

# GEO-PAL UGANDA



# Geo-Pal Uganda

## 1 Aims and Scope

Geo-Pal Uganda is a scientific journal whose aim is to provide a vehicle for the dissemination of knowledge concerning the geology and palaeontology of Uganda. It publishes original papers that contribute to scientific debate on issues in geology and palaeontology relevant to Uganda and neighbouring countries where there may be an overlap in interests. Its scope embraces all fields of investigation in palaeontology and in the case of

geology, all fields that may throw light on the context of its fossil record (geological context, radio-isotopic age determinations, stratigraphy, palaeoclimatology, palaeoenvironments, etc.). Original articles, as well as review articles are accepted. Each publication will appear as a separate issue of the journal and will be published as soon as possible after the editors are satisfied that the scientific quality of the article warrants its dissemination.

## 2 Submission of manuscripts

Authors should submit their articles to Geo-Pal Uganda in electronic format in order to facilitate the editorial and reviewing process and thereby to shorten publication time. Manuscripts should be

sent to the Uganda Museum, Kira Road, P.O. Box 5718, Kampala, Uganda by mail or preferably by email to the editor.

Contact <[saramussasarah@yahoo.com](mailto:saramussasarah@yahoo.com)>

## 3 Copyright Information

Submission of a manuscript implies that the work has not been published before (except in the form of an abstract, a review or thesis), that it is not under consideration for publication elsewhere; that its publication has been approved by all co-authors and by the authorities at the establishment where the research was carried out. Transfer of copyright to the Uganda Museum becomes effective if and when the article is accepted for publication.

The copyright covers the exclusive right to reproduce and distribute the article, including reprints, translations, photographic reproductions, microform, electronic form (offline, online) or other reproductions of similar nature. All articles published in this journal are protected by copyright, which covers the exclusive rights to reproduce and distribute the article (e.g. as offprints, pdfs), as well as all translation rights. No material published in this journal may be reproduced photographically or stored on microfilm, in electronic data bases, video disks etc., without first obtaining written permission from the copyright owners.

## 4 Subscription information

**ISSN 2076-5746**

Copies of published articles can be obtained from the Uganda Museum, P.O. Box 5718, Kampala, Uganda, by requesting the article either printed on paper, or in pdf format. Articles printed on paper will imply a charge of \$20 to cover handling and postal fees. Articles in pdf format will be sent free of charge.

Requests for articles should preferably be made by email to the Chief Commissioner of the Uganda Museum <[mwanjankale@gmail.com](mailto:mwanjankale@gmail.com)> copied to <[saramussasarah@gmail.com](mailto:saramussasarah@gmail.com)> and <[jacksseb@yahoo.com](mailto:jacksseb@yahoo.com)>.

## 5 Production

Uganda Museum, P.O. Box 5718, Kampala

© Uganda Museum, Kampala

# Observations on Anthracotheriidae (Mammalia : Artiodactyla) from Napak, early Miocene, Uganda

Martin Pickford

UMR 7207 CR2P – MNHN-CNRS-SU, Muséum national d'Histoire naturelle, Paris (martin.pickford@mnhn.fr)

To cite this article : Pickford, M. 2020 - Observations on Anthracotheriidae (Mammalia : Artiodactyla) from Napak, early Miocene, Uganda. *Geo-Pal Uganda*, 13: 1-29.

## ABSTRACT

Since the mid-1960's fossils of the extinct artiodactyl family Anthracotheriidae have been recorded from early Miocene volcano-sedimentary deposits at Napak, Uganda, but the material basis for the listings has never been made clear in a scientific context. The aim of this contribution is to describe the fossils and to discuss their systematic and palaeoecological implications.

**Key Words.**- Early Miocene, Artiodactyla, dentognathic, post-cranial, sexual dimorphism

## INTRODUCTION

Anthracothere fossils were first recorded from the early Miocene deposits at Napak, Uganda, by Bishop (unpublished field notes) (Musalizi et al. 2009). The fossils were found at Napak V in 1961, and Napak IX in the Napak Member in 1962 and 1964, and at Napak II in the Iriiri Member in 1965. Additional fossils were collected from time to time, with hints that they represented the large species, *Brachyodus aequatorialis* MacInnes, 1951, but the material has never been formally described. This was largely due to the fact that the specimens in the early collections lacked diagnostic features, comprising as they did, isolated tooth fragments and edentulous jaw fragments, meaning that identification was based mainly on size criteria.

Since 1999, the Uganda Palaeontology Expedition has collected additional fossils of a species of large anthracothere at Napak IX, Napak I, Napak V and Napak XV (Table 1) some specimens of which are informative enough to throw light on their taxonomic and systematic affinities, but overall, the sample is rather too restricted to solve all the problems in these domains. The upper molars and one of the premaxillae from Napak, in particular, differ from the Rusinga holotype of the Kenyan early Miocene species *Masritherium aequatorialis*, which raises questions about its generic affinities. Are the differences observed due to sexual dimorphism or do they indicate individual variation, or the presence of taxonomic diversity?

Anthracothere fossils have now been collected at five localities in Uganda – Napak (this paper), Moroto (Pickford & Mein, 2006), Bukwa (Pickford, 2017), Kakara (Pickford, 1991) and Kisegi (Pickford, 1994) (Fig. 1).

Comparisons have been made with material of *Brachyodus onoideus* from Europe, including the type specimen and other fossils from Neuville-aux-Bois, France (Blainville, 1847; Gervais, 1859; Déperet, 1895; Mayet, 1908; Antunes & Ginsburg, 2003) and other samples of anthracotheres that have, at one time or another, been attributed to the genus *Brachyodus*, including fossils from Moghara, Egypt (Andrews, 1899; Hamilton, 1973; Miller et al. 2014) Bugti, Pakistan (Forster-Copper, 1913, 1924) Ban Na Sai, Thailand (Ducrocq et al. 2003) and Shansi and Yunnan, China (Xu, 1962). The conclusion is that few of the African fossils can convincingly be included in the genus *Brachyodus*, there being important differences in dental and cranial anatomy from the type species. Nevertheless, there are basic dental resemblances between all these forms, such as the presence of wrinkled enamel in the cheek teeth and five main cusps in the brachyselenodont upper molars, and no anterior cristid from the metaconid, and a junction between the posthypocristid and postentocristid in the lower molars (Holroyd et al. 2010)

which accounts for many of the taxonomic decisions of previous students of the fossils (Andrews, 1899; Arambourg, 1933; MacInnes, 1951; Hooijer, 1963, 1968; Dineur, 1982). However, there have been dissenting voices, such as those of Fourtau (1920) and Black (1978) who included the African forms in the genus *Masritherium*. The aim of this paper is thus to describe the Napak fossil anthracotheres, and to discuss the generic affinities of these and other African early Miocene large anthracotheres from the continent.

## GEOLOGICAL CONTEXT, AGE, PALAEOECOLOGY

The geology and geochronology of the Napak volcano-sedimentary deposits have been published on several occasions (Musalizi et al. 2009; Pickford et al. 2010, 2013, 2019). In brief, the fossiliferous deposits accumulated on the flanks of a carbonatite-nephelinite volcano as sub-aerial tuffs and superficially reworked slope deposits, which were subjected to varying degrees of pedogenesis before being buried by subsequent eruptions of tuff, agglomerate and lava. For this reason, many of the Napak fossils are damaged and comprise isolated skeletal elements. Furthermore, burrowing and plowing activities in recently developed surface soils by rodents and bush pigs have damaged and displaced some of the fossils even more. The anthracothere fossils found at the various sites are all broken, but some pieces, notably specimens from Napak IX and Napak V, could be fitted back together.



**Figure 1.** Fossiliferous localities in Uganda which have yielded Anthracotheres.

On the basis of radio-isotopic dating of biotite crystals in the tuffs at Napak, it is estimated that the volcano was active between 19-20.5 Ma and this is inferred to be the age of the enclosed fossils, corresponding to East African Faunal Set I of Pickford (1981).

The bulk of fossils from Napak is of terrestrial affinities (Pickford, 2004) with only two localities in the Napak Member (above the Lomorutoit Nephelinite Lava) having yielded the occasional fossil with aquaphile affinities. These are Napak V and Napak XV, both of which have yielded crocodiles. Napak IX, which yielded anthracothere fossils has not yielded any other specimens with aquaphile habits, nor has Napak I. The Iriiri Member, beneath the Lomorutoit Lava, in contrast, contains abundant freshwater snails and gastropods, fish, turtles and crocodiles, as well as a few fragments of anthracotheres (Napak II, not described herein due to their extremely fragmentary condition). From this it is inferred that the oft-quoted preferred aquaphile habitat of anthracotheres is not put in doubt by the Napak discoveries.

## MATERIAL

**Table I. Fossil anthracotheres from Napak (institution prefix UM) described in this paper**

Catalogue (locality, register N° and year of collection)	Anatomy
Nap I 9'99	Right p/4
Nap V 61	Premaxilla
Nap V 12'03	Incisor
Nap V 139'08	Canine
Nap V 96'09	Mandible with three teeth
Nap V 35'10	2nd phalanx
Nap V 6'11	Left premaxilla
Nap V 69'12	3rd phalanx
Nap V 92'13	Proximal radius
Nap IX Aug 62	Premaxilla with incisor
Nap IX 22'99	Maxilla with M1/ and half M2/
Nap IX 40'99	Premaxilla
Nap XV 63'07	Upper right molar
Nap XV 125'07	Incisor
Nap XV 162'15	Calcaneum

## METHODS

Comparisons of the Napak fossil anthracotheres were made with material of *Brachyodus onoides* (Gervais, 1859) from France, *Brachyodus intermedius* Mayet, 1908, from France (which may represent a separate genus), *Brachyodus africanus* Andrews, 1899 (now attributed to *Afromeryx africanus* by Pickford, 1991), *Brachyodus aequatorialis* MacInnes, 1951, from Kenya (herein attributed to the genus *Masritherium*), *Brachyodus mogharensis* Pickford, 1991, *Masritherium depereti* Fourtau, 1920 and *Jaggermeryx naida* Miller et al. 2014, from Moghara, Egypt. Comparisons were also made with fossils from Bugti, Pakistan (Forster-Cooper, 1913, 1924), Ban Na Sai, Thailand (Ducrocq et al. 2003) and China (Xu, 1962). A possibly relevant lower jaw fragment from Wadi Sabya, Saudi Arabia attributed to *Masritherium* sp. by Madden et al. (1978) was investigated, but the publication shows only a lingual view of the specimen which does not provide enough information to verify the identification.

## ABBREVIATIONS

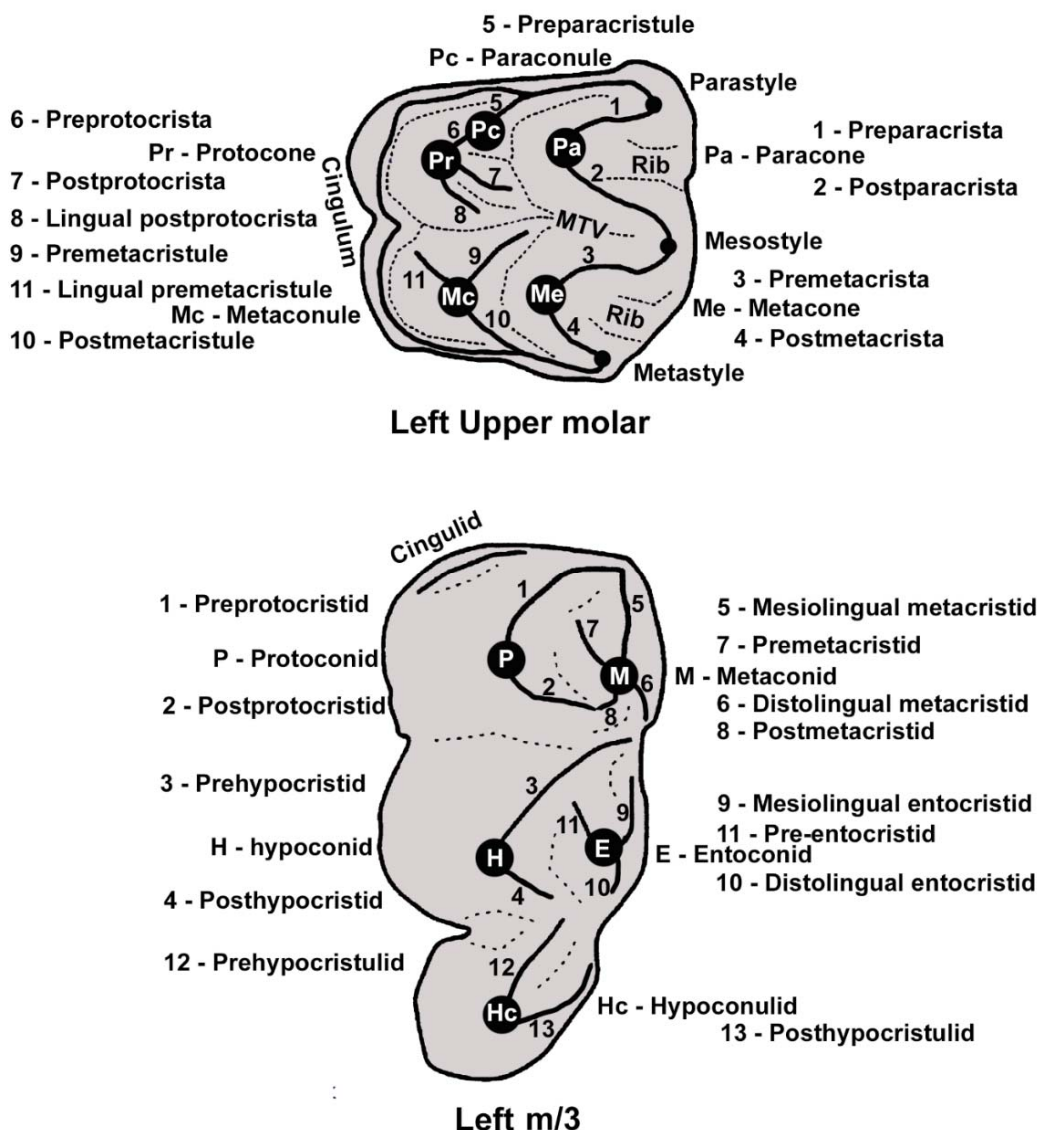
**BLB** - Bucco-lingual breadth  
**CGM** - Cairo Geological Museum, Cairo  
**CH** - Chilleurs-aux-Bois, France  
**CNRS** - Centre National de Recherche Scientifique  
**CUWM** - Cairo University Moghara collection, Cairo  
**FS** - Faluns Savigné, France  
**KNM** - Kenya National Museum, Nairobi  
**LH** - Lokichar, Kenya  
**MDL** - mesio-distal length

**MGP-PD** - Museo di Geologia e Paleontologia of the Università di Padova  
**MN** - Mammal Neogene (biostratigraphic zone)  
**MNHN** - Muséum National d'Histoire Naturelle, Paris  
**Nap** - Napak, Uganda  
**Neu** - Neuville-aux-Bois, France  
**NHMUK** - Natural History Museum of the United Kingdom, London  
**UM** - Uganda Museum, Kampala

## NOMENCLATURE OF THE MOLARS

In the literature there are several ways of referring to the cusps and crests of anthracothere molars. The convention used in this paper is adapted from Lihoreau & Ducrocq (2007) with the addition of a lingual premetacristule in the upper molars (11 in Fig. 2), a crest that occurs in some, but not all, anthracotheres (Dineur, 1982; Pickford, 2006). In the system of Lihoreau & Ducrocq (2007) the posterior cristule of the paraconule is not numbered but it is nevertheless present between the central parts of the protocone and paracone and in some taxa it extends as far as the median transverse valley. Coombs & Coombs (1977) called this crest the postparaconule crista.

References to upper teeth are abbreviated as capital letters (M - molar, P- premolar, I - incisor, C - canine, D - deciduous cheek tooth) followed by a number representing the meristic position, followed by a forward slash which represents the occlusal plane (eg M1/ - first upper molar). Lower teeth are abbreviated using a lower case letter (m, p, i, c, d) with the meristic position beneath the forward slash (eg m/1 - lower first molar).



**Figure 2.** Nomenclature of the cusps and crests of upper and lower molars of Anthracotheriidae (adapted from Lihoreau & Ducrocq, 2007). Forster-Cooper (1913, 1924) called the ribs ‘barrels’ and the paraconule the « protoconule » because it is more closely linked to the protocone than to the paracone.

## TAXONOMIC NOTE

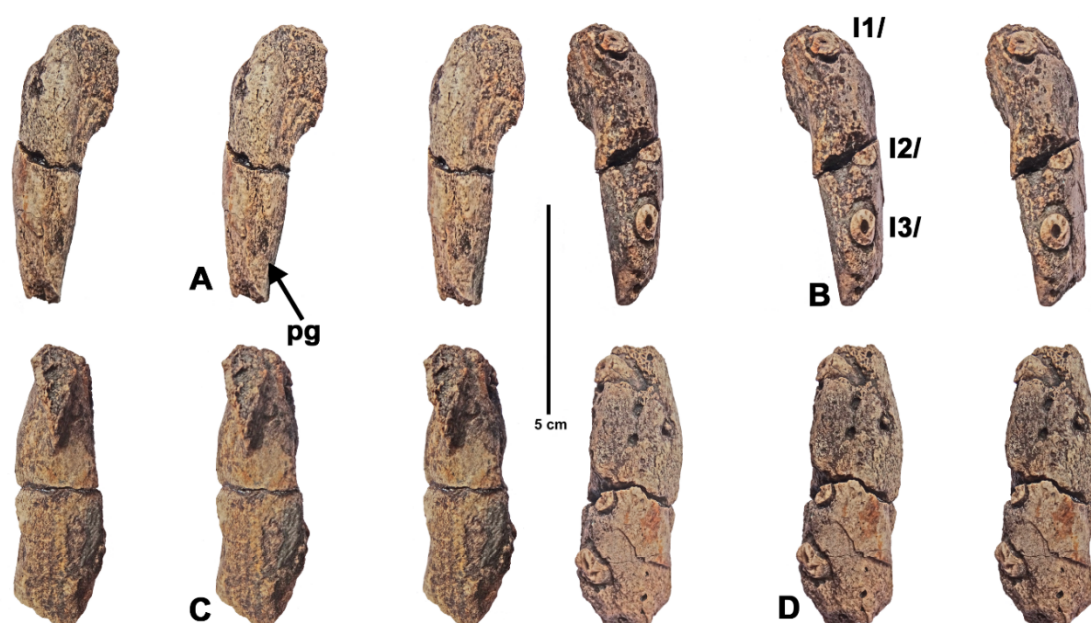
The study of the Napak anthracotheres reveals that a general revision of the brachyselenodont anthracotheres is required. Fossils attributed to the genera *Brachyodus* and *Masritherium* show too many differences in cranial and dental morphology for them to continue to be subsumed under a single genus *Brachyodus*. Furthermore, the East African species traditionally classified as *Brachyodus aequatorialis* differs in substantial details of the skull from the European genus *Brachyodus*, as well as from the Egyptian taxon *Masritherium*. In addition, it is likely that some of the molars from Moghara, Egypt, previously attributed to *Masritherium depereti*, belong to *Jaggermeryx naida*, there being overlap in the ranges of metric variation of their molars. Of the two species, *Jaggermeryx naida* possesses the larger molars.

Such an in-depth taxonomic and systematic revision is beyond the scope of this paper. In this article, the East African species will be classed within the genus *Masritherium*, as was done by Black (1978) but with the proviso that it could belong to a different genus.

## ANATOMICAL DESCRIPTIONS OF THE FOSSILS

### Upper jaws and teeth

An almost complete premaxilla (UM Nap IX 40'99) from Napak IX, Uganda, reveals that there are three incisors in this bone (Fig. 3). The upper central incisor in the specimen is small, which indicates that it is likely to represent a female individual, in which case the holotype of *Brachyodus aequatorialis* from Rusinga (herein attributed to the genus *Masritherium*), with its large incisor (MacInnes, 1951) would represent a male. In the Napak IX specimen, the I2/ alveolus is separated from that for the I1/ by a diastema 19 mm long, and the space between I2/ and I3/ is 10 mm long. The incisor roots are inclined in the premaxilla, all of them pointing antero-ventrally. In the Napak IX fossil there is a buttress projecting mesially from the alveolus of the central incisor, suggesting that the two premaxillae met in the midline. If this is so, then the space between the two central incisors is estimated to have been about 21 mm.



**Figure 3.** Stereo views of Nap IX 40'99, right premaxilla with roots of I1/, I2/ and I3/ from the early Miocene of Napak IX, Uganda, interpreted to belong to a female individual. A) dorsal view, B) occlusal view, C) lingual view, D) buccal view (pg : groove in dorsal part of premaxilla) (scale : 5 cm).



**Figure 4.** Stereo views of Nap IX Aug 62, unerupted left upper second incisor in its alveolus in a fragment of premaxilla. A) dorsal view, B) lingual view (scale : 10 mm).

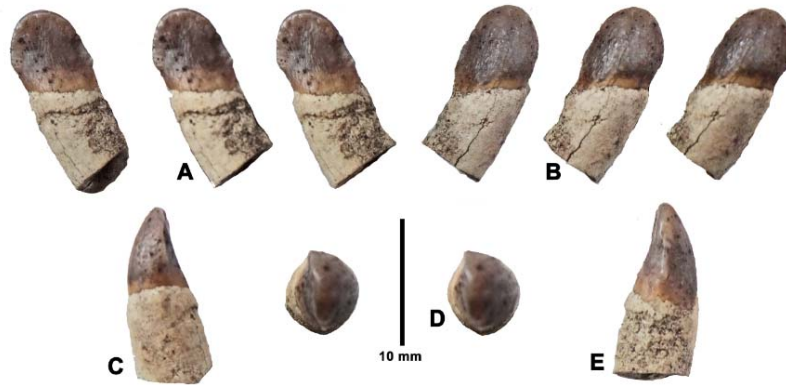
Of pertinence to the analysis is a specimen from Napak IX, Uganda (Fig. 4). The fossil is a fragment of left premaxilla with a single-rooted tooth inside its crypt. The crown is labio-lingually compressed, is concave on the lingual side with a central swelling, and it has sharp mesial and distal edges. Overall it resembles an incisor. On the dorsal surface of the specimen, there is part of the alveolus of the upper central incisor which extends well over the radicular part of the I2/. The dimensions of what remains of the alveolus of the I1/ indicates that the individual was probably a male.



**Figure 5.** Stereo views of premaxillae of *Masritherium aequatorialis* from Napak V, early Miocene, Uganda. A) Nap V 61, right premaxilla, B) Nap V 97'09, left premaxilla (1 : occlusal views, 2 : labial views, 3 : lingual views) (scale : 5 cm).

Locality Napak V yielded edentulous left and right premaxillae of an anthracothere with large alveoli for the central incisors, and are accordingly interpreted to belong to male individuals of *Masritherium aequatorialis*, the holotype of which possesses large alveoli (MacInnes, 1951). In the Napak specimens (Fig. 5) there are short diastemata between I1/ and I2/ (14 mm on the right, ca 12 mm on the left). Unfortunately the distal parts of these premaxillae are broken off. There appear to be no buttresses on the mesial side of the premaxilla, suggesting that the two premaxillae did not meet interproximally.





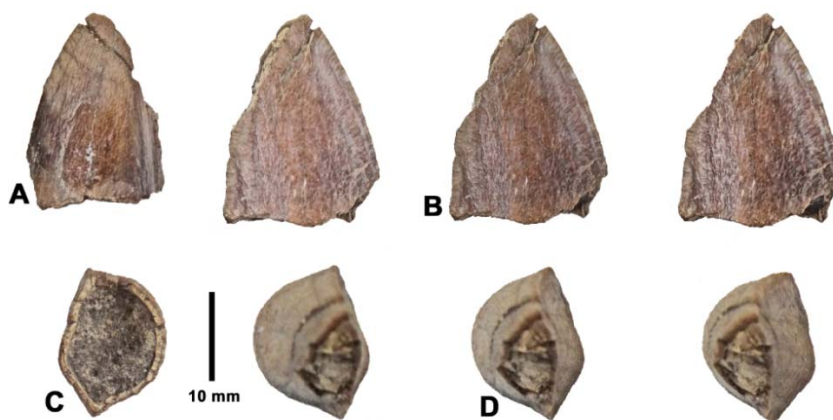
**Figure 6.** Nap V 12'03, isolated incisiform tooth from Napak V, Uganda. A) stereo lingual views, B) stereo labial views, C) mesial view, D) occlusal view, E) distal view. Note that the root is larger than the crown (scale : 10 mm).

An incisiform tooth from Napak (Nap V 12'03) probably the left I2/, is labio-lingually compressed, with a concave lingual surface and a convex labial one (Fig. 6). The cervix is slanted with respect to the root, suggesting that the crown leaned mesially in the premaxilla, and the root is larger than the crown. The precrista and postcrista are rounded and terminate a short way above the cervix such that at cervix the tooth is shorter than the main part of the crown.



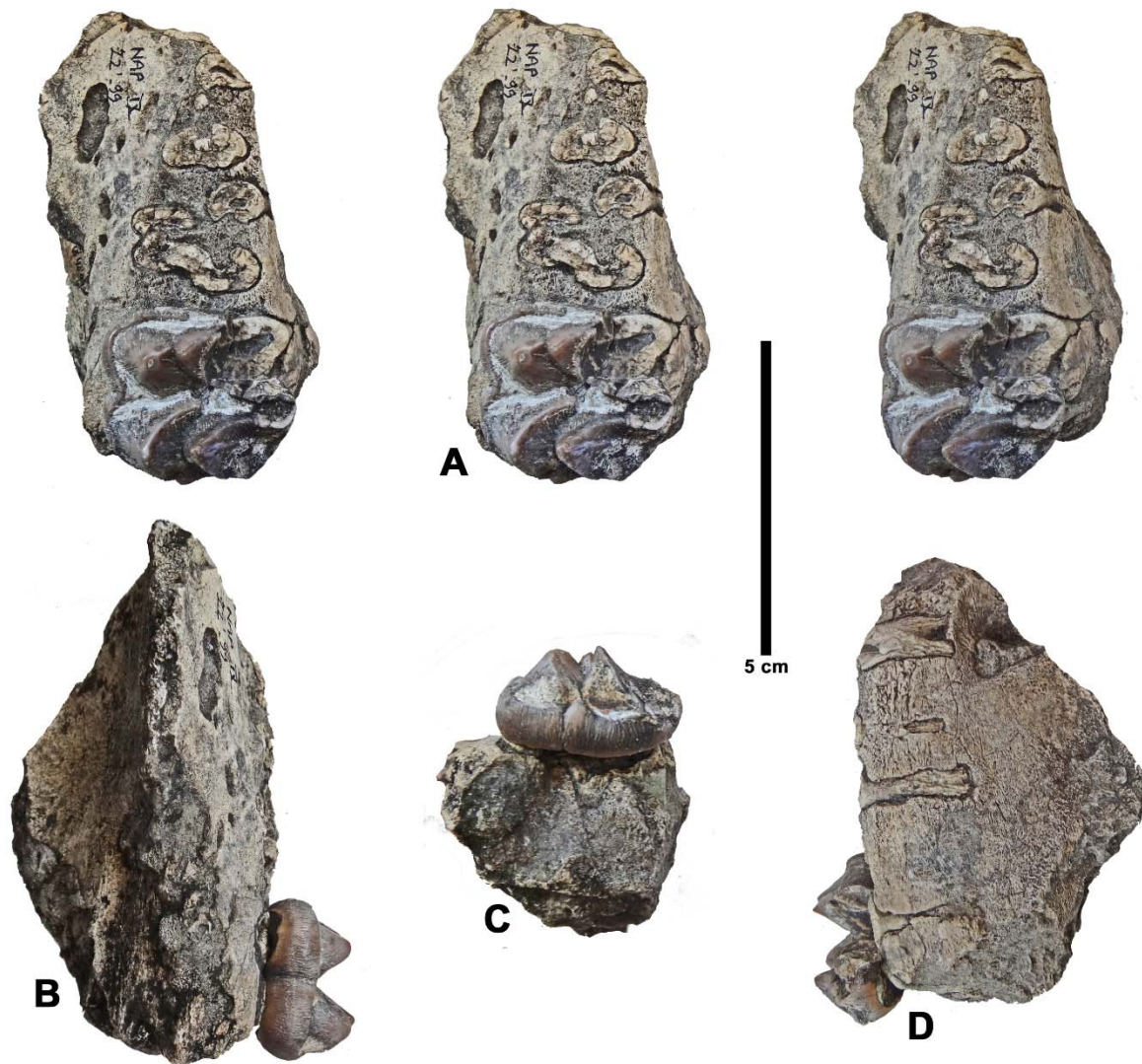
**Figure 7.** Nap XV 125'07, damaged incisiform tooth from Napak XV, Uganda. A) lingual view, B) occlusal view, C) stereo labial view. Note that the root is larger than the crown (scale : 10 mm).

Napak XV yielded an incisiform tooth lacking the apex of the crown (Fig. 7). The cervix in Nap XV 125'07 is slanted with respect to the root, and the root is larger than the crown. The crown is slightly labio-lingually compressed and there are blunt precrista and postcrista. This specimen, despite its limitations, likely corresponds to an upper right second incisor.

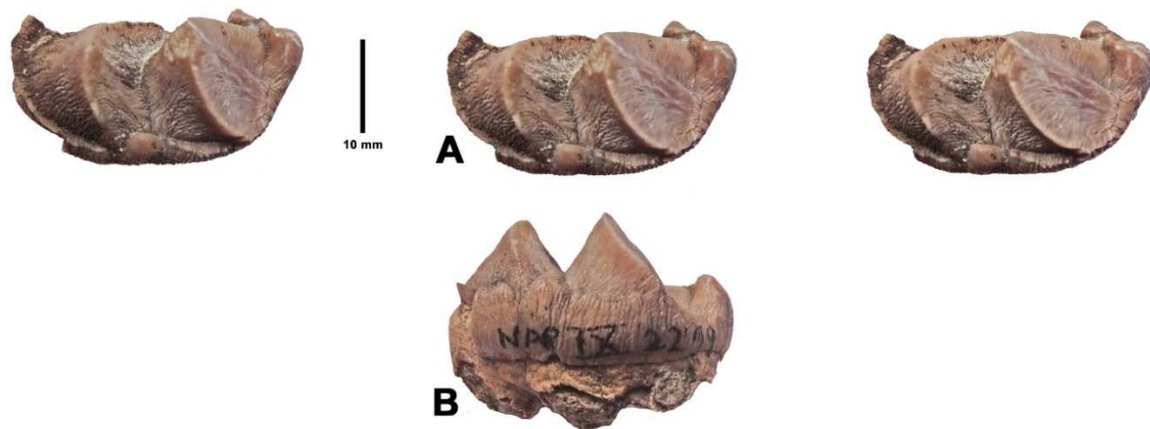


**Figure 8.** Nap V 139'08, damaged isolated caniniform tooth from Napak V, Uganda. A) lingual view, B) stereo buccal view, C) radicular view of base of crown, D) stereo apical views. This tooth is likely from a male individual (scale : 10 mm).

Napak V yielded an incomplete caniniform tooth (Nap V 139'08) which lacks the apex, and in which the open radicular part is infilled with sediment (Fig. 8). The crown is tall, somewhat compressed and has prominent precrista and postcrista. The buccal surface is lightly concavo-convex (almost flat) but the lingual surface is strongly convex. This tooth is interpreted to be an upper left canine by comparison with the corresponding tooth in *Nabotherium aegyptiacum* (see specimen CGM 67200 from the Fayum, Egypt, described by Sileem et al. 2016) and to the upper canine of *Brachyodus onoideus* from Eggenburg, Austria, described by Déperet (1895).



**Figure 9.** Nap IX 22'99, left maxilla with roots of P3/ and P4/ and crown of M1/. A) stereo occlusal views, B) lingual view, C) distal view, D) buccal view (scale : 5 cm).



**Figure 10.** Nap IX 22'99, distal loph of unworn left M2/ from Napak IX, Uganda. A) stereo occlusal views, B) distal view (scale : 10 mm).

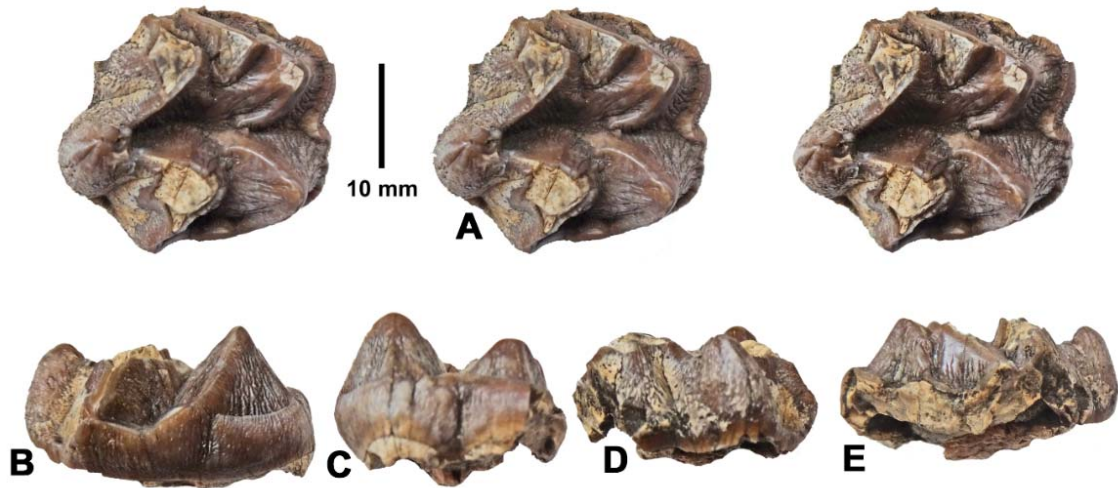
Napak IX 22'99 comprises parts of a snout of a large anthracothere (Fig. 9). The teeth had broken off but the unworn left M1/ (lacking the paracone) was found nearby and fits cleanly onto the exposed roots, while the rear part of the unerupted (rootless) left M2/ is inferred to belong to the same individual. Only the left maxilla and molars are described herein, the right maxilla being in poor condition. The infraorbital foramen is immediately above the anterior root of the P3/. On the palatal surface several small holes are preserved, possibly remnants of foramina related to the palatine groove.

The maxilla retains the roots of the P3/ and P4/. On the basis of the roots, the P3/ is inferred to have been triangular in occlusal outline, broad behind, narrowing anteriorly, while the P4/ was more ovoid in outline, with four roots, two separate roots buccally, and two lingual ones which are coalescent on their lingual sides. In *Brachyodus onoideus*, the lingual root of the P4/ is usually single (one specimen was observed with a shallow lingual groove) and the same applies to *Masritherium aequatorialis*.

The M1/ is pentacuspidate (most of the paracone is broken off) with a prominent paraconule between the protocone and paracone. The posterior cristule of the paraconule extends into the median transverse valley thereby separating the postprotocrista from the base of the paracone. The protocone is distinctly smaller than the metaconule and the preprotocrista and lingual postprotocrista are weak. The rib on the buccal surface of the metacone is narrow and low. The premetacrista and postmetacrista are sharp and the metastyle is weakly developed.

The premetacristule is strongly developed and terminates in the centre of the tooth, but there is no lingual premetacristule. The postprotocrista and premetacrista meet at the buccal end of the median transverse valley, forming a loop-like mesostyle which is bulbous buccally. The cingulum is well-developed lingually and extends along the mesial edge. Distally it reaches round the metaconule to fuse with the postmetacristule.

The distal loph of the M2/ from Napak IX is basically similar in morphology to that of the M1/ (Fig. 10). There is a weak 'rib' on the buccal surface of the metaconule and a better-defined, but low, rib on the metacone. The metastyle is almost obsolete but the distal portion of the mesostyle is strong and bulbous in shape. The distal cingulum is quite strongly developed.



**Figure 11.** Nap XV 63'07, right M1/ from Napak XV, Uganda. A) stereo occlusal views, B) distal view, C) lingual view, D) buccal view, E) mesial view (scale : 10 mm).

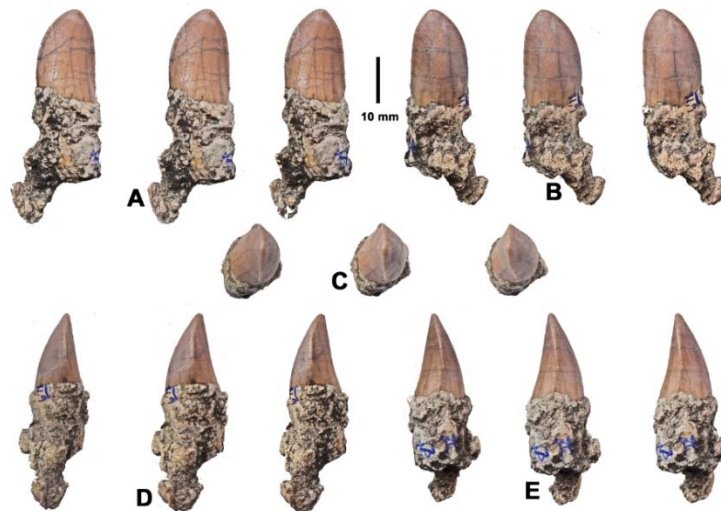
The upper molar from Napak XV (Nap XV 63'07) has suffered slight damage to the apices of the paracone and metacone, and most of the parastyle is missing, but overall, the specimen is in good condition and was only slightly worn at the time of death (Fig. 11). On the basis of the thickness of enamel, it is most likely to represent a permanent tooth, but the possibility of it being a D4/ cannot, for the moment, be excluded, because it has long been known that the D4/s of brachyselenodont anthracotheres closely resemble their permanent counterparts (Kowalevsky, 1874; Ducrocq et al. 2003). The Napak tooth (MDL x BLB - 24.2 x 28.6 mm) is as large as specimens of *Brachyodus onoideus* and the enamel is wrinkled, but more coarsely than in the European species as well as in East African *Masritherium aequatorialis*.

The paraconule is large and positioned between the anterior halves of the protocone and paracone. Its posterior cristule does not reach the median transverse valley, a swollen crista (the postprotocrista) leading buccally from the apex of the protocone to the base of the paracone blocking its way - somewhat similar to the situation in *Anthracotherium bumbachense* Stehlin, 1910 (Roman & Boucher, 1936) and *Brachyodus hui* (Chow, 1958) (Xu, 1962) from China, and to some extent, in specimens from Ban Na Sai, Thailand, attributed to *Brachyodus cf. onoideus* by Ducrocq et al. (2003). This is unlike the situation in European specimens of *Brachyodus onoideus* and African *Masritherium aequatorialis*, in which the posterior cristule of the paraconule extends as far as the median transverse valley, but it does resemble the morphology in *Sivameryx palaeindicus* and *Sivameryx africanus* which are much smaller species. The preparacristule (5 in Fig. 2) is long, extending antero-buccally as far as the base of the preparacrista, but the anterior part is broken off, so its original extent cannot be determined accurately.

The preprotocrista is short, ending at the paraconule, and the lingual postprotocrista (8 in Fig. 2) curves disto-buccally terminating in the middle of the tooth in the floor of the median transverse valley, where it forms a low barrage. The mesostyle is large and bulbous and is not pinched in buccally, and it completely blocks the buccal end of the median transverse valley. The metastyle is weakly developed, comprising a narrow vertical crest at the base of the postmetacrasta where the buccal end of the postmetacrastule fuses with the postmetacrasta. The premetacrastule (9 in Fig. 2) extends antero-buccally towards the middle of the crown, ending slightly buccally from the end of the postprotocrista, but without blocking the median transverse valley. There is no sign of a lingual premetacrastule (11 in Fig. 2) in this tooth.

The cingulum is well-developed on the lingual sides of the protocone and metaconule and it extends along the mesial edge of the tooth (mostly broken off) but only a short way onto the distal surface of the metaconule. The ribs on the buccal surfaces of the paracone and metacone are weak.

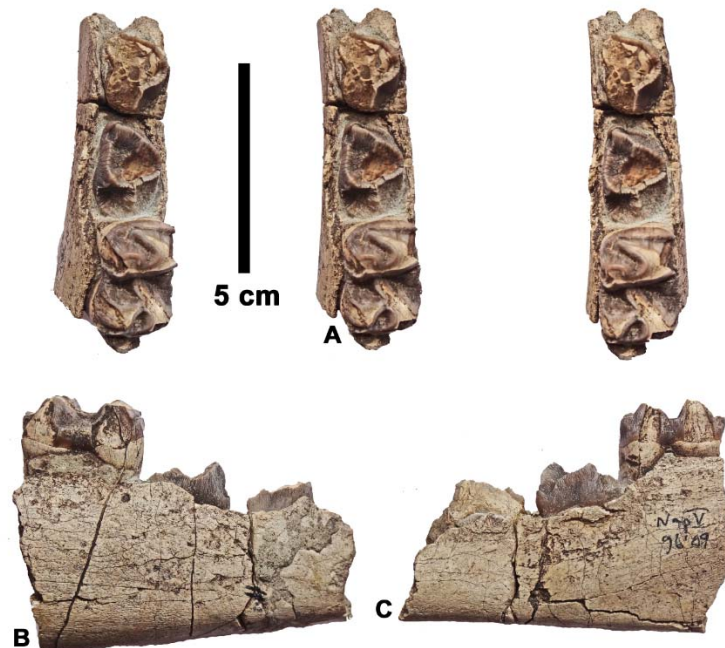
## Lower jaws and teeth



**Figure 12.** Stereo views of Nap V 6'11, an isolated left i/3 from Napak V, Uganda. A) lingual view, B) labial view, C) occlusal view, D) distal view, E) mesial view (scale : 10 mm).

Napak V yielded an unerupted left lower incisor (Nap V 6'11) which is significantly larger and taller than other incisors from the site (Fig. 12). It is interpreted to correspond to the tooth in the anterior corners of the mandibular symphysis - see for example *Masritherium aequatorialis* (KNM RU 1014 in Black, 1978; Holroyd et al. 2010) and *Masritherium depereti* (CGM 30798, Fourtau, 1920; Miller et al. 2014).

Napak V 6'11 is considered to be a lower left third incisor, but the question of meristic position is far from being resolved (see discussion below).

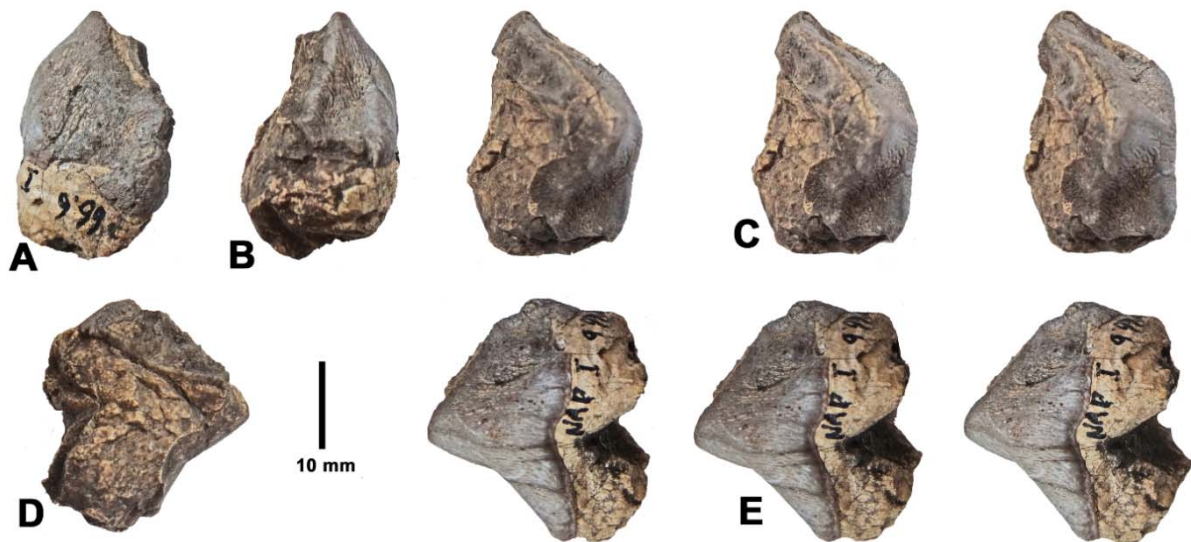


**Figure 13.** Nap V 96'09 + Nap V 61 (506), right mandible fragments containing p/3 and p/4 in crypt and fully erupted m/1. A) stereo occlusal views, B) buccal view, C) lingual view (scale : 5 cm).

Napak V yielded three fragments of an anthracothere right mandible that fit together (Nap V 96'09 + Nap V 61 (506)) (Fig. 13). The p/3 and p/4 were still in their crypts at the time of death, whereas the m/1 is moderately deeply worn, indicating the presence of delayed eruption of the permanent premolars as in other examples of brachyselenodont anthracotheres (Macdonald, 1956).

The crown of the p/3 is badly damaged, but what remains resembles the p/4. The p/4 has a main cusp (apex broken off) with a strong precrisid directed towards the mesio-lingual corner of the tooth. There is a well-formed lingual cingulum separated from the protoconid by a capacious fovea closed distally by a lingually orientated distal protoconid crest. The talonid of the tooth is broad with a low cingulum linguallly, distally and buccally, and there is a central cristid rising towards the protoconid.

The m/1 is rather worn, but it is possible to discern that there was a distolingual metacristid, but no anterior cristid from the metaconid. The preprotocristid terminates anteriorly close to the lingual margin of the tooth, but the prehypocristid ends almost in the midline of the crown, obstructing the median transverse valley. The posthypocristid is linguallly directed and joins the distolingual entocristid, behind which there is a small posterior cingulid with a small cusplet (hypoconulid).



**Figure 14.** Napak I, 9'99, right p/4 from Napak I, Uganda. A) mesial view, B) distal view, C) stereo occlusal views, D) lingual view, E) stereo buccal views (scale : 10 mm).

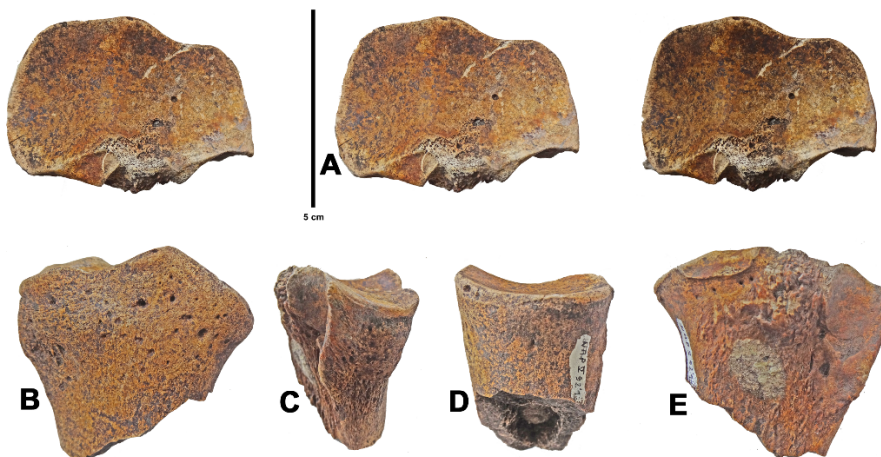
Napak I yielded a damaged right p/4 (Napak I 9'99) in light wear, but missing much of the lingual part of the crown (Fig. 14). The protoconid has a preprotocristid that ends anteriorly in a low stylid, and a postcristid that ends in the midline of the crown, separating the talonid into two parts. There is a shallow depression on the antero-lingual aspect of the protoconid separated from a similar shallow depression on the disto-lingual part of the crown by an oblique cristid, suggesting that there was likely an endprotocristid (terminology in Boissarie et al. (2010)).

A low, rounded cingulid forms a margin to the talonid, but much of it has broken away, leaving only a short portion on the bucco-distal corner of the tooth, where it forms a rounded rim to the distobuccal fovea. There are two robust roots.

**Table 2. Measurements (in mm) of the teeth of Anthracotheres from Napak, Uganda.**

Locality	Catalogue N°	Tooth	MDL	BLB	Comments
Nap I	9'99	Right p/4	28.0	18.0	
Nap IX	22'99	Left P3/ roots	24.0	16.0	
Nap IX	22'99	Left P4/ roots	20.5	22.5	
Nap IX	22'99	Left M1/	27.2	30.0	
Nap IX	40'99	Right I1/ root	7.0	4.0	
Nap IX	40'99	Right I2/ root	5.0	5.5	
Nap IX	40'99	Right I3/ root	7.0	4.5	
Nap IX	22'99	Right P2/ roots	16.0	11.0	
Nap IX	22'99	Right P3/ roots	25.0	14.5	
Nap IX	22'99	Right M2/ rear loph	--	32.0	
Nap IX	Aug 62	Left I2/	8.0	6.5	10.0 height
Nap IX	Aug 62	Right I2/ root	7.8	6.3	
Nap V	96'09	Right p/4	24.6	16.2	
Nap V	96'09	Right m/1	29.0	20.0	
Nap V	139'08	Left i/3	18.3	13.2	25.0 height
Nap V	12'03	Left upper incisor	6.0	5.0	
Nap V	6'11	Right i/3	12.8	11.8	
Nap V	61	Right I1/ alveolus	30.5	15.0	
Nap V	61	Right I2/ alveolus	9.5	7.0	
Nap V	97'09	Left I1/ alveolus	29.5	15.2	
Nap V	97'09	Left I2/ alveolus	--	9.0	
Nap V	61	Right p/3	21.5	15.6	fits 96'09
Nap XV	63'07	Right M1/	24.2	28.6	
Nap XV	125'07	Right I2/	9.5	7.6	

**Post-cranial skeleton**



**Figure 15.** Nap V 92'13, proximal end of right radius from Napak V, Uganda. A) stereo proximal views, B) cranial view, C) medial view, D) lateral view, E) caudal view (scale : 5 cm).

Only a few postcranial bones of anthracotheres have been found at Napak, and none of them throws much light on their taxonomy or systematics, but they do reveal the presence of a large species at the sites where they have been collected (Napak V, Napak XV).

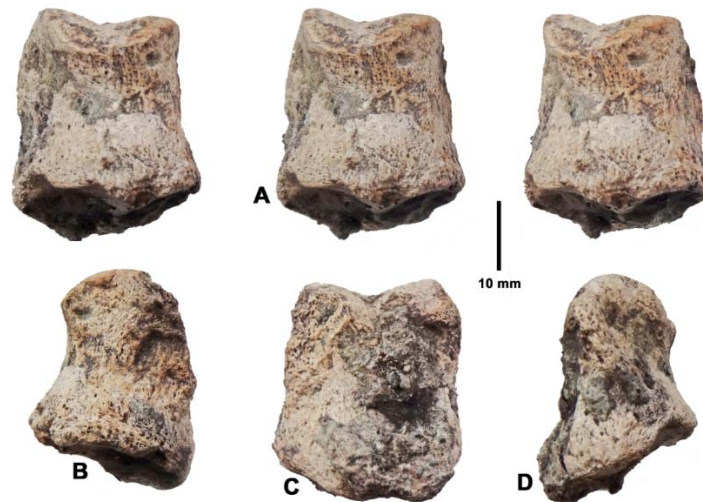
The proximal radius (Fig. 15) has two prominent facets in its caudal part for articulation with the ulna, a small one on the medial side of the caudal face restricted to the epiphysis, and a large facet on the lateral side which descends about 3 cm down onto the diaphysis. From this it is inferred that the radius and ulna were not fused solidly together, probably because the individual was juvenile. The proximal breadth of the articular part is 68 mm and the cranio-caudal diameter is 43.7 mm.



**Figure 16.** Nap XV 169'12, right calcaneum from Napak XV, Uganda, A) talar view, B) stereo caudal views, C) lateral view, D) cranial view, E) medial view (scale : 5 cm).

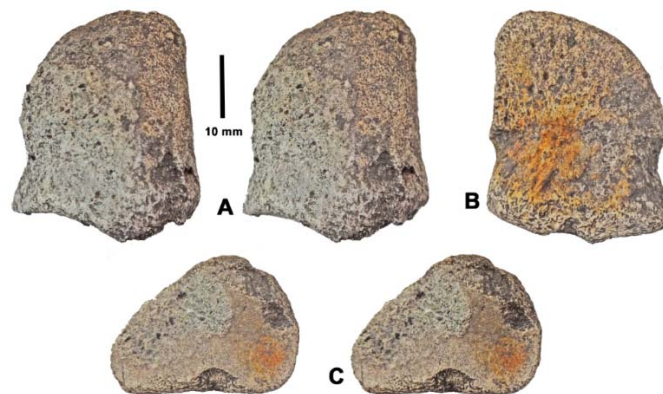
The only anthracothere calcaneum from Napak (Nap XV 169'12) is damaged, lacking the epiphysis of the tuber calcis, the sustentaculum and the lateral process (Fig. 16). In its preserved part it is similar to specimens from Moghara, Egypt (Fourtau, 1920) and Moruorot, Kenya (Arambourg, 1933). The sustentaculum extends almost right across the bone.





**Figure 17.** Nap V 35'10, axial 2nd phalanx from Napak V, Uganda. A) stereo dorsal views, B) side view, C) volar/plantar view, D) side view (scale : 10 mm).

There are two phalanges from Napak V (Nap V 35'10 and Nap V 69'12) which are attributed to a large species of anthracothere (Figs 17 & 18). Both of them appear to be axial phalanges (i.e. from rays III or IV) but it is not possible to determine with confidence whether they are from the manus or the pes. Both are proximo-distally short, and dorso-ventrally low, as in suiforms in general. The distal articular surface of the second phalanx shows a curved shallow valley approximately in the middle which corresponds to a low ridge in the proximal articular surface of the third phalanx. The termination of the third phalanx is rounded, and blunt, and on the volar/plantar side, there is a low transverse ridge at about half the length of the bone, presumably corresponding to the insertion of the hoof which, if correct, would indicate the presence of small hooves in the species.



**Figure 18.** Nap V 69'12, 3rd phalanx from Napak V, Uganda. A) stereo dorsal view, B) volar/plantar view, C) stereo proximal view (scale : 10 mm).

**Table 3. Measurements (in mm) of anthracothere post-cranial bones from Napak, Uganda.**

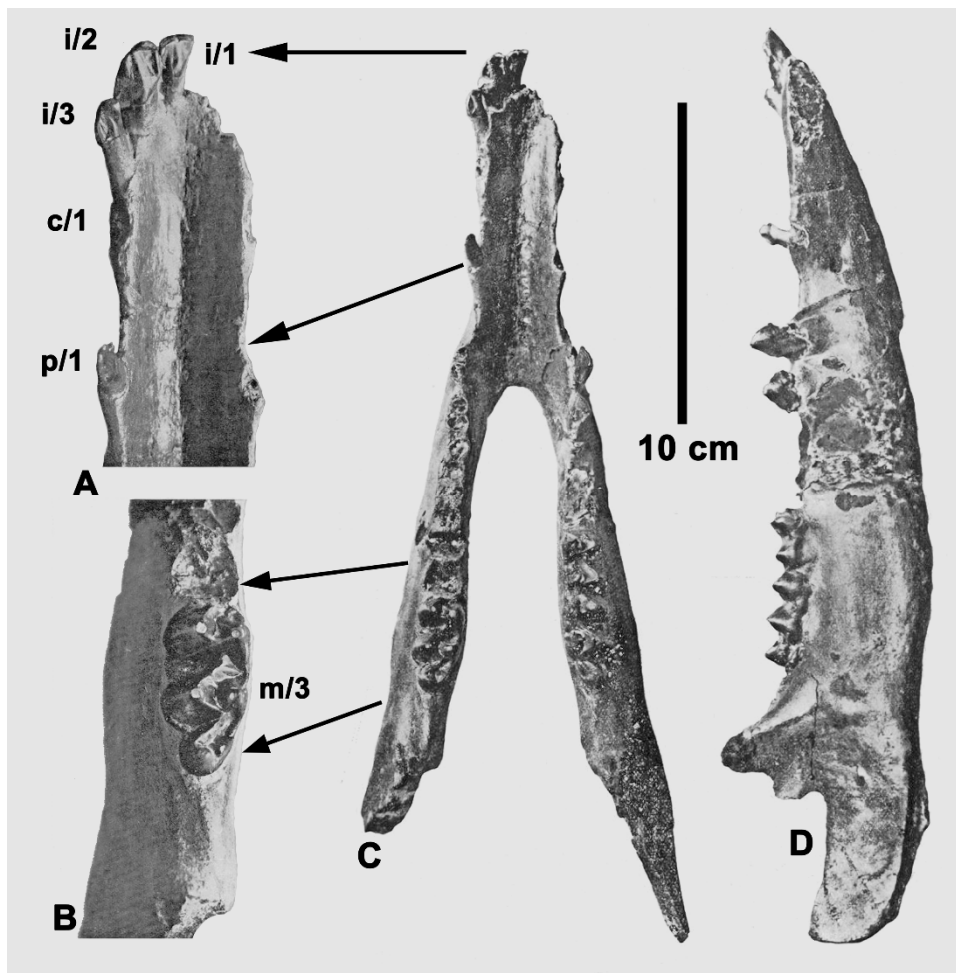
Locality	Catalogue N°	Specimen	Length	Proximal breadth	Proximal height	Distal breadth	Distal height
Nap V	15'06	Distal metapodial	--	--	--	29.0	28.0
Nap V	69'12	3rd phalanx	32.5	29.1	22.5	--	--
Nap V	35'10	2nd phalanx	38.0	28.0	25.0	25.8	18.0
Nap V	92'13	Right proximal radius	--	68.0	43.7	--	--
Nap XV	25'07	Navicular	61.0	--	28.0	47.0	32.0
Nap XV	169'12	Right calcaneum	--	--	--	--	--

## DISCUSSION

### Lower incisors

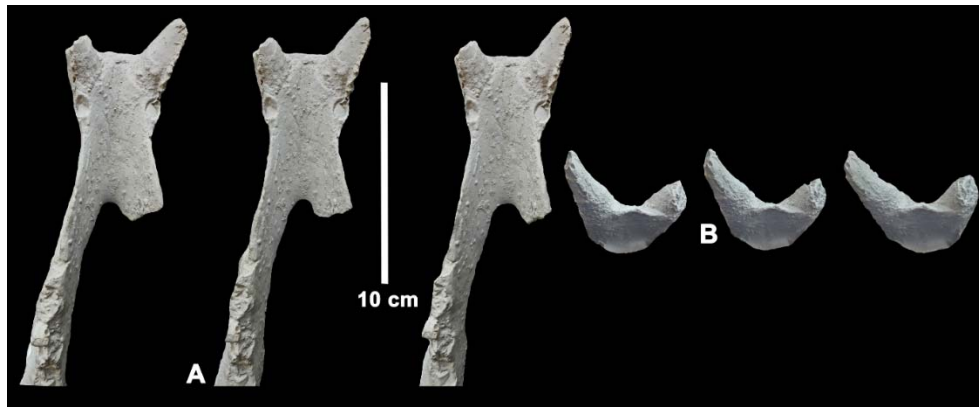
The literature reveals that there has been a great deal of confusion concerning the determination of the meristic position of the anterior teeth (incisors, canines) of large brachyselodont anthracotheres. There are few specimens with all the anterior teeth in their alveoli associated with the premolars and molars (Roman, 1907; Fourtau, 1920; Astre, 1926; Macdonald, 1956; Dineur, 1982). This renders direct observations difficult, to which can be added the fact that diverse lineages suppressed one or two anterior teeth, enlarged some, reduced the dimensions of others and developed diastemata of variable lengths between successive teeth. In addition, it is clear that in most lineages there was an important element of dimorphism and bimodality.

A small, almost complete bothriodont mandible from Oligocene deposits at Briatexte, France (Fig. 19) possesses all the incisors on the left side which reveals that in this form, it is the i/2 which is the largest tooth (Astre, 1926). Not only that, but it is positioned in the corner of the symphysis, with the i/3 distal to it, followed by the canine which is small. Behind the canine is a long diastema, then the p/1, a second diastema, then the p/2, followed by a short diastema and then the p/3 to m/3 in a continuous series. The fossil was attributed to *Brachyodus porcinus* (Gervais, 1859) by the author.



**Figure 19.** Small anthracothere mandible from Briatexte, France (Oligocene). A) occlusal view of symphysis, B) occlusal view of m/3, C) occlusal view, D) right lateral view. Note the enlarged i/2, the position of the i/3 behind the i/2, the completely fused symphysis and the elongated diastemata (adapted from Astre, 1926, who identified the specimen as *Brachyodus porcinus*) (scale : 10 cm).

Roman (1907) illustrated a juvenile mandible from the Burdigalian deposits at Horta das Tripas, Lisbon, Portugal which he identified as *Brachyodus onoideus* (but which was attributed to *Brachyodus intermedius* by Antunes & Ginsburg, 2003). He recognised four alveoli in the anterior part of the jaw in front of the diastema, three for the incisors and a small one for the canine close behind the alveolus of *i*/3. He described the alveolus of the first incisor as being longitudinally compressed, those for the *i*/2 and *i*/3 as being circular, and that for the canine as being reduced, short and longitudinally compressed. There followed a long diastema separating the canine from the *p*/1.



**Figure 20.** Stereo views of the anterior part of the holotype mandible of *Masritherium depereti* from Moghara, Egypt (CGM 30798) (cast in the NHMUK). A) occlusal views, B) anterior views to show the absence of alveoli between the tall teeth in the corner of the symphysis (scale : 10 cm).

Fourtau (1920) noted that the well-preserved anterior margin of the holotype mandibular symphysis of *Masritherium depereti* from Moghara, Egypt, was devoid of alveoli, from which he concluded that the lower central incisors had been suppressed (Fig. 20). In the main text, the bilaterally compressed, rather tall teeth in the corners of the symphysis were interpreted by him to be the second incisors, which are separated by short diastemata from what he interpreted to be premolariform canines. Thus he concluded that the *i*/1 and *i*/3 were suppressed in this species. In résumé, he wrote that the lower dental formula of *Masritherium depereti* is 1-1-4-3 (incisors, canine, premolars, molars). At the very end of his paper however, Fourtau (1920) overturned all this, and wrote that *Masritherium depereti* possessed no lower incisors at all, and that the tall tooth in the anterior corner of the mandibular symphysis was the canine. If so, then the small alveolus close behind it would be for the *p*/1, which poses a problem in that there are four premolariform teeth behind the long diastema.

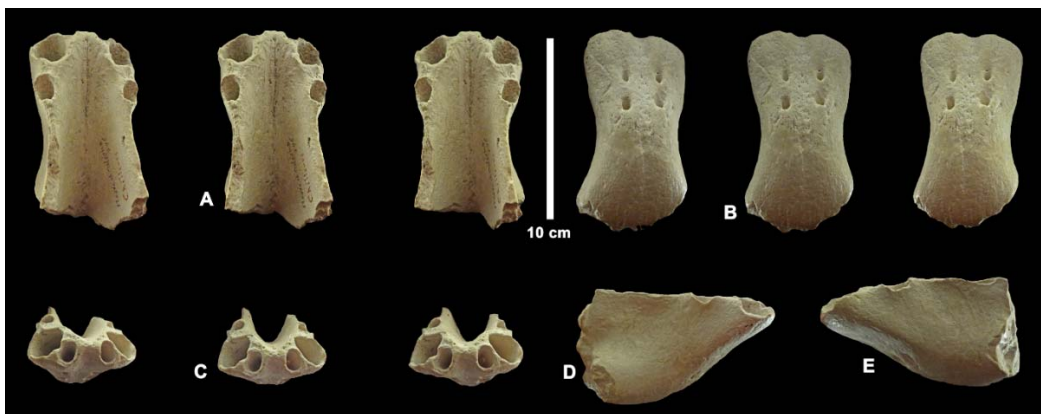
Two mandibular symphyses attributed by Fourtau (1920) to Proboscidea, belong in fact to Anthracotheriidae (Pickford, 2003). The latter author wrote, « *Two isolated symphyses from Wadi Moghara were described by Fourtau (1918, p. 88) who identified them as M. angustidens var. libyca. One of these retained a fragment of the right lower tusk which is “légèrement comprimée sur les côtés et dont le plus grand diamètre est 33 millimètres”. This suggested that the lower tusk was oval in section, but not flattened, a view accepted by Tobien (1973) who concluded that the specimen might indicate the peg type of lower tusk. Unfortunately, both symphyses (specimens CGM 32984 and CGM 32985) assigned to this species belong to the large anthracothere Brachyodus depereti* ».

The lower canine, still in its crypt, is preserved in the holotype young adult mandible of *Gelasmodon gracilis* Forster-Cooper (1913) from Bugti, Pakistan, well-separated from the *p*/1 by an elongated diastema. It is positioned a short distance behind the corner of the symphysis. According to Forster-Cooper (1913, 1924) the holotype specimen appears to have possessed no incisors.

Black (1978) mentioned in the diagnosis of the genus *Masritherium* « *jaws elongate with long diastema between p/1-c/1, shorter between c/1-incisor* » and for the species *Masritherium depereti* he specified « *i/2 enlarged, c/1 possibly absent in females* ». Concerning *Masritherium aequitorialis* (sic) he diagnosed it as possessing « *long diastemata between P1/-C1/ and C1/-I3/; long p/1-c/1 diastema, short*

*c/1-i/3* ». This followed and expanded on the work of MacInnes (1951) based on the holotype skull in which the alveolus that was identified as that of the I2/ is in fact of the I3/, and of a lower jaw (KNM RU 1014) that was collected after MacInnes' (1951) study. In these interpretations the tall tooth in the corner of the symphysis would be the *i/2* and the small alveolus behind it would be for the canine, essentially in agreement with the findings of Roman (1907) concerning the European species *Brachyodus onoideus*.

Dineur (1982) illustrated a mandibular symphysis of *Brachyodus onoideus* from Chilleurs-aux-Bois, which has three alveoli in each half of the anterior part (Fig. 21). The two alveoli at the front of the jaw were interpreted to be for the first and third incisors, followed by a small one behind for the lower canine. The supposed third incisors in the corners of the symphysis were considered to be strongly dimorphic and Dineur (1982) illustrated several isolated teeth in support of this interpretation. Thus, for this author, the enlarged 'caniniform' teeth in the anterior corners of the symphysis were the third incisors, from which it followed that the second incisors had been suppressed. He deduced the same meristic position for the caniniform tooth in the lower jaw of the Moghara species (*Masritherium depereti*) but unlike Fourtau (1920) he considered that this species had suppressed the *i/1* and the *i/2*.



**Figure 21.** Cast of a mandibular symphysis of *Brachyodus onoideus* from Chilleurs-aux-Bois, France (MN 3b). Dineur & Ginsburg (1986) identified the large alveolus at the corner of the symphysis as that of the *i/3*. A) stereo occlusal views, B) stereo ventral views, C) stereo anterior views, D) right lateral view, E) left lateral view (scale : 10 cm).

The same interpretation was voiced by Dineur & Ginsburg (1986). When discussing the anterior teeth of *Brachyodus*, they explained that « *La dentition montre une disposition inhabituelle des dents antérieures (Dineur, 1981; Cabard et al. 1980). La canine est petite, et c'est une incisive qui, très développée, assure le rôle joué par la canine chez les autres Anthracothères. Ce caractère se retrouve chez deux espèces africaines, B. depereti (Fourtau) et B. aequatorialis MacInnes, rapportées généralement à Masritherium, genre créé par Fourtau (1920) en raison précisément de cette disposition originale de la dentition antérieure. Masritherium est donc un synonyme junior de Brachyodus* ». In the same paper the authors concluded that the enlarged tooth in the symphysis of *Brachyodus onoideus* is the *i/3*.

In their diagnosis of *Brachyodus depereti*, Miller et al. (2014) wrote « *i/1–i/2 absent, i/3 tusk-like, at least in males, p/1 occasionally absent* ». This diagnosis suggests that the small alveolus behind the caniniform *i/3* is for a reduced canine.

Thus, over the years, the enlarged tooth in the anterior corner of the mandibular symphysis of large brachyselenodont anthracotheres has been variably interpreted as an *i/2*, an *i/3* or a canine, and the tooth a short distance behind it has been inconsistently called the *i/3* or the canine or the *p/1*.

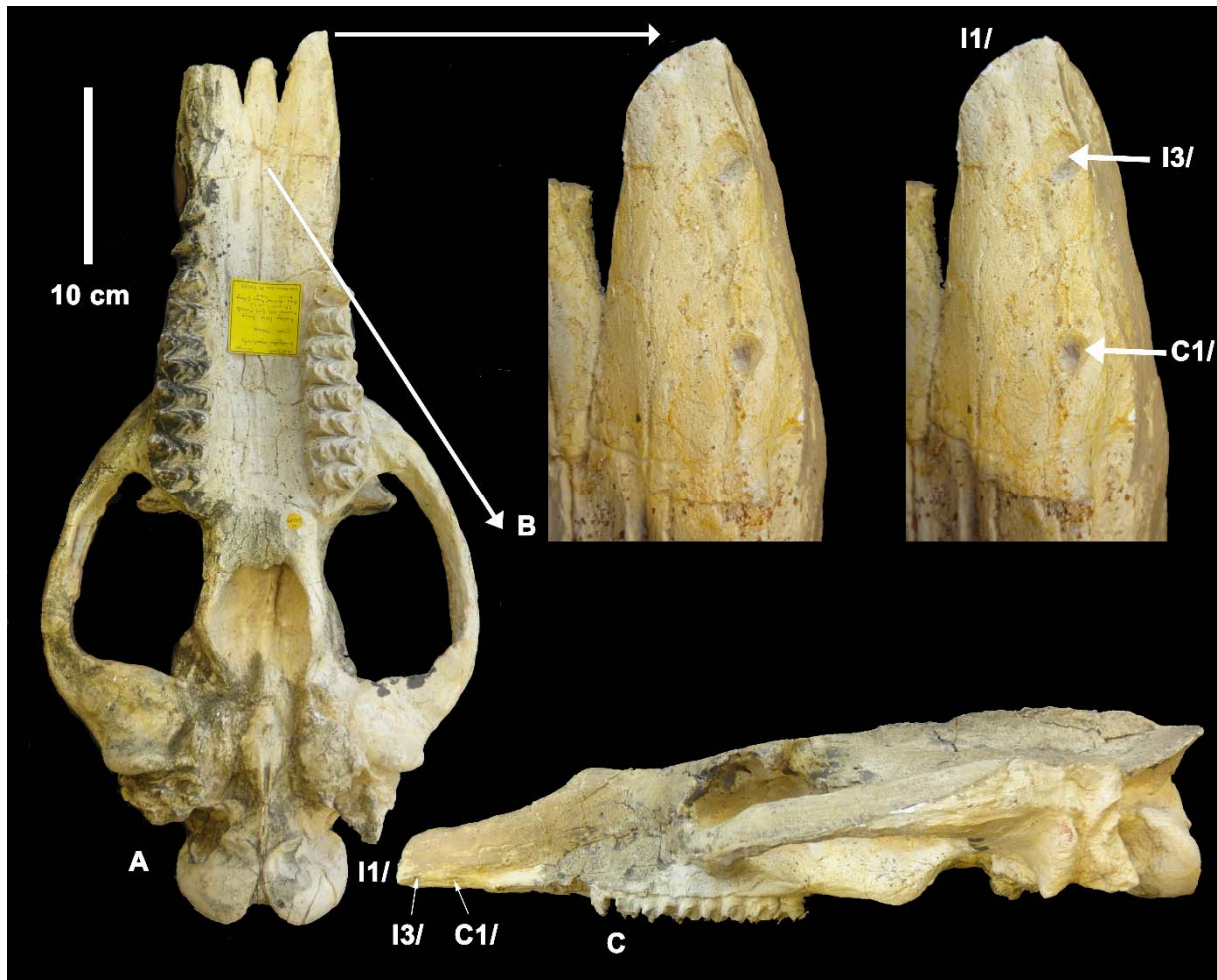
In summary, the majority of authors considers that the enlarged caniniform tooth in the corner of the symphysis in large brachyselenodont anthracotheres is the *i/3*, but the Briatexte specimen attributed by

Astre (1926) to *Brachyodus porcinus* (but generally included in the genus *Elomeryx*) indicates an alternative scenario - that the said tooth could be an *i*2. A better fossil record of symphyses of *Brachyodus* and *Masritherium* is required to settle the issue.

### Premaxilla

The discovery of the Napak anthracothere premaxillae prompts re-examination of the holotype skull of *Brachyodus aequatorialis* from Rusinga, Kenya (MacInnes, 1951).

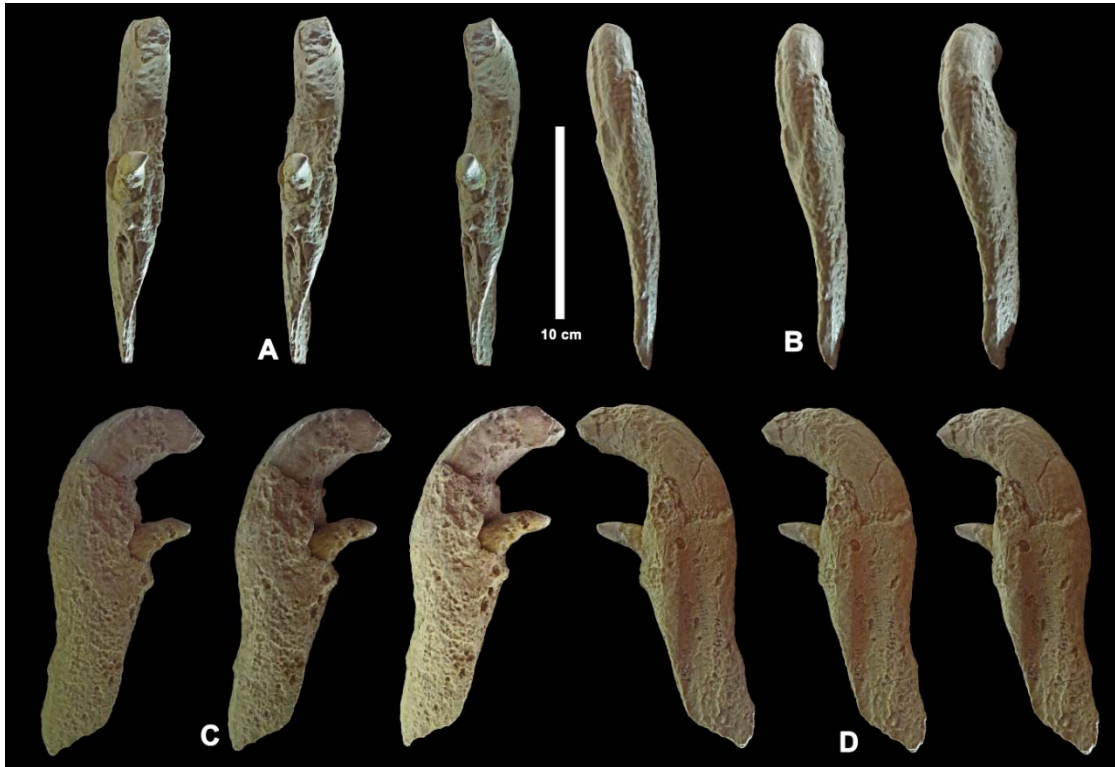
MacInnes (1951) wrote that, in the broken anterior part of the premaxilla of the holotype of *Brachyodus aequatorialis*, there were massive tooth cavities which he interpreted to represent large central upper incisors. Separated from these alveoli by a space estimated to be some 30 mm long, are alveoli which he took to belong to the I2/ and 30 mm behind these alveoli there is a second set of alveoli that he interpreted to belong to the upper canines. The premaxillo-maxillary suture is visible ventrally, so the identification of the upper canine alveoli is probably secure. However, the alveolus identified by MacInnes as that of the I2/ is in fact that of the I3/, that for the I2/ having broken away on both sides (Fig. 22).



**Figure 22.** NHMUK M 34389, cast of KNM RU 1009, the holotype of *Brachyodus aequatorialis* from the early Miocene of Rusinga, Kenya, highlighting the left premaxilla. The alveolus considered by MacInnes, 1951, to be for the I2/ is in fact that of the I3/ (scale of complete skull : 10 cm).

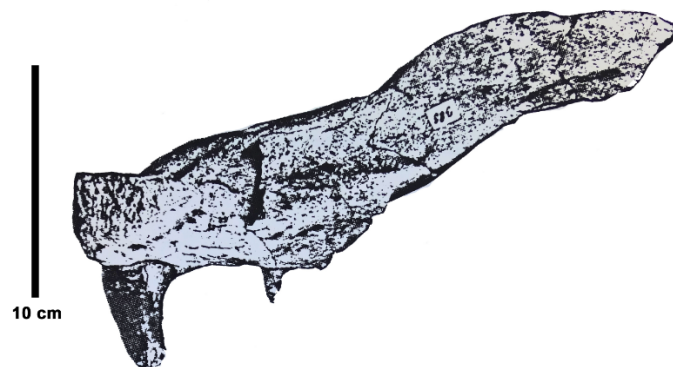
Comparison of the Ugandan premaxillae with specimens of *Brachyodus onoideus* from Chilleurs-aux-Bois and Neuville, France (Dineur, 1982) reveals that there are major differences between the two samples. Dineur (1982) remarked on the tendency for reduction of the quantity of incisors in the genus

*Brachyodus*. The two French specimens have only two incisors, probably the I1/ and I2/, although Dineur (1982) interpreted the second tooth as an I3/. In both specimens, the central upper incisor is large, indicating that they are likely to represent male individuals. In contrast, the only specimen from Africa complete enough to yield unequivocal information (Nap IX 40'99) reveals that there were three upper incisors in the premaxillae.



**Figure 23.** Stereo views of MNHN 2369, cast of right premaxilla of *Brachyodus onoideus* (original specimen in Musée d'Orléans) containing I1/ and I2/. A) occlusal view, B) dorsal view, C) labial view, D) lingual view (scale : 10 cm).

The premaxilla of *Brachyodus onoideus* is more gracile than that of the East African *Masritherium aequatorialis*, especially in its distal half, it does not have a dorsal groove and its ventral margin rises behind the I2/ (Figs 23 & 24). Lingually there is a ridge projecting towards the midline which is absent in the East African forms. These differences pose questions concerning the generic identity of the two samples.



**Figure 24.** MNHN Neu 89, right premaxilla of a male individual of *Brachyodus onoideus* from Neuville, France. Image modified from Dineur (1982, Plate II, Figure 1). Note the prominent buttress medial to the I1/ indicating that the two premaxillae probably met in the midline (scale : 10 cm).

In summary, the premaxilla of the large anthracothere from Napak shows that it possessed three incisors, whereas premaxillae of *Brachyodus onoideus* carry only two teeth. Furthermore the morphology of the African and European premaxillae differ significantly from each other, opening up the possibility that we are in the presence of more than one genus of large brachyselenodont anthracothere.

### Identification of deciduous cheek teeth

Some authors have experienced difficulties determining the correct meristic position of deciduous teeth of anthracotheres. Kowalevsky (1874, Plate XIII, fig. 78) correctly identified the D3/ and D4/ of *Brachyodus onoideus* (in the figure caption identified as *Anthracotherium* from the Sables de l'Orléanais). The D4/ of this taxon is fully molariform, as are the D4/s of artiodactyls in general. However, MacInnes (1951, plate 4, fig. 4) identified the teeth in a juvenile maxilla from Rusinga as the DM3/, DM4/ and M2/, but the teeth preserved in the specimen are the D2/, D3/ and M1/. MacInnes (1951) attributed the fossil to *Brachyodus* sp. indet. despite writing that the permanent molar resembles those in the holotype skull of *Masritherium aequatorialis*, both in morphology and dimensions. However, as an M1/, the tooth is rather larger than the corresponding teeth in the holotype (MDL x BLB - 33 x 34 mm in the juvenile specimen versus 30-31 x 30.5 mm in the holotype). Further study of this specimen is required.

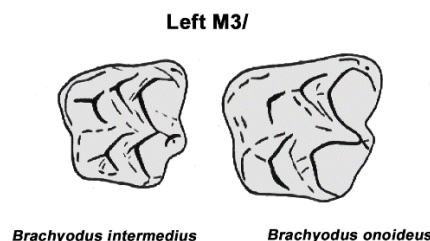
Pandolfi et al. (2016, fig. 21b) made a similar error when describing the skull of *Anthracochœrus stehlini* Dal Piaz, 1930 (1931) from Oligocene deposits at Monteviale, Italy (holotype MGP-PD 26554). The figure of the maxilla is captioned as containing the D3/ to M3/, but in fact the teeth preserved are the D2/-D4/ and M1/-M2/. These errors in the determination of the meristic positions of the teeth naturally affect down-line analyses, in particular any metric comparisons. This is one of the few specimens in which the upper and lower cheek teeth are preserved in articulated upper and lower jaws, so it is a particularly informative specimen.

Sallam et al. (2016) described important samples of deciduous dentitions of *Bothriogenys fraasi* from the Fayum, Egypt, in which the D4/ is observed to be completely molariform. It is interesting to note that the d/3 in this species is trilophid, whereas in most other anthracotheres it is bilophid.

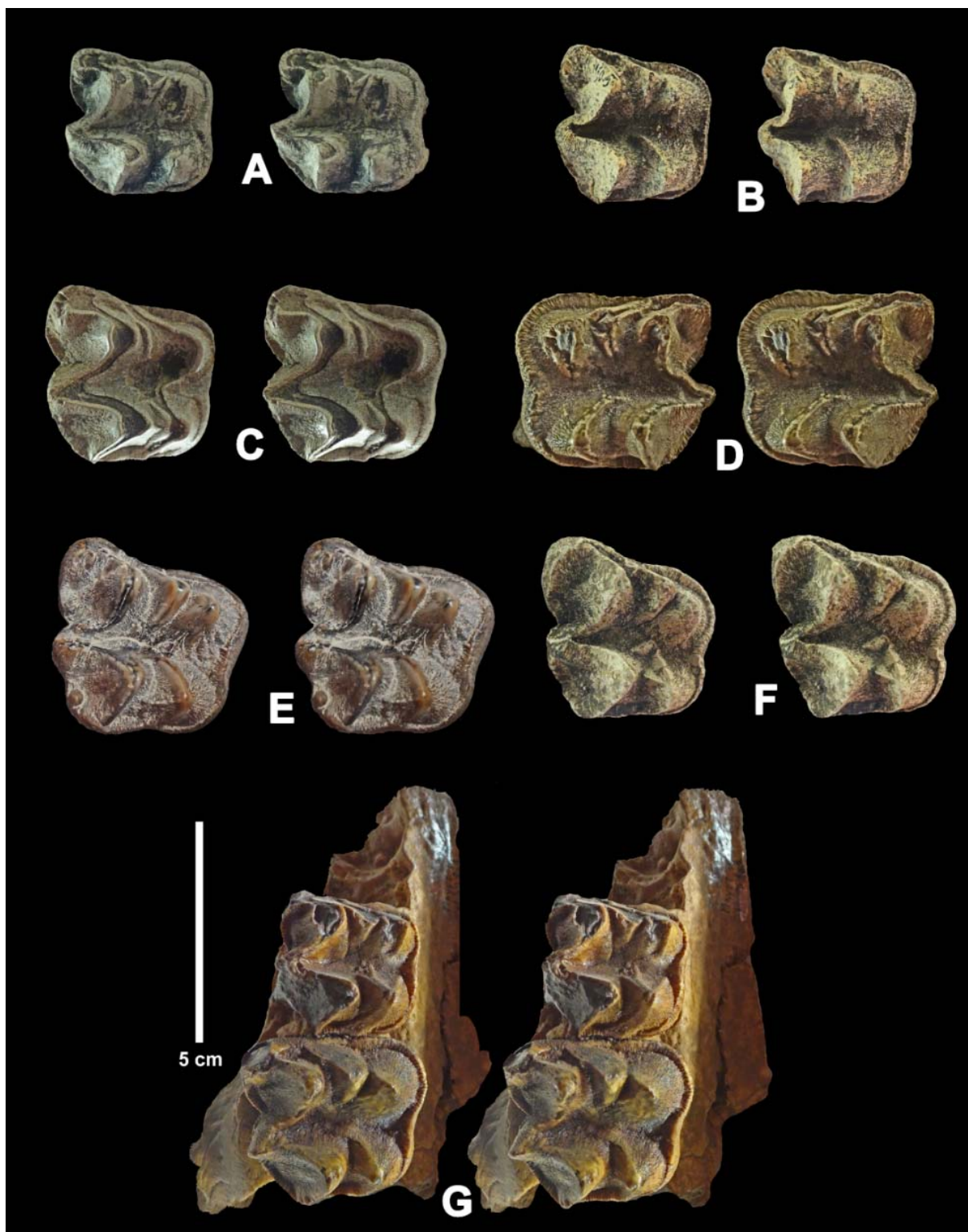
Whilst on the subject of the meristic position of teeth, it is worth pointing out that some researchers such as Kowalevsky (1874) Mayet (1908) and Stehlin (1910) counted the premolars from back to front. Thus the premolar next to the m/1 is called the p/1 by these authors, and the tooth at the front of the premolar row is called p/4, which is the opposite of the convention employed by most researchers in which the p/1 is the most anterior premolar, and the p/4 is the most posterior tooth in the premolar row.

### Diagnosis of *Brachyodus*

It has often been remarked that a distinguishing feature of *Brachyodus* is the « pinched-in » form of the mesostyle in the upper molars (Dineur, 1982; Dineur & Ginsburg, 1976). For Lihoreau & Ducrocq (2007) Holroyd et al. (2010) and Ducrocq et al. (2010) the « pinched » mesostyle was a diagnostic generic feature of *Brachyodus*.



**Figure 25.** Comparison between the upper third molars of *Brachyodus intermedius* and *Brachyodus onoideus* from France showing the « pinched » mesostyle (adapted from Dineur & Ginsburg, 1986).



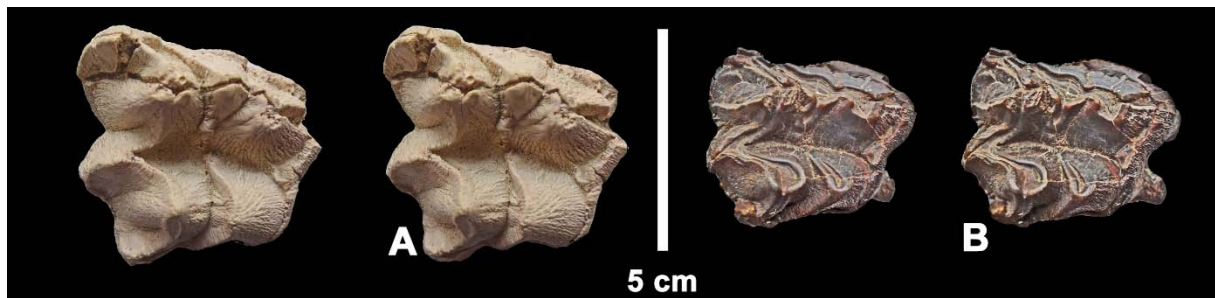
**Figure 26.** Stereo occlusal views of upper molars of *Brachyodus onoideus* from France, to show the variation in the morphology of the mesostyle. A) CH 175, right M1/, mesostyle pinched anteriorly, B) CH 171, right M1/, mesostyle rounded, C) CH 181, right M2/, mesostyle rounded D) Neu 83, left M2/, mesostyle pinched anteriorly, E) FS 1389, right M3/, mesostyle rounded and subdivided, F) CH 137, right M3/, mesostyle rounded, G) CH 304, right maxilla with M2/ and M3/, mesostyle rounded in M2/, pinched in M3/ (scale : 5 cm).



Dineur & Ginsburg (1986) recognised two species of *Brachyodus* in the early Miocene deposits of France - a relatively small species, *Brachyodus intermedius* and a larger species *Brachyodus onoideus* (Fig. 25). These taxa were reported to be time successive, with the smaller species being common in fluvial sands (Les Beilleaux, La Brosse, Pontigné - MN 3a) while the larger species is found in the faluns (Savigné etc – MN 3b and MN 4) (Gagnaison, 2013).

For Dineur & Ginsburg (1986) there were not only metric differences between the two assemblages of French early Miocene anthracotheres, but also some morphological differences. *Brachyodus intermedius* possessed a mesostyle in which the crests are disposed in a Y-shape and which join each other well inside the buccal margin of the tooth, it has weak development of the caniniform lower incisors, and a premaxilla that shows three alveoli (specimen from La Brosse). *Brachyodus onoideus*, in contrast had a V-shaped mesostyle, the mesial breadth of the m/2 is greater than, or equal to, the distal breadth of the tooth, it has lost the i/1 and I3/ and it has great development of the I1/ and i/3. Antunes & Ginsburg (2003) wrote that the « type » of *Brachyodus onoideus* was collected at Eggenburg, Austria, but this is not correct. The type specimen of the species is from Neuville-aux-Bois, France (Gervais, 1859).

Examination of anthracotheres from France reveal that the « pinched » mesostyle in the upper molars is far from being expressed in all the specimens (Fig. 26), most of them having a rounded or even bulbous buccal profile to the mesostyle. None of them possesses as clear a crest as expressed in the mesostyles of upper molars from Moghara (see for example Fourtau, 1920; Black, 1978) attributed to *Masritherium* by these authors but possibly belonging to *Jaggermeryx* Miller et al. (2014) (Fig. 27).

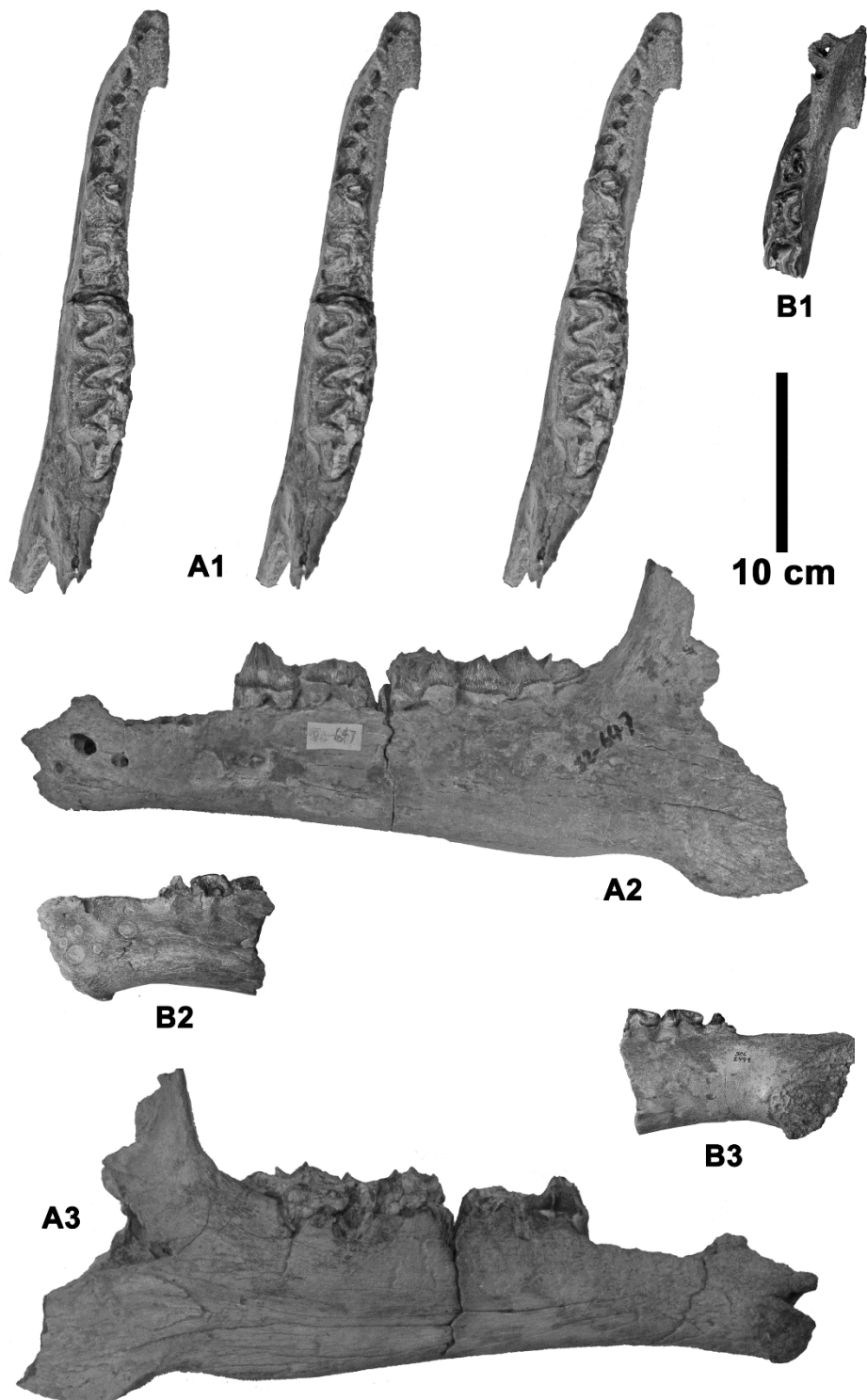


**Figure 27.** Stereo occlusal views of right upper molars with posteriorly pinched mesostyles from Moghara, Egypt. A) CGM 7210 attributed to *Masritherium depereti* by Fourtau (1920) (cast in NHMUK), B) CUWM 10, interpreted to be an M3/ of *Masritherium depereti* by Miller et al. (2014). Note the prominent posteriorly concave crest extending from the apex of the mesostyle towards cervix and thence distally towards a moderately sized metastyle (scale : 5 cm).

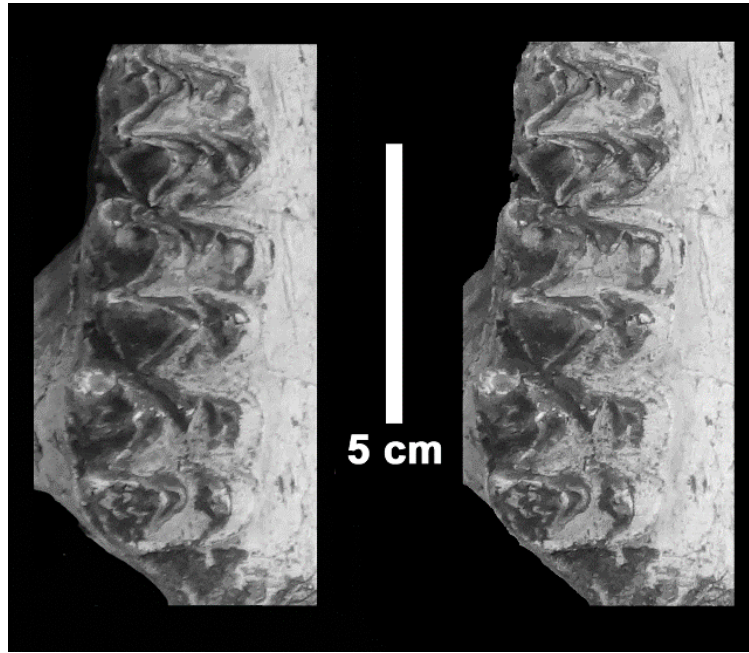
The early and middle Miocene strata at Moghara, Egypt, have yielded two taxa of very large anthracotheres, *Masritherium depereti* Fourtau, 1920, and *Jaggermeryx naida* Miller et al. 2014 (Fig. 27). Both of these taxa were defined on the basis of mandibles (incomplete in the case of *Jaggermeryx naida*) with very different symphyseal portions. Bivariate analyses of the third molars from Moghara indicate that on average specimens of *Jaggermeryx naida* are bigger than those of *Masritherium depereti*, but that there is significant overlap in dimensions. Traditionally, the large upper molars of anthracotheres from the region have been attributed to *Masritherium depereti* (Fourtau, 1920; Hamilton, 1973; Black, 1978; Miller et al. 2014) but the possibility exists that some of them could belong instead to *Jaggermeryx naida*. An almost complete unpublished mandible of *Jaggermeryx naida* in Cairo (CGM 82647, Fig. 28) retaining the p/4-m/3 has the largest m/3 known from the region (MDL x BLB : 65 x 37 mm versus 61.4 x 29.6 mm for the holotype of *Masritherium depereti*).

The anthracothere upper molar from Napak V differs from those of *Masritherium aequatorialis* MacInnes (1951) in a number of features (Fig. 29). The mesostyle of the Napak fossil is bulbous and extends well outside the buccal cervical margin of the tooth, whereas in the Rusinga molars, the mesostyle is pinched in posteriorly and the apex of the mesostyle is in a position well inside the buccal

cervical margin. The tooth from Napak is somewhat similar in this respect to fossils from Thailand attributed to *Brachyodus cf. onoideus* by Ducrocq et al. (2003) although the postparaconule cristule is longer in the Thai fossils than in the specimen from Uganda.



**Figure 28.** Mandibles of *Jaggermeryx naida* from Moghara, Egypt. A) CGM 82647, left ramus containing the p/4-m/3 and the alveoli of p1-p/3, B) DPC 2499, anterior half of holotype left mandible containing p/2-p/4. A1) stereo occlusal views, A2) buccal view, A3) lingual view, B1) occlusal view, B2) buccal view, B3) lingual view (images of DPC 2499 modified from Miller et al. 2014) (scale : 10 cm).



**Figure 29.** Stereo occlusal view of the upper right molars of the holotype of *Masritherium aequatorialis* from Rusinga, Kenya (KNM RU 1009) (cast in the NHMUK). Note the postparaconule cristule separating the posterior parts of the protocone and paracone and the posteriorly pinched mesostyle (scale : 5 cm).

There is no detailed similarity between the Napak anthracothere molar (Nap XV 63'07) (MDL x BLB - 24.2 x 28.6 mm) and a slightly smaller left M1/ or M2/ from supposedly late Oligocene deposits at Lokichar, Kenya (KNM LH 11642 : MDL x BLB - ca 19 x 20 mm) attributed to aff. *Bothriogenys* sp. by Ducrocq et al. (2010).

The m/3 in the mandible fragment from Wadi Sabya, Saudi Arabia (Madden et al. 1978) is too small (MDL - 43.7 mm) to belong to *Masritherium depereti* or to *Masritherium aequatorialis*. It falls within the range of metric variation of *Afromeryx africanus* and *Brachyodus mogharensis* from Moghara, Egypt (Pickford, 1991). On this basis, it is considered unlikely that there is a close relationship between the Wadi Sabya anthracothere and the one from Napak.

## CONCLUSIONS

Fossil anthracotheres have been known to occur at Napak, Uganda, since the early 1960's, but due to the fragmentary nature of the specimens, no anatomical descriptions of the fossils have been published. The material has usually been attributed to *Brachyodus aequatorialis* and biostratigraphic inferences have been made on the basis of this identification, but more complete specimens collected by the Uganda Palaeontology Expedition reveal that the fossils differ from the type specimen of the species from Rusinga, Kenya (MacInnes, 1951). The premaxilla from Napak has a small central incisor unlike the large central incisor in the Rusinga fossil, while the upper molar has a large bulbous mesostyle that extends well beyond the buccal border of the cervix, unlike the smaller more centrally positioned mesostyle in the Rusinga specimen, and in the Napak molar, the postprotoconule cristule stops well short of the median transverse valley, being blocked by the postprotocrista which extends buccally to the base of the paracone, again, unlike the Rusinga sample.

The question arises whether the Napak fossils represent a genus and species distinct from the Rusinga one, or whether the differences observed could be due to sexual dimorphism (small upper central incisor) or to ontogenetic variation within a single species as implied by previous attributions of the fossils to *Brachyodus aequatorialis* or to misidentification of the correct meristic position of the tooth (could the

upper molar from Napak V be a deciduous tooth rather than a permanent one). Two premaxillae from Napak V possess large alveoli for the upper central incisors, an observation that favours the hypothesis that the differences observed are related to sexual dimorphism. The D4/ of *Masritherium aequatorialis* has not been described (a specimen identified as such by MacInnes, 1951, is in fact a D3/) so it is not possible to make direct comparisons between the samples.

Comparisons of the Napak anthracotheres with fossils from Moghara, Egypt (Fourtau, 1920; Miller et al. 2014) and Bugti, Pakistan (Forster-Cooper, 1913, 1924; Pickford, 1987) reveal no special similarities between them. There is however a measure of similarity between one of the Napak fossils (upper molar) and some of the anthracothere specimens from the middle Miocene of Thailand (Ducrocq et al. 2003).

Until more informative fossils are found, the taxonomic status of the Napak anthracothere will remain enigmatic. Currently available specimens indicate the possibility of the existence of an undescribed taxon, but the sample is not informative enough to permit a secure diagnosis. For this reason, the fossils are left in open nomenclature, pending the recovery of diagnostic material. Suffice to report that a large species of anthracothere occurs at Napak in deposits aged ca 19-20.5 Ma and that previous attributions of the fossils to *Brachyodus aequatorialis* (or *Masritherium aequatorialis*) are not secure. As such the names should not be employed to support biostratigraphic arguments about correlations of the Napak volcano-sedimentary deposits.

#### ACKNOWLEDGEMENTS

Thanks to members of the Uganda Palaeontology Expedition which has been funded by the Ministry of Foreign Affairs (Commission des Fouilles archéologiques à l'Étranger), the Collège de France, the CNRS (CR2P, GDRI 193, PICS 1048), Sorbonne Université and the Muséum National d'Histoire Naturelle, Paris. The Uganda National Council for Science and Technology authorised research and the Uganda Museum (Mrs Rose Mwanja) issued excavation permits. Sarah Musalizi and Jack Ssebuyungu (Uganda Museum) are thanked for providing access to the fossils in their care. Brigitte Senut (MNHN), Loïc Ségalen (Sorbonne Université) and Dominique Gommery (CNRS) are thanked for their input and support. Thanks are extended to local leaders who facilitated access to the sites and to villagers in Iriiri who worked with us in the field - Bala John, Naduko Paul, Lomulen Julius, Maruk Robert, Korobe Philip, Nakee Betty, Nalem Sarah, Longoli Anna, Ilukol Celestina, Putan Rachel, Lomongin William, Lowanyang Madalena, Adiaka Madalena, Aleper Juliana, Sagal Peter, Iiko William, Lokee Lomokol and Loduk Paul.

I am also anxious to acknowledge the help of curators of the fossils examined during this study – Mohamed Abdel Gawad (Cairo University), Medhat Said Abdel Ghany, Afifi Said Hassan Sileem and Mohamed Magdi Gamil (CGM), Christine Argot and Guillaume Billet (MNHN), Pip Brewer, Spyridoula Pappa and Nadine Gilbert (NHMUK). I benefitted from e-mail correspondence with Ellen Miller (Wake Forest University).

#### REFERENCES

- Andrews, C.W. 1899 - Fossil Mammalia from Egypt. *The Geological Magazine*, New Series, Decade IV, **6**: 481-484.
- Andrews, C.W. 1914 - On the lower Miocene vertebrates from British East Africa, collected by Dr Felix Oswald. *Quarterly Journal of the Geological Society of London*, **70**: 163-186.
- Antunes, M. & Ginsburg, L. 2003 - The last Anthracothere *Brachyodus onoideus* (Mammalia, Artiodactyla) from westernmost Europe and its extinction. *Ciências da Terra*, **15**: 161-172.
- Arambourg, C. 1933 - Mammifères miocènes du Turkana, Afrique orientale. *Annales de Paléontologie*, **22**: 121-148.
- Astre, G. 1926 - Le *Brachyodus porcinus* de Briatexte et les caractères de la mandibule des petits *Brachyodus* oligocènes. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **44**: 337-344.

- Black, C.C. 1978 - Anthracotheriidae. In: Maglio, V.J. & Cooke, H.B.S. (Eds), *Evolution of African Mammals*. Harvard University Press, Cambridge, pp 423-434.
- Blainville, H.M.D. de, 1847 - Ostéographie ou Description iconographique comparée du Squelette et du Système dentaire des Mammifères Récents et fossiles pour servir de base à la Zoologie et à la Géologie, volume 4, Quaternatès-Maldentés, AA, Ongulogrades, G. *Hippopotamus*. Paris, pp. 1-104 and 233-245. Atlas, volume 4, plates I-VIII.
- Boisserie, J.R., Lihoreau, F., Orliac, M., Fisher, R.E., Weston, M. & Ducrocq, S. 2010 - Morphology and phylogenetic relationships of the earliest known hippopotamids (Cetartiodactyla, Hippopotamidae, Kenyapotaminae). *Zoological Journal of the Linnean Society*, **158**: 325-366.
- Cabard, P., Huin, J. & Locher, J.P. 1980 - Le *Brachyodus onoideus* (Gervais) 1869 (Mammalia, Anthracotheriidae) des Beilleaux, Savigné-sur-Lathan (Indre et Loire). *Bulletin de l'Association des naturalistes Orléanais*, Série III, **32**: 11-17.
- Chow, M.C. 1958 - Some Oligocene mammals from Lunan, Yunnan. *Vertebrata Palasiatica*, **2** (4): 263-268.
- Coombs, W.P. & Coombs, M.C. 1977 - The origin of Anthracotheres. *Neues Jahrbuch der Geologie und Paläontologie Monatshefte*, **1977** (10): 584-599.
- Dal Piaz, G.B. 1930 - Nuovo genere e nuova specie di artiodattili dell'Oligocene veneto. *Rendiconti della Reale Accademia Nazionale dei Lincei, Classe di Scienze Fisiche Matematiche e Naturali*, Serie 6, **12**: 61-64.
- Dal Piaz, G.B. 1931 - I mammiferi dell'Oligocene Veneto. *Anthracochœrus* n. g., *A. stehlini* n. sp. *A. fabianii* n. sp. *Memorie del Regio Istituto Geologico dell'Università di Padova*, **9**: 1-36.
- Depéret, C. 1895 - Über die Fauna von miocänen Wirbelthieren aus der ersten Mediterranstufe von Eggenburg. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch - Naturwissenschaftliche Klasse. Abteilung 1, Mineralogie, Biologie, Erdkunde*, **104** (4): 395-416.
- Dineur, H. 1982 (sometimes cited as 1981) - Le genre *Brachyodus*, Anthracotheriidae (Artiodactyla, Mammalia) du Miocène inférieur d'Europe et d'Afrique. *Mémoires des Sciences de la Terre, Université Paris VI*. Thèse 3ème Cycle.
- Dineur, H. & Ginsburg, L. 1986 - Les variations de taille chez *Brachyodus* (Mammalia, Artiodactyla, Anthracotheriidae) dans le bassin miocène de la Loire: implications systématiques et stratigraphiques. *Comptes Rendus de l'Académie des Science, Paris*, **303**, série II, (7): 633-636.
- Ducrocq, S., Boisserie, J.-R., Tiercelin, J.-J., Delmer, C., Garcia, G., Manthi, F.K., Leakey M.G., Marivaux, L., Otero, O., Peigné, S., Tassy, P. & Lihoreau, F. 2010 - New Oligocene vertebrate localities from Northern Kenya (Turkana Basin). *Journal of Vertebrate Paleontology*, **30** (1): 293-299.
- Ducrocq, S., Chaimanee, Y., Suteethorn, V. & Jaeger, J.-J. 2003 - Occurrence of the anthracotheriid *Brachyodus* (Artiodactyla, Mammalia) in the early Middle Miocene of Thailand. *Comptes Rendus Palevol*, **2**: 261-268.
- Forster-Cooper, C. 1913 - New Anthracotheriidae and allied forms from Baluchistan - Preliminary Notice. *Annals and Magazine of Natural History*, Series 8, **12**: 514-522.
- Forster-Cooper, C. 1924 - The Anthracotheriidae of the Dera Bugti deposits in Baluchistan. *Palaeontologia Indica*, (n.s.) **8** (2): 1-60.
- Fourtau, R. 1920 - Contributions à l'étude des vertébrés miocènes de l'Égypte. *Geological Survey of Egypt*, pp. i-vii+1-121.
- Gagnaison, C. 2013 - Les assemblages de vertébrés dans deux sites paléontologiques du bassin miocène de Savigné-sur-Lathan/Noyant-sous-le-Lude : La Guimardière et Pelmer (Maine-et-Loire, France). *Geodiversitas*, **35** (1): 67-103.
- Gervais, P. 1859 - *Zoologie et Paléontologie Françaises : animaux vertébrés, ou nouvelles recherches sur les animaux vivants et fossiles de la France*. Ed. Arthus Bertrand, Paris, 544 pp.
- Hamilton, W.R. 1973 - A lower Miocene mammalian fauna from Siwa, Egypt. *Palaeontology*, **16**: 275-281.
- Holroyd, P., Lihoreau, F., Gunnell, G. & Miller, E. 2010 - Anthracotheriidae. In: Werdelin, L. & Sanders, W. (Eds) *Cenozoic Mammals of Africa*. University of California Press, Berkeley, Los Angeles, London, pp. 843-851.
- Hooijer, D.A. 1963 - Miocene Mammalia of Congo. *Annales du Muséum Royale du Congo belge*, Series 8, **46**: 1-77.

- Hooijer, D.A. 1968 - Evidence for a pentadactyl manus in *Brachyodus aequatorialis* MacInnes from the East African Miocene. *Koninklijke Nederlandse Akademie van Wetenschappen*, **B71**: 91-97.
- Kowalevsky, W. 1874 - Monographie der Gattung *Anthracotherium* Cuv. und Versuch einer natürlich Classification der fossilen Hufthiere. *Palaeontographica*, **22**: 133-346.
- Lihoreau, F. & Ducrocq, S. 2007 - Family Anthracotheriidae: Systematics and Evolution. In: Prothero, D. & Foss, S. (Eds) *The Evolution of Artiodactyls*. Johns Hopkins University Press, Baltimore. pp. 89-105.
- Macdonald, J.R. 1956 - The North American Anthracotheres. *Journal of Paleontology*, **30** (3): 615-645.
- MacInnes, D.G. 1951 - Miocene Anthracotheriidae from East Africa. *Fossil Mammals of Africa*, **4**: 1-24.
- Madden, C.T., Schmidt, D.L. & Whitmore, F.C. 1978 - *Masritherium* (Artiodactyla, Anthracotheriidae) from Wadi Sabya, southwestern Saudi Arabia : an earliest Miocene age for the continental rift valley volcanic deposits of the Red Sea margin. *Open File Rept. USGS*, **1978**: 1-26.
- Mayet, L. 1908 - Etude des Mammifères miocènes des sables de l'Orléanais et des faluns de la Touraine. *Annales l'Université Lyon, Nouvelle série, I, Sciences, Médecine*, **24**: 1-336.
- Miller, E.R., Gunnell, G.F., Abdel Gawad, M., El-Barkooky, A.M., Clementz, M. & Hassan, S.M. 2014 - Anthracotheres from Wadi Moghra, early Miocene, Egypt. *Journal of Paleontology*, **88** (5): 967-981.
- Musalizi, S., Senut, B., Pickford, M. & Musiime, E. 2009 - Geological and palaeontological archives relating to Early Miocene localities of Uganda, 1957-1969. *Geo-Pal Uganda*, **1**: 2-96.
- Pandolfi, L., Carnevale, G., Costeur, L., Del Favero, L., Fornasiero, M., Ghezzi, E., Maiorino, L., Mietto, P., Piras, P., Rook, L., Sansalone, G. & Kotsakis, T. 2017 - Reassessing the earliest Oligocene vertebrate assemblage of Monteviale (Vicenza, Italy). *Journal of Systematic Palaeontology*, **15** (2): 83-127.
- Pickford, M. 1981 - Preliminary Miocene Mammalian biostratigraphy for Western Kenya. *Journal of Human Evolution*, **10**: 73-97.
- Pickford, M. 1987 - Revision des Suiformes (Artiodactyla: Mammalia) de Bugti (Pakistan). *Annales de Paléontologie*, **73**: 289-350.
- Pickford, M. 1991 - Late Miocene anthracothere (Mammalia, Artiodactyla) from tropical Africa. *Comptes Rendus de l'Académie des Sciences, Paris*, **313**: 709-715.
- Pickford, M. 1994 - Anthracotheriidae from the Albertine Rift Valley. In: Senut, B. & Pickford, M. (Eds). *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire*. Vol. 2: Palaeobiology-Paléobiologie. *Occasional Publication CIFEG*, **29**: 309-319.
- Pickford, M. 2003 - New Proboscidea from the Miocene strata of the lower Orange River Valley, Namibia. *Memoir of the Geological Survey of Namibia*, **19**: 207-256.
- Pickford, M. 2004 - Palaeoenvironmental reconstruction of Early Miocene hominoid-bearing deposits at Napak, Uganda, based on terrestrial molluscs. *Annales de Paléontologie*, **90**: 1-12.
- Pickford, M. 2006 - Sexual and individual morphometric variation in *Libycosaurus* (Mammalia, Anthracotheriidae) from the Maghreb and Libya. *Geobios*, **39**: 267-310.
- Pickford, M. 2017 - Bukwa II Suiformes, *Geo-Pal Uganda*, **11**: 71-79.
- Pickford, M. & Mein, P. 2006 - Early Middle Miocene Mammals from Moroto II, Uganda. *Beiträge zur Paläontologie*, **30**: 361-386, Wien.
- Pickford, M., Musalizi, S., Senut, B., Gommery, D. & Musiime, E. 2010 - Small Apes from the Early Miocene of Napak, Uganda. *Geo-Pal Uganda*, **3**: 1-111.
- Pickford, M., Senut, B., Musalizi, S. & Musiime, E. 2013 - The osteology of *Nonanomalurus soniae*, a non-volant arboreal rodent (Mammalia) from the Early Miocene of Napak, Uganda. *Geo-Pal Uganda*, **7**: 1-33.
- Pickford, M., Senut, B., Musalizi, S., Gommery, D. & Ssebuyungu, C. 2019 - Early Miocene Victoriapithecoid Monkey from Napak, Uganda. *Geo-Pal Uganda*, **12**: 1-17.
- Roman, F. 1907 - Le Néogène continental dans la Basse Vallée du Tage (Rive Droite). Deuxième Partie : Mammifères Terrestres. *Commission du Service Géologique du Portugal*. Lisbonne, pp. 41-74, Pls II-V.
- Roman, F. & Boucher, J. 1936 - Les Mammifères stampiens du Bassin de Roanne (Loire) I.-*Anthracoherium bumbachense*. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon, Mémoire*, **24**: 1-40.

- Sallam, H.M., Sileem, A.H., Miller, E.R. & Gunnell, G.F. 2016 - Deciduous dentition and dental eruption sequence of *Bothriogenys fraasi* (Anthracotheriidae, Artiodactyla) from the Fayum Depression, Egypt. *Palaeontologia Electronica*, **19.3.38A**: 1-17.
- Sileem A.H., Sallam, H.M., Hewaidy, A.G.A., Miller, E.R. & Gunnell, G.F. 2016 - A new anthracothere (Artiodactyla) from the early Oligocene, Fayum, Egypt, and the mystery of African 'Rhagatherium' solved. *Journal of Paleontology*, **90** (1): 170-181.
- Stehlin, H.G. 1910 - Zur Revision der europäischen Anthracotherien. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, **21**: 165-185.
- Tobien, H. 1973 - On the evolution of the mastodonts (Proboscidea, Mammalia) Part I : the bunodont trilophodont groups. *Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden*, **101**: 202-276.
- Xu Yu-xuan, 1962 - Some new anthracotheres from Shansi and Yunnan. *Vertebrata Palasiatica*, **6** (3): 232-250.

# **GEO-PAL UGANDA**

## **Editorial Board**

### **Editor-in-Chief**

Sarah Musalizi, Uganda Museum, Kampala

### **Associate Editors**

Brigitte Senut, Muséum National d'Histoire Naturelle, Paris  
Martin Pickford, Muséum National d'Histoire Naturelle, Paris  
Rose Mwanja, Uganda Museum, Kampala  
Jorge Morales, Museo Nacional de Ciencias Naturales, Madrid  
Israel Sanchez, Museo Nacional de Ciencias Naturales, Madrid  
Yoshihiro Sawada, Kurashiki, Okayama Prefecture

### **Web Site Maintenance**

Nelson Abiti, Uganda Museum, Kampala



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