Morotochoerus from Uganda (17.5 Ma) and *Kenyapotamus* from Kenya (13-11 Ma): implications for hippopotamid origins

Morotochoerus *de Uganda (17.5 Ma) y* Kenyapotamus *de Kenia (13-11 Ma): implicaciones sobre el origen de los hipopotámidos*

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ABSTRACT

The aim of this paper is to describe and interpret suiform teeth from Moroto, Uganda, and Ngorora, Kenya, which contribute to the debate about hippo-anthracothere-whale relationships. The early stages of hippopotamid evolution are relatively poorly known on account of the paucity of their fossil record older than 7 Ma. New specimens of *Morotochoerus* from Uganda reveal that it is not closely related to Hippopotamidae; the superficial resemblances of the cheek teeth to those of hippos represent convergences and not homologies. Restricted samples of *Palaeopotamus ternani* are available from the Middle Miocene of Kenya {Maboko, ca 16 Ma; Muruyur, ca 14.5 Ma; Fort Ternan, ca 13.7 Ma} while from the base of the late Miocene, *Kenyapotamus coryndonae* is known from Kenya {Ngerngerwa, ca 10.5-10 Ma; Nakali, ca 10.5 Ma; Samburu Hills, ca 9.5 Ma}, Ethiopia {Ch'orora, ca 10.5 Ma} and Tunisia {Beglia Formation ca 11-10 Ma}. The recovery of specimens of *Kenyapotamus* from the Ngorora Formation, Kenya, aged ca 11 Ma, is of interest because it includes well preserved teeth, including an m/3 in good condition. These specimens support the hypothesis that hippopotamids descended from palaeochoerids and not from anthracotheres.

Keywords: Morotochoerinae, *Morotochoerus*, *Kenyapotamus*, Hippopotamidae, Palaeochoeridae, Cetartiodactyla, Africa, Miocene, Evolution

RESUMEN

El objetivo de este trabajo es describir e interpretar los dientes suiformes de Moroto, Uganda, y Ngorora, Kenia, que contribuyen al debate sobre las relaciones hipo-anthracothere-whale. Las primeras etapas de la evolución de los hipopotámidos son relativamente poco conocidas a causa de la escasez de su registro fósil en edades superiors a los 7 Ma. Nuevos ejemplares de *Morotochoerus* en Uganda revelan que no están estrechamente relacionados con *Hippopotamidae*, las semejanzas superficiales de los dientes de la mandíbula con los de los hipopótamos representan convergencias y no homologías. Algunas muestras de *Palaeopotamus ternani* aparecen en el Medio Mioceno de Kenia {Maboko, ca 16 Ma; Muruyur, ca 14.5 Ma; Fort Ternan, ca 13.7 Ma}, mientras que desde la base del Mioceno tardío, *Kenyapotamus coryndonae* aparece en Kenia {Ngerngerwa, ca 10.5-10 Ma; Nakali, ca 10.5 Ma; Samburu Hills, *ca* 9,5 Ma}, {Ch'orora Etiopía, *ca* 10.5 Ma} {y Túnez Beglia Formación ca 11-10 Ma}. La obtención de especímenes de *Kenyapotamus* de la Formación Ngorora, Kenya, con edad ca 11 Ma, es de interés porque incluye dientes bien conservados, incluyendo un m/3 en buenas condiciones. Estos ejemplares apoyan la hipótesis de que los hipotámidos descienden de paleoquéridos y no de antracotéridos.

Palabras clave: Morotochoerinae, *Morotochoerus*, *Kenyapotamus*, Hippopotamidae, Palaeochoeridae, Cetartiodactyla, Africa, Mioceno, Evolución

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Introduction

Convergence in tooth form has confused palaeontologists for over two centuries, with famous examples among the proboscideans and suiforms including the 'tapir gigantesque" of Cuvier, 1804 (a deinotherian proboscidean), *Tapirus pentapotamiae* of Falconer, 1868, a suid, *Hesperopithecus haroldcookei* Osborn, 1922, a peccary tooth misidentified as a hominoid, and many others. Canines of females of *Conohyus*, a middle Miocene suid, were for many years confused with those of *Sivapithecus* (Kelley, 2005), and isolated suid molars have often been misidentified as hominoids (Pickford & Tiwari, 2010). So have specimens of hyracoids and even fish (Andrews, 1978). In all these cases, more complete specimens or restudy of the original fossils led to the correct elucidation of the affinities of the specimens.

Cheek tooth rows have been less commonly misattributed, as they contain more information than isolated teeth, and complete skeletons are even less commonly misidentified, although inappropriate analyses have on occasion misled palaeontologists. A pertinent example is the interpretation of *Oreopithecus bambolii* (a late Miocene hominoid) as a cercopithecid (Delson, 1979) based on a cladistic analysis of its cheek teeth, and omission of the skull, mandible and post-cranial skeleton from the analysis.

Convergence also touches the post-cranial skeleton. An example comes from the Early Miocene of Napak, Uganda, where the distal humerus and proximal femur of an arboreal rodent species, *Paranomalurus bishopi*, were interpreted to represent a galagid (Gebo *et al*., 1997a) and a lorid (MacLatchy & Kityo, 2002) respectively, were used to estimate different body weights, and to deduce radically divergent locomotor repertoires, and, at a higher level of analysis, were taken to mean that the divergence between galagids and lorids must be more ancient than the Early Miocene. Convergence of post-cranial features of this rodent with those of primates, due to its arboreal adaptations, were thus inappropriately utilised to deduce the phylogenetic relationships among two families of strepsirrhine primates.

Hooijer (1952) provided a list of fossils misidentified as hippopotamids (*hippopotami spurii*), and of hippopotamid remains misattributed to other taxa (*hippopotami veri*). Another example is the identification of hippopotamid dental remains from Sri Lanka (Ceylon) as those of the anthracothere, *Merycopotamus*, by Deraniyagala (1944). The latter author was confused by the convergence in superficial cheek tooth enamel characters (coarsely wrinkled enamel) between the two taxa. On the basis of this misattribution, he proposed the extension of Siwaliks stratigraphy to southern Sri Lanka.

Confusion due to convergence of characters is on-going (Boisserie *et al*., 2009a, 2009b; Orliac *et al*., 2010), and failure to take it into account produces weak phylogenetic scenarios, even using the most sophisticated of digital analytical methods.

In the particular case of *Morotochoerus ugandensis*, Orliac *et al*. (2010) had available some partial tooth rows from Moroto I and Moroto II, Uganda, spanning the posterior lower premolar to the m/3 in a mandible and the DP4/-M1/ in a maxilla fragment. It should be noted that the maxilla with DP4/-M1/ of *Morotochoerus* (MOR II BUMP 350) described by Orliac *et al*. (2010) was originally attributed to a cercopithecid by MacLatchy *et al*. (2003), confusion flowing from the somewhat convergent morphology between the teeth of this suiform and those of monkeys. Re-interpretation of the BUMP 350 maxilla as that of a diminutive hippopotamid by Orliac *et al*. (2010) is equally suspect, the slight morphological resemblances in the cheek teeth to those of hippos being due to convergent evolution rather than to closeness of phylogenetic relationships.

Undescribed specimens of *Morotochoerus ugandensis* collected by the Uganda Palaeontology Expedition include anterior teeth and some fragmentary post-cranial bones which reveal that, whatever it is, *Morotochoerus* is not a hippopotamid, but has closer affinities with Anthracotheriidae, as shown by its talar and phalangeal morphology, as well as the shape and dimensions of its incisors and canines. The family relationships of *Morotochoerus* remain poorly understood on account of the paucity of its fossil record (it is here attributed to a new subfamily within Anthracotheriidae) but it is unlikely to be closely related to Hippopotamidae.

Molecular phylogenetic studies have stimulated interest in the relationships between whales and artiodactyls, with a consensus emerging that among Cetartiodactyla, extant hippopotamids are more closely related to whales than are any of the other artiodactyls (Montgelard *et al*., 1997). The fossil record is rather silent on the matter, the oldest known hippopotamids being about 16.5 Ma (Pickford, 2007a) and the oldest known whales being of Eocene age (ca 50 Ma) (Gingerich & Uhen, 1998) implying the existence of a ghost lineage of prehippos of more than 30 million years duration.

Because of this huge gap in the fossil record, some researchers have proposed that anthracotheres (specifically the bothriodontines) represent the missing lineage that links whales and hippos (Boisserie *et al.*, 2005a, 2005b) or that the genera *Kulutherium* and *Morotochoerus* are primitive hippopotamids which extend the fossil record of the family back to the early Miocene of East Africa (Orliac *et al.*, 2010). The former hypothesis has not found general acceptance, mainly because anthracothere skeletal and dental morphology is widely divergent from that of hippos on the one hand (Pickford, 2008) and that of whales on the other, but also because the group (*Libycosaurus – Merycopotamus*) proposed to fill the morphological gap between whales and hippos occurs appreciably later in time than the earliest known hippos. The latter hypothesis, by the same authors as the former, is not supported by fossils from Moroto, Uganda, described herein. Other researchers (Pickford, 2007a, 2008) have proposed that hippopotamids evolved from Palaeochoeridae which is a better candidate for the group that links whales to hippos than bothriodont anthracotheres are.

In view of the hippo-anthracothere-whale debate, it is important to describe and interpret unpublished fossils of *Morotochoerus* from Moroto, Uganda, aged about 17.5 Ma (Fig. 1) and newly discovered remains of *Kenyapotamus* from the Ngorora Formation, Kenya, aged ca 11 Ma (Fig. 2, 3). The Ngorora fossils throw light on some details of the morphological transition from *Palaeopotamus* to *Kenyapotamus* and provide support for the palaeochoerid hypothesis of hippo origins. *Morotochoerus* has nothing to do with hippopotamid origins, the few (superficial) resemblances between its cheek teeth and those of hippos being due to convergent evolution and not to commonality of descent.

Location. Material and methods

Geological context is provided in figures 1 to 3.

The fossils described here are curated at the Uganda Museum, Kampala and the Orrorin Community Organisation; Tugen Hills, Kenya. Abbreviations are as follows: bl – bucco-lingual; BUMP - Boston University/Uganda Museum Palaeontology; ll – labio-lingual; md – mesio-distal; MOR – Moroto; OCO – Orrorin Community Organisation.

Measurements were taken with sliding callipers to the nearest tenth of a mm. Images were obtained
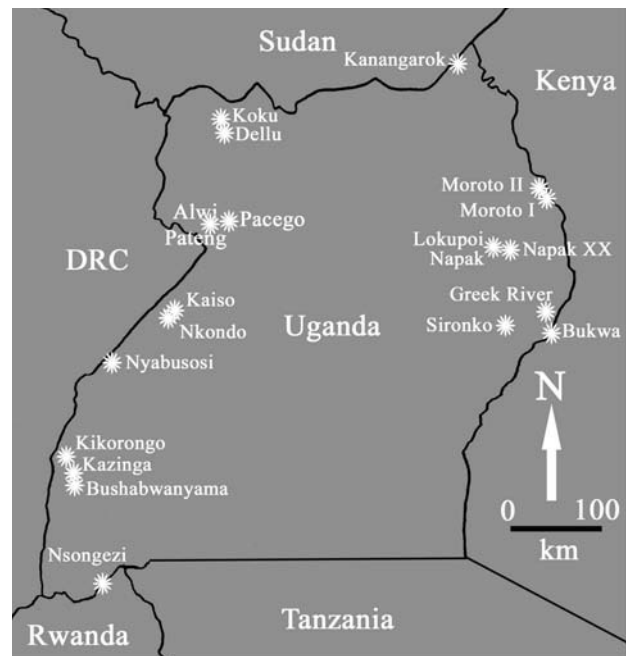

Fig. 1.—Map of Uganda showing position of Moroto in the northeast.

with a Sony Cyber-Shot digital camera and treated with Photoshop to improve contrast and balance.

Dental nomenclature is based on Hünermann (1968), Pickford (1988) and Van der Made (1996) (Fig. 4, 5). We do not follow the nomenclature proposed by Boisserie *et al.* (2009b) and Orliac *et al.* (2010). It adds little to previously available nomenclature schemes, but it does omit important structures such the anterior, median and posterior accessory cusps and their naming of crista (ids) eliminates one groove on each main cusp, a fundamental feature of suiform teeth. Besides, the naming of cusps in the scheme of Boisserie *et al.* (2009b) suggests homology between anthracotheres and hippos, where none exists, thereby compromising their character coding, and all that flows from it.

Systematic descriptions

Family Anthracotheriidae Leidy, 1869
Subfamily Morotochoerinae nov.

*Diagnosis***:** Anthracotheres with pentacuspidate upper molars lacking parastyle, mesostyle and metastyle.

Type genus: *Morotochoerus* Pickford, 1998b

Included genera: *Kulutherium* Pickford, 2007

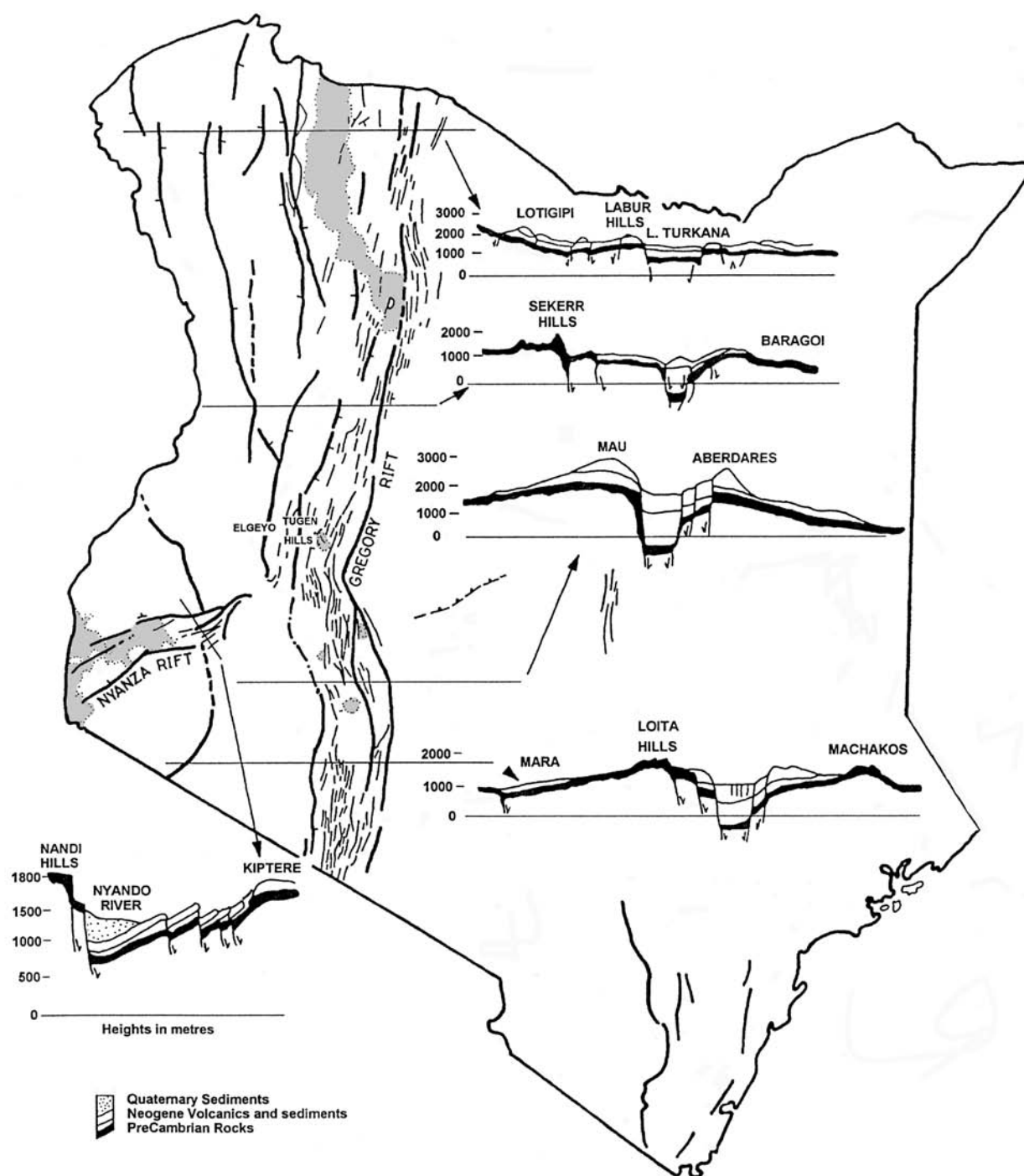Genus *Morotochoerus* Pickford, 1998b

Fig. 2.—Map of Kenya showing the Tugen Hills within the Gregory Rift Valley.

Species *Morotochoerus ugandensis* Pickford, 1998b

Description: MOR I 15'98 and MUZM 50 are parts of the same maxilla, and join together perfectly to comprise a right M2/-M3/ (Fig. 6A). The state of wear is compatible with that of the holotype mandible, and the specimens were found close to

the type specimen, which means that the maxilla is likely part of the holotype individual, a possibility borne out by occluding the specimens together. The M3/ has already been described by Pickford (1998b). The M2/ is deeply worn and is broken anteriorly and lingually, and, as a consequence, does not yield a great deal of information, save to show that the M2/ was as large as
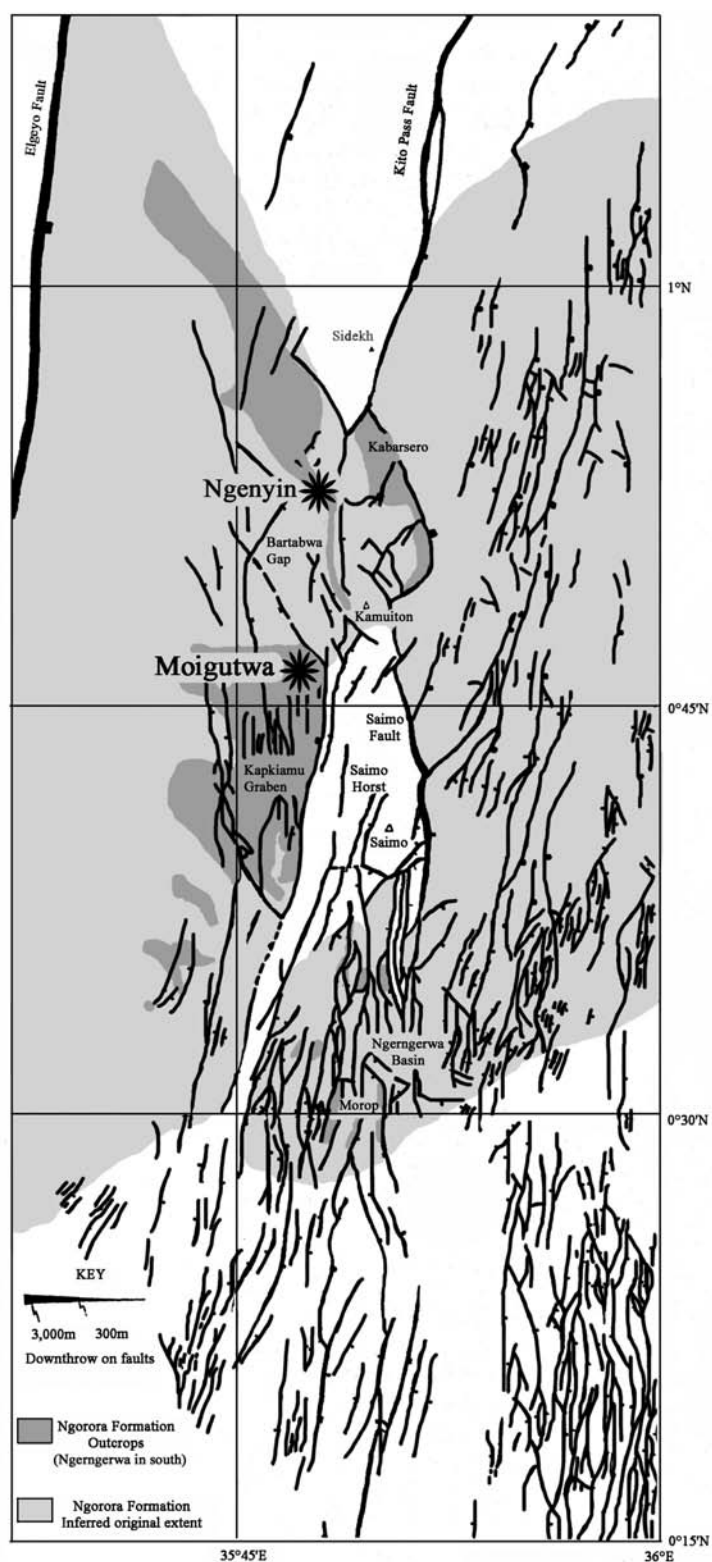
Fig. 3.—Map of outcrop (dark grey) and subcrop (light grey) of the Late Middle Miocene Ngorora Formation, Tugen Hills, Kenya, and the position of Moigutwa and Ngenyin (black stars). Note also the basal Late Miocene Ngerngerwa Basin in the south (type area of *Kenyapotamus coryndonae*). *Palaeopotamus* comes from older strata (Middle Miocene Muruyur Formation, ca 14.5 Ma) exposed west of Saimo.
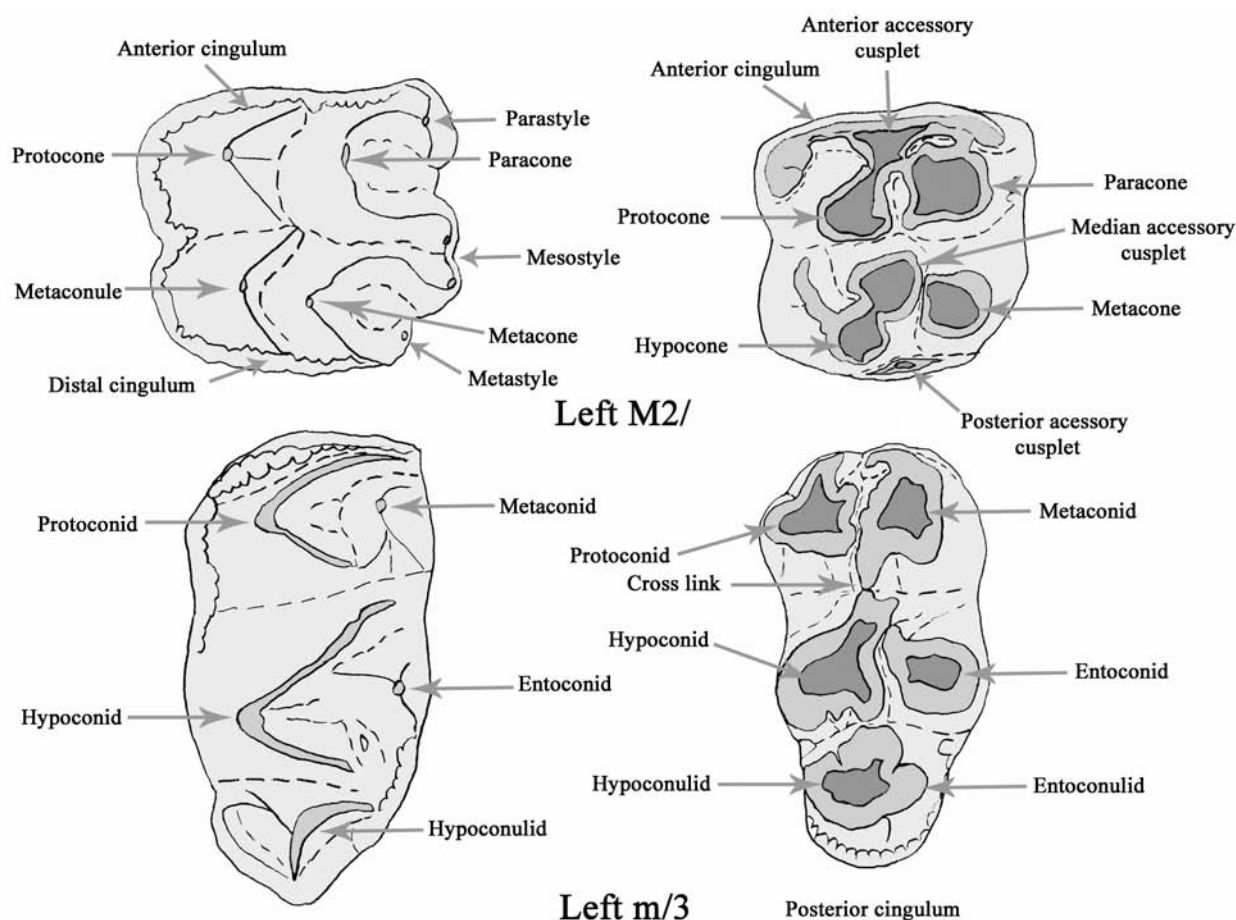
Fig. 4.—Dental nomenclature of suiform molars: left column, Late Miocene bothriodont anthracothere *Libycosaurus petrocchii;* right column, Late Middle Miocene kenyapotamine hippopotamid *Kenyapotamus coryndonae*.

the M3/, but with a squarer occlusal outline, rather than the slight posteriorly tapering outline shown by the M3/.

MOR II 20'01, a moderately to deeply worn left M2/ (13.3 x 14.0 mm) shows a well-developed preprotocrista which extends obliquely anteriorly towards the buccal side of the crown (Fig. 7A). This makes the paracone much narrower than the protocone, as in selenodont anthracotheres and Sanitheriidae (Pickford, 1984). Wear has proceeded to the stage where the paraconule is no longer recognisable as a distinct cusplet, although there are slight indentations in the margins of the preprotocone crista suggesting its former presence. The postprotocone crista is broad and ends in the middle of the tooth, but with no connection to the hypocone. The buccal part of the paracone is damaged, but it is possible to see that the buccal cusps comprised only about one third of the breadth of the crown.

Lower teeth

MOR I 3'99 is a left i/3 (Fig. 8B). The crown is small, labiolingually compressed with lightly wrinkled to smooth enamel. The root is appreciably taller than the crown (6.7++ mm versus 4.2 mm height for the crown) and it swells distinctly some dis-
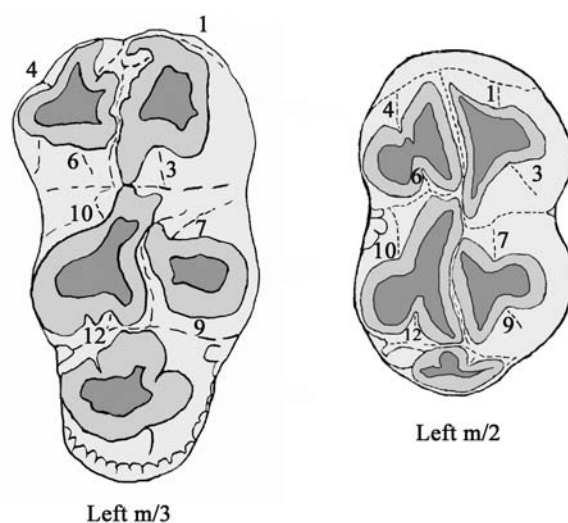

Fig. 5.—Fürchenmuster of hippopotamid teeth, right m/3 (reversed) of Late Middle Miocene *Kenyapotamus coryndonae* and left m/2 of extant *Hippopotamus amphibius* (1-12, groove numbers following the system of Hünermann (1968)).
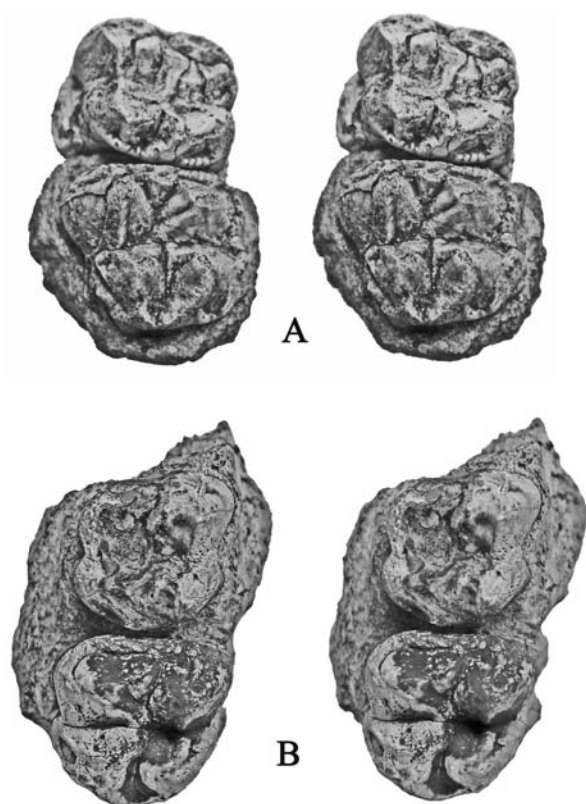
Fig. 6.—Stereo occlusal views of maxilla fragments of *Morotochoerus ugandensis*. A) MOR I 15'98 + MUZM 50, right maxilla fragment containing M2/ and M3/ (cast made prior to damage to the M2/), B) MOR II BUMP 350, left maxilla containing D4/-M1/. (Scale: 10 mm).
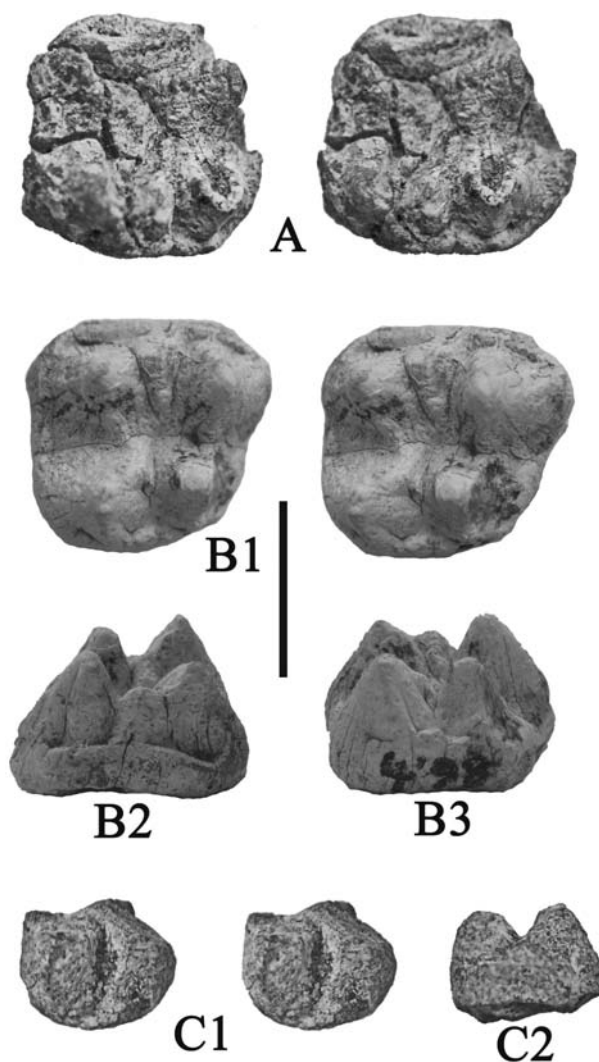

Fig. 7.—Upper and lower molars of *Morotochoerus ugandensis*. A) MOR II 20'01, left M2/, stereo occlusal view; B) MOR II 4'98, left M3/, B1 – stereo occlusal view, B2 - mesial view, B3 – distal view; C) MOR II 62'04, distal half of right m/2, C1 – stereo occlusal view, C2 – distal view.

tance beneath the cervix. The crown measures 3.7 x 3.1 mm and the root, at its largest diameter, is 4.2 x 3.9 mm. The cervix has no indentation but it rises slightly mesially.

MOR I 10'09 is a left lower incisor (probably i/3) in moderate wear (Fig. 8A) (md x bl = 4.7 x 3.9). The root (15.4 mm) is much taller than the crown (4.7 mm). It was found close to the place where the holotype of the species was collected, and could well represent the same individual. The root, which is swollen some distance beneath the cervix, is about 3.5 times taller than the crown. The buccal surface of the crown is convex, delimited mesially and distally by the preprotocristid and the postprotocristid respectively. The lingual side is gently concave with a prominent central ridge subdividing it into two broad, shallow foveae. There is a low basal swelling lingually but not to the extent of forming a cingulum. The enamel is finely wrinkled to smooth where worn, similar to the wrinkling that patterns the molar enamel of giraffids and cervids, but finer. The cervix has no indentation.

MOR I 4'11 is a left incisor with a labio-lingually compressed crown, with sharp mesial and distal crests (Fig. 8D). The crown is hook shaped, the root almost circular in section swelling from cervix towards the apex in the upper third before narrowing apically where the root is closed, and marked by longitudinal ridges and furrows. The crown measures 4.3 x 3.0 (md x bl) the crown height is 3.3 mm and the root height is 13 mm.

MOR II 62'04 is the distal half of an unworn right lower molar (— x 8.9 mm) probably m/2 (Fig. 7C). The hypoconid has clear pre- and posthypocristids, the latter ending beneath a prominent hypoconulid (posterior accessory cusplet). The entoconid is slightly bucco-lingually compressed and has sharp pre- and post-cristids.

MOR II BUMP 351 is a fragment of right mandible containing a worn m/2 missing part of the posterior half. The tooth measures 13.0 x 9.2 (md x bl). It was previously identified as a hyracoid (unpublished catalogue BUMP).

Post-cranial bones

MOR I 17'09 is a fragment of left talus attributed to *Morotochoerus* on the basis of its morphology, dimensions and prove-
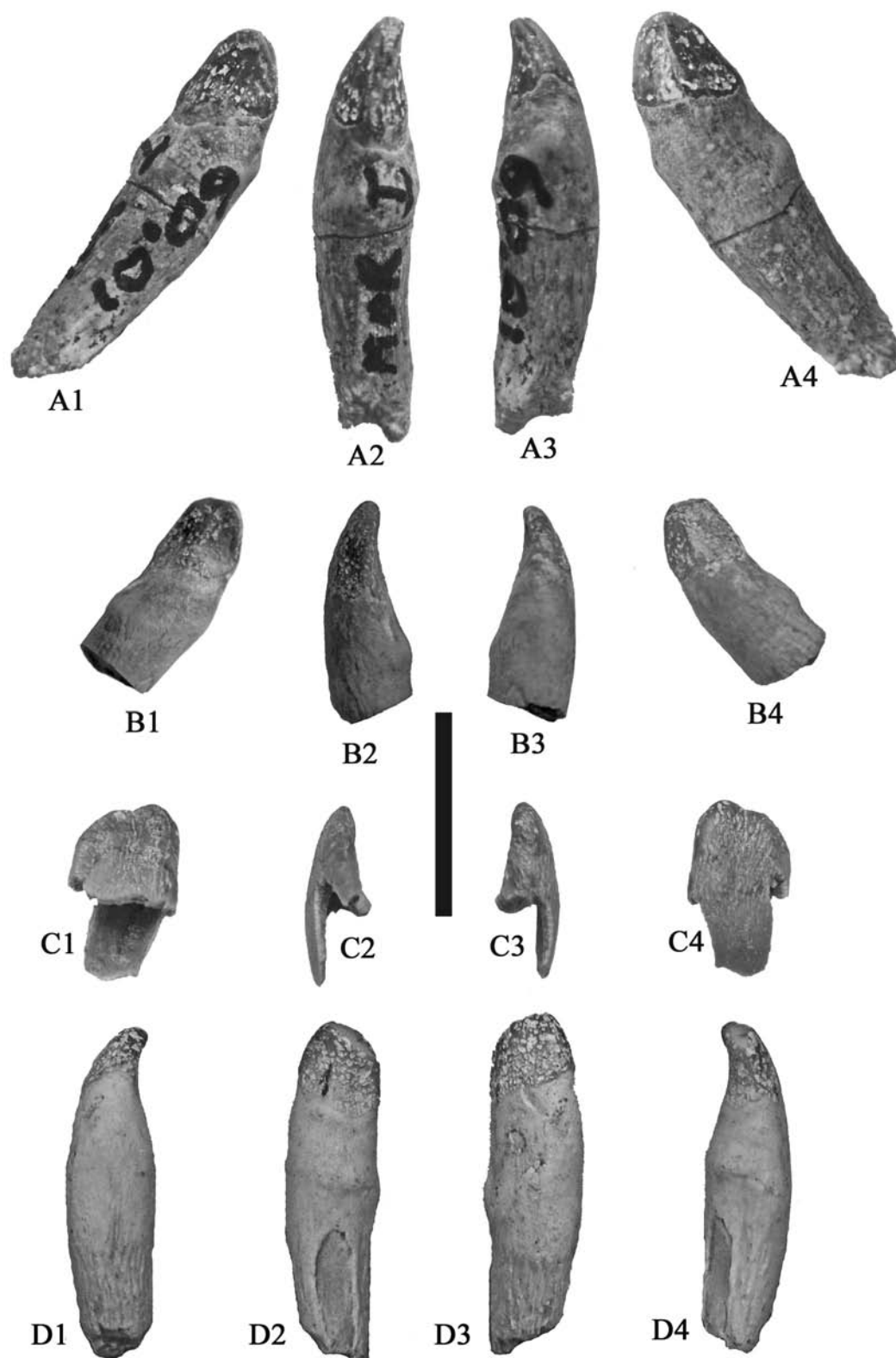
Fig. 8.—Anterior lower teeth of *Morotochoerus ugandensis*. A) MOR I 10'09, left lower i/3, B) MOR I 3'99, left lower i/3, C) Mor I 34'09, left lower i/1 or i/2, D) MOR I 4'11 left incisor. All four teeth possibly represent the same individual as the holotype mandible. 1) lingual, 2) distal, 3) mesial, 4) labial views except for D) which are mesial, lingual, buccal and distal respectively (Scale: 10 mm).
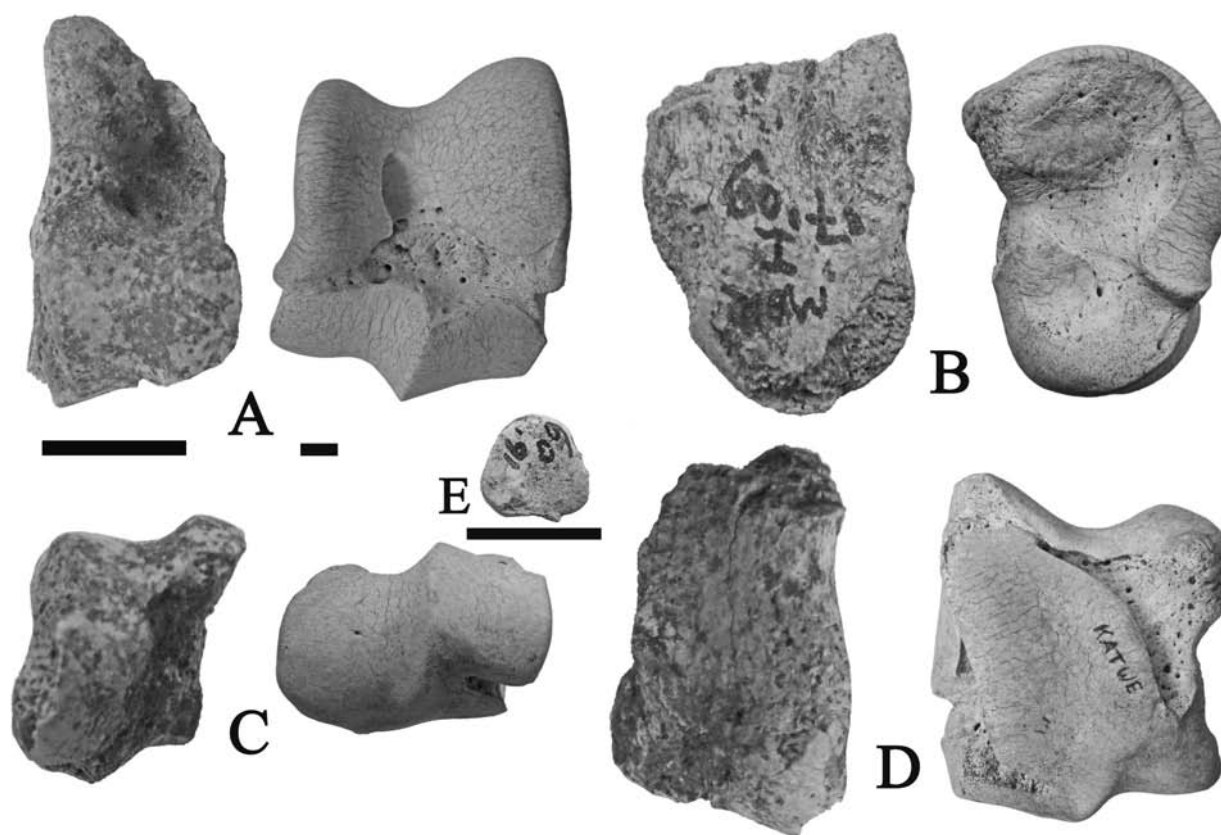
Fig. 9.—Postcranial bones of *Morotochoerus ugandensis* compared with those of *Hippopotamus amphibius*. A-D) left talus, E) axial first phalanx. A) anterior view, B) medial view, C) distal view, D) posterior view, E) proximal view. In A-D the left images are of *Morotochoerus* (MOR I 17'09) and the right ones are of *Hippopotamus*; E is *Morotochoerus* (MOR I 16'09) (Scales: 10 mm).

nance. The navicular facet is medio-laterally narrow, unlike the broad facet that characterises hippopotamids. In *Morotochoerus* the navicular facet is 7.7 mm broad (medio-laterally) which is about half the height (46.9%) of the bone measured at the junction between the navicular and tibial articulations (16.4 mm). In hippos the navicular facet is proportionally much broader, a specimen of extant *Hippopotamus amphibius* from Katwe, Uganda, measured 36 mm compared to a mid-talar height of 44 mm (81.8%). The diameter of the navicular facet in MOR 17'09, is 14.8 mm, whereas that of the Katwe hippo is 41.5 mm (Fig. 9A-9D).

Thus, it is clear that in *Morotochoerus*, the navicular facet does not share the proportions of hippopotamid tali, a key character of the family (Pickford, 2008; Boisserie *et al*., 2009b). This feature alone indicates that *Morotochoerus* has no close relationship with hippos, and that it should not be included in the same family. The proportions and preserved morphology of this fragment of talus most closely resemble those of anthracotheres (narrow navicular facet) rather than suids (broader navicular facet), palaeochoerids (extremely broad navicular facet) and hippopotamids (broad navicular facet), and they tilt the balance towards the hypothesis that *Morotochoerus* belongs to the Anthracotheriidae. Because of dental divergences from classic anthracotheres (most of which possess well developed parastyle, mesostyle and metastyle), *Morotochoerus* is here attributed to a new subfamily, Morotochoerinae, defined by the lack of buccal styles in the upper molars. The possibility of anthracothere affinities for *Morotochoerus* was already evoked by Pickford *et al*., 1986, when the first specimens were collected in 1985 (described in 1998).

MOR I 16'09 is the proximal epiphysis of a first phalanx. It is 8.4 mm broad by 8.2 mm high (Fig. 9E). There is a prominent concave proximal facet flanked basally by two swollen processes. This morphology suggests that the distal articulation of the metapodial has a rounded superior part and that ventrally there is a keel, somewhat as in tragulids and palaeochoerids. In its preserved parts, this axial phalanx does not resemble those of hippos which are broader relative to height.

Other post-cranial bones from Moroto probably pertain to *Morotochoerus*. One is a scapula glenoid previously interpreted to be that of a hominoid primate (*Morotopithecus*, now *Afropithecus turkanensis*) by Gebo *et al*. (1997b) (Pickford *et al*., 1999; Young & MacLatchy (2004). Another is a proximal tibia BUMP 174, in which the fibula is fused proximally to the tibia.

Interpretation and discussion

Orliac *et al*. (2010) interpreted *Morotochoerus ugandensis* as a diminutive hippopotamid. Indeed

they have proposed that it is the earliest known true hippopotamid. There are two points of contention regarding their claim – one concerns the age, Moroto being basal Middle Miocene (ca 17.5 Ma) rather than basal Early Miocene (ca 21 Ma) (Gebo *et al.*, 1997b), the other its systematic affinities. Although there is a superficial resemblance between the gross morphology of the molars of *Morotochoerus* and those of hippopotamids, in detail there are important differences between them which effectively remove the genus from Hippopotamidae and approach it to Anthracotheriidae (it is here attributed to a new subfamily Morotochoerinae).

Orliac *et al.* (2010) wrote that "traits unambiguously characterizing the node Hippopotamidae notably include six non-homoplastic synapomorphies". Of these six supposed synapomorphic dental characters, we are now able to score two for *Morotochoerus*, thereby testing the prediction of the hypothesis that this genus belongs to the family: 1- "lower incisor crown circular in transverse section", and 2- "the presence of a deep indentation in the cervix of the lower incisor crown". In neither case does *Morotochoerus* conform to the prediction. A further prediction implied by classing *Morotochoerus* as Hippopotamidae, is that the navicular facet on the talus should be as broad as the cuboid one. However, the prediction fails: the talus of *Morotochoerus* possesses a narrow navicular facet. The fact that even slight augmentation of the hypodigm of *Morotochoerus* (incisors, fragment of talus) radically modifies the predicted character scoring of the genus reveals that it is not a hippopotamid. This means that the supposed hippopotamid dental synapomorphies of *Morotochoerus* are more likely to represent convergences than synapomorphies.

Pickford (2008) considered that a lineage of Palaeochoeridae gave rise to Hippopotamidae. Currently, the palaeochoerid with dental and post-cranial morphology closest to that of hippos, is *Propalaeochoerus* from the Late Oligocene to Early Miocene of Europe. *Morotochoerus* is morphologically more distant from hippopotamids than *Propalaeochoerus* is. Among the fundamental differences are the style of enamel wrinkling, which in *Morotochoerus* is more akin to that of certain ruminants such as giraffids and cervids, or to some anthracotheres such as *Merycopotamus* and other bothriodonts, than it is either to that of *Palaeopotamus* and *Kenyapotamus* on the one hand, or that of *Propalaeochoerus* on the other. The surface orna-

mentation of the enamel of the latter genus is similar to that of *Palaeopotamus* and *Kenyapotamus*. Furthermore the available post-cranial evidence, even though scanty, shows that *Morotochoerus* has no close relationship to hippos, and should not be included in the same family.

In addition, the lower incisors of *Morotochoerus* from Moroto described here are unlike those of any hippopotamid, but are more similar to those of anthracotheres and incidentally to some palaeochoerids. The supposed « hippopotamid » features of *Morotochoerus* are here interpreted to represent convergent characters, not especially linking the genus to hippopotamids. The genus *Propalaeochoerus* is a more suitable candidate for hippopotamid origins than is *Morotochoerus*, as it requires fewer morphological changes and only modest metric changes to yield the hippopotamid dental grundplan, not only of the molars, but also of the premolars, canines, incisors and the post-cranial bones.

Propalaeochoerus did not feature in the cladistic analysis of Orliac *et al.* (2010), although *Palaeochoerus* did. It should be noted that Orliac *et al.* (2010) used a skull of *Doliochoerus quercyi* to score the characters of *Palaeochoerus* (in the paper there is inconsistency between the text, in which the taxon is called *Palaeochoerus quercyi*, and the figure legends in which it is called *Doliochoerus quercyi*) but since *Doliochoerus* is divergent from *Palaeochoerus* in cranial and some dental features, this procedure is inappropriate for demonstrating that palaeochoerids cannot be the ancestral group from which hippos emerged. Boisserie *et al.* (2009b) used the same taxon in their analyses but correctly called it *Doliochoerus quercyi*.

Family Hippopotamidae Gray, 1821
Subfamily Kenyapotaminae Pickford, 1983
Genus *Kenyapotamus* Pickford, 1983
Species *Kenyapotamus* sp.

Material: OCO 3'08, right m/3; OCO 4'08, right M2/, OCO 2'09, left M1/.

Locality: Moigutwa, Tugen Hills, Kenya {GPS WGS 84, 00°46'04.0"N: 35°22.9"E} for 2008 specimens and Ngenyin, Tugen Hills, Kenya {GPS 00°49'57.9"N: 35°49'22.3"E} for 2009 specimen.

Stratigraphy: Ngorora Formation, Member D or E.

Age: Late Middle Miocene ca 11 Ma.

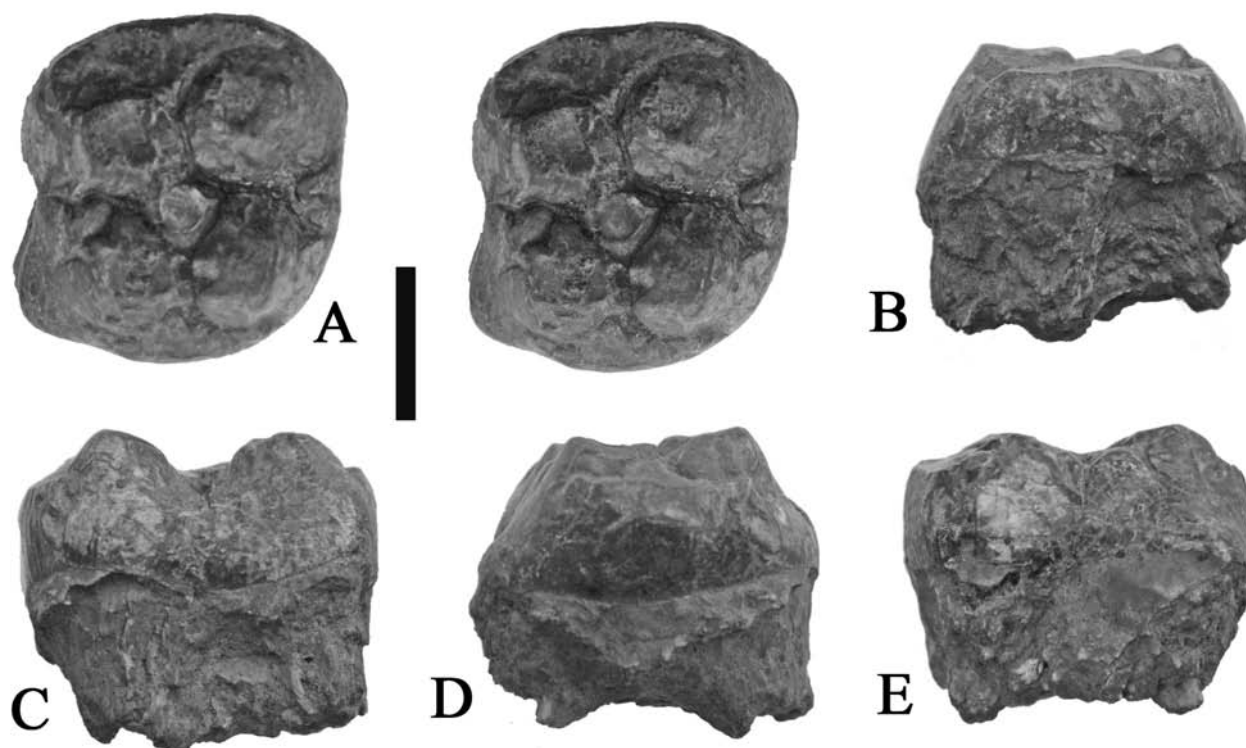*Associated fauna*: Gomphotheriidae, Rhinocerotidae, Fish, Crocodiles

Fig. 10.—OCO 2'09, left M1/, *Kenyapotamus* sp. from Ngenyin, Tugen Hills, Kenya, ca 13-12.5 Ma). A) stereo occlusal view, B) mesial view, C) buccal view, D) distal view, E) lingual view (scale - 10 mm).

Description: OCO 2'09, a left M1/ (Fig. 10) is in medium wear, as is the upper molar, OCO 4'08, (Fig. 11B). The morphology of the two teeth is similar, and they are described together. There are four main cusps arranged in two lophs. The crown is posed on a solid root at least 10 mm deep from which the five roots diverge, four from the corners supporting the main cusps and a small one mesially in the centre line supporting the anterior accessory cusplet. Wear has produced two transverse ridges rather than a flat wear surface. The anterior accessory cusplet (protopreconule of Van der Made, 1996) is well developed and is joined to the protocone by the obliquely directed preprotocrista. The protocone and paracone are separated from each other by a sagittal valley. The median accessory cusp (the tetrapreconule of Van der Made, 1996) is prominent and is strongly joined by wear to the metacone via the premetacrista. The metacone is separated from the hypocone by a sagittal valley. The four main cusps have poorly developed « Fürchen » (Hünermann, 1968; Pickford, 1988) such that the trefoil wear pattern of the cusps, so typical of hippos, is not well developed in these specimens, although careful examination reveals that the grooves of the trefoil are present near the bases of the cusps. The posterior accessory cusplet is small and centrally positioned in the distal cingulum. There are prominent and deep mesial and distal cingula, the mesial one extending lingually where it forms a low but thick swelling with two beads. The metacone sports a swelling of enamel in its mesiolingual corner, probably a remnant of a lingual cingulum. There is a small, low basal pillar at the buccal end of the median transverse valley, but this valley traverses the tooth almost

unobstructed, the median accessory cusplet making only a slight encroachment into the valley on its distal side. The crown has appreciable flare, which extends onto the root base, especially on the buccal side.

The lower third molar, OCO 3'08, is moderately worn (Fig. 11A). There are five main cusps arranged in three lophids. The crown, like that of the upper molar, sits on a solid root base at least 10 mm thick, from which the five roots diverge beneath the main cusps. The distal root is inclined distally, but is joined by a ridge to the root beneath the hypoconid. The mesial cingulum is 8.5 mm deep in its centre. There is no sign of cingular development at the buccal and lingual ends of the median transverse valley, but the posterior valley sports low basal pillars on the two sides, and the hypoconulid has a low pustular cingulum basally. The protoconid has well developed pre- and postcristids, the latter swelling basally as it approaches the median transverse valley, but without forming a distinct cusplet or pillar. The metaconid possesses well developed pre- and postcristids, the latter obliquely directed towards the centre of the median transverse valley, where it touches the prehypocristid, thereby obstructing the middle of the valley. The entoconid has weakly expressed pre- and postcristids, but it possesses clear but shallow anterior and posterior grooves representing Fürchen 7 and 9 (Pickford, 1988) (Fig. 5). The hypoconid has a large precristid oriented obliquely towards the centre of the median transverse valley, but it does not form a distinct median accessory cusplet. The posthypocristid is short and oriented in the centre line of the tooth. « Fürchen » 10 and 12 are clearly visible, even though shallow (Fig. 5). The
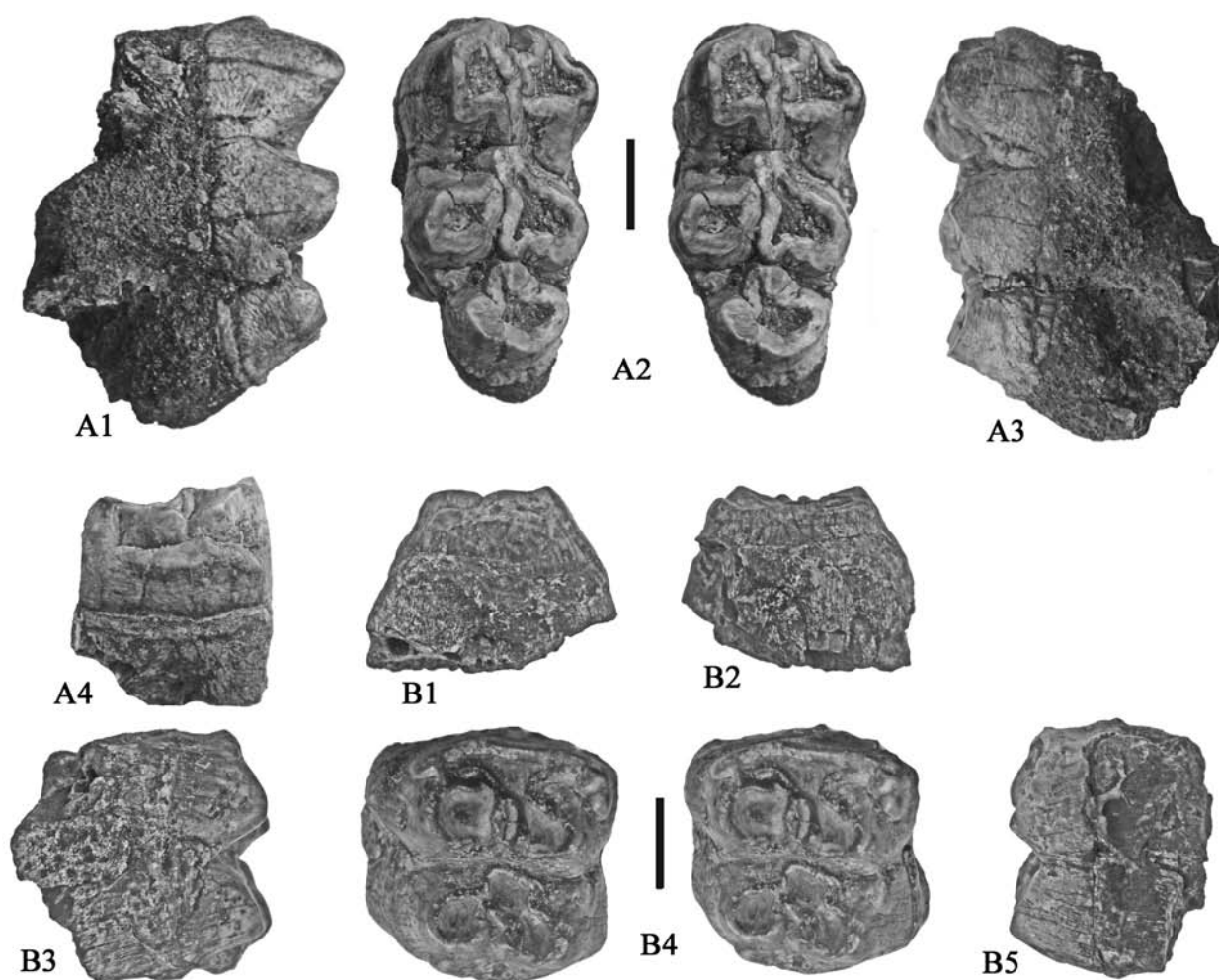
Fig. 11.—A) OCO 3'08, right m/3, and B) OCO 4'08, left M2/, of *Kenyapotamus* sp. from Moigutwa, Late Middle Miocene, Ngorora Formation, Tugen Hills, Kenya. A1 – lingual, A2 – stereo occlusal, A3 – buccal, and A4 – mesial views (note the deep cingulum and substantial root base); B1 – distal, B2 – mesial (note small central root beneath anterior accessory cusplet), B3 – buccal, B4 stereo occlusal, and B5 – lingual views (note substantial root base) (Scale – 10 mm).

hypoconulid is centrally positioned and is comprised of two closely appressed cusps. It has a precristid analogous to that in the hypoconid and lingually it is contiguous with a small cusp analogous to the entoconid, from which it is separated by two shallow grooves, one mesial the other distal. With deep wear the hypoconulid becomes unicuspid. The enamel is rough where unworn.

Tabla 1.—**Measurements (in mm) of the teeth of *Kenyapotamus* sp. from the Ngorora Formation, Tugen Hills, Kenya (ca 11 Ma)**

Specimen	Mesio-distal length	Bucco-lingual breadth
OCO 3'08, right m/3	47.5	24.6
OCO 4'08, right M2/	27.5	26.0
OCO 2'09, left M1/	21.3	20.9

Discussion

The upper molars from Ngenyin and Moigutwa, Ngorora Formation, Kenya, are, in general, similar in dimensions, overall morphology and wear pattern to material from Ngerngerwa, Kenya, the type locality of the species *Kenyapotamus coryndonae* (Pickford, 1983; Orliac *et al.*, 2010). The anterior and median accessory cusplets are prominent, as in the Ngerngerwa and Nakali fossils and the « Fürchen » are somewhat subdued. However, there are some differences, notably the stronger median accessory cusp, which is more like that of *Palaeopotamus ternani* (Pickford, 2007a). There can be little doubt that these teeth represent the
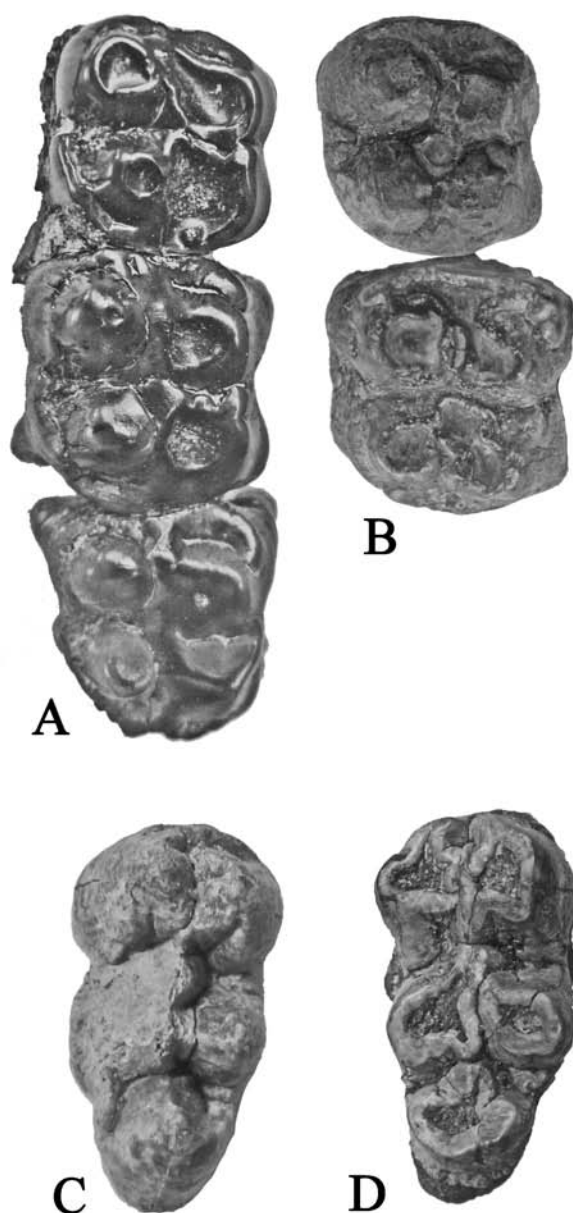
Fig. 13.—Comparison of right m/3 of *Kenyapotamus* sp. from the Late Middle Miocene of Ngorora, Kenya, and left m/3 of *Hexaprotodon pantanelli* from the Late Miocene of La Portera, Spain (image reversed from Van der Made, 1999) to show similar basic structure of the teeth, especially the well developed cross-link between the postmetaconid cristid and the prehypoconid cristid (Scale: 10 mm).

Fig. 12.—Comparison of upper and lower molars of A) right upper molar row of *Propalaeochoerus* sp. from the Oligocene (MP 26) of St Henri, France, C) left m/3 of *Propalaeochoerus elaverensis* from the Oligocene (MP 30) of Coderet, France, and B) and D) *Kenyapotamus* sp. from the Late Middle Miocene of Ngorora, Kenya. The two upper molars from Ngorora are presented as right teeth and the m/3 as a left tooth, and have been reduced to the same size as the palaeochoerid teeth to simplify comparisons.

same genus as that from Ngerngerwa, but possibly a different species.

The lower third molar from Ngorora (Fig. 11A) is similar to a specimen from Nakali (Orliac *et al.*, 2010) attributed to *Kenyapotamus coryndonae*. The Samburu Hills mandible of *Kenyapotamus* (Tsujikawa, 2005) has deeply worn cheek teeth, but it too shows the cross contact of the prehypocristid and the postmetacristid, which touch each other in the median transverse valley, thereby obstructing its centre, as in other hippos (Fig. 4). This same structure is evident in *Palaeopotamus ternani* from Fort Ternan and Maboko (Pickford, 2007a) and appears to be a stable structural element of hippo lower teeth, as it also occurs in Late Miocene, Pliocene and extant hippos {*Hippopotamus aethiopicus* from Omo, Ethiopia (Coryndon & Coppens, 1975), *Hexaprotodon pantanelli* from La Portera, Spain (Van der Made, 1999)} (Fig. 13).

The morphology of the third lower molar of *Propalaeochoerus elaverensis* Viret, 1929, is basically similar to that of hippos, with well-developed prehypocristid and postmetacristid meeting in the mid-line of the crown forming a cross link, and obstructing the median transverse valley (Fig. 12). From this evidence we conclude that the basic dental structural elements of hippo molars were already established in some taxa of Oligocene Palaeochoeridae, and that changes that occurred during the Oligo-Miocene, culminating in hippopotamid dentitions, consisted of relatively minor modifications of crown and root morphology, accompanied by an increase in dimensions.

In contrast, if hippopotamid molars were to be derived from those of bothriodont pattern, then a wholesale reorganisation of molar morphology would be required (Pickford, 2008). For instance the lower molars of bothriodont anthracotheres possess a prehypocristid that is directed towards the lingual margin of the tooth which it almost reaches, wrapping round the anterior face of the entoconid, and the postmetacristid is also lingually positioned. There is thus no central obstruction of the median transverse valley (Fig. 14). Enamel in bothriodont molars is thinner than that of hippos, the fine structure of the enamel is divergent (wrinkled in bothriodonts like that of many ruminants, pustulate in hippos), the root base is shallow in bothriodonts, deep in hippos, the cusp proportions are highly divergent (in bothriodonts lingual cuspids are narrow, buccal cuspids are broad: in hippos, the buccal and lingual cuspids are subequal in breadth), absence in bothriodonts of anterior, median and posterior accessory cusplets, presence of these cusplets in kenyapotamine hippos, selenodont molar cusps in bothriodonts, bunodont, brachyodont cusps in kenyapotamines, presence of prominent styles in upper molars of bothriodonts, no sign of parastyle, mesostyle and metastyle in hippo molars, and highly divergent « Fürchenmuster » in bothriodonts and hippos.

The affinities of *Kulutherium*

In the type description of *Kulutherium kenyensis*, cogent reasons were given by Pickford (2007b) explaining why the genus could not be included in Hippopotamidae. The fine structure of the enamel is incompatible with its interpretation as a hippopotamid, as is the gross morphology of its molars and its enamel thickness. The supposed similarities in morphology between the molars of *Kulutherium* and later hippos evoked by Orliac *et al*. (2010) are due to convergence, and not to closeness of phylogenetic relationship. Pickford (2007) considered that it belonged to Anthracotheriidae, and it is here assigned to this family, provisionally within the subfamily Morotochoerinae subfam. nov.

Conclusions

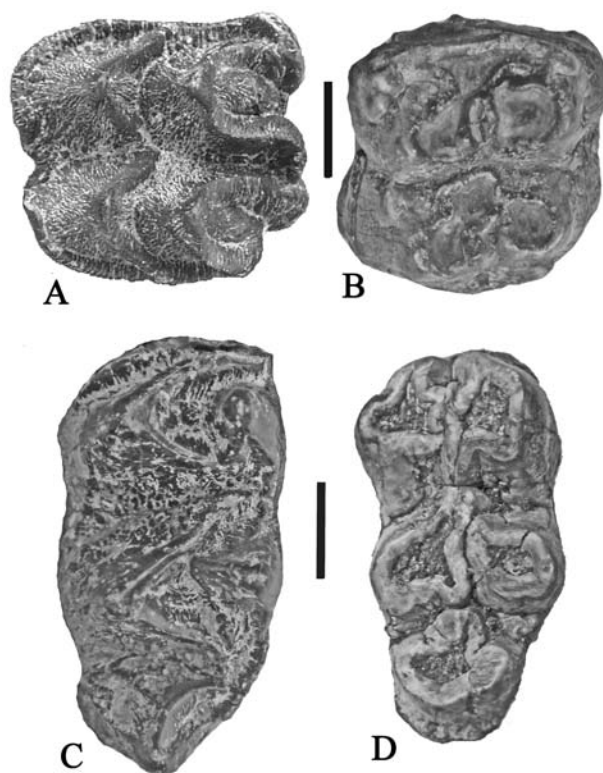Uncertainty about hippopotamid origins and the family relationships to Cetacea and other Artio-

Fig. 14.—Comparison of upper and lower molars of *Libycosaurus* from the basal Late Miocene of Beglia, Tunisia (upper left M2/) and the Late Miocene of Agranga, Chad (lower left m/3) and *Kenyapotamus* sp. from the Late Middle Miocene of Ngorora, Kenya. The upper and lower molars from Ngorora have been flipped over in order to simplify comparisons. Note, in particular, the relative sizes of the main cusps, the lingual cusps in *Libycosaurus* being extremely narrow and the buccal ones covering ca 2/3rds of the breadth of the crown, whereas in *Kenyapotamus*, the breadths of the lingual and buccal cusps are more equal (Scale: 10 mm).

dactyla persists. Having abandoned the hypothesis that the sister group of hippopotamids are the bothriodonts *Merycopotamus-Libycosaurus*, (previously, characters such as a descending plate at the angle of the jaw and the raised orbits, initially considered to represent "apomorphies" perceived to link the two groups, (Boisserie *et al*., 2005b) are now accepted to be the result of convergent evolution) Boisserie *et al*. (2009b) continue to espouse an origin within Bothriondontinae (sic) on the basis of analyses of teeth, whereas Orliac *et al*. (2009, 2010), propose that "*Kulutherium* and *Morotochoerus* are sister taxa.... closely related to Miocene hippopotamids". *Kulutherium* is an anthracothere (Pickford, 2007b), but is not a bothriodont (smooth, thin molar enamel, no signs of enlarged buccal styles, absence of selenodont tendencies in the molars, minute paraconule
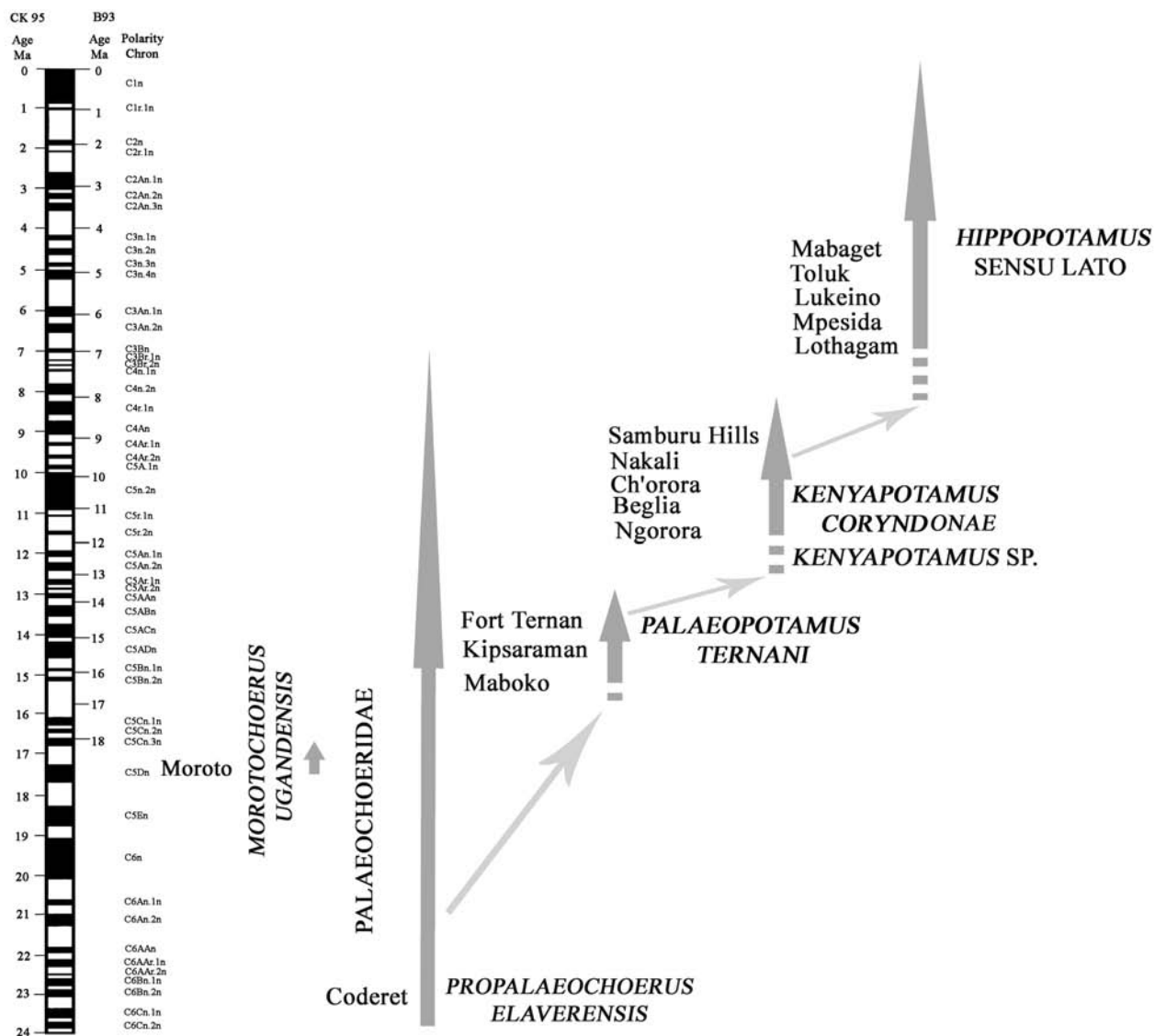
Fig. 15.—Summary of the broad traits of hippopotamid evolution from a palaeochoerid ancestor. Palaeochoerids survived in Eurasia until about 8 Ma. Coderet (MP 30, Late Oligocene) is correlated to polarity chron C6Cn.1n or C6Cn.2n on the basis of palaeomagnetic stratigraphy and is therefore likely aged ca 24 Ma (Baksi, 1993; Cande & Kent, 1995; Kempf et al., 1997; Pickford, 1998a). (Note the slight differences in the age tick marks on the GPTS of the two papers cited). African localities are dated, for the most part, by radio-isotopic age determinations (Pickford, 1998a).

linked to the preprotocrista in upper molars). *Morotochoerus* is likely an anthracothere and is here assigned to a new subfamily, Morotochoerinae, an identification supported by the recovery of new fossils from Moroto I (Fig. 6-9) (possibly representing parts of the type specimen), and Moroto II, including lower incisors which are characteristic of this family, but markedly divergent from the corresponding teeth in hippopotamids. We note that additions to the hypodigm of *Morotochoerus* by Orliac

et al. (2010, fig. 1C, 1D) include a maxilla with two teeth (MOR II BUMP 350) that was previously identified as a cercopithecoid monkey (MacLatchy *et al*., 2003).

Apart from their considerably smaller dimensions, the molars of *Morotochoerus* differ from those of *Kulutherium* in several ways (the enamel is finely wrinkled, the paraconule in upper molars is relatively large and centrally positioned between the mesial ends of the protocone and paracone, but not

linked to the protocone by a preprotocrista (as it is in bothriodonts), height of molar cusps above the cervix is low in *Morotochoerus*, taller in *Kulutherium*, cusps pyramidal rising from near the cervix in *Morotochoerus*, more rounded, conical, disposed on a deep crown base in *Kulutherium*. A major weakness of the two analyses by Boisserie *et al.* (2009b) and Orliac *et al.* (2010) is that the authors did not take into account the pervasive suite of cranial and postcranial characters by which hippos and anthracotheres have been shown to differ markedly (Pickford, 2008).

The "deep nesting" of *Morotochoerus ugandensis* in Hippopotamidae (Orliac *et al.*, 2010) reveals the perils of using restricted character sets when analysing the phylogeny of taxa (see a comparable case resulting in interpretation of the Late Miocene hominoid, *Oreopithecus*, as a cercopithecid (Delson, 1979). In the case of *Morotochoerus*, even slight additions to the hypodigm of the species (incisors, fragment of talus, and proximal epiphysis of axial first phalanx) reveal that its identification as Hippopotamidae has a high probability of being incorrect. This example provides a cautionary tale to cladists - convergence is a major pitfall of this approach to phylogeny reconstruction, a weakness amplified by restricted and/or incomplete data sets.

In contrast, the remains of *Palaeopotamus ternani* from Kipsaraman (14.7 Ma) (Pickford, 2007a) and the new fossils from the Ngorora Formation described herein, reveal that hippopotamids are closely related to and probably descended from palaeochoerids (Fig. 15).

Some Oligocene and Miocene palaeochoerids possess cheek teeth with basic structural elements similar to those of hippopotamids, so much so that only relatively minor morphological and metric changes would be necessary to evolve a hippopotamid dentition from a palaeochoerid one. Similarities are not only confined to overall crown morphology, but also include finer details of radicular structure, enamel thickness, relative cusp proportions, enamel ornamentation and « Fürchenmuster ».

It is concluded that the Ngorora specimens attributed to *Kenyapotamus* sp., when combined with the evidence from *Palaeopotamus* and *Propalaeochoerus*, strengthen the hypothesis that Hippopotamidae developed from Palaeochoeridae, and that the scenario of an anthracothere link between hippos and whales is obsolete (Pickford, 2008). Likewise, the proposed classification of *Kulutheri-*

um and *Morotochoerus* as members of the family Hippopotamidae is considered to be invalid for reasons already published (Pickford, 2007b) but also because newly available elements of the anterior dentition (incisors) and post-cranial bones of *Morotochoerus* reveal that it differs radically from hippopotamids, much more so than do incisors of *Propalaeochoerus*.

The discovery of teeth of *Kenyapotamus* in ca 11-13 Ma deposits of the Ngorora Formation, Kenya, is important for several reasons. Firstly, it helps to fill a gap in the fossil record between early hippopotamids from Maboko (ca 16.5 Ma) Kipsaraman (14.5 Ma) and Fort Ternan (13.7 Ma) (Pickford, 1983, 2007a) attributed to *Palaeopotamus ternani*, on the one hand, and younger material from Nakali, Samburu Hills and Ngerngerwa aged between 10.5 and 9.5 Ma, attributed to *Kenyapotamus coryndonae*, on the other (Pickford, 1983, 2007a). Secondly, the specimens from Ngorora include a well preserved m/3 which shows closely similar morphology to teeth of Late Miocene, Pliocene, Pleistocene and Extant hippos, but which also shows similarities in basic structure to the teeth of *Palaeopotamus ternani* from the Middle Miocene of Kenya, and to teeth of Oligocene Palaeochoeridae such as *Propalaeochoerus elaverensis* from France (Viret, 1929). Thirdly, the Ngorora specimens show highly divergent morphology from all known bothriodont anthracotheres, in particular the teeth of *Libycosaurus* and *Merycopotamus* species.

If bothriodonts represent the link between hippopotamids on the one hand and Cetacea on the other, as was recently postulated (Boisserie *et al.*, 2005a, 2005b) then one needs to address two points which flow from the proposal. Firstly, one would need to hypothesise, as was done by Boisserie *et al.* (2005b) and Orliac *et al.* (2010) that the structure of the dentitions of bothriodonts is so 'plastic' that, in a short period of time during the Late Miocene, the selenodont dentition of bothriodonts could give rise to the brachyodont, bunodont dentition of early hippopotamids, accompanied by major changes in the detailed structure of the radicular system, cusp morphology, relative cusp dimensions, enamel thickness, enamel surface ornamentation and groove system (Fürchenmuster). This runs counter to evidence that the basic structure of bothriodont cheek teeth, like that of hippopotamids, was stable over extended periods of geological time. Throughout their long history (Eocene to Pleistocene (Matthew, 1934)) bothriodonts show no signs of developing dental structures

comparable to those that occur in hippopotamids (Middle Miocene to Recent). A second difficulty with this scenario is that the earliest known hippopotamids (*Palaeopotamus ternani*) occur earlier in time than *Libycosaurus* species (Pickford, 2007a) the supposed sister group of hippos taken to link hippos to whales. We note that a recently published paper by these authors (Orliac *et al.*, 2010) refutes the hypothesis of Boisserie *et al.* (2005a, 2005b).

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