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The axial skeleton of *Brachyodus onoideus* (Mammalia, Anthracotheriidae): taxonomic and functional implications

El esqueleto axial de *Brachyodus onoideus* (Mammalia, Anthracotheriidae): implicaciones taxonómicas y funcionales

Martin PICKFORD

Abstract: Vertebrae of *Brachyodus onoideus* from Europe have never been described, yet several specimens have been curated in diverse museums for more than a century. The importance of the cervical vertebrae lies in the fact that they reveal that this species possessed a moderately elongated neck that in neutral posture was oriented upwards, somewhat as in some extant artiodactyls (Okapi, Eland and camels), unlike the low-slung head and neck posture of the two extant genera of hippopotamuses. The sacrum of *Brachyodus* is markedly different from those of *Hippopotamus* and *Choeropsis*. In morpho-functional terms it is closer to those of large ruminants and equids, indicating the possession of a less muscular tail than in hippos which wag their tails energetically during defecation.

Resumen: Las vértebras de *Brachyodus onoideus* de Europa nunca se han descrito, a pesar de que algunos ejemplares se han conservado en diversos museos durante más de un siglo. La importancia de las vértebras cervicales radica en el hecho de revelar que esta especie poseía un cuello moderadamente alargado que en postura neutra estaba orientado hacia arriba, como ocurre en algunos artiodáctilos actuales (Okapi, Eland y camellos), a diferencia del cuello corto y posición baja de la cabeza de los dos géneros de hipopótamos actuales. El sacro de *Brachyodus* es marcadamente diferente de los de *Hippopotamus* y *Choeropsis*. En términos morfofuncionales se acerca más al de los grandes rumiantes y équidos, lo que indica la posesión de una cola menos musculosa que en los hipopótamos que mueven la cola enérgicamente durante la defecación.

INTRODUCTION

The axial skeleton of anthracotheres, an extinct superfamily of artiodactyls, was extremely poorly documented until a specimen of '*Brachyodus*' *aequatorialis* was excavated at Grillental VI, Namibia, comprised of a damaged skull, six of the seven cervical vertebrae articulated together, and a thoracic and a lumbar vertebra in connection associated with some limb bones (Pickford, 2008a, 2015). This specimen yields evidence that the neck of the genus was moderately elongated, and that the head was habitually held in an above-the-shoulder posture when at rest, contrasting fundamentally with the foreshortened neck of hippopotamuses (*Choeropsis*, *Hippopotamus*) in which, at rest, the head is held in a low-slung posture beneath the level of the shoulders.

The fact that the splanchnocranium and neurocranium of *Brachyodus* have seldom been found in correct anatomical relationship to each other, has caused confusion and uncertainty. The best preserved specimen was described by MacInnes (1951). '*Brachyodus*' *aequatorialis*, from Rusinga Island, Kenya, has a platycephalic cranium in which the occipital condyles and glenoid fossa are at almost the same level as the roots of the maxillary teeth. This specimen has served as a proxy for reconstruction of the head of *Brachyodus onoideus*, although we now know that there are major differences in proportions of the skulls of these two taxa (see below). The specimen of '*Brachyodus*' *aequatorialis* from Grillental VI, Namibia (Pickford, 2008a, 2008b, 2015) has the most complete known series of neck vertebrae of this

species, but the associated cranium is rather poorly preserved even though it does preserve parts of the maxillae with the molars, the posterior nares, the base of the neurocranium and the occipital condyles.

On the basis of specimens from Saint-Antoine-de-Ficalba (one crushed cranium) and Chilleurs-aux-Bois (many cranio-dental remains), Orliac *et al*. (2013) reconstructed *Brachyodus onoideus* as platycephalic, but the neurocranium in the fossil from Saint-Antoine-de-Ficalba is crushed and distorted and neither specimen has the maxillae attached to the neurocranium, rendering it impossible to determine the relationship betweeen the basicranium and the level of the cheek teeth. The platycephalic reconstruction was accepted by Pickford (2020b) but the subsequent recognition of the subcomplete skull of *Brachyodus onoideus* preserving the correct relationship between the splanchnocranium and neurocranium, indicates that *Brachyodus onoideus* is not platycephalic. The specimen, which is curated at the Geology Department of the University of Liège preserves the left maxilla with cheek teeth in correct anatomical relationship to the neurocranium showing that its glenoid fossa and occipital condyles are positioned well above the roots of the maxillary cheek teeth, revealing that *Brachyodus onoideus* was considerably more hypsicephalic than '*Brachyodus*' *aequatorialis*.

A major difference between the cervical vertebrae of anthracotheres and hippopotamids is that, in anthracotheres, the bones are generally in compression relative to one another, the head being at the upper end of a long, upwardly sloping neck with the weight of the head pushing the vertebrae together, whereas in hippopotamuses, the cervical vertebrae are generally held at a low angle slightly above horizontal, with the weight of the head tending to pull the vertebrae away from the thorax and from each other when on land (when in the water, the head is partly bouyed up like the rest of the body, so the force of gravity on the limbs and vertebrae is reduced). As a consequence of the extensive or compressive forces acting on the vertebrae, the system of sinews, muscles, intervertebral discs and other soft tissues of the neck, differs in the two groups. For example, the hypaphosyseal process in the cervical vertebrae of hippos (and other mammals with low-slung heads such as suids and carnivores) is V- or Y-shaped, whereas in anthracotheres (and other mammals with heads held high) it is a simple undivided process (Pickford, 2015).

The presence of a moderately elongated neck in the Namibian specimen of '*Brachyodus*' *aequatorialis*, implying an above-the-shoulder posture of the head, prompted Pickford (2015) to question the oft-repeated hypotheses that anthracotheres possessed body plans similar to those of hippopotamuses (Geais, 1934; Orliac *et al*., 2013) and by inference that they had similar ecological requirements such as amphibiosis.

The presence of a medium length neck in *Brachyodus* casts doubt on the notion that hippopotamuses,

which have extremely short necks, descended from anthracotheres (Lihoreau & Boisserie, 2004; Boisserie *et al*., 2005a, 2005b, 2006). Pickford (2008) concluded that *Brachyodus* was morphofunctionally closer to ruminants (in particular traguloids) in its dentition, skeleton, overall body plan and cursorial locomotor repertoire, than to hippopotamids which, in these complexes, are closer to some families of Old World «peccaries» (at the time called Palaeochoeridae, but now known as doliochoeroids, not to be confused with New World Peccaries, which are rather different from them, Pickford, 2017). The vertebral column of *Brachyodus* supports this inference, the morphology of the atlanto-axial articulation being derived with respect to those of «suiformes» but not as derived as those of ruminants, being in some ways intermediate between the two extremes. In hippopotamids the atlanto-axial articulation is plesiomorphic, an observation that essentially refutes the notion that hippos descended from anthracotheres, because, if so, then one would have to invoke a reversal from a derived morphological state to a plesiomorphic condition of this articulation.

The sacrum of *Brachyodus*, like the cervical vertebrae, differs fundamentally in morphology from those of hippopotamuses. The anthracothere sacrum narrows distally and has short transverse processes, as in many large-bodied terrestrial cursorial ungulates, whereas in *Hippopotamus* and *Choeropsis*, all the sacral vertebrae posterior to the first one are subequal in breadth, with some individuals having a 5th sacral vertebra in which the transverse processes are slightly broader than those on the second and third ones. The tail vertebrae are correspondingly large in hippos, with prominent, robust, elongated transverse processes.

In hippopotamuses, the short but fleshy tails are endowed with strong musculature which actively and rapidly swish the tail from side to side during defecation, acting somewhat like a dung-spreader (both in the water and on land) (Skinner & Smithers, 1990; Klingel, 2013; Robinson, 2013). In these animals, the coccygeal vertebrae have elongated transverse processes to support the muscle mass. The caudally narrowing sacrum of *Brachyodus onoideus*, in contrast, indicates that the coccygeal vertebrae would have been narrow with reduced or absent transverse processes, as in *Anthracotherium* (Kowalevsky, 1874) and thus would probably have been similar in general morphology to those of large ruminants and equids, and if so, then its tail would have been more gracile and not as muscular as those of hippopotamuses.

The aim of this contribution is to describe the occipital region, atlas, axis and sacrum of *Brachyodus onoideus* and to discuss the relevance of these bones for understanding aspects of head and neck posture, as well as the anatomy of the pelvic region, and what these imply in terms of taxonomy among anthracotheres. It is concluded that the African species previously classified as '*Brachyodus*' *aequatorialis* belongs to a separate genus for which a new name is created (see below).

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The new data also prompt a reassessment of the systematic and phylogenetic relationships between anthracotheriids and hippopotamids, which have been an active subject of debate ever since it was hypothesised that hippos are more closely related to whales than to artiodactyls (Montgelard *et al*., 1997a, 1997b; Gatesy, 1998, 1999; Gatesy *et al*., 1996, 1999; Boisserie *et al*., 2005a, 2005b; Gomes-Rodrigues *et al*., 2021). It is herein concluded that hippopotamids are unlikely to have descended from anthracotheres, because such a scenario would require evolutionary reversals in several anatomical complexes (dentition, atlas, axis, sacrum, radio-ulna, talus and metapodials among others). Whilst the possibility of reversals in morphology should not be discarded a priori, it would be surprising if they occurred in so many anatomical complexes within a single evolving lineage. This is especially so, if one considers the pervasive resemblances that are present between the skeletons of some doliochoerids and hippopotamids.

Abbreviations. **CGM,** Cairo Geological Museum; **GSN,** Geological Survey of Namibia, Windhoek; **GT,** Grillental, Namibia; **KNM,** Kenya National Museum, Nairobi; **MNHN,** Muséum National d'Histoire Naturelle, Paris; **NHMB,** Naturhistorische Museum, Basel; **NHMUK,** Natural History Museum of the United Kingdom, London; **SO,** Sables de l'Orléanais; **Ulg,** Université de Liège.

PREVIOUS STUDIES

Despite almost two centuries of research on anthracotheres, few vertebrae have been described, most of which are incomplete, crushed or otherwise distorted. Part of the problem seems to be related to the preconceived notion, often repeated in the literature, that anthracotheres were expected to have possessed hippo-like skeletal elements. Partly for this reason, because the cervical vertebrae and sacrum of anthracotheres are morphologically divergent from those of hippopotamuses, they remained unidentified in the collections, except in rare cases where they were found in close association with dental elements (Kowalevsky, 1874; Geais, 1934). Cervical vertebrae of *Brachyodus* are curated in collections in Cairo (Cairo Geological Museum and the University of Cairo), Basel (Naturhistorisches Museum) and the Loire Valley (various municipal museums), some for more than a century, yet none of them have been described.
Falconer and Cautley (1847) illustrated neck vertebrae of Indian Pleistocene hippopotamuses, which closely resemble those of the extant species, but they did not figure any vertebrae of the medium-sized Pleistocene anthracothere *Merycopotamus dissimilis*. Lydekker (1876) however, described two axis vertebrae of *M. dissimilis*, specifically commenting on the great elongation of the bone compared to those of *Sus*

and *Hippopotamus*. However, he did not illustrate the specimens, merely providing some measurements and commenting on their resemblance in some features to those of ruminants.
Kowalevsky (1874) illustrated several vertebrae from the thorax, lumbar region, sacrum and tail of *Anthracotherium* from La Rochette, Switzerland, but the specimens are generally poorly preserved even if reasonably complete. He did not illustrate any cervical vertebrae, but he did propose a reconstruction of the skeleton with a complete neck. In this genus the sacrum narrows caudally as in many medium- to large-bodied terrestrial, cursorial mammals, and the caudal vertebrae have short transverse processes. On the basis of the Rochette fossils he reconstructed the body plan of *Anthracotherium magnum* (Kowalevsky, 1874, pl. XV) showing it with a neck that is much shorter than the skull (reillustrated by Renevier, 1880) but this needs to be verified.
Scott (1894, 1940) reconstructed the skeleton of *Elomeryx armatus* from North America, showing the neck to be about the same length as the head (reillustrated by Kron & Manning, 1998).
Fourtau (1918) described several thoracic and lumbar vertebrae from Moghara, Egypt, that he attributed to *Brachyodus africanus* and *Masritherium depereti*. He provided measurements of some of the material, and commented that the centrum of the lumbar vertebra of *M. depereti* was much longer than that of *B. africanus*. He did not illustrate any of the fossils and no mention was made of cervical vertebrae or the sacrum.
Geais (1934) described several medium-sized anthracothere vertebrae and post-cranial elements from St-Henri, France, belonging to *Brachyodus borbonicus* (now classified as *Elomeryx borbonicus*). The specimens are badly crushed (she did not illustrate the vertebrae) but they permitted her to propose a body plan for the species, showing that it had relatively long legs, with the entire humerus positioned beneath the level of the rib cage. The neck in her reconstruction is slightly shorter than the skull.
Crusafont-Pairo (1979) described an atlas of the large anthracothere *Libycosaurus anisae* from Beglia, Tunisia but, on account of its great length, he erroneously attributed it to Giraffidae.
Neither of the monographic treatments by Dineur (1982) and Ginsburg and Chevrier (2005) on *Brachyodus* from the Sables de l'Orléanais and the French Faluns mention any vertebrae.
Finally, Pickford (2015) described six articulated neck vertebrae associated with a partial cranium, and articulated thoracic and lumbar vertebrae of '*Brachyodus*' *aequatorialis* from Grillental, Namibia, which revealed that this species possessed a moderately long neck (longer than that of the Okapi) that was held in a steep posture in which, in neutral position, the head would have been well above the shoulders.

DESCRIPTION OF THE AXIAL SKELETON OF *BRACHYODUS ONOIDEUS* (GERVAIS, 1859)

Occipital condyles

Brachyodus onoideus (Gervais, 1859) possessed large occipital condyles, described as «gigantic» by Orliac *et al.* (2013) (Fig. 1). They are distinctly keeled, unlike the condyles of *Hippopotamus* in which the keeling is subtle to weak over most of their surface (Fig. 2). The Liège fossil indicates that the occipital condyles and the glenoid fossae are positioned well above the alveolar margin of the maxillary dentition. Other specimens of the species housed in London and Basel show that the left and right occipital condyles are well separated from each other both dorsally and ventrally. The nuchal bone above the foramen magnum has a distinct but narrow slot that rises about 2 cm towards the top of the skull. The bone between the brain cavity and the rear of the nuchals is thick and comprised of coarsely spongy bone.

Discussion. In contrast to *Brachyodus onoideus*, the neurocranium of '*Brachyodus*' *aequatorialis* from Rusinga Island, Kenya, is platycephlic, the occipital condyles and glenoid fossae are low down, at the same levels as the roots of the cheek teeth, and the rear of the squamosal flanges lie at an angle of ca 30° with respect to the alveolar margins of the maxillary cheek teeth, as opposed to an angle of ca 45° in *Brachyodus onoideus* (Fig. 2). A further distinction between *Brachyodus onoideus* and '*Brachyodus*' *aequatorialis*, concerns the spacing between the occipital condyles. In the former species, the two condyles are well separated from each other, both dorsally and ventrally, but in the latter species the two condyles almost contact each other ventrally, being separated by a narrow, shallow slit (Fig. 3).

The skulls of *Hippopotamus* are platycephalic, the occipital condyles and glenoid fossae being even lower relative to the alveolar margin of the upper cheek teeth than in '*Brachyodus' aequatorialis* (Fig. 4). In contrast, the external auditory meatus of *Hippopotamus* is greatly elevated above the level of the occipital condyles, compared to their position in *Brachyodus* in which they are more-or-less at the same level as the condyles (Fig. 2). According to Orliac *et al.* (2013) the external auditory meatus of *Brachyodus onoideus* was elevated as in hippos, but this is not the case. In *Brachyodus*, relative to the plane of the alveolar process of the cheek teeth, the meatus is at the same height as the occipital condyles, whereas in *Hippopotamus*, it is well above the occipital condyles.

In lateral view the external auditory meatus of *Hippopotamus* is located slightly beneath the base of the orbit (Fig. 2). In *Brachyodus onoideus*, in contrast, it is positioned close to the upper margin of the orbit, and in '*Brachyodus*' *aequatorialis* it is in line with the base of the orbit.

Atlas

The atlas of *Brachyodus onoideus* is similar in construction and proportions to the specimen of '*Brachyodus' aequatorialis* from Namibia described by Pickford (2015), but the fossil from Neuville-aux-Bois (NHMB SO 241) is much better preserved (Fig. 5). The other specimen from Chilleurs-aux-Bois (NHMB 1608) lacks parts of the dorsal arch, but is otherwise similar to SO 241 (Fig. 6).

The cranial articular facets for the atlanto-occipital joint are deep, broad and keeled, and quite close to each other ventrally but separated by a large gap dorsally where the dorsal arch intervenes between them. Within the neural canal, there is no obvious ridge for attachment of the odontoid strap, the canal being almost circular in outline.

In ventral view the two atlantal fossae are well developed with the alar foramen close to the atlanto-occipital sector (*i.e.*, closer to the cranial end of the bone than to the caudal end). The caudal parts of the wings are broader than the cranial parts.

There is a prominent ventral tubercle close to the caudal end of the centrum and there is a narrow V-shaped incision in the cranial end of the centrum between the two atlanto-occipital facets.

In dorsal view, the dorsal tubercle is low and centrally positioned flanked by steep walls of the dorsal arch, at the anterior base of which are the large alar foramina (one on each side).

The base-plate morphology of the atlanto-axial articular surface dominates the caudal view of the atlas, above which is the thin dorsal arch, and either side of which are the alae (wings), each of which has a small foramen emerging close to its base. The lower two-thirds of the neural canal has a facet for the odontoid process and the two flanges of the axis, above which is the thin dorsal arch. The ventral tubercle is obvious in the caudal view.

Discussion. The atlas of *Brachyodus onoideus* is similar in morphology to that of '*Brachyodus*' *aequatorialis* from Grillental, Namibia (Pickford, 2015) but it is slightly longer and broader (106–110% depending on the parts compared, Tab. 1). In the cited paper, the morphological differences from the corresponding bone of hippopotamuses were listed, so it is not necessary to repeat them. A figure of an atlas vertebra of *Archaeopotamus andrewsi* from Wadi Natrun, Egypt, is provided for comparative purposes (Fig. 7).

In addition to differences in length/breadth proportions (short in hippopotamuses, longer in *Brachyodus*), the atlas of *Archaeopotamus* has articular facets for the occipital condyles that are separated further from each other ventrally than they are in *Brachyodus*. The same applies to the atlanto-axial facets at the caudal end of the atlas. Furthermore, the articular facets on the caudal end of the bone are of the cone-in-cone type, constrasting strongly with the base-plate morphology that occurs in the atlas of *Brachyodus*.
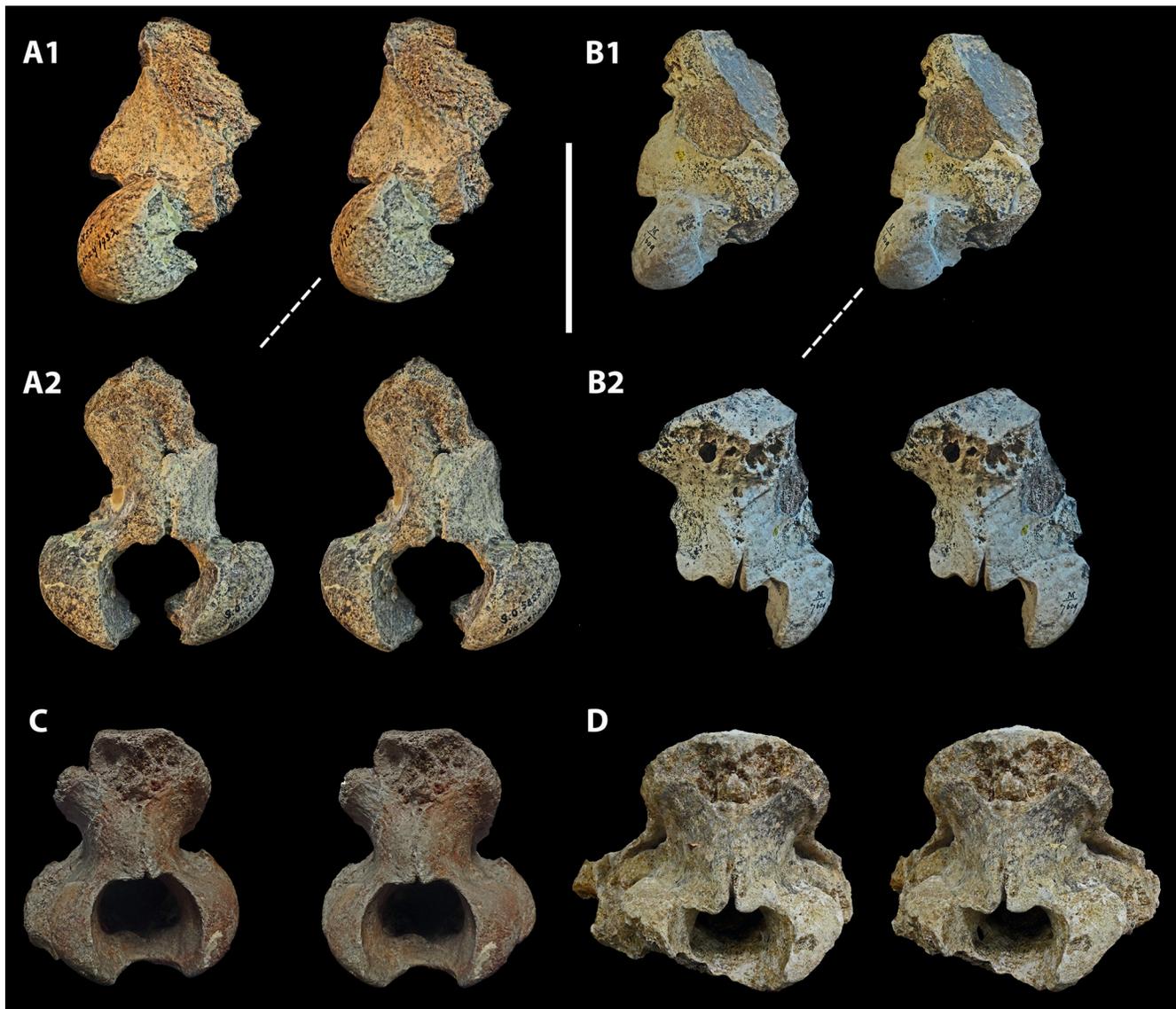
Figure 1. Stereo images of nuchal and occipital parts of neurocrania of *Brachyodus onoideus*. **A,** NHMB SO 5855 from Nancray, France; **A1,** right lateral view; **A2,** caudal view; **B,** NHMUK M 7609 from Chilleurs-aux-Bois; **B1,** right lateral view; **B2,** caudal view; **C,** ULg M5000b, locality unknown, caudal view; **D,** NHMB 5600, from Chilleurs-aux-Bois, caudal view. Dashed lines show the orientation of the keel on the occipital condyles; scale bar = 10 cm.

Axis

The axis vertebra of *Brachyodus onoideus* from Nancray lacks the spinous process and the dorsal arch (Fig. 8). The body is reasonably well preserved except caudally where it has been reinforced with resin. The specimen is similar in morphology to the Grillental axis of '*Brachyodus*' *aequatorialis* (Pickford, 2015) but is substantially longer (Tab. 2). The dens is short and is flanked on either side by flanges that rise dorsally in front of the base plate (atlanto-axial articular surface). The base plate is slightly angled with respect to the inferior profile of the bone, sloping from antero-inferior to postero-dorsal, and the articular surface is gently convex rather than flat. On each side, the vertebrarterial canal enters the bone close to the dorsal end of the base plate at the base of the pedicle. The intravertebral foramen is large (broken superiorly in the fossil) and is located midway between the base plate and the caudal epiphysis of the centrum. The hypapophyseal process is at the caudal end of the body at the end of the median inferior ridge. The transverse processes are damaged but the root of the right one is preserved as a sharp ridge angled at ca 30° to the sagittal plane and pointing postero-laterally.

Discussion. The axis of *Brachyodus onoideus* is longer (123%, Tab. 2) than that of '*Brachyodus*' *aequatorialis* described by Pickford (2015) but the morphology is closely similar after allowing for damage and slight distortion of the fossils. The differences from the axis of hippopotamuses were enumerated in detail in the cited reference, including the fact that the hypapohyseal
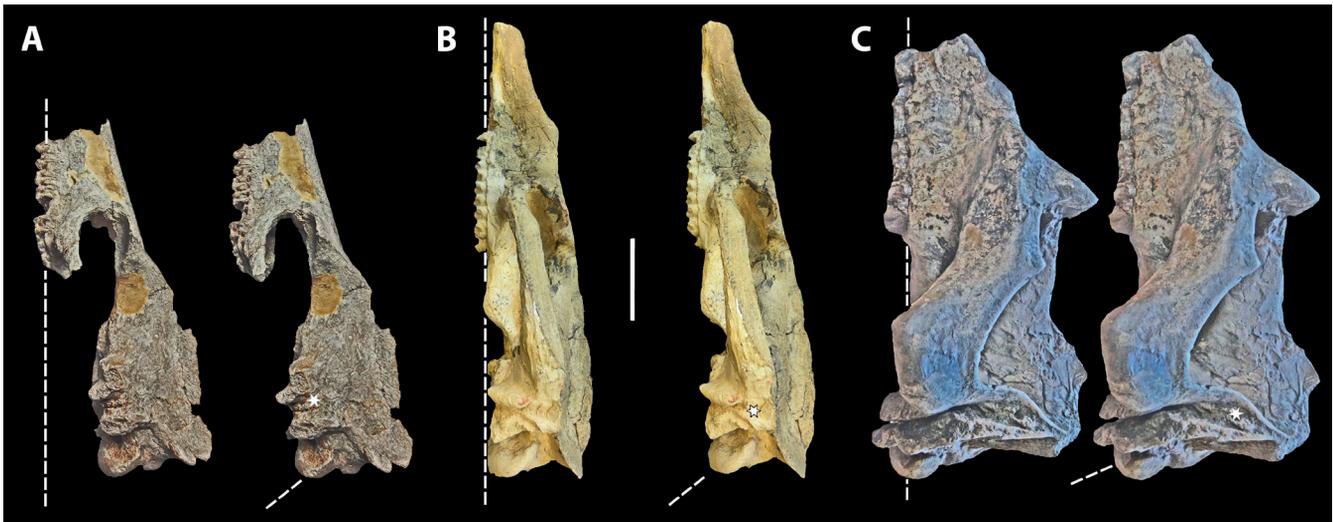
Figure 2. Stereo left lateral views of crania of *Brachyodus* and *Hippopotamus* with the alveolar process of the cheek teeth oriented vertically (long dashed lines in left images of each stereo pair). **A,** ULg M5000b *Brachyodus onoideus*; **B,** KNM RU 1009 (cast) *'Brachyodus' aequatorialis*; **C,** MNHN AC3864, *Hippopotamus antiquus* from Val d'Arno, Italy (right side reversed). White star is the external auditory meatus, short dashed lines in the right hand images of each stereo pair show the orientation of the keel on the occipital condyles (weakly expressed in *Hippopotamus*). Note the position of the occipital condyles relative to the alveolar process, and the height of the external auditory meatus relative to the occipital condyles and the orbits; scale bar = 10 cm.
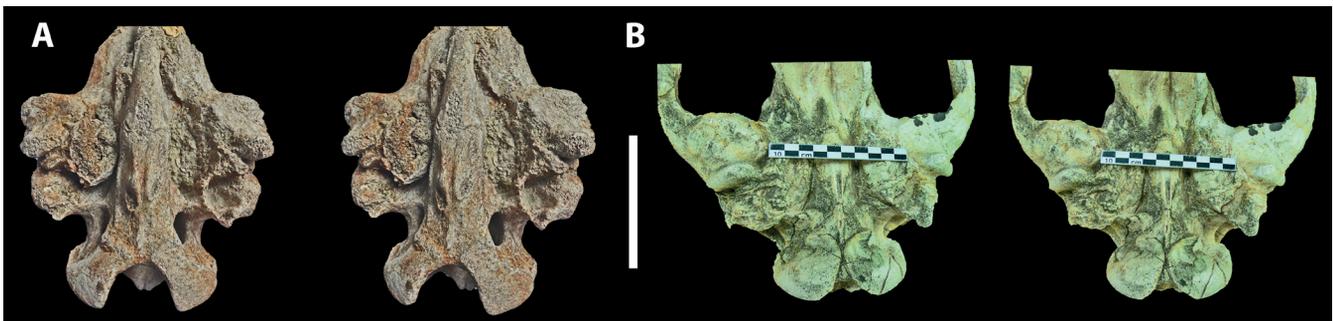
Figure 3. Stereo ventral views of basicrania of: **A,** ULg 5000b *Brachyodus onoideus* and **B,** KNM RU 1009 (cast) *'Brachyodus' aequatorialis*. Note the occipital condyles separated from each other ventrally in (**A**) and touching each other in (**B**); scale bar = 10 cm.

Table 1. Measurements (in mm) of the atlas vertebrae of *Brachyodus*.

| Measurement/ Taxon, catalogue N°	*Brachyodus onoideus* NHMB SO 241	*Brachyodus onoideus* NHMB SO 1608	*'Brachyodus' aequatorialis* GSN GT 88'06
Greatest breadth	232	--	--
Width of facets for occipital condyles	121	112	110
Height of facets for occipital condyles	58	--	--
Height of neural canal	51.5	--	--
Width of neural canal	58	--	--
Breadth of axis facet	128	--	--
Width between facets for axial flanges	56.5	--	--
Ventral length of centrum	49	49	46.3
Greatest ventral length at alae	62.3	--	--
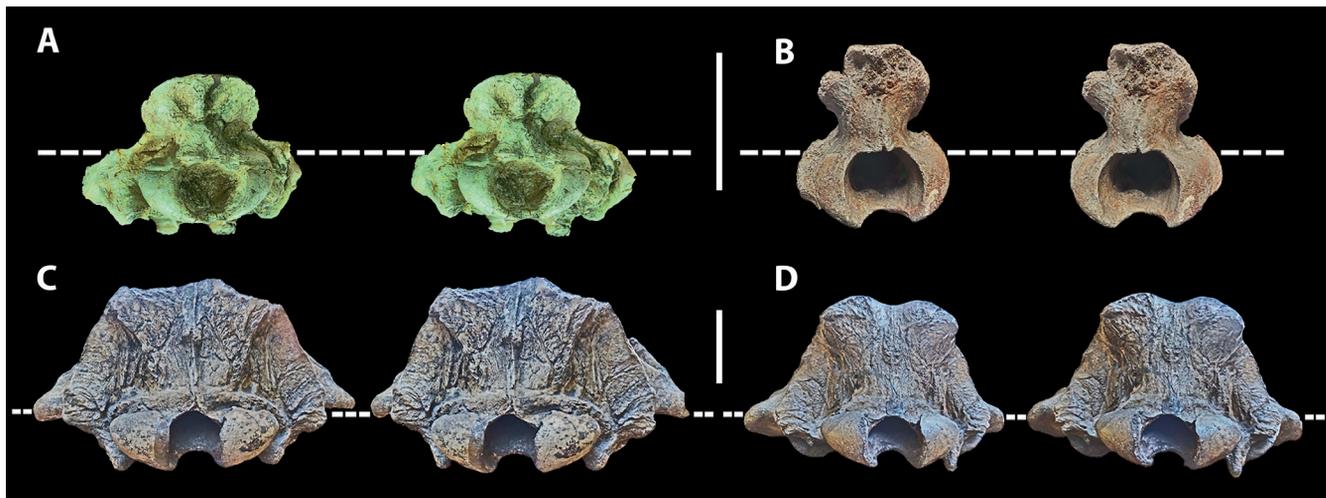
Figure 4. The occipital regions of early Miocene anthracotheres and Plio-Pleistocene *Hippopotamus*. **A,** KNM RU 1009, holotype cranium of *'Brachyodus' aequatorialis* from Rusinga Island, Kenya (cast in NHMUK); **B,** ULg M5000b, *Brachyodus onoideus* from an unknown locality; **C,** MNHN AC3866, *Hippopotamus antiquus*, from Val d'Arno, Italy; **D,** MNHN AC3864, *Hippopotamus antiquus* from Val d'Arno. The dashed lines are at the dorsal margins of the occipital condyles; scale bar = 10 cm.

process is undivided in *Brachyodus*, whereas it is V- or Y-shaped in *Hippopotamus* and *Choeropsis*.

A major difference between the axis vertebrae of *Brachyodus* and *Hippopotamus* concerns the length of the atlantal articulation (dens plus base plate) relative to the total length of the bone. In *Brachyodus* it comprises 27.6% of the length of the vertebra, whereas in *Hippopotamus* from Madagascar it is 57.1% of its length (Fig. 9). Furthermore, in ventral view, the base plate in the axis of *Brachyodus* is oriented at right angles to the long axis of the bone whereas in *Hippopotamus* it slants towards the rear at an angle of ca 45° resulting in a cone-in-cone articulation with the atlas. In addition, in *Hippopotamus* there are no flanges accompanying the dens.

Sacrum

The sacrum of *Brachyodus onoideus* from Nancray (NHMB SO 5896) is almost complete, lacking small parts of the right alae (Fig. 10). A portion of the right iliac blade is attached to the first sacral vertebrae, while the rest of the os coxae, although present in the collection, is poorly preserved. The sacrum has five vertebrae solidly ankylosed to each other, the first (S1) being extremely broad but with a low dorsal spine, the second (S2) much narrower with a tall spinous process, and the third, fourth and fifth ones even narrower and with tall spinous processes (Tab. 3). In S2-S5, the transverse processes are greatly reduced in lateral extent, each being less than a quarter of the breadth of the centrum. The transverse processes are fused together laterally, leaving small "intervertebral foramina" between successive vertebrae. The form and extent of S5 indicate that the tail of *Brachyodus onoideus* would probably have been rather small in medio-lateral diameter, with reduced to absent transverse processes in the coccygeal vertebrae (cf. *Anthracotherium magnum* from La Rochette, Kowalevsky, 1874).

The dorsal spine of S1 is low and narrow, and it is well separated at its base from the taller and more robust spinous process of S2. The spinous processes of S2-S5 are fused together at their apices, forming a solid dorsal ridge (sacral crest) along the centre of the bone, that swells and narrows as it goes. The sacral (intervertebral) foramina between the vertebrae

Table 2. Measurements (in mm) of the axis of *Brachyodus*.

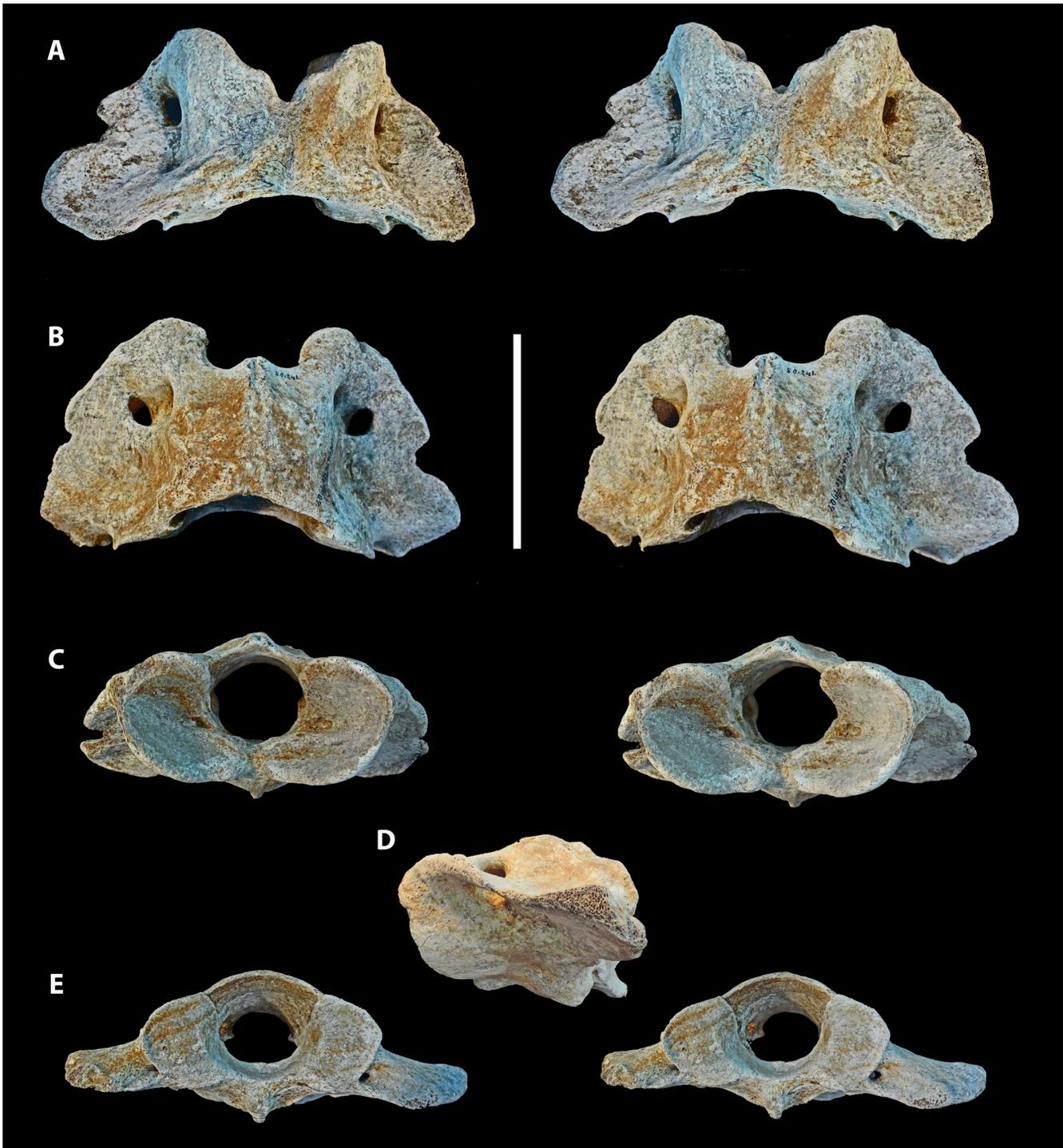| Measurement/Taxon Catalogue Number	*Brachyodus onoideus* NHMB S0 5896	*'Brachyodus' aequatorialis* GSN GT 88'06
Anterior breadth	109.2	--
Breadth neural canal	49.4	--
Length of neural canal (including dens)	131	--
Ventral length	148	120.3

Figure 5. NHMB SO 241, atlas vertebra of *Brachyodus onoideus* from Neuville-aux-Bois, France. **A,** stereo ventral view; **B,** stereo dorsal view; **C,** stereo cranial view; **D,** left lateral view; **E,** stereo caudal view; scale bar = 10 cm.

are rather small in dorsal view, but are slightly more prominent in ventral view.

In dorsal view the iliac blade makes a large contact with the lateral surface of S1, and a restricted contact with the cranial part of S2.

As is usual in mammals, the sacrum of *Brachyodus onoideus* has a slightly concave longitudinal profile to its ventral side.

A second sacrum from Nancray housed in the NHMB (SO 5897) lacks S1 and part of S5, but is otherwise similar to NHMB SO 5896. The importance of this specimen is that it is associated with a damaged lumbar vertebra, parts of the os coxae, a complete femur (Dineur, 1982; Ginsburg & Chevrier, 2005; Houssaye *et al*., 2021) and some upper and lower molars, providing proof that the axial material represents *Brachyodus onoideus*.
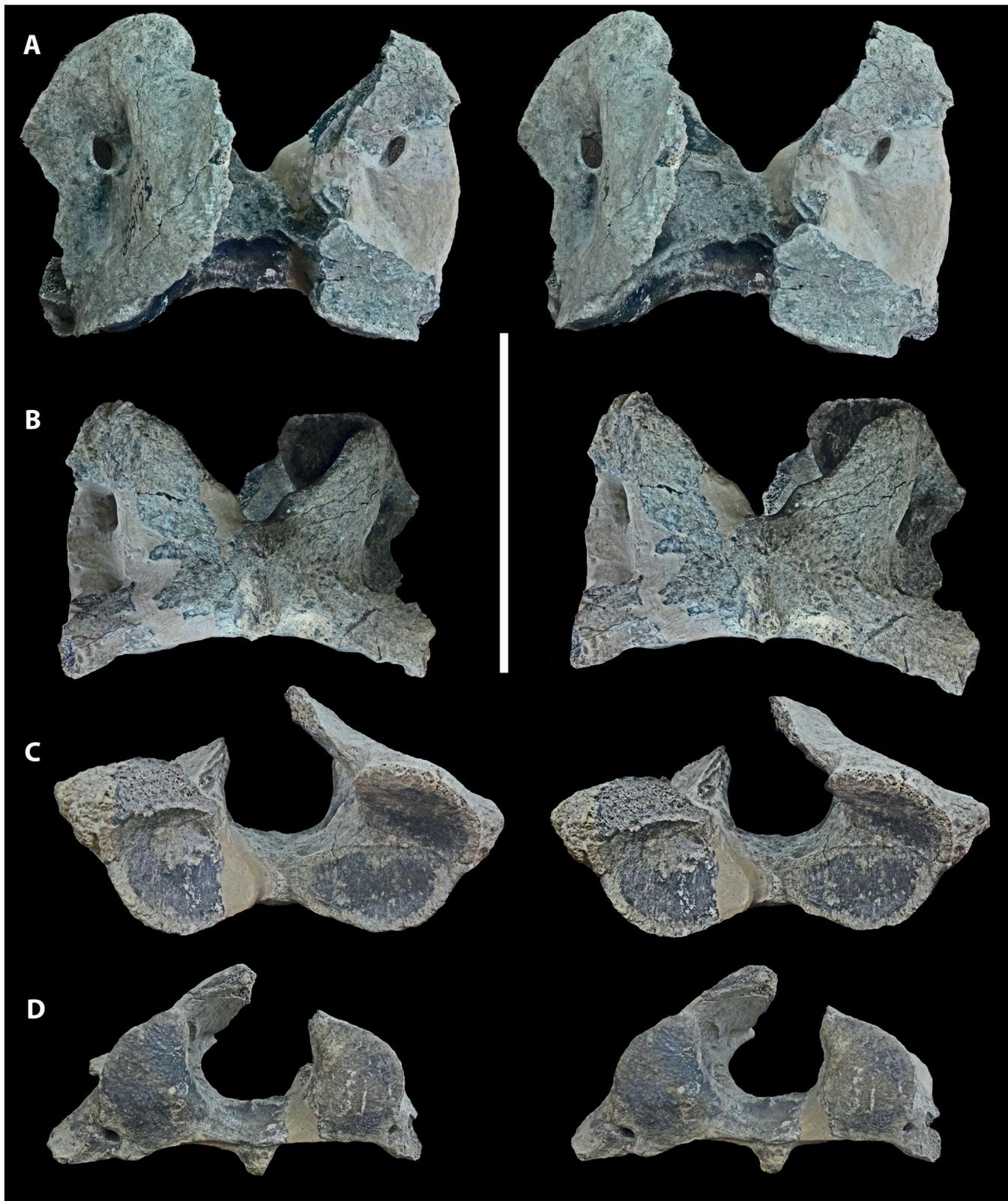
Figure 6. Stereo images of NHMB SO 1608, atlas vertebra of *Brachyodus onoideus* from Chilleurs-aux-Bois, France. **A,** dorsal view; **B,** inferior view; **C,** cranial view; **D,** caudal view; scale bar = 10 cm.

Discussion. In both species of extant hippopotamuses (*Hippopotamus amphibius* and *Choeropsis liberiensis*) the sacrum is almost as broad at S5 as it is at S2, with well-developed transverse processes that are fused to each other laterally, but leaving large "intervertebral foramina" between successive vertebrae (Figs. 11, 12). In S2-S5, the medio-lateral extent of each transverse processes is as great as, or slightly greater than, the

Table 3. Measurements (in mm) of sacral vertebrae of *Brachyodus onoideus*, *Hippopotamus amphibius* and *Choeropsis liberiensis*.

Measurement/taxon-Catalogue N°	*Brachyodus onoideus* NHMB SO 5896	*Hippopotamus amphibius* NHMB 2767	*Hippopotamus amphibius* MNHN A7985	*Hippopotamus amphibius* MNHN A7986	*Choeropsis liberiansis* MNHN A67
Total length S1-S5	257.5	332	347	346	143
Cranial breadth	240	--	267	264	139
Breadth at caudal end of S1	95	96	--	--	--
Breadth at caudal end of S2	65	95	123.5	118	47
Breadth at caudal end of S3	57	115	102	111	47
Breadth at caudal end of S5	41	128	108.5	116	42.3
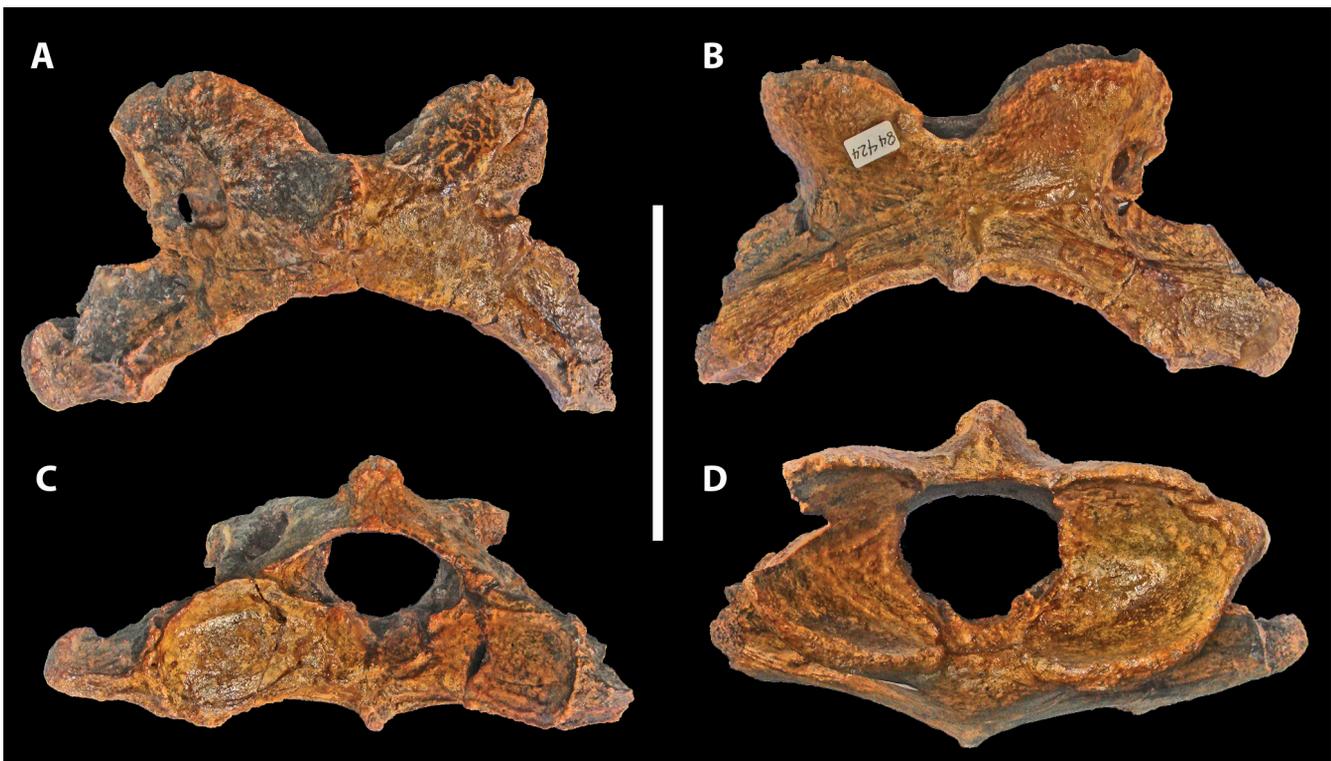
Figure 7. CGM 84-424, atlas vertebra of *Archaeopotamus andrewsi* from the late Miocene deposits at Wadi Natrun, Egypt. **A,** dorsal; **B,** ventral; **C,** caudal; **D,** cranial views; scale bar = 10 cm.

breadth of the centrum. In aged individuals, the first coccygeal vertebrae is sometimes fused to S5, but in young subjects it is not.

The coccygeal vertebrae of both *Hippopotamus* and *Choeropsis* have elongated transverse processes which extend laterally for more than the breadth of the centrum, contrasting strongly with the corresponding vertebrae in *Anthracotherium* in which the transverse processes are greatly reduced in dimensions (Kowalevsky, 1874). The elongated transverse processes in the coccygeal vertebrae of *Hippopotamus* and *Choeropsis* provide a solid framework for the strong caudal musculature that is especially active during defecation.

The tails of both extant species of hippos are short but thick at the base, and they are wagged actively and rapidly during defecation to spread the dung and urine,

both in the water (Fig. 13) and on land where defecation often takes place in habitually used «latrines» (Klingel, 2013; Robinson, 2013) such as particular bushes, gaps between bushes along their trails and other landmarks. The rapid wagging of the tail has, at times, been compared to the twirling of a propellor, although the action is not rotatory, but predominantly from side to side.

Concerning *Hippopotamus amphibius*, Klingel (2013) wrote "*Territories are advertised by the bulls through their presence, their dominant behaviour and their ritualized defecation combined with urination. By rapidly wagging their tails, faeces and urine are scattered in the vicinity. This type of defecation is repeated in the same places and results in impressive dung heaps, measuring several square metres in area. The dung heaps certainly do not function as boundary markers*
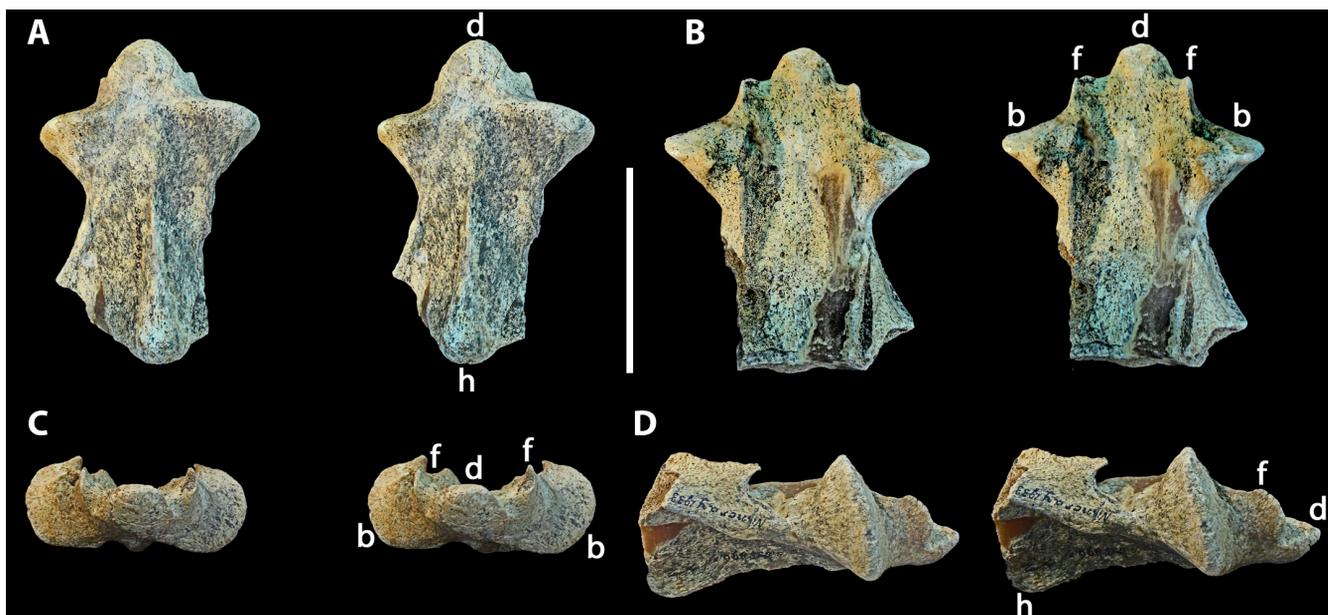
Figure 8. Stereo images of NHMB SO 5896, axis vertebra of *Brachyodus onoideus* from Nancray, France. **A,** inferior view; **B,** superior view of neural canal; **C,** cranial view; **D,** right lateral view (**b**, base plate; **d**, dens [odontoid process]; **f**, flange; **h**, hypapophyseal process); scale bar = 10 cm.
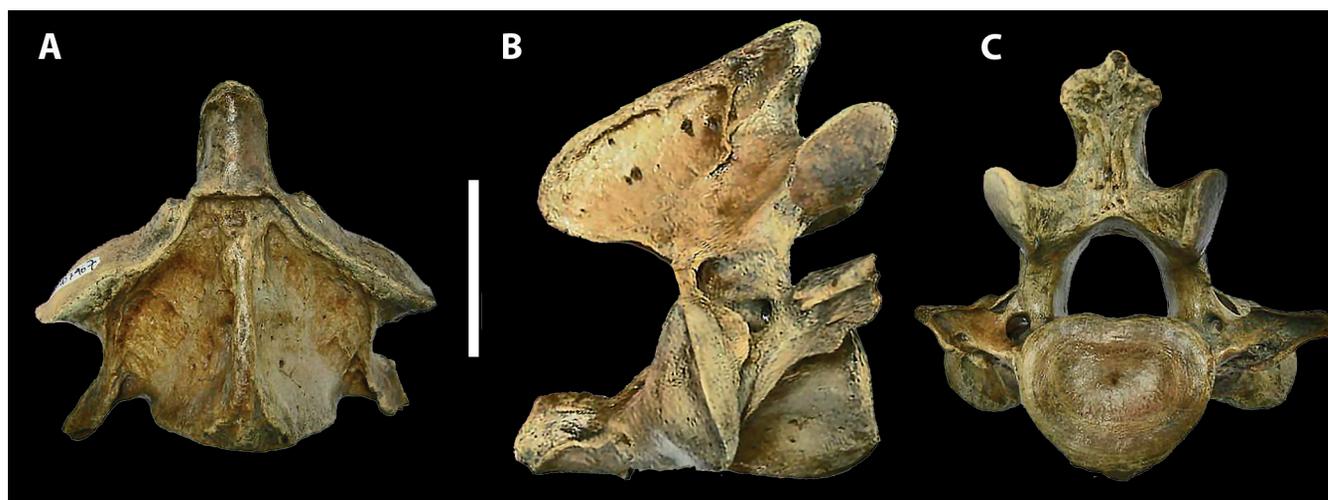

Figure 9. MNHN MAD 7967, axis vertebra of *Hippopotamus* sp. from Madagascar. **A,** ventral view; **B,** left lateral view with dens oriented horizontally; **C,** caudal view; scale bar = 5 cm.

and they do not prevent other bulls from entering the territory, but they are thought to serve as orientation marks for the territorial individual as well as for other common Hippos. Dung heaps are not produced by the territorial animal alone, but by virtually all passing males, and they are also found outside the territories in the grazing areas and along the inland tracks. They are rarely found in the open grassland but are regularly produced and maintained at the edges of bushes, at narrow passages between bushes, sometimes at corners of houses.

Territorial neighbours often display ritualized simultaneous defecation at their common boundary in the water. They then stand side by side a few metres apart facing in the same or opposite direction, both demonstrating strength and dominance by holding their heads high and ears forward. In this situation it is quite clear that the behaviour serves as a visual signal, as dung heaps are not produced. Smell is likely to be of importance as well."

As for *Choeropsis liberiensis*, Robinson (2013) wrote "*Heaped dung and tail-splattered excrement are commonly found along trailside vegetation*" suggesting somewhat similar habits to those of the common hippopotamus.
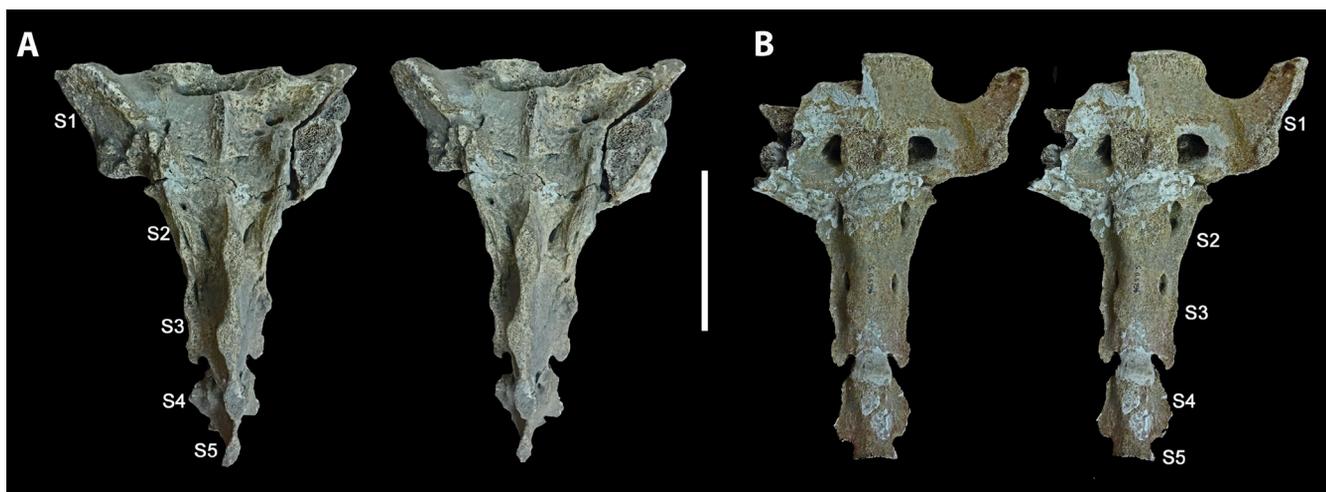
Figure 10. Stereo images of NHMB SO 5896, sacrum and portion of right iliac of *Brachyodus onoideus* from Nancray, France. **A,** dorsal view; **B,** inferior view (S1-S5, the five sacral vertebrae); scale bar = 10 cm.
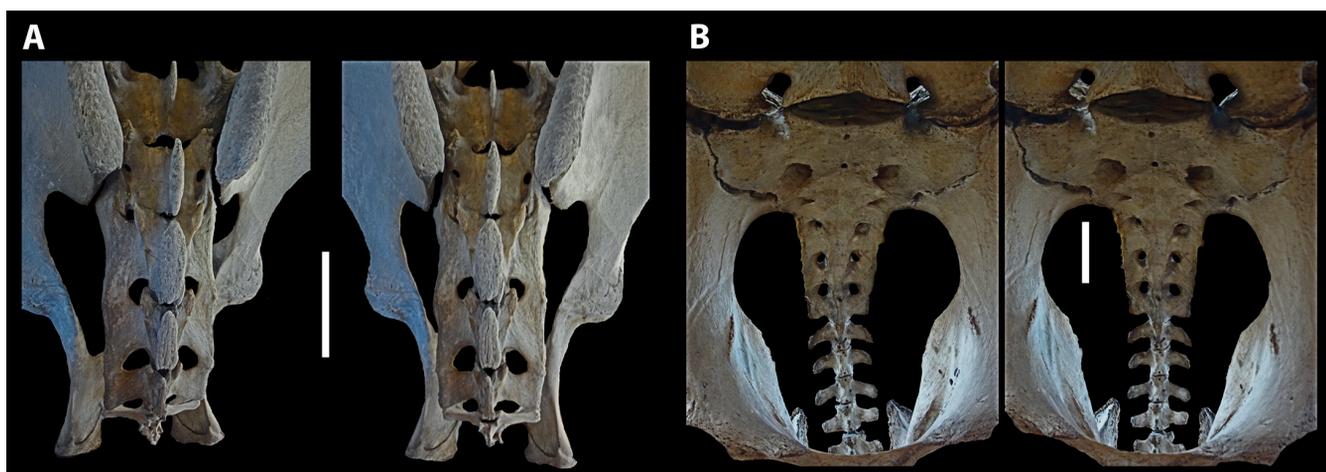

Figure 11. Stereo images of MNHN A7985, sacrum and os coxae of *Hippopotamus amphibius*. **A,** dorsal view; **B,** inferior view. Note the strongly developed transverse processes in the caudal vertebrae (scales are for the sacral vertebrae); scale bars = 10 cm.
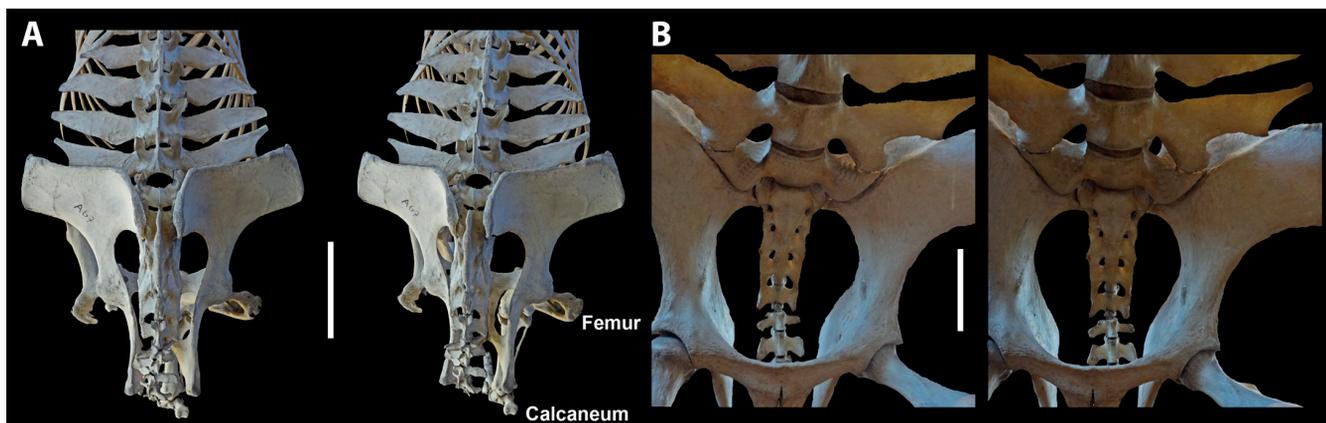

Figure 12. Stereo dorsal (**A**) and inferior (**B**) views of the pelvis and lumbar region of *Choeropsis liberiensis* (MNHN A67) (scales are for the sacral vertebrae); scale bars = 10 cm.

Figure 13. **A,** Tail morphology in *Hippopotamus amphibius*; and **B**, view of the dung-spreading action of the tail during defecation.

THE TAXONOMIC STATUS OF '*BRACHYODUS*' *AEQUATORIALIS*

The skull of *Brachyodus onoideus* is now known to be so divergent from that of '*Brachyodus*' *aequatorialis* (Fig. 14) that it is no longer realistic to maintain the two species in the same genus. On other grounds, this conclusion has been anticipated by previous authors such as Black (1978) who transferred the Kenyan form to *Masritherium* Fourtau, 1918, but he was unaware that Fourtau's hypodigm of the species was a mixture of specimens from two (or perhaps three) species in two genera and that the holotype of the species is inseparable morphologically from the mandible of *Brachyodus onoideus*. Other authors such as Dineur (1982) and Holroyd *et al*. (2010) considered *Masritherium* to be a synonym of *Brachyodus* and thus reunited the two species under the same genus.

Masritherium depereti Fourtau, 1918 is a junior synonym of *Brachyodus onoideus*, because its holotype mandible is extremely similar to the mandible in the Liège skull (ULg M5000a) of *Brachyodus onoideus*. However, most of the remainder of Fourtau's (1918) hypodigm of the species *M. depereti* belongs to a different genus, *Jaggermeryx* Miller *et al*., 2014. The Rusinga anthracothere does not belong to *Jaggermeryx* because the latter genus has a hypsicephalic skull, divergent upper molar morphology and radically different morphology of the symphyseal region of the mandible. This means that the large, platycephalic anthracothere from Rusinga requires a new genus name.

Family Anthracotheriidae Leidy, 1869

Rusingameryx n. gen.

Type-species. *Brachyodus aequatorialis* MacInnes, 1951. Early Miocene; Kenya, Uganda, Namibia.

Etymology. *Rusinga* for the type locality, with the suffix *meryx* – Greek noun meaning Ruminant.

Diagnosis. Large-bodied, platycephalic anthracothere in which the glenoid fossae and occipital condyles are positioned at the same level as the roots of the maxillary cheek teeth; external auditory meatus at the level of the middle of the orbit; no post-orbital process rising from the jugal; posterior pole of the anterior nares positioned above the P1/; ventral parts of the occipital condyles close together, separated by a narrow slit; nuchals bent downwards and overhanging the occipital condyles; upper margin of orbits in line with the elongated sagittal crest. Upper molars pentacuspidate with prominent parastyle and mesostyle, and variable metastyle; mandibular symphysis solidly fused when adult; long diastema anterior to the p/1; p/1-m/3 form a closed series of teeth, i/2 with tall crown, positioned at the antero-labial corner of the symphysis.

Differential diagnosis. *Rusingameryx* differs from *Brachyodus* Depéret, 1895, and *Jaggermeryx* Miller *et al*., 2014, by its platycephalic cranium. It differs from *Libycosaurus* Bonarelli, 1947, which has quadricuspidate upper molars, five upper premolars and a post-orbital process rising from the jugal; it differs from *Afromeryx* Pickford, 1991, by its greater dimensions and pentacuspidate upper molars. It differs from *Sivameryx* Lydekker, 1877, by its greater dimensions, and by its more platycephalic cranium and its less selenodont lower molars and its paraconule being well separated from the protocone in the upper molars. It differs from *Epirigenys* Boisserie *et al*., 2005a, by its less bunodont cheek teeth with weaker cingula in the upper molars. It differs from *Bothriogenys* Schmidt, 1913, by its greater dimensions, by the longer diastema between i/3 and p/1, and by the loss of the lower canine.
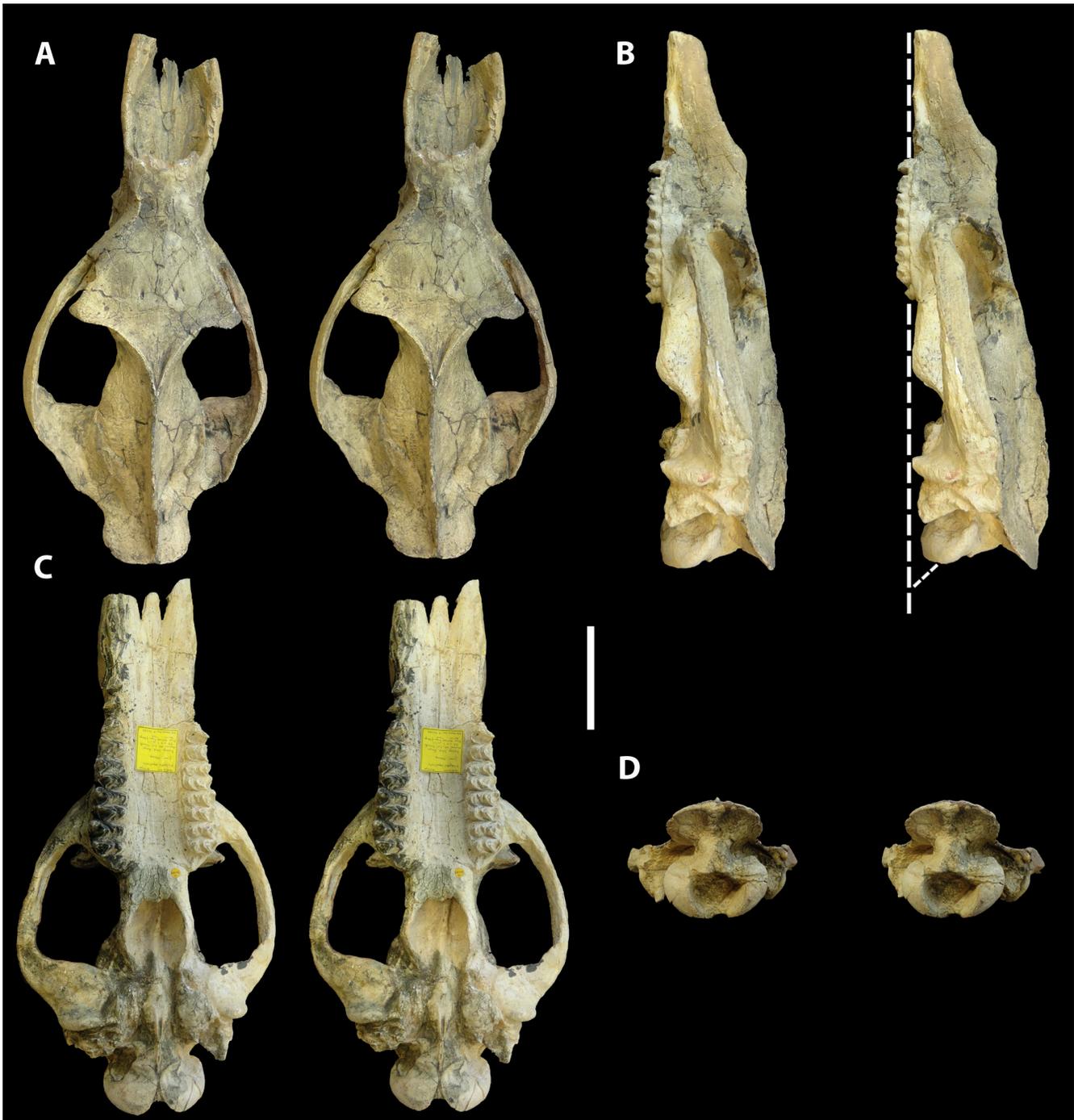
Figure 14. Stereo images of KNM RU 1009 (cast in NHMUK M34389), holotype cranium of *Rusingameryx aequatorialis* (MacInnes, 1951). **A,** dorsal view; **B,** left lateral view (long dashed line shows the level of the alveolar process of the maxilla, short dashed line shows the orientation of the keel of the occipital condyle); **C,** ventral view; **D,** caudal view; scale bar = 10 cm.

Rusingameryx is similar to *Kukusepasutanka* Macdonald, 1956, in its degree of platycephaly, the overall shape of the cranium and the tubular form of the snout, but it differs from this genus by the possession of P1/, by the lesser inflation of the styles in the upper molars and the mesostyle not invaded by the transverse valley, by the absence of a post-orbital process rising from the jugal, and by the weak to

absent protocones in the P3/ and P2/. *Rusingameryx* differs from *Arretotherium* Douglass, 1901, which has tetracuspidate upper molars (no paraconule) with loop-like mesostyle invaded by the transverse valley.
Rusingameryx differs from *Merycopotamus* Falconer & Cautley, 1847, by its less strongly descending angle of the mandible and the presence of a strongly developed paraconule in the upper molars and its compact

mesostyle. It differs from *Parabrachyodus* Forster-Cooper, 1915, by its more developed selenodonty and longer muzzle (Pickford, 1987). It differs from *Gonotelma* Pilgrim, 1908, which has open, loop-shaped mesostyles in the tetracuspidate upper molars. It differs from *Telmatodon* Forster-Cooper, 1924, which has quadricuspidate upper molars. It differs from *Hemimeryx* Lydekker, 1878, which possesses tetracuspidate upper molars with loop-shaped mesostyles.

Rusingameryx aequatorialis (MacInnes, 1951)

Figure 14

1991 *Brachyodus aequatorialis*; Pickford, p. 1495–1497.
2010 *Brachyodus aequatorialis*; Holroyd *et al*., p. 846.
2014 *Brachyodus aequatorialis*; Miller *et al*., p. 968, 970.
2020a *Masritherium aequatorialis*; Pickford, p. 6.
2020b *Brachyodus aequatorialis*; Pickford, p. 62.
2020b *Masritherium aequatorialis*; Pickford, p. 59, 60, 66.

Diagnosis. See Pickford (1991) and annex in Pickford (2020b).

Holotype. KNM RU 1009, almost complete cranium lacking the anterior parts of the premaxillae (Fig. 14 is of a cast of the holotype, housed at the NHMUK under the catalogue number M34389).

Type locality and age. Rusinga Island, Kenya (precise locality on the island not recorded), early Miocene, Faunal Set II of Pickford (1981, 1986) *ca* 17.8 Ma.
Rincon *et al*. (2013) wrote that *Kukusepasutanka*, like *Arretotherium*, does not have a paraconule in the upper molars. However, Macdonald (1956) explained that *Kukusepasutanka* possesses a large protoconule (= paraconule of Rincon *et al*., 2013).

DISCUSSION

In the literature on anthracotheres and hippopotamids there has been a strange ambivalence about the relationships between these two groups of mammals, with many authors inferring that they are closely related, yet at the same time remarking that they differed from each other in many morphological features of the skeleton and dentition as well as in their overall body plan (*e.g.*, the length of neck, Lydekker, 1876) (Pickford, 2008b).
The Plio-Pleistocene Indian anthracothere, *Merycopotamus* Falconer & Cautley, 1847, was so named by its discoverers because its teeth resemble those of ruminants (Greek – *meryx*) and it was thought to have inhabited rivers (Greek – *potamus*), the name mirroring that of the hippopotamus (from the Greek *hippo* – horse, *potamus* – river). Thus, from the outset, some ruminant-like attributes were noted in this Indian genus.
Lydekker (1876) concluded that "*From the dimensions of the axis vertebra,* Merycopotamus *must have been a much longer-necked animal than either the* Pig *or the* Hippopotamus*, in this respect also showing* Ruminant *tendencies*". He also pointed out that some

of the post-cranial bones of *Merycopotamus* were propotionally longer than those of hippos or pigs (talus, femur, separated radius and ulna) implying longer, more slender limbs, yet in his discussion he wrote "*the osteology of* Merycopotamus*, as we know it, is very closely allied to that of* Hippopotamus *and* Sus*, but it presents certain characters different from that of both genera …. I should be inclined to place the genus (*Merycopotamus*) in the family Hippopotamidae, forming a link between that and the Anthracotheriidae*». He subsequently pointed out (Lydekker, 1877) that the last sentence had the family names transposed, thereby misrepresenting the systematic position of *Merycopotamus*. Lydekker (1883) reiterated the fact that «*the limb bones of* Merycopotamus *are proportionally longer than those of* Hippopotamus *exemplified by the more elongated form of the astragalus …. the separation of the radius and ulna, and their more elongated form. The axis vertebra….. is an elongated bone like that of* Hyopotamus".
Dineur (1982) wrote that "*La forme svelte et allongée de l'astragale et des métapodes chez* Brachyodus onoideus *oppose cette espèce aux Hippopotamidae et aux autres Anthracothères de grande taille (*Anthracotherium*,* Merycopotamus*). Elle indique un mode de vie nettement plus terrestre, que confirme la stucture du crâne de* Brachyodus onoideus*, qui ne montre aucune adaptation à la vie amphibie, à la différence du crâne de* Merycopotamus".
Telles-Antunes and Ginsburg (2003) wrote that "*As an overall view, the skeleton of* Brachyodus onoideus *seems to point out to basically terrestrial animals. They certainly were much less aquatic-adapted than hippos even if probably living (as indicated by other, ecologic data) in swamps or close by rivers, in areas with a dense plant-covering*".
Ginsburg and Chevrier (2005) wrote that "*La squelette de* Brachyodus *ressemble morphologiquement de très près à celui d'*Hippopotamus*, ce qui est logique puisque les deux genres appartiennent à deux familles voisines, les Anthracotheriidae et les Hippopotamidae, qui entrent dans une même superfamille, celle des Anthracotherioidea. Seules les proportions changent, et parfois considérablement, entre les deux genres. Les éléments des extrémités montrent le plus de différences de proportions. Celles de* Brachyodus *sont élancées, l'animal étant svelte et coureur, celui d'*Hippopotamus *sont au contraire courtes et trappues, ce dernier étant lourd, gros, bas sur pattes et amphibie*".
Unlike Dineur (1982), Orliac *et al*. (2013) considered that *Brachyodus* was amphibious, partly on the basis of the morphology of the petrosal (inflated tegmen tympani for example) but also on the form of the cranium (orbits reported to be dorsally protruding – now known to be erroneous). However, contrasting with this result, Houssaye *et al*. (2021) after studying scans of the femur of *Brachyodus onoideus* and other long bones of diverse mammals, concluded that "*the extinct taxa* Microbunodon minimum, Bothriodon

velaunus, Elomeryx borbonicus, Merycopotamus medioximus, Paenanthracotherium bergeri, *and probably also* Saotherium *cf* S. mingoz *are inferred as essentially terrestrial animals,* Brachyodus onoideus *as slightly water-dependent, and* Libycosaurus bahri *and* Hexaprotodon garyam *as clearly semi-aquatic, although less specialised for this ecology than* Hippopotamus amphibius".

Pickford (2015) showed that the cervical vertebrae of 'Brachyodus' aequatorialis from Grillental, Namibia, were elongated, so much so that its neck was longer than those of the extant Okapi and Eland. He postulated that *Brachyodus* was adapted to what might be termed a hydrophilic lifestyle as exemplified by the swamp deer, lechwe and other ruminants that spend alot of their time in shallow water, but are not amphibious like hippos, nor even semi-aquatic.

Pickford (2008b, 2015) showed that most of the bones in the skeleton of anthracotheres (including *Brachyodus*) differ from the corresponding bones of hippopotamuses. Addition of the sacrum of *Brachyodus onoideus* and *Anthracotherium magnum* to the list, underlines the marked differences that this family has from hippopotamuses, rendering it unlikely that the latter descended from the former.

As already discussed by Pickford (2015) the elongated dens of the axis in hippos is of the primitive peg-like type that occurs in mammals as diverse as suids, peccaries and carnivores, whereas the presence of flanges associated with a somewhat flattened and abbreviated dens in *Brachyodus* represents a departure from the primitive morphotype. Ruminants possess even more derived morphology in which the dens and flanges form a hemi-cylindrical articulation with the atlas (Flower, 1876). If one is to derive hippopotamuses from anthracotheres, then one would need to invoke a reversal from a derived pattern towards a primitive condition of the atlanto-axial articulation. Whilst on this theme of reversed evolution, Lydekker (1877) hypothesised that "Hippopotamus *is descended from a selenodont and not a bunodont ancestor….If this view be true, the bunodont teeth of* Hippopotamus *are an instance of reversion to an older type*".

It is perhaps more likely that hippopotamuses descended from an ancestral group that possessed a peg-like dens of the axis and a bunodont dentition, rather than an alternative scenario featuring evolutionary reversals in the dentition and axial skeleton which would be the case if one attempts to derive them from anthracotheres. Among the bunodont artiodactyls with a peg-like dens with a cone-in-cone atlanto-axial articulation, the Doliochoeridae and Siderochoeridae are the closest to hippopotamuses (Pickford, 2017). The «phylogenetic» analyses of Gomes-Rodrigues *et al.* (2021) did not include any doliochoeroids which is the group that Pickford (2008a, 2008b, 2015, 2017) considered to be the source of the hippopotamid radiation. Their analyses therefore did not test the

hypothesis proposed by Pickford (2008a, 2008b, 2015). The missing taxa and missing characters of the taxa included in the data base compiled by Gomes-Rodrigues *et al.* (2021) render their results unlikely in a biological context.

Interpreting the evidence from the sacrum is less easy because the fossil record of this bone in doliochoeroids is poor, the sole published specimen (*Choeromorus petersbuchensis*) preserving only the S1 and S2 (Pickford, 2017). The two available specimens of the sacrum of *Brachyodus* reveal that its morphology was markedly different from that of hippos.

CONCLUSIONS

Study of elements of the axial skeleton of the early Miocene European anthracothere, *Brachyodus onoideus*, especially the cervical vertebrae and sacrum, reveals marked differences from the corresponding bones in Hippopotamidae, but shows some resemblances to those of tragulids and other ruminants. In contrast the equivalent bones of Hippopotamidae are close to those of some doliochoeroids such as *Siderochoerus* and *Choeromorus* as shown by Pickford (2017).

The new evidence from the atlas, axis and sacrum of *Brachyodus* underscores the conclusion published by Pickford (2008a, 2008b, 2015) that it is extremely unlikely that hippos descended from anthracotheres, but more likely that they are related to doliochoeroids and/or siderochoerids (sometimes known as Old World Peccaries, not to be confused with New World Peccaries, which are rather different from them) (Pickford, 2017). If this is so, then the concept of Hippopotamoidea as employed by Gomes-Rodrigues *et al.* (2021) to embrace anthracotheres and hippopotamids within the same superfamily, needs to be tested by adding characters from the postcranial skeleton (especially the axial skeleton) and taxa (especially the Doliochoeridae and Siderochoeridae) to their character matrix which included 221 characters gleaned from 70 taxa.

Comparisons of the crania of *Brachyodus onoideus* and 'Brachyodus' aequatorialis reveal that the former species is hypsicephalic while the latter is platycephalic. It is now clear that these two species can no longer be subsumed under the same genus name. A new genus *Rusingameryx* is created to accomodate the East African and Namibian species in the combination *Rusingameryx aequatorialis* (MacInnes, 1951).

Pickford, M. - The axial skeleton of *Brachyodus* (Anthracotheriidae) - *Spanish Journal of Palaeontology* 37 (1), 35–52, 2022

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