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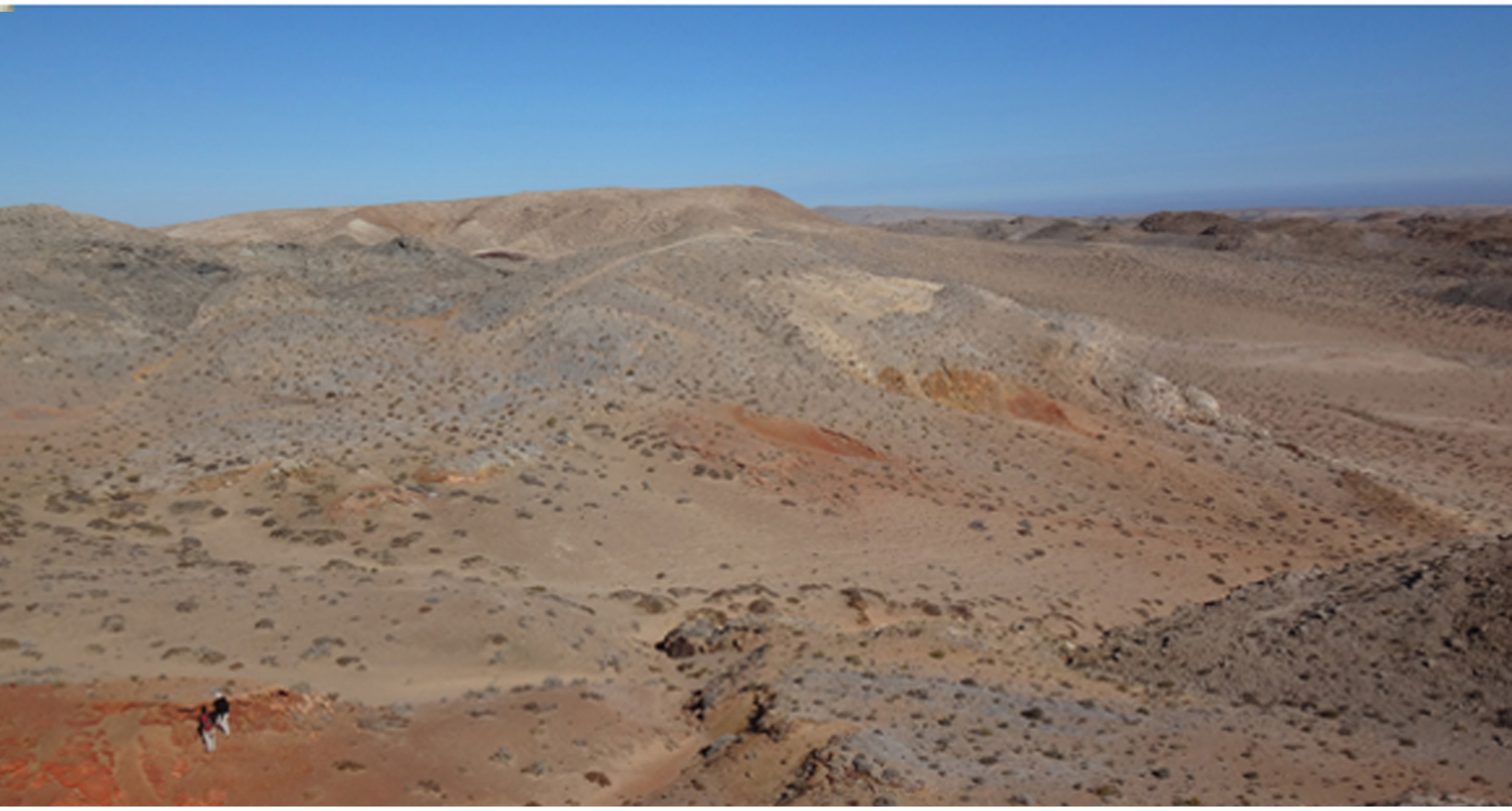

MINISTRY OF MINES AND ENERGY

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### PAPERS

**Cover Image** : Geologists studying the Bo Alterite in the type outcrops 1 km north of Chalcedon Tafelberg (in the background), Sperrgebiet, Namibia

# Encore Hippo-thèses: Head and neck posture in *Brachyodus* (Mammalia, Anthracotheriidae) and its bearing on hippopotamid origins

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**Abstract**: Five almost complete cervical vertebrae and fragments of the sixth, associated with a partial cranium and limb bones of the bothriodontine *Brachyodus aequatorialis* from Early Miocene fluvial deposits at Grillental VI, Northern Sperrgebiet, Namibia, reveal not only that this anthracothere possessed a relatively elongated neck in contrast to hippopotami which have considerably shorter necks, but also that the morphology of the neck vertebrae in these two families is radically divergent, those of *Brachyodus* are closer morphologically to those of tragulids, while hippopotamid vertebrae are most similar to those of Palaeochoeridae. This discovery adds to the long suite of characters by which the skeleton of anthracotheres differs from that of hippopotamids, making it unlikely that the former gave rise to the latter, thereby running counter to repeated claims in recent literature to the effect that hippopotamids descended from anthracotheres.

**Key Words**: *Brachyodus*, Cervical vertebrae, Neck, Head posture, Anthracotheriidae, Hippopotamidae, Neogene, Namibia

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Submitted in 2015.

## Introduction

In 2006, a partial skeleton of an adult individual of *Brachyodus aequatorialis* was discovered embedded in Early Miocene fluvial silts at Grillental VI, Northern Sperrgebiet, Namibia (Pickford, 2008a, 2008b). The fossiliferous deposits were partly covered by a dune which gradually shifted northwards exposing more of the skeleton. Two years later the neck vertebrae in articulation were exposed 50 cm from where the skull had been collected. They were excavated in a block, protected in a plaster jacket, and transported to Paris for preparation. The bones are traversed by numerous fine cracks which rendered preparation delicate, but with careful use of glue and consolidant they were extracted from the matrix in relatively good condition by Philippe Richir, showing minor distortion and minimal matrix expansion damage. During cleaning a manual second phalanx and two sesamoids were found in the sediment suggesting that the fore foot of the individual was buried close to its neck. A year later two vertebrae from the trunk - the last thoracic and first lumbar vertebrae - were found in connection but they are less well preserved, being represented mainly by the centra and detached transverse processes. A calcaneum was collected in 2011 and a navicular in 2015, both bones within half a metre of the skull, and thus likely from the same individual.

Anthracothere vertebrae are poorly represented in the palaeontological literature, partly due to the fact that not much attention is given to fossil mammalian vertebrae in general, but partly because isolated vertebrae can be difficult to attribute to taxa which are usually defined on the basis of skulls and teeth. Thus, the discovery, in the Early Miocene of Namibia, of vertebrae associated with a skull and limb bones of *Brachyodus aequatorialis* provides a rare opportunity to study aspects of the vertebral column of this extinct group of mammals.

There are a few descriptions of anthracothere vertebrae available, accompanied by illustrations (Falconer & Cautley, 1848; Kowalevsky, 1874; Scott, 1894, 1895, 1896, 1940; Geais, 1934; Kron & Manning, 1998). This paper aims to describe the Grillental specimens and to compare them to the cervical vertebrae of Hippopotamidae and other artiodactyls (pecorans, tragulids, palaeochoerids, tayasssuids, entelodonts) in order to determine whether the supposedly close relationship between hippos and anthracotheres repeatedly postulated in recent literature (Boisserie & Lihoreau, 2006; Boisserie *et al.* 2005a, 2005b; Lihoreau & Boisserie, 2004; Lihoreau *et al.* 2015; Orliac *et al.* 2010) is tenable or not (Pickford, 2008b, 2011).

Pickford (2008b) mentioned the discovery of the neck vertebrae of *Brachyodus* at Grillental, Namibia, but at the time of writing the specimen was still in its plaster jacket. Despite this it was possible to see that the neck of this genus was long, as is that of *Merycopotamus* Falconer & Cautley, 1845 (Lydekker, 1876) and unlike those of hippopotamids which are considerable shorter. Crusafont-Pairo (1979) misattributed an atlas of the anthracothere *Libycosaurus anisae* to Giraffidae on account of its unusual length (Pickford, 2008b).

The paper sets out with some general observations about neck length, head carriage (posture) and osteology of cervical vertebrae in artiodactyls as background information for interpreting the fossil specimens from Namibia (Table 1).

**Table 1. Cervical vertebrae and other material studied**

- Anthracotheriidae
  - *Brachyodus aequatorialis* GSN GT 88’06
  - *Elomeryx borbonicus* UCBL Sciences de la Terre 1408 (St Henri, Geais, 1934, pl. 3, fig. 9)
  - *Morotochoerus ugandensis* UM MOR I, 15’98
- Palaeochoeridae
  - *Propalaeochoerus elaverensis* FSL, Collection Hugueney (Coderet)
  - *Choeromorus inonuensis* Maden Tetkik ve Arama, Ankara, Turkey, Aki 3/4
- Hippopotamidae
  - *Hippopotamus amphibius* MNHN A 7985, MNHN A 7986, MNHN Sans N° A, Sans N° B.
  - *Choeropsis liberiensis* MNHN A 67, MNHN 1948-1
- Tayassuidae
  - *Pecari tajacu (*labelled *Dicotyles torquatus)* MNHN A 12587 (1870-132), A 9871 (1898-304)
- Suidae
  - *Sus scrofa* MNHN A 8794
  - *Potamochoerus porcus* MNHN 1878-454
  - *Phacochoerus aethiopicus* MNHN A 14037
- Camelidae
  - *Camelus dromedarius* MNHN A 7984
- Tragulidae
  - *Tragulus javanicus* MNHN A 3370
  - *Tragulus napu* MNHN A 3373
  - *Hyaemoschus aquaticus* MNHN 1914-97
- Giraffidae
  - *Okapia johnstoni* MNHN A 14703 (1904-57)
  - *Giraffa camelopardalis* MNHN A 10617, A 7977
- Bovidae
  - *Taurotragus oryx* MNHN A 8001

For the purposes of this paper, individual vertebral centra were measured on the ventral side from the proximal to the distal epiphysis, excluding the hypapophyseal tubercle, which can extend distally somewhat, even overlapping the proximal part of the next vertebra in line. By this means the lengths of the centra of the various sectors of the vertebral column can be compared in a relatively precise way, and this acts as a proxy for neck length relative to trunk length, for example. The data can be presented in a graphic way.

**Table 2. Abbreviations**

FSL – Faculté des Sciences, Lyon
GSN – Geological Survey of Namibia
GT – Grillental
MNHN – Muséum National d'Histoire Naturelle, Paris
MOR - Moroto
NHMUK – Natural History Museum, London, UK
UCBL – Université Claude Bernard, Lyon
UM – Uganda Museum, Kampala

## Genera and species mentioned in this paper (Table3)

**Table 3**. Alphabetical list of genera and species mentioned in this paper.

| Genus | Author, year | Species | Author, year |
|---|---|---|---|
| *Blastocerus* | Illiger, 1815 | | |
| *Brachyodus* | Depéret, 1895 | *Brachyodus aequatorialis*<br>*Brachyodus onoideus* | MacInnes, 1951<br>(Gervais, 1859) |
| *Camelus* | Linnaeus, 1758 | *Camelus domedarius* | Linnaeus, 1758 |
| *Cervus* | Linnaeus, 1758 | *Cervus unicolor* | Kerr, 1792 |
| *Choeropsis* | Leidy, 1854 | *Choeropsis liberiensis* | (Morton, 1849) |
| *Choeromorus* | Gervais, 1850 | *Choeromorus inonuensis* | Pickford & Ertürk, 1979 |
| *Doliochoerus* | Filhol, 1882 | *Doliochoerus quercyi* | Filhol, 1882 |
| *Dorcabune* | Pilgrim, 1910 | *Dorcabune anthracotherioides* | Pilgrim, 1915 |
| *Elomeryx* | Marsh, 1894 | *Elomeryx borbonicus* | (Geais, 1934) |
| *Elotherium* | Pomel, 1847a | | |
| *Epirigenys* | Lihoreau *et al.* 2015 | *Epirigenys lokonensis* | Lihoreau *et al.* 2015 |
| *Giraffa* | Brisson, 1756 | *Giraffa camelopardalis* | (Linnaeus, 1758) |
| *Hippopotamus* | Linnaeus, 1758 | *Hippopotamus amphibius* | Linnaeus, 1758 |
| *Hyemoschus* | Ogilby, 1841 | *Hyemoschus aquaticus* | Ogilby, 1841 |
| *Libycosaurus* | Bonarelli, 1947 | | |
| *Merycopotamus* | Falconer & Cautley, 1845 | | |
| *Morotochoerus* | Pickford, 1998 | *Morotochoerus ugandansis* | Pickford, 1998 |
| *Okapia* | Lankester, 1901 | *Okapia johnstoni* | Sclater, 1901 |
| *Palaeochoerus* | Pomel, 1847b | | |
| *Palaeopotamus* | Pickford, 2007 | *Palaeopotamus ternani* | (Pickford, 1983) |
| *Panthera* | Oken, 1816 | *Panthera leo* | (Linnaeus, 1758) |
| *Pecari* | Linnaeus, 1758 | *Pecari tajacu* | Linnaeus, 1758 |
| *Pecarichoerus* | Colbert, 1935b | | |
| *Phacochoerus* | F. Cuvier, 1826 | *Phacochoerus aethiopicus* | (Pallas, 1767) |
| *Potamochoerus* | Gray, 1854 | *Potamochoerus porcus* | (Linnaeus, 1758) |
| *Propalaeochoerus* | Stehlin, 1899-1900 | *Propalaeochoerus elaverensis* | Viret, 1929 |
| *Schizoporcus* | Van der Made, 2010 | | |
| *Sus* | Linnaeus 1758 | *Sus scrofa* | Linnaeus, 1758 |
| *Taurotragus* | Wagner, 1855 | *Taurotragus oryx* | (Pallas, 1766) |
| *Tayassu* | Fischer de Waldheim, 1814 | | |
| *Tragulus* | Pallas, 1767 | *Tragulus javanicus*<br>*Tragulus napu* | (Osbeck, 1765)<br>(F. Cuvier, 1822) |

## Generalities Concerning the Osteology of Artiodactyl Cervical Vertebrae

In mammals the neck is generally comprised of seven vertebrae (Flower, 1876). Artiodactyls provide no exceptions to this general rule, even those with extremely elongated necks such as camels and giraffes (but for a discussion of this point see Lönnig, 2011), but the aquatic manatees do, since they possess only six cervical vertebrae (Flower, 1876).

Flower (1876) wrote "*Among the Ungulata, the atlas in the Pecora is very long, with deep articular cavities for the occipital condyles. The transverse processes are not wide, but much extended from before backwards, and flattened from above downwards. Each is perforated by a foramen which gives exit to the inferior division of the first cervical nerve, but not by the vertebral artery, which usually enters the neural canal between the arches of the second and third vertebrae. The odontoid process of the axis is of peculiar shape, being like a spout, or hollow half-*

*cylinder, with a prominent sharp semicircular rim. The canal for the second cervical spinal nerve pierces the lamina of the axis near its anterior border. The other vertebrae have more or less elongated bodies, which are opisthocoelus, i.e. concave behind and convex in front. They are keeled below, the keel being often developed into a hypapophysial spine posteriorly; the neural spines are moderately long, and inclined forwards……… The Suina and Tragulina differ from the remaining existing Artiodactyles in the form of the odontoid process, which is conical; while on the other hand the Horse and Tapir* among the Perissodactyles have this process wide, flat, and hollowed above, approaching the form it presents in the Ruminants. In the Pig, the broad pedicles of all the cervical vertebrae are perforated by canals for the passage of the upper division of the spinal nerves. The bodies of the cervical vertebrae in the Rhinoceros, Tapir, and Horse are markedly opisthocoelous, but in the Pig and* Hippopotamus *very slightly so*".

(* Flower (1876) is incorrect about the form of the odontoid process in tapirs – it is peg-like, with a cone-in-cone morphology of the atlanto-axial articulation).

## Functional significance of cervical vertebral morphology

The neck of an animal not only links the head to the body, but it also constitutes a remarkable organ with multiple functions related to head posture and cranio-cervical mobility among others. Leaving aside the soft tissues, since in palaeontology we usually deal mainly with bones, the morphology of the cervical vertebrae reveals a great deal about the animal's carriage of the head and how it and the neck bones may have moved relative to each other and as a chain of connected bones.

As concerns intervertebral movements, they can be subdivided into three categories reflecting three axes of movement which are at right angles to each other (Fig. 1) - pitch, roll and yaw - which can be combined into a bewildering variety of complex movements, such as the "necking" behaviour of giraffes (dominance behaviour) (MacDonald, 2001). Change of pitch refers to the up-and-down movements (extension and flexion) of the head and neck vertebrae, as when nodding (in humans signifying YES!). Yaw refers to the side-to-side movements (bending) of the head and vertebrae, as in humans when lowering the head towards the shoulders, whereas roll refers to the rotation of the vertebrae relative to each other (turning the head) as, for example, when shaking the head (in humans to signify NO!), the latter movement being minimal at the occipital condyles (cranio-atlantal joint) but maximal at the atlanto-axial joint. Joints between the axis and the third to seventh cervical vertebrae (C3-C7) are via intervertebral discs which are slightly flexible cartilaginous plates, more or less thick, often with low concentric ridges proximally and distally (reflected as imprints in the surface of the epiphyses). The intervertebral discs are tough, but they permit minor stretching and compression and even slight rotation (roll), meaning that minor intervertebral movements of pitch, yaw and to a lesser extent, roll, are possible all down the neck. When combined along the length of the neck, these minor movements between individual vertebrae can add up to significant potential for bending, twisting and rolling the neck.

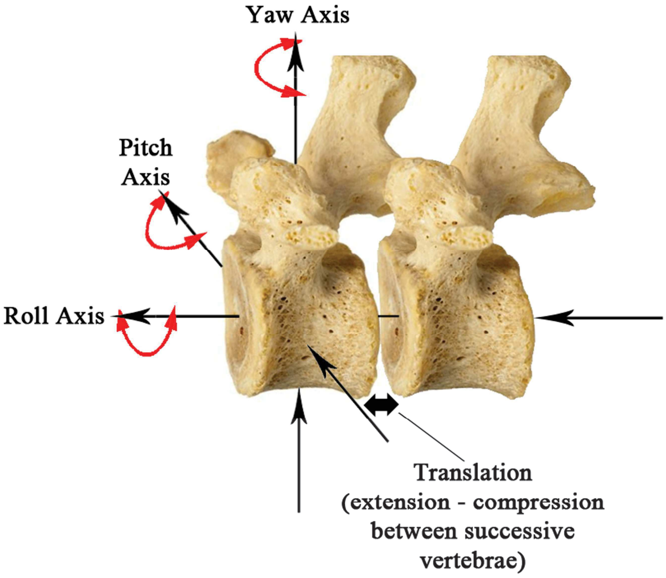

**Figure 1**. Definition of the three axes of movements possible in the neck of vertebrates (roll, pitch and yaw). The vertebrae shown are of a human being. In addition, a small degree of compression and extension of the intervertebral discs is possible, called translation.

Opisthocoely refers to the curvature of the epiphyses of the vertebrae. In mammals the anterior epiphysis is usually convex or flat, the posterior one concave or flat. In mammals in which intervertebral yaw movements are emphasised over pitch and roll, the epiphyses are dorso-ventrally taller than the bilateral dimension. In those in which pitch movements are emphasised, the bilateral dimension of the epiphysis is greater than the dorso-ventral one. In animals such as snakes, in which the intervertebral joint permits extensive pitch, roll and yaw, the epiphyses are almost hemi-spherical. Table 4 summarises some of the main points about cervical vertebrae studied in this paper

**Table 4.** Summary of functional significance of cervical vertebrae.

| **Morphology** | **Functional significance** | **Remarks** |
|---|---|---|
| Occipital condyle morphology | Permits pitch and yaw movements of the cranium relative to the atlas but prevents roll at this joint | General condition in mammals |
| Atlanto-axial articular surface | Permits roll movements of the atlas relative to the axis, but restricts pitch and yaw movements | General condition in mammals |
| Opisthocoely of C3-C7 | Permits relatively minor pitch and yaw movements by stretching and compressing the intervertebral discs, minimises but does not completely prevent roll movements depending on the outline of the epiphysis (tall and narrow epiphysis emphasises yaw at the expense of pitch, broad and low epiphysis emphasises pitch over yaw) | Present in anthracotheres, tragulids and pecorans, absent in hippopotamids, tayassuids, palaeochoerids and suids |
| Flattening of the epiphyses of the centra of C2-C7 | Levels or lowers the head, restricts pitch, yaw and roll movements | Present in hippopotamids, tayassuids, palaeochoerids and suids, absent in anthracotheres, tragulids and pecorans |
| Canting of centra of C2-C7 | Elevates the head | Accented in anthracotheres, tragulids and many pecorans, reduced in hippopotamids |
| Elongation of centra of C3-C7, relative to thoracic and lumbar centra | Lengthens the neck relative to the body | Long in anthracotheres and many ruminants, shorter in hippopotamids |
| Conical atlanto-axial articulation | Cone-in-cone articular surfaces allow minor extensional-compressional (telescoping) movements of vertebrae in head-down posture, and minimise possibility of dislocation of the joint during yaw and pitch movements | Present in hippopotamids, tayassuids, palaeochoerids and suids, absent in anthracotheres, tragulids and pecorans |
| Conical, peg-like odontoid | Forms an anteriorly projecting continuation of | Present in hippopotamids, tayassuids, |

| | | |
|---|---|---|
| process of axis | the cone-in-cone morphology of the atlanto-axial joint | palaeochoerids and suids, absent in anthacotheres, tragulids and pecorans |
| Planar atlanto-axial articulation (base plate morphology) with hemi-cylindrical odontoid process anteriorly | Provides flattened support surface for elevated head, hinders telescoping of joint in head-up postures | Present in anthracotheres, tragulids and pecorans, absent in hippopotamids, tayassuids, palaeochoerids and suids |
| Shortening of vertebrae C3-C7 relative to thoracic and lumbar vertebrae | Shortens the neck relative to the body | Short in hippopotamids, tayassuids, suids (and probably palaeochoerids) : long in anthracotheres, tragulids and pecorans |
| Compressed odontoid process with lateral flanges in axis | Forms an atlanto-axial joint surface comprising two articular surfaces at right angles to each other (base plate and dens) | Present in anthracotheres and tragulids, taken to extreme in pecorans, absent in hippopotamids, tayassuids, palaeochoerids and suids |
| V-shaped hypapohyseal tubercle of axis | Provides increased surface area for attachment of the ventral longitudinal ligament and provides two areas of attachment for intervertebral ligaments | Present in hippopotamids, tayassuids and palaeochoerids and suids, absent in anthracotheres, tragulids and pecorans |
| Undivided hypapophyseal tubercles of axis | Provides a single point of attachment for ventral longitudinal ligament and intervertebral ligaments | Present in anthracotheres, tragulids and pecorans, absent in hippopotamids, tayassuids, palaeochoerids and suids |
| Ventral hypapophyseal process | Subdivides the ventral surface of the centrum into two halves and provides attachment surfaces for the ventral longitudinal ligament and intervertebral ligaments | Low and blunt in hippopotamids, suids and tayassuids, taller and sharper, increasing in relief posteriorly, in ruminants and *Brachyodus* |

## Definition of neck length

There are several loose definitions of neck length in mammals, most of them comparing neck length with trunk length, or length of the thoracic chain. There are various factors that can make such comparison of sectors of the vertebral column rather imprecise. The number of vertebrae in a sector can vary, but this is not a serious problem among artiodactyls except for the tail in which the number of vertebrae, and thus tail length, varies tremendously. Hippopotamids generally have 15 thoracic vertebrae (Gratiolet, 1867; Milne-Edwards, 1868), suids, tayassuids and *Okapia* generally have 14, and *Tragulus* and *Taurotragus* have 13. Cartilaginous inter-vertebral discs and other soft tissues can increase the length of a sector by up to 15% compared to dry vertebrae articulated together. For curved sectors of the vertebral column such as the thorax there is the problem of determining the linear length of a curved complex, the ventral length measured along the curve being different from the dorsal length, for example. In fossil mammals in which the intervertebral discs are usually missing or damaged, and in which the vertebral column is often incomplete, it is usually not possible to compare entire sectors of the vertebral column.

In short necked artiodactyls such as *Hippopotamus* and *Choeropsis*, the individual centra of C3-C6 are shorter than all but the shortest of the centra of individual thoracic or lumbar vertebrae of the same individual. Long necked artiodactyls such as *Brachyodus* and *Taurotragus* show the opposite relationship, with the cervical centra being longer than those of the thoracic and lumbar vertebrae. In very long necked artiodactyls such as *Giraffa* and *Okapia*, the centra of the cervical vertebrae are two to three times longer than those of the thoracic and lumbar vertebrae.

## Vertebral canting

The “cant” of vertebral centra refers to the angle between the floor of the neural canal and the epiphyseal surfaces. These two surfaces can be almost a right angles to each other (low canting as in Hippopotamidae) or can be at up to 30° from the right angle (high canting, as in many pecorans). Anthracotheres show high canting of the neck vertebrae (Fig. 2).

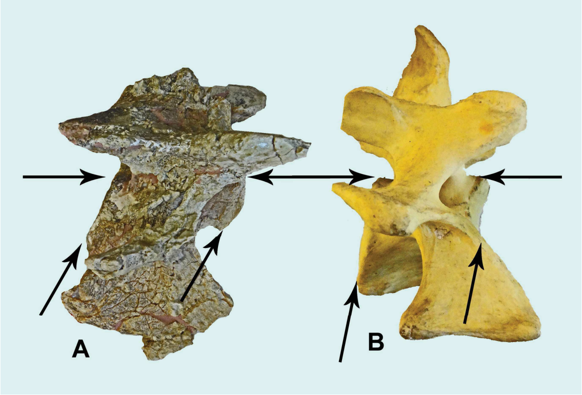

**Figure 2**. Canting in cervical vertebrae of A) *Brachyodus*, B) *Choeropsis* with the floor of the neural canal oriented horizontally. Note the difference between the orientations of the plane of the epiphyses, more inclined in *Brachyodus* than in *Choeropsis* (not to scale).

## Definition of Head Posture

For the purposes of this paper, head posture is assessed while the animal is walking or resting in a relaxed way (Fig. 3). During feeding and other behaviour (such as threat displays, neck fighting, head butting and so on) the head can be held in many different poses ranging from extremely low (while grazing on short grass, for example) to extremely high (while stretching upwards to reach leaves high in trees, for instance), or more or less in line with the vertebral column (during male-to-male head butting, for example) and these positions are often significantly different from the relaxed walking posture.

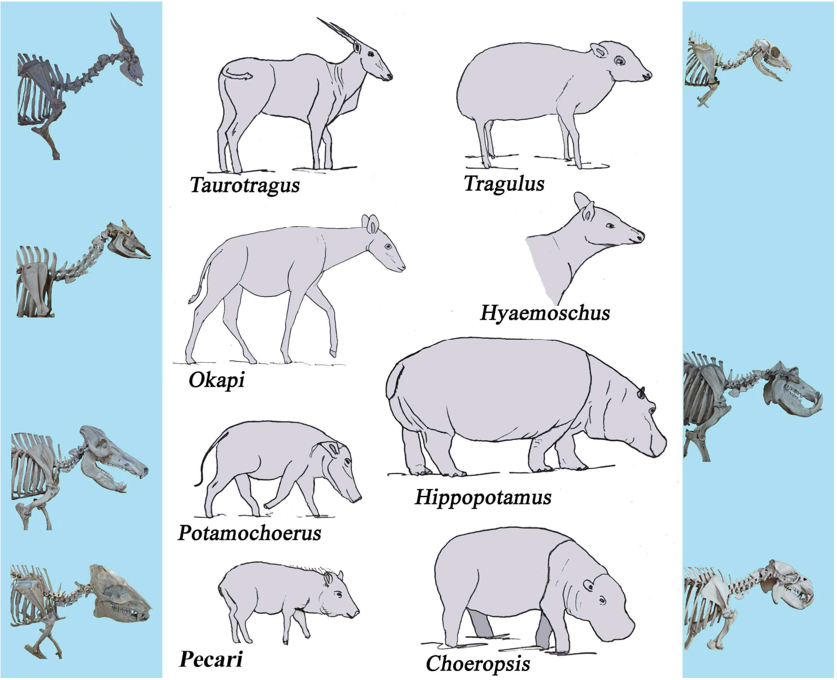

**Figure 3**. Head posture and neck length in diverse artiodactyls. Pecorans (*Taurotragus* and *Okapia*) have relatively long necks with the top of the head usually held above the shoulders, tragulids (*Tragulus* and *Hyaemoschus*) possess shorter necks, but the head is still held above the shoulders and the occiput is low. Suidae (*Sus*) and Tayassuidae (*Pecari*) have short necks with the head usually held lower than the shoulders, and Hippopotamidae (*Hippopotamus* and *Choeropsis*) have short necks with the head habitually held lower than the shoulders. On the basis of their neck vertebrae, anthracotheres are closer to tragulids and pecorans in terms of neck length and head posture.

## Generalities on head posture and neck length in Artiodactyla

Artiodactyls display a wide range of head posture and neck length which is reflected in the osteology of the cervical vertebrae and the height of the occiput relative to the occipital condyles. Despite the wide range of osteological variation of the neck bones that is encountered in this order, the diversity can be grouped into three broad categories on the basis of the shape and function of the atlanto-axial joint and other parts of the cervical chain. These broad groups are capable of further subdivision on the basis of additional morphological characters.

The first category comprises hippopotamids, suids, tayassuids and palaeochoerids. The second group consists of the traguloids (*Tragulus*, *Hyaemoschus*) and the third group assembles the pecorans (bovids, cervids and giraffids). Anthracotheres possess an atlanto-axial articulation close to the second category, and which is markedly different from that of the first and third.

In the first category (eg suoids), the odontoid process of the axis is conical (peg-like) and the lateral articular facets face strongly antero-laterally at an angle of about 45° to the sagittal plane, the ensemble forming a conical articular surface (cone-in-cone when articulated with the atlas). In the second category (ie traguloids), the odontoid process is somewhat compressed dorso-ventrally, separated from small anteriorly directed flanges on the medial part of the lateral facets and the articulation is comprised of two surfaces at right angles to each other, comprising a cylinder-in-cylinder odontoid part, and a plate-on-plate centrum part (the base plate). The lateral facets face antero-laterally but are more anteriorly facing than in the first category, ca 30° to the sagittal plane. In the third category (ie pecorans), the odontoid process is highly compressed in the dorso-ventral direction, and is confluent with the flanges on the lateral facets, which face almost directly anteriorly (ie parallel to the roll axis) comprising the half-cylinder morphology described by Flower (1876), behind which is the plate-on-plate articulation (base plate) of the anterior epiphysis of the centrum.

Examination of other morphological features of the cervical column, of which there are many, result is similar tripartite groupings, the taxa in the first group generally possessing short necks, while those in the second group longer necks than those in the first group, and the third category much elongated necks.

There are other differences, such as the degree of opisthocoely developed, the first group having relatively flat vertebral epiphyses in the 3rd to 7th cervical vertebra and at the rear of the axis. The second and third categories tend to have slight to marked opisthocoely in the homologous joints (ie the distal end of the centrum is concave, the anterior end convex).

In artiodactyls, the anterior epiphysis of the cervical vertebrae tends to be more hemispherical in the long necked forms (*Giraffa*, *Okapia*) and almost flat in the short-necked forms such as *Hippopotamus* (Blainville, 1847). When measuring centrum length, the protocol used was to measure the length at the ventral border of the epiphysis rather than in its centre mainly in order to avoid the effects of opisthocoely, but also because in mounted specimens, the middle of the centrum is not usually accessible. This protocol provides accurate estimates of centrum length in taxa with relatively flat centra, but underestimates total centrum length in long-necked taxa such as *Giraffa*.

The cervical vertebrae are held in position relative to one another by a variety of tissues, such as ligaments and tendons (attached to muscles) which insert onto processes, flanges and tubercles on the dorsal, lateral and ventral surfaces (Saban, 1971). Between the vertebrae (from the rear of C2 (the axis) to the rear of C7) the epiphyses are strongly connected to each other via cartilaginous intervertebral discs which hold the joints together, but which are pliable enough to allow slight bending movements (up and down, side to side) but only minor rotatory movement. The bony column is surrounded by ligaments, muscular tissues, nerves, and blood vessels, all of which have some relation with the cervical vertebrae. For example, each vertebra possesses foramina for the passage of nerves and blood vessels. The position and extent of these foramina vary from taxon to taxon. For example, the axis of the suids possess a posterior foramen for the second vertebral nerve which pierces the base of the transverse process, whereas, in anthracotheres, the nerve passes backwards in a similar position, but it lies above the transverse process in a groove rather than passing through it.

The centrum of the axis is usually marked by a ventral antero-posterior ridge which terminates backwards in a swelling, the hypapophyseal tubercle, which usually extends a short distance beyond the body of the centrum. In most artiodactyls, the hypapophyseal tubercle is simple, but in the Suoidea the central ridge bifurcates or forks before reaching the hypapophyseal tubercle, forming a broad triangular, v-shaped structure with a central depression. This morphology is found in Hippopotamidae (*Hippopotamus* and *Choeropsis*), the Suidae (*Sus*, *Potamochoerus*), Tayassuidae (*Pecari*, *Tayassu*) and Palaeochoeridae (*Propalaeochoerus*). Scott (1898) reported a similar morphology in the entelodont genus *Elotherium* (he described the ventral tubercles as being trifid and wrote that *Hippopotamus* presented very similar morphology). It has not been observed in any traguloids or pecorans and it does not occur in the few anthracotheres for which the axis is known. Somewhat similar v-shaped morphology of the tubercle occurs in the lion, *Panthera leo*, but in the latter species the centre of the "v" has a low accessory bony mound, not found in any of the Artiodactyla which possess such a v-shaped hypapophyseal tubercle on the axis. The third cervical vertebra of the suoids and entelodonts also shows the v-shaped posterior termination of the hypapophyseal process, but the forking tends to diminish in the fourth and subsequent vertebrae, although in *Pecari*, it is evident right back to the 5th cervical vertebra (Fig. 8).

## Osteological Specificities of Cervical Vertebrae

The proximal cervical vertebra is the atlas (C1) which articulates with the occipital condyles of the head in front and with the axis vertebra behind. It is usually considerably broader than long with deep articular facets anteriorly for the occipital condyles of the skull and shallower facets posteriorly for the axis. In the posterior ventral part of the neural canal, there is an articular surface for the odontoid process of the axis which extends from the base of the canal upwards either side terminating at the base of the laminae. In suoids, the neural canal is comprised of two moieties, a broader dorsal part occupied by the spinal cord, and a narrower lower part occupied by the odontoid process of the axis. The two parts are separated by the odontoid strap, a strong ligament that inserts into ridges on the lateral walls inside the neural canal (Fig. 4, 5). In anthracotheres and ruminants, the neural canal is not noticeably wider where the spinal cord is housed than the odontoid part and there are no ridges on the walls of the canal.

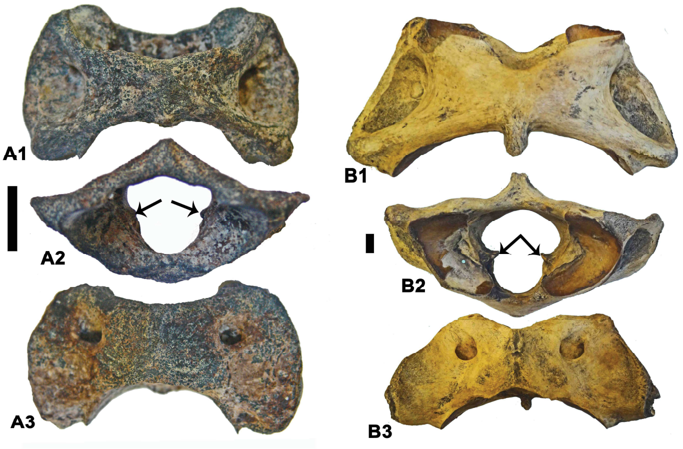

**Figure 4**. Atlas vertebra (A - FSL sans n°) of *Propalaeochoerus elaverensis* from Coderet, France, and (B) *Hippopotamus amphibius* (with damaged alae): 1) ventral, 2) anterior, 3) dorsal views. Note the ridges inside the neural canal to which the odontoid strap is inserted (arrows) which separates the canal into two moieties, a large dorsal part for the spinal cord, and a narrower, lower part occupied by the odontoid process of the axis vertebra (scales : 10 mm).

In pecorans the atlas is longer than in most other artiodactyls. The spinous process and ventral ridge tend to be subtle and low, the wings (alae) broad and longer antero-posteriorly than the centrum. The bone is pierced by foramina for the superior and inferior branches of the first spinal nerve. Ventrally there is often a crest, the hypapophyseal process (Flower, 1876), which terminates posteriorly at a projection called the ventral tubercle (Sisson & Grossman, 1953).

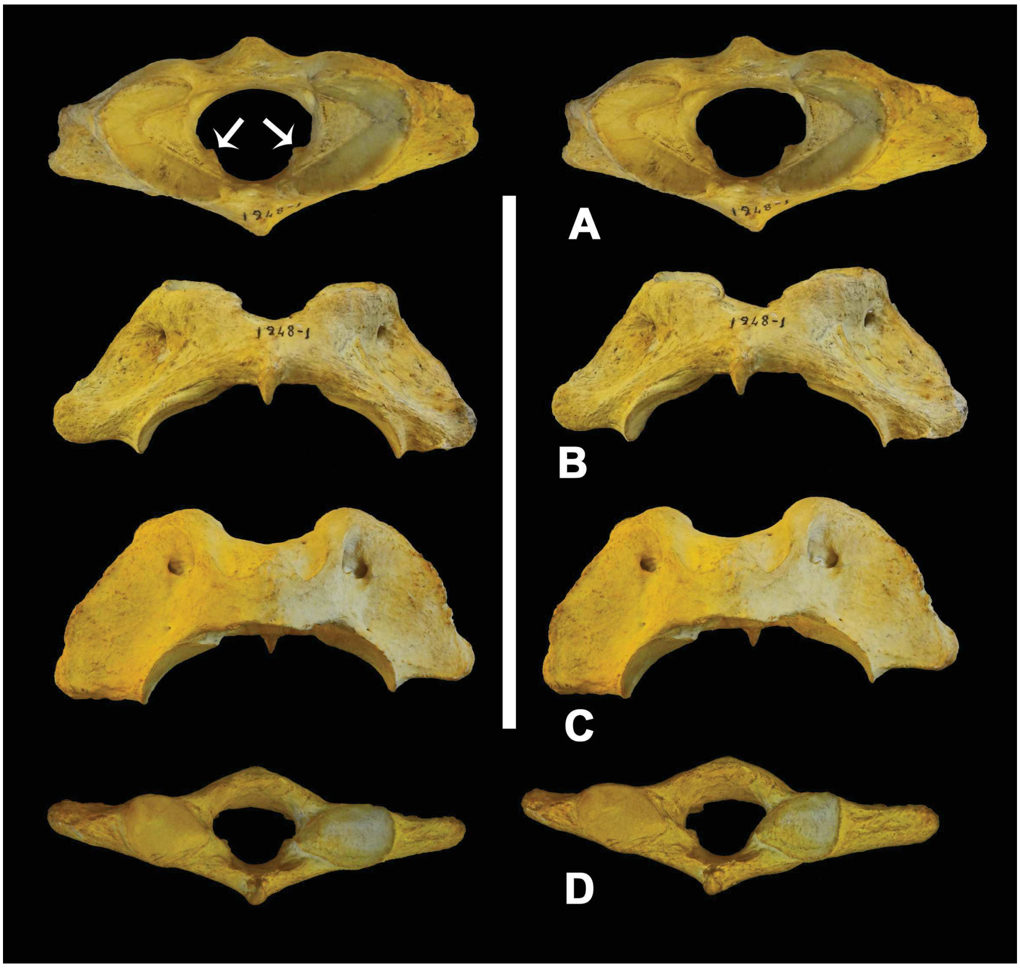

**Figure 5**. Stereo images of the atlas of *Choeropsis liberiensis* (MNHN 1948-1) A) anterior view (arrows show ridge for insertion of odontoid strap), B) ventral view, C) dorsal view and D) posterior view (note that the odontoid articular surface is separated from the epiphyseal articular surface) (scale: 10 cm).

The axis (C2) of artiodactyls is generally longer than the atlas and all the other cervical vertebrae, with a more massive centrum which terminates anteriorly in an odontoid process (or dens: Sisson & Grossman, 1953) which articulates with the floor of the neural canal of the atlas in front. The odontoid process of the axis ossifies from a separate centre in front of the anterior epiphysis of the centrum (Flower, 1876). In primitive artiodactyls, the odontoid process is generally peg-like (conical) and points anteriorly (suids, tayassuids, hippopotamids) (Fig. 6-9) but in traguloids (Fig. 10) and pecorans, it develops lateral flanges which become confluent with the anterior facing facets of the axis, resembling a spout with flanges posed on a base plate. In pecorans the odontoid process loses its peg-like morphology and becomes like a “spout or hollow half-cylinder with a prominent sharp semicircular rim” (Flower, 1876) orthogonal to the base plate. The anterior facets which articulate with the atlas, are prominent either side of the base of the neural canal extending upwards to the base of the pedicles of the neural arch.

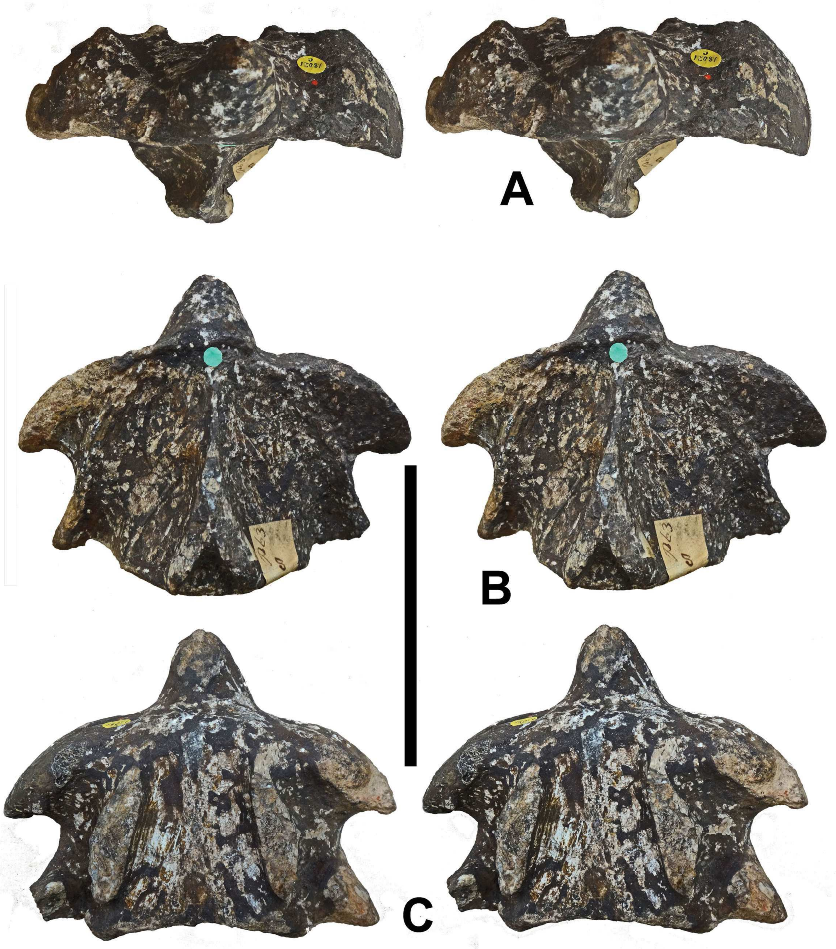

**Figure 6**. NHMUK M 18021, stereo images of an axis vertebra of *Hippopotamus sivalensis* from the Siwaliks of India. A) anterior view, B) ventral view, C) dorsal view. Note that the specimen lacks the pedicles and neural spine so the view in C) is of the floor of the neural canal. This is the same specimen as that figured by Falconer & Cautley (1848, plate 63, fig. 8). Note the conical, peg-like odontoid process confluent with the conical epiphyseal articular surfaces and the forked hypapophyseal tubercle (B) (scale: 10 cm).

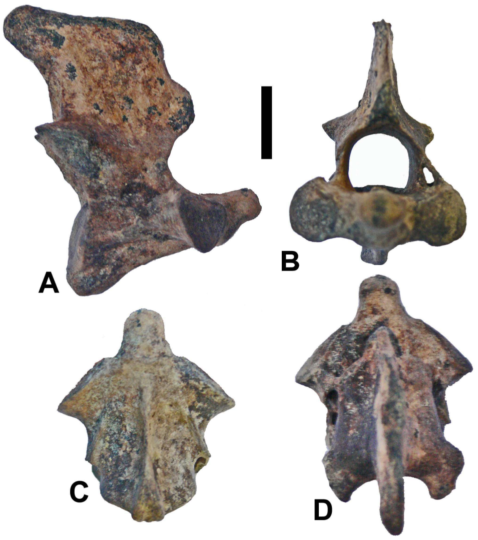

**Figure 7**. Axis vertebra of *Propalaeochoerus elaverensis* from Coderet, France (FSL sans n°). A) right lateral view, B) anterior view, C) ventral view showing forked hypapophyseal process, D) dorsal view (scale: 10 mm).

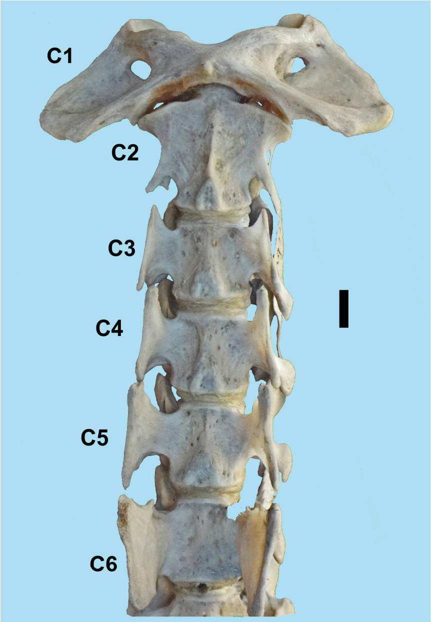

**Figure 8**. Ventral view of the cervical vertebrae of *Pecari* MNHN A 12587. Note the forked hypapophyseal processes in C2-C5, similar to *Propalaeochoerus*, *Hippopotamus* and *Choeropsis*, but different from anthracotheres.

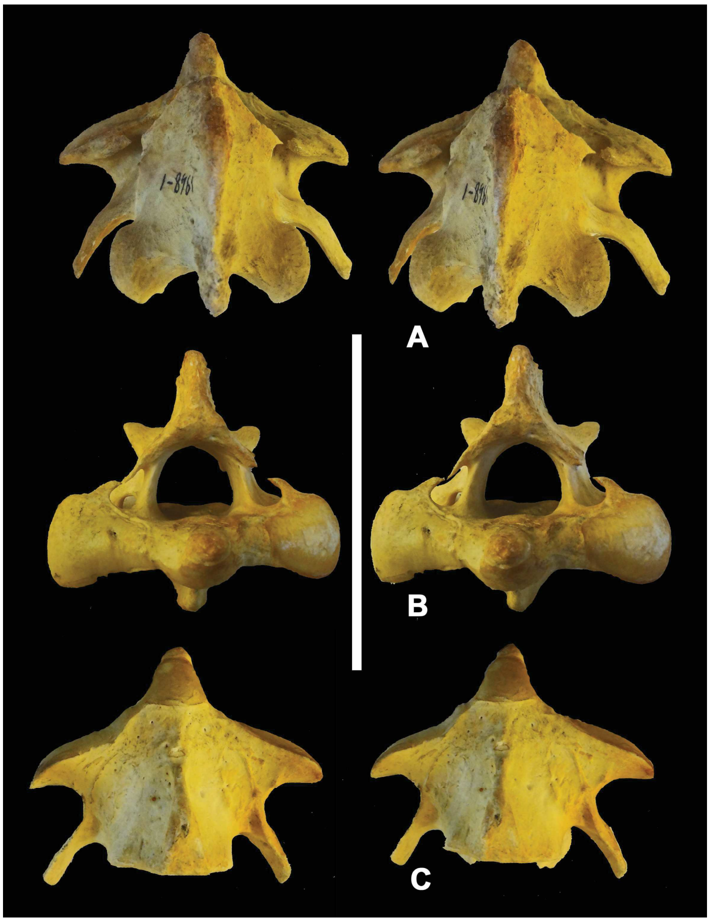

**Figure 9**. Stereo images of the axis of *Choeropsis liberiensis* (MNHN 1948-1). A) dorsal view, B) anterior view and C) ventral view (scale: 10 cm).

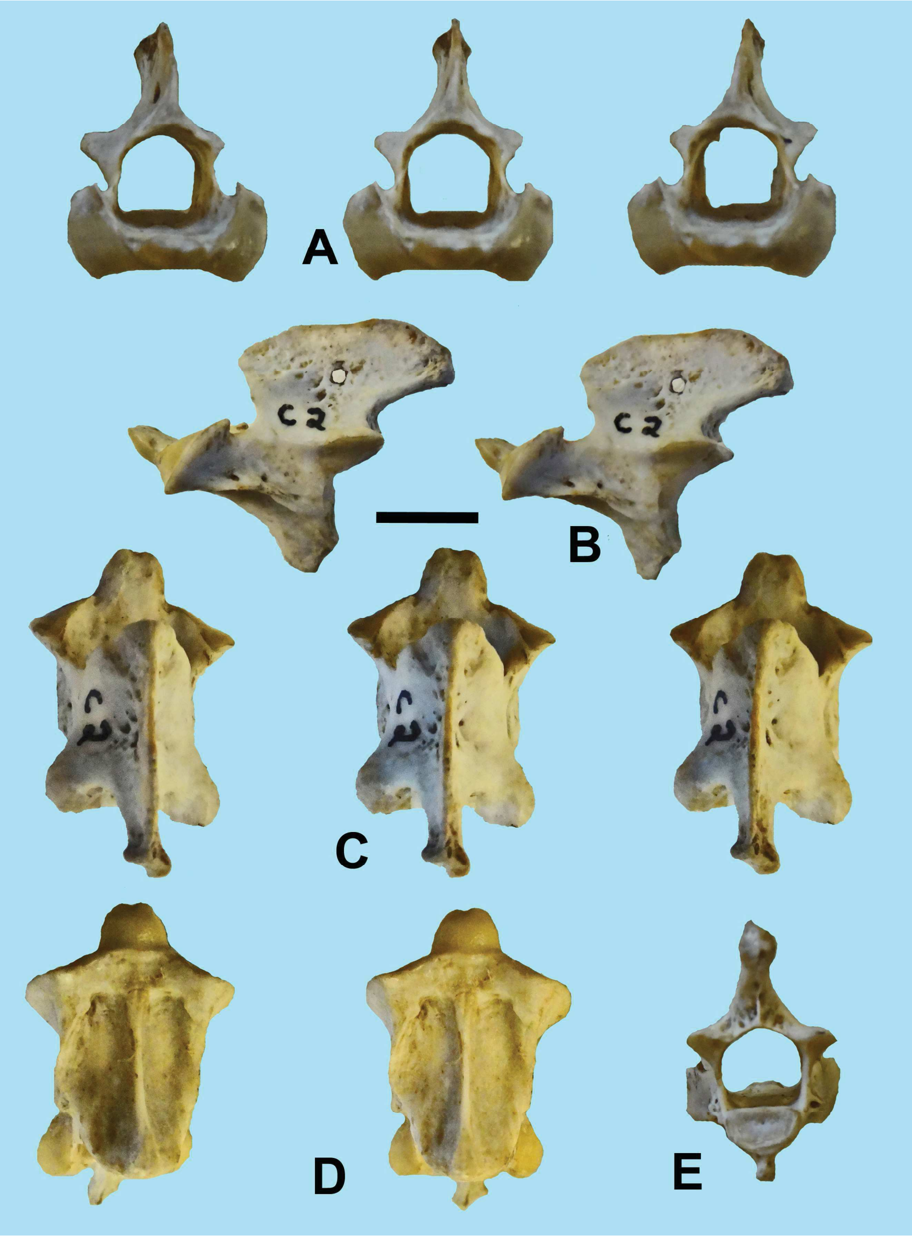

**Figure 10**. The axis of *Tragulus javanicus* (MNHN A 3370). A) stereo triplet of the anterior view, B) stereo left lateral view, C) stereo triplet of the dorsal view, D) stereo ventral view, E) posterior view (scale: 10 mm).

The spinous process of the axis is generally tall, bilaterally compressed and proximo-distally elongated, the ventral ridge of the centrum is low but sharp with a posterior tubercle (the hypapophyseal spine or tubercle) which can be simple and peg-like as in most artiodactyls or bifurcating (v-shaped) as in hippopotami (Chapman, 1881; Milne-Edwards, 1868; Hooijer, 1950) suids, tayassuids and palaeochoerids (and some carnivores such as the Lion, *Panthera leo*). Weakly trifid hypapophyses also occur in some Tylopoda, but the posterior ends terminate in larger tubercles in *Camelus* than occur in suoids and hippopotamids. The hypapophyseal tubercles are associated with the ventral longitudinal ligament which "*lies on the ventral surface of the bodies of the vertebrae and the intervertebral fibro-cartilages, to which it is firmly attached*" (Sisson & Grossman, 1953). Distally there is a pair of dorsally positioned posterior zygapophyses, the facets of which face ventrally and articulate with the anterior zygapophyses of the third cervical vertebra (C3) behind. The transverse process of C2 tends to be poorly developed, but may have a more or less elongated posterior inferior lamina. The foramen for the second spinal nerve is located close to the base of the pedicle. The posterior articulation of the centrum with the anterior articulation of C3 is via a cartilaginous plate, the intervertebral disc. The surface of the posterior epiphysis is slightly concave to flat and is angled (canted) more or less steeply relative to the body of the centrum, depending on the taxa examined.

The third to sixth cervical vertebrae (C3, C4, C5 and C6) resemble each other in overall morphology but show progressive differences from each other concerning the development of the transverse processes, the zygapophyses and other structures. All articulate with each other via cartilaginous plates which are slightly flexible allowing bending of the neck up and down or sideways, but not allowing a significant amount of rotation. The anterior epiphysis is generally positioned higher than the posterior one, the centrum sloping downwards distally to a greater or lesser degree depending on the habitual orientation of the neck. In artiodactyls which habitually hold the neck at a low angle, the centrum is less canted than in those that hold their necks at a steep angle. The epiphyses are more or less opisthocoelus (anterior epiphysis convex, posterior one concave) with some taxa such as hippopotami having almost planar epiphyseal surfaces. C3-C6 have a flattened dorsal "table" linking the prominent pair of anterior zygapophyses, in which the articular facets face dorsally, to the pair of posterior zygapophyses in which the articular facets face ventrally. On the top of this table there is a more or less strongly developed spinous process which is tall, elongated antero-posteriorly and compressed from side to side. The bilateral distance between the zygapophyses increases slightly from C3 to C6. Laterally there is a transverse process which may develop an inferior lamina, usually stronger in C5 and C6 than in C3 and C4. The ventral hypapophyseal ridge of the centrum is sharp but generally low, often terminating distally in a swollen tubercle or short process, the hypapophyseal spine. In suoids, the hypapophyseal process of C3 tends to be trifid (forked, v-shaped posterior part) (Fig. 11) whereas in ruminants it is simple with a posterior tubercle. The same trifid morphology of the hypapophyseal ridge can be present in C4 of suoids (in *Pecari* for example) but it fades out on the posterior cervical vetebrae, and has not been observed in C6 and C7.

**Figure 11**. Stereo image of C3 of *Choeropsis liberiensis* (MNHN 1948-1) ventral view (note the forked hypapophyseal process) (scale: 10 cm).

### Occiput height

A general rule among mammals is that in taxa which hold the head high above the shoulders (most ruminants) the occiput tends to be short and low, whereas in species which hold the head lower than the shoulders (suids and hippopotamids) the occiput tends to be tall and its apex high above the occipital condyles (MacDonald, 2001). In this respect, anthracotheres are more like ruminants than suoids (Falconer & Cautley, 1848: MacInnes, 1951).

## Systematic Palaeontology

### Family Anthracotheriidae Gill, 1872

### Genus *Brachyodus* Depéret, 1895

Type species *Brachyodus onoideus* (Gervais 1859)

### Species *Brachyodus aequatorialis* MacInnes, 1951

### Description

#### Atlas of *Brachyodus*

In the Grillental *Brachyodus* specimen the proper centrum of the atlas (Sisson & Grossman, 1953) is reduced compared to those of many other artiodactyls, but it has a prominent base for the hypapophyseal tubercle (ventral tubercle) from which the apex has broken (Fig. 12). The anterior articular surface is comprised of two deeply curved depressions almost confluent ventrally, but well separated from each other dorsally. These depressions receive the occipital condyles of the skull and are constructed such that the occipital condyles of the skull can extend upwards and flex downwards (pitch) and sideways (yaw) relative to the atlas vertebrae but cannot rotate within it (roll). The neural arch is mesio-distally longer than the ventral part of the centrum, and it has no spine, only a low swelling in its centre, the dorsal tuberosity. The foramen for the first spinal nerve pierces the lateral wall of the vertebra just behind the anterior articular facet. The transverse processes, or alae, are narrow and flange-like anteriorly, curving inferiorly, but are damaged such that their full extent cannot be assessed.

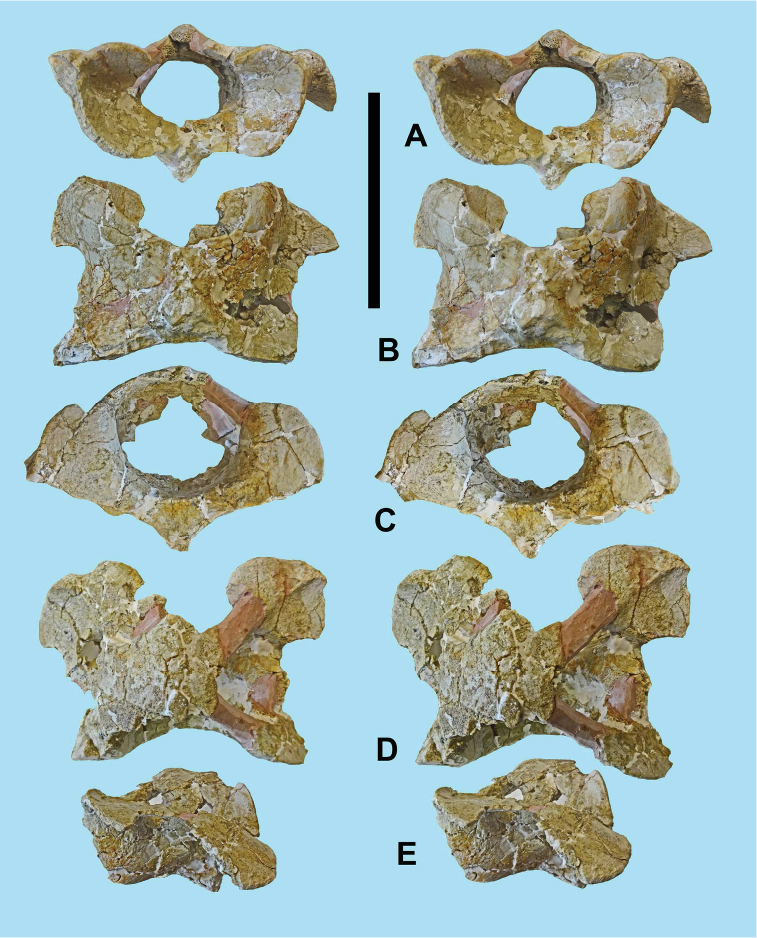

**Figure 12**. GSN GT 88'06, stereo views of the atlas vertebra of *Brachyodus aequatorialis* from Grillental VI, Sperrgebiet, Namibia. A) anterior, B) dorsal, C) posterior, D) ventral, E) left lateral view, anterior to the left (scale: 10 cm). Note the lack of ridges for insertion of the odontoid strap, a significant difference from Hippopotamidae and Palaeochoeridae.

In posterior view, the surface for the dens of the axis vertebra (odontoid process of the axis) is well developed in the floor of the neural canal extending into the neural canal about half the way along the superior surface of the centrum and terminating internally at a low ridge. Laterally this articular surface extends upwards either side of the centrum ending near the base of the pedicles and blends into the posterior articular surfaces which are almost flat and face posteriorly (for the anterior-facing articular surface of the axis). The two posterior articular surfaces of the axis are separated from each other dorsally by the pedicles and superior arch, and ventrally by the vertical part of the centrum behind the ventral tubercle. The neural canal is oval and shows no sign of crests of flanges where the odontoid strap would insert. Indeed the odontoid articular facet terminates upwards by blending into the neural arch, completely different from the conformation in the *Hippopotamus* in which a prominent ridge subdivides the neural canal into two moieties, a broad superior one for the spinal cord and a narrow lower one for the odontoid process of the axis, the two being separated by a strong ligamentous belt called the odontoid sling or strap (Fig. 4, 5).

## Axis of *Brachyodus*

The centrum of the axis is considerably larger and longer than that of the atlas (Fig. 13, 14, 15). The posterior surface of the centrum is concave, triangular in outline with rounded apices of the triangle. The inferior lamina of the transverse process is weak, projecting backwards slightly beyond the limit of the centrum. In ventral view the odontoid process of the axis is bilaterally broad and laterally it blends sharply but smoothly into the vertically oriented facets located beneath the pedicles of the neural arch. In dorsal view, the odontoid process is seen to comprise a central “dens” which projects anteriorly, flanked either side by a flange from which it is separated by a furrow (Fig. 13, 14). In anterior view, the flange sweeps steeply upwards to terminate beneath the pedicles of the neural arch. The under surface of the flange blends into the forward facing facet (base plate) which articulates with the posterior surface of the atlas. In ventral view there is a depression behind the dens which occupies about one third of the length of the centrum, behind which there is a sharp sagittal crest or ventral keel (hypapophyseal process) which extends as far as the posterior epiphysis, terminating at the hypapophyseal tubercle, which shows no sign of bifurcation. The neural canal is triangular with rounded apices, taller than broad, and broadest at the base. The pedicles are slender and are pierced by a prominent foramen, the canal for the second nerve. The transverse processes are weakly developed. There are no anterior zygapophyses, but the posterior zygapophyses are prominent with ventrally (and slightly laterally) facing articular facets for contact with the anterior zygapophyses of the 3rd cervical vertebra (C3). The spinous process is tall and bilaterally compressed anteriorly, but its posterior end in broken.

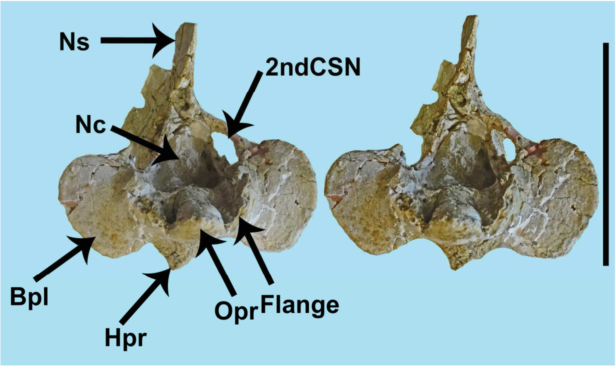

**Figure 13**. Nomenclature of the atlanto-axial articulation and surrounding structures in GSN GT 88’06, anterior stereo view of the axis of *Brachyodus aequatorialis* frpm Grillental VI, Sperrgebiet, Namibia, to show the morphology of the atlanto-axial articulation (Bpl – Base plate, Hpr – Hypapophyseal process, Nc – Neural canal (filled with sediment), Ns – Neural spine, Opr – Odontoid process, 2nd CSN – Foramen for passage of the second cervical spinal nerve) (scale: 10 cm).

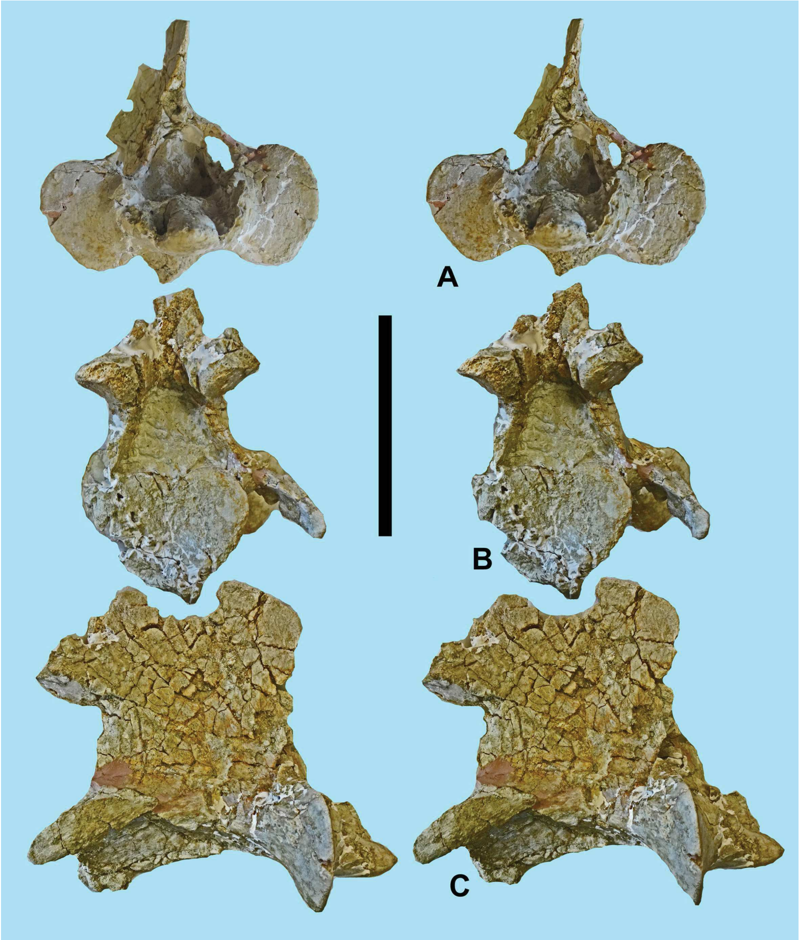

**Figure 14**. GSN GT 88’06, stereo images of axis of *Brachyodus aequatorialis*. A) anterior, B) posterior, C) right lateral view with anterior to the right (scale: 10 cm).

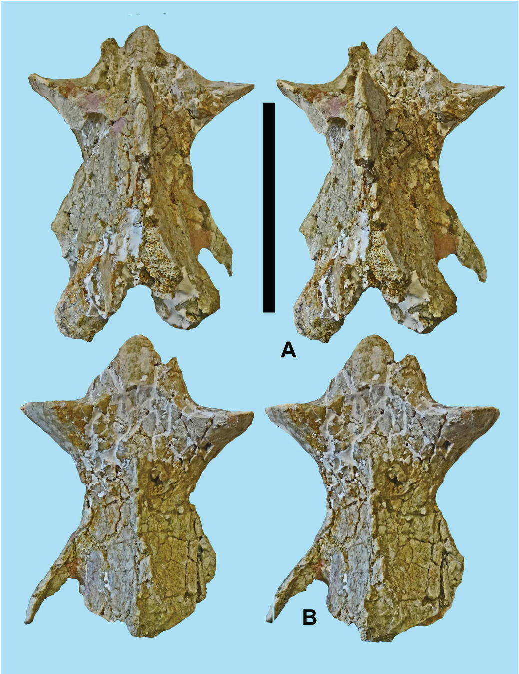

**Figure 15**. GSN GT 88’06, stereo views of the axis of *Brachyodus aequatorialis*. A) dorsal, B) ventral views (scale: 10 cm). Note the unforked hypapophseal process in (B).

The anterior articular facets for the atlas face anteriorly and are almost orthogonal to the roll axis, facing slightly upwards (Fig. 15). They form an angle of almost 90° with the lateral articular surface of the odontoid process. The conformation of the atlanto-axial articulation permits substantial rotatory movement parallel to the neural canal (roll) but restricts up and down movements (pitch) and side-to-side movements (yaw) (Fig. 16).

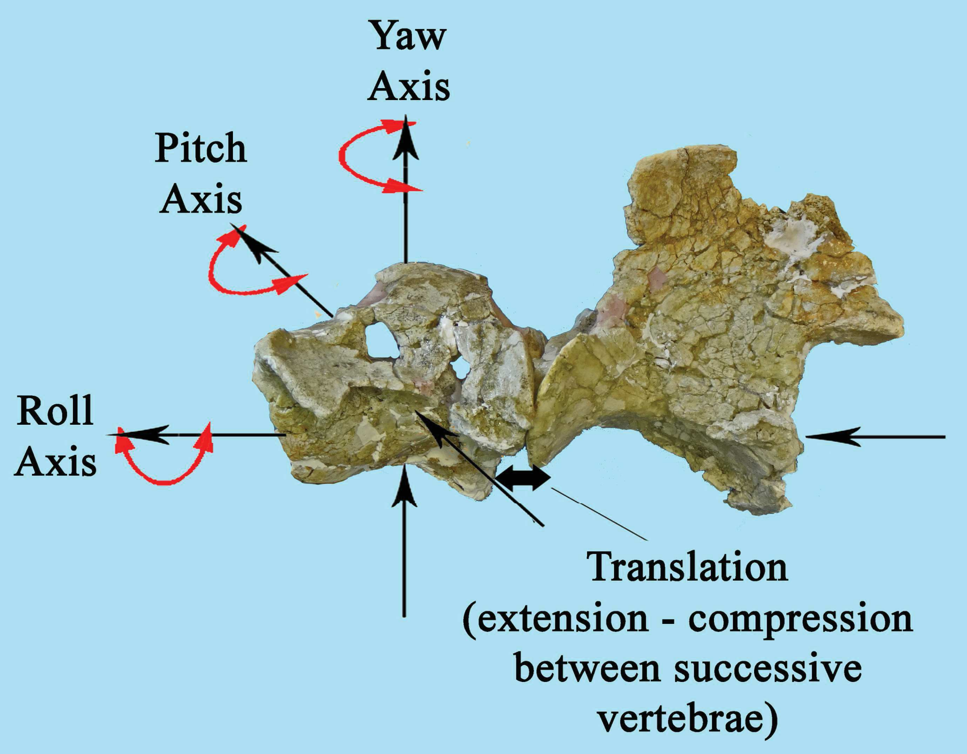

**Figure 16**. Definition of pitch, roll, yaw and translation movements in the atlas and axis of *Brachyodus aequatorialis* from Grillental VI, Namibia.

Combined, the joint surfaces of the atlas and axis permit substantial head movements in all three planes (pitch and yaw in the cranio-atlantal joint – roll in the atlanto-axial joint). In other cervical vertebrae (C3-C7) pitch and yaw are possible but restricted and roll even more so, with most movement being permitted by the flexibility and compressibility of the cartilaginous intervertebral discs. A small degree of compression and extension of the intervertebral discs is possible leading to translation of the vertebrae relative to one another, which permits minor amounts of shortening or lengthening of the neck.

## <u>C3-C5 of *Brachyodus*</u>

The post-axis neck vertebrae of *Brachyodus* are similar to each other in most details and can be described together (Fig. 17-20). The centrum is quite opisthocoelus, with convex anterior and concave posterior epiphyseal surfaces (unlike the pig and hippo in which they are flatter) but not nearly as opisthocoelus as those of the Giraffe and Okapi. The ventral keel (hypapophyseal process) is low forming a rounded to sharp ridge and is developed into a broad triangular hypapophyseal tubercle posteriorly, but the crest shows no sign of bifurcating, unlike *Hippopotamus*, *Choeropsis*, Tayassuidae and Palaeochoeridae which have a strong bifurcation posteriorly (the forked or trifid conformation). The centrum is "canted" such that its body forms an angle of about 30° with the intervertebral surfaces as measured along the base of the neural canal (ca 45° if measured along the ventral keel). The neural canal is ovoid, taller than broad, with a flat base. The pedicles are thicker than those of the axis, and are pierced by the foramen for the nerves (third in C3, fourth in C4 etc). These foramina are slightly below the level of the base of the neural canal. The pedicles are capped by a flat table-like platform which has a dorsal central ridge or spinous process. The shape of the spinous process cannot be determined in the Grillental specimen since in all the posterior cervical vertebrae available, its apex is broken off or damaged. The transverse processes are flange-like, projecting laterally before curving ventrally and terminate distally in a ventrally directed lamina which extends beyond the posterior surface of the centrum. The anterior zygapophyses have articular surfaces that face upwards and slightly inwards. They project substantially beyond the intervertebral surface of the centrum. The posterior zygapophyses have ventrally facing articular surfaces which extend beyond the surface of the posterior intervertebral disc, thereby ensuring substantial contact between neighbouring vertebrae. The conformation of the zygapophyseal articular surfaces permits a certain degree of yaw movement but little pitch and very little roll.

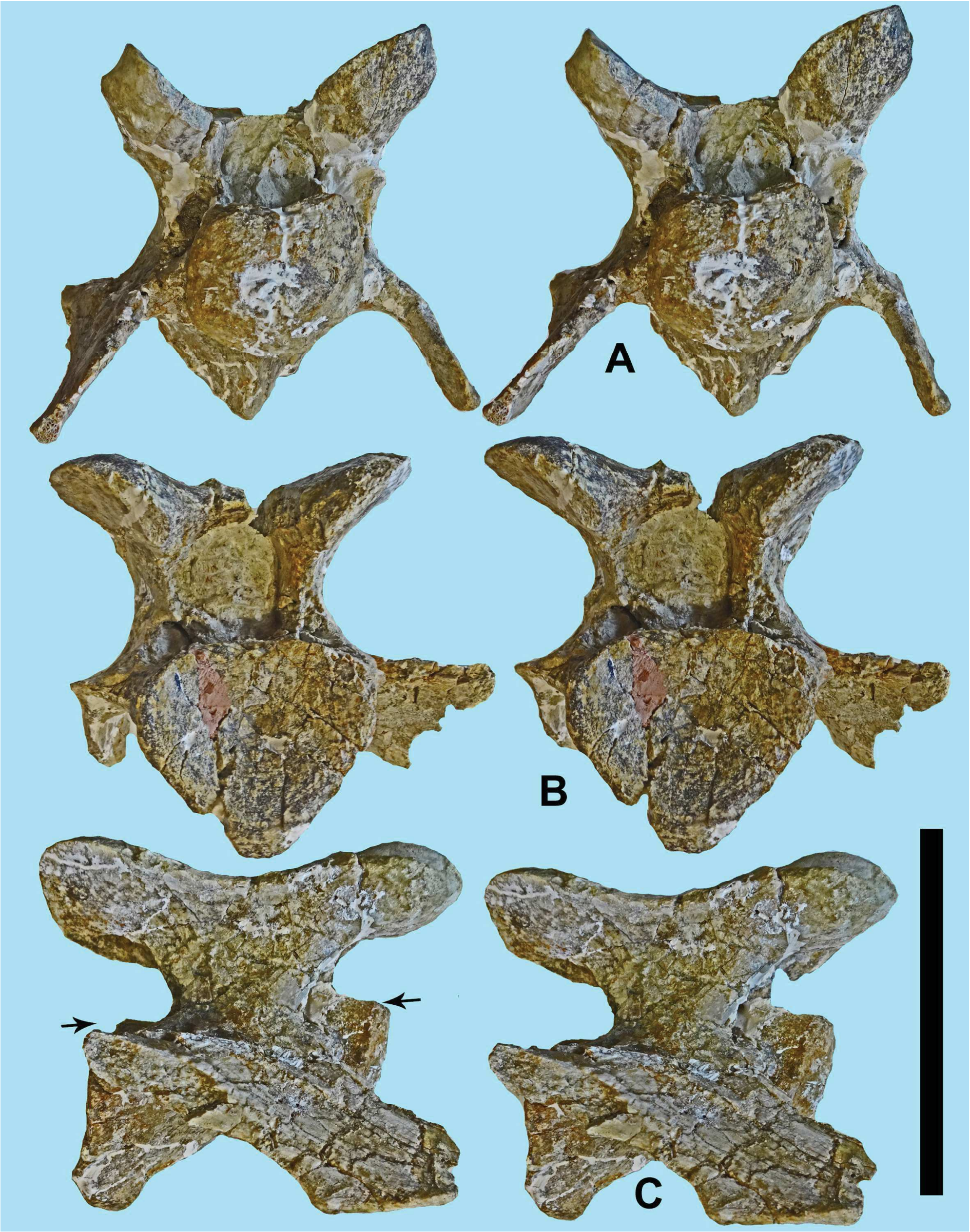

**Figure 17**. GSN GT 88'06, stereo views of the 3rd cervical vertebra of *Brachyodus aequtorialis* from Grillental VI, Namibia. A) anterior, B) posterior and C) right lateral view (arrows show the level of the floor of the neural canal) (scale: 10 cm).

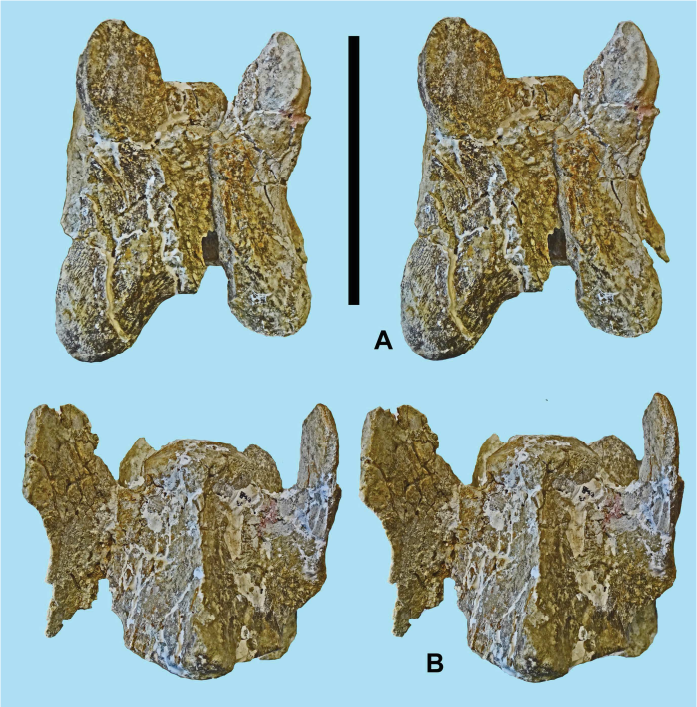

**Figure 18**. GSN GT 88'06, stereo views of the 3$^{rd}$ cervical vertebra of *Brachyodus aequatorialis* from Grillental VI, Namibia. A) dorsal, B) ventral views (scale: 10 cm). Note the unforked hypapophyseal process in (B).

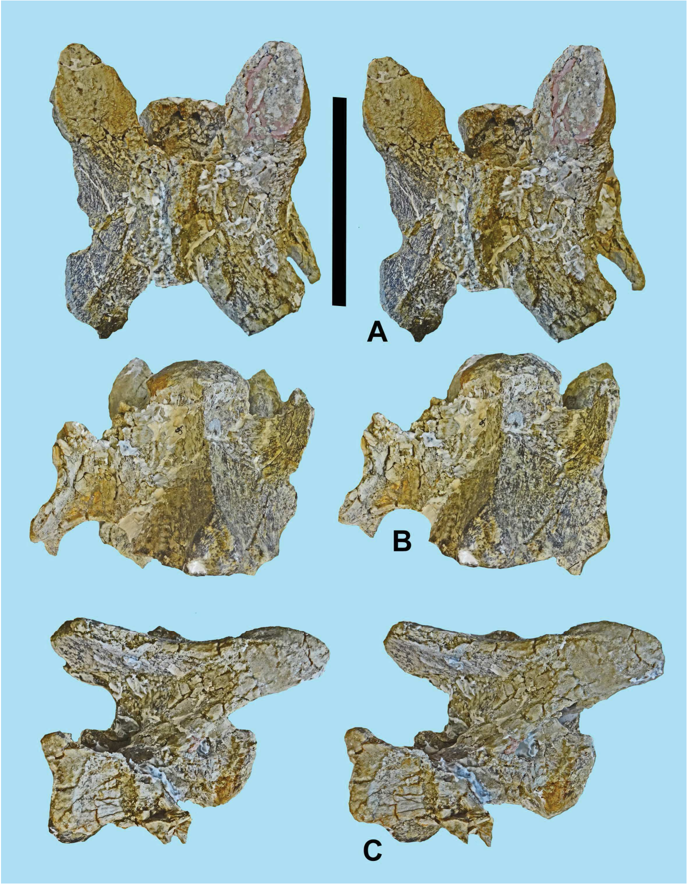

**Figure 19**. GSN GT 88'06, stereo images of the 4$^{th}$ cervical vertebra of *Brachyodus aequatorialis* from Grillental VI, Namibia. A) dorsal, B) ventral, C) right lateral views (scale: 10 cm). Note the swollen, but unforked hypapophyseal process in (B).

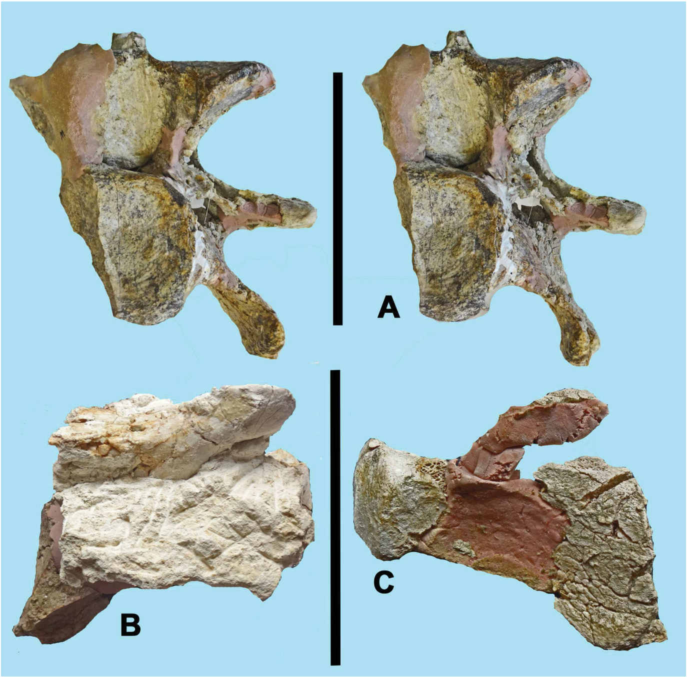

**Figure 20**. GSN GT 88'06, cervical vertebrae of *Brachyodus aequatorialis* from Grillental VI, Namibia, (A) stereo posterior view of C5, (B-C) medial and lateral views of C6 (scales : 10 cm).

### Thoracic and lumbar vertebra

Grillental VI yielded two posterior vertebrae in articulation, the last thoracic vertebra and the first lumbar vertebra (Fig. 21). The centra are reasonably well preserved and yield accurate measurements of the centrum length, but the arches and apopohyses are poorly preserved. Both these vertebra are shorter than any of the cervical vertebrae.

**Figure 21**. GSN GT 88'06, stereo image of the ventral surfaces of two posterior trunk vertebrae of *Brachyodus aequatoralis*, the last thoracic (top) and the first lumbar vertebra (bottom). Between the two vertebrae is a natural cast (in sandstone) of the intervertebral disc (scale: 10 cm).

## Other post-cranial bones associated with GSN GT 88'06

In order to complete the description of the Grillental *Brachyodus aequatorialis* specimen, the post-cranial bones of the same individual are briefly described and illustrated.

Manual phalanx and sesamoids

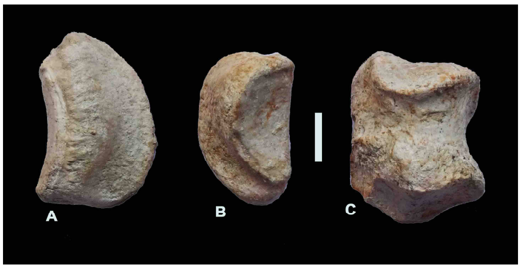

**Figure 22**. GSN GT 88'06, two sesamoids (A, B) and manual second phalanx (C) of *Brachyodus aequatorialis* from Grillental VI, found while extracting the cervical vertebrae from the silt matrix encasing them; A) lateral view, B) articular view, C) dorsal view (scale: 10 mm).

The manual sesamoids of *Brachyodus aequatorialis* are robust with large articular surfaces (Fig. 22). The volar part is narrower than the articular part. The second phalanx is relatively short and broad.

**Figure 23**. GSN GT 2'11, tarsal sesamoid fused to a cuneiform (A - medial view) and GSN GT 1'11, left calcaneum (B - medial, C - lateral views) from Grillental VI, Namibia, associated with specimen GT 88'06 of *Brachyodus aequatorialis* (scale: 10 cm).

The calcaneum of *Brachyodus aequatorialis* has a long tuber calcis and a relatively gracile articular facies (Fig. 23). The sustentaculum tali is somewhat narrower mesio-distally than the base of the tuber and measures 55 mm medio-laterally. The cuboid articulation is gently concave. The total length of the bone is 195 mm and the diaphysis measures 31.2 mm medio-lateral diameter and 51.2 mm antero-posterior diameter.

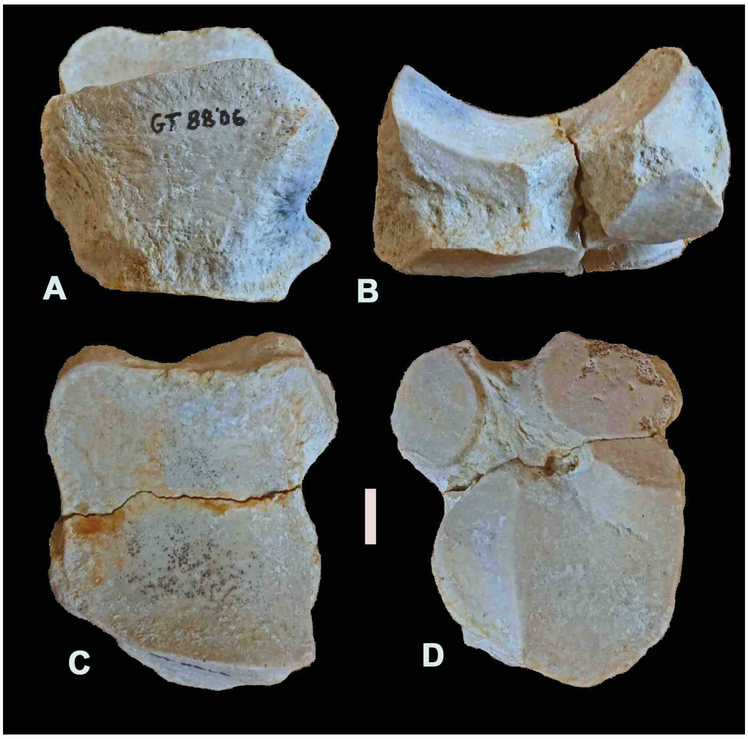

**Figure 24**. GSN GT 88'06, left navicular of *Brachyodus aequatorialis* from Grillental VI, Namibia, A) anterior view, B) lateral view, C) proximal view, D) distal view (scale: 10 mm).

The navicular of *Brachyodus aequatorialis* is quite small, with a single concave articular surface proximally which is longer in the cranio-caudal direction than the medio-lateral one (Fig. 24). Distally there are four main articular surfaces, one separated from the other three by wide but shallow grooves, the other three for the third tarsal bone (lateral cuneiform) confluent with each other.

### Comparisons

Our comparison of the neck and trunk vertebrae of *Brachyodus aequatorialis* from Namibia (Fig. 25), reveal that the species shares a large number of traits with Ruminantia, and few if any derived features with Suoidea (Suidae, Tayassuidae, Palaeochoeridae, Sanitheriidae, Hippopotamidae) or entelodonts. The neck vertebrae of *Brachyodus* are longer relative to thoracic and lumbar vertebrae than in suoids, but can be matched in ruminants with medium length necks. The opisthocoely is like that in ruminants with medium-length necks, while the high degree of canting of the vertebral centra accords with the same group, unlike suoids in which the vertebral epiphyses are almost flat and the centra barely canted, if at all. The hypapophyseal process in *Brachyodus* is sharp, increasing in height posteriorly without bifurcation, as in ruminants, unlike the low, rounded process in suoids, which bifurcates posteriorly, noticeably in *Hippopotamus*, *Choeropsis* and *Propalaeochoerus*.

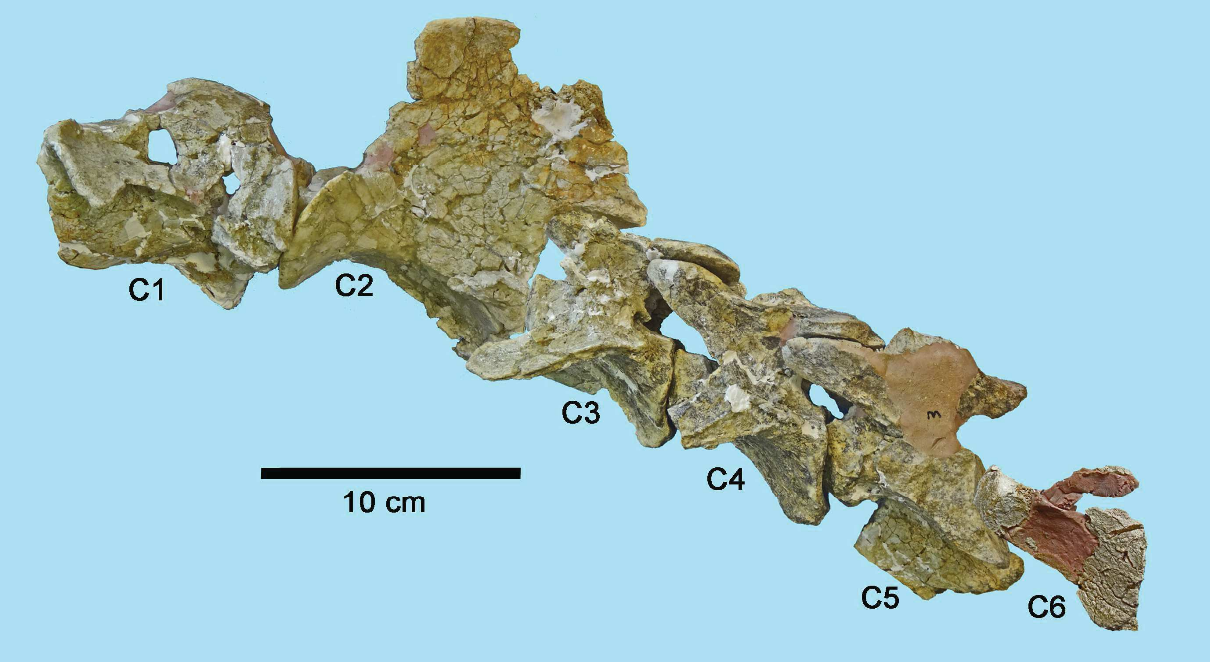

**Figure 25**. The neck skeleton of *Brachyodus aequatorialis* from Grillental VI, Namibia, in left lateral view. Note the canted centra of C2-C6 with opisthocoelus articulations, indicating that the head was habitually held well above the shoulder in this species. The intervertebral discs have been omitted, so the neck would have been somewhat longer than depicted here (scale: 10 cm).

The form of the odontoid process of the axis of *Brachyodus* is ruminant-like (hemi-cylinder) and its articular surface is continuous with the flat, forward facing "base-plate" articular surface of the epiphysis, as in ruminants, and completely different from the peg-like, conical odontoid process of suoids which is confluent with more laterally facing anterior articular surfaces of the epiphysis, which results in a cone-in-cone articulation. In *Brachyodus* there are low flanges between the odontoid process and the epiphyseal articular surface, somewhat similar to the morphology found in Tragulidae, but absent in pecorans and suoids.

## Metric analysis of the vertebrae of *Brachyodus* and other Artiodactyla

Metric comparisons of the neck vertebrae relative to the thoracic and lumbar vertebrae reveal that the genus *Brachyodus* possessed a long neck, as in many ruminants, whereas *Hippopotamus* and *Choeropsis* possess short necks as in Tayassuidae and Suidae (Table 6, 7). Furthermore, comparison of the lengths of C3-C5 relative to the length of the axis points to the same conclusion, with C3-C5 of *Hippopotamus* and *Choeropsis* being shorter relative the length of the axis than are the homologous vertebrae in *Brachyodus*, *Taurotragus* and *Okapia*. These two ways of examining the metric data support the conclusion that *Brachyodus* was a relatively long necked artiodactyl in the style of many ruminants, and that its neck was appreciably longer relative to other body sectors than those of *Hippopotamus* and *Choeropsis* (Fig. 26, 27).

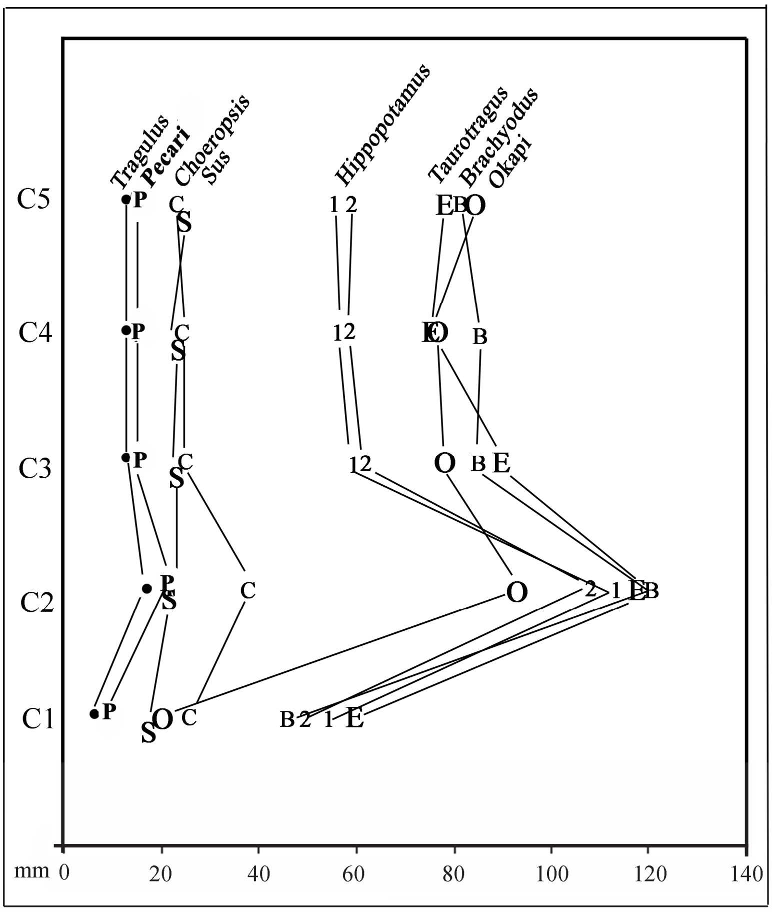

**Figure 26**. Metric comparison of the neck vertebrae of various Artiodactyla. C3-C5 are distinctly longer relative to C2 length in *Okapia*, *Taurotragus* and *Brachyodus*, than they are in *Hippopotamus* (Dots – *Tragulus napu*; 1 & 2 – *Hippopotamus amphibius*; B – *Brachyodus aequatorialis*; C – *Choeropsis liberiensis*; E – *Taurotragus oryx*; O – *Okapia johnstoni*; P – *Pecari tajacu*; S – *Sus scrofa*)

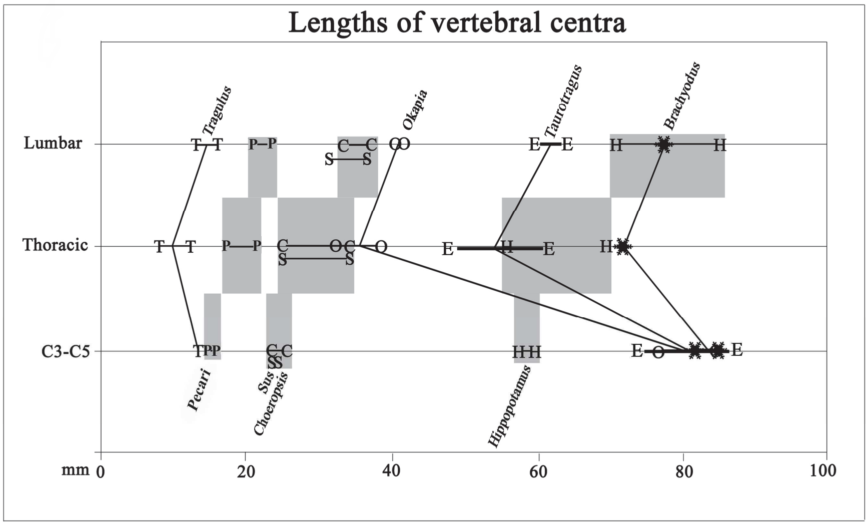

**Figure 27**. Lengths of vertebral centra (with shortest and longest centra plotted) arranged by sector of the vertebral column. Cervical vertebrae C3-C5 are shorter than most thoracic and lumbar vertebrae in *Pecari (Dicotyles)*, *Sus*, *Choeropsis* and *Hippopotamus*, whereas they are longer than thoracic vertebrae and most lumbar vertebrae in *Tragulus*, *Okapia*, *Taurotragus* and *Brachyodus*. This comparison indicates that *Brachyodus* possessed a long neck, not as greatly elongated as in *Okapia*, but longer relative to body dimensions than that of the Eland, *Taurotragus*.

## Functional meaning of the cervical vertebrae of *Brachyodus aequatorialis*

The cervical chain of *Brachyodus aequatorialis* from Namibia indicates that the species possessed a somewhat elongated neck relative to trunk length, and that it habitually held its cranium in a head-up position (ie the head was habitually held well above the shoulders, as for example when walking) (Table 5). The length of the neck of *Brachyodus* exceeds that of the Okapi (*Okapia johnstoni*) and the Eland (*Taurotragus oryx*) but the proportions of neck length to trunk length in these three forms are rather different, the Okapi and Eland having smaller bodies than *Brachyodus*.

In contrast the necks of *Hippopotamus* and *Choeropsis* are short relative to trunk length, and the head is habitually held in a head-down posture while walking. The few available neck vertebrae of the Palaeochoeridae, *Propalaeochoerus elaverensis*, indicate that it was hippo-like in miniature.

The atlanto-axial articular surfaces of *Brachyodus* are closest to the ruminant type, most closely resembling that of Tragulidae, but with minor differences such as the strength of the flanges linking the odontoid process to the anterior epiphyseal base-plate articular surface. Suoids have a radically different atlanto-axial articulation of the cone-in-cone type, with antero-laterally facing epiphyseal surfaces and no flanges. Thus in *Brachyodus*, the way of rotating the head (roll axis) was ruminant-like and not like that occurring in hippopotamids and palaeochoerids.

**Table 5**. Comparison of the morphology of the cervical vertebrae of selected artiodactyls. In order to standardise the comparisons, vertebrae are oriented with the base of the neural canal horizontal.

**Atlas**

| **Morphology** | ***Brachyodus*** | ***Hyaemoschus*** | ***Propalaeochoerus*** | ***Hippopotamus*** | ***Choeropsis*** |
|---|---|---|---|---|---|
| Posterior articulation for axis | Faces posteriorly | | Faces postero-laterally | Faces postero-laterally | Faces postero-laterally |
| Ventral tubercle (hypapophyseal tubercle) | Short, thick, well beneath odontoid articulation | | Short, narrow, positioned immediately beneath the odontoid articulation | Long, narrow, pointed, immediately beneath the odontoid articulation | Long, narrow, pointed, immediately beneath odontoid articulation |
| Articular surface on inside wall of the neural canal | Contiguous with that for the odontoid process of the axis and extends upwards to the base of the pedicle | | Stops beneath the pedicles | Stops short well beneath the pedicle | Not in contact with the part for the odontoid process of the axis, only slightly developed inside the neural canal |
| Neural canal | Ovoid almost circular | | Ventral half narrower than dorsal half | Broad dorsal and narrow ventral portions | Ventral half narrower than dorsal half |
| Ridge between odontoid and neural moieties of the neural canal | Absent | | Strong | Strong | Strong |

**Axis**

| **Morphology** | ***Brachyodus*** | ***Hyaemoschus*** | ***Propalaeochoerus*** | ***Hippopotamus*** | ***Choeropsis*** |
|---|---|---|---|---|---|
| Anterior articular facets | Face anteriorly and slightly antero-laterally | Face anteriorly and slightly antero-laterally | Face strongly antero-laterally | Face strongly antero-laterally | Face strongly antero-laterally |
| Anterior extremity of ventral ridge | Separated from odontoid process by a wide, shallow depression | Separated from odontoid process by a wide, shallow depression | Close to odontoid process | Close to odontoid process | Close to odontoid process |
| Ventral ridge (hypapophyseal process) | Simple, straight, sharp, swollen distally without bifurcation | Straight, swollen distally without bifurcation | Low, rounded, bifurcates distally, v-shaped (forked) | Low, rounded, bifurcates distally, v-shaped (forked) | Low, rounded, bifurcates distally, v-shaped (forked) |
| Odontoid process | Dorsoventrally somewhat compressed | Dorsoventrally compressed | Conical, peg-like, uncompressed | Conical, peg-like, uncompressed | Conical, peg-like, uncompressed |

| | | | | | |
|---|---|---|---|---|---|
| Lateral articular flanges separated from odontoid process by valleys | Present | Present | Absent | Absent | Absent |
| Posterior foramen for second nerve | Absent, passing in a groove above the transverse process, groove above process | Absent, not affecting transverse process, groove above process | Area not preserved | Present, piercing base of transverse process | Present, piercing base of transverse process |
| Articular surface of posterior zygapophyses | Horizontal, facing ventrally | Horizontal facing ventrally | Steep, almost vertical, facing ventro-latero-posteriorly | Steeply angled, facing ventro-latero-posteriorly | Steeply angled, facing ventro-latero-posteriorly |
| Base of distal epiphysis | Lower than odontoid process | | In line with base of odontoid process | In line with base of odontoid process | In line with base of odontoid process |
| Ventral lamina of transverse process | Slender, projecting ventro-posteriorly | | Broken | Projecting posteriorly | Weak projecting posteriorly |

**C3**

| **Morphology** | ***Brachyodus*** | ***Hyaemoschus*** | ***Propalaeochoerus*** | ***Hippopotamus*** | ***Choeropsis*** |
|---|---|---|---|---|---|
| Centrum | Canted | Canted | Not canted | Not canted | Not canted |
| Opisthocoely | Medium | Medium | Weak, almost flat | Weak, almost flat | Weak, almost flat |
| Hypapophyseal process | No bifurcation | No bifurcation | Not known | Bifurcates distally (forked) | Bifurcates distally (forked) |
| Hypapophyseal process | Sharp, increasing in height posteriorly | | Not known | Low rounded, bifurcates | Low, rounded, bifurcates |

**Table 6. Measurements (in mm) of various artiodactyls** (*B.a. – Brachyodus aequatorialis*, *Ch – Choeropsis liberiensis*, *H – Hippopotamus amphibius*) (e – estimated measurement).

| **Vertebra** | **Measurement** | ***B.a.*** | ***H* 1** | ***H* 2** | ***H* A** | ***H* B** | ***Ch* 1** | ***Ch* 1948-1** |
|---|---|---|---|---|---|---|---|---|
| Atlas | Dorsal sagittal length | 46.3 | 49.6 | 54 | 54.4 | | 26.4 | 22.2 |
| | Breadth at occipital condyles | 110 | 155 | 147 | 147.5 | | 75.4 | 78.6 |
| Axis | Centrum ventral length | 120.3 | 108.4 | 113 | 97.6 | 85 | 38 | 47 |
| | Breadth at anterior zygapophyses | 122.5 | 160 | 150 | 178 | 171 | 84 | 86.7 |
| C3 | Centrum ventral length | 85 | 60 | 62.4 | | | 25 | 31 |
| | Breadth at posterior zygapophyses | $84^{e}$ | 112 | 110 | | | 48 | 58.5 |
| C4 | Centrum ventral length | 85 | 58 | 56 | | | 24 | 29 |
| | Breadth at posterior zygapophyses | 96.6 | 114 | 115 | | | 61.5 | 60.1 |
| C5 | Centrum ventral length | 81.6 | 59 | 55.5 | | | 23.4 | 27 |
| | Breadth at posterior zygapophyses | 113 | 116.3 | 119 | | | 59 | 64.5 |

**Table 7**. Lengths (in mm) of vertebral centra in *Brachyodus*, hippopotamids, other suoids, tragulids and other ruminants, measured along the ventral keel (° : no measurement taken; -- : no measurement possible; xx : vertebra not present (end of series)). *B.a. - Brachyodus aequatorialis; C.l. - Choeropsis liberiensis; H.a. - Hippopotamus amphibius; O.j. – Okapia johnstoni; P.t. – Pecari tajacu; S.s. - Sus scrofa; T.n. - Tragulus napu; T.o. – Taurotragus oryx*).

| **Vertebra** | ***B.a.*** | ***H.a. 1*** | ***H.a. 2*** | ***C.l.*** | ***P.t.*** | ***S.s.*** | ***T.n.*** | ***O.j.*** | ***T.o.*** |
|---|---|---|---|---|---|---|---|---|---|
| **C1** | 46.3 | 49.6 | 54 | 26.4 | 9.1 | 17.6 | 6.7 | 21 | 58.3 |
| **C2** | 120.3 | 108.4 | 113 | 38 | 21.7 | 21.7 | 16.3 | 93 | 115 |
| **C3** | 85 | 60 | 62.4 | 25 | 15.3 | 23.4 | 13.5 | 78.3 | 87.6 |
| **C4** | 85 | 58 | 56 | 24 | 15.2 | 23.6 | 13.2 | 77 | 74 |
| **C5** | 81.6 | 59 | 55.5 | 23.4 | 15.8 | 24.6 | 13.2 | 85 | 77 |
| **C6** | -- | 55.2 | 58.5 | 26.7 | 16.5 | 25.7 | 11.6 | 77.5 | 67.8 |
| **C7** | -- | 59.6 | 55.5 | 26 | 16.5 | 25.6 | 11.6 | 62 | 64 |
| **T1** | -- | 56 | 62 | 25 | 18.4 | 28.8 | 8 | 33.5 | 61.5 |
| **T2** | -- | 60.4 | 62 | 28 | 18.4 | 28.6 | 8 | 32.7 | 59.5 |
| **T3** | -- | 60 | 58.5 | 28 | 18.2 | 28.1 | 8.1 | °° | 60 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **T4** | -- | 58.7 | 54 | 28 | 18.3 | 27.1 | 8.1 | °° | 58 |
| **T5** | -- | 51 | 56.5 | 29.5 | 18.3 | 25 | 8.1 | 36.5 | 47.5 |
| **T6** | -- | 58.4 | 57.5 | 31.5 | 18.3 | 25.4 | 8.1 | 35.6 | 50 |
| **T7** | -- | 65 | 58.7 | 31.5 | 18.3 | 27 | 9.8 | 36 | 50 |
| **T8** | -- | 65.9 | 63.3 | 31.5 | 18.3 | 27.7 | 9.7 | 35 | 51 |
| **T8** | -- | 65.4 | 64 | 31 | 18.3 | 27.8 | 10.7 | 35.7 | 52.7 |
| **T10** | -- | 68.8 | 64.8 | 30.8 | 18.6 | 28.3 | 12.4 | 36.7 | 53 |
| **T11** | -- | 68.2 | 65.4 | 32.8 | 18.6 | 29.3 | 10.6 | 36.7 | 57 |
| **T12** | -- | 68.2 | 71 | 32.7 | 18.7 | 29.6 | 11 | 37.6 | 57 |
| **T13** | -- | 69 | 71.3 | 34 | 20.3 | 29.8 | 12 | 37.6 | xx |
| **T14** | -- | 68.2 | 72.3 | 33.5 | 21.4 | 32 | xx | 39 | xx |
| **T15** | 72 | 70 | 71.8 | 34.2 | xx | xx | xx | xx | xx |
| **L1** | 77.5 | 71.6 | 74 | 35.7 | 21.4 | 33.2 | 15.7 | 41.1 | 61.3 |
| **L2** | -- | 82.3 | 82 | 37.5 | 21.4 | 37 | 16 | 42.1 | 64.2 |
| **L3** | -- | 85.5 | 82.4 | 37 | 23.4 | 35.7 | 15 | 42.1 | 62 |
| **L4** | -- | 71 | 76.5 | 34 | 22.7 | 35.9 | 15.7 | 42.1 | 63.4 |
| **L5** | | xx | xx | xx | 21.4 | 31.7 | 16.2 | 42.5 | 62.5 |
| **L6** | | xx | xx | xx | xx | xx | 13.6 | xx | 59.7 |

## The neck in other Anthracotheriidae

Geais (1934) described poorly preserved atlas and axis (UCBL Sciences de la Terre 1408) which she attributed to *Brachyodus borbonicus* (now usually classified in the genus *Elomeryx*). The axis shows the forward facing epiphyseal articular facet shaped like a base-plate and the broadened base of the odontoid process characteristic of anthracotheres, unlike the narrower peg-like or conical odontoid process and laterally facing epiphyseal articular surface that occurs in suids, palaeochoerids, tayassuids and hippopotamids (Hooijer, 1950). Thus *Elomeryx* had an axis which was like that of *Brachyodus*, indicating that this was likely the usual morphology of the family, or at the least in the subfamily Bothriodontinae.

## Commentary on recent cladistic analyses of Hippopotamidae and Anthracotheriidae

Lihoreau *et al*. (2015) proposed for the third time a scenario of hippopotamid-cetacean relationships in which anthracotheres were concluded to comprise the group that links the two together, thereby eliminating or greatly reducing the duration of the ghost lineage between the earliest known cetaceans on the one hand (early Eocene) and the earliest known hippopotamids on the other (early Miocene). However, the cladistic analyses carried out by these authors were based only on dental characters, of which 172 are listed in the supplementary information.

As concerns the most recent version of the hypothesis that hippos descended from anthracotheres (Lihoreau *et al.* 2015), our interpretation confirms that it is essential to include cranial and post-cranial morphology in phylogenetic analyses (Kowalevsky, 1873, 1874). No post-cranial remains of *Epirigenys* were described, so the analysis by the authors depended solely on dental remains. The rearrangement of crista and styles proposed by the authors along with the suppression of cusps and styles, in order to obtain a tetracuspidate hippopotamid upper molar morphology with trefoliate cusps and no styles, from a bothriodont anthracothere starting morphology in which the molars are pentacuspidate with strong buccally positioned styles and divergently oriented crista, and with selenodont cusps, represents an extreme example of the concept of odontological plasticity. This concept was previously employed by the same authors when proposing first *Libycosaurus* (Late Miocene) and subsequently *Morotochoerus* (Early Miocene) as the ancestral hippopotamid (Boisserie, 2005; Boisserie *et al.* 2005a, 2005b; Lihoreau, 2003; Orliac *et al.* 2010). When each of these hypotheses was refuted (Pickford, 2008b, 2011) the authors abandoned or modified their previous hypotheses by selecting another, older, anthracothere genus as the ancestor of the hippos. The nomination of Oligocene *Epirigenys* as the ancestor of hippopotamids by Lihoreau *et al.* (2015) follows the same logic (Fig. 28, 29) uses almost the same dental nomenclature (slightly modified and extended) and employs the same cladistic methodology as for the previous scenarios, and it fails for the same reasons (it presents no cranial or post-cranial data and the nomenclature employed for anthracothere and hippopotamid teeth suggests the presence of homologies where few exist). As such the nomenclature employed anticipates the phylogeny, producing a circular argument.

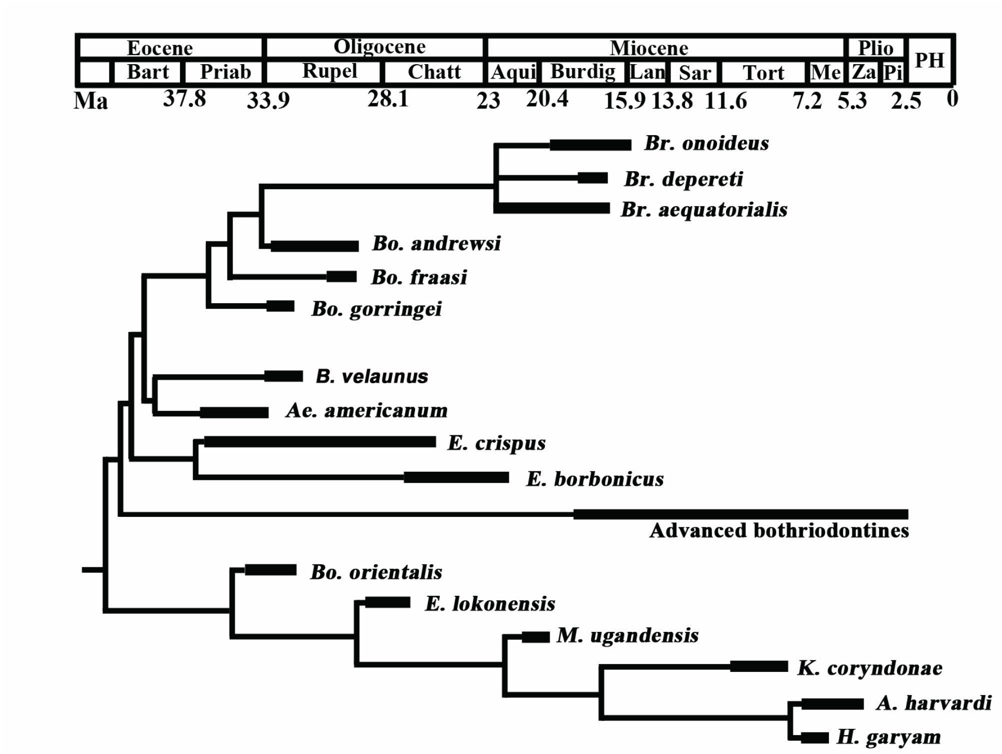

**Figure 28**. Hypothesis of the phylogeny of Hippopotamidae and Anthracotheriidae according to Lihoreau *et al.* (2015, fig. 3) (Abbreviations from Lihoreau *et al.* 2015: *A – Archaeopotamus, Ae – Aepinacodon, B – Bothriodon, Bo – Bothriogenys, Br – Brachyodus, E – Elomeryx* and *Epirigenys, H - Hippopotamus, K – Kenyapotamus, M - Morotochoerus*). The linking of *Kenyapotamus coryndonae*, *Archaeopotamus harvardi* and *Hippopotamus garyam* (ie Hippopotamidae) to *Morotochoerus ugandensis*, *Epirigenys lokonensis* and *Bothriogenys orientalis* (ie Anthracotheriidae) is refuted in the present paper.

Our data reveal that anthracotheres are more closely related to traguloids and other ruminants than they are to Suoidea and Hippopotamidae. The new information about the vertebral column reveals a close relationship between Hippopotamidae and Palaeochoeridae (the sister group of Tayassuidae, the New World Peccaries) and only a very distant one between these families and Ruminantia, especially Anthracotheriidae.

Therefore, the most recent proposal that hippopotamids originated from Eocene, Oligocene and Miocene anthracotheres (Lihoreau *et al.* 2015) is refuted.

Dental character definitions

The definition of dental characters by Lihoreau *et al.* (2015) can be criticised. On a linguistic level the authors consistently use the word "labial" for check teeth, when the more usual terminology for the outer surface of the molars and premolars is "buccal". The name ectocrystile/id is applied by these authors to both the 'labial' and 'lingual' cusplet at the ends of the median transverse valley (perhaps this is simply a typographic error). On a more substantive level, for many of the minor dental structures, the authors have proposed a terminology that implies homology between anthracotheres and hippopotamids where none exists (Fig. 29). Many of these minor structures are known to be highly variable in bunodont and bunoselenodont mammals, most of them representing developments in parallel or by convergence from cingula.

**Figure 29**. Left sketch - nomenclature and morphological scheme of an upper molar of early hippopotamids according to Lihoreau *et al.* (2015, text fig. 3, one of a series of four sketches to explain the morphological evolution of the upper molar, specifically the stage representing *Morotochoerus ugandensis*) compared with UM MOR I, 15'98, an upper molar of the species from Moroto I, Uganda, stereo occlusal view (centre) and interpretive drawing (right) (scale: 10 mm). Numerous inconsistencies are apparent between the left hand sketch and the fossil itself.

The early Miocene small anthracothere, *Morotochoerus ugandensis* was interpreted as an "early hippopotamid" by Orliac *et al.* (2010) and by Lihoreau *et al.* (2015) but its upper molars lack several of the supposed hippopotamid characters illustrated in a sketch by these authors, including all the styles (Fig. 29), and it has features that are not mentioned by these author, such as the enlarged centrally positioned paraconule separated from the protocone by a groove, divergent orientations of the cristae of the main cusps, mesial, lingual and distal cingula, and even a posterior cingular cusplet separated from the end of the postmetacone crista (in the position of, but not homologous to, the metastyle). Thus the upper molar morphology of *Morotochoerus* is not close to that of the Hippopotamidae, but it shares several characters with anthracotheres as shown by Pickford (2008b, 2011).

Atomising of morphology

Furthermore, Lihoreau *et al.* (2015) do not implicitly state that many of the characters that they define are linked into functional complexes. It is generally the functional complexes that are subjected to natural selection, more so than the individual minor structures in isolation from each other. For example, a crista in an upper molar generally has an antagonistic cristid in the lower molar, the two structures being part of a single occlusal relationship, both of which are subjected to the same natural selection forces. The question is - "Should this complex be atomised into two characters or into one?" The authors consistently count such linked complexes as multiple characters, thereby biasing their data base from the outset of the analysis. In effect, the authors have 'atomised' the dentition in order to increase the quantity of characters to include in the analysis.

Taxon choice

The choice of taxa included in the cladistic analysis by Lihoreau *et al.* (2015) is remarkable for the fact that only one poorly known "palaeochoerid" is included (*Doliochoerus quercyi*) when far more complete taxa of this group are known (*Propalaeochoerus*, *Palaeochoerus*, *Pecarichoerus*, *Choeromorus*, *Schizoporcus*), some of which were discussed by Pickford (2008b, 2011). Since *Doliochoerus* is not a typical palaeochoerid, either dentally or cranially (its post-cranium is undescribed), the combination of using solely this taxon to represent the Palaeochoeridae, and the omission of other palaeochoerids results in a questionable refutation of Pickford's (2008b, 2011) hypothesis of hippopotamid origins. Also peculiar is the absence of any discussion of the most primitive known hippopotamid, *Palaeopotamus ternani* (Pickford, 1983, 1989) from the Middle Miocene of East Africa, which possesses a dentition close to those of palaeochoerids (Pickford, 2007).

Absence of post-cranial characters

No post-cranial bones of *Epirigenys* have been described, so they could not be included in the analysis by Lihoreau *et al.* (2015). However, post-cranial bones of other anthracotheres, palaeochoerids and hippopotamids are known (Pickford, 2008b, 2011) and should be included in cladistic analyses wherever possible.

Lihoreau *et al*. (2014) wrote that "*Few post-cranial elements from Chad have been attributed with certainty to anthracotheres. Fragmentary and eroded specimens appear very difficult to differentiate from the post-cranials of hippopotamids that are equivalent in size, anatomically close and similarly display substantial morphological variations*". This sentence gives the false impression that it is difficult to differentiate the post-cranial bones of hippopotamids from those of anthracotheres, and it runs counter to the findings of Lihoreau (2003). Pickford (2008b) showed that every bone and tooth in the skeleton of anthracotheres is readily distinguished from those of hippopotami, a finding already anticipated by Falconer & Cautley (1848). The failure by Lihoreau *et al*. (2015) to employ the post-cranial bones in their cladistic analysis represents a major weakness which effectively nullifies their results.

MacAlister (1873) and Fisher *et al*. (2007) described aspects of the soft anatomy of *Choeropsis*, and it is clear from their work that the forelimb bones and details of muscle insertions and origins of the Pygmy Hippo differ markedly from those of anthracotheres (Pickford, 2008b).

## Systematic and phylogenetic implications of the vertebrae of *Brachyodus aequatorialis*

The morphology of the neck vertebrae of *Brachyodus*, and the length of the neck relative to the trunk vertebrae, indicate that *Brachyodus* shares a great deal with ruminants, especially with Tragulidae. Its neck vertebrae are radically different from those of *Hippopotamus* and *Choeropsis*, as well as *Propalaeochoerus*, the latter three of which resemble each other to a high degree.

From this we conclude that Anthracotheriidae should be removed from Suiformes in which they have generally been classified (McKenna & Bell, 1997) usually on the basis of their talar morphology, and should instead be assigned, either to the Ruminantia, or to a separate suborder in a sister-group relation with the Ruminantia (Fig. 30-33). Among the ruminants, *Brachyodus* is morphologically closer to Tragulidae than to Pecorans.

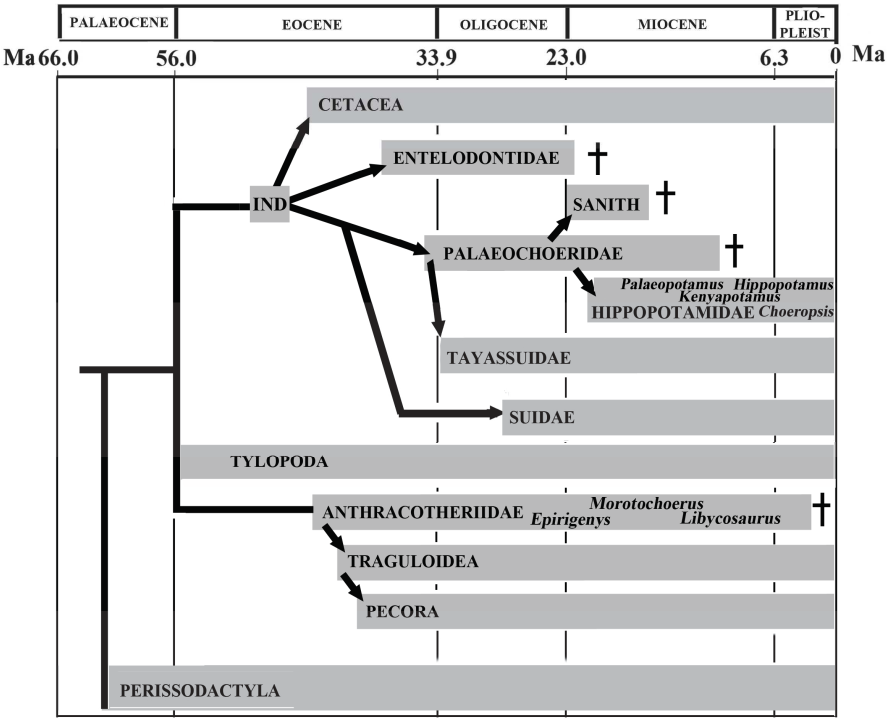

**Figure 30**. Proposed phylogeny of Artiodactyls taking into account the cranio-dental morphology as well as the post-cranial skeleton, in particular the vertebral column (Ind – *Indohyus*, Sanith – Sanitheriidae)

In contrast, the neck vertebrae of *Hippopotamus* and *Choeropsis* are virtually isometrically upscaled versions of the vertebrae of Old World Peccaries, Palaeochoeridae, such as *Propalaeochoerus elaverensis* and *Choeromorus inonuensis* and they also share morphological features with Tayassuidae (New World Peccaries) (Fig. 33).

Among Artiodactla a v-shaped (or trifid) hypapophyseal tubercle at the distal termination of the ventral ridge of the axis and C3 (the forked ventral spine of Hooijer, 1950; the trifid spine in the Entelodontidae, *Elotherium*, Scott, 1898) occurs in Hippopotamidae, Palaeochoeridae and Tayassuidae, and in a weakened version in the Suidae, *Sus* and *Potamochoerus*. This character not only provides strong evidence of a close relationship between these families but also yields information concerning the time of origin of the character which must have evolved before the Early Oligocene, the time of divergence of Old World Palaeochoeridae and New World Tayassuidae (Pearson, 1927, 1929). It occurs in Entelodontidae which indicates that it may well be a primitive character among Artiodactyla. It does not occur in Ruminantia, which have a derived morphology of the hypapophyseal process, nor does it occur in Anthracotheriidae, indicating that the divergence between Anthracotheres on the one hand, and the Palaeochoeridae-Tayassuidae-Suidae-Hippopotamidae on the other, probably occurred earlier than the Oligocene, and likely in the Early or Middle Eocene.

What all this signifies is that Anthracotheriidae and Hippopotamidae are so divergent in cervical vertebral parameters that it is exceedingly unlikely that the former group gave rise to the latter (Fig. 31). If anthracotheres are postulated to give rise to hippopotamids as was done by Lihoreau *et al.* (2015), then one needs to invoke an evolutionary yoyo, starting with forked hypapophysis in C2 and C3, the morphology found in primitive artiodactyls such as entelodonts and suoids, evolving into an unforked morphology in anthracotheres, then reverting to a forked morphology in hippopotamids. It is more parcimonious to derive the forked hypapophyseal process in hippopotamids directly from an ancestral group that possessed the same morphology. The same argument applies to the form of the odontoid process of the axis, conical peg-like in hippopotamids and suoids, spout-like in anthracotheres and ruminants. From this we conclude that anthacotheres do not form the link between Cetacea on the one hand, and Hippopotamidae on the other. The vertebrae of Palaeochoeridae, in contrast, are so close morphologically to those of *Hippopotamus* and *Choeropsis*, that the hypothesis that hippos emerged from palaeochoerids proposed by Pickford (2008b, 2011) represents a far more likely scenario than the recently published alternative view that they descended from anthracotheres (Lihoreau *et al.* 2014, 2015).

This re-arrangement of the families renders the concept of Whippomorpha (Cetacea + Hippopotamidae + Anthracotheriidae) and Cetruminantia (Whippomorpha + Ruminantia) (Waddell *et al.,* 1999) untenable, as it groups Hippopotamidae with Palaeochoeridae + Tayassuidae + Suidae. In contrast, it fits better, but not perfectly, with the arrangement published by Spaulding *et al.* (2009) in which Anthracotheriidae (with the exception of *Merycopotamus*) are positioned close to Tragulidae and Pecorans. However, the cladogram of Spaulding *et al.* (2009) has a vast separation between Suidae + Tayassuidae on the one hand, and Hippopotamidae on the other, which our study suggests does not exist (Fig. 33). Our results indicate that the Cetancodontamorpha of these same authors is an unnatural grouping of divergent taxa. Our grouping of taxa agrees partly with the cladogram of Price *et al.* (2005), with one major difference, the branching of Suiformes prior to the split between the Pecora and Whippomorpha (Hippopotamidae + Cetacea). Minor adjustment of the arrangement would rectify the contradiction (Fig. 32). However, a major drawback to the Price *et al.* (2005) phylogeny is that the authors failed to include the anthracotheres and tragulids and did not mention the Palaeochoeridae.

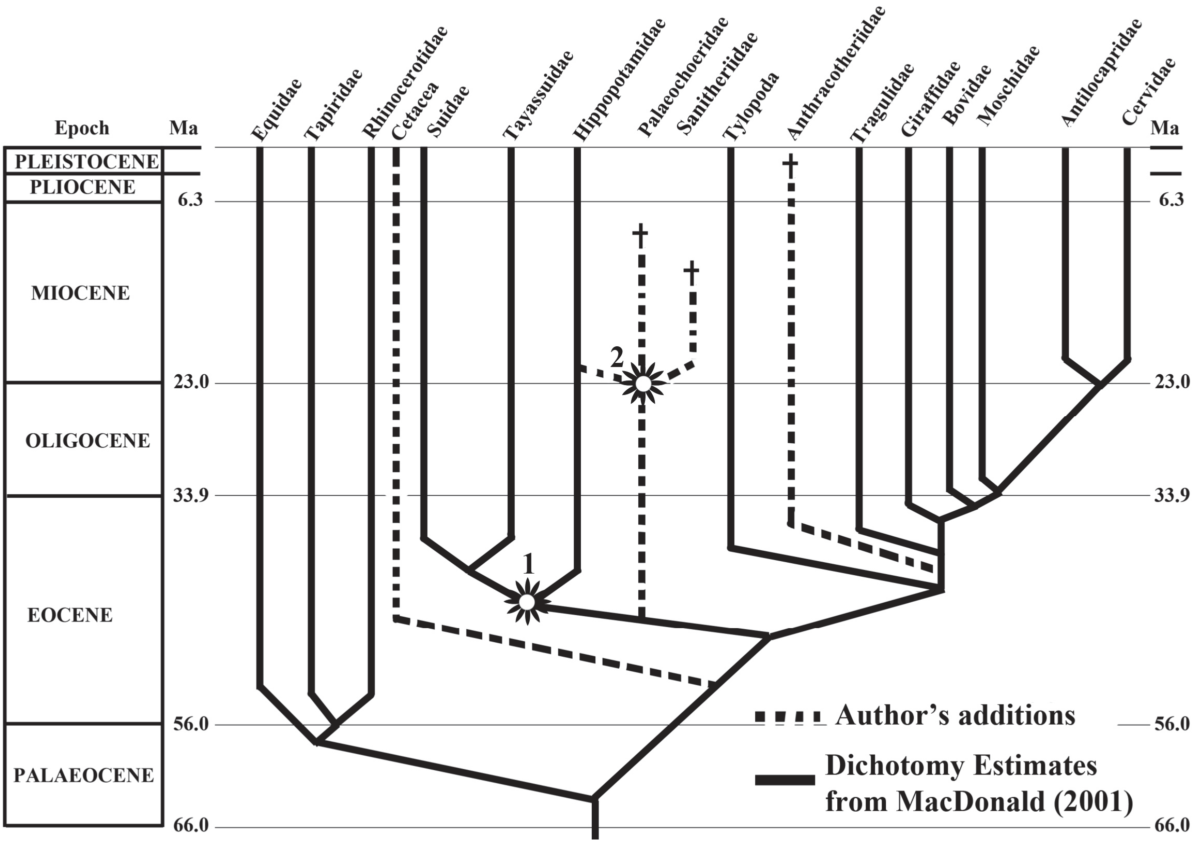

**Figure 31**. Phylogeny of extant families of Ungulates showing the Hippopotamidae close to the Suidae and Tayassuidae (modified from MacDonald, 2001). The Anthracotheriidae, Palaeochoeridae, Sanitheriidae (all extinct) and Cetacea (dotted lines) have been added to this phylogeny. MacDonald, 2001, postulated a Middle Eocene split between Tayassuidae and Hippopotamidae (1 in the figure) not inconsistent with the hypothesis proposed herein in which Palaeochoeridae diverged from Tayassuidae during the Eocene and Hippopotamidae diverged from Palaeochoeridae during the Early Miocene (2 in figure).

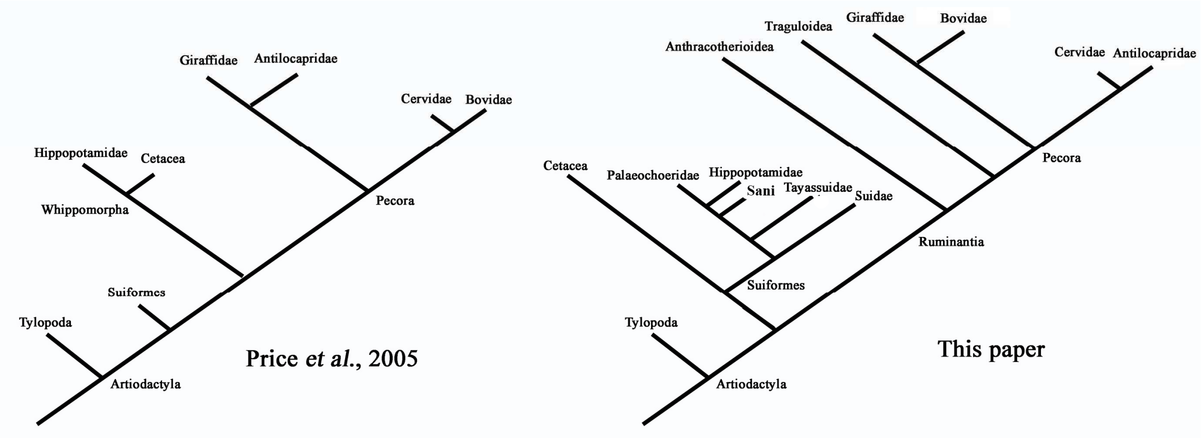

**Figure 32**. Phylogeny of Artiodactyla according to Price *et al.* 2005, which is based predominantly on molecular evidence, compared to the hypothesis proposed herein based on dental and skeletal morphology. Note the revised position of the Hippopotamidae relative to the Suiformes and the transposed positions of Antilocapridae and Bovidae (Sani – Sanitheriidae).

The new analysis of the cervical vertebrae of *Brachyodus* (and *Elomeryx*) reveals that the anthracotheres possess several morphological features shared with ruminants, whereas hippopotamids share none of these features with ruminants, but all of them with Palaeochoeridae, Tayassuidae and some with Suidae. Data on the non-axial post-cranial skeleton were already given by Pickford (2008b) who showed that anthracotheres were highly divergent from hippopotamids in many features of the dentition, cranium and appendicular skeleton. The new information obtained from the cervical vertebrae confirms the vast morphological difference that exists between anthracotheres and hippopotamids. The former have relatively elongated necks and the cranium is habitually held in a head-up posture, whereas the latter have short necks with the cranium habitually held in a head-down posture. In their neck and head posture, anthracotheres are more like ruminants than hippopotamids, with particular resemblances in some vertebral features to Tragulidae. On the basis of this new data, it is proposed to classify Anthracotheriidae either within the Ruminantia, or as the sister-group of the Ruminantia. Hippopotamidae, in contrast, fit comfortably close to Palaeochoeridae, not only dentally (Pickford, 2008b, 2011) but also post-cranially (Pickford, 2008b and this paper), and the probability that Hippopotamidae descended from Palaeochoeridae is strengthened by the study of the vertebral column.

Old anatomical literature reveals soft tissue similarities between hippopotamids and tayassuids which are pertinent to the debate about the affinities of Hippopotamidae. For example, Chapman (1881) wrote that "*The female generative apparatus of the Peccary and of* Hippopotamus *are almost identical*". Combining the findings made during the present study of the vertebral column with the soft anatomy (Garrod, 1880) indicates that it is no longer possible to dismiss lightly the probability that Hippopotamidae are more closely related to other suoids than they are to an extinct family Anthracotheriidae which, as its skeleton is more completely analysed, shows an increasing number of features shared with Ruminantia. Palaeontological, biogeographic and biostratigraphic data indicate strongly that Hippopotamidae share close phylogenetic signals with Palaeochoeridae, a family often referred to as Old World Peccaries, with the New World Peccaries (Tayassuidae) in a slightly more remote relationship.

## Relationship between Anthracotheriidae and Tragulidae

An unexpected result of this analysis of the neck vertebrae of *Brachyodus*, is that it indicates a closer relationship of the Anthracotheriidae to the Ruminantia than to the Suiformes. Among the Ruminantia, the Tragulidae show the closest relationship to Anthracotheriidae. Dental resemblances between anthracotheres and ruminants have been noticed in the past (Lydekker, 1876; Pickford, 2008b) but the form of the talus has generally been given greater weight in deciding the systematic position of the family, which is almost universally attributed to the Suiformes on that account (Simpson, 1945; McKenna & Bell, 1997). Pickford (2008b) showed that anthracotheres shared many features of their skeletal body plan and limb length to aquaphile ruminants such as the South American marsh deer (*Blastocerus* Illiger 1815) and the Indian swamp deer, the Sambar (*Cervus unicolor* Kerr, 1792). The neck of *Brachyodus* confirms this viewpoint, but reveals in addition, that the morphological resemblances beween anthracotheres and ruminants are not due so much to convergence, but to shared ancestry (Spaulding *et al.* 2009)

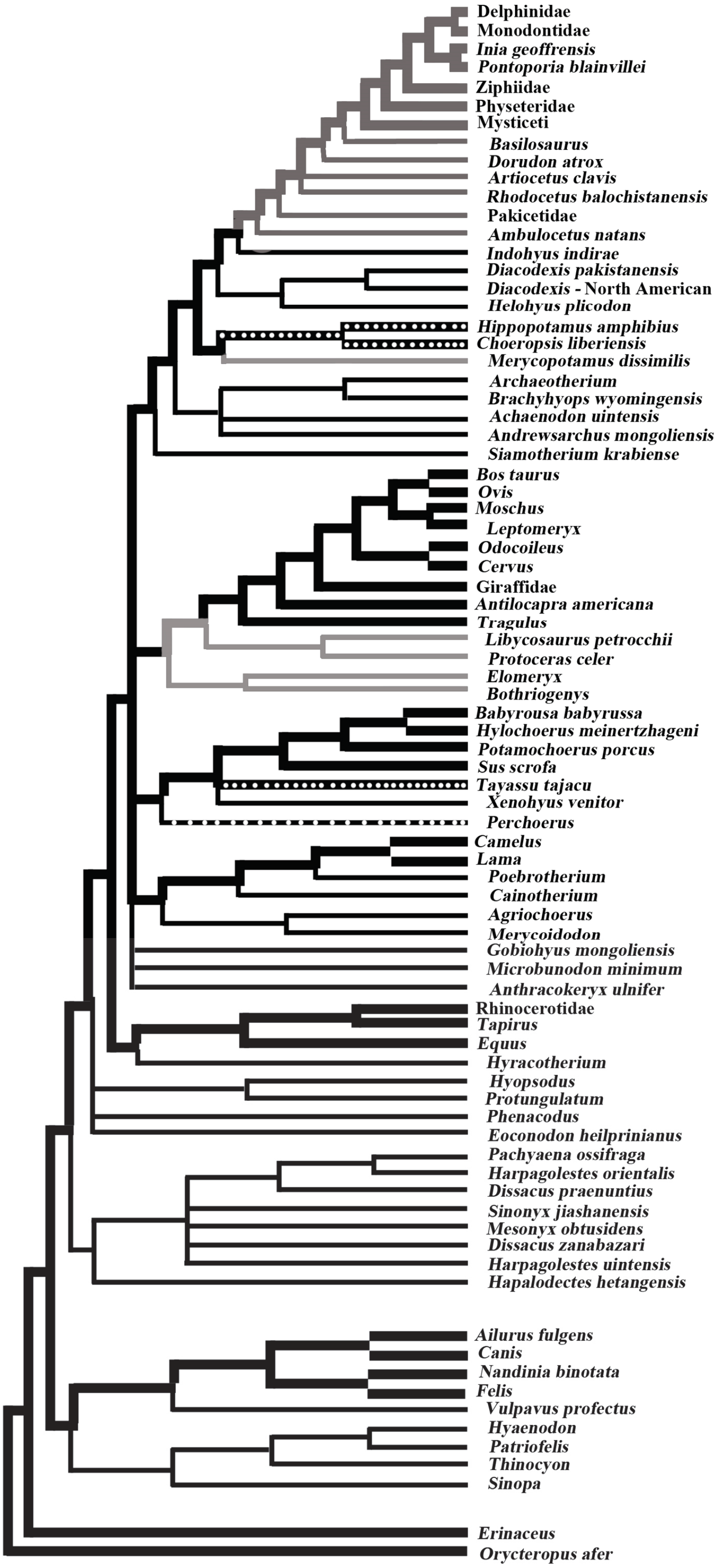

**Figure 33**. Phylogeny of Mammalia proposed by Spaulding *et al.* 2009, in which the Anthracotheriidae (with the exception of *Merycopotamus*) (grey lines) nest close to Traguloidea and other ruminants, in agreement with the dento-skeletal evidence discussed in this paper, which in addition indicates that Tayassuidae and Hippopotamidae (dotted lines) are more closely related to each other than the phylogeny would suggest. Taxa positioned slightly to the right are extinct, those to the left are extant. (Figure modified from Spaulding *et al.* 2009).

(Fig. 33). In this respect it is pertinent to recall that Metais *et al*. (2001) wrote "*Although Colbert (1935a) considered its unquestionable tragulid affinities, Gentry (1978) claimed that* Dorcabune *might be a primitive anthracothere. With the exception of the M structure and the presence of a weak entoconidian groove,* Dorcabune *does not display other apomorphies with* Archaeotragulus. *The former differs from the Thai form by its larger size and by its molars more bunodont and less transversely compressed. It is therefore clear that no close relationship exists between the two taxa, and according to Gentry (1978) the tragulid status of* Dorcabune *can be questioned*». This discussion reveals that the supposed tragulid *Dorcabune* Pilgrim (1910) from the Siwaliks of Indo-Pakistan, could well be an anthracothere rather than a tragulid. Pilgrim (1910, 1915) already noted the dental resemblances between his new genus and anthracotheres, and for this reason, named a species of the genus *Dorcabune anthracotherioides*. This history underlines the similar morphology that some anthracotheres share with some tragulids, interpreted here as being due to proximity of ancestry rather than to convergence among widely separated lineages.

## Conclusions

It is shown that the cervical vertebrae of the bothriodontine anthracothere *Brachyodus*, are radically divergent from those of extant and fossil Hippopotamidae. When combined with previously published data about anthracothere and hippopotamid cranial, dental and post-cranial morphology (Pickford, 2008b), it effectively refutes the notion that hippopotamids may have descended from anthracotheres (Lihoreau *et al.* 2015).

A second conclusion of this study is that the cervical vertebrae of *Brachyodus* reveal closer morphofunctional relations with Ruminantia than with Suiformes, an observation that indicates that the family Anthracotheriidae should be removed from Suoidea, in which it is usually classified on the basis of its talar morphology, and moved towards the Ruminantia. Some resemblances between the vertebrae of *Brachyodus* and those of Tragulidae, suggest that the most likely systematic position for Anthracotheriidae would be close to, or within, Ruminantia. In phylogenetic terms, Anthracotheriidae would occupy a basal position in Ruminantia, followed by Traguloidea, and then by Pecora. This finding generally supports a phylogeny of Artiodactyla recently proposed by Spaulding *et al*. (2009).

A third conclusion of this contribution is that neglect of post-cranial data in cladistic analysis (Lihoreau *et al.* 2014, 2015) generally produces poor results. With respect to systematics and phylogenetics, this sentiment was already stressed by Kowalevsky (1873, 1874) and his words are as relevant today as they were when they were published over 140 years ago.

The fourth conclusion of the present study is that the removal of anthracotheres from the ancestry of Hippopotamidae does not *per se* weaken the molecular-based hypothesis that Hippopotamidae and Cetacea are more closely related to each other than either is to other Artiodactyla (Fisher *et al.* 2007; Price *et al.* 2005), but it does indicate that previously published molecular-based phylogenetic relationships between Tayassuidae, Hippopotamidae and Cetacea need to be reassessed.

Finally, the fifth conclusion of this article is that the Hippopotamidae are osteologically so close to Palaeochoeridae in so many ways, that there remains little doubt that this is the group from which Hippopotamidae emerged. The available fossils of primitive hippopotamids indicates that the divergence of Hippopotamidae from Palaeochoeridae occurred during the Early Miocene, soon after palaeochoerids had dispersed into Africa (Pickford, 2007).

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