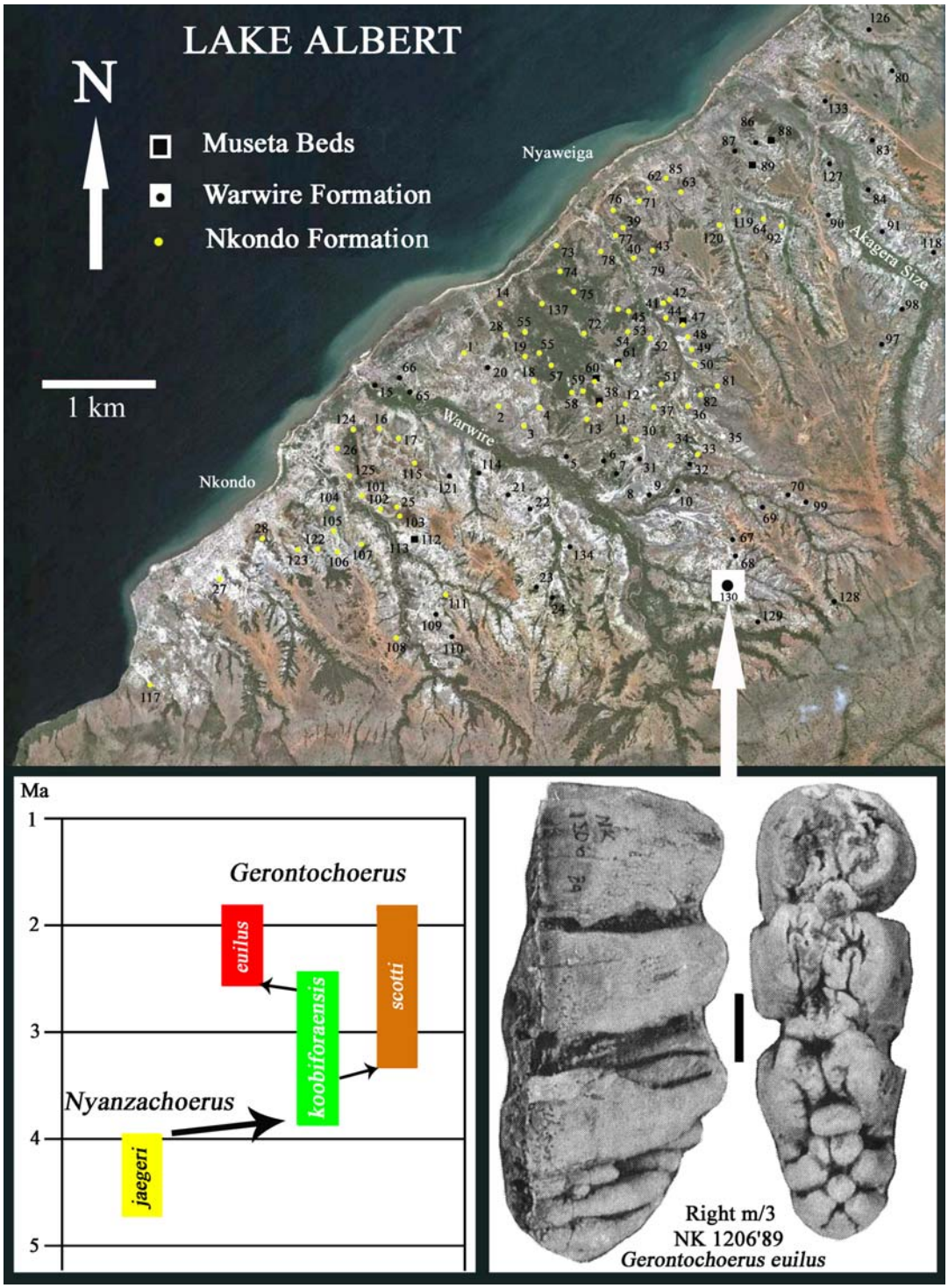
Number 6, 2013
ISSN 2076-5764

GEO-PAL UGANDA



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Geo-Pal Uganda

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Reappraisal of *Hylochoerus euilus* Hopwood, 1926 (Suidae, Mammalia) from the Albertine Rift (Pliocene) Uganda

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

ABSTRACT

The lectotype of *Hylochoerus euilus* Hopwood, 1926a, from the Plio-Pleistocene of Uganda is shown to be an upper third molar and not a mandibular tooth. This determination radically modifies its interpretations, and has repercussions on the taxonomy of Late Neogene tetraconodonts of Africa. It is concluded that *Notochoerus* is a suine and not a tetraconodont, and that the use of this genus name for species of tetraconodonts is not defensible. The genus name *Gerontochoerus* Leakey, 1943, is resurrected for the species that, in recent literature, has become known as "*Notochoerus*" *euilus* (Hopwood, 1926a) and "*Notochoerus*" *scotti* (Leakey, 1943). It is shown that the species "*Notochoerus*" *clarki* White & Suwa, 2004, is a junior synonym of *Gerontochoerus euilus* and that *Notochoerus harrisi* Van der Made, 1998, is a junior synonym of *Gerontochoerus scotti*. A new species, *Gerontochoerus koobiforaensis*, is erected for material intermediate in dimensions between *Gerontochoerus euilus* and *Gerontochoerus scotti*.

Key Words : Pliocene, Uganda, Suidae, Tetraconodontinae, Taxonomy, Metric variation

INTRODUCTION

As part of a general revision of the Tetraconodontinae, the author re-examined in detail the type series of *Hylochoerus euilus* from Kaiso, Uganda. This species was transferred to the genus *Notochoerus* by Leakey (1958) at the time thought to belong to the Suinae, close to *Metridiochoerus* and *Kolpochoerus*, but it was later classified as Tetraconodontinae by Cooke & Wilkinson (1978) who hypothesised that it descended from *Nyanzachoerus jaegeri*. This subfamilial attribution has been widely accepted by subsequent researchers, and in recent literature (Bishop, 2010) there has been a tendency to include the species formerly known as *Nyanzachoerus jaegeri* Coppens, 1971, in *Notochoerus*.

Two conclusions emerge from the re-examination of the Kaiso fossils. First, the lectotype third molar, which was interpreted as a lower molar by Hopwood (1926a) and all subsequent students, turns out to be an upper third molar, a finding that radically modifies the taxonomy of the group to which it belongs and all the down-line interpretations that flow from this change in meristic position. Secondly, direct comparison of the Kaiso lectotype with the type specimen of *Notochoerus capensis* reveals that they do not belong to the same genus.

The principal aim of this paper is to describe and interpret the lectotype and other fossils from the Albertine Rift Valley attributed to *Hylochoerus euilus* and to examine their relationships to specimens from the Eastern Branch of the African Rift System attributed to *Notochoerus euilus*, *Notochoerus scotti* and *Notochoerus clarki*.

The second purpose of this article is to determine whether the type species of *Notochoerus* (*No. capensis*) from Longlands, Vaal River Gravels, South Africa, represents the same genus as the Kaiso

sample attributed to *Notochoerus euilus*. The fragmentary nature of its fossil record renders the subfamily affinities of *Notochoerus capensis* dubious, a finding that echoes the conclusion of Van der Made (1998) that *Notochoerus capensis* is a nomen dubium, throwing into doubt the utility of the genus name *Notochoerus* and its extension to a diversity of suids which may belong to a distinct genus. What is clear is that it does not represent the same genus as the Kaiso lectotype of *Hylochoerus euilus*.

It is concluded that the type species of the genus, *Notochoerus capensis*, differs fundamentally from the three (or more) East African species usually attributed to the same genus, and that it is no longer feasible to continue attributing the latter taxa to this genus. The genus name with priority for the latter group is *Gerontochoerus* Leakey, 1943, type species *G. scotti* Leakey, 1943, lectotype KNM OS 5 (Omo 1), right maxilla containing M2/-M3/ from Omo, Shungura, Ethiopia.

BACKGROUND TO THE STUDY OF *HYLOCHOERUS EUILUS*

Hypsodont, polylophid molars of African and Asian extant and fossil suids have attracted attention for well over a century (Owen, 1840-45; Thomas, 1884; Thomas, 1904; Shaw, 1938, 1939; Leakey, 1942; Arambourg, 1947; Cooke, 1949; Cooke & Coryndon, 1970; Cooke & Ewer, 1972; Cooke & Maglio, 1972; Cooke, 1976; Cooke, 1978; Cooke & Wilkinson, 1978; Harris & White, 1979; Harris, 1987; Cooke, 2005; Bishop, 2011). Increase in hypsodonty and the addition of more or less complex talons(ids) to the third molars differs so markedly from the usual bunodont suid dental pattern, as exemplified by *Sus scrofa*, *Dasychoerus verrucosus*, *Potamochoerus porcus* and many Miocene suids, that it has been noted on numerous occasions. It is now generally accepted that at least five groups of suids evolved hypsodont teeth independently from each other. *Hippohyus* from Indo-Pakistan evolved from *Propotamochoerus* (Pickford, 1988), *Notochoerus Kolpochoerus*, *Metridiochoerus*, *Hylochoerus* and *Phacochoerus* developed from *Dasychoerus* (Pickford, 2012). *Gerontochoerus* evolved from *Nyanzachoerus* (Cooke & Wilkinson, 1978).

As hypsodont teeth wear down, the enamel pattern expressed at the occlusal surface changes as a function of changes in the cusp morphology from crown apex to crown base, the presence of accessory cusplets which are often curved from apex to cervix, differences in the depths and position of the Fürchen on each cusp, fusion between the enamel of cusps and accessory cusplets which are separated at their apices but which fuse together towards the cervix, variation in the depths of the foveae between cusps, longitudinal rotation of the molars (especially the upper one) as they wear down, and the presence or absence of roots, and differences in the slope of the wear surface. This combination of phenomena has caused endless problems with the interpretations of such teeth, to such an extent that genera such as *Afrochoerus* Leakey, 1958, were erected for senile individuals of *Metridiochoerus*. As teeth become more and more hypsodont, the tendency to develop roots is delayed until, in some lineages such as *Phacochoerus*, many individuals may not develop roots at all. The presence or absence of roots has on occasion been employed to distinguish and separate some species from others of the same lineage (Leakey, 1958) (eg *Pronotochoerus* with roots is the same lineage as *Metridiochoerus* which often has no roots, at least in highly hypsodont forms). As a consequence, a tremendously complex literature has developed around the interpretation of such suid lineages, with little sign that consensus is approaching.

It has often proved difficult to determine the side from which isolated hypsodont molars came, and whether they belong to the upper or lower tooth row (Broom, 1925; Van Hoepen & Van Hoepen, 1932; Shaw, 1939). As a result, in the literature, there are several misattributions of teeth to the upper and lower tooth rows and this has introduced error into the metric analyses and the down-line biochronology that flows from them. Not only were the type specimens of *Notochoerus capensis* and *Hylochoerus euilus* initially misattributed to the lower tooth row, but there are other instances in the literature. For example, HCRP U 15 442 from Malawi (Sandrock *et al*., 2007) is likely an upper third molar on the basis of the marked angle between the occlusal plane and the cervix, and the strong mesially concave curvature of the posterior cusplets of the talon, but Kullmer (1999, 2008) identified it as a lower third molar. Siding of isolated teeth has also proved problematic. For example, Harris &

White (1979) wrote that the holotype of *Metridiochoerus andrewsi*, from Homa Mountain, is an upper right M3/, yet it is a left M3/, as shown by comparing it with the Kagua specimen (NHML M 15880) which can be sided confidently due to the fact that it occurs in the maxilla (Leakey, 1958). The lectotype of *Hylochoerus euilus* was reported by Cooke and Coryndon (1970, p. 148) to be from the left side in the text, but from the right side in the captions of the text-figure and plate (Cooke & Coryndon, 1970 text-fig. 11, plate 7 figures A, B). The incorrect siding of teeth affects their interpretation because the buccal cusps are described as though they are lingual ones, and vice versa, and when compared with correctly sided teeth, inappropriate comparisons are made between protocone and paracone for the first loph, and between the hypocone and metacone for the second loph.

Since 1958 (Leakey, 1958) the species *euilus* has been attributed to *Notochoerus* Broom, 1925, and since 1978 the genus has been included in the subfamily Tetraconodontinae (Cooke & Wilkinson, 1978) usually as a descendant of *Nyanzachoerus* Leakey, 1958. These interpretations of the generic and subfamilial status of the species have become deeply entrenched, yet the original reasons for including *euilus* in *Notochoerus* were weakly argued, and boil down to three features – the third molars are hypsodont, they are polylophid and possess roots. However, these features are also common to early stages of *Metridiochoerus* and to *Kolpochoerus*.

Leakey (1958) was the first person to classify the Kaiso species in *Notochoerus* as the combination *Notochoerus euilus* (Hopwood, 1926a) because he considered the lectotype to be compatible with what was expected to be the morphology of a lower third molar of the genus. It should be recalled that at that time no lower third molar of *Notochoerus capensis* had been described (some specimens from "Sterkfontein" attributed to the species by Shaw, 1938, were subsequently identified as *Metridiochoerus andrewsi* and some fossils from Makapansgat described by Ewer (1958) were later identified as *Metridiochoerus andrewsi* by Cooke, 1993). The difference in dimensions between the type specimens of *Notochoerus capensis* and *Notochoerus euilus* prompted Leakey (1958) to classify the South African and East African material in two distinct species, and he added the larger species *Gerontochoerus scotti* to the genus as the combination *Notochoerus scotti* (Leakey, 1943).

During the 1970's many new fossils of hypsodont suids were described from the eastern branch of the African Rift System (Cooke & Ewer, 1972; Cooke, 1978; Harris & White, 1979) including complete skulls and mandibles. The attribution of the material to four genera - *Notochoerus*, *Metridiochoerus*, *Kolpochoerus* and *Phacochoerus* - was not accomplished without differences of opinion and much resorting of fossils. The uncertainty was mainly fuelled by the fragmentary nature of the type specimens of the type species of the three extinct genera.

The holotype of *Notochoerus capensis* is an upper third molar lacking part of the anterior loph (originally interpreted as a lower molar), the holotype of *Metridiochoerus andrewsi* is an isolated upper third molar, the holotype of *Kolpochoerus paiceae* (= *Kolpochoerus sinuosus*) is a deeply worn lower third molar in a fragmentary mandible. The difficulties of proposing a robust taxonomy for these suids were increased by the presence of rampant synonymy, not only at the species level, but also at the genus level.

The lectotype of *Hylochoerus euilus* Hopwood, 1926a, from the Kaiso Peninsula, Albertine Rift, Uganda (NHML M 12613A) is an upper third molar and not a lower third molar as thought by all researchers since Hopwood (1926a). The tooth, which is missing part of the first loph, appears to be rather narrow, and this undoubtedly influenced the original and subsequent assessments of the tooth as a lower molar, especially when it is compared with the broader holotype of *Notochoerus capensis* Broom, 1925, an incomplete upper third molar (incidentally, also first interpreted as a lower tooth (Broom, 1925)). There is a fragment of lower m/3 from Kaiso (NHML M 12613B) which shows sub-parallel occlusal surface and cervix. However, one of Hopwood's (1926a) specimens from Kaiso (NHML M 12613C), probably belongs to *Metridiochoerus andrewsi* judging from the morphology of the cusps and the thick cementum, and this may have influenced previous interpretations of the species *Gerontochoerus euilus*.

Attempts to reconstruct the incomplete type specimen of *Notochoerus capensis* were not greeted with acclaim. Broom's (1925) reconstruction of the M3/ of *Notochoerus capensis* was forcefully criticised by Shaw (1939) who proposed his own, shorter version, which was in its turn criticised by Cooke (1949). Van der Made (1998) commented that it was difficult to work with reconstructions which yield a wide range of possible measurements for the length of the teeth. For example, the different reconstructions of the holotype of *No. capensis* yield lengths that vary from 72 to 81 mm.

Cooke & Coryndon (1970) attempted a reconstruction of the Kaiso lectotype of *Gerontochoerus euilus*, at the time called *Notochoerus euilus*, but because they thought it was a lower molar they added on one loph too many. The form of the cervix reveals that only half the first loph is missing (along with the anterior cingular complex) and in any case the tooth is an upper molar. My own measurements of the lectotype of *Gerontochoerus euilus* suggest that its length is about 60 mm (breadth ca 26 mm), whereas the reconstruction by Cooke & Coryndon (1970) would make its length about 79 mm and its breadth ca 23 mm, which would imply that it has the same length and breadth as small lower third molars of *Gerontochoerus koobiforaensis* sp. nov. and large ones of "*Notochoerus*" *clarki* (Fig. 6). It is perhaps for this reason that the material attributed by many authors to *Notochoerus euilus* (here attributed to *G. koobiforaensis*) was for so long identified as a species which is larger than the lectotype, and that when a smaller species was recognised at Gamadeh and other sites in Ethiopia, it was taken to indicate the existence of a new species by White & Suwa (2004) who did not realise that it has in fact the same dimensions as the lectotype of *G. euilus*. The presence of an admixture of two species in erstwhile *Notochoerus euilus* as concluded by White & Suwa (2004) is not contested by the present study - indeed, it is supported by the new data and interpretation, but the names applied to the entities need to be reconsidered in light of the morphometrics of the lectotype of *Hylochoerus euilus*, and not on the basis of the fossils from the Eastern branch of the African Rift that erroneously became the "reference model" for the species.

Over the years the following species have been rightly or wrongly attributed to *Notochoerus* (Table 1).

Table 1. Species of suids which have at one time or another been attributed to the genus *Notochoerus*. The list is in chronological order of publication. (Species highlighted in grey are tetraconodonts, those left clear are suines).

Taxon	**Comment and reidentification of type specimen**
Notochoerus capensis Broom, 1925	Type species is a suine
Notochoerus euilus (Hopwood, 1926a)	*Gerontochoerus euilus* (Hopwood, 1926a)
Notochoerus dietrichi Hopwood, 1934	*Metridiochoerus andrewsi* Hopwood, 1926b
Notochoerus meadowsi Broom, 1928	*Metridiochoerus andrewsi* Hopwood, 1926b
Notochoerus paiceae Broom, 1931	*Kolpochoerus* Van Hoepen & Van Hoepen, 1932
Notochoerus dietrichi Hopwood, 1934	*Metridiochoerus andrewsi* Hopwood, 1926b
Notochoerus broomi Shaw & Cooke, 1941	*Phacochoerus modestus* (Van Hoepen & Van Hoepen, 1932)
Notochoerus serengetensis Dietrich 1942	*Metridiochoerus andrewsi* Hopwood, 1926b
Notochoerus scotti (Leakey, 1943)	*Gerontochoerus scotti* Leakey, 1943
Notochoerus compactus Leakey, 1958	*Kolpochoerus compactus* (Leakey, 1958)
Notochoerus hopwoodi Leakey, 1958	*Metridiochoerus hopwoodi* (Leakey, 1958)
Notochoerus harrisi Van der Made, 1998	*Gerontochoerus scotti* Leakey, 1943
Notochoerus clarki White & Suwa, 2004	*Gerontochoerus euilus* (Hopwood, 1926a)

MATERIALS, METHODS AND DENTAL NOMENCLATURE

Diverse authors have devised many terms to describe hypsodont suid teeth. Some of the terms such as dental skirt, pillars, columns, prisms, laterals, medials, anterior complex, and posterior complex, are poorly defined and often leave room for doubt. Few authors have used the classic tribosphenic cusp terminology for hypsodont suid teeth, yet it is clear that the two anterior loph(id)s are comprised of protocone and paracone for upper teeth, protoconid and metaconid for lower teeth, and that the second loph(id) is comprised of the hypocone and metacone for upper teeth, and hypoconid and entoconid for lower teeth (Fig. 1). In addition, suid molars possess anterior and posterior cingula(ids) and three

cusplets in the sagittal valley called the anterior, median and posterior accessory cusplets (aac, mac, pac) (Fig. 1).

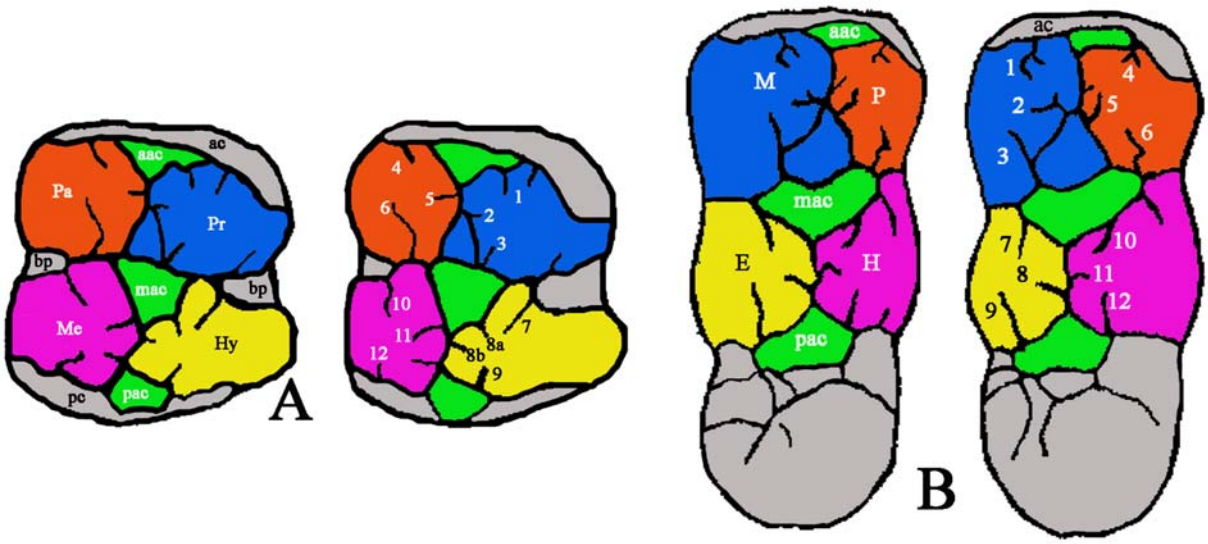

Figure 1. Dental nomenclature used in this paper (stereo drawings of teeth of *Hippopotamodon sivalense*). A - right M2/ : Pr – protocone, Pa – paracone, Hy – hypocone, Me – metacone, ac – anterior cingulum, pc – posterior cingulum, bp – basal pillars; B - right m/3 : P – protoconid, M – metaconid, H – hypoconid, E – entoconid, aac – anterior accessory cusplet, mac – median accessory cusplet, pac – posterior accessory cusplet, 1-12 – grooves or Fürchen (modified from Pickford, 1988; Fürchenmuster after Hünermann, 1968).

There are cingular accessory tubercles called basal pillars that may become enlarged and heightened in hypsodont teeth. Each of the main cusps of suid teeth are scored by three or more grooves called Fürchen (Hünermann, 1968; Pickford, 1988) which are numbered 1 to 12 (see Fig. 1). It is the depth and position of these grooves that give rise to the complicated enamel figures observed in the occlusal surface, often described as H-shaped, dumb-bell shaped, stellate and so on. Additional grooves can score the buccal surfaces of the buccal cusps and the lingual surfaces of the lingual cusps, and these contribute to the complexity of the enamel figures exposed at the occlusal surface of the teeth. In some taxa the Fürchen can reach each other, thereby slicing off a separate cusplet, but which is formationally part of the main cusp. This is particularly important in upper molars of some hypsodont suids, in which the Fürchen known as 8a (8 anterior) and 8p (8 posterior) may join each other thereby isolating a rounded cusplet to the inner side of the hypocone. This cusplet has sometimes been interpreted to be a neoformation, but it is in fact part of the hypocone.

Measurements of the teeth follow the method outlined by Harris & White (1979) but it is evident that inter-observer measurements can vary quite considerably (Annex 1).

Institution Abbreviations

HCRP – Hominid Corridor Research Project
KNM – Kenya National Museum, Nairobi
MNHN - Muséum National d'Histoire Naturelle, Paris
NHML – Natural History Museum, London
NME – National Museum of Ethiopia, Addis Ababa
UM – Uganda Museum, Kampala

MORPHOMETRIC COMPARISON BETWEEN *HYLOCHOERUS EUILUS* AND OTHER SUIDS

Description of the lectotype of *Hylochoerus euilus*

NHML M 12613A is a right M3/ lacking part of the anterior loph and cingulum. The tooth is rather narrow which is undoubtedly the reason why it was previously interpreted to be a lower molar. However, there are two main features of the specimen which reveal that it is from the maxillary tooth row – 1) the marked angle between the occlusal surface and the cervix, and 2) the strong anterior inclination of the cusps and notches relative to the cervix in buccal and lingual views (Fig. 2). A lower third molar of the species from the Kaiso Peninsula, UM NK 1206'89, Locality NK 130 in the Warwire Formation (Pickford *et al*., 1993) (see front cover) shows sub-parallel occlusal surface and cervix, and in lingual and buccal views, the cusps are more rectilinear and more vertically oriented with respect to the cervix than is the case in the upper third molar (Pickford, 1994).

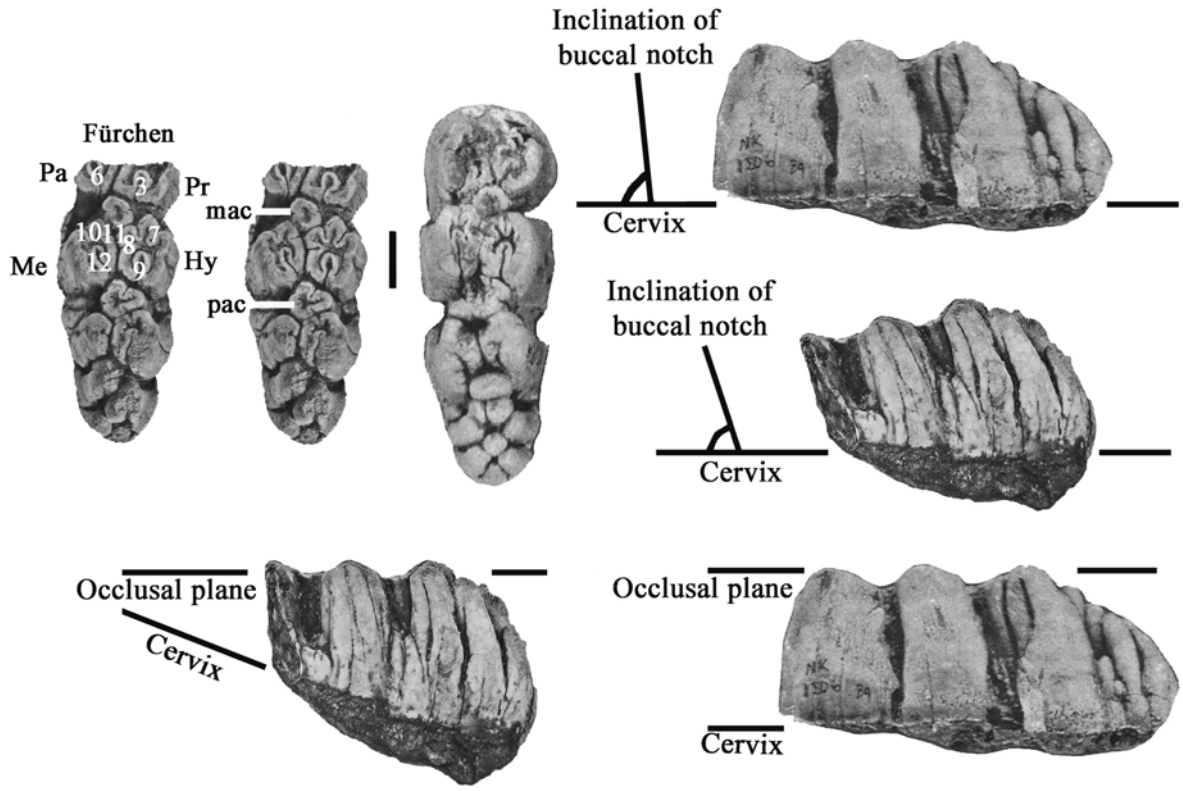

Figure 2. Distinguishing upper and lower third molars of *Gerontochoerus euilus* from the Kaiso Peninsula, Albertine Rift, Uganda. NHML M 12613A an incomplete right M3/ and UM NK 1206'89, right m/3 (For abbreviations see Fig. 1) (scale : 10 mm).

The median accessory cusplet of the lectotype is positioned between the first and second lophs but does not intervene between the protocone and paracone of the first loph, nor between the metacone and hypocone of the second loph. The posterior accessory cusplet (hypoconule) occupies a position between the second loph and the talon, and does not intervene between the hypocone and metacone. As a consequence of the position of the median and posterior accessory cusplets, the lingual and buccal notches are mesio-distally broad with a U-shaped base, somewhat recalling the morphology observed in *Hylochoerus*, as was noted by Hopwood (1926a) as well as in *Nyanzachoerus* species. In the base of the buccal and lingual notches, there are low basal pillars. The talon is comprised of a loph accompanied distally by a complex of four cusplets decreasing in height distally. The lingual surfaces of the protocone, hypocone and the lingual cusp of the talon are scored by vertical slits that contribute

to the stellate occlusal enamel pattern, but since the slits do not extend to the apices of the cusps, nor to their bases, the enamel pattern at the occlusal surface varies greatly as wear advances. Slits are present on the lingual surfaces of the metacone and the main talon cusp, but they are not as deeply incised as those on the buccal side and they die out basally. In occlusal view the Fürchen (Hünermann, 1968; Pickford, 1988) are clearly expressed. In the protocone and paracone, the posterior Fürchen (N° 3 and N° 6) are deeply incised and even open up anteriorly to form a rounded enamel outline (Fig. 2) sometimes referred to as dumbell-shaped. The same applies to Furchen 9 and 12 of the hypocone and metacone respectively. The anterior Fürchen (N° 7 and 10) of the hypocone and metacone are narrower and not as deeply incised as the posterior ones (N° 9 and 12) of the same cusps and they do not open up into rounded enamel outlines. Fürchen 8 of the hypocone consists of two grooves, one anteriorly (8a) the other posterior (8p). Fürchen 11 of the metacone is clear but narrow. The median accessory cusplet and the posterior accessory cusplet are small and subrounded in outline, broadening basally, with weakly developed vertical slits (Fig. 2). The surface of the enamel on the buccal and lingual sides of the tooth is coarsely but not deeply vertically wrinkled. The crown is hypsodont, the height of the cusps being ca 1.6 times the basal breadth of second loph of the tooth.

Comparison of the holotype of *Notochoerus capensis* and the lectotype of *Hylochoerus euilus*

The holotype of *Notochoerus capensis* and the lectotype of *Hylochoerus euilus* are upper right third molars which facilitates comparisons. There are manifest differences between these two specimens. In *Notochoerus capensis*, the anterior, median and posterior accessory cusplets are bigger and more complex in enamel outline than those of *H. euilus* and they intervene largely between the protocone and paracone of the anterior loph, and the hypocone and metacone of the second loph (Fig. 3). Thus the inner sides of the main cusps are well separated from each other, unlike the situation in the Kaiso fossil in which the inner parts of the main cusps are largely in contact with each other.

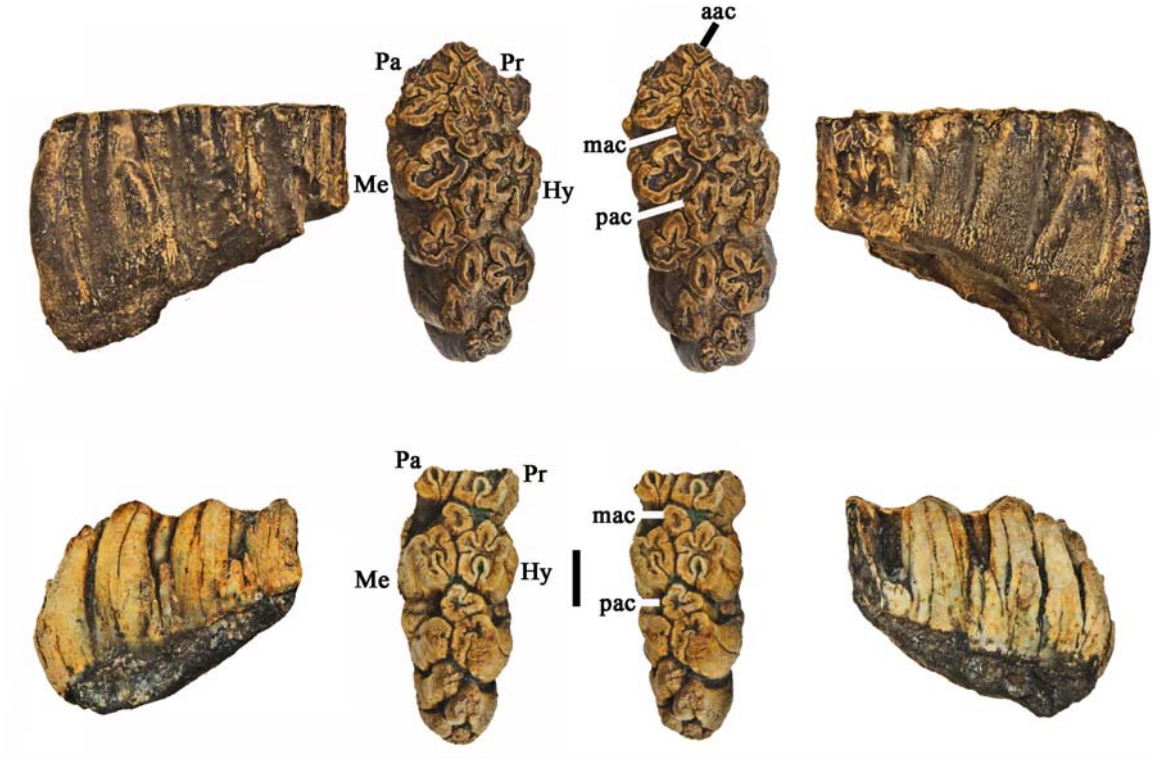

Figure 3. Comparison of the type specimens of *Gerontochoerus euilus* and *Notochoerus capensis*. Note in particular the positions of the median (mac) and posterior accessory cusplets (pac) relative to the hypocone and metacone (scale : 10 mm). (for abbreviations see Fig. 1).

The result is that the M3/ of *Notochoerus capensis* is occlusally broader than that of *Hylochoerus euilus*. The more complicated occlusal outlines of the accessory cusplets in *Notochoerus capensis* are

achieved by the presence of anterior and posterior extensions separated from the central part by well-expressed vertical grooves. It is the anterior and posterior extensions of the accessory cusps that separate the buccal main cusps from the lingual ones.

The buccal main cusps (paracone, metacone) of *Notochoerus capensis* are rounded buccally, contrasting with the more flattened profile that occurs in *Hylochoerus euilus*, but it should be noted that closer to cervix there is some flattening of the cusps in *No. capensis* and they become more elongated mesio-distally. Thus, the buccal notches are broader near the occlusal surface than they are near the cervix. The lingual main cusps (protocone, hypocone) in contrast, are more flattened and more mesio-distally elongated in *Notochoerus capensis* than in *Hylochoerus euilus*.

The degree of hypsodonty in the two teeth is comparable, but the enamel surface of *Notochoerus capensis* is more finely and densely wrinkled than that of *Hylochoerus euilus*.

It should be 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. The Olduvai tooth differs markedly from the lectotype of *Hylochoerus euilus*, reinforcing the view that the Kaiso specimen does not belong to *Notochoerus*. Harris & White (1979) identified the Olduvai tooth as *Mesochoerus limnetes*, but this attribution seems to be unlikely.

Comparison of the lectotypes of *Hylochoerus euilus* and *Gerontochoerus scotti*

Figure 4. Comparison of right upper third molars of *Gerontochoerus scotti* (top row) *Notochoerus capensis* (middle row) and *Gerontochoerus euilus* (bottom row). All three fossils are type specimens (scale : 10 cm).

The lectotype of *Gerontochoerus scotti* Leakey, 1943, is a right maxilla fragment from Shungura, Omo, Ethiopia, containing worn M2/ and M3/ (KNM OS 5 (Omo 1) cast in NHML M 26590) (Fig. 4). The M3/ is more deeply worn than the Kaiso tooth, and it is appreciably bigger (87.7 x 28.3 mm versus ca 60 x 26 mm).

The overall morphological similarities between the teeth prompted Leakey (1958) to include the Omo specimen in *Notochoerus euilus*, along with a left lower jaw fragment (cast in NHML M 26592) containing m/2-m/3 of more modest dimensions (m/3 measures 79 x 22.2 mm which compares with measurements of 70.8 x 25 mm for a right lower molar from the Warwire Formation, Albertine Rift, Uganda, attributed to *Notchoerus euilus* by Pickford (1994)).

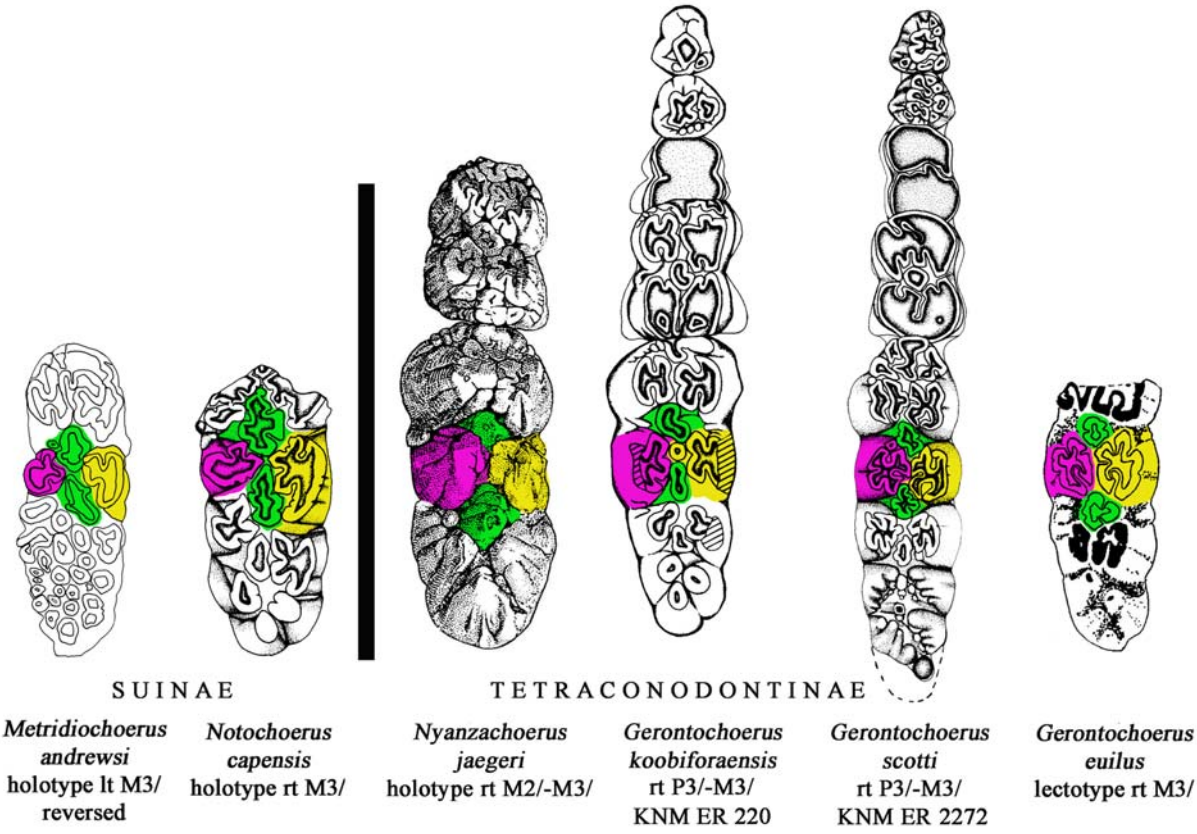

Figure 5. Comparison of the second lophs of right M3/s of *Metridiochoerus andrewsi*, *Notochoerus capensis*, *Nyanzachoerus jaegeri*, *Gerontochoerus koobiforaensis*, *Gerontochoerus scotti* and *Gerontochoerus euilus*. Note how the median and posterior accessory cusplets (in green) intervene between the hypocone (yellow) and metacone (rose) in the suines *M. andrewsi* and *No. capensis*, whereas in the tetraconodonts *Ny. jaegeri*, *G. euilus*, *G. koobiforaensis* and *G. scotti*, the hypocone and metacone retain contact in the midline of the crown. Note also the role of Fürchen N° 8a and 8p (see Fig. 1 for the position of these Fürchen) in contributing to the slicing off of a distinct pillar or cusplet in *Gerontochoerus*, but not in *Metridiochoerus* and *Notochoerus*. The figure of *Ny. jaegeri* is modified from Coppens, 1971, *G. euilus* is modified from Cooke & Coryndon (1970) and those of *No. capensis*, *G. koobiforaensis* and *G. scotti* are modified from Harris & White (1979) (scale : 10 cm).

There are however, a few differences between the lectotypes of *Gerontochoerus scotti* and *Hylochoerus euilus* in addition to the obvious ones of dimensions and wear stage. The anterior, median and posterior accessory cusplets are small in both teeth and they do not separate the buccal cusps from the lingual ones, unlike the situation in *Notochoerus capensis*. In this the Omo and Kaiso teeth are similar, but in *G. scotti*, there is a small almost circular enamel island between the hypocone and the metacone. In the Kaiso tooth, there are two grooves on the inner side of the hypocone

corresponding to Fürchen N° 8a and 8p, along with well-formed and deeply invading Fürchen 7 (the anterior one) and 9 (the posterior one) (Fig. 5). In the Kaiso tooth, the two grooves on the inner side of the hypocone, corresponding to N° 8a and 8p almost meet each other, thereby forming a small but tall cusplet lingual to the rest of the hypocone. Note that this cusplet is part of the hypocone, not an accessory cusplet. In *G. scotti*, the two grooves corresponding to Fürchen N° 8a and 8p have met each other, and thereby separate off a narrow pillar between the rest of the hypocone and the metacone.

The situation in *Notochoerus capensis* is completely different. The two Fürchen N° 8a and 8p show no tendency to meet each other, and it is the posterior part of the median accessory cusplet and the anterior part of the posterior accessory cusplet which are responsible for separating the hypocone from the metacone.

On the basis of these observations, it is concluded that the Kaiso species *Hylochoerus euilus* belongs to the same genus as the Omo *Gerontochoerus scotti*, as thought by Leakey, 1958, a decision generally accepted by subsequent researchers, but that both of these species differ fundamentally from the South African *Notochoerus capensis*, meaning that it is no longer possible to classify all three species together in a single genus. For this reason, the genus *Gerontochoerus* Leakey, 1943, is resurrected for the species *scotti* (the type species) and *euilus* (hereafter called *Gerontochoerus euilus*).

Comparison of the lectotype of *Gerontochoerus euilus* and the holotype of *Notochoerus clarki*

White & Suwa, 2004, erected the species *Notochoerus clarki* for material from Ethiopia which was perceived to be significantly smaller than material attributed by them to *Notochoerus capensis*, *Notochoerus euilus* and *Notochoerus scotti*. The type material of *No. clarki* is from Gamadeh, Middle Awash, Ethiopia, and consists of a cranium with dentition (NME GAM-VP-1/20).

The holotype of *Notochoerus clarki* is similar dentally to the lectotype of *Gerontochoerus euilus*, but it is not significantly smaller than it, as thought by White & Suwa (2004). The lectotype M3/ of "*No*". *euilus* (ca 60 x 26 mm) falls within the range of metric variation to "*No*". *clarki* (55-65 x 24-27 mm) (Fig. 6). It, and other material from Bouri, Middle Awash, and the Omo Valley, is smaller than material which, at the time of their study, was generally reported to belong to *Notochoerus euilus*, but it is now clear that the bulk of the specimens from the Ethiopian, Kenyan and Tanzanian sectors of the African Rift System attributed to the species *euilus*, belongs in fact to a species distinct from the Kaiso lectotype, and thus should not continue to be called *euilus*.

The metric and morphological similarities between the Kaiso and Gamadeh specimens indicates that they represent a single species, for which the name with priority is *Gerontochoerus euilus* (Hopwood, 1926a). This means that many of the specimens hitherto attributed to a highly variable *Notochoerus euilus*, need to be classified into two different species as proposed by White & Suwa, 2004. Although many of the fossils are close in dimensions to the holotype of *Notochoerus capensis*, they differ morphologically from this species to such a fundamental extent, that they cannot be attributed to the subfamily Suinae, nor to the genus *Notochoerus*, nor to the species *capensis*. The material is considerably smaller than *Gerontochoerus harrisi* (Van der Made, 1998), which is in any case a junior synonym of *Gerontochoerus scotti*.

The new species is here called *Gerontochoerus koobiforaensis* sp. nov. The holotype is KNM ER 3541, a skull and mandible from Unit 2 of the Koobi Fora Formation, East Turkana, Kenya (Harris & White, 1979, Plates 1-3). It is defined as a species of *Gerontochoerus* intermediate in dimensions between *Gerontochoerus euilus*, which is smaller, and *Gerontochoerus scotti*, which is larger (Fig. 6). The new species is clearly a tetraconodont suid, on the basis of the premolar morphology (small P2/, p/2 compared to much larger P3/-P4/ and p/3-p/4), the presence of zygomatic knobs (also present in *Nyanzachoerus jaegeri*) (Gebreyesus, 2011) and other dental and cranial features. It likely descended from *Nyanzachoerus jaegeri* Coppens, 1971, which should be kept in a distinct genus on account of its shorter and broader third molars which are distinctly less hypsodont and which have less complicated talon(id)s than those of the three described species of *Gerontochoerus*.

Metric analysis of *Gerontochoerus* species

Annex 1 presents measurements of teeth attributed in the literature to *Nyanzachoerus jaegeri* and various species of *Notochoerus* (here called *Gerontochoerus*). It has not been possible to verify all the identifications made by the authors (Leakey, 1943; Coppens, 1971; Cooke & Ewer, 1972; Harris, 1983; Harris *et al*., 1988; Harris, 2003; White & Suwa, 2004; Kullmer, 2008; Gebreyesus, 2011) meaning that there is a risk of the presence of extraneous taxa in the sample. For example, Harris (1983) included KNM ER 448 in *Notochoerus scotti* whereas in a previous paper (Harris & White, 1979, figs 36, 37) it was identified as *Notochoerus capensis*. Examination of the figures indicates that the specimen is a suine rather than a tetraconodont on the basis of the morphology of the premolars and the M3/, which is close to that of the holotype of *Notochoerus capensis*.

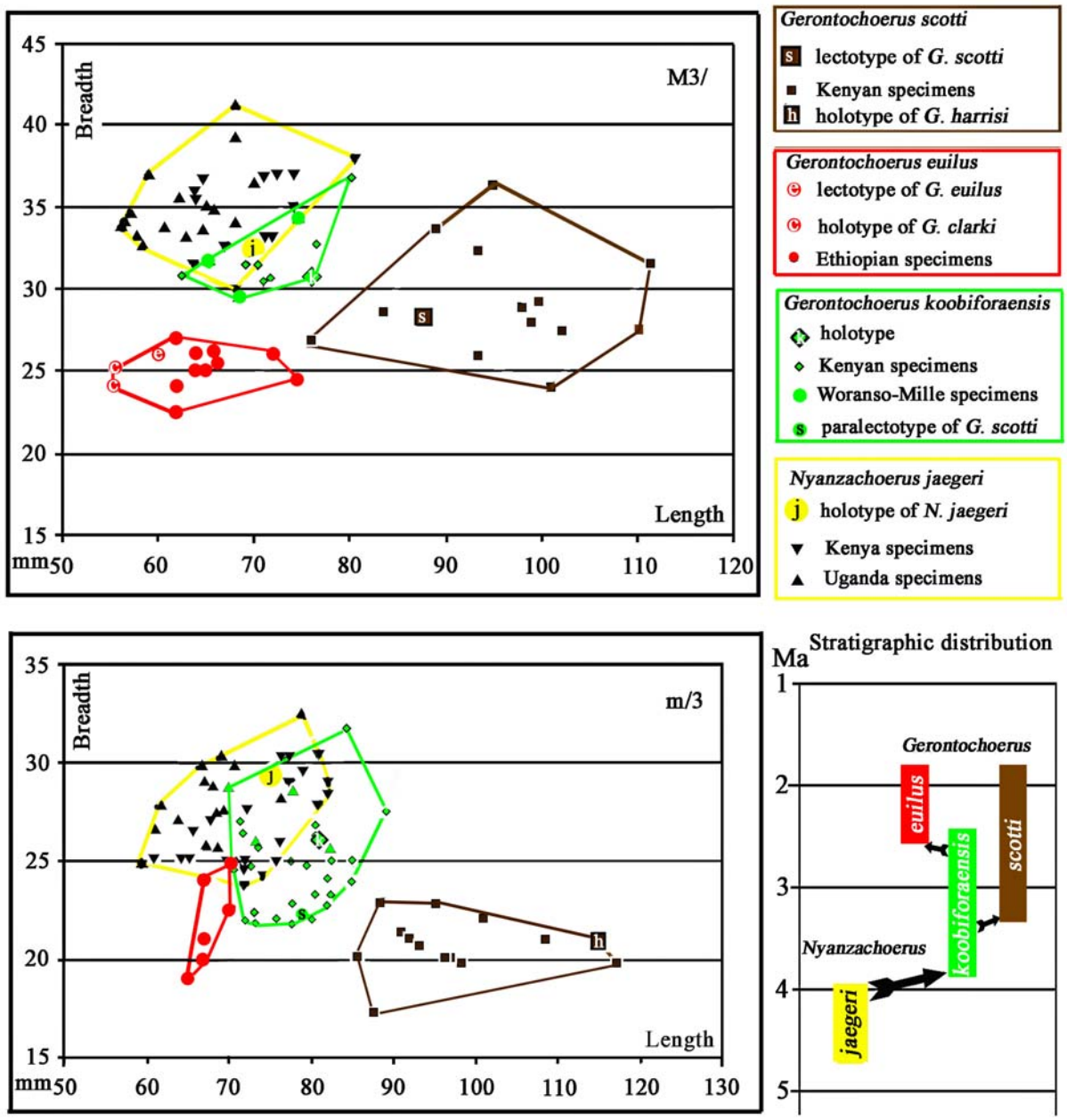

Figure 6. Bivariate plots (length x breadth) of upper and lower third molars of Plio-Pleistocene African tetraconodont suids. One specimen from Galili, NME GLL 345, is listed as a left m/3 by Kullmer *et al*., (2008) but its great breadth suggests that it might be an upper third molar. It is omitted from this figure (Annex 1).

Figure 6 presents bivariate plots of the third molars of the three species of *Gerontochoerus* recognised in this paper and of *Nyanzachoerus jaegeri*, its likely ancestor.

This metric analysis of East African Plio-Pleistocene tetraconodont suids indicates that there are four groups (Figs 6, 7, 8). The earliest group has relatively short and broad molars and large premolars, the youngest groups the narrowest molars and smallest premolars.

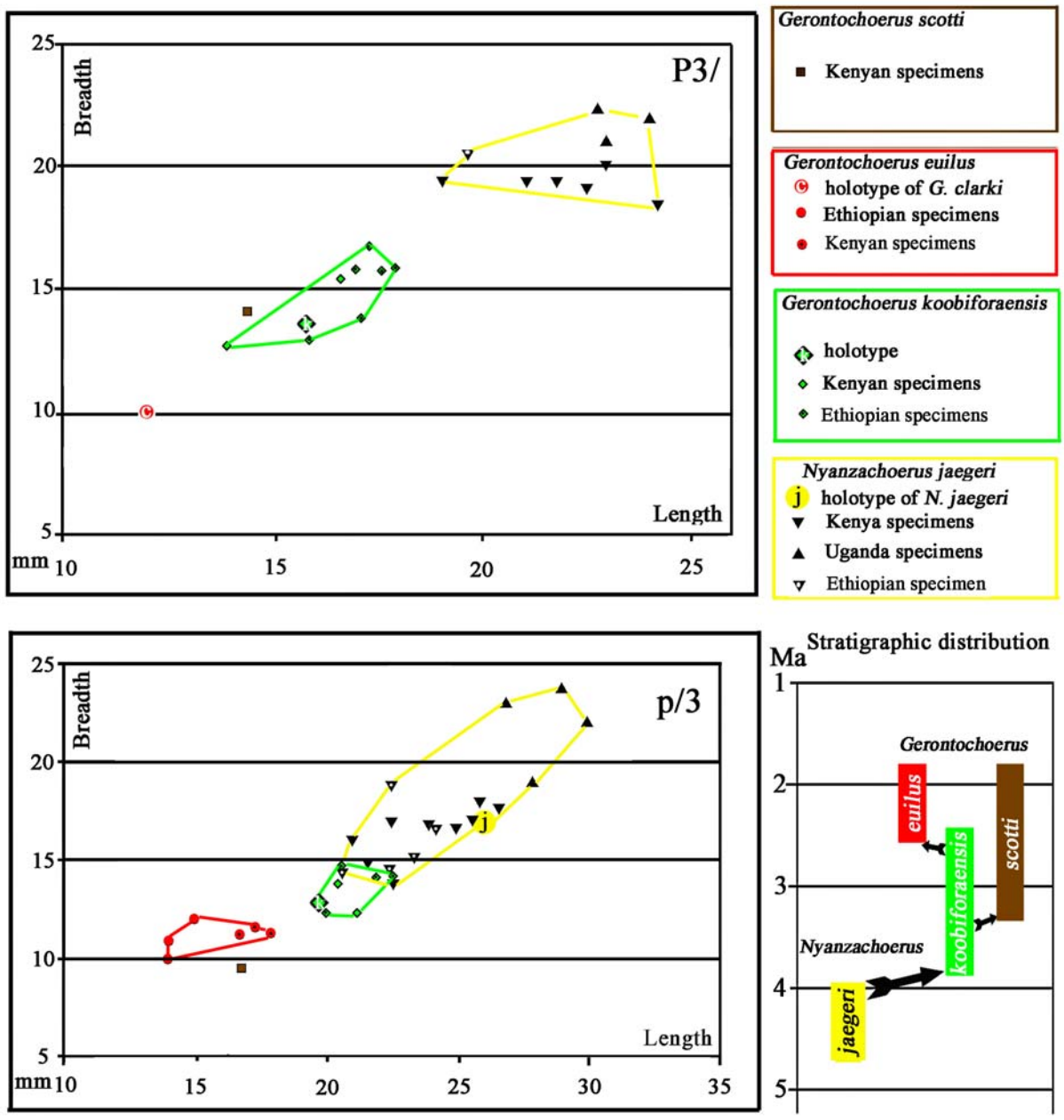

Figure 7. Bivariate plots of upper and lower third molars of Plio-Pleistocene African tetraconodonts. There was a tendency for reduction in the dimensions of the posterior premolars.

It is noted that the fossils in the Ugandan sample of *Nyanzachoerus jaegeri* are generally larger than material attributed to this species from the Eastern branch of the African Rift System, but the differences are not sufficient to warrant identification as a distinct taxon. Morphologically the specimens are close to the holotype from Hamada Damous in Tunisia (not Chad as reported by Leakey *et al*., 2003).

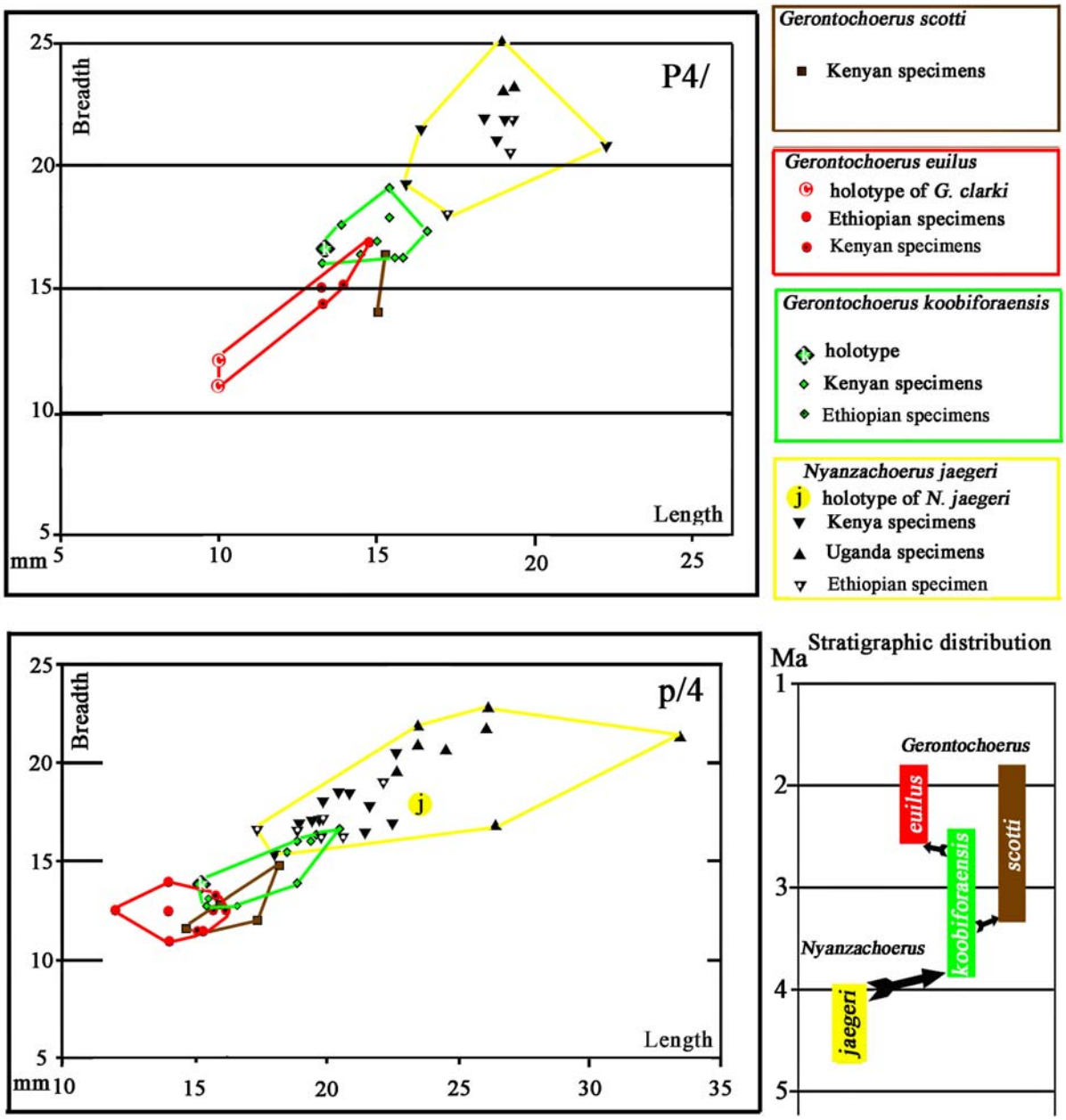

Figure 8. Bivariate plots of upper and lower fourth molars of Plio-Pleistocene African tetraconodonts. There was a tendency for reduction in the dimensions of the posterior premolars, but less marked than in the third premolars.

There is slight overlap in dimensions between the lower premolars and m/3s attributed to *Gerontochoerus koobiforaensis* and *Gerontochoerus euilus* (ex *clarki*). The upper teeth in contrast plot into distinct clouds of points, with only one P4/ of *Gerontochoerus euilus* plotting within the range of variation of *Gerontochoerus koobiforaensis*. This overlap could mean that one or more specimens has been misattributed in the literature. Further study of the original fossils is required to remove doubt introduced by inter-observer measurement differences or simple misidentification, for example.

It should be noted that, even if Cooke & Coryndon's (1970) reconstruction of the lectotype of NHML M 12613A is correct (it has one lophid too many in the reconstruction) and even if it is a lower m/3, its dimensions (79 x 23) plot out in the zone of overlap between the clouds of points for what was called *Notochoerus clarki* by White & Suwa (2004) and *Gerontochoerus koobiforaensis* sp. nov. The author's own assessment of the possible original dimensions of the tooth (60 x 26) and its appurtenance to the upper tooth row, plot it only within the range of variation of what White & Suwa

(2004) called *Notochoerus clarki*. There can be little doubt that, from a morphometric perspective, the latter species is a junior synonym of *Gerontochoerus euilus*.

BIOCHRONOLOGICAL IMPLICATIONS

In the Ethiopian Rift deposits, the small species *Gerontochoerus euilus* (previously identified as *Notochoerus clarki*) ranges in age from 2.5 – 1.8 Ma (White & Suwa, 2004; Cooke, 2007) (Fig. 6). Specimen UM NK 1206'89 is from locality NK 130 near the top of the Warwire Formation, the age of which is likely to be Late Pliocene, although the base of the formation is basal Pliocene as it occurs in strata which contain molluscs typical of assemblage G5a, in the Warwire sub-phase of Palaeolake Obweruka (Van Damme & Pickford, 2010). The type area of the Kaiso Village Formation (from which the lectotype of *Gerontochoerus euilus* could have come (Hopwood, 1926a)) is aged ca 2.3 Ma, Pickford *et al*., 1993) which accords with the age range of the species.

DISCUSSION

Although there have been differences of opinion concerning details of the evolution of Plio-Pleistocene tetraconodonts of Africa, and above all, of their taxonomy, there has been a common thread of thought linking Late Miocene and Basal Pliocene *Nyanzachoerus* to what was generally called *Notochoerus* from Plio-Pleistocene deposits. Recent literature (Bishop, 2010) accepts the presence of four species of *Notochoerus*, with what used to be called *Nyanzachoerus jaegeri* being transferred to the genus *Notochoerus*, following the proposals of Harris & Leakey (2003) and Harris *et al*., (2003). The basis for the subdivision of *Notochoerus* into various species was largely based on metric data, allied with assessments of hypsodonty and talon(id) elongation in third molars. The dimensional data was largely exploited for biochronology (White & Harris, 1977; Cooke & Wilkinson, 1978; Harris & White, 1979; Cooke, 2007).

With the realisation that the type species of *Notochoerus* is not a tetraconodont, but a suine related to the *Pronotochoerus-Potamochoeroides-Metridiochoerus* lineage, it has become necessary to resurrect the name *Gerontochoerus* Leakey, 1943, for the Plio-Pleistocene tetraconodonts of Africa. With the finding that the lectotype of *Gerontochoerus euilus* falls comfortably into the range of metric variation of the small species "*Notochoerus*" *clarki*, it is necessary to examine the status of all the other material previously attributed to *Notochoerus euilus*. It turns out that much of the latter material has third molars which are appreciably larger (Fig. 6) than the Kaiso lectotype and what was called *Notochoerus clarki* by White & Suwa, 2004. It is here named *Gerontochoerus koobiforaensis* sp. nov. Note that one of the specimens attributed to *Hylochoerus euilus* by Hopwood (1926a) probably belongs to *Metridiochoerus andrewsi* (Fig. 9).

Figure 9. Hypsodont third molar fragments from Kaiso, Uganda, included in *Hylochoerus euilus* by Hopwood, 1926a. (A) NHML M 16213B, *Gerontochoerus euilus* and (B) NHML M 16213C, *Metridiochoerus andrewsi*. Note the positions of the median and posterior accessory cusplets, not intervening between hypoconid and entoconid in A, but largely intervening between hypocone and metacone in B. Note also the thick cementum in B.

It is evident from the data in Figs 6-8, that, with the passage of time, there was a trend towards narrowing and elongation of the third molars, with *Nyanzachoerus jaegeri* possessing relatively short and broad third molars, *Gerontochoerus koobiforaensis* somewhat narrower and longer third molars, *Gerontochoerus scotti* even narrower and longer third molars, and *Gerontochoerus euilus* even narrower and shorter third molars. Over the same period, there was a trend towards decrease in dimensions of the posterior premolars (Figs 7-8).

CONCLUSIONS

Reappraisal of the Kaiso lectotype of *Hylochoerus euilus* Hopwood, 1926a, indicates that it is an upper right third molar, and not a lower molar as previously thought. Comparison with other hypsodont suids from Africa reveals that the species belongs to the genus *Gerontochoerus* Leakey, 1943, and not to *Notochoerus* Broom, 1925, as widely reported in the literature. *Gerontochoerus* is a tetraconodont suid probably descended from *Nyanzachoerus* Leakey, 1958. In contrast, *Notochoerus* Broom, 1925, is a suine close to *Metridiochoerus* Hopwood, 1926b, *Pronotochoerus* Leakey, 1943, and *Potamochoeroides* Dale, 1948.

Much material from the Eastern Branch of the African Rift System, previously attributed to *Notochoerus euilus*, belongs to a species appreciably larger than the Kaiso lectotype. A new species, *Gerontochoerus koobiforaensis*, is created to accommodate this sample, which is intermediate in dimensions between *G. euilus* (Hopwood, 1926a) and *Gerontochoerus scotti* Leakey, 1943, the type species of the genus.

The species *Notochoerus clarki* White & Suwa, 2004, is a junior synonym of *Gerontochoerus euilus*. The species *Notochoerus harrisi* Van der Made, 1998, is a junior synonym of *Gerontochoerus scotti*.

The results of this research suggest that it is essential to base taxonomic decisions on detailed comparisons with type material. In this particular case, even though the type specimens of *Notochoerus capensis* and *Gerontochoerus euilus* are incomplete upper third molars, they retain enough morphometric information to throw light on their subfamilial affinities, in this case Suinae for the former and Tetraconodontinae for the latter.

ACKNOWLEDGEMENTS

Thanks are extended to Pip Brewer, NHML, for access to fossils in her care. Thanks also to Ezra Musiime, Sarah Musalizi and Rose Mwanja, Kampala, for access to fossils in the Uganda Museum. Dominique Gommery is thanked for providing access to suid fossils from Bolt's Farm, South Africa, which throw light on *Notochoerus capensis* and *Metridiochoerus andrewsi*.

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Annex 1. Measurements (in mm) of teeth of *Nyanzachoerus jaegeri* and various species of *Gerontochoerus* (in previous literature attributed to *Notochoerus*). ("Own" are the author's measurements with the year of acquisition). In the last column, note the inter-observer differences in measurements. (L – mesio-distal length; B – bucco-lingual breadth, lt – left; rt - right).

Catalogue	Tooth	L	B	Locality	Species	Data source and comments
NME KGA 4-1858	m/1 lt	19	13	Middle Awash	*G. euilus*	White & Suwa, 2004
NME KGA 4-1549	m/1 rt	17	14	Middle Awash	*G. euilus*	White & Suwa, 2004
KNM ER 186	m/1	20,6	12,3	Koobi Fora	*G. euilus*	Harris, 1983
KNM ER 2773	m/1	18	0	Koobi Fora	*G. euilus*	Harris, 1983
NME KGA 4-318	m/2 lt	27	16,5	Middle Awash	*G. euilus*	White & Suwa, 2004
NME KGA 4-1549	m/2 rt	25	20	Middle Awash	*G. euilus*	White & Suwa, 2004
KNM ER 2773	m/2	28,5	16,5	Koobi Fora	*G. euilus*	Harris, 1983
KNM ER 2791	m/2	29,9	17,2	Koobi Fora	*G. euilus*	Harris, 1983
KNM ER 3338	m/2	30	18,8	Koobi Fora	*G. euilus*	Harris, 1983
NME Omo 244-1973-489	m/3 lt	60	0	Omo	*G. euilus*	White & Suwa, 2004
NME Omo 299-1976-175	m/3 lt	65	0	Omo	*G. euilus*	White & Suwa, 2004
NME KGA 4-709	m/3 rt	77	0	Middle Awash	*G. euilus*	White & Suwa, 2004
NME Omo 75s-1970-958	m/3 lt	65	19	Omo	*G. euilus*	White & Suwa, 2004
NME Omo 29-1970-1156	m/3 lt	67	20	Omo	*G. euilus*	White & Suwa, 2004
NME Bou VP 8/4	m/3 rt	67	21	Bouri	*G. euilus*	White & Suwa, 2004
NME KGA 4-1882	m/3 lt	72	22	Middle Awash	*G. euilus*	White & Suwa, 2004
NME KGA 4-166	m/3 rt	70	22,5	Middle Awash	*G. euilus*	White & Suwa, 2004
NME Bou VP 15/9	m/3 rt	67	24	Bouri	*G. euilus*	White & Suwa, 2004
UM NK 1206'89	m/3 rt	70,8	24,9	Nkondo	*G. euilus*	Pickford, 1994 as 70,8 x 26,1
HCRP 289	m/3 lt	64	18,7	WK 27, Wayi-Kasimba	*G. euilus*	Kullmer, 2008
KNM ER 186	m/3	76,3	0	Koobi Fora	*G. euilus*	Harris, 1983
KNM ER 2773	m/3	73	21,8	Koobi Fora	*G. euilus*	Harris, 1983
KNM WT 16199	M1/ lt	27,2	21,4	West Turkana, LO6	*G. euilus*	Harris et al., 1988
KNM WT 16368	M3/ lt	65,9	26,2	West Turkana, LO5	*G. euilus*	Harris et al., 1988
NME KGA 4-2606	M3/ lt	62	27	Middle Awash	*G. euilus*	White & Suwa, 2004
NME L 559-5	M3/ lt	64	25	Middle Awash	*G. euilus*	White & Suwa, 2004
NME Omo 270-1974-1104/5	M3/ lt	62	22,5	Omo	*G. euilus*	White & Suwa, 2004
NME Omo 29-1970-1160	M3/ lt	64	26	Omo	*G. euilus*	White & Suwa, 2004
HCRP 118	M3/ rt	74,6	24,5	MP 1, Mwangwabila-Phapa	*G. euilus*	Kullmer, 2008
HCRP 173	M3/ rt	66,2	25,6	PM 12, Phapa-Masapa	*G. euilus*	Kullmer, 2008
NME KGA 4-165	M3/ rt	72	26	Middle Awash	*G. euilus*	White & Suwa, 2004
NME L 25-157	M3/ rt	62	24	Middle Awash	*G. euilus*	White & Suwa, 2004
NME Omo 118-1972-14	M3/ rt	62	0	Omo	*G. euilus*	White & Suwa, 2004
NME Omo 76-1969-260	M3/ rt	65	25	Omo	*G. euilus*	White & Suwa, 2004
NME Bou VP 15/9	p/3 lt	14	10	Bouri	*G. euilus*	White & Suwa, 2004
NME KGA 4-1596	p/3 lt	14	11	Middle Awash	*G. euilus*	White & Suwa, 2004
NME KGA 4-1549	p/3 rt	15	12	Middle Awash	*G. euilus*	White & Suwa, 2004
KNM ER 186	p/3	16,7	11,2	Koobi Fora	*G. euilus*	Harris, 1983
KNM LT 26079	p/3	17,3	11,6	Lothagam	*G. euilus*	Harris, 2003
KNM ER 3395	p/3	17,9	11,4	Koobi Fora	*G. euilus*	Harris, 1983
NME Bou VP 15/9	p/4 lt	12	12,6	Bouri	*G. euilus*	White & Suwa, 2004
NME KGA 4-1998	p/4 lt	14	11	Middle Awash	*G. euilus*	White & Suwa, 2004
NME KGA 4-2325	p/4 lt	14	12,5	Middle Awash	*G. euilus*	White & Suwa, 2004
NME KGA 4-1549	p/4 rt	14	14	Middle Awash	*G. euilus*	White & Suwa, 2004
NME L 495-1	p/4 rt	15,5	13	Middle Awash	*G. euilus*	White & Suwa, 2004
KNM BC 1807	p/4 rt	15,2	11,5	Chemeron KO 19	*G. euilus*	Tsujikawa 2012, ms
KNM ER 2773	p/4	15,3	11,5	Koobi Fora	*G. euilus*	Harris, 1983
KNM ER 2791	p/4	15,6	12,6	Koobi Fora	*G. euilus*	Harris, 1983
KNM ER 3338	p/4	15,8	13,3	Koobi Fora	*G. euilus*	Harris, 1983
KNM ER 186	p/4	16,2	12,5	Koobi Fora	*G. euilus*	Harris, 1983
NME MSD-VP-2/144	P4/	13,3	15	Woranso-Mille	*G. euilus*	Gebreysus, 2011
KNM WT 16192	P4/ lt	13,3	14,4	West Turkana, LO10	*G. euilus*	Harris et al., 1988
KNM WT 16199	P4/ lt	13,9	15,2	West Turkana, LO6	*G. euilus*	Harris et al., 1988

KNM WT 16268	P4/	14	15,1	West Turkana	*G. euilus*	Harris et al., 1988
KNM WT 16448	P4/ lt	14,8	16,8	West Turkana, LO4	*G. euilus*	Harris et al., 1988
NME GAM VP 1/20	M1/ rt	15	0	Gamadeh	*G. euilus* holotype of *No. clarki*	White & Suwa, 2004
NME GAM VP 1/20	M2/ lt	23,5	23	Gamadeh	*G. euilus* holotype of *No. clarki*	White & Suwa, 2004
NME GAM VP 1/20	M2/ rt	23	20	Gamadeh	*G. euilus* holotype of *No. clarki*	White & Suwa, 2004
NME GAM VP 1/20	M3/ lt	55	24	Gamadeh	*G. euilus* holotype of *No. clarki*	White & Suwa, 2004
NME GAM VP 1/20	M3/ rt	55,5	25	Gamadeh	*G. euilus* holotype of *No. clarki*	White & Suwa, 2004
NME GAM VP 1/20	P3/ rt	12	10	Gamadeh	*G. euilus* holotype of *No. clarki*	White & Suwa, 2004
NME GAM VP 1/20	P4/ lt	10	11	Gamadeh	*G. euilus* holotype of *No. clarki*	White & Suwa, 2004
NME GAM VP 1/20	P4/ rt	10	12	Gamadeh	*G. euilus* holotype of *No. clarki*	White & Suwa, 2004
NHML M 12613A	M3/ rt	60	26	Kaiso	*G. euilus* lectotype	Own, 2013, Hopwood, 1926, as lt m/3
NHML M 26592 cast (Omo 2)	m/2 lt	28	19	Omo, Shungura	*G. koobiforaensis* paralectotype *N. scotti*	Leakey, 1943
NHML M 26592 cast (Omo 2)	m/3 lt	79	22,2	Omo, Shungura	*G. koobiforaensis* paralectotype *N. scotti*	Own, 2013; Leakey, 1943 as 82 x 24
NME AMA-VP-2/10	m/1	15,3	10,8	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME ARI-VP-1/367	m/1	19,8	15,3	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-2/103	m/1	16,2	11,5	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM WT 14519	m/1 lt	21,8	15,2	West Turkana, LK1	*G. koobiforaensis*	Harris et al., 1988
KNM WT 16191	m/1 lt	31,2	20,6	West Turkana, LO10	*G. koobiforaensis*	Harris et al., 1988
KNM WT 16360	m/1 lt	22,1	14,4	West Turkana, LO5	*G. koobiforaensis*	Harris et al., 1988
KNM KP 30184	m/1 rt	21	14,9	Kanapoi	*G. koobiforaensis*	Harris et al., 2003
NME L 495-1	m/2 rt	28	17	Middle Awash	*G. koobiforaensis*	White & Suwa, 2004 as *No. clarki*
KNM ER 2779	m/2	31,5	17,2	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM LT 23765	m/2	34,3	18,7	Lothagam	*G. koobiforaensis*	Harris, 2003
KNM LT 289	m/2	34,8	23,4	Lothagam	*G. koobiforaensis*	Harris, 2003
NME MKM-VP-1/291	m/2	31,4	22,1	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSDF-VP-3/9	m/2	0	20,1	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-1/7	m/2	29,5	20,5	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-2/54	m/2	34,8	21,7	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM WT 14519	m/2 lt	33,1	22,5	West Turkana, LK1	*G. koobiforaensis*	Harris et al., 1988
KNM KP 30184	m/2 rt	32,4	21,4	Kanapoi	*G. koobiforaensis*	Harris et al., 2003
KNM WT 16445	m/2 rt	29,7	19,9	West Turkana, LO4	*G. koobiforaensis*	Harris et al., 1988
KNM WT 16487	m/2 rt	28,5	20,3	West Turkana, LO4	*G. koobiforaensis*	Harris et al., 1988
NME L 495-1	m/3 lt	80	22	Middle Awash	*G. koobiforaensis*	White & Suwa, 2004 as *No. clarki*
KNM ER 2884	m/3	75,8	22,1	Koobi Fora	*G. koobiforaensis*	Harris, 1983
NME AMA-VP-2/44	m/3	82,3	25,6	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM ER 1608	m/3	77,5	25,1	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 1609	m/3	79,4	24,8	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 1985	m/3	85	24	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 2772	m/3	82	24,2	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 2779	m/3	73	22,4	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 2782	m/3	77,5	25,1	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 2823	m/3	92,6	0	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 3337	m/3	82,2	23,3	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 3340	m/3	89	27,6	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 4988	m/3	77,7	22,9	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM LT 23723	m/3	80,5	23,4	Lothagam	*G. koobiforaensis*	Harris, 2003
KNM LT 26136	m/3	71,4	27	Lothagam	*G. koobiforaensis*	Harris, 2003
KNM LT 574	m/3	82	22,8	Lothagam	*G. koobiforaensis*	Harris, 2003
NME MKM-VP-1/179	m/3	0	25,7	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MKM-VP-1/185	m/3	70	28,7	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-1/7	m/3	73,1	26	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-5/27	m/3	77,7	28,6	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME GLL 283	m/3	0	25,1	Galili	*G. koobiforaensis*	Kullmer et al., 2008
KNM WT 16494	m/3	85,1	25	West Turkana, LO4	*G. koobiforaensis*	Harris et al., 1988
HCRP 435	m/3 lt	77,7	21,6	U 28, Uraha	*G. koobiforaensis*	Kullmer, 2008
KNM WT 14519	m/3 lt	84,5	31,7	West Turkana, LK1	*G. koobiforaensis*	Harris et al., 1988
NME GLL 345	m/3 lt	94,1	34,8	Galili	*G. koobiforaensis*	Kullmer et al., 2008
KNM KP 30184	m/3 rt	73,5	25,8	Kanapoi	*G. koobiforaensis*	Harris et al., 2003
KNM WT 16369	m/3 rt	71,6	26,5	West Turkana, LO5	*G. koobiforaensis*	Harris et al., 1988

KNM WT 16370	m/3 rt	82,3	25,1	West Turkana, LO5	*G. koobiforaensis*	Harris et al., 1988
KNM WT 16450	m/3 rt	72,6	24,7	West Turkana, LO4	*G. koobiforaensis*	Harris et al., 1988
KNM WT 16490	m/3 rt	80,5	26,6	West Turkana, LO4	*G. koobiforaensis*	Harris et al., 1988
KNM WT 14871	m/3	80,5	26,4	West Turkana, KK	*G. koobiforaensis*	Harris et al., 1988
NME ARI-VP-1/454	M1/	20,3	18,4	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME ARI-VP-3/267	M1/	21	0	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-1/58	M1/	20,5	17,7	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-2/67	M1/	22	17,1	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME ARI-VP-1/454	M2/	29,6	24,5	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME ARI-VP-1/46	M2/	27,5	0	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM ER 220	M2/	23,8	21,7	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 2880	M2/	28,6	23,6	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 3498	M2/	29,6	24,2	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 3540	M2/	25	24,6	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM WT 16647	M2/	28,5	25,6	West Turkana, LO4	*G. koobiforaensis*	Harris et al., 1988
NME MKM-VP-1/55	M2/	27	26,7	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-1/10	M2/	29,1	23,6	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NHML M 12613D	M2/ lt	28	21	Kaiso	*G. koobiforaensis*	Own, 2013; Hopwood, 1926, 26 x 18.5 est. fig. as rt m/2, *H. eulius*
KNM WT 16429	M2/ rt	28,9	22,5	West Turkana, LO4	*G. koobiforaensis*	Harris et al., 1988
NME ARI-VP-1/299	M3/	74,7	34,4	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM ER 220	M3/	62,7	30,9	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 2880	M3/	76,5	32,7	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 3498	M3/	69,2	31,5	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 3540	M3/	71	30,4	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 430	M3/	70,4	31,4	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM LT 298	M3/	0	32,7	Lothagam	*G. koobiforaensis*	Harris, 2003
KNM WT 14532	M3/	71,7	30,7	West Turkana	*G. koobiforaensis*	Harris et al., 1988
NME MKM-VP-1/51	M3/	0	33,8	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MKM-VP-1/55	M3/	65,3	31,8	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-1/10	M3/	68,5	29,6	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-5/54	M3/	72,9	0	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM WT 16647	M3/	80,2	36,8	West Turkana, LO4	*G. koobiforaensis*	Harris et al., 1988
KNM WT 14526	p/2 lt	18	10,1	West Turkana, LO4	*G. koobiforaensis*	Harris et al., 1988
KNM WT 14526	p/3 lt	20	12,3	West Turkana, LO4	*G. koobiforaensis*	Harris et al., 1988
KNM WT 14519	p/3 lt	20,5	13,7	West Turkana, LK1	*G. koobiforaensis*	Harris et al., 1988
NME MKM-VP-1/132	p/3	20,6	0	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-3/8	p/3	20,6	14,5	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM ER 3540	p/3	21,2	12,3	Koobi Fora	*G. koobiforaensis*	Harris, 1983
NME MSD-VP-2/105	p/3	21,9	14,1	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-2/70	p/3	22,5	14,3	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM ER 2782	p/4	15,5	12,7	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 2884	p/4	16,6	12,8	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 3540	p/4	17,3	0	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM WT 14519	p/4 lt	18,5	15,5	West Turkana, LK1	*G. koobiforaensis*	Harris et al., 1988
KNM LT 26136	p/4	18,9	13,9	Lothagam	*G. koobiforaensis*	Harris, 2003
NME MSD-VP-3/9	p/4	18,9	16,1	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-2/225	p/4	19,4	16,1	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-2/70	p/4	19,6	16,4	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM KP 30184	p/4 rt	20,5	16,7	Kanapoi	*G. koobiforaensis*	Harris et al., 2003; Geraads et al., 2013 as 21 x 16,5
KNM ER 220	P3/	13,9	12,6	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 3540	P3/	14,5	0	Koobi Fora	*G. koobiforaensis*	Harris, 1983
NME MSD-VP-5/6	P3/	15,9	12,8	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM ER 2880	P3/	16,6	15,4	Koobi Fora	*G. koobiforaensis*	Harris, 1983
NME MKM-VP-1/53	P3/	17	15,8	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-5/24	P3/	17,1	13,7	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MKM-VP-1/271	P3/	17,3	16,7	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME ARI-VP-1/440	P3/	17,6	15,6	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-3/9	P3/	17,9	15,8	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM ER 220	P4/	13,3	16	Koobi Fora	*G. koobiforaensis*	Harris, 1983
KNM ER 2880	P4/	13,9	17,5	Koobi Fora	*G. koobiforaensis*	Harris, 1983

NME ARI-VP-1/46	P4/	14,5	16,4	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM ER 3540	P4/	15	16,9	Koobi Fora	*G. koobiforaensis*	Harris, 1983
NME MKM-VP-1/271	P4/	15,4	19,1	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MKM-VP-1/55	P4/	15,4	17,9	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MKM-VP-1/53	P4/	15,6	16,2	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME MSD-VP-2/16	P4/	15,8	16,2	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
NME ARI-VP-1/53	P4/	16,6	17,3	Woranso-Mille	*G. koobiforaensis*	Gebreysus, 2011
KNM ER 3541	m/2	28,5	18,6	Koobi Fora	*G. koobiforaensis* holotype	Harris, 1983
KNM ER 3541	m/3	81	26,4	Koobi Fora	*G. koobiforaensis* holotype	Harris, 1983 as 81 x 36,4
KNM ER 3541	M2/	27,1	24,7	Koobi Fora	*G. koobiforaensis* holotype	Harris, 1983
KNM ER 3541	M3/	76	30,8	Koobi Fora	*G. koobiforaensis* holotype	Harris, 1983
KNM ER 3541	p/3	19,8	12,8	Koobi Fora	*G. koobiforaensis* holotype	Harris, 1983
KNM ER 3541	p/4	15,3	13,9	Koobi Fora	*G. koobiforaensis* holotype	Harris, 1983
KNM ER 3541	P3/	15,7	13,5	Koobi Fora	*G. koobiforaensis* holotype	Harris, 1983
KNM ER 3541	P4/	13,4	16,5	Koobi Fora	*G. koobiforaensis* holotype	Harris, 1983
KNM ER 3155	m/1	18,8	14,8	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 4174	m/1	32,8	16	Koobi Fora	*G. scotti*	Harris, 1983
KNM WT 16193	m/1 lt	21,9	14,3	West Turkana, LO3	*G. scotti*	Harris et al., 1988
KNM WT 16259	m/1 lt	0	12,1	West Turkana, KU 2	*G. scotti*	Harris et al., 1988
KNM ER 1611	m/2	30,6	19,2	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 2647	m/2	36,3	18,6	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3155	m/2	28,2	19	Koobi Fora	*G. scotti*	Harris, 1983
KNM WT 16256	m/2	30,8	17,5	West Turkana, KU 2	*G. scotti*	Harris et al., 1988
KNM WT 16193	m/2 lt	27	21,3	West Turkana, LO3	*G. scotti*	Harris et al., 1988
KNM WT 16259	m/2 lt	23,4	16,2	West Turkana, KU 2	*G. scotti*	Harris et al., 1988
KNM ER 205	m/3	101	22,1	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 2663	m/3	98,2	19,8	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 2725	m/3	117	19,8	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3155	m/3	90,8	21,4	Koobi Fora	*G. scotti*	Harris, 1983 as *No. euilus*
KNM ER 3359	m/3	93	20,6	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3365	m/3	92	21	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 446	m/3	108,5	21	Koobi Fora	*G. scotti*	Harris, 1983
KNM LT 26124	m/3	88,5	22,9	Lothagam	*G. scotti*	Harris, 2003 as *No. euilus*
HCRP 445	m/3 lt	87,7	17,3	U 16, Uraha	*G. scotti*	Kullmer, 2008
HCRP 762	m/3 lt	85,8	20,1	RC 11, Ruasho-Chomolo	*G. scotti*	Kullmer, 2008
KNM WT 16193	m/3 lt	95	22,8	West Turkana, LO3	*G. scotti*	Harris et al., 1988
KNM WT 16259	m/3 lt	76,5	0	West Turkana, KU 2	*G. scotti*	Harris et al., 1988
HCRP UR3 159	m/3 rt	96,4	20	Karonga	*G. scotti*	Own, 2011; Kullmer 2008, as 88,9 x 19,7
KNM ER 2272	M1/	19	16,7	Koobi Fora	*G. scotti*	Harris, 1983
KNM WT 16195	M1/ rt	18,4	24,3	West Turkana, KU 1	*G. scotti*	Harris et al., 1988
KNM ER 2272	M2/	26,7	20,1	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3154	M2/	33,3	21,1	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3556	M2/	35,2	22,2	Koobi Fora	*G. scotti*	Harris, 1983
KNM WT 14874	M2/ rt	23,5	20,7	West Turkana, KG 1	*G. scotti*	Harris et al., 1988
KNM WT 16203	M2/ rt	34	24,3	West Turkana, LO9	*G. scotti*	Harris et al., 1988
KNM ER 2272	M3/	76	26,6	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 1163	M3/	93,4	25,9	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 1777	M3/	97,9	28,9	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 2731	M3/	87,6	28,3	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3428	M3/	99	28	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3438	M3/	102,1	27,5	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3461	M3/	101	24	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3502	M3/	111,4	31,6	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 5556	M3/	92	0	Koobi Fora	*G. scotti*	Harris, 1983
HCRP U15 442	M3/ lt	110,2	27,6	Karonga	*G. scotti*	Kullmer 2008, as *No. euilus* lt m/3; Own, 2011 as 119 x 28,6
KNM WT 14872	M3/ lt	99,7	29,2	West Turkana, KG	*G. scotti*	Harris et al., 1988
KNM WT 16208	M3/ lt	93,4	32,4	West Turkana, KU 2	*G. scotti*	Harris et al., 1988
KNM WT 14876	M3/ rt	104,3	0	West Turkana, KG	*G. scotti*	Harris et al., 1988
KNM WT 16363	M3/ rt	95	36,3	West Turkana, LO5	*G. scotti*	Harris et al., 1988
KNM WT 16449	M3/ rt	83,4	28,6	West Turkana, LO4	*G. scotti*	Harris et al., 1988

KNM ER 3464	p/3	15,4	0	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3440	p/4	16	13	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 3464	p/4	17,4	12,1	Koobi Fora	*G. scotti*	Harris, 1983
KNM WT 16259	p/4 lt	14,7	11,7	West Turkana, KU 2	*G. scotti*	Harris et al., 1988
KNM ER 2272	P3/	14,4	14,1	Koobi Fora	*G. scotti*	Harris, 1983
KNM ER 2272	P4/	15,3	16,4	Koobi Fora	*G. scotti*	Harris, 1983
KNM WT 14876	P4/ rt	15	14,1	West Turkana, KG	*G. scotti*	Harris et al., 1988
KNM ER 3429	m/2	34	19	Koobi Fora	*G. scotti* holotype *No. harrisi*	Harris, 1983
KNM ER 3429	m/3	114,8	21	Koobi Fora	*G. scotti* holotype *No. harrisi*	Harris, 1983
KNM ER 3429	p/3	16,8	9,6	Koobi Fora	*G. scotti* holotype *No. harrisi*	Harris, 1983 as *No. scotti*
KNM ER 3429	p/4	18,2	15	Koobi Fora	*G. scotti* holotype *No. harrisi*	Harris, 1983
KNM OS 5 (NHML M 26590 cast)	M2/ rt	30	22	Omo	*G. scotti* lectotype	Leakey, 1943 as 30 x 22
KNM OS 5 (NHML M 26590 cast)	M3/ rt	87,7	28,3	Omo	*G. scotti* lectotype	Leakey, 1943 as 83 x 30
NME ARI-VP-1/477	m/1	17,9	14,8	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME ARI-VP-3/132	m/1	20,6	17,8	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
KNM KP 32801	m/1	19,4	15	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
UM NK 311'86	m/1	21,5	17,7	Nkondo NK 32	*Ny. jaegeri*	Pickford, 1994
UM NK 312'86	m/1	22,4	14,7	Nkondo NK 32	*Ny. jaegeri*	Pickford, 1994
UM NK 43'86	m/1	18	18	Nkondo NK 9	*Ny. jaegeri*	Pickford, 1994
UM NK 609'88	m/1	22,6	15,3	Nkondo NK 101	*Ny. jaegeri*	Pickford, 1994
KNM KP 235	m/1 lt	19	19	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 252	m/1 rt	20,4	13,8	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 26944	m/1 rt	26,6	14,1	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 235	m/2	27,5	22	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 32258	m/2	35,6	23,6	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
NME MKM-VP-1/261	m/2	29,1	20,9	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
UM NK 311'86	m/2	31,4	24,1	Nkondo NK 32	*Ny. jaegeri*	Pickford, 1994
UM NK 312'88	m/2	34	21,8	Nkondo NK 28	*Ny. jaegeri*	Pickford, 1994
UM NK 43'86	m/2	26,8	21	Nkondo NK 9	*Ny. jaegeri*	Pickford, 1994
UM NK 538'86	m/2	29,5	22,2	Nkondo NK 55	*Ny. jaegeri*	Pickford, 1994
UM NK 609'88	m/2	34,6	22,3	Nkondo NK 101	*Ny. jaegeri*	Pickford, 1994
KNM KP 30178	m/2 lt	34,1	25,8	Kanapoi	*Ny. jaegeri*	Harris et al., 2003 as 34,1 x 35,8
KNM KP 30180	m/2 lt	31	22	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30178	m/2 rt	35,8	24,7	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30180	m/2 rt	32	20,2	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30182	m/2 rt	35,5	20	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 254	m/3	77	29	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 262	m/3	74	24,3	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 30402	m/3	76,6	30,3	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30550	m/3	82	29	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 32258	m/3	78,9	29,6	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 32801	m/3	76	26	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
UM NK 131'86	m/3	61	26,5	Nkondo NK 13	*Ny. jaegeri*	Pickford, 1994
UM NK 1'88	m/3	68,5	25,6	Nkondo NK 76	*Ny. jaegeri*	Pickford, 1994
UM NK 227'86	m/3	59,4	24,8	Nkondo NK 29	*Ny. jaegeri*	Pickford, 1994
UM NK 269'86	m/3	69	30,3	Nkondo NK 28	*Ny. jaegeri*	Pickford, 1994
UM NK 2706'89	m/3	67	25,7	Nkondo NK 72	*Ny. jaegeri*	Pickford, 1994
UM NK 311'86	m/3	67	29	Nkondo NK 32	*Ny. jaegeri*	Pickford, 1994
UM NK 343'86	m/3	66,3	24,9	Nkondo NK 35	*Ny. jaegeri*	Pickford, 1994
UM NK 385'89	m/3	78,8	32,4	Nkondo NK 103	*Ny. jaegeri*	Pickford, 1994
UM NK 430'86	m/3	68,5	27,4	Nkondo NK 44	*Ny. jaegeri*	Pickford, 1994
UM NK 43'86	m/3	66,3	25	Nkondo NK 9	*Ny. jaegeri*	Pickford, 1994
UM NK 538'86	m/3	61,5	27,8	Nkondo NK 55	*Ny. jaegeri*	Pickford, 1994
UM NK 538'86	m/3	63,8	27	Nkondo NK 55	*Ny. jaegeri*	Pickford, 1994
UM NK 593'88	m/3	66,6	29,7	Nkondo NK 101	*Ny. jaegeri*	Pickford, 1994
UM NK 609'88	m/3	67,8	28,7	Nkondo NK 101	*Ny. jaegeri*	Pickford, 1994
UM NK 609'88	m/3	70,6	29,8	Nkondo NK 101	*Ny. jaegeri*	Pickford, 1994
UM NK 642'89	m/3	69	27,5	Nkondo NK 76	*Ny. jaegeri*	Pickford, 1994
UM NK 756'89	m/3	76,3	28,1	Nkondo NK 32	*Ny. jaegeri*	Pickford, 1994
KNM KP 235	m/3 lt	67,7	27,1	Kanapoi	*Ny. jaegeri*	Harris et al., 2003; Cooke &

						Ewer, 1972 as 68,5 x 28 *Ny. plicatus*
KNM KP 267	m/3 lt	82	28,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30178	m/3 lt	77,3	30,3	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30180	m/3 lt	70,2	24,9	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30180	m/3 lt	72	25	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30452	m/3 lt	71,5	24,7	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
NME GLL 937	m/3 lt	65,4	25	Galili	*Ny. jaegeri*	Kullmer et al., 2008
NME SKW 226	m/3 lt	72,4	27,6	Galili	*Ny. jaegeri*	Kullmer et al., 2008
HCRP 568	m/3 rt	75,9	24,8	U 46, Uraha	*Ny. jaegeri*	Kullmer, 2008
KNM KP 210	m/3 rt	80,6	27,9	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30178	m/3 rt	80,8	30,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30452	m/3 rt	71,7	23,8	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
NME GLL 1039	m/3 rt	65,8	26,4	Galili	*Ny. jaegeri*	Kullmer et al., 2008
NME MSD-VP-1/27	M1/	18,3	19,9	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME MSD-VP-2/59	M1/	19,3	18,8	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
UM NK 266'86	M1/	19	0	Nkondo NK 27	*Ny. jaegeri*	Pickford, 1994
UM NK 312'88	M1/	20,3	18,8	Nkondo NK 28	*Ny. jaegeri*	Pickford, 1994
KNM KP 257	M1/ lt	18,5	19	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 257	M1/ rt	18	19	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 206	M2/	37,6	27	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 262	M2/	39	26,7	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
NME MSD-VP-1/27	M2/	28,1	28,6	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME MSD-VP-5/5	M2/	31,7	28,8	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
UM NK 357'86	M2/	31	29	Nkondo NK 36	*Ny. jaegeri*	Pickford, 1994
UM NK 380'86	M2/	28	26	Nkondo NK 40	*Ny. jaegeri*	Pickford, 1994
UM NK 385'88	M2/	34,2	34,2	Nkondo NK 38	*Ny. jaegeri*	Pickford, 1994
KNM KP 225	M2/ lt	25,6	26,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 257	M2/ lt	32,1	25,5	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 257	M2/ lt	30,9	29,8	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30617	M2/ lt	35,8	25,9	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 225	M2/ rt	24	24,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 257	M2/ rt	29,8	25,7	Kanapoi	*Ny. jaegeri*	Harris et al., 2003; Cooke & Ewer, 1972 as 32,8 x 26,2
KNM KP 30617	M2/ rt	0	27	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
NME AMA-VP-2/56	M3/	55,7	0	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME ARI-VP-1/430	M3/	62,2	35,6	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
KNM KP 253	M3/	71,5	33,2	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 26944	M3/	71,2	36,8	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM LT 23741	M3/	64,7	36,7	Lothagam	*Ny. jaegeri*	Harris, 2003
NME MKM-VP-1/274	M3/	0	34,5	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME MSD-VP-1/27	M3/	65,9	34,8	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
UM NK 34'86	M3/	80,6	38	Nkondo	*Ny. jaegeri*	Pickford, 1994
NME GLL 477	M3/	73,5	32,7	Galili	*Ny. jaegeri*	Kullmer et al., 2008
UM NK 242'89	M3/	65	35	Nkondo NK 115 G3a/b	*Ny. jaegeri*	Pickford, 1994
UM NK 2498'89	M3/	63	33	Nkondo NK 60 G3b	*Ny. jaegeri*	Pickford, 1994
UM NK 266'86	M3/	70	36,3	Nkondo NK 27 G3a/G4	*Ny. jaegeri*	Pickford, 1994
UM NK 2705'89	M3/	56,5	34	Nkondo NK 72 G3b	*Ny. jaegeri*	Pickford, 1994
UM NK 2705'89	M3/	57,6	33,1	Nkondo NK 72 G3b	*Ny. jaegeri*	Pickford, 1994
UM NK 272'88	M3/	60,7	33,5	Nkondo NK 46 G3b	*Ny. jaegeri*	Pickford, 1994
UM NK 312'88	M3/	57	34,5	Nkondo NK 28 G3a/G4	*Ny. jaegeri*	Pickford, 1994
UM NK 357'86	M3/	56,2	33,8	Nkondo NK 3 G3a/b	*Ny. jaegeri*	Pickford, 1994
UM NK 370'86	M3/	64,5	33,5	Nkondo NK 39 G3b	*Ny. jaegeri*	Pickford, 1994
UM NK 380'86	M3/	58,3	32,6	Nkondo NK 40 G3a	*Ny. jaegeri*	Pickford, 1994
UM NK 385'89	M3/	68	41,2	Nkondo NK 103 G3b	*Ny. jaegeri*	Pickford, 1994
UM NK 385'89	M3/	68	39,3	Nkondo NK 103 G3b	*Ny. jaegeri*	Pickford, 1994
UM NK 391'86	M3/	68	34	Nkondo NK 41 G3a	*Ny. jaegeri*	Pickford, 1994
UM NK 490'89	M3/	59	37	Nkondo NK 122 G3a	*Ny. jaegeri*	Pickford, 1994
UM NK 773'88	M3/	60,5	33,6	Nkondo NK 115 G3a/b	*Ny. jaegeri*	Pickford, 1994
KNM KP 234	M3/ lt	66,9	32,6	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 235	M3/ lt	63,5	31,5	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 257	M3/ lt	63,8	35,5	Kanapoi	*Ny. jaegeri*	Harris et al., 2003; Cooke & Ewer, 1972 as 66,6 x 35,7

KNM KP 26944	M3/ lt	72,3	37	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30617	M3/ lt	74	35	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 225	M3/ rt	68	30	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 253	M3/ rt	71,8	33,2	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 257	M3/ rt	63,8	36	Kanapoi	*Ny. jaegeri*	Harris et al., 2003; Cooke & Ewer, 1972 as 67,8 x 35,2
KNM KP 30617	M3/ rt	74,2	36,9	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
NME GLL 368	M3/ rt	78,2	35,7	Galili	*Ny. jaegeri*	Kullmer et al., 2008
KNM KP 235	p/2	9	7	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
UM NK 609'88	p/2	20,4	11,1	Nkondo NK 101	*Ny. jaegeri*	Pickford, 1994
NME ARI-VP-3/222	p/3	23,4	15,1	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
KNM KP 226	p/3	0	13,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 32801	p/3	23,6	16,5	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
NME MSD-VP-2/188	p/3	22,4	14,5	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME MSD-VP-5/26	p/3	24,2	16,5	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME GLL 377	p/3	20,6	14,3	Galili	*Ny. jaegeri*	Kullmer et al., 2008
UM NK 311'86	p/3	26,9	23	Nkondo NK 32	*Ny. jaegeri*	Pickford, 1994
UM NK 312'88	p/3	27,9	19	Nkondo NK 28	*Ny. jaegeri*	Pickford, 1994
UM NK 43'86	p/3	30	22	Nkondo NK 9	*Ny. jaegeri*	Pickford, 1994
UM NK 609'88	p/3	29	23,7	Nkondo NK 101	*Ny. jaegeri*	Pickford, 1994
KNM KP 235	p/3 lt	25	16,5	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 30178	p/3 lt	25,9	17,9	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30180	p/3 lt	23,6	16,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30452	p/3 lt	26,5	0	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM BC 1818	p/3 rt	21,6	14,8	Chemeron KO 18	*Ny. jaegeri*	Tsujikawa 2012, ms
KNM KP 235	p/3 rt	21	16	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 241	p/3 rt	23,9	16,7	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 267	p/3 rt	22,6	13,7	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30178	p/3 rt	25,6	17	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30182	p/3 rt	26,6	17,6	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
NME GLL 1039	p/3 rt	22,5	18,7	Galili	*Ny. jaegeri*	Kullmer et al., 2008
KNM KP 32801	p/4	19,5	17,1	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
NME MKM-VP-1/146	p/4	18,9	16,6	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME MKM-VP-1/261	p/4	22,2	19,1	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME MSD-VP-2/105	p/4	17,4	16,6	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME MSD-VP-2/187	p/4	19,8	16,3	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME MSD-VP-5/26	p/4	21,7	17,9	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
UM NK 110'86	p/4	26,1	21,9	Nkondo NK 11	*Ny. jaegeri*	Pickford, 1994
UM NK 311'86	p/4	23,5	22	Nkondo NK 32	*Ny. jaegeri*	Pickford, 1994
UM NK 312'88	p/4	24,6	20,6	Nkondo NK 28	*Ny. jaegeri*	Pickford, 1994
UM NK 385'89	p/4	33,5	21,5	Nkondo NK 103	*Ny. jaegeri*	Pickford, 1994
UM NK 391'86	p/4	23,5	21,1	Nkondo NK 41	*Ny. jaegeri*	Pickford, 1994
UM NK 43'86	p/4	26,5	17	Nkondo NK 9	*Ny. jaegeri*	Pickford, 1994
UM NK 538'86	p/4	22,7	19,7	Nkondo NK 55	*Ny. jaegeri*	Pickford, 1994
UM NK 609'88	p/4	26,2	23	Nkondo NK 101	*Ny. jaegeri*	Pickford, 1994
KNM KP 235	p/4 lt	21,5	16,5	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
KNM KP 30178	p/4 lt	20,9	18,5	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30180	p/4 lt	19,7	17,1	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM LT 23741	p/4 lt	20,5	18,5	Lothagam	*Ny. jaegeri*	Harris, 2003
KNM KP 235	p/4 rt	22,5	17	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972; Harris et al. 2003 as 21 x 0
KNM KP 267	p/4 rt	18,1	15,3	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 30178	p/4 rt	0	17,8	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM LT 23741	p/4 rt	22,7	20,5	Lothagam	*Ny. jaegeri*	Harris, 2003
NME GLL 1039	p/4 rt	19,9	18,1	Galili	*Ny. jaegeri*	Kullmer et al., 2008
KNM KP 257	P2/	10,5	6,7	Kanapoi	*Ny. jaegeri*	Cooke & Ewer, 1972
UM NK 312'88	P2/	12,9	8,3	Nkondo NK 28	*Ny. jaegeri*	Pickford, 1994
KNM KP 225	P2/ lt	11,5	7,2	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 225	P2/ rt	11,4	7,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM BC 838	P3/	19,1	19,4	Chemeron JM 511	*Ny. jaegeri*	Tsujikawa 2012, ms
NME MSD-VP-1/27	P3/	19,7	20,4	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
UM NK 266'86	P3/	24	22	Nkondo NK 27	*Ny. jaegeri*	Pickford, 1994

UM NK 312'88	P3/	22,8	22,2	Nkondo NK 28	*Ny. jaegeri*	Pickford, 1994
UM NK 357'86	P3/	23	20,8	Nkondo NK 36	*Ny. jaegeri*	Pickford, 1994
KNM KP 211	P3/ lt	23	20	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 225	P3/ lt	22,5	19,1	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 257	P3/ lt	21,8	19,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003; Cooke & Ewer, 1972 as 22,5 x 18
KNM KP 225	P3/ rt	21,1	19,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 257	P3/ rt	24,2	18,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003; Cooke & Ewer, 1972 as 22,5 x 18,2
KNM KP 30617	P3/ rt	23	21	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
NME AMA-VP-2/38	P4/	19,3	21,8	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME ARI-VP-1/311	P4/	19,2	20,5	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
NME ARI-VP-1/98	P4/	17,2	18	Woranso-Mille	*Ny. jaegeri*	Gebreysus, 2011
UM NK 266'86	P4/	19	23	Nkondo NK 27	*Ny. jaegeri*	Pickford, 1994
UM NK 380'86	P4/	19,3	23,2	Nkondo NK 40	*Ny. jaegeri*	Pickford, 1994
UM NK 391'86	P4/	19	25	Nkondo NK 41	*Ny. jaegeri*	Pickford, 1994
KNM KP 211	P4/ lt	15,9	19,2	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 225	P4/ lt	19,1	21,8	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 257	P4/ lt	18,8	21	Kanapoi	*Ny. jaegeri*	Harris et al., 2003; Cooke & Ewer, 1972 as 18,4 x 19,8
KNM KP 30617	P4/ lt	22,3	20,8	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 225	P4/ rt	18,4	21,9	Kanapoi	*Ny. jaegeri*	Harris et al., 2003
KNM KP 257	P4/ rt	16,4	21,4	Kanapoi	*Ny. jaegeri*	Harris et al., 2003; Cooke & Ewer, 1972 as 18,2 x 20,3
KNM KP 251	m/1 lt	19	0	Kanapoi	*Ny. jaegeri (*holotype *plicatus)*	Cooke & Ewer, 1972
KNM KP 251	m/2 lt	26	20	Kanapoi	*Ny. jaegeri (*holotype *plicatus)*	Cooke & Ewer, 1972
KNM KP 251	m/3 lt	64,6	25	Kanapoi	*Ny. jaegeri (*holotype *plicatus)*	Harris et al., 2003
KNM KP 251	m/3 rt	61,2	25,1	Kanapoi	*Ny. jaegeri (*holotype *plicatus)*	Harris et al., 2003
KNM KP 251	p/3 lt	24	16,8	Kanapoi	*Ny. jaegeri (*holotype *plicatus)*	Harris et al., 2003; Cooke & Ewer, 1972 as 23 x 17
KNM KP 251	p/3 rt	22,5	16,8	Kanapoi	*Ny. jaegeri (*holotype *plicatus)*	Harris et al., 2003; Cooke & Ewer, 1972 as 23,2 x 16,2
KNM KP 251	p/4 lt	19,9	17,2	Kanapoi	*Ny. jaegeri (*holotype *plicatus)*	Harris et al., 2003, Cooke & Ewer, 1972 as 21,4 x 16,7
KNM KP 251	p/4 rt	19	17	Kanapoi	*Ny. jaegeri (*holotype *plicatus)*	Cooke & Ewer, 1972
MNHN sans n°	m/1 rt	23,1	18	Hamada Damous	*Ny. jaegeri* holotype	Coppens, 1971
MNHN sans n°	m/2 rt	37	21,3	Hamada Damous	*Ny. jaegeri* holotype	Coppens, 1971
MNHN sans n°	m/3 rt	74,8	29	Hamada Damous	*Ny. jaegeri* holotype	Coppens, 1971
MNHN sans n°	M2/ lt	36,7	27	Hamada Damous	*Ny. jaegeri* holotype	Coppens, 1971
MNHN sans n°	M3/ lt	69,2	32	Hamada Damous	*Ny. jaegeri* holotype	Coppens, 1971
MNHN sans n°	p/2 rt	11,6	7	Hamada Damous	*Ny. jaegeri* holotype	Coppens, 1971
MNHN sans n°	p/3 rt	26	17	Hamada Damous	*Ny. jaegeri* holotype	Coppens, 1971
MNHN sans n°	p/4 rt	23,5	18	Hamada Damous	*Ny. jaegeri* holotype	Coppens, 1971

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Published by the Uganda Museum
Kira Road,
P.O. Box 5718,
Kampala,
Uganda