculated by the authors are somewhat different, especially at the lower end of the range, with minimum lengths significantly shorter in Harris & White (1979) than in Cooke (2007).

On the basis of the number of cusp pairs in the talonid (two plus a cingular pillar behind the two anterior cusps, making a total of four cusp pairs for the whole tooth), the m/3 from Brad Pit ‘A’ belongs to *Gerontochoerus koobiforaensis*, an identification which agrees with the relatively low distal pillar which, even though slightly worn, would have been only ca 30 mm tall. Appurtenance to *Gerontochoerus scotti* can be discounted, because this taxon has more cusp pairs in the talonid, and it is considerably more hypsodont. The Brad Pit ‘A’ tooth plots well outside the range of metric variation of *Gerontochoerus euilus*.

The BPA 852 third molar is large within the context of *Gerontochoerus koobiforaensis*, agreeing best with specimens from Hadar (Sidi Hakoma) and Koobi Fora (Tulu Bor) but it is

General Discussion

Several teeth from Brad Pit ‘A’, Bolt’s Farm Karst System, South Africa, belong to the tetraconodont suid *Gerontochoerus koobiforaensis*, implying an age of ca 3.7 Ma (span 4 to 3.2 Ma) for the deposits in which it occurs. The genus was previously represented in the subcontinent by the more derived taxon *Gerontochoerus scotti*, some specimens of which were for a long time misattributed to the suine *Notochoerus capensis*.

Pickford (2013) showed that the lectotype of *Hylochoerus euilus* from Kaiso, Uganda, was an upper molar and not a lower one, as had been thought since its erection by Hopwood (1926) and that, as such, the specimen plots within the range of morphometric variation of *Notochoerus clarki* White & Suwa (2004) meaning that the latter species falls into synonymy with the former. This decision was

appreciably shorter than specimens from Ekuma River (Pickford *et al.* 2016) and Makapansgat (Pickford & Gommery, 2016) (Fig. 13). On this basis, it is considered to be likely that the BPA specimen correlates best to the time period spanned by the Sidi Hakoma and Tulu Bor successions, which would imply an age of ca 3.7 +/- 0.4 Ma, but an age as old as 4 Ma or as young as 3.2 Ma cannot be ruled out.

The quantity of upper and lower premolars of these suids is restricted, but Harris & White (1979) noticed a tendency towards reduction in the dimensions of the third and fourth premolars through time. Thus *Nyanzachoerus kanamensis* possessed larger premolars than those of *Gerontochoerus koobiforaensis* which are larger than those of *Gerontochoerus scotti* and *Gerontochoerus euilus* (Fig. 13). The BPA 1356 and BPA 1481 specimens plot close to the range of variation of *Gerontochoerus koobiforaensis*, thereby supporting the identification based on the m/3.

Two suid lower third molars, one (GSN EKR 63’13, see below) from Ekuma Rhino Site, Namibia (Pickford *et al.* 2016) the other (M 2077) from Makapansgat are here attributed to *Gerontochoerus scotti*, but are appreciably broader than the other specimens attributed to the species, perhaps because the cementum cover is thick (thereby increasing the breadth measurement compared with teeth that have lost the cementum).

accepted by Geraads & Bobe (2017). Furthermore, Pickford (2013) showed that the holotype of *Notochoerus capensis* Broom, 1925 (the type species of the genus considered by its creator to be a lower left tooth but which is in fact an upper right one) differs fundamentally in its morphology from the lectotype of *Hylochoerus euilus* (both teeth are upper third molars, so can be compared directly with each other) so much so that the two teeth can no longer be considered to represent the same genus. Pickford (2013) therefore resurrected the name *Gerontochoerus* Leakey, 1943 (type species *Gerontochoerus scotti*). This recommendation was not accepted by Geraads & Bobe (2017) who continued to attribute the species *euilus* to the genus *Notochoerus*. Nevertheless, the holotype of *Notochoerus capensis* does not resemble any of the East

African specimens which have traditionally been admitted within the genus (Pickford & Gommery, 2016).

Pickford (2013) noted that « *an upper left third molar attributed to Notochoerus hopwoodi Leakey, 1958 (NHML M 17115) from Olduvai Bed IV, Tanzania, is similar in many respects to the holotype of Notochoerus capensis, but it is less deeply worn. The tooth is slightly narrower than the South African tooth (25 mm versus 30 mm) but in toto the two specimens are very similar to each other and probably belong to the same species* ». Harris & White (1979) attributed M 17115 to *Mesochoerus limnetes*, but there are no particular similarities between it and the holotype of the species from Kaiso, Uganda, which is a relatively brachyodont tooth (Hopwood, 1926; Cooke & Coryndon, 1970)

which probably belongs to the genus *Nyanzachoerus* (Pickford, 1994) (but see Cooke, 1997, who considered it to be closer to the small primitive suine *Kolpochoerus afarensis*, which he transferred to *Potamochoerus*).

Images of the Olduvai tooth are provided (Fig. 14) which reveal the similarities between this tooth and the holotype of *Notochoerus capensis* from Longlands (South Africa) and highlight how divergent it and the Longlands specimen are from the Kaiso lectotype of *Hylochoerus euilus*. A particular morphological similarity which is rare in suids concerns the positions of the median and posterior accessory cusplets intervening between the hypocone and metacone. In other suids, the inner margins of the hypocone and metacone are close to each other and the accessory cusplets far apart.

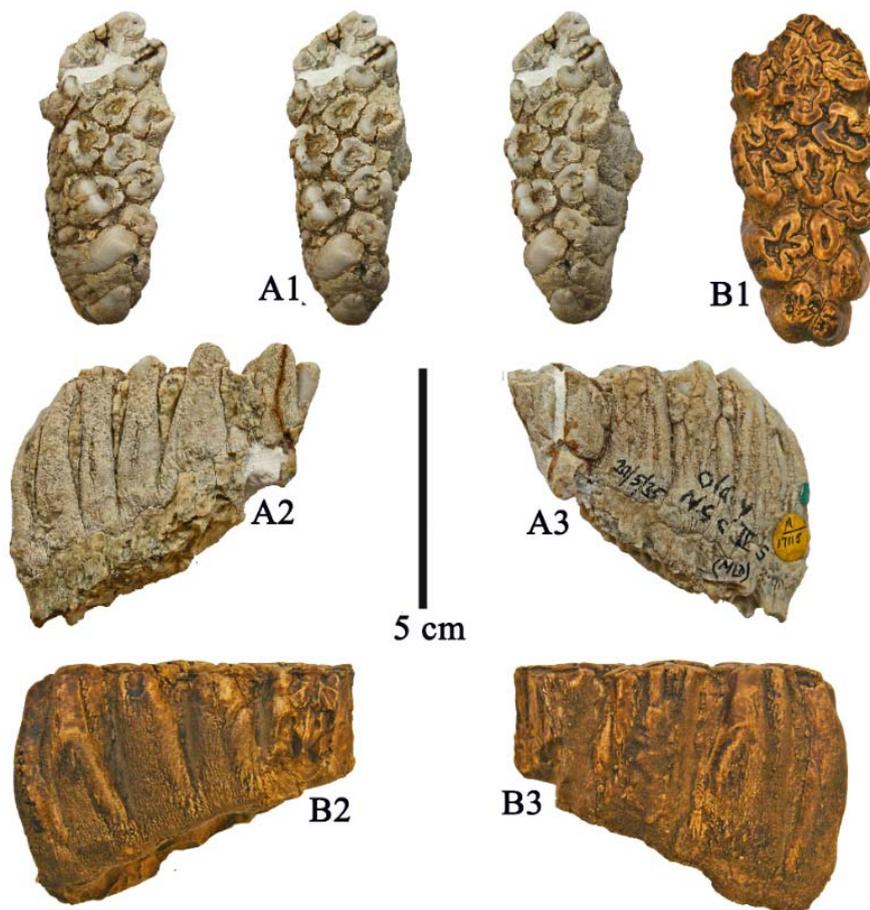


Figure 14. A) NHMUK M 17115, left M3/ from Olduvai Bed IV, Tanzania, attributed by Leakey, 1958, to *Notochoerus dietrichi* Hopwood, 1934. A1) stereo occlusal views, A2) lingual view, A3) buccal view. B) cast of holotype right M3/ of *Notochoerus capensis* from Longlands, Vaal River, South Africa (images reversed for ease of comparison). B1) occlusal, B2) lingual, B3) buccal views. Teeth are oriented with the occlusal plane horizontal (scale : 5 cm).

Assuming that the provenience of the Olduvai tooth (M 17115) is correctly reported (Leakey, 1958) then it follows that *Notochoerus capensis* may have survived later than species of the genus *Gerontochoerus* which died out about 1.8 Ma (Cooke, 2007). Olduvai Bed IV is Pleistocene (0.6-0.8 Ma) (Ashley *et al.* 2010).

Our estimates of the dimensions of the holotype of *Notochoerus capensis* are 72 x 30 mm (Van der Made, 1998, gave two estimates for the length : 72 and 81 mm, depending on how its mesial end is reconstructed). Harris & White (1979) identified skull KNM ER 448 as *Notochoerus capensis*, giving the measurements of its M3/ as 91.8 x 31.6 mm, but the fossil was later removed from this species and identified as *Notochoerus scotti* by Harris (1983) who gave its M3/ measurements as 89 x 33.7 mm. With the removal of this skull from *Notochoerus capensis*, the species is no longer recognised by that author in the East African fossil record.

Pickford & Gommery (2016) described some large suid remains from Aves Cave 1, South Africa, not far from Brad Pit 'A'. Among the specimens is a partial M3/ with marked resemblances to the holotype of *Notochoerus capensis*. From the same strata there are upper and lower premolars of large dimensions which are of typical suine morphology and are radically different from the corresponding teeth in Tetraconodontinae. This evidence supports the hypothesis that *Notochoerus* is a suine rather than a tetraconodont. The deposits at Aves Cave I are estimated to be ca 3.0-2.7 Ma (Pickford & Gommery, 2016).

Recently, Lazagabaster *et al.* (2018) reported the presence of *Notochoerus capensis* at Lee Adoyta in the Ledi-Geraru area, Ethiopia (ca 2.7 - 2.5 Ma). The specimens accord with this species not only in dimensions, but also in some

Conclusions

Three suid teeth from Brad Pit 'A' in the Bolt's Farm Karst System are identified as *Gerontochoerus koobiforaensis* Pickford, 2013. The inflated morphology of an upper third premolar and half a lower third premolar indicate affinities with the subfamily Tetraconodontinae and the teeth plot within the range of metric variation of *G. koobiforaensis*. A lower third molar has four lophids (each comprised of two cusps) accessory cusplets in the transverse valleys between the lophids and there is a cingular pillar at the distal extremity

aspects of crown morphology, notably by the fact that the median and posterior accessory cusplets intervene between the hypocone and metacone and the 'H'-shape of the lingual cusps is not as fully developed as it is in the buccal cusps. However, their definition of the species was based on the work of Harris & White (1979) in which the upper third molars of *Notochoerus capensis* (i.e. in reality *Gerontochoerus scotti*) are illustrated as possessing six lophs and the lower third molars seven lophids. However, the holotype M3/ of the *Notochoerus capensis* possesses only four lophs (Shaw, 1938; Pickford, 2013) or five if one accepts Broom's (1925) reconstruction of the missing parts (Cooke, 1949; Cooke & Coryndon, 1970). The definition of the taxon used by Lazagabaster *et al.* (2018) was therefore based on two fossils, neither of which matches the holotype of *Notochoerus capensis* in dimensions or in morphology : a) skull KNM ER 448, with an M3/ 89 mm long, which has subsequently been transferred to *Notochoerus scotti* by Harris (1983) (*Gerontochoerus scotti* in this paper (Pickford & Gommery, 2016)) and B) a lower third molar from Makapansgat (M 2077) which is far too large to belong to the same species as the holotype (length of the holotype M3/ of *Notochoerus capensis* is ca 72 mm : and the length of the m/3 from Makapansgat is 116.7 mm). Thus, even though the Lee Adoyta specimens have a distinct possibility of belonging to *Notochoerus capensis*, they do not represent the same species as the fossils from East Turkana and Makapansgat attributed to this species by Harris & White (1979). The latter specimens are more properly attributed to *Gerontochoerus scotti*. It is noted that the Lee Adoyta stratigraphic sequence spans the period 2.8 to 2.5 Ma (Lazagabaster *et al.* 2018).

of the crown. The crown is moderately hypsodont, is covered in cementum and possessed roots, and its dimensions accord with *Gerontochoerus koobiforaensis*.

The recognition of this species at Brad Pit 'A' accords with previous age estimates of the deposits based on other faunal elements found there (Pickford & Gommery, in press). The most likely age based on the suids is ca 3.7 +/- 0.4 Ma, but the deposits could be as old as 4 Ma or as young as 3.2 Ma. The hypsodont nature of its m/3 together with the presence of cementum

suggests that *Gerontochoerus koobiforaensis* included grass in its diet.

Species *Gerontochoerus scotti* Leakey, 1943

Holotype: KNM OS 5 (old number CM Omo I), (cast in NHMUK M26590), right maxilla fragment containing M2/ and M3/.

Type locality and age: Shungura, Omo, Ethiopia.

Original diagnosis: A *Gerontochoerus* of very large size in which the enamel pattern of the third molars exhibits an extreme degree of folding in the upper third molars, the lateral pillars of each pair are separated from each other by median pillars except in the case of the

the anterior pair of pillars, but in the lower third molars the enamel of the lateral pillars comprising each pair touches along the median line and the median pillars merely separate each pair from the next succeeding pair (from Leakey, 1943).

Emendation to diagnosis: A species of *Gerontochoerus* larger than *Gerontochoerus koobiforaensis* and *Gerontochoerus euilus*, in

which the talonid complex behind the fourth pair of cusps is itself multicusped often forming a fifth pair of cusps or more.

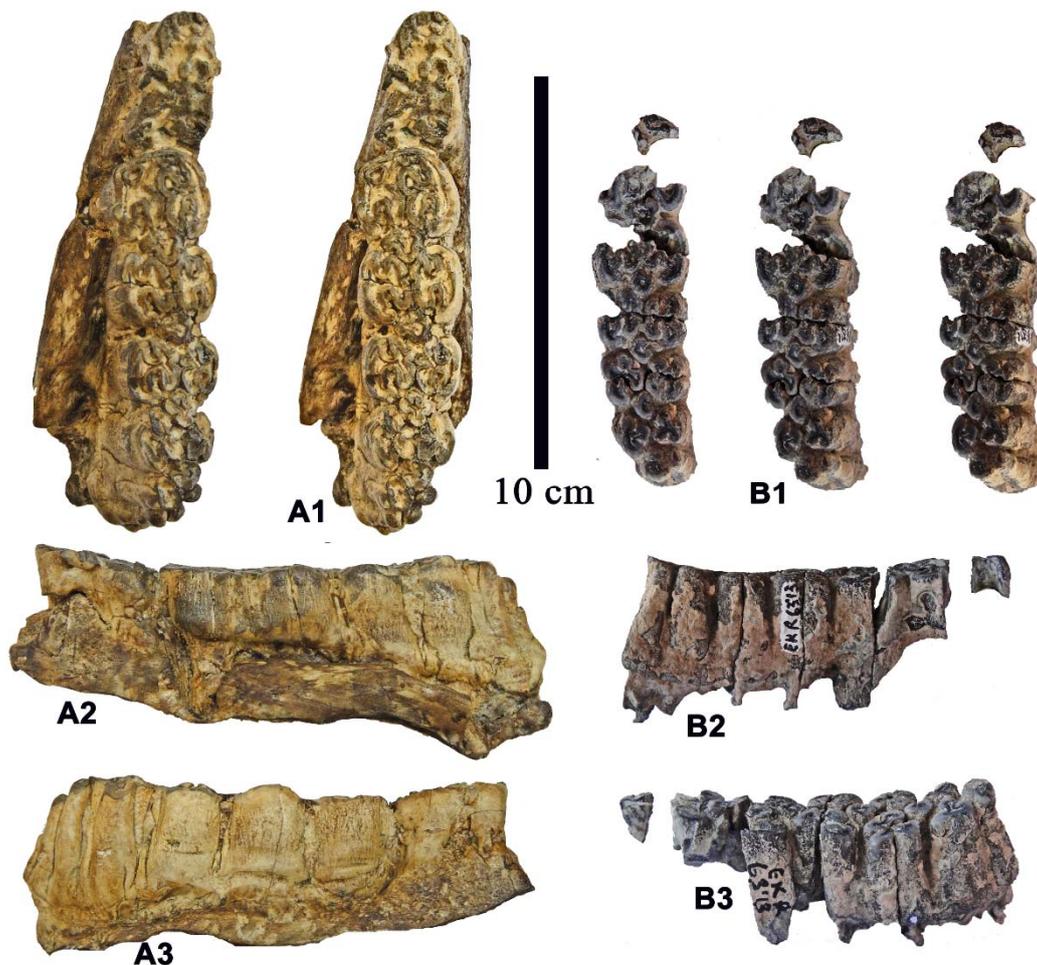


Figure 15. Comparison between m/3s of *Gerontochoerus scotti*. A) CM Omo 2, the paratype left mandible containing m/2 and m/3 from Ethiopia (Leakey, 1943) (cast in NHMUK) and B) GSN EKR 63'13, right m/3 from Ekuma Rhino Site, Etosha, Namibia. 1 - stereo occlusal views, 2 - buccal views, 3 - lingual views (scale : 10 cm).

Description of the m/3 from Ekuma Rhino Site

As preserved the right m/3 from Ekuma Rhino Site comprises a moderately worn crown missing fragments of the first pair of cusps (protoconid, metaconid) and some of the anterior cingular complex, which is detached from the rest of the tooth (Fig. 15b). In total there are five pairs of cusps (lophids) and a posterior cingular pillar. The median and posterior accessory cusplets are tall, and block the median and posterior transverse valleys in their middle. The talonid consists of three pairs of cusps constructed along the same lines as the

Discussion

The suid from Ekuma Rhino Site was previously attributed to *Gerontochoerus koobiforaensis* by Pickford *et al.* (2016) but it has five lophids in the m/3, so in this respect it agrees better in morphology with *Gerontochoerus scotti*. However, the tooth appears to be rather broad for the latter taxon (range of breadths 17-23 mm) (Fig. 13) and thus closer to *G. koobiforaensis*, but this is likely due

anterior lophids, but the enamel outlines are less clearly defined. The Furchen are deeply indented, there is a thick cover of cementum and the cervix is well-defined and almost rectilinear. There are remnants of roots preserved beneath the hypoconid-entoconid pair and beneath the distal end of the talonid.

Because of the damage to the mesial end of the tooth it is not possible to provide an accurate measurement of its length, but it was in the neighbourhood of 10 cm long and the second lophid is 27 mm broad.

in part to the fact that there is a thick cover of cementum on the lingual and buccal sides of the crown, which is lacking in many of the specimens from East Africa. The estimated crown length of ca 100 mm agrees with the larger subset of specimens attributed to *Gerontochoerus scotti* (sometimes classified as a separate species *Gerontochoerus harrisi* Van der Made, 1998).

Conclusions

The tetraconodont fossil record of Southern Africa is generally rather poor except at selected sites such as Langebaanweg, Cape Province (*Nyanzachoerus kanamensis australis* Cooke & Hendey 1992) and the Chiwondo Beds, Malawi (Kullmer, 2008). A few specimens of *Gerontochoerus scotti* from Makapansgat were for a long time misattributed to *Notochoerus capensis*, but the specimens are far too large to belong to this species, which is, in any case, a suine and not a tetraconodont. A mandible from Hondeklip Bay was attributed to *Nyanzachoerus australis* by Pickford & Senut (1997).

The discovery of additional tetraconodont specimens from sites in South Africa and Namibia extends the known geographic range of the subfamily in the subcontinent to the west coast of Namibia and to the Etosha Basin in northern Namibia. Of particular value is a small sample from Brad Pit 'A' in the Cradle of Humankind, Gauteng, South Africa, part of the Bolt's Farm Karst System. At this site an m/3 was found associated with a P3/ and a p/3 which

provide sound evidence of the tetraconodont affinities of the species, the premolars of this subfamily being highly diagnostic and radically different from those of suines. It is worth pointing out that a karst infilling at Aves Cave I, not far from Brad Pit 'A', yielded large premolars that are typical of suines associated with a broken upper molar that closely resembles the holotype of *Notochoerus capensis*. For this reason, among others, *Notochoerus capensis* is considered to belong to Suinae rather than to Tetraconodontinae. It is stressed, however, that most of the East African and Malawi specimens previously attributed to *Notochoerus capensis* do not belong to this species, but are tetraconodonts more properly classified in *Gerontochoerus*.

It is concluded that the grits at Kaukausib Fontein which are interbedded with onyx-like travertine accumulated about 5 Ma (range 6-4 Ma), the karst infilling at Brad Pit 'A' was deposited about 3.7 Ma (range 4-3.2 Ma), and the Ekuma Delta clays at the Rhino Site, about 3.2 Ma.

Acknowledgements

We thank the Geological Survey of Namibia, Windhoek, and the Ditsong National Museum of Natural History, Pretoria, for providing access to the fossils.

We are anxious to thank Namdeb Diamond Corporation (Pty) Ltd for financial and logistic support (J. Jacob, G. Grobbelaar, H. Fourie, B. Wood, K. Prinsloo, U. Witbooi, L. Kastoor, W. Muyamba, E. Pinehas). Research authorisation was provided by the Namibian National Heritage Council (E. Ndalikokule, A. Nankela, H. Elago), and administrative and logistic support by the Geological Survey of Namibia (G. Simubali, A. Nguno, V. Do Cabo, J. Eiseb, H. Mocke, U. Schreiber) and the Sperrgebiet National Park (H. Tjihukununa). The Namibia Palaeontology Expedition was supported by UMR 7207 of the CNRS. Particular thanks to

Hendrick Steenkamp and Amon Iitula who carefully extracted the blocks of grit at Kaukausib Fontein which contained the fossil suid teeth so that they could then be treated in the laboratory.

The excavation permit for the Brad Pit excavation (permit ID2672) was delivered by the South African Heritage Agency (R. Redelstorff and P. Hine). We thank Mrs C. Klinkert for providing access to her property. The MPFSA (Mission Paléolithologique Franco-Sud-Africaine) is financed by the French Ministry of Europe and Foreign Affairs (Pôle Sciences humaines et sociales, Archéologie et Patrimoine – Sous-directions de l'enseignement supérieur et de la recherche) and the IRL HOMEN is financed by the French CNRS and the South African NRF.

References

- Ashley, G., Dominguez-Rodrigo, M., Bunn, H., Mabulla, A. & Baquedano, E. 2010. Sedimentary geology and human origins : A fresh look at Olduvai Gorge, Tanzania. *Journal of Sedimentary Research*, **80**, 703-709.
- Bennett, R.S. & Kalbskopf, S. 1978. *An Investigation of the Area between the Klinghardt Mountains and the Eastern Boundary of the Sperrgebiet*. The Consolidated Diamond Mines of South West Africa (Pty) Ltd. Sperrgebiet Geological Investigation, Oranjemund, Unpublished Report, Accession N° 69033, File Index N° Rpt 238, 1978, 11 pp.
- Bishop, L.C. 2010. Suoidea. In: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*. Chapter 42, pp. 821-842, Berkeley, Los Angeles, London, University of California Press.
- 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.
- 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. 1976. Suidae from Plio-Pleistocene strata of the Rudolf Basin. In: Coppens, Y., Howell, F., Isaac, G. & Leakey, R. (Eds) *Earliest Man and Environments in the Lake Rudolf Basin*, pp. 251-263, Chicago, University of Chicago Press.
- Cooke, H.B.S. 1997. The status of the African fossil suids *Kolpochoerus limnetes* (Hopwood, 1926), *K. phacochoeroides* (Thomas, 1884) and "*K.*" *afarensis* (Cooke, 1978). *Geobios*, **30**, 121-126.
- Cooke, H.B.S. 2007. Stratigraphic variation in Suidae from the Shungura Formation and some coeval deposits. In: Bobe, R., Alemseged, Z. & Behrensmeyer, A.K. (Eds). *Hominin Environments in the East African Pliocene : An Assessment of the Faunal Evidence*, pp. 107-127, Dordrecht, Springer.
- Cooke, H.B.S. & Coryndon, S.C. 1970. Pleistocene mammals from the Kaiso Formation and other related deposits in Uganda. *Fossil Vertebrates of Africa*, **2**, 107-224.
- Cooke, H.B.S. & Ewer, R.F. 1972. Fossil Suidae from Kanapoi and Lothagam, North-western Kenya. *Bulletin of the Museum of Comparative Zoology*, **143**, 149-296.
- Cooke, H.B.S. & Hendey, Q.B. 1992. *Nyanzachoerus* (Mammalia: Suidae: Tetraconodontinae) from Langebaanweg, South Africa. *Durban Museum Novitates*, **17**, 1-20.
- Coppens, Y. 1971. Une nouvelle espèce de Suidé du Villafranchien de Tunisie, *Nyanzachoerus jaegeri* nov. sp. *Comptes*

- Rendus de l'Académie des Sciences, Paris, Séries Ila*, **272**, 3264-3267.
- Geraads, D. & Bobe, R. 2017. Suidae from Kanapoi. *Journal of Human Evolution*, <http://dx.doi.org/10.1016/j.jhevol.2017.05.004>, 9 pp. + 1 page of Supplementary Online Material.
- Gommery, D., Badenhorst, S., Sénégas, F., Potze, S., Kgasi, L. & Thackeray, J.F. 2012. Preliminary results concerning the discovery of new fossiliferous sites at Bolt's Farm (Cradle of Humankind, South Africa). *Annals of the Ditsong National Museum of Natural History*, **2**, 33-45.
- Gray, J.E. 1821. On the natural arrangement of vertebrate 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.
- Harris, J.M. 1983. Family Suidae. In: Harris J.M. (Ed.). *Koobi Fora Research Project: Volume II: The Fossil Ungulates, Proboscidea, Perissodactyla, and Suidae*, pp. 215-300. Oxford, Oxford University Press.
- Harris, J. & White, T. 1979. Evolution of the Plio-Pleistocene African Suidae. *Transactions of the American Philosophical Society*, Philadelphia, **69**, 1-128.
- Hopwood, A. 1926. The Geology and Palaeontology of the Kaiso Bone Beds. *Uganda Protectorate Geological Survey Department Occasional Paper*, **2** (2), 19-23.
- Hopwood, A. 1934. New fossil mammals from Olduvai, Tanganyika Territory. *Annals and Magazine of Natural History*, **14** (10), 546-550.
- Hünemann, K.A. 1968. Die Suidae (Mammalia, Artiodactyla) aus den Dinotheriensanden (Unterpliozän = Pont) Rhein Hessens (Südwestdeutschland). *Schweizerische Paläontologische Abhandlungen*, **86**, 1-96.
- Kullmer, O. 1999. Evolution of Plio-Pleistocene suids (Artiodactyla, Suidae) based on tooth pattern analysis. *Kaupia Current Research*, **2**, 1-34.
- Kullmer, O. 2008. The fossil Suidae from the Plio-Pleistocene Chiwondo Beds of Northern Malawi, Africa. *Journal of Vertebrate Paleontology*, **28** (1), 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. 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.
- Miller, R. McG., Pickford, M. & Senut, B. 2010. The geology, palaeontology and evolution of the Etosha Pan, Namibia: implications for terminal Kalahari deposition. *South African Journal of Geology*, **113**, 307-334.
- Morales, J., Senut, B. & Pickford, M. 2011. *Crocuta dietrichi* from Meob, Namibia: implications for the age of the Tsondab Sandstone in the coastal part of the Namib Desert. *Estudios geológicos*, **67** (2), 207-215.
- Pether, J. 1986. Late Tertiary and Early Quaternary marine deposits of the Namaqualand coast, Cape Province: New perspectives. *South African Journal of Science*, **82**, 464-470.
- Pickford, M. 1994. Fossil Suidae of the Albertine Rift Valley, Uganda-Zaire. In: Senut, B. & Pickford, M. (Eds). *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire. Vol. 2 : Palaeobiology-Paléobiologie*. Orléans, *Occasional Publication, CIFEG*, **1994/29**, 339-373.
- Pickford, M. 1998. Onland Tertiary marine strata in southwestern Africa: eustasy, local tectonics and epeirogenesis in a passive continental margin setting. *South African Journal of Science*, **94**, 5-8.
- Pickford, M. 2002. Neogene and Quaternary vertebrate biochronology of the Sperrgebiet and Otavi Mountainland, Namibia. *Communications of the Geological Survey of Namibia*, **12**, 359-365.
- 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. 2013. Reappraisal of *Hylochoerus euilus* Hopwood, 1926 (Suidae, Mammalia) from the Albertine Rift (Pliocene) Uganda. *Geo-Pal Uganda*, **6**, 1-26.
- Pickford, M. 2018. Onyx travertine in the northeastern Sperrgebiet, Namibia.

- Communications of the Geological Survey of Namibia*, **20**, 87-99.
- 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. & Gommery, D. In press. Fossil suids from Bolt's Farm Palaeokarst System, South Africa : implications for the taxonomy of *Potamochoeroides* and *Notochoerus* and for biochronology. *Estudios geologicos*.
- 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.
- Pickford, M. & Senut, B. 1996. Namibia Palaeontology Expedition : 6 April to 6 July, 1996. Unpublished field report, 25 pp.
- Pickford, M. & Senut, B. 1997. Cainozoic mammals from coastal Namaqualand, South Africa. *Palaeontologia Africana*, **34**, 199-217.
- Pickford M. & Senut, B. 2019. Namibia Palaeontology Expedition : 20 April to 14 May, 2019. Unpublished field report, 30 pp.
- Pickford, M., Senut, B., Hipondoka, M., Person, A., Ségalen, L., Plet, C., Jousse, H., Mein, P., Guérin, C., Morales, J. & Mourer-Chauviré, C. 2013. Mio-Plio-Pleistocene geology and palaeobiology of Etosha Pan, Namibia. *Communications of the Geological Survey of Namibia*, **15**, 16-68.
- Pickford, M. & Tsujikawa, H. 2019. Revision of African Kubanochoerinae (Suidae : Mammalia) with descriptions of new fossils from the Middle Miocene Aka Aiteputh Formation, Nachola, Kenya. *Münchner Geowissenschaftliche Abhandlungen*, **48**, 1-105.
- Reda, H., Lazagabaster, I.A. & Haile-Selassie, Y. 2017. Newly discovered crania of *Nyanzachoerus jaegeri* (Tetraconodontinae, Suidae, Mammalia) from the Woranso-Mille (Ethiopia) and reappraisal of its generic status. *Journal of Mammalian Evolution*. DOI 10.1007/s10914-017-9398-5.
- 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 précisions paléoenvironnementales*. PhD Thesis, University of Montpellier II, Montpellier, France, 232 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** (3), 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*, **2**, 25-37.
- Thackeray, 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.
- 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.
- White, T.D. & Suwa, G. 2004. A new species of *Notochoerus* (Artiodactyla, Suidae) from the Pliocene of Ethiopia. *Journal of Vertebrate Paleontology*, **24** (2), 474-480.
- White, T.E. 1959. The endocrine glands and evolution, No. 3: Os cementum, hypsodonty, and diet. *Contributions from the Museum of Paleontology University of Michigan*, **13**, 211-265.