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Reassessment of the generic attribution of *Numidotherium savagei* and the homologies of lower incisors in proboscideans

CYRILLE DELMER

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Near the end of the twentieth century, a medium-sized early proboscidean found in Dor El Talha (late Eocene to early Oligocene), Libya, originally identified as a small species of *Barytherium*, was described as a new species of *Numidotherium* and designated *Numidotherium savagei*. Poorly known, this taxon has been excluded from most of the recent debate about the origin and diversification of the order Proboscidea. New specimens described herein show strong structural similarities of the upper teeth with those of bunolophodont early proboscideans (e.g., *Moeritherium* and *Phiomia*) and document the shared presence of derived traits in the postcranial skeleton. The newly referred material also demonstrates some unique characteristics of this taxon, notably in its mandibular morphology and the microstructure of its dental enamel. Included for the first time in a cladistic analysis (207 anatomical characters applied to all early tethytheres), *N. savagei* is distinct from both *Numidotherium* and *Barytherium,* and lies in an "intermediate" position between the strictly lophodont Eocene proboscideans and the bunolophodont moeritheres and elephantiforms. Accordingly, the species is herein referred to a new genus, *Arcanotherium*. New data on its mandibular symphysis and, especially, on its lower incisors loci and morphology, bring new support to a hypothesis of homology between the lower incisors of early proboscideans and the ever-growing lower tusks of the elephantiforms, which are identified here as di1 and i1.

Key words: Proboscidea, *Numidotherium*, *Barytherium*, Elephantiformes, phylogeny, Palaeogene, Libya.

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Introduction

First mentioned in the 1950s (Bellair et al. 1954), the fossil vertebrates in the Dor El Talha escarpment in Libya were investigated throughout the 1960s by two scientific teams: a French expedition, led by Philippe Magnier, explored the area in 1960 (Arambourg and Magnier 1961) and was shortly followed in 1968 and 1969 by a British team led by Professor Robert J.G. Savage (see Savage 1969). Both unearthed numerous fossil remains from a rich terrestrial and marine fauna, which were brought back to the museums in Paris and Bristol respectively. The estimated late Eocene/early Oligocene age of this fauna (Arambourg and Magnier 1961; Savage 1969; Wight 1980), together with the presence of numerous terrestrial mammals, make Dor El Talha among the richest Palaeogene mammal localities in Africa. This fauna shows a generic composition similar to that of the Fayûm in Egypt, estimated to be of similar age (Said 1962, 1990; Simons 1968; Vondra 1974; Bown et al. 1982; Fleagle et al. 1986; Bown and Kraus 1988; Gingerich 1992; Rasmussen et al. 2008; Seiffert et al. 2008). This similarity remains one of the main arguments supporting contemporaneity of the two assemblages (Wight 1980; Court 1995).

One of the major differences between the Dor El Talha and Fayûm faunas lies in the abundance of the early proboscidean genus *Barytherium* at the former. The recovery of a few weathered remains of an old individual at the beginning of the twentieth century in the Qasr El Sagha Formation of the Fayûm led to the description of its type species, *B. grave* Andrews, 1901. Very few discoveries (consisting of isolated remains only) referable to the genus have been reported in the region since (Harris 1978; Holroyd et al. 1996), though many new specimens have been recovered from the Birket Qarun Formation in recent years (Seiffert 2007; Liu et al. 2008; Seiffert et al. 2008). In contrast, hundreds of cranial, dental and postcranial elements referable to *Barytherium*, including a partial skeleton, were discovered at Dor El Talha (Savage 1969). Among these remains, a few smaller specimens were identified initially as a smaller species of *Barytherium*, usually referred to as *Barytherium* sp. (Savage 1969; Harris 1978; Savage and Court 1989; Shoshani et al. 1989). However, the discovery of *Numidotherium koholense* Mahboubi, Ameur, Crochet, and Jaeger, 1986 in Algeria, then the oldest representative of the Proboscidea, shed new light on the emergence and diversification of the order. Its primitive cranial and postcranial anatomy, associated with a strictly lophodont dentition, was the first key that led later to the reconsideration of the ancestral morphotype of the order

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(Gheerbrant et al. 1996, 2002, 2005a; Delmer 2005a), as well as the generic attribution for the small Libyan barythere. Thus, Court (1995), in his study of the available specimens referred previously to *Barytherium* sp. in the Dor El Talha collection at Bristol, emphasised their resemblance with *N. koholense* and concluded, on the grounds of dental, mandibular and postcranial similarities, that this taxon should be referred to the genus *Numidotherium*. He therefore created a new species that was named for R.J.G. Savage, *Numidotherium savagei* Court, 1995. Although Court included in his paper a cladistic analysis of all early proboscideans known at that time, he did not use it to test his attribution of *N. savagei* to the genus *Numidotherium* by including it in the matrix.

Since the description of *N. savagei*, knowledge of stem proboscideans has been greatly increased by the description of three new very primitive taxa: *Phosphatherium escuilliei* Gheerbrant, Sudre, and Capetta, 1996, *Daouitherium rebouli* Gheerbrant and Sudre, 2002, and *Moeritherium chehbeurameuri* Delmer, Mahboubi, Tabuce, and Tassy 2006. The first two are among the oldest and most primitive proboscideans known, and all three support the hypothesis of a strictly lophodont primitive dental state for the order Proboscidea (Gheerbrant et al. 1996, 2002; Delmer et al. 2006). This has led to the re-evaluation of the hypotheses on evolution and phylogenetic relationships among early proboscideans as well as the phylogenetic relationships of the order itself. At the same time, *Barytherium* collections from Dor El Talha became fully accessible and resulted in a revision of the available data on the emergence of the proboscideans (Delmer 2005a). Within these unpublished collections, a few specimens referable to Court's species *N. savagei* were identified, and their characteristics lead here not only to a re-evaluation of the systematic status of this taxon, but also to a reconsideration of the evidence for homology of the ever-growing lower tusks of the elephantiforms and the lower incisors of early proboscideans.

Institutional abbreviations.—BMNH, Natural History Museum, London, UK; CGM, Cairo Geological Museum, Cairo, Egypt; CH, Chilga specimens housed in the National Museums of Ethiopia, Addis Ababa, Ethiopia; MNHN, Muséum National d'Histoire Naturelle, Paris, France: LBE, Tertiary Egyptian/Libyan specimens at the MNHN; UO, Earth Sciences Institute, Oran University, Oran, Algeria: UO-K for the El Kohol locality.

Other abbreviations.—CI, consistency index; L., length; RI, retention index.

Material and methods

Material examined.—The specimens studied and described by Court (1995) were part of the vast collection of fossil mammals brought back from Dor El Talha to Bristol by Professor Robert J.G. Savage in 1968 and 1969. These specimens are held today within the collections of the BMNH, together with the rest of the early proboscidean material collected at Dor El Talha. All the newly referred specimens discussed in this paper were found incorrectly identified and/or isolated in BMNH collection, with the exception of two (MNHN LBE 20, MNHN LBE 30) which were identified in Magnier's collection held at MNHN. Some previously undescribed material (anterior elements of the holotype BMNH 6821/10) was found to belong to the same individual as those described by Court (1995).

Remark concerning the collection numbers of the specimens held within the collections of BMNH.—Court (1995) published the specimens, found in Dor El Talha and referred to *N. savagei*, without official catalogue numbers from the BMNH, instead using their field numbers. Mistakes were made in some cases, some field numbers having either been misread or attributed to the wrong specimen (personal observation; see list of referred specimens). These specimens have now been given formal catalogue numbers, which are used in this paper. Moreover, following the International Commission on Zoological Nomenclature (1999: article 72), the specimens referred to *Numidotherium savagei* in the original description (Court 1995), including the new elements of the holotype mandible, are identified here as paratypes.

Enamel analysis.—In order to check their identification, the enamel microstructure of the upper teeth referred to *Arcanotherium savagei* in this paper was analysed. This was carried out following the same protocol that Tabuce et al. (2007) used when they investigated the microstructure of the enamel of the lower teeth of *N. savagei* described by Court (1995). Without reducing the gross morphological information content, the enamel fragments were, when available, removed from an identified part of the tooth and their positions recorded. Enamel fragments were embedded in polyester resin and sectioned vertically, horizontally, or tangentially. The samples were then ground and polished with frequent checking under a binocular microscope. Surfaces of original fractures and natural wear facets were investigated when the material was too rare to be sectioned. After slight etching for 30 seconds with 37% phosphoric acid (to make morphological details visible), the specimens were successively rinsed with 10% ammonia and distilled water. After air drying, samples were sputter-coated with platinum and examined under a JEOL® scanning electron microscope at magnifications between ×15 and ×4000. A binocular microscope under tangential light (Boyde 1976; Koenigswald and Pfretzschner 1987) was used to improve the observations in detecting Hunter-Schreger bands (HSB).

The dental nomenclature used in this paper is that of Tassy (1996). The Latin anatomical nomenclature used is from the Nomina Anatomica Veterinaria (Fifth Edition).

Systematic palaeontology

Mirorder Tethytheria McKenna, 1975

Order Proboscidea Illiger, 1811

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Family indet.

Genus *Arcanotherium* nov.

Type species: *Arcanotherium savagei* (Court, 1995).

Etymology: the genus name is derived from the Latin word *arcanus* for secret, enigmatic, hidden.

Diagnosis.—As for the type and only species.

Stratigraphic and geographic range.—Evaporite and Idam Units (late Eocene/early Oligocene) of Dor El Talha, Libya.

Arcanotherium savagei (Court, 1995)

Figs. 1–5.

1995 *Numidotherium savagei* sp. nov.; Court 1995: 651, figs. 2–7.

Type material: Holotype: BMNH M. 82163a (field no. 6821/10), partial right mandibular ramus with p2–m3. Paratypes: BMNH M. 82163b, partial left mandibular ramus with eroded m2–m3, undoubtedly from the same individual as the holotype (field no. 6821/?, listed by Court (1995) as m1–m2); BMNH M. 82167, left and right lower mesial incisors associated with holotype (field no. 6821/11); BMNH M. 82165, associated lower dentition comprising right p2–m2 and left p3–m3 (field no. 686/2); BMNH M. 82168, isolated left m3 (field no. 684/21, listed as 6821/21 by Court (1995); this is surely incorrect, as there are no more than 15 field numbers allocated to proboscideans from locality 6821); BMNH M. 82174, left scapular glenoid (field no. 6821/1); BMNH M. 82175, left ulna (field no. 6821/3); BMNH M. 82179, this specimen does not display any number), right cuneiform (field no. 6821/?, listed as 6821/9 by Court (1995)); BMNH M. 82180, right lunar (field no. 6821/8); BMNH M. 82177a–b, associated left and right femoral fragments (field nos. 6821/7–8); BMNH M. 82170, isolated left m2 talonid (field no. 684/11; listed by Court (1995) as 684/25; no specimen bearing this number is present in the collection, but 684/11 fits the description); BMNH M. 82169, right m3 (field no. 6955/1, mentioned by Court (1995) as a talonid of m3; this specimen is now complete, the missing protolophid having been found since in the collection); BMNH M. 82173, fragmentary atlas vertebra (field no. 6821/2); BMNH M. 82181, ?metacarpal (field no. 6821/ 1); BMNH M. 82182, ?metapodial (field no. 6821/14).

Type locality: Dor El Talha, Libya.

Type horizon: Idam Unit, early Oligocene.

Other referred specimens.—BMNH M. 82164, mandibular symphysis (field no. 686/2); BMNH M. 82166, right mandibular ramus with erupting p4 and m2, and numerous associated fragments of mandible and skull (field no. 686/8); BMNH M. 82183, partial symphysis with erupting mesial incisor (field no. 696/9); BMNH M. 82398, right M2 (field no. 686/2); BMNH M. 82171, lophid of indeterminate lower molar (field no. 684/32); BMNH M. 82172, right M1 (field no. 6816/3); MNHN LBE 20, left M1; MNHN LBE 30, fragmented upper molar; BMNH M. 82176, left ulna (field no. 6816/4); BMNH M. 82178, partial tibia (field no. 6821/4).

Emended diagnosis (modified from Court 1995).—Medium-sized proboscidean, intermediate in size between *Numidotherium koholense* and *Barytherium grave*. Mandible with a symphysis extending posteriorly to the level of p2 and an ascending ramus rising at the level of the junction between m2 and m3. Dental formula I?/i2 C?/c0 P?/p3 M3/m3; i_1 and i2 roots of similar size, those of i2 growing deeper in the symphysis; i1 mesio-lingually flattened, with distal edge crenulated buccally when unworn. Lophodont cheek dentition. Premolars more molarised than those of the early (non-elephantiform) proboscidean taxa *Phosphatherium*, *Daouitherium*, *Numidotherium*, *Barytherium*, and *Moeritherium*, with a metaconid distinguishable on p2 and strongly developed lingual to the protoconid on p3. Upper molars with a small paraconule, mesial to the protoloph, and massive mesial and lingual cingula.

Overall, the cheek dentition of *Arcanotherium savagei* is less lophodont than those of *Barytherium* and *Numidotherium*, with tips of cusps distinguishable and slightly elevated above the lophs. The scapula displays a tuberculum supraglenoidale which is smaller than that of *B. grave* and which lacks the distinct medially deflected coracoid process of *N. koholense*. The ulna of *A. savagei* shows a distinct lateral articular facet for the capitulum of the humerus, which is incipient in *Barytherium* and *N. koholense*, and a strong widening of its distal epiphysis. The lunate is wider anteriorly than posteriorly, with a small contact for the ulna. The cuneiform carpal is more rectangular than that of *N. koholense*, with a contact facet for the pisiform larger than that of deinotheres and elephantiforms.

Description

Since Court (1995) adequately described the specimens of this taxon available to him, with the exception of the metapodials BMNH M. 82181 and BMNH M. 82182 and of the atlas BMNH M. 82173, the following description includes only details of the latter and additional data obtained from the specimens referred herein.

Mandible (Fig. 1).—Court (1995) based the species *Arcanotherium savagei* on the holotype for the species, BMNH M. 82163a, and a contralateral part of the same jaw, which consisted of right and left posterior halves of the mandibular horizontal rami from a single individual, bearing right p4–m3 and left m3, with isolated but associated right p2–p3. Among the specimens from the same locality, the anterior portion of this mandible (BMNH M. 82163c), a badly damaged symphysis and the anterior portion of the left mandibular ramus, has been recovered, together with an isolated left p2 and the mesial incisors. The symphyseal elements were originally identified and labelled as *Moeritherium*. Although no definite contact between these elements and the holotype can be found, their colour, size and preservation show undoubtedly that they belong to the same individual (Fig. 1A). This now almost complete mandible reveals some important characters and allows a reconstruction (Fig. 1B). The mandibular symphysis of *A. savagei* is massive yet short like *Barytherium* (Delmer 2005a), extending posteriorly to the level of p2. It bears two pairs of incisors, identified as i1 and i2, with roots of similar width, those of the i2s growing deeper than those of the i1s. Such an arrangement suggests that the two lower incisors of this taxon are of similar size.

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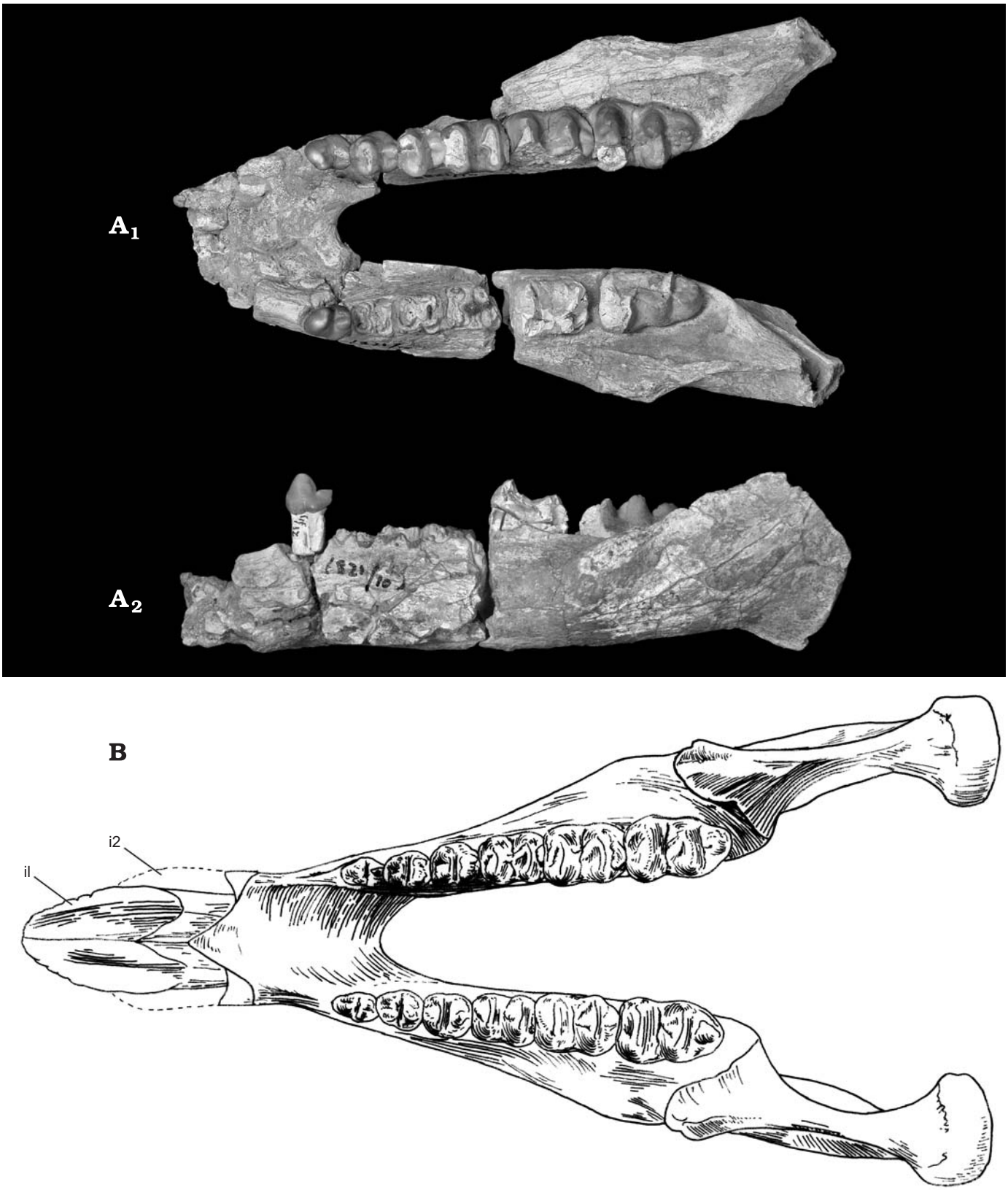


Fig. 1. Holotype mandible (BMNH M. 82163a, b, c) of the proboscidean *Arcanotherium savagei* (Court, 1995), from the Idam Unit (early Oligocene) of Dor El Talha, Libya in occlusal (**A**), lateral (**B**), reconstructed occlusal (**C**) views.

Another mandibular symphysis (BMNH M. 82164) found in the Dor El Talha collection in London was originally labelled as *Moeritherium* (Fig. 2A) and assigned the same field number as the isolated but associated lower dentition de-

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scribed by Court (1995: fig. 3C, D). Its incorrect identification seems to be due to the collapse of the i1 loci on this specimen, which makes the i1s appear smaller than i2s, as in *Moeritherium* (Fig. 2A$_3$). However, the posterior extension of its symphysis to the level of p2, in contrast with *Moeritherium* where it reaches p3/p4 (personal observation), together with the morphology of the root of the p2, which has a narrower mesial root fused to a broader distal one (as described by Court (1995) for *A. savagei*) clearly supports its attribution to this taxon. An estimation of the original size of the loci of i1 indicates a similar width to that of the loci of the i2, as on BMNH M. 82163c (Fig. 2A$_3$).

Lower dentition.—The complete lower cheek dentition has been thoroughly described by Court (1995). He also described a pair of incisors, identified as i1s, belonging undoubtedly to the holotype (Court 1995: fig. 2C, D). An additional lower incisor (BMNH M. 82183) is here referred to this species (Fig. 3A): it was found at the same locality as an associated but isolated lower dentition (BMNH M. 82165) described by Court (1995: fig. 3C, D), together with numerous mandibular and cranial fragments including a partial horizontal mandibular ramus with erupting p4 and m2 (Fig. 2B). The dissociated elements found in this locality suggest that they constitute the remains of at least two crushed mandibles referable to *A. savagei*, one adult and one juvenile. The size, shape, and preservation of the incisor BMNH M. 82183 is consistent with it being that of a juvenile *A. savagei* and is therefore identified here as such. Due to its mesial location in the symphysis, with the remnants of the deciduous incisor's root present medially to its own root, this incisor is identified here as an i1 (see discussion on the homology of incisors It consists mainly of the tip of the crown of the incisor, which provides new information on the morphology of this tooth, since those described originally by Court (1995) were worn. As Court (1995) observed, the crown of this incisor is surprisingly flat mesiodistally. The mesial edge is straight, and joined anteriorly by the slightly curved distal one. It bears 10 blunt serrations on its distal edge, whereas on BMNH M. 82167, only three are visible owing to wear. Such a crenulated lateral edge is very similar to that found on the unworn di1 of *Phiomia* (CGM C.10007). The curvature and shape of this crown fit exactly with the worn, missing tip of the incisors described by Court (1995). Entirely reconstructed and placed in the symphysis (Fig. 1B), these incisors display a shape radically different from those of the other early proboscideans and are strongly reminiscent of lower tusks of the early elephantiforms.

Upper dentition.—No upper teeth were attributed by Court (1995) to *A. savagei*. Three upper molars in the Dor El Talha BMNH and MNHN collections are here referred to this taxon. Only one of them can be unequivocally positioned in the maxillary row (MNHN LBE 13), and only one of them can be confidently referred to *A. savagei* (BMNH M. 82398, see description below). However, as the three teeth share numerous structural similarities, and since no other strictly lophodont proboscidean of this size is known from the locality, they are all here referred to *A. savagei*.

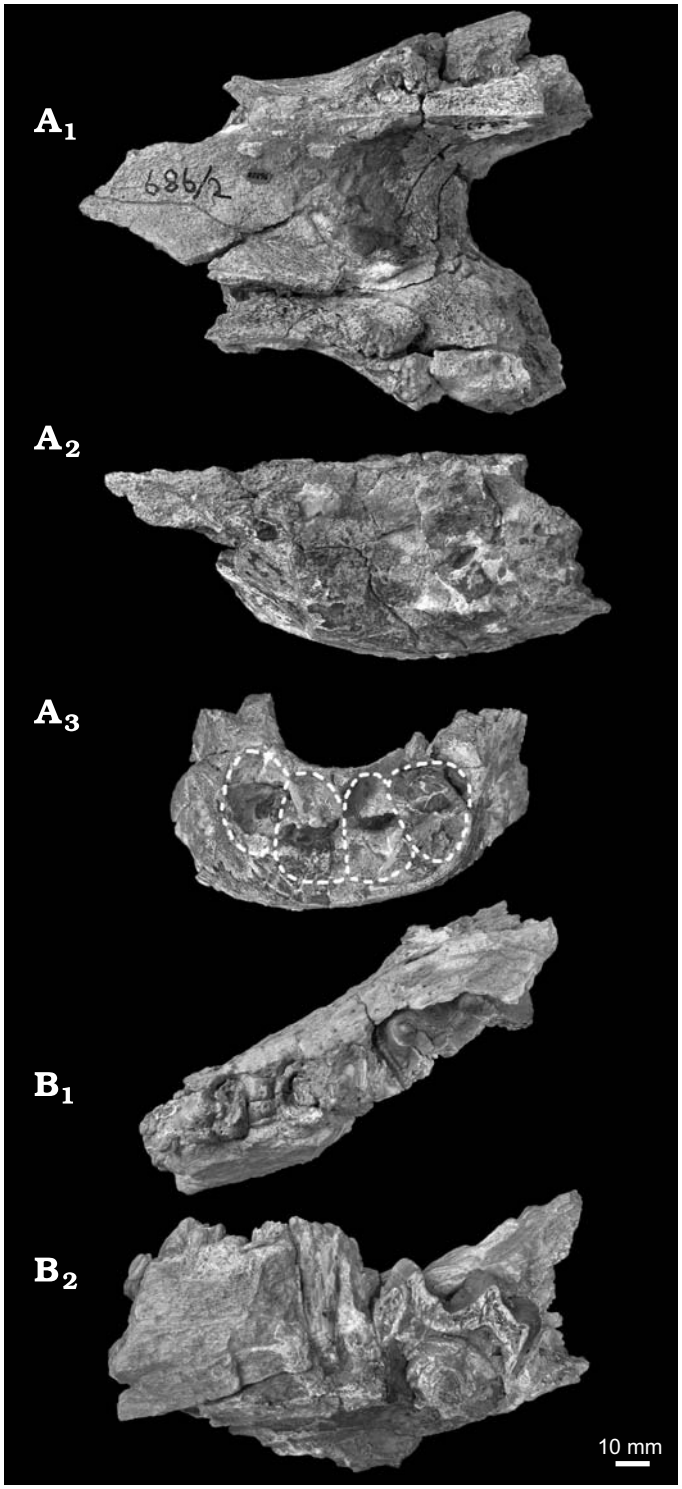


Fig. 2. Mandibular elements of the proboscidean *Arcanotherium savagei* (Court, 1995), from the Evaporite Unit (late Eocene) of Dor El Talha, Libya. **A**. Symphysis (BMNH M. 82164) in occlusal (A$_1$), lateral (A$_2$), and anterior (A$_3$) views; uncrushed incisor loci are outlined in white on A$_3$. **B**. Part of right mandibular ramus (BMNH M. 82166) with erupting m2 and p4 in occlusal (B$_1$) and lateral (B$_2$) views.

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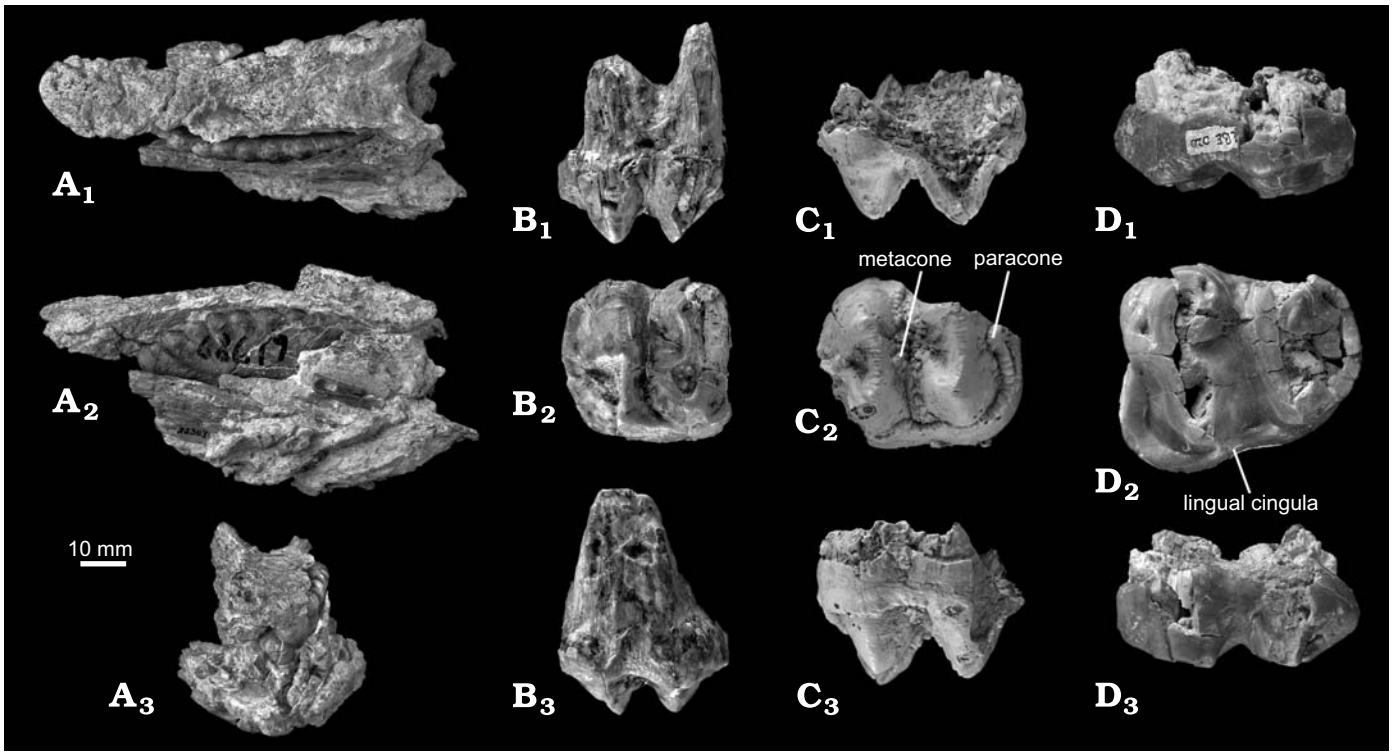


Fig. 3. Dental elements of the proboscidean *Arcanotherium savagei* (Court, 1995), from the Evaporite (A and C, late Eocene) and Idam (B, early Oligocene) units of Dor El Talha, Libya. **A**. Erupting left i1 (BMNH M. 82183) in occlusal (A_1), lateral (A_2), and anterior (A_3) views. **B**. Right M1 (BMNH M. 82172) in buccal (B_1), occlusal (B_2), and lingual (B_3) views. **C**. Right M2 (BMNH M. 82398) in buccal (C_1), occlusal (C_2), and lingual (C_3) views. **D**. Left M3 (MNHN LBE 20) in buccal (D_1), occlusal (D_2), and lingual (D_3) views.

An incomplete and worn tooth, identified here as an M1 (BMNH M. 82172; Fig. 3B) because of its size and shape, was found in a locality where remains of *Palaeomastodon*, *Barytherium grave*, and *A. savagei* are present. With a square outline in occlusal view, it is bilophodont and shows a distinct ectoflexus and a reduced entoflexus associated with a massive lingual cingulum. Although most of the mesial part of the protoloph is broken, a distinct and significant mesial cingulum can be seen on the mesio-lingual side of the crown. This tooth shows a massive, although very worn, postprotocrista which extends distobucally to the middle of the interloph, and a small but distinct, slightly curved, postparacrista. Although much worn, the metaloph bears the trace of a strong distocrista which extends to the distal wall of the crown.

Another incomplete right upper molar (BMNH M. 82398; Fig. 3C), identified as an M2 because of its size and shape, is the only upper tooth which can be unequivocally referred to *A. savagei*. In addition to bearing the same field number as the associated lower dentition described by Court (1995) and the mandibular symphysis described above (BMNH M. 82398; Court 1995: fig. 5H), its enamel displays the same three layered Schelzmuster (Rodolphe Tabuce, personal communication 2006) observed on that of the lower molars of *A. savagei* (Tabuce et al. 2007). This enamel structure, unique among early proboscideans, is observed only in more derived elephantiforms and elephantoids (Tabuce et al. 2007), and therefore is a key character in identifying *A. savagei* and in establishing its phylogenetic relationships. This tooth is bilophodont and rectangular in outline, and shares with the M1 the presence of a developed lingual and mesial cingulum, associated with a weak entoflexus. From the middle of the mesial cingulum, a small enamel cusp, identified here as a paraconule, extends proximally on the mesial wall of the protoloph. On this tooth, the postparacrista, postprotocrista and posthypocrista are well defined, as in other strictly lophodont proboscideans such as *Numidotherium koholense* or *Barytherium grave*. A small metaconule is present at the base of the mesial wall of the metaloph, in the middle of the interloph.

A left M3 (MNHN LBE 20; Fig. 3D), although much worn, is the only tooth whose position in the row can be ascertained, owing to its shape and lack of a contact facet on its distal wall. Triangular-shaped in occlusal view, this tooth displays the same strong lingual and mesial cingula observed on both the other molars, with the presence of a distinct paraconule and metaconule. Owing to the level of wear of this tooth, very few observations can be made on the presence or absence of crests. The only observable feature is the presence of a strong distocrista extending distally.

Postcranial anatomy.—Court (1995) thoroughly described and figured all of the postcranial elements that he referred to *A. savagei*, with the exception of the atlas, BMNH M. 82173, and the metapodials, BMNH M. 82181 and BMNH M.

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82182. The atlas is described here for the first time. However, since the identification of the metapodials is still ambiguous, and because very few metapodials, or indeed any other podial elements, have been attributed to early proboscideans, they will not form part of the discussion. New information on the ulna of *A. savagei* is also provided here. Since all the element found associated to the holotype of *A. savagei* in the locality 6821 share similar wear and colour as the latter, together with proportions and size consistent with that of an unique individual, and since no other vertebrate remains were recovered from that locality, it is considered here that all the elements found in this locality belong to the same individual.

Atlas (Fig. 4): the partial, worn atlas (BMNH M. 82173), only mentioned by Court (1995), displays a few characteristics of phylogenetic significance. In anterior view, the neural spine (tuberculum dorsale) forms an elongate transverse ridge, almost as wide as the neural canal. Although abraded postmortem, its robustness and lateral extension are very similar to those observed on the atlas of *Moeritherium*. This morphology is much different from that of the neural spine of the atlas of *Numidotherium koholense* (UO-K 1-1–22), which exists as a small transverse ridge, much narrower than the neural canal. Proportional to its size, the neural arch of the atlas of *A. savagei* is thicker than that of *N. koholense*, and therefore much more similar to that of *Moeritherium* or *Phiomia*. The neural canal is wide, as in *N. koholense* or *Phiomia*, while it is much more constricted in *Barytherium* and *Moeritherium*. The anterior facets for the occipital condyles are therefore widely spaced, comma-shaped and deeply concave, and extend to the lower border of the neural arch. The posterior facets that articulated with the axis are triangular in shape and, in dorsal view, are obliquely set at about 45° with respect to the transverse plane. Such orientation is found on the atlas of *Moeritherium* and *Phiomia*, while on that of *N. koholense* or *B. grave*, the posterior facets are almost parallel to the mediolateral axis. The transverse processes are damaged, but they are clearly dorsoventrally flattened, with a slight posteroventral inclination, as in *Moeritherium*, *Phiomia*, and *N. koholense*. They are perforated near their dorsal border by the transverse foramina.

Ulna (Fig. 5): an almost complete ulna, lacking only its olecranon process, was described by Court (1995; BMNH M. 82175). The transfer and re-organisation of the Dor El Talha collection from Professor Robert J.G. Savage in London led to the discovery of the missing olecranon process of this specimen, providing additional information on this bone (Fig. 5B). Moreover, another almost complete ulna (BMNH M. 82176; Fig. 5A) is here referred to *A. savagei* and sheds new light on the original description of the bone. The olecranon of the ulna of *A. savagei* extends strongly posteriorly and proximally. It is mediolaterally compressed near the shaft of the bone, thickens rapidly (notably medially) but only weakly laterally. The shape of this olecranon process, and especially its posterior extension, is quite different from that seen in early elephantiforms and more derived proboscideans, which is much more massive, but weakly elevated proximally and much less extended posteriorly. The olecranon process of *A. savagei* appears quite similar to that of UO-K 061, attributed to *N. koholense*, as figured by Mahboubi et al. (1986: text-fig. 11A). Both of them differ from that of *Barytherium*, which is much more proximally orientated and less posteriorly extended, with a more symmetrical thickening of its extremity (Delmer 2005b; own unpublished data). However, the similarity of the olecranon processes of *N. koholense* and *A. savagei* remains ambiguous: the ulna of *N. koholense* (UO-K 061) shows distinct

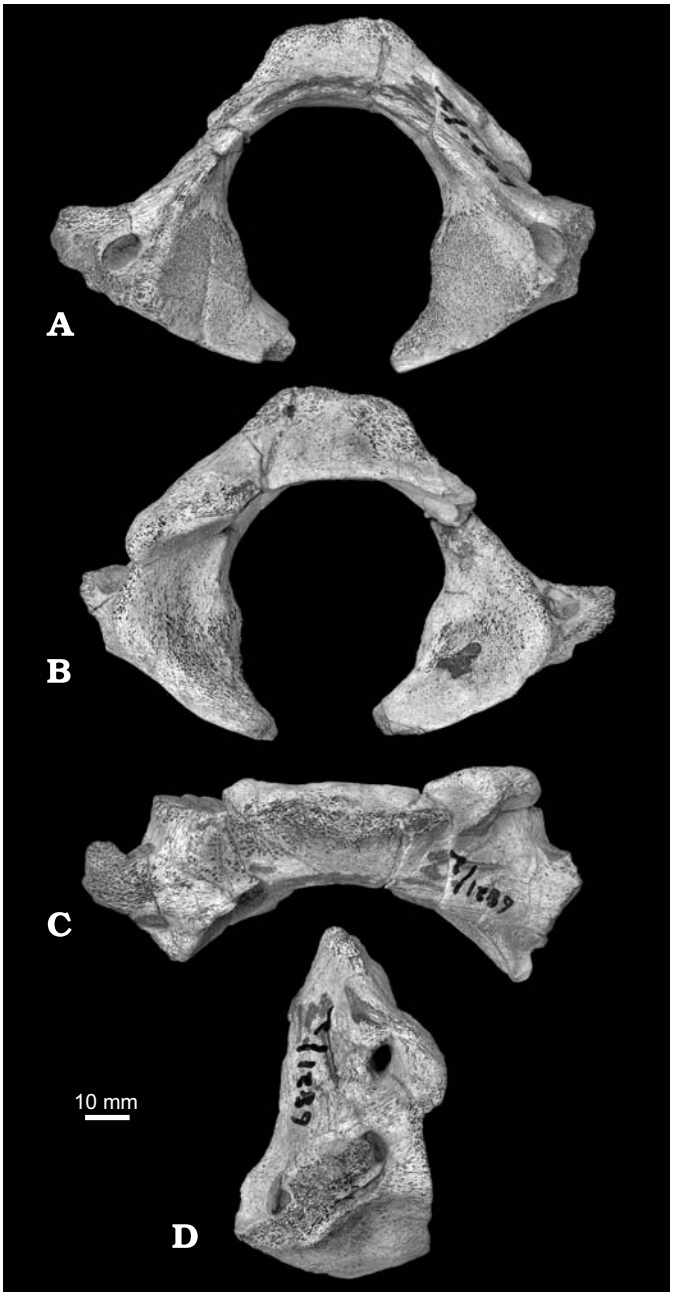


Fig. 4. Atlas (BMNH M. 82173) of the proboscidean *Arcanotherium savagei* (Court, 1995) from the Idam Unit (early Oligocene) of Dor El Talha, Libya in anterior (**A**), posterior (**B**) dorsal (**C**), and lateral (**D**) views.

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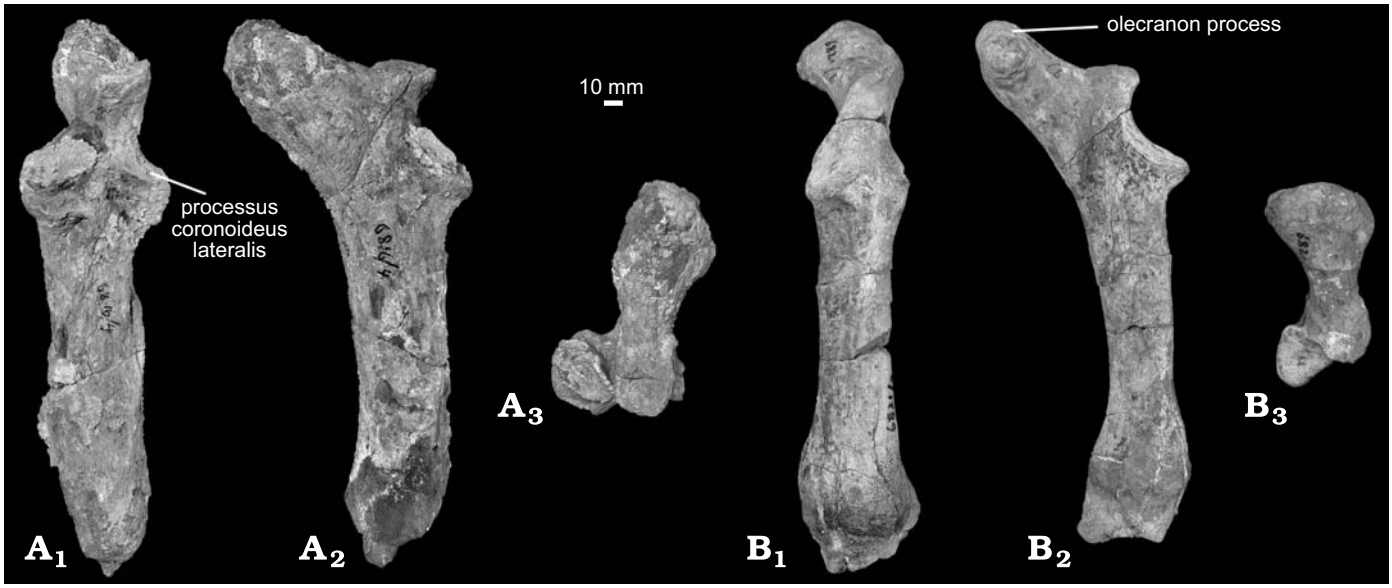


Fig. 5. Ulnae of the proboscidean *Arcanotherium savagei* (Court, 1995), from the Idam Unit (early Oligocene) of Dor El Talha, Libya. **A**. Left ulna (BMNH M. 82176) in anterior (A_1), lateral (A_2), and proximal (A_3) views. **B**. Left ulna (BMNH M. 82175), repaired since its first publication (Court 1995) in anterior (B_1), lateral (B_2), and proximal (B_3) views.

traces of teratology, with pathologic bone growth which connects the proximal half of the radius to the ulna. On this specimen, the radius is abnormally massive, with a diaphysis almost twice as large as that of the other known radii of *N. koholense* of similar length. Moreover, only one other ulna with a preserved olecranon process is available in the El Kohol collection, and this specimen displays a shape very similar to that observed on the known ulnae of *Barytherium* (Delmer 2005b, own unpublished data). Therefore, it is still difficult to ascertain the shape of the olecranon process of *N. koholense*, and therefore to judge the meaning of its similarities with *B. grave* or *A. savagei*. Another ulna referable to *A. savagei* has been identified in the Dor El Talha collection in London (BMNH M. 82176; Fig. 5A). Slightly larger than that described by Court (1995), it shares with the latter most of the structural details described by Court (1995) and herein. However, its displays a surprising feature: its proximal articulation shows a distinct lateral articulation facet (processus coronoideus lateralis) for the lateral condyle of the humerus (Fig. 5A_1), whereas Court (1995) mentioned that such facet is not present and that the whole lateral support of the ulna in this taxon is provided by the radius. A close re-examination of the specimen described by Court (1995) shows that its entire proximal articulation is badly abraded, and that no clear judgement can be made on the extension of the medial and lateral facets for the humeral condyles. The second ulna described here contradicts Court's (1995) observation and has strong phylogenetic significance, since a lateral articular facet is undoubtedly absent from the ulnae of *N. koholense* and *Barytherium*, while it is present as a similar feature on the ulna of *Moeritherium* and is even more developed on that of early elephantiforms (Delmer 2005b, own unpublished data).

Discussion on the generic attribution of *Arcanotherium savagei*

Problems with the previous attribution of *A. savagei* to *Numidotherium*.—For Court (1995), the attribution of the species *A. savagei* to the genus *Numidotherium* is mainly supported by the features he observed to be shared between *N. koholense* and *A. savagei* and that distinguish them from *Barytherium*. He listed them as an extension of the diagnosis of the genus *Numidotherium* (Court 1995: 651). However, even without the new data described in this paper, this decision can be questioned.

First, many of the distinctions that Court (1995) listed cannot be observed on at least one of the taxa concerned: the presence of a fovea for the ligamentum teres on the head of the femur, the presence of an entepicondylar foramen on the humerus and the respective size of sustentacular and ectal facets of the astragalus cannot be verified for *A. savagei*, since such parts of its anatomy are still unknown. Court (1995) also mentioned the transverse compression of the diaphysis of the ulna and the semi-supinated position of its distal articulation in *Numidotherium*, which differs from the triangular section and the more pronated carpal articulation of other proboscideans, including *Barytherium*. However, it appears that the ulna of the latter is still incompletely known, but shares with *N. koholense* and *A. savagei* some of the features described by Court (1995): e.g., the proximal half of its diaphysis shows the same transverse compression as that of *N. koholense* and *A. savagei*. Moreover, no distal ulna that

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could belong to *Barytherium* has been found in the Dor El Talha collections (Delmer 2005b).

Secondly, many of the characteristics listed by Court (1995) as diagnostic for the genus *Numidotherium* can be found in other early proboscideans such as *Moeritherium* (i.e., incisors compressed buccolingually and completely covered with enamel) or can be regarded as plesiomorphic at a higher rank within mammals (i.e., presence of an entepicondylar foramen on the humerus, of a facet for a free os centrale on the lunar or of a fovea for the ligamentum teres on the head of the femur).

Thirdly, it appears also that most of the dissimilarities emphasised by Court (1995) between the genera *Numidotherium* and *Barytherium* rely on the few extraordinary features displayed by the latter, shared by very few, and in many case by no other, proboscideans. For example, the massive scapular supraglenoidal tubercle (i.e., coracoid process sensu Andrews 1906, Court 1995, and Shoshani et al. 1996) that Andrews (1906) described for *Barytherium grave* is shared only by *Moeritherium* among proboscideans. Shoshani et al. (1989) proposed that this tubercle should be regarded as an autapomorphy of *Barytherium* and therefore reported the presence of the small *Barytherium* sp. in the Fayûm. However, a careful re-evaluation of the scapulae of *Moeritherium* available in the major Fayûm collections in the world shows that they undoubtedly show a supraglenoidal tubercle as well developed as that of *Barytherium*, and that the specimens referred to *Barytherium* sp. by Shoshani et al. (1989) are in fact scapulae of *Moeritherium* (Delmer 2005b). Moreover, the presence in *Barytherium* of an extensive facet for articulation of the ulna with the lunate (Court 1995; Delmer 2005b) is found in no other known proboscidean, and therefore the absence of such a facet cannot be regarded as a synapomorphy of the genus *Numidotherium*, as suggested by Court (1995), since it is shared by all other proboscideans known. Finally, the relative difference in the height of the horizontal ramus between *A. savagei* and *Barytherium* emphasised by Court (1995) is really only significant if the specimen chosen for comparison is the holotype of *B. grave*. The detailed study of the *Barytherium* remains from Dor El Talha has revealed a large size variation in the mandible of the genus, especially regarding the height of the horizontal ramus, which appears to be related to sexual dimorphism (Delmer 2005b, own unpublished data). At least one mandible undoubtedly referred to *Barytherium* shows a horizontal ramus height dimension proportionally similar to that of *A. savagei* (Delmer 2005b; own unpublished data).

Finally, Court (1995) also mentioned some distinctions between the genera *Numidotherium* and *Barytherium* that do not exist, as they both share the same orientation of their cristid obliqua and a similar development of the talonid with respect to the trigonid on their lower molars, together with the trace of contact for a free os centrale on the lunar (Delmer 2005b, own unpublished data).

It appears therefore that Court's (1995) attribution of the species *A. savagei* to the genus *Numidotherium* relies mainly on plesiomorphies or the absence of features known as autapomophic in the genus *Barytherium*. Court did not test its attribution by including the characteristics of *A. savagei* in his phylogenetic analysis, as he chose to analyse the phylogenetic relationships of early proboscideans at the generic level and incorrectly regarded the features of *N. koholense* as characterising both species. In light of the new data available for this taxon and for the other early proboscideans, the inclusion of the morphological features of *A. savagei* in a cladistic analysis is essential to assess its relationships.

Impact of new observations on the generic attribution of *Arcanotherium savagei* and early proboscidean phylogeny.—The newly referred specimens described here reveal new information about the anatomy of *A. savagei,* and lead to surprising observations. Its mandible, now almost completely known, displays an extraordinary mosaic of features shared with the other strictly lophodont early proboscideans and derived characteristics observed in *Moeritherium* and early elephantiforms. It also has unique features. The distal extension of the symphysis to the level of p2 (Fig. 1) is shared with *Numidotherium koholense*, whereas it is more distally extended in *Moeritherium* (at the level of p3/p4) or *Barytherium* (at the level of p4/m1). As Court (1995) noticed, the horizontal rami are significantly more robust in *A. savagei* than in *N. koholense*, with a gradual thickening starting at the level of the first premolar very similar to that observed on the mandible of *Barytherium grave* and *Moeritherium* (Delmer 2005b). Like *N. koholense*, the horizontal rami of the mandibles of *Daouitherium rebouli* and *Phosphatherium escuilliei* show no significant thickening, while the mandibles of the early elephantiforms *Phiomia* and *Palaeomastodon* are even more robust than those of *Barytherium* or *Moeritherium*, with a symphysis wider than the cheek teeth rows. Moreover, the anterior margin of the ascending ramus of the mandible of *A. savagei*, level with the middle of the m3, is located more anteriorly than in *N. koholense*, where it is behind the m3. Deinotheres and early elephantiforms share this state with *A. savagei*, whereas the early proboscideans *Phosphatherium escuillei* and *Daouitherium rebouli* display the same position as *N. koholense*. *Moeritherium* and *Barytherium* show a different state, with an anterior border of the ascending ramus respectively at the level of m2/m3 and of m2. Finally, the possession of two pairs of lower incisors of significant and equal size is an entirely new arrangement within the early proboscideans: strictly lophodont taxa (*Barytherium*, *N. koholense*, and *P. escuillei*) share an i1 significantly larger than i2, while *Moeritherium* displays enlarged i2 and reduced i1, and early elephantiforms and deinotheres possess only one (ever-growing) lower tusk. In relation to the enlargement of i2, the mandibular symphysis of *A. savagei* displays a shape very close to that of *Moeritherium*, which led to the misidentification of both isolated symphyses found at Dor El Talha.

The premolar and molar dentition of *A. savagei* also shows a surprising combination of features. As Court (1995) empha-

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sised, the lower dentition of *A. savagei* displays an overall morphology very similar to that of the strictly lophodont early proboscideans *N. koholense*, *B. grave*, *P. escuillei*, and *D. rebouli*. It shares with *B. grave* the square outline of its p3 and p4, and the presence of a small accessory cusp in front of the metaconid on p4, characteristics unknown in any other early proboscideans (Delmer 2001, 2005b; Gheerbrant et al. 2005a). An accessory cusp in front of the metaconid is also found on all lower molars of *A. savagei*, *B. grave*, and *P. escuilliei*, and on the m3 of *D. rebouli* (Delmer 2005b). However, the degree of lophodonty of the dentition of *A. savagei* is not as high as in the other strictly lophodont early proboscideans, showing cusps that are more individualised from the lophs, especially on the premolars. Such a pattern is found associated with a level of molarisation of the lower premolars greater in *A. savagei* than in any other early proboscideans. Its p2 shows a distinct metaconid, absent in *P. escuilliei*, *D. rebouli*, *N. koholense*, and *Moeritherium*, and incipient in *B. grave*, while the protolophid of its p3 is wide and bears distinct protoconid and metaconid. In *N. koholense* and *D. rebouli*, the metaconid is present but small and weakly individualised from the protoconid, while *Moeritherium* and *B. grave* display a narrower, less developed protolophid than that of *A. savagei*. This combination, unique among early proboscideans either bunolophodont or lophodont, is associated with features found in bunolophodont taxa but not yet known in strictly lophodont early forms. Thus, the lower molars of *A. savagei* display a preprotocristid that is much more developed than the premetacristid, like those of *Moeritherium* or *Phiomia*, while both cristids have a similar size in the other strictly lophodont early proboscideans. Moreover, its m1–m2 does not display the postmetacristid and preentocristid shared by all other Eocene strictly lophodont proboscideans, but absent in deinotheres and early elephantiforms. The upper molars referred to *A. savagei* and described above possess a paraconule and metaconule, together with a strongly developed lingual cingulum and a reduced entoflexus, features only found on the bunolophodont moeritheres and early elephantiforms. The similarity of the M3 of *A. savagei* with that of *Moeritherium* is so striking that this isolated tooth was first recognised as belonging to an unknown, enormous, lophodont *Moeritherium* (personal observation). Finally, analysis of the enamel microstructure of *A. savagei* revealed that this taxon does not display the typical Schmelzmuster composed of 3-D enamel that is shared exclusively with the other strictly lophodont proboscideans *N. koholense*, *B. grave* or the deinotheres (Remy 1976; Bertrand 1989; Tabuce et al. 2007). Instead it displays a three-layered Schmelzmuster with 3-D enamel limited near the enamel-dentine junction, overlain by HSB (a specific mode of decussation in which prisms decussate in transversely oriented bands) then radial enamel in the outer zone, which is shared by all elephantoids (Bertrand 1989; Pfretzschner 1994; Ferretti 2003), and is therefore even more derived than that of some early elephantiforms (Tabuce et al. 2007).

In light of these unique features and character combinations of both the mandible and the dentition of *A. savagei*, the differences noted by Court (1995) between the postcranial elements of *A. savagei* and *N. koholense*, which he regarded as intra-generic variation, need to be re-evaluated. As such, the triangular shape of the lunate of *A. savagei* (BMNH M. 82180), which is significantly wider anteriorly than posteriorly, is shared by all elephantiforms and elephantoids, while *Barytherium* and *N. koholense* share a more rectangular lunate that is longer than wider and more similar to that of "primitive" condylarths such as *Phenacodus* (Delmer 2005b). Moreover, as in all other known proboscideans, the scapula of *A. savagei* does not display the massive coracoid process medially deflected, as observed on *N. koholense*, while its supraglenoidal process is, as noticed by Court (1995), smaller than that observed in *Barytherium* and *Moeritherium*. Finally, as documented above, the atlas and ulna of *A. savagei* share features with moeritheres and elephantiforms, but not with *Barytherium* or *N. koholense*.

In order to assess the systematic attribution and phylogenetic position of *A. savagei*, its anatomical characters were added to a data matrix of 207 cranial, mandibular, dental and postcranial characters scored for all early proboscideans known, including the recently described *Phosphatherium escuilliei* Gherbrant, Sudre and Capettat, 1996 and *Chigatherium harrisi* Sanders, Kappelmann, and Rasmussen, 2004, together with early tethytheres and relevant related taxa (Appendices 1 and 2). The family Prorastomidae, which contains *Pezosiren portelli* Domning, 2001 and *Prorastomus sirenoides* Owen, 1855, was chosen to represent the order Sirenia, while the genus *Behemotops* was used as the representative of the order Desmostylia. The genus *Anthracobune* was also included as the best known representative of the family Anthracobunidae, whose phylogenetic relationships with, or within, the tethytheres is regularly cited by authors (Sahni and Kumar 1980; Wells and Gingerich 1983; West 1984; Domning et al. 1986; Tassy and Shoshani 1988; Kumar 1991). The embrithopod *Arsinoitherium*, also occasionally proposed as a member of the Tethytheria (Court 1992; Fischer and Tassy 1993; Gheerbrant et al. 2005b), was not included in this analysis since its highly derived dental states are difficult to homologise with the other taxa analysed and have been shown to reduce phylogenetic resolution (Delmer 2005a, b). *Arsinoitherium* will be the object of a separate paper. In order to reduce the impact of a priori hypotheses, all multistate characters were here regarded as unordered.

The data matrix was analysed with unweighted parsimony, using the exhaustive algorithm ("ie" command) of Hennig86 program. Only one most parsimonious tree (L = 381; CI = 0.64; RI = 0.70) was found (Fig. 6). The entire analysis of the distribution of characters of this tree, together with the respective phylogenetic relationships within the early proboscideans and early tethytheres, is not the object of this paper, as it includes numerous unpublished data, mainly on the genus *Barytherium*. Such work will be published together with the monographic description of the new data of this enigmatic genus. The main purpose of this analysis is to test the validity of the genus *Arcanotherium* using a cladistic approach.

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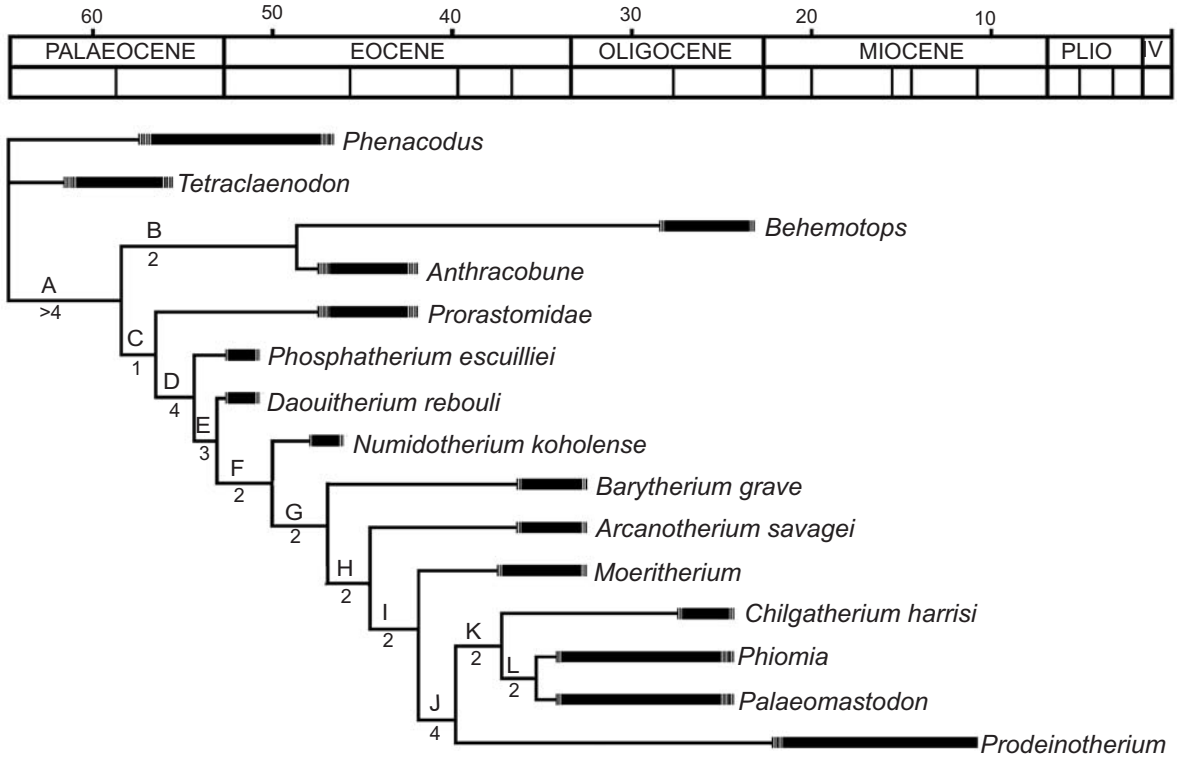


Fig. 6. Phylogenetic relationships among early tethytheres. Most parsimonious tree (L = 381; CI = 0.64; RI = 0.70) obtained from 207 morphological characters. Nodes are identified by letters (A to L). Bremer support is indicated in black under each node.

In the most parsimonious tree obtained in this analysis, *A. savagei* appears as a unique taxon, distinct from any other proboscidean taxa, and lying at an "intermediate" node between the strictly lophodont Eocene proboscideans and *Moeritherium* together with the late Oligocene/Miocene strictly lophodont proboscideans (*Chilgatherium* and deinotheres) (Fig. 6 node H). Such a node is supported by 11 unambiguous synapomorphies: paraconule present on the M1–2–3 (character 69; state 0); metaconule present on the M1–2 (71: 0); centrocrista absent on the M1 (80: 1); lingual cingulum present on the M3 (95: 0); low hypoconid, significantly lower than the protoconid, on the p2 (101: 0); paracristid more massive than the premetacristid on the m1–2–3 (117: 0); postmetacristid absent on the m1–2 (118: 1); preentocristid absent on the m1–2 (119: 1); significant dorsoventral flattening of the transverses processes of the atlas (133: 1); developed lateral sigmoid facet of the ulna (153: 1); and lunate triangular in proximal view (156: 1). Five of these synapomorphies come from the observations made on the specimens newly referred to *A. savagei* in this paper (69: 0; 71: 0; 80: 1; 95: 0; 153: 1). The vast number of characters supporting the independence of *A. savagei* from both genera *Barytherium* and *Numidotherium*, but also from any other proboscideans taxon, confirms the re-attribution of this species to a new genus proposed in this paper.

Remarks on the similarity between *Arcanotherium savagei* and *Chilgatherium harrisi*.—In 2004, a new early proboscidean named *Chilgatherium harrisi* Sanders, Kappelman, and Rasmussen, 2004 was described from a late Oligocene locality in Ethiopia (Sanders et al. 2004). It was the first non-elephantiform proboscidean ever recorded in the late Oligocene of Africa. Only known from its teeth, it has been described as a primitive representative of the family Deinotheriidae, separated from other deinotheres at the sub-familial level. Detailed comparison of the teeth referred to *C. harrisi* and those of *A. savagei* emphasise the extraordinary similarity of the lower molars of both taxa (Fig. 7E–H): their m2 and m3 are almost exactly the same size, and share the features that distinguish *A. savagei* from the other strictly lophodont early proboscideans: a preprotocristid more massive than the premetacristid, a postmetacristid and preentocristid absent on the m2, and a weaker level of lophodonty, with cusps easily distinguishable from the lophs. The difference between *C. harrisi* and the other strictly lophodont early proboscideans is even more marked, as its m3 does not display the postmetacristid and preentocristid retained in *A. savagei*. As noted by Sanders et al. (2004), the talonid of the lower molars is more developed than in any other early proboscideans, and its m2 can be recognised as trilophodont, even though the lophid joining the cusps of the talonid is low. On the other hand, the m1 of *C. harrisi* appears to be clearly trilophodont. Known only from a distal fragment of the crown (CH35-d; Fig. 7E), it displays a complete distal lophid and the distal wall of a mesial one. The size of this fragment clearly supports the identification of the distal lophid as a tritolophid, as its identification as a metalophid would suggest a size for the m1 too small with respect to that of the other molars.

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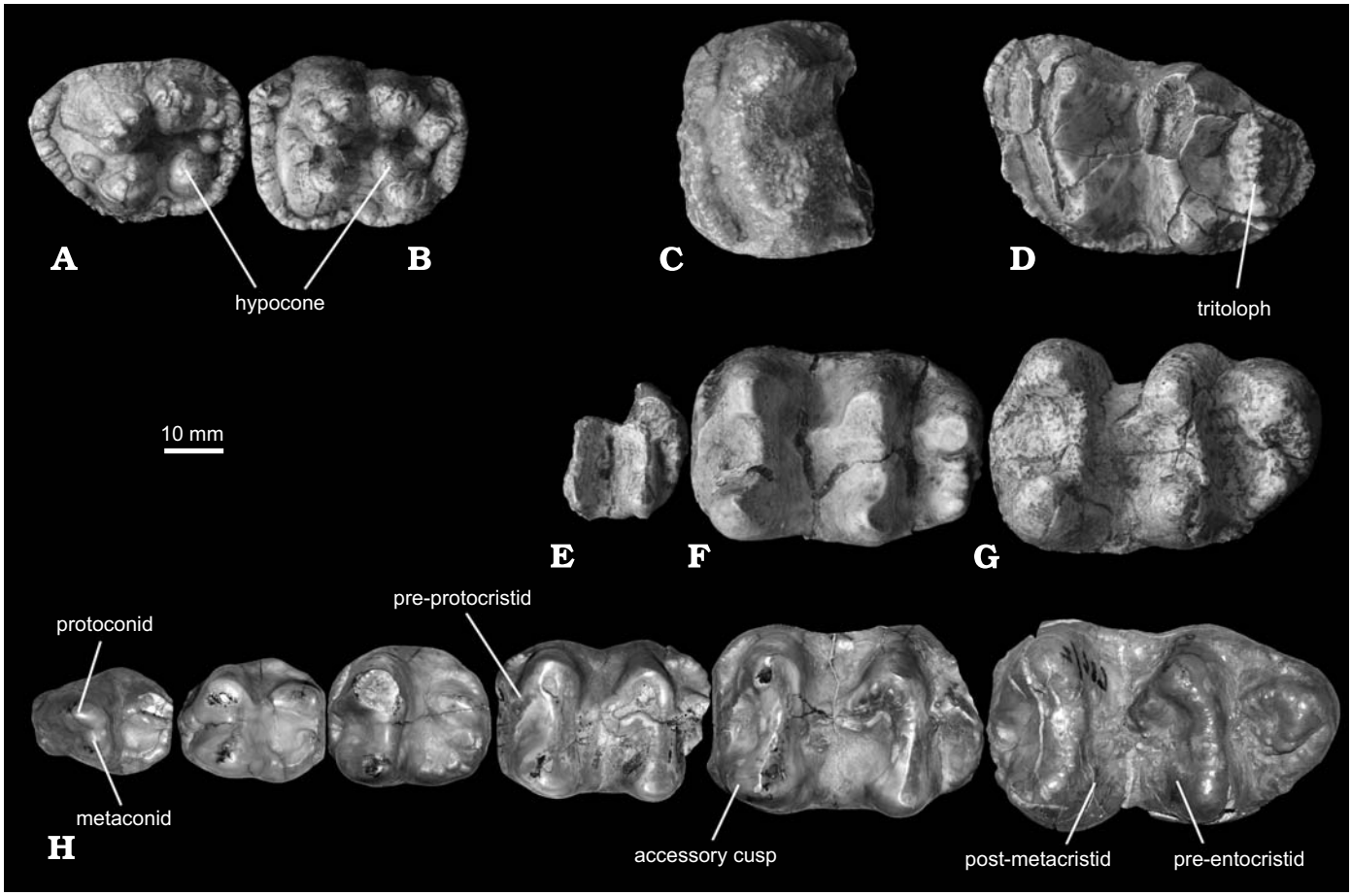


Fig. 7. Dental elements of the proboscidean *Chilgatherium harrisi* Sanders, Kappelman, and Rasmussen, 2004, from the Upper Guang and Gahar Valley sections (late Oligocene), Chilga region, Ethiopia. **A**. Right P3 (CH9–22) reversed for consistency. **B**. Left P4 (CH9–7). **C**. Protoloph of left ?M2 (CH12–4). **D**. Right M3 (CH35–1) reversed for consistency. **E**. Tritolophid of right m1 (CH35–3d) reversed for consistency. **F**. Left m2 (CH35–3a). **G**. Right m3 (CH35–3c) reversed for consistency. All in occlusal views. Dental elements of the proboscidean *Arcanotherium savagei* (Court, 1995), from the Evaporite Unit (early Oligocene) of Dor El Talha, Libya. **H**. Right p2, p3, m1, m3 and left p4, m2 (BMNH M. 82165) in occlusal view (p4 and m2 reversed for consistency).

It appears therefore that *C. harrisi* could easily be interpreted as a slightly more derived, more "molarised" form of *A. savagei*. However, the upper teeth referred to *C. harrisi* are very different from those referred here to *A. savagei*. Two upper premolars, identified by Sanders et al. (2004) as P4, were referred to *C. harrisi*. Found in a different locality than the lower teeth, they are strictly bunodont and strongly molarised, both of them displaying distinct hypocones, as their cusps in general are either crenulated or sub-divided into 2 to 3 cuspules. Such morphology would not fit in an occluding pattern of an even more molarised p3 of *A. savagei*. Sanders et al. (2004) regarded the differences between the two teeth as individual variation but a re-examination of the specimens indicates that those differences are too great for this to be the case. Their clear difference in shape (CH9-22 is more constricted anteriorly than CH9-7), together with the significantly greater development of the hypocone on the latter (Fig.7A, B), clearly suggest that the teeth had different positions in the tooth row, and should most probably be identified as right P3 (CH9-22) and left P4 (CH9-4) from the same individual. It also seems unlikely that a mammal would display simultaneously bunodont premolars and strictly lophodont molars. It is suggested here that these premolars should not be referred to the same taxon as the holotype of *C. harrisi*. As for the M3 referred to *C. harrisi* (CH35-1; Fig. 7D) and found at the same locality as the holotype, it is quite different from that identified here as the M3 of *A. savagei*. Much narrower and longer, it bears an almost complete tritoloph, albeit not completely separate from the metaloph (Fig. 7D). Badly damaged, this tooth does not seem to have an individualised paracone, though it does have a strong centrocrista. It also shares with the M3 of *A. savagei* the presence of strong mesial and lingual cingula. The morphology of this tooth, supposed to occlude with the m3 of the holotype (CH35-3c; Fig. 7G), is surprising, considering the morphology of the latter. It suggests that, in occlusion, a considerable part of its distal cingulum would have extended distally beyond the talonid of the m3. It is also very narrow, as narrow as the m3, while the upper teeth of the other strictly lophodont early proboscideans are wider than the lower ones. This difference

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in width between upper and lower molars is much less significant in the early elephantiforms *Phiomia* and *Palaeomastodon*. The presence of a tritoloph still connected to the metaloph can be interpreted as precluding a dentition with the tritoloph of the early elephantiforms or elephantoids or the convolute (sensu Gräf 1957) observed in deinotheres. Moreover, the presence of a sharp centrocrista and the apparent absence of an individualised paracone also suggest an affinity of *C. harrisi* with deinotheres, as they display both characteristics. On the other hand, the M3 of the early elephantiform *Phiomia* displays a strong paracone and no centrocrista. It appears therefore that if the attribution of this tooth is confirmed, *C. harrisi* displays a surprising combination of lower molars very similar to those of *A. savagei*, slightly more complex, together with an M3 displaying features of both deinotheres and early elephantiforms.

In the same cladistic analysis, the dental features of *C. harrisi* place it in the most parsimonious tree as the sister-group of the clade uniting the early elephantiforms *Palaeomastodon* and *Phiomia* (Fig. 6 node K). This node is supported by 4 unambiguous synapomorphies: the presence of a strong parastyle present on its P3 (56: 1); the presence of a tritoloph on its M3 (84: 1); absence of postmetacristid on the m3 (126: 1); and the presence of two cusps on the talonid of the m3 (129: 1). Such a position does not confirm its proposed attribution to the family Deinotheriidae, as it shares more anatomical features with the early Elephantiformes. However, this taxon remains still too poorly known to be sure of its phylogenetic position, especially since some questions remain concerning the identification of the premolars referred to it. On the other hand, deinotheres display a combination of primitive and derived characteristics, either cranial, dental or postcranial, that influence strongly the phylogenetic tree of early proboscideans (Delmer 2005a, b; Delmer et al. 2005). More data on the anatomy of *C. harrisi* is required in order to confirm the association of its upper and lower teeth and clarify its resemblances to *A. savagei*. Both taxa appear to be key elements to the understanding in the divergence of both elephantiforms and deinotheres, one of the major events in the evolution of the order Proboscidea.

Considerations on the homology of incisors among proboscideans

Most early proboscideans still possess an anterior dental formula close to that of the primitive mammalian state: *Numidotherium koholense* and *Moeritherium* share the presence of three upper incisors and two lower ones, while *Barytherium* only retains two upper and two lower incisors. Gheerbrant et al. (2005a) demonstrated that *Phosphatherium escuilliei* had two lower incisors; no information on its upper anterior dentition is available. However, deinotheres have only one lower ever-growing tusk, while elephantiforms share the presence of one ever-growing tusk on their lower and upper jaw, the lower one being lost by elephantids. The identity of the incisors retained as tusks by both elephantiforms and deinotheres has long been the subject of controversy among palaeontologists.

Upper incisors.—When he described *Moeritherium*, Andrews (1906) proposed that its enlarged I2s were homologous with the upper tusks of elephantiforms. This was the favoured hypothesis throughout the 20th century (Matsumoto 1923; Osborn 1936; Sikes 1971), with most authors regarding the deciduous tusks of young elephantoids to be homologous with the dI2s of *Moeritherium* (Schaub 1948; Sikes 1971). However, Anthony (1933) proposed that both of these successively erupting tusks were in fact homologous with the dI2 and dI3 of *Moeritherium*, based on the observation of a calcified primordium for the permanent tusk in the foetus of an elephant in which the deciduous tusk was still growing. Tassy (1985, 1987) later modified this interpretation by proposing that deciduous and permanent tusks of elephantoids are homologous with the dI3 and dI2, respectively, of early proboscideans. Recent ontogenetic studies (Luckett 1996) emphasised the presence of a single epithelial primordium for the two tusks in the foetuses and new-born calves of elephants. The absence of a second epithelial primordium contradicts the hypothesis that the tusks originate from two different deciduous teeth, and led to the acceptance of the idea that the deciduous and permanent tusks of elephantoids and elephantiforms are homologous with the dI2 and I2 of early proboscideans, which, conveniently, are significantly enlarged in all of the latter.

Lower incisors.—The identity of the lower tusk of elephantiforms and deinotheres is still debated, since two different patterns are observed among early proboscideans. The strictly lophodont taxa, *Phosphatherium escuilliei*, *Numidotherium koholense*, and *Barytherium grave* share the presence of two incisors on each side of the mandible, the mesial one being significantly larger than the distal one. In contrast, *Moeritherium* retains two incisors on each side but the distal one is significantly larger than the mesial one. It is widely accepted that the two lower incisors retained in all early elephantiforms are the i1 and i2. As *Moeritherium* has been generally recognised throughout the 20th century as the most primitive proboscideans, it was widely considered that the lower tusks of elephantiforms and deinotheres were homologous with the enlarged di2 and i2 of moeritheres and therefore of other early proboscideans. Later, Tassy (1987) proposed that the lower tusks of elephantiforms are homologous with the di1 and di2 of early proboscideans. One of his main arguments was the delay in timing of eruption of the permanent tusks of elephantiforms (simultaneously with that of dp4), and that of the permanent i2 of *Moeritherium* (just before or simultaneously with that of m3). However, this work was done before the discovery of primitive proboscideans with an enlarged mesial incisor, *Barytherium* having been excluded from most work on proboscideans throughout the 20th century. The successive discoveries of *N. koholense* and *P. escuilliei*, both displaying a mesial incisor more enlarged than the distal one, led to the re-

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consideration of the homology of lower tusks among proboscideans. In the light of the recently proposed phylogeny of early proboscideans (Gheerbrant et al 2005a; Fig. 6, based on the analysis presented herein, is similar in topology), the hypothesis suggesting that the enlarged lateral incisor of *Moeritherium* is homologous with the tusks of elephantiforms requires the following succession of evolutionary events: reduction of the mesial incisors and enlargement of the distal ones, followed by acquisition of the ever-growing state for the distal incisors within the elephantiforms. However, the description here of a strictly lophodont early proboscidean, *A. savagei*, phylogenetically intermediate between the strictly lophodont early proboscideans and the *Moeritherium*-elephantiform-deinothere clade, displaying mesial and distal incisors of the same size and whose i1s are morphologically very similar to the lower tusks of elephantiforms (see description above), suggests that the lower tusks of elephantiforms are homologous with the enlarged i1 of the strictly lophodont early proboscideans. The reduction of the i1 in *Moeritherium* appears therefore to be autapomorphic for the genus, whereas they retained the enlarged i2 displayed by *A. savagei*. This hypothesis is more parsimonious, as it requires fewer evolutionary changes. The hypothesis of identity of the tusks of elephantiforms proposed here is therefore:

Upper tusks: dI2/I2 – Lower tusks: di1/i1.

This hypothesis is consistent with the position of upper and lower tusks in the jaws of elephantiforms and elephantoids, where the upper ones always occlude distal to the lower ones.

Conclusion

Although excluded from most of the debate on the origin and first phases of differentiation of the proboscideans of the last twenty years, *Arcanotherium savagei* is shown here to be a key element in the understanding of the emergence of the elephantiforms and deinotheres. Its unusual combination of primitive, strictly lophodont, dental features and of derived dental features shared by the early elephantiforms, together with derived mandibular and postcranial characteristics, finally allow us to understand the relationships between the extraordinarily primitive morphology of the strictly lophodont early proboscideans and that of the elephantiforms and elephantoids. Questions still remain about the events involved in the diversification of the deinotheres and elephantiforms, and the description of new forms such as *Chilgatherium harrisi* now appears to be essential to the understanding of this event. This divergence seems to have been correlated with the evolution of graviportal stance within the proboscideans: while deinotheres, elephantiforms and elephantoids display the typical columnar limbed posture of elephants, the early representatives of the order, *N. koholense* and *B. grave*, display limbs with much stronger angulation, together with almost plantigrade hands and feet (Court 1994; Delmer 2005b, c). Such postcranial morphology suggests locomotion and habitat radically different from that of the more derived proboscideans. The recent isotope analysis of *Barytherium*'s enamel suggested that it grazed freshwater vegetation in a swamp or riverine environment (Liu et al. 2008), supporting this suggestion. Similar results were obtained from the enamel of *Moeritherium*. The acquisition of graviportal stance by the proboscideans, which is likely to have occurred during the Oligocene, increased their locomotor efficiency and surely played a key role in their dispersal during the Neogene. This transition deserves now to be thoroughly investigated.

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Appendix 1

Character list

1. Skull – Frontal = in contact (0), or not in contact with the premaxillary (1)
2. Skull – Posterior extension of the nares = weak (0), or strong (1)
3. Skull – Opening of the orbit = into the jugal (0), or into the maxillary (1)
4. Skull – Position of the orbit = above the molars (0), above the premolars (1), or in front of the premolars (2)
5. Skull – *Processus orbitalis* of the palatine = present (0), or absent (1)
6. Skull – Jugal = extends to the anterior border (0), or to the rear border of the glenoid fossa (1)
7. Skull – External auditory meatus = low (0), or high (1)
8. Skull – External auditory meatus = open (0), or closed ventrally by post-tympanic and postglenoid parts of the squamosal (1)
9. Skull – Squamosal = cerebral part not inflated (0), or inflated dorsally (1)
10. Skull – Parietal = in contact with the alisphenoid (0), or not contact with the alisphenoid (1)
11. Skull – Periotic bone = with a pars mastoidea smaller (0), or larger than the pars cochlearis (1)
12. Skull – Periotic bone = foramen ovale separated from foramen lacerum medium (0), or confluent (= foramen metoticum) (1)
13. Skull – Pneumatisation = weak (0), medium (1), or significant (2)
14. Skull – Sagittal crest = present (0), or absent (1)
15. Skull – Postorbital process of the frontal = massive (0), or small (1)
16. Skull – Maxillary = processus pyramidalis reduced (0), weakly extended anteriorly (1), or strongly extended anteriorly (2)
17. Skull – Maxillary = processus pyramidalis extends posteriorly to the level of M3 (0), of M2/M3 (1), or of P4/M1 (2)
18. Skull – Zygomatic arches = weakly (0), or strongly divergent (1)
19. Skull – Position of the postglenoid foramen = lateral (0), weakly medial (1), or strongly medial (i.e., homologuous of the canal temporalis) (2)
20. Skull – Condylar foramina = present (0), or absent (1)
21. Skull – Zygomatic extension of the squamosal = low (0), or high (1)
22. Mandible – Symphysis = short (0), or lengthened (1)
23. Mandible – Origin of the vertical ramus = behind the M3 (0), at the level of M3 (1), between M2 and M3 (2), or at the level of M2 (3).
24. Mandible – Angle between vertical and horizontal rami = obtuse (0), sharp (1), or at 90°(2)
25. Mandible – Coronoid process of the vertical ramus = high (0), or low above the teeth (1)
26. Mandible – Coronoid process of the vertical ramus = higher (0), or lower than the condyle (1)
27. Mandible – Angular process = very massive (0), massive (1), or small (2)
28. Mandible – Symphysis = not fused (0), or fused (1)
29. Mandible – Posterior extension of the symphysis = in front of P1 (0), at the level of P2 (1), between P2 and P3 (2), between P3 and P4 (3), between P4 and M1 (4), between M1 and M2 (5), or in front of the premolars (6)
30. Mandible – Lateral thickening of the horizontal ramus = poor (0), significant, starting at the level of the premolars (1), or significant, starting at the level of the symphysis (2)
31. Mandible – Coronoid foramen = absent (0), or present (1)
32. Mandible – Diastema between the jugal and anterior teeth = reduced to absent (0), or significant (1)
33. Teeth – M11 = much shorter than M22 (30% or more) (0), slightly shorter than M22 (10% or less) (1), or of the same length than M22 (2)
34. Teeth – Incisor = not evergrowing (0), or evergrowing (1)

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35. Teeth – I1 = present (0), or absent (1)
36. Teeth – I3 = present (0), or absent (1)
37. Teeth – Upper incisors = of similar size (0), or I2 significantly larger than other (1)
38. Teeth – Upper canine = present (0), or absent(1)
39. Teeth – Lower incisors = upwards vertically oriented (0), proclives (1), or downward vertically oriented (2)
40. Teeth – I1 = with enamel covering the whole crown (0), with enamel covering half of the crown (1), or without enamel (2)
41. Teeth – I2 = present (0), or absent (1)
42. Teeth – I3 = present (0), or absent (1)
43. Teeth – Lower incisors = of similar size (0), I1 significantly larger than the others (1), or I2 significantly larger than the others (2)
44. Teeth – Lower canine = present (0), or absent (1)
45. Teeth – P1 = present (0), or absent (1)
46. Teeth – P2 = reduced (0), or inflated and caniniform (1)
47. Teeth – P2 = parastyle absent (0), or present (1)
48. Teeth – Shape of the P2 in occlusal view = oval, longer than wide (0), or wider posteriorly (1)
49. Teeth – P2 = protocone absent (0), or present (1)
50. Teeth – P2 = metacone present (0), or absent (1)
51. Teeth – P2 = metacone reduced (0), or enlarged, easily distinguishable from protocone (1)
52. Teeth – P2 = metastyle absent (0), or present (1)
53. Teeth – P2 = lingual cingulum absent (0), or present (1)
54. Teeth – P2 = mesial cingulum present (0), or present (1)
55. Teeth – P3–4 = mesial cingulum present (0), or present (1)
56. Teeth – P3 = parastyle present (0), or absent (1)
57. Teeth – P3 = metacone fused with the paracone (0), or individualised from the paracone (1)
58. Teeth – P3 = metastyle absent (0), or present (1)
59. Teeth – P3 = hypocone absent (0), or present (1)
60. Teeth – P3 = lingual cingulum present (0), or absent (1)
61. Teeth – P3 = lingual cingulum incomplete (0), or complete (1)
62. Teeth – P4 = paraconule present (0), or absent (1)
63. Teeth – P4 = metacone massive and fused with the paracone (0), reduced (1), massive, forming an ectoloph with the paracone (2), or massive and independant from the paracone (3)
64. Teeth – P4 = hypocone absent (0), or present (1)
65. Teeth – P4 = lingual cingulum présent (0), or absent (1)
66. Teeth – P4 = lingual cingulum incomplete (0), or complete (1)
67. Teeth – P4 = mesial cingulum complete (0), or incomplete (1)
68. Teeth – M1–2 = parastyle massive (0), or reduced to absent (1)
69. Teeth – M1–2–3 = paraconule present (0), or absent (1)
70. Teeth – M1–2 = paraconule individualised from the protoloph (0), or forming a massive crest on the anterior wall of the protoloph (1)
71. Teeth – M1–2 = metaconule present (0), or absent (1)
72. Teeth – M1–2 = metaconule individualised from the metaloph (0), consituting a massive crest on the anterior wall of the metaloph (1), or reduced to a fine crest on the anterior wall of the metaloph (2)
73. Teeth – M1–2 = mesostyle present (0), or absent (1)
74. Teeth – M1–2–3 = post-paracrista II absent (0), or present (1)
75. Teeth – M1–2–3 = crista obliqua oblique (0), or lingually positioned, oriented in the antero-posterior axis of the crown (1)
76. Teeth – M1–2 = convolute absent (0), or present (1)
77. Teeth – M1–2 = lingual cingulum absent (0), or present (1)
78. Teeth – M1 = postentoconule absent (0), or present (1)
79. Teeth – M1 = postentoconule reduced, only defined by a small groove at the top of the distocrista (0), well individualised from the hypocone (1), or independent from the hypocone (2)
80. Teeth – M1 = centrocrista present (0), or absent (1)
81. Teeth – M1 = tritoloph absent (0), or present (1)
82. Teeth – M1 = mesial cingulum present (0), or absent (1)
83. Teeth – M2–3 = centrocrista present (0), or absent (1)
84. Teeth – M2–3 = tritoloph absent (0), or present (1)
85. Teeth – M2–3 = mesial cingulum present (0), or absent (1)
86. Teeth – M2 = postentoconule absent (0), or present (1)
87. Teeth – M2 = postentoconule reduced, only define by a small groove at the top of the distocrista (0), well individualised from the hypocone (1), or independent from the hypocone (2)
88. Teeth – M2 = metaloph slightly less wide than the protoloph (0), or significantly less wide than the protoloph (1)
89. Teeth – M3 = parastyle reduced to absent (0), or massive (1)
90. Teeth – M3 = paraconule individualised from the protoloph (0), or constituting a crest on the anterior wall of the loph (1)
91. Teeth – M3 = metaconule present (0), or absent (1)
92. Teeth – M3 = metaconule individualised from the metaloph (0), constituting a massive crest on the anterior wall of the metaloph (1), or reduced to a fine crest on the anterior wall of the metaloph (2)
93. Teeth – M3 = mesostyle present (0), or absent (1)
94. Teeth – M3 = metaloph bucally displaced from the dental axis (0), or in the dental axis (1)
95. Teeth – M3 = lingual cingulum present (0), or absent (1)
96. Teeth – P1 = present (0), or absent (1)
97. Teeth – P2 = present (0), or absent (1)
98. Teeth – P2 in occlusal view = sub-oval (0), or triangular (1)
99. Teeth – P2 = paraconid reduced to absent (0), or massive (1)
100. Teeth – P2 = metaconid absent (0), or present (1)
101. Teeth – P2 = low, hypoconid significantly lower than the protoconid (0), hogh, slightly lower than the protoconid (1)
102. Teeth – P2–3–4 = mesial cingulum present (0), absent (1)
103. Teeth – P3–4 = protostylid present (0), or absent (1)
104. Teeth – P3 in occlusal view = rectangular (0), square (1)
105. Teeth – P3 = paraconid massive and anteriorly positioned (0), small, on the mesial side of the anterior face of the crown (1)
106. Teeth – P3 = metaconid lower than the protoconid, posterior to him (0) , as high as the protoconid, lingual to him (1), small, at the lingual side of the protocnid (2), or reduced to a small enlargement of the postero-lingual wall of the protoconid (3)
107. Teeth – P3 = entoconid absent (0), or present (1)
108. Teeth – P3 = pre-metacristide absent (0), present (1)
109. Teeth – P4 = rectangular in occlusal view (0), or square (1)
110. Teeth – P4 = paraconid present (0), or absent (1)
111. Teeth – P4 = paraconid massive, in anterior position (0), small, on the antero-vestibular side of the crown (1)
112. Teeth – P4 = accessory cusp in font of the metaconid absent (0), or present (1)
113. Teeth – P4 = entoconid absent (0), or present (1)
114. Teeth – P4 = pre-metacristid absent (0), or present (1)
115. Teeth – P4 = metalophid absent (0), or present (1)
116. Teeth – M1–2 = acessory cusp in front of the metaconid absent (0), or present (1)

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117. Teeth – M1–2–3 = pre-protocristid more massive than the pre-metacristid (0), or as developped as the pre-metacristid (1)
118. Teeth – M1–2 = post-metacristid present (0), or absent (1)
119. Teeth – M1–2 = pre-entocristid present (0), or absent (1)
120. Teeth – M1–2 = pre-entocristid = straight (0), curved (1)
121. Teeth – M1–2–3 = cristida obliqua oblique, joining the metaconid (0), strongly oblique, joining a vertical post-protocristid in the midle of the protolophid (1), or straight in the mesio-distal axis of the crown (2)
122. Teeth – M1 = tritolophid absent (0), or present (1)
123. Teeth – M2 = tritolophid absent (0), or present (1)
124. Teeth – M2–3 = buccal cingulum present (0), or absent (1)
125. Teeth – M3 = accessory cusp on the pre-metacristid absent (0), or present (1)
126. Teeth – M3 = post-metacristid present (0), or absent (1)
127. Teeth – M3 = pre-entocristid present (0, or absent (1)
128. Teeth – M3 = pre-entocristid straight (0), or curved (1)
129. Teeth – M3 = talonid bearing only one cusp (0), or bearing two cusps (1)
130. Teeth – M3 = talonid bucally displaced (0), or in the mesio-distal axis of the crown (1)
131. Skeleton – Atlas = distal articular facets strongly posteriorly extended (0), or weakly posteriorly extended (1)
132. Skeleton – Atlas = proximo-distal flattening weak (0), or significant (1)
133. Skeleton – Atlas = dorso-ventral flatening of the transverses processes weak (0), significant (1)
134. Skeleton – Scapula = supraglenoidal tubercle massive (0), very massive (1), or reduced (2)
135. Skeleton – Scapula = scapular spine ventrally positionned (0), medially positionned (1), or dosally positionned (2)
136. Skeleton – Scapula = coracoid process massive, easily distinguishable from the supraglenoidal tubercle (0), or reduced, weakly distinguishable from the supraglenoidal tubercle (1)
137. Skeleton – Scapula = glenoid cavity oval (0), or rectangular (1)
138. Skeleton – Humerus = humeral crest weakly laterally extended (0), laterally laterally extended (1), or significantly laterally extended (2)
139. Skeleton – Humerus = deltoid process medium-sized (0), reduced to a scar on the humeral crest (1), or massive (2)
140. Skeleton – Humerus = medial supra-condylar crest strongly (0), or poorly extended laterally (1)
141. Skeleton – Humerus = entepicondylar foramen present (0), or absent (1)
142. Skeleton – Humerus = lateral supracondylar crest low (0), high (1/4 of the length of the femur) (1), very high (1/3 of the length of the femur) (2)
143. Skeleton – Humerus = lateral supracondylar crest not (0), weakly (1), or strongly (2) extended laterally
144. Skeleton – Humerus = humeral trochlea strongly concave (0), or almost flat (1)
145. Skeleton – Humerus = medial condyle of the trochlea narrower (0), wider (1), or as wide as the lateral condyl (2)
146. Skeleton – Humerus = olecranon fossa deep (0), or shallow (1)
147. Skeleton – Humerus = trochiter anterior (0), or lateral to the head (1)
148. Skeleton – Ulna = diaphysis antero-medially flatenned (0), or tiangular to quadrangular (1)
149. Skeleton – Ulna = synovial groove present (0), or absent (1)
150. Skeleton – Ulna = proximal surface for the radius rugose (0), smooth, wiht a well delimited facet (1)
151. Skeleton – Ulna = olecranon narrow (0), weakly enlarged posteriorly (1), or significantly enlarged posteriorly (2)
152. Skeleton – Ulna = olecranon strongly extended proximally (of more than the height of the sigmoid cavity) (0), extended proximally (of less than the height of the sigmoid cavity) (1), ornot extended proximally (olecranon perpendicular to the sigmoid cavity) (2)
153. Skeleton – Ulna = lateral sigmodd facet reduced to absent (0), developped (1)
154. Skeleton – Radius = as massive as the ulna (0), less massive than the ulna (1)
155. Skeleton – Radius = proximal extremity as wide (0), or narrower than the proximal articulation of the ulna
156. Skeleton – Lunar = rectangular, longer than wider (0), or triangular in proximal view (1)
157. Skeleton – Lunar = contact facet for the ulna absent (0), or present (1)
158. Skeleton – Lunar = contact facet for a free central bone present (0), or absent (1)
159. Skeleton – Lunar = contact facet for the unciform present (0), or absent (1)
160. Skeleton – Lunar = unique (0), or double contact for the scaphoid (1)
161. Skeleton – Lunar = contact facet for the scaphoid perpendicular (0), or inclined with respesct of the distal articulation of the lunar
162. Skeleton – Cuneiform = in occlusal view, lateral hook perpendicular (0), or at 45° to the mediolateral axis of the bone
163. Skeleton – Cuneiform = unique (0), or double contact for the lunar (1)
164. Skeleton – Cuneiform = ulnar facet antero-posteriorly concave (0), or antero-posteriorly concave and medio-laterally convex (1)
165. Skeleton – Cuneiform = contact facet for the Mc V absent (0), or present (1)
166. Skeleton – Cuneiform = contact facet for the pisiform wide (0), or narrow (1)
167. Skeleton – Cuneiform = contact facet for the pisiform concave (0), or flat (1)
168. Skeleton – Magnum = facet for the Mc II absent (0), or present (1)
169. Skeleton – Magnum = facet for the lunar concave (0), or convex in lateral or medial view (1)
170. Skeleton – Magnum = anterior half wider (0), as wide (1), or narrower than the posterior half
171. Skeleton – Unciform = contact facet for the Mc III reduced to absent (0), or long (1)
172. Skeleton – Ilion = narrow (0), or wide (1)
173. Skeleton – Femur = diaphysis quadrangular (0), or antero-posteriorly flattened (1)
174. Skeleton – Femur = neck present (0), or absent (1)
175. Skeleton – Femur = head medially inclined (0), parallel (1), or perpendicular to the diaphysis axis (2)
176. Skeleton – Femur = greater trochanter massive, high above the head (0), massive, lower than the head (1), or reduced (2)

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177. Skeleton – Femur = neck long (0), or short (1)
178. Skeleton – Femur = small trochanter massive and medially extended (0), reduced and poorly medially extended (1), or massive and posteriorly extended (2)
179. Skeleton – Femur = third trochanter present (0), or absent (1)
180. Skeleton – Femur = third trochanter massive and srongly laterally extended (0), or reduced (1)
181. Skeleton – Femur = distal extremity as wide (0), or narrower than the proximal extremity (1)
182. Skeleton – Femur = trochlea extending strongly (0), or weakly proximally extended on the anterior face of the diaphysis (1)
183. Skeleton – Femur = head antero-medially oriented (0), or medially oriented (1)
184. Skeleton – Femur = medial condyle as wide (0), or wider than the lateral condyle (1)
185. Skeleton – Femur = as long as the tibia (0), or much longer than the tibia (1)
186. Skeleton – Tibia = section of the diaphysis triangular (0), or oval (1)
187. Skeleton – Tibia = tuberuculum intercondylare absent (0), or present (1)
188. Skeleton – Tibia = area intercondilaris cranialis horizontal (0), at 45° (1), or vertical (2)
189. Skeleton – Tibia = anterior tuberosity developed (0), massive (1), or very reduced (2)
190. Skeleton – Tibia = diaphysis straight (0), postero-laterally (1), or postero-medially twisted (2)
191. Skeleton – Tibia = tibial cochlea with two (0), or one concavity (1)
192. Skeleton – Fibula = facet for the astragalus strongly (0), or weakly (1) inclined with respect of the facet for the calacaneum
193. Skeleton – Astragalus = tuberculum mediale absent (0), or present (1)
194. Skeleton – Astragalus = sustentacular facet as long (0), shorter (1), or longer than the ectal facet
195. Skeleton – Astragalus = sustentacular facet does not join (0), or joins the navicular facet (1)
196. Skeleton – Astragalus = ectal facet as wide (0), narrower (1), or wider than the than the sustentacular facet
197. Skeleton – Astragalus = fibular facet wide (0), or narrow (1)
198. Skeleton – Astragalus = foramen astragali present (0), or absent (1)
199. Skeleton – Astragalus = fibular facet weakly inclined with respect of the tibial facet (0), or perpendicular to the tibial facet (1)
200. Skeleton – Astragalus = in lateral view, navicular facet anteriorly oriented (0), or antero-ventrally oriented (1)
201. Skeleton – Astragalus = in anterior view, navicular facet horizontally oriented (0), or disto-medially oriented (1)
202. Skeleton – Astragalus = neck long (0), or short (1)
203. Skeleton – Astragalus = crista capitatis present (0), or absent (1)
204. Skeleton – Astragalus = tibial facet strongly concave (0), weakly concave (1), or flat (2)
205. Skeleton – Calcaneum = ectal and sustentacular facets inclined with respect of the facet for the cuboid (0), or perpendicular to the facet for the cuboid (1)
206. Skeleton – Calcaneum = tuber calcanei narrow (0), or enlarged posteriorly (1)
207. Skeleton – Calcaneum = sustentacular facet strongly convex in its posterior half (0), strongly convex in its anterior half (1), or flat (2)

Appendix 2

Data matrix

Phenacodus

0000000000	0000000000	0000000010	0020000000	0000000100	0000011100	0000000000
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0000000000	0000000000	0000000000	?000000000	0000000000	0000000000	0000000

Tetraclaenodon

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0000000000	0000000000	0000000000	?000000000	0000000000	0000000000	0000000

Anthracobune

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Behemotops

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0010-01???	??10011100	1-10000???	?010020000	1010000100	1000011-00	??????????
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Prorastomidae

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Phosphatherium escuilliei

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1-00-00100	000001001-	1-10100???	?010100000	1000011000	2001100000	??????????
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Daouitherium rebouli

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Numidotherium koholense

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1-11-000-0	010010-01-	1-10110000	1110100000	1000001001	1001000100	1100201200
0120000001	?100001010	1101100110	1110011101	10001?1???	1010020110	0111010

Arcanotherium savagei

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021?101??1	01001??001	??100??101	0111110111	-10101011-	1001100100	011021????
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Barytherium grave

?012?1111?	??10?221??	103111?141	?100011111	0111101110	1111100001	-1101-11-
1-11-000-0	010010-00-	1-10110101	1111110111	-101011001	1001100100	1101210200
1120?00011	1100001010	1???101111	?11111-101	1110101011	1112110110	011201?

Moeritherium

0012111111	1100112121	1021111131	11?0001010	0121101?00	1100?01100	1100010101
0?10111111	0?10111001	0?10010010	0?00??00?0	?00000011-	200001?-??	0011110110
100110001?	101???????	??????????	?01020121-	111010122?	?010020110	011?00?

Prodeinotherium

1111111111	1?21021121	1112111132	112111-122	11111-----	----101110	11211--11-
1-10-10121	110010-00-	1-11111---	-110011000	001010011-	2101011-00	1102211111
1111111110	2211111111	0111111102	111112-11-	1111111221	1011021111	1112111

Phiomia

1110111111	?110011121	1112111112	1101111112	1111110001	-001010000	1131010101
0110111121	1011012000	0111011---	-110-30000	001010011-	2111011-11	001????201
1111111110	2211111111	0111111???	1?????????	?????11101	1110121111	1112111

Palaeomastodon

??10??????	?????211??	?112111162	1101111112	1111110001	-001010000	1121010101
011011112?	10?111200?	???1?11---	-??0????0?	??1?10011-	2111011-10	0012211201
111111????	??????????	??????????	??10021101	1101111101	1?????????	????111

Chilgatherium harrisi

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