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The Late Miocene hippopotamid, *Archaeopotamus pantanellii* nov. comb., from the Casino Basin (Tuscany, Italy): paleobiogeographic implications

R. Martino ^{a,b}, L. Rook ^c, O. Mateus ^{a,b} and L. Pandolfi ^d

^aDepartment of Earth Sciences, GeoBioTec, School of Science and Technology, FCT-NOVA, Universidade NOVA de Lisboa, Campus de Caparica, Caparica, Portugal; ^bMuseu da Lourinhã, R. João Luís Moura, Lourinhã, Portugal; ^cDipartimento di Scienze della Terra, Università degli Studi di Firenze, Florence, Italy; ^dDipartimento di Scienze, Università degli Studi della Basilicata, Campus di Macchia Romana, Potenza, Italy

ABSTRACT

Fossil remains from the latest Messinian of Casino Basin (Tuscany, Italy) are known since the beginning of the nineteenth century. Among the others, the mammal assemblage includes *Mesopithecus pentelicus*, *Tapirus arvernensis*, *Propotamochoerus provincialis* and scarce and poorly preserved remains of a hippopotamid, consisting of a mandibular symphysis fragment, an apical fragment of a lower canine, some isolated lower incisors, a fragmented second upper premolar and a second lower molar. These specimens were initially referred as *Hippopotamus hipponensis* and later ascribed to the new species *Hippopotamus pantanellii* (recently reported as *Hexaprotodon? pantanellii*). However, this attribution has been disputed during the past years. The hippopotamid remains from the Casino Basin are revised here in order to clarify their systematic position and to infer paleobiogeographic and evolutionary patterns within the Mediterranean fossil record of Hippopotamidae. The morphology of the remains collected from the Casino Basin more closely resembles the African than the Asian hippopotamids' lineage and therefore the Tuscan remains should be more properly referred as *Archaeopotamus pantanellii*. The latter species probably dispersed into Tuscany from the Iberian Peninsula where the presence of *Archaeopotamus crusafonti* is well documented.

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Introduction

Hippopotamidae (Gray 1821) representatives appeared in the African and Arabic fossil record around 8 Ma (Boisserie et al. 2017b). The first and archaic Hippopotaminae include the poorly known genus *Chororatherium*, for now represented by a single described species, *C. roobi* from Chorora, Ethiopia (ca. 8 Ma) (Boisserie et al. 2017b). Starting from 7.5 Ma the 'narrow-muzzle' species belonging to the genus *Archaeopotamus* (Boisserie 2005; Boisserie et al. 2017a) started to be fairly represented in Africa and in the Arabian Peninsula. From 6 Ma onwards, the representatives of the genus *Hexaprotodon* Falconer and Cautley, 1836, which mainly comprises the Asian lineage of hippopotamids, also began to be common in mammal assemblages (Boisserie 2005). The poorly known genus *Saotherium* appeared in Chad (Central Africa) during the Early Pliocene (Boisserie et al. 2003; Boisserie 2005). In addition to the previous genera, Geraads et al. (2021) ascribed some Plio-Pleistocene (2.9–2.4 Ma) remains from Mille-Logya in the Lower Awash Valley, Ethiopia, to '*Trilobophorus*' but its validity needs more evidence. Further studies also need to be carried out on Pliocene materials from Kenya, Hadar (ca. 3 Ma), Kanapoi (ca. 4 Ma), lower parts of Koobi Fora Formation at Allia Bay (4.2–4.1 Ma), Nachukui Formation (Apak Member, more than 4.3 Ma), Omo Group formations (3.4–2.9 Ma) and Kantis (3.4–3.5 Ma), where most of the remains are currently ascribed as aff. *Hippopotamus* (Gèze 1985; Harris 1991; McDougall and Feibel 1999; Harris et al. 2003; Weston 2003; McDougall and Brown 2008; Mbua et al. 2016). The North African peri-Mediterranean

area during that time frame was marked by several hippopotamids occurrences. *Hexaprotodon? sahabiensis* was described from As Sahabi, Libya, Late Miocene (Gaziry 1987; Pavlakis 2008), *Hex.? hipponensis* from Pont-de-Duvivier, Algeria, earliest Pliocene (Gaudry 1876) and *Hex.? protamphibius andrewsi* from Wadi Natrun, Egypt, Late Miocene-Early Pliocene (Andrews 1902; Stromer 1914; Arambourg 1947). *Hexaprotodon? sahabiensis* material is quite abundant, mainly represented by isolated teeth and a fragment of a mandible with right canine, right incisors and the left first incisor (Gaziry 1987; Pavlakis 2008). *Hexaprotodon? sahabiensis* is quite peculiar and it probably represents an evolutionary branch with both archaic and advanced characteristics (Gaziry 1987). *Hexaprotodon? hipponensis* was established on scarce and fragmentary material, including some isolated incisors, a premolar and a canine fragment (Gaudry 1876). *Hexaprotodon? protamphibius andrewsi* is represented by numerous cranial, mainly isolated teeth, and post-cranial remains (Andrews 1902; Stromer 1914; Arambourg 1947). Lately, *Hex.? protamphibius andrewsi* was reassigned to *Archaeopotamus andrewsi*, as an extensive revision based on all the abundant material collected from Wadi Natrun (Egypt) revealed a closer relationship with *Archaeopotamus* rather than with *Hexaprotodon* (Pickford et al. 2022).

The first dispersal wave of Hippopotamidae outside Africa towards Europe took place around 6 Ma (Boisserie 2007). In the European area, hippopotamids remains were collected from several Late Miocene deposits of Spain (Aguirre 1963; Crusafont et al. 1964; Aguirre et al. 1973; Morales 1984;

CONTACT R. Martino  r.martino@campus.fct.unl.pt  Department of Earth Sciences, GeoBioTec, School of Science and Technology, FCT-NOVA, Universidade NOVA de Lisboa, Campus de Caparica, Caparica, Portugal

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Lacomba et al. 1986; Alcalá 1994; Alcalá and Montoya 1998; Morales et al. 2011), from an Early Pliocene locality of France (Faure and Méon 1984) and from latest Miocene sites of Italy (Pantanelli 1879; Seguenza 1902, 1907; Hooijer 1946; Martino et al. 2021). Hippopotamid occurrence in the Late Miocene deposits of Greece, at Panaghia sta Éria (Euboea Island), should be considered doubtful (Athanassiou 2022). The rich hippopotamid material, represented by cranial and post-cranial remains, collected from Spain (Las Casiones, Venta del Moro, La Portera, Arenas del Rey, El Arquillo I) is ascribed to *Hex.? crusafonti* (= *Hex. primaevus*) (Aguirre 1963; Crusafont et al. 1964; Aguirre et al. 1973; Morales 1984; Lacomba et al. 1986; Alcalá 1994; Alcalá and Montoya 1998; Morales et al. 2011). However, in a recent revision, Martino et al. (2021) suggested that this Late Miocene species should be referred to the genus *Archaeopotamus*, based on the peculiar mandibular characters shared by the material from La Portera (Lacomba et al. 1986). The remains ascribed to *Hex.? crusafonti* should therefore be more properly indicated as *A. crusafonti*. The latter species is also reported from La Mosson (France), dated to the earliest Pliocene (Faure and Méon 1984).

In Italy, between the end of the nineteenth century and the beginning of the twentieth one, Late Miocene hippopotamid remains were found in four localities (Pantanelli 1879; Seguenza 1902, 1907). Seguenza (1902, 1907) described a considerable number of fossils collected from Gravitelli (Messina, Sicily, southern Italy) and some isolated remains unearthed from two different localities near Gravitelli, San Pier Niceto and Scirpi (Messina, Sicily, southern Italy). Unfortunately, all the fossil records collected went lost in 1908 due to a catastrophic earthquake. The remains collected from Sicily are currently dubiously assigned to *Hex.? siculus* (Seguenza 1902, 1907; Hooijer 1946; Boisserie 2005; Martino et al. 2021). Some years before Seguenza (1902, 1907), Pantanelli (1879) reported some fragmentary Late Miocene hippopotamid material from a Tuscan locality, the Casino Basin (Siena). These remains were originally assigned by Pantanelli (1879) to *Hippopotamus hipponensis* Gaudry, 1876 (now *Hex.? hipponensis* following Boisserie 2005). Hereafter Joleaud (1920) revised the material described from the Casino Basin and agreed with Stehlin (1899-1900), Forsyth Mayor (1875) and Andrews (1902) in considering 'la forme de Casino diffère de celle de Duvivier et confine plus directement aux Suilliens par le dessin de la surface d'usure des molaires qui ne présentent pas encore la tréfle caractéristique des Hippopotames pliocène, quaternaires et actuels' (the Casino specimens differ from the material from Pont-de-Duvivier by the design of the molars, which do not yet display the characteristic trefoil wear pattern of the Pliocene, Quaternary and modern hippopotamuses). For the abovementioned reasons, Joleaud (1920) rejected the attribution to *Hip. hipponensis* (now *Hex.? hipponensis*) and assigned the poorly represented material from the Casino Basin to a new species, *Hippopotamus pantanellii* Joleaud (1920). An extensive revision by Boisserie (2005) doubtfully attributed, on the base of the tables in Pantanelli (1879), the Tuscan remains to the genus *Hexaprotodon*, rejecting the attribution to the more evolved *Hippopotamus*.

The original hippopotamid remains collected from the Casino Basin are here revised in detail and figured for the first time in order to clarify and update their systematic position and their paleobiogeographic implications. Despite the fragmentary nature of the remains collected from the Casino Basin, a detailed revision is important to shed light on the scant Late Miocene hippopotamid material collected from the peri-Mediterranean area. Hippopotamids, thanks to their peculiar semi-aquatic lifestyle, represent a *unicum* among large mammals and therefore they can

contribute for a better understanding of the great changes that affected the peri-Mediterranean area during the Late Miocene.

Geological setting

Fossil presence in the Casino Basin, Tuscany, Central Italy (Casino Basin location is indicated with the black star in Figure 1) was firstly reported by Capellini (1872). Casino Basin's area (around 40 km²) is mainly characterised by two different sedimentary sequences. The geological setting of the Casino Basin was firstly defined as a combination of an Upper Lacustrine Cycle and a Lower Lacustrine Cycle (Lazzarotto and Sandrelli 1977). Bossio et al. (2002) indicated the Upper Lacustrine Cycle as 'Argille del Casino' (Casino clays). Later, Abbazzi et al. (2008) recognised a unit lithologically and palaeontologically coinciding with Casino clays along the Borro Strolla Creek. The UM2 lithofacies, outcropping in Piaggiolo A quarry of the Borro Strolla synthem, deposited simultaneously to similar sedimentation in the second Casino's Lake (Abbazzi et al. 2008). This unit, as the Casino clays, can be ascribed to the latest Messinian, 'Lago-Mare' bio-facies.

The faunal list of the second Casino Lake includes *Dipoides problematicus*, *Eucyon* sp., *Thalassictis* cf. *hipparionum*, *Tapirus arvernensis*, *Propotamochoerus provincialis*, *Parabos* sp., *Paracervulus* cf. *australis*, Hippopotamidae indet., *Mesopithecus pentelicus* and *Hippotherium* cf. *malpassi* (Rook 1992; Rook et al. 1999; Rook and Bernor 2013; Cirilli et al. 2020; Martino et al. 2020; Iannucci et al. 2021; Pandolfi et al. 2021a, 2021b). Some remains display bitemarks on posterior bones, and carnivores may have therefore played a role in their

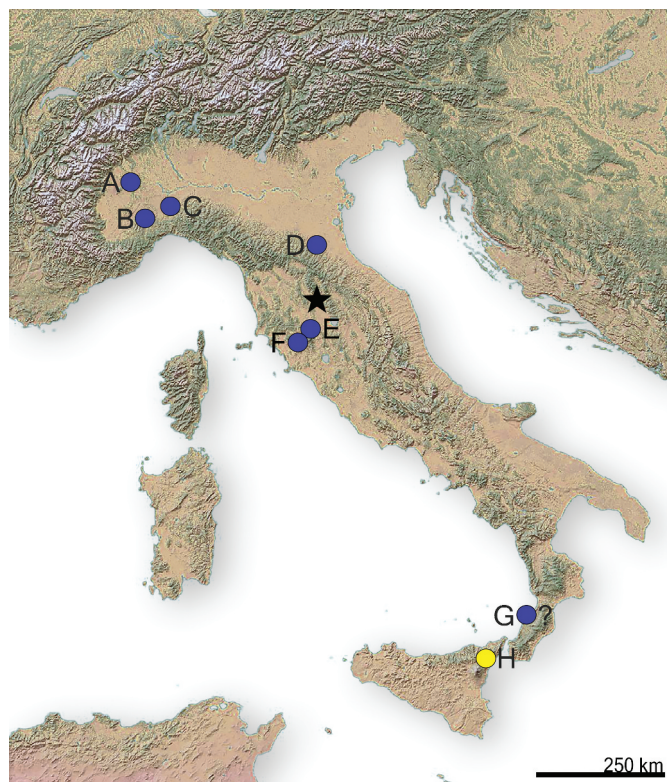


Figure 1. Casino Basin locality indicated with the black star. A. Moncucco Torinese, B. Verduno, C. Ciabot Cagna, D. Monticino Quarry, E. Velona, F. Baccinello V3, G. Cessaniti, H. Sicilian localities (Gravitelli, San Pier Niceto, Scirpi). Borro Strolla locality coincides with Casino Basin one. Yellow = hippopotamids presence, blue = hippopotamids absence.

accumulation (Gallai 2005). The mammals' assemblage of the Casino Basin can be ascribed to the upper part of the Mammal Neogene Zone 13.

Material and methods

The morphological terminology for the teeth followed Thenius (1989) and Boisserie et al. (2010). The revised remains were morphologically and morphometrically compared with Late Miocene and Early Pliocene hippopotamids from direct observations and published data. The species analysed from bibliography are *Archaeopotamus harvardi* (Coryndon 1977), *Archaeopotamus qeshta* (Boisserie et al. 2017a), *Archaeopotamus lothagamensis* (Weston 2000), *Archaeopotamus crusafonti* (Aguirre 1963), *Archaeopotamus andrewsi* (Arambourg 1947), *Hexaprotodon bruneti* (Boisserie and White, 2004), *Hexaprotodon garyam* Boisserie, Likius, Vignaud, & Brunet, 2005, *Hexaprotodon sivalensis* Falconer & Cautley, 1836, *Hexaprotodon? hipponensis* (Gaudry, 1876), *Hexaprotodon? sahabiensis* (Gaziry 1987), *Hexaprotodon? siculus* (Hooijer 1946) and *Saotherium mingoz* Boisserie, 2005. R.M. studied *A. crusafonti* remains stored in the Museo Nacional de Ciencias Naturales of Madrid (Spain), collected from Arenas del Rey, El Arquillo and La Portera. All specimens are reported in Aguirre (1963), Lacombe et al. (1986) and Alcalá and Montoya (1998). The specimens from the Casino basin were also compared with the remains of *Hippopotamus amphibius* Linnaeus, 1758 and *Choeropsis liberiensis* (Morton 1844).

Historical framework

Fossiliferous remains from the Casino Basin were firstly reported by Capellini (1872), Rüttimeyer (1876) and Major (1874, 1877). A more detailed study regarding the Casino Basin was tackled by Pantanelli (1879, 1886). Pantanelli (1879) briefly described and depicted the faunistic remains from the Casino Basin and ascribed the hippopotamid remains to *Hip. hipponensis* (now *Hex.? hipponensis*), previously described by Gaudry (1876) in Algeria. However, the morphology of the material figured by Pantanelli (1879) was highly simplified. An attempt to revise the hippopotamid remains from the Casino Basin was made by Joleaud (1920). However, the author never revised the original specimens from the Casino Basin, but only the description and tables depicted in Pantanelli (1879). Joleaud (1920) erected the new species, *Hip. pantanellii*, in honour of Dante Pantanelli, who firstly described these remains. However, Joleaud (1920) never described the diagnostic characters of *Hip. pantanellii*, which are still currently undefined. All the remains collected from the Casino Basin are now stored in the Museo di Storia Naturale dell'Accademia dei Fisiocritici, Siena, Italy, with the exception of the second lower molar that is currently in the Museo di Storia Naturale e del Territorio, Certosa di Calci, Pisa, Italy.

Institutional Abbreviations

MSNAF, Museo di Storia Naturale dell'Accademia dei Fisiocritici, Siena, Italy; MSNCC, Museo di Storia Naturale e del Territorio, Certosa di Calci, Pisa, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain.

Other Abbreviations

C/c, canines; I/i, incisors; P/p, premolars; M/m, molars; L, greatest length; W, width; MD, mesiodistal diameter; LL: labiolingual diameter; MN, Mammal Neogene Zone.

Systematic Palaeontology

Class **Mammalia** Linnaeus 1758

Cetartiodactyla Montgelard et al. 1997

Superfamily **Hippopotamoidea** Gray 1821 (sensu Gentry and Hooker 1988)

Family **Hippopotamidae** Gray 1821

Subfamily **Hippopotaminae** Gray 1821

Genus ***Archaeopotamus*** Boisserie, 2005

Type species. *Archaeopotamus lothagamensis* (Weston 2000)

Included species. *Archaeopotamus harvardi* (Coryndon 1977); *A. qeshta* (Gentry 1999; Boisserie et al. 2017a; Boisserie and Bibi 2022); *A. crusafonti* (Aguirre 1963; Crusafont et al. 1964; Aguirre et al. 1973; Morales 1984; Lacombe et al. 1986; Alcalá 1994; Alcalá and Montoya 1998; Morales et al. 2011); *A. andrewsi* (Andrews 1902; Stromer 1914; Pickford et al. 2022); *A. aff. harvardi* from Rawi (see Boisserie 2005).

Archaeopotamus pantanellii (Joleaud, 1920) nov. comb.

(Figures 2, 3)

1879: *Hippopotamus hipponensis* in Pantanelli 1879, p. 318, plate IV, 1–7.

1920: *Hippopotamus pantanellii* in Joleaud 1920, p. 18.

2005: *Hexaprotodon? pantanellii* in Boisserie 2005, p. 20.

Material

Holotype, MSNAF2821, fragmented mandible with right i1, left i1, i2, i3 in cross-section. The rest of the remains from the type locality are defined as paratypes.

Other referred specimens

MSNAF2829, isolated lower incisors; MSNAF2820, apical fragment of a right c; MSNAF2828, a right P2 and severely fragmented tooth (probably a p1); MSNCCI10501, left m2; MSNAF2862, fragmented mandible with undeterminable teeth in cross-section. All remains probably belong to at least two different individuals, a sub-adult (p2 and c) and an adult (mandible and m2).

Derivation of name

Archaeopotamus pantanellii, in honour of Dante Pantanelli, the first scholar who described the hippopotamid from the Casino Basin.

Stratigraphical range

Late Miocene (MN 13).

Type locality

Upper lacustrine level of Casino Lignite mine (also known as Casino clays or second Casino's Lake), near Siena, Tuscany, Italy (coordinates 43.3° N, 11.3° E).

Emended diagnosis

Archaeopotamus pantanellii is a medium-small European hexaprotodont species clearly distinguished from other hippopotamids by

the following combination of characters: incisors arrangement $i1 > i2 \geq i3$ with rounded-oblate cross-section; c with a D-shaped cross-section, a groove on the mesial side, finely crenulated enamel, and slightly visible transversal lines; P2 triangular shaped without accessory cuspids; m2 with four main cuspids, well-developed cingulid on lingual, mesial and distal sides, crenulated enamel and feebly developed trefoil wear pattern.

Differential diagnosis

Archaeopotamus pantanellii diverges from *A. harvardi* in having transversal fine lines on the c; the former species is also characterised by smaller dimensions. *Archaeopotamus pantanellii* differs from *A. lothagamensis* in showing a groove on the c mesial side and larger dimensions and can be distinguished from *A. qeshta* for the $i3 > i2 \geq i1$ arrangement. *Archaeopotamus pantanellii*, differently from *A. andrewsi*, shows transversal lines on the c enamel and a m2 with acingulid more crenulated. *Archaeopotamus pantanellii* differs from *A. crusafonti* in being hexaprotodont and showing overall larger dimensions, the Tuscan species also differs from *Hex.? sículus* in having a single groove on the mesial side of the c and straight incisors without grooves. *Archaeopotamus pantanellii* differently from *Hex.? sahabiensis* displays m2 with four main cuspids instead of five. *Archaeopotamus pantanellii* is recognisable from *Hex.? hipponensis* for straight incisors without peculiar wear surface.

General description

The mandible (MSNAF2821) is highly damaged and displays four teeth in cross-section that could be right i1, left i1, i2, i3 or right c, i3, i2 and i1 (Figure 2A). The mandibular fragment is probably a part of the mandibular symphysis, close to the teeth emergence. Among the two options, probably the first one is the more conservative. The putative right i1 does not show a different internal structure or visible enamel, and the cross-section is likewise similar to the other teeth. In cross-section the putative i3 is the smallest

incisor, and the i2 displays slightly smaller dimensions to i1, whilst the i1 is the largest one. A small diastema is present between the two i1s. The i2 and the i3 have rounded cross-section, while the i1s are more elliptic-shaped. The diastema between the right i1 and the left i1 is well visible, while it is absent between i1 and i2 and i2 and i3. In the light of that, the Casino Basin hippopotamid was thus characterised by a hexaprotodont condition. A lignite vein well visible along the mandibular fragment could attest the possible action of intense taphonomic activities that could have altered the original morphology of the remains. The action of post-depositional processes could explain the partially folded aspect of the incisors in the mandibular fragment.

The right c is severely fragmented and only represented by the apical part MSNAF2820 (Figure 2B-E). The mesial side (Figure 2D) is better preserved than the lateral one (Figure 2B). On the former side is visible a longitudinal groove that runs on the upper-central part of the canine, no similar structure is visible on the lateral side. The enamel is thin, finely crenulated with peculiar slightly visible transversal lines. The apical part in the occlusal view (Figure 2C) displays a deflection towards the mesial side. The cross-section (Figure 2E), although if incomplete because it includes the wear surface, shows a cross-section that is mostly D-shaped, and it presents a small groove on the mesial side that contributes to a bean-shaped aspect of the cross-section.

The isolated lower incisors (Figure 2F-I), three well preserved (Figure 2F-H) and two undetermined fragments (Figure 2I), are mainly cylindrical with a round or mostly rounded cross-section (MSNAF2829). All the incisors lack the distal part. The enamel is just slightly visible on some specimens (Figure 2F, 2H). All remains show an apical bevelled wear facet. One incisor (Figure 2F) is long and slender, while the other two are smaller and with a stockier aspect (Figure 2G-H). The incisor depicted in Figure 2G has a cross-section more elliptic, with a mesial-lateral diameter greater than the ventral-dorsal one.

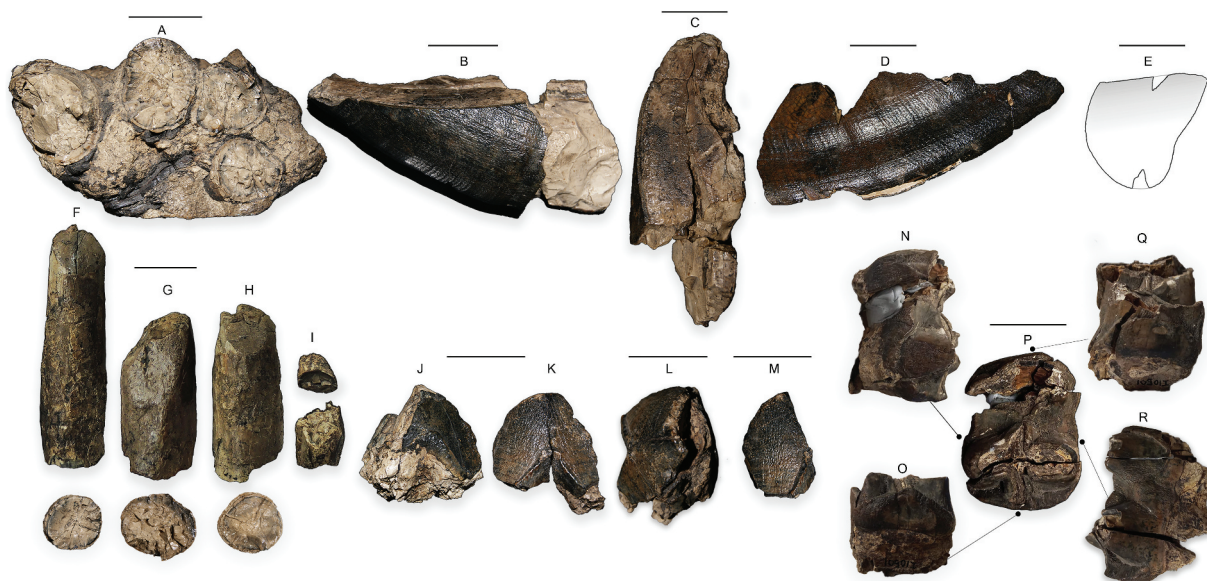


Figure 2. A. Mandible fragment with right i1, left i1, i2, i3 (MSNAF2821). B-E, right lower canine (MNSAF2820). B, lateral view; C, occlusal view; D, mesial view; E, cross section. F-I, lower incisors (MSNAF2829). F, i2-i3; G, i1-i2; H, i1-i2; I, lower undeterminable incisors fragments. J-L, right P2 (MSNAF2828). J, lingual view; K, labial view; L, occlusal view. M, lower premolar fragment (p1?) (MSNAF2828). N-R, left m2 (MSNCCI10501). N, labial view; O, distal view; P, occlusal view; Q, mesial view; R, lingual view. Scale bars 2 cm.

The right P2 MSNAF2828 (Figure 2J-L) is broken along the longitudinal plane, distal and mesial parts are partially missing, roots are almost entirely damaged and therefore not investigable. The P2 is mainly triangular and does not show accessory cusps, the enamel is finely crenulated. The cingulum is pustulated on the lingual side (Figure 2J). On the labial side (Figure 2K), the cingulum looks less developed than on the lingual side. In occlusal view (Figure 2L), the main cusp of the P2 curves lingually towards the apex. The P2 is just slightly worn. On the lower part of the lingual side are visible several transversal thin bands. The same bands are also visible on the other fragmented premolar (probably a lower p1, Figure 2M). These bands are probably growth lines (perikymata).

The left m2 is transversally damaged MSNCCI10501 (Figure 2N-R). The enamel is rough, and accessory cusps are absent. The hypoconid in occlusal view is the largest cuspid, and it is linked with the mesial cusps (metaconid and protoconid) as well as the

cingulid distally (Figure 2P). The metaconulid is reduced, mostly ovoid shaped. The cingulid is well developed on the labial part (Figure 2N), particularly on the protoconid. The cingulid is almost visible on the lingual part, poorly developed on the metaconid and absent on the entoconid (Figure 2R). The cingulid is particularly high and slightly pustulated on the distal part of the tooth (Figure 2O), while less developed on the mesial part (Figure 2Q). On the medial labial side is present a mesostylid. The m2 looks fairly worn in occlusal view (Figure 2P) in particular, on the anterior cusps. The distal part is better preserved, and the trefoil wear pattern typical of the Hippopotamidae family is almost completely developed. The roots are nearly entirely damaged.

The last remain is probably another mandible part; only two cross-sections of indeterminable incisors are visible that are neither diagnostic nor significant for an anatomical attribution (MSNAF2862).

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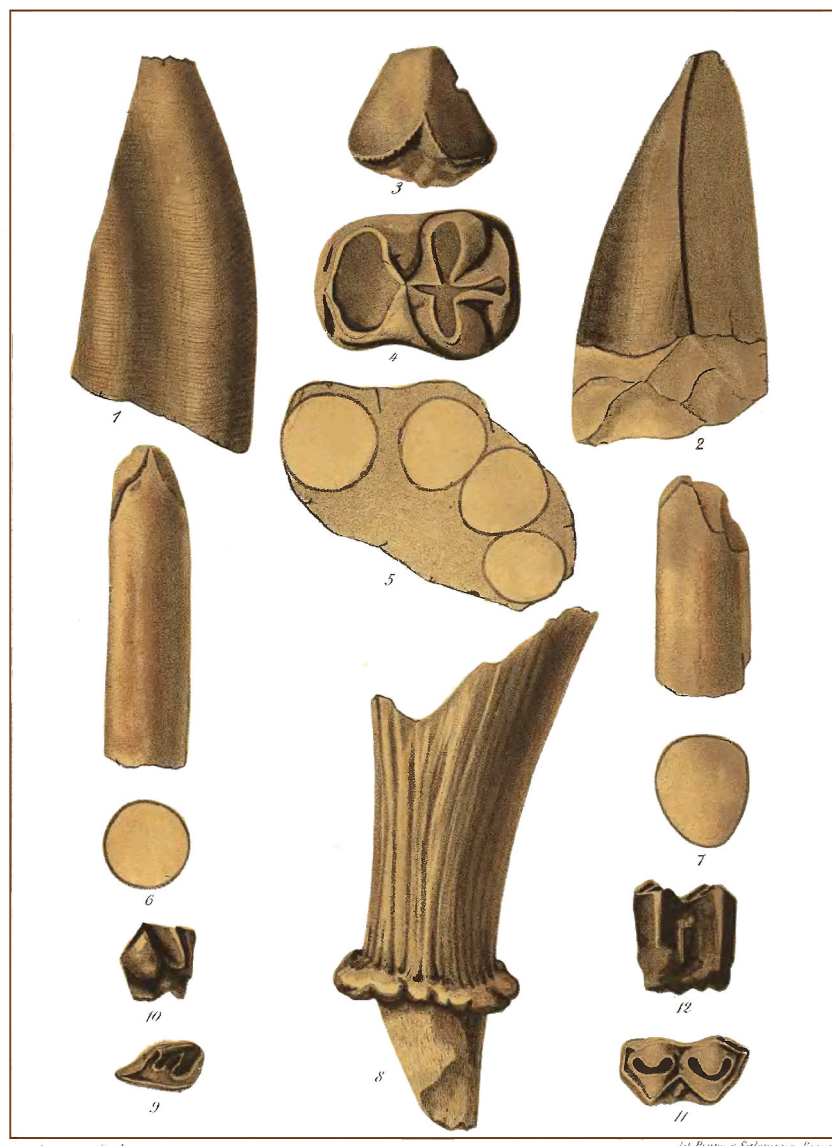


Figure 3. Original table of Casino Basin remains (Pantanelli 1879), Tab. IV, Figures 1-7. 1-2, MNSAF2820. 3, MNSAF2828. 4, MSNCCI10501. 5, MNSAF2820. 6-7, MNSAF2829.

Morphological and morphometrical comparison

Morphological comparison

A comparison with the hippopotamids unearthed from coeval localities is not easy due to the fragmentary and scant nature of the material collected from the Casino Basin. The morphology of the mandible fragment was highly simplified in Pantanelli (1879) (Figure 3). The cross-sections of the teeth were depicted as perfectly sub-rounded, although the real morphology is more complex. The largest incisor in the mandibular fragment is the i1, while the i2 and the i3 appear dimensionally similar, with the i2 slightly larger than the i3. This incisors arrangement ($i1 > i2 \geq i3$) is quite common in hippopotamids. *Archaeopotamus harvardi* displays the i1 bigger than i2 and i3, while in *A. qeshta* i2 is the largest incisor (Weston 2000, 2003; Boisserie et al. 2017a). Boisserie et al. (2017a) reported an $i3 > i2 > i1$ arrangement for *A. lothagamensis*, while, conversely, Weston (2000) described these incisors as equal-sized. However, the measurements reported in Boisserie et al. (2017a) supported the $i3 > i2 > i1$ condition. *Archaeopotamus crusafonti* displays only four incisors in the mandible, with the i1 slightly larger than the i2 (Lacombe et al. 1986; Martino et al. 2021). *Hex. sivalensis* usually has the i2 smaller than the i1, while the i3 in some specimens can be bigger than the i1 (Boisserie et al. 2005b). For de Visser (2008), in Asian species belonging to *Hexaprotodon*, the relative size of the lower incisors may be variable. *Hexaprotodon garyam* shows the i1 and the i3 equal in size or the i1 slightly larger than the i3, while the i2 is always the smallest one (Boisserie et al. 2005b). *Hex. bruneti* is characterised by a particularly enlarged i3 and by i2 and i1 similar in size (Boisserie and White 2004). The relative dimension of the six incisors in the mandible of *Hex.? siculus* is unknown (Seguenza 1902, 1907; Martino et al. 2021). In *Hex.? hipponensis* the i1 is reported as the largest incisor (Gaudry 1876). Nevertheless, a mandible of *Hex.? hipponensis* with incisors *in situ* has never been recovered, and therefore this assertion is not necessarily correct. *Hexaprotodon? sahabiensis* has the i2 smaller than the i1 and the i3, whilst the i1 and the i3 are almost sub-equal in size (Pavlakis 2008). *Soatherium mingo* shows similar dimensions for the i1 and the i3, while the i2 is always the smallest incisor (Boisserie et al. 2003). *Hippopotamus amphibius* usually displays a tetraprotodont condition, with the i1 bigger than the i2. Nevertheless, Falconer (1868, p. 406 footnote), Gaudry (1876) and Stuenes (1989) described a supernumerary incisors' anomaly in some *H. amphibius* specimens affecting one side of the lower jaw in adult individuals. *Choeropsis liberiensis* is characterised by a diprotodont condition, and the mandible has therefore only two first incisors. The morphology of the lower incisors is likewise poorly informative. Weston (2003) stated that in *A. harvardi* the morphology is variable, some isolated incisors collected from Lothagam are curved, with longitudinal lateral grooves (LT-26207), while others have a wear facet highly irregular. *Archaeopotamus crusafonti* i2 (MNCN72803) reported in Alcalá and Montoya (1998), is mainly cylindrical with a flattened mesial side, almost straight and with a cross-section that shows a feeble groove on the lateral side, similarly to the specimen depicted in Figure 2H. The fragmented left hemimandible (MNCN62837) displays the cross-section of the alleged i1 slightly elliptical, a general cylindrical aspect, and two poorly developed grooves on the labial and mesial sides, respectively. *Archaeopotamus andrewsi* had mainly cylindrical incisors with a smooth or slightly grooved enamel (Stromer 1914; Pickford et al. 2022). Nevertheless, one incisor (p. 54, fig. 85, D1-D2) depicted by Pickford et al. (2022) displays the 'tracked margin' of the wear surface typical of *Hex.? hipponensis* (Gaudry 1876). In *Hex. bruneti* the i1 has a circular cross-section, whereas the i2 may be mesial-laterally compressed.

The i3, the largest incisor, can exhibit both a circular cross-section and a mesial-lateral compressed one (Boisserie and White 2004). *Hexaprotodon? sahabiensis* mandible described in Pavlakis (2008) displays large incisors with a simple morphology, cylindrical and straight. Pavlakis (2008) did not describe the enamel surface of the lower incisors in *Hex.? sahabiensis*. The incisors of *Hex.? siculus* depicted by Seguenza (1907, Tab. VII figs. 13–16) probably belonged to a single individual, since the author referred to a mandible, destroyed during the excavation, with several teeth *in situ*. Some of these incisors were slightly apically curved (figs 14 and 16), others exhibited a well-visible groove (figs. 14 and 15), while one (fig. 13) was mainly cylindrical. The morphology of the incisors collected from the Casino Basin is probably one of the simplest among all the Late Miocene hippopotamids.

The c from the Casino Basin displays a longitudinal groove on the mesial side and an enamel finely crenulated, similarly to *A. harvardi* (Weston 2003). In *A. harvardi*, the cross-section of the c is slightly bean-shaped and, despite the cross-section of the c from the Casino Basin is not fully investigable, the D-section resembles the one displayed by *A. harvardi* (Weston 2003, p. 456, fig. 10.16). In *A. harvardi* collected from Tanzania the c cross-section is more D-shaped than bean-shaped (Harrison 1997). *Archaeopotamus lothagamensis* has a c compressed from side to side with an enamel finely striated and a flattened mesial border (Weston 2000). No grooves are reported by Weston (2000) on the severely fragmented c described from Lothagam (Kenya). The cross-section of the c of *A. lothagamensis* is mainly D-shaped (Weston 2000). The c from the Casino Basin is similar, but less transversally compressed. The fine striated enamel similarly characterised *A. qeshta*, which displays a bean-shaped cross-section and a flat-to-concave mesial side (Boisserie et al. 2017a). *Archaeopotamus crusafonti* c (MNCN72765) displays thin finely crenulated enamel, a groove on the mesial side that is less marked than in *H. amphibius* and an additional groove barely developed more ventrally (pers. observ. R.M.). The cross-section of the c is visible on the mandibular symphysis collected from La Portera (MNCN62837), it is bean-shaped with a groove on the mesial side and a more rounded aspect on the lateral side. *Archaeopotamus andrewsi* c has a flat mesial side and a more rounded lateral one, the enamel is finely striated, and a well-visible groove runs along the mesial side (Pickford et al. 2022). The groove on the c of *A. andrewsi* (Pickford et al. 2022, p. 55, fig. 86 A and p. 60, fig. 97) seems narrower and deeper than in the Casino Basin specimen. A small groove on the lateral side of the *A. andrewsi* c (Pickford et al. 2022, p. 55, fig. 86 B) is well visible, but the latter is placed more ventrally than in the Casino Basin specimen. The cross-section of the c in *A. andrewsi* is mainly D-shaped, as in most *Archaeopotamus* specimens (Pickford et al. 2022). Regarding *Hexaprotodon* genus, *Hex. garyam* has a finely wrinkled enamel, while *Hex. sivalensis* can show fine, coarse or smooth enamel (Boisserie et al. 2005b; de Visser 2008). Iqbal et al. (2019) described lower canines relatively well striated and with shallow grooves. de Visser (2008) reported the presence of a groove on the lateral side on several specimens of *Hexaprotodon*, while the mesial side may be grooved or smooth. Nevertheless, on many canines it was not possible to investigate grooves' occurrence (de Visser 2008). In *Hex. sivalensis* the c has a peculiar 'pear-shaped' cross-section (Falconer and Cautley 1868; de Visser 2008). The c cross-section in the Casino Basin is markedly different from that the one of *Hex. sivalensis*. The canine of *Hex. bruneti* is characterised by a gently wrinkled enamel (Boisserie and White 2004). *Hexaprotodon? siculus* c displays well-visible striae on the enamel and two grooves on the supposedly mesial side, the only one figured by Seguenza (1907). However, Seguenza (1907) described an additional groove

on the lateral side, missing in the Casino Basin specimen. *Hexaprotodon? sahabiensis* is characterised by a significantly large *c*, bigger than *A. harvardi* and *Hex. sivalensis*, with finely crenulated or smooth enamel (Gaziry 1987). The mesial side of the *c* of *Hex.? sahabiensis* is flat, while the lateral one is more rounded, the *c* cross-section is defined as ‘kidney-shaped’, and it is peculiar among hippopotamidae (Gaziry 1987; Pavlakis 2008). The enamel is finely crenulated or almost smooth, no lateral grooves were mentioned (Gaziry 1987; Pavlakis 2008). Gaudry (1876) reported fine striations and no strong grooves on the *c* lateral side of *Hex.? hipponensis* (Gaudry 1876, p. 501, fig. 5). Arambourg (1944) figured the *c* mesial side of *Hex.? hipponensis*, the latter is characterised by fine striae, while distinctive grooves are not detectable. The enamel of the *c* of *S. mingozi* can be finely ridged or smooth, and grooves on lateral and mesial sides were not reported by Boissier et al. (2003). The enamel of the *c* of *C. liberiensis* is finely striated, almost smooth. The *c* of the *Hip. amphibius* is longitudinally well striated, with grooves on both mesial and lateral sides. The groove on the mesial side is usually more developed than the one on the lateral one. The groove on the lateral side of the *c* is more or less developed in several hippopotamid species and usually well expressed in later ontogenetic stages (Boissier 2005).

The P2 (MSNAF2828) is not well preserved. The outline is triangular, with no visible accessory cusps. However, the mesial and distal sides are partially missing, so possible small accessory cusps could have been lost. P2s of *A. harvardi* are usually characterised by a single cusp curved lingually towards the apex and by a well-developed cingulum, in particular on the lingual side. In addition, pustulated enamel can be seen running mesio-lingually and disto-labially (Weston 2003). These characters are shared also by the hippopotamid from the Casino Basin. Currently, no P2s of *A. lothagamensis*, *A. crusafonti* and *A. qeshta* are known (Lacomba et al. 1986; Weston 2000; Boissier et al. 2017a). Regarding *Hex. garyam*, Boissier et al. (2005b) reported a P2 with a main triangular cusp, a strong mesial and distal cingulum as well as a mesial crest lingually curved. de Visser (2008) highlighted great variability in upper premolars of *Hexaprotodon*, P2 usually displays one main cusp and in most of the teeth is also present a posterior platform, covered by crenulated ridges or cusplets, and the latter character is absent in the specimen collected from the Casino Basin. *Hex. bruneti* P2 is bad preserved, and therefore its morphology is unknown (Boissier and White 2004). *Soatherium mingozi* has a triangular P2 in lateral view (Boissier et al. 2003). *Hex.? siculus* is characterised by a simple-built P2, with a gently wrinkled enamel (Martino et al. 2021). The P2s of *Hex.? sahabiensis* and *Hex.? hipponensis* are both unknown (Gaziry 1987; Pavlakis 2008). The P2 of *H. amphibius* is mainly triangular and mono-cusp P2 in *C. liberiensis* appears mainly triangular, with a possible distal accessory cusp, wrinkled enamel and pustulated cingulum.

The m2 from the Casino Basin (MSNCCI10501) was rediscovered recently in the MSNCC. The morphology of the m2 depicted in the original table (Pantaneli 1879, Tab. IV, fig. 4), is highly simplified (Figure 3). Hooijer (1946) argued that the m2 collected from the Casino Basin shows the hypoconid more simply built than the entoconid, differently from *Hippopotamus* and Asian *Hexaprotodon*. In Hippopotamidae, the entoconid is usually characterised by a comma-shaped wear surface, differently from the hypoconid that is usually trifoliated and therefore more complex (Mazza 1995). The lower molars of *A. harvardi* are characterised by a great variation. In general, these molars possess four low cusps with a prominent cingulid that forms shelves mesially and distally. In *A. harvardi* the entoconid is usually comma-shaped (Weston 2003). In *A. lothagamensis* a medial stylid is present on the m2 that also possesses a well-developed distal cingular shelf, the entoconid is comma shaped (Weston 2000, 2003). Weston (2000) described a hemi-mandible from Lothagam ascribed to *A. cf. lothagamensis* (KNM-LT 23871). The m2 from this mandible

is similar in occlusal view to the one from the Casino Basin in displaying a large hypoconid and a more ovoid-shaped entoconid. *Archaeopotamus qeshta* displays a m2 morphologically similar to the one from the Casino Basin (Boissier et al. 2017a, p. 5, fig. 3B). The m2 of *A. qeshta* is slightly more worn than the one from Tuscany, but a large hypoconid and a smaller entoconid are well distinguishable. This m2 probably possesses a mesostylid on the labial part. Boissier et al. (2017a) provided just the occlusal view of the m2 of *A. qeshta*, therefore it is not possible to investigate the labial and lingual sides. An unworn m2 of *A. crusafonti* is described in Alcalá and Montoya (1998). This tooth (MNCN72805) displays a well-developed cingulid, in particular on the mesial and distal parts. The hypoconid is way larger than the entoconid, the cingulid is high and crenulated distally and mesially, the cingulid is not high on both sides and it is also well visible on a mesostylid. In *A. andrewsi* the second lower molars depicted in Pickford et al. (2022) are almost unworn, and thus comparison with the Tuscan specimen is difficult. However, the labial side (Pickford et al. 2022, p. 53, fig. 107, A3) displays a cingulid that looks less developed and less crenulated than in the m2 from the Casino, and in occlusal view (Pickford et al. 2022, p. 53, fig. 107, B1) the hypoconid looks noteworthy larger than the entoconid. On the m2s of *Hex. sivalensis* are visible an anterior lobe, some posterior cusps (heptaconid, pentaconid, hexaconid), and most of them do not display cingulid (de Visser 2008). An accessory cusp and the absence of cingulid on the m2 of *Hex. sivalensis* is also reported by Iqbal et al. (2019). These characters of *Hex. sivalensis* are not shared with the hippopotamus collected from the Casino Basin. The m2 of *Hex. garyam* is characterised by a trefoil wear pattern not fully developed and a cingulid thicker mesially and distally but attenuated laterally. In *Hex. bruneti*, the cingulid is well developed and the entoconid has a mesial lobe (Boissier and White 2004). The m2 of *Hex.? siculus* was only figured by Seguenza (1907) in the lingual and labial views. The m2 of the Sicilian species displayed a cingulid better developed on the lingual side rather than on the labial one. The cingulid is quite crenulated and it is high mesially and distally (Seguenza 1907). *Hexaprotodon? sahabiensis* is characterised by five well-developed cusps on the m2 (Gaziry 1987). In *S. mingozi*, the m2 is low-crowned and the cingulid is missing lingually and labially, low and thick mesially and distally (Boissier et al. 2003). *Choeropsis liberiensis* displays an m2 with four cusps, trefoil wear pattern, high cingulid on the anterior cusps of the m2, while less developed in the posterior ones. In *H. amphibius* the m2 is high crowned, with a trefoil wear pattern perfectly developed, high cingulid, four main cusps and sometimes by an accessory distal cusp. The main characteristics of Late Miocene and Early Pliocene species are listed in Table 1.

Morphometric comparison

The dimensions of the remains from the Casino Basin are not easily comparable with other hippopotamid specimens. The P2 partially misses proximal and distal parts, and the maximum length is therefore underestimated. Isolated incisors are equally uninformative because their position cannot be deduced with certainty and thus compared with that of other hippopotamids. The dimensions of the incisors in the mandible are reported in Tab. 2 and compared to different Late Miocene and earliest Pliocene hippopotamid species. However, the possible deformation of the true morphology does not permit a good morphometrical comparison. The second lower molar is almost complete and probably the best specimen collected from the Casino Basin. Nevertheless, the dimensions of the m2 are usually little diagnostic at specific level. (Tab. 3). It can only be concluded therefore that the specimen collected from the Casino Basin was a medium-size species of hippopotamidae.

Table 1. Characters shared by *A. pantanellii* compared to Late Miocene and Early Pliocene hippopotamids. *Archaeopotamus harvardi* (Harrison 1997; Weston 2003), *A. lothagamensis* (Weston 2000, 2003), *A. qeshta* (Gentry 1999; Boisserie et al. 2017a), *A. crusafonti* (Martino et al. 2021 and references therein), *A. andrewsi* (Pickford et al. 2022 and references therein), *Hex. garyam* (Boisserie et al. 2005), *Hex. sivalensis* (Falconer and Cautley 1836; de Visser 2008; Iqbal et al. 2019), *Hex.? siculus* (Martino et al. 2021 and references therein), *Hex.? sahabiensis* (Gaziry 1987; Pavlakis 2008), *Hex.? hipponensis* (Gaudry 1876) and *S. mingoz* (Boisserie et al. 2004).

species	Incisors arrangement	c section	c enamel	c groove	m2 aspect
<i>Archaeopotamus pantanellii</i>	i1 > i2 > i3	D-shaped	Finely crenulated, transversal striated	A single groove on the mesial side	No additional cuspids. Cingulid well visible. Mesostyliid. Hyp > ent
<i>Archaeopotamus harvardi</i>	i1 > i2 > i3	D-shaped or bean shaped	Finely crenulated	A single groove on the mesial side	No additional cuspids. Cingulid well developed mesially and distally.
<i>Archaeopotamus lothagamensis</i>	i3 > i2 > i1	D-shaped	Enamel finely striated	No grooves reported	No additional cuspids. Cingular shelf. Mesostyliid
<i>Archaeopotamus qeshta</i>	i2 always the largest one	Bean-shaped	Finely longitudinally striated	//	No additional cuspids. Mesostyliid. Hyp > ent
<i>Archaeopotamus crusafonti</i>	i1 > i2	D-shaped	Finely crenulated	A single groove on the medial side	No additional cuspids. Mesostyliid. Hyp > ent
<i>Archaeopotamus andrewsi</i>	//	D-shaped	Finely striated	A groove on the medial side and one on the lateral side	No additional cuspids. Cingulid less developed and crenulated than <i>A. pantanellii</i> . Hyp > ent
<i>Hexaprotodon garyam</i>	i1 and i3 similar in size, i2 always the smallest one	D-shaped	Finely wrinkled enamel	A single groove on the medial side	No additional cuspids. Cingulid attenuated lingually and labially
<i>Hexaprotodon sivalensis</i>	i1 > i2, i3 can be bigger than i1	Pear-shaped	Fine, coarse, or smooth enamel	A single shallow groove on the lateral side, mesial side can be grooved or smooth	Several additional posterior cusps. Cingulid usually absent
<i>Hexaprotodon? siculus</i>	//	//	Well-visible striae	Two grooves on the (supposedly) mesial side. One groove on the lateral side	Cingulid better developed on the lingual side than on the labial one Five well-developed cuspids
<i>Hexaprotodon? sahabiensis</i>	i1 = i3 > i2	Kidney-shaped	Finely crenulated or smooth	No grooves reported	
<i>Hexaprotodon? hipponensis</i>	//		Fine striations	No grooves reported	//
<i>Soatherium mingoz</i>	i1 and i3 similar in size, i2 always the smallest one	Kidney-shaped	Finely ridged or smooth	No grooves reported	No additional cuspids. Cingulid absent lingually and labially

Discussion

Characters of the Casino Basin hippopotamid in the framework of late Miocene hippopotamids variability

The hippopotamid remains collected from the Casino Basin are scarce and fragmentary. Nevertheless, some features can be highlighted. The Tuscan hippo displays an hexaprotodont condition probably with an $i1 > i2 \geq i3$ arrangement, a c with finely crenulated and slightly transversally striated enamel with a groove on the mesial side, an m2 without accessory cuspids, well-developed cingulid on labial, mesial and distal sides, with a feebly trefoil wear pattern on the posterior cusps.

Among all the Late Miocene species, *A. crusafonti* is the earliest hippopotamid that shares a supposedly tetraprotodont condition, which is less archaic than the hexaprotodont one. This evolutionary trend is well observable in the different specimens of *Hex. protamphibius* collected from several strata with distinct ages in Shungura (Ethiopia): hippopotamids shifted from the hexaprotodont condition towards the more advanced tetraprotodont one (Coryndon 1978). However, the tetraprotodont condition of *A. crusafonti* should probably be confirmed by further findings, as anomalies in the number of incisors have been extensively described in the literature (Falconer and Cautley 1868; Gaudry 1876; Stuenes 1989). The mandible collected from La Portera is currently under detailed studies since it was only described by Lacombe et al. (1986) and never revised more recently. The $i1 > i2 > i3$ condition displays by the Casino Basin specimen is shared by *A. harvardi* (Weston 2003).

In *Hex. garyam* the i2 is always the smallest one (Boisserie et al. 2005b). The overall aspect and dimensions of the incisors from the Casino Basin are different from the ones collected from the peri-Mediterranean area, Spain (*A. crusafonti*), Italy (*Hex.? siculus*), Egypt (*A. andrewsi*), Libya (*Hex.? sahabiensis*) and Algeria (*Hex.? hipponensis*) (Martino et al. 2021 and references therein; Pickford et al. 2022).

The c collected from the Casino Basin shows a distinctive structure of the enamel. The Casino basin specimen displays feeble transversal striae, finely crenulated enamel, and a longitudinal groove on the mesial side, while the c cross-section is D-shaped. *Archaeopotamus crusafonti* shares a c morphology really close to the one of the Casino Basin (pers. observ. R.M.). The finely crenulated enamel is also shared by *A. harvardi*, while Asian *Hexaprotodon* shows a great variability, from smooth to grooved enamel (Weston 2003; de Visser 2008). *Hexaprotodon garyam* shows an enamel smooth or finely striated (Boisserie et al. 2005). *Hex.? siculus* displayed two grooves on the medial side and one on the lateral side (Seguenza 1907). The cross-section in the c of the Casino Basin, even if partially incomplete, is mainly D-shaped with a groove on the mesial side. The c cross-section of *A. crusafonti* (MNCN62837) is similar to the one of the Casino Basin, mainly D-shaped with a groove on the mesial side, but probably more slightly mesial-labially compressed. A compressed canine in cross-section is displayed by *A. lothagamensis*, while other hippopotamids display more peculiar cross-section, pear-shaped, bean-shaped or D-shaped (Weston 2000, 2003; de Visser 2008; Boisserie et al. 2017a).

Table 2. Comparative dimensions of m2 (L: max length; W: max width) of Miocene hippopotamids, minimum (m)–maximum (M) dimensions in mm; mean in mm; number of specimens (N). Data for *Hex.? siculus* from Seguenza (1902, 1907) and Hooijer (1946); *Hex.? sahabiensis* from Gaziry (1987) and Pavlakis (2008); *A. harvardi* (1) from Coryndon (1977) and Boisserie et al. (2017a); *A. harvardi* (2) from Harrison (1997); *A. lothagamensis* from Weston (2000, 2003); *A. qeshta* from Boisserie et al. (2017a); *A. crusafonti* from Faure and Méon (1984) and Gentry and Hooker (1988); *A. andrewsi* from Pickford et al. (2022); *Hex. garyam* from Boisserie et al. (2005); *Hex. sivalensis* from Hooijer (1950) and de Visser (2008); *Hex. bruneti* from Boisserie and White (2004).

	L (m-M) (mm)	L mean (mm)	N	W (m-M) (mm)	W mean (mm)	N
Casino basin		44.6	1		33	2
<i>A. harvardi</i> (1)	41.2–51.3	47.44	11	33.0–38.4	36.16	3
<i>A. harvardi</i> (2)	45.5–56	50.63	3	34.9–40.7	38.03	2
<i>A. lothagamensis</i>	41.1–42.7	41.90	2	27.8–34.0	30.90	2
<i>A. qeshta</i>	41.5–44.8	43.15	2	31.8–33.7	32.75	2
<i>A. crusafonti</i>	36–40.4	37.8	3	28–29	28.5	2
<i>A. andrewsi</i>	39–40.4	39.8	3	26–32	28.67	3
<i>Hex. garyam</i>	41.6–54.0	49.28	31	30.8–45.2	37.53	26
<i>Hex. sivalensis</i>	43–52	48.17	9	31–40	36.5	10
<i>Hex. bruneti</i>		49	1		33	1
<i>Hex.? siculus</i>	46–50	48	2	35–39	37	2
<i>Hex.? sahabiensis</i>	36.42–39	37.7	2	26.38–34	30.2	10

The c cross-section of *Hex. garyam* is figured in Boisserie et al. (2005b, p. 667–668, fig. 2A–3A) and it looks more rounded than in the Casino Basin specimen, *A. lothagamensis* and *A. crusafonti*. The cross-section of the c of most advanced Hippopotamidae is usually to triangular to D-shaped, while in more archaic forms the cross-section is more compressed (Weston 2000; Boisserie and White 2004).

Kenyapotamus coryndonae, a basal Hippopotamidae, shows an ovate-triangular c cross-section (Tsujiikawa 2005; Tsubamoto et al. 2015). Anthracotheriines in general have a c cross-section more rounded than hippopotamids (Boisserie et al. 2005a, 2010).

The m2 collected from the Casino Basin does not display prominent additional cusps, and the cingulid is well visible. *A.*

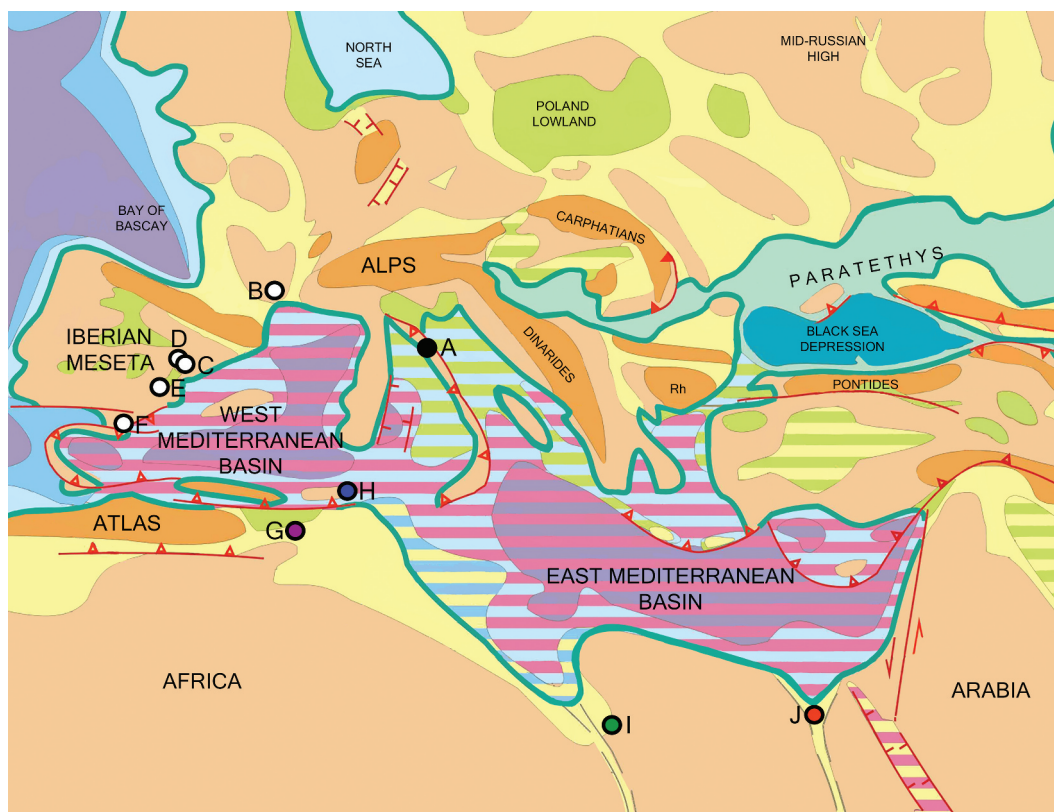


Figure 4. Paleobiogeographical reconstruction of Late Miocene–Early Pliocene localities with hippopotamids from the peri-Mediterranean area, modified from Popov et al. (2004). For further information regarding colours and symbology check Map. 9 (latest Miocene), Contents Annexe in Popov et al. (2004). **A**, *Archaeopotamus pantanellii*, Casino Basin, Tuscany, Italy; **B**, *Archaeopotamus crusafonti*, La Mosson, Montpellier, France; **C**, *Archaeopotamus crusafonti*, Las Casiones, Teruel, Spain; **D**, *Archaeopotamus crusafonti*, El Arquillo, Teruel, Spain; **E**, *Archaeopotamus crusafonti*, Venta del Moro and La Portera, Valencia, Spain; **F**, *Archaeopotamus crusafonti*, Arenas del Rey, Granada, Spain; **G**, *Hexaprotodon? hipponensis*, Pont-de-Duvivier, Algeria; **H**, *Hexaprotodon? siculus*, Gravittelli, Scirpi, San Pier Niceto, Sicily, Italy; **I**, *Hexaprotodon? sahabiensis*, As Sahabi, Libya; **J**, *Archaeopotamus andrewsi*, Wadi Natrun, Egypt.

harvardi usually possesses four low cuspids with a prominent cingulid that forms shelves mesially and distally. Almost all *Hexaprotodon* m2s described in de Visser (2008) show additional cuspids, heptaconid (present in 18 specimens out of 18 specimens analysed), pentaconid (15 out of 16) and hexaconid (13 out of 14). Cingulid is absent in most cases (16 out of 26), while rarely present on the lingual side (2 out of 26) and slightly more frequently on the labial side (7 out of 26). A similar lower molars complexity is also shared by *Hex. palaeindicus* (Falconer and Cautley 1868, p. 57, fig. 4a). In the light of the above-mentioned statements, the m2 from the Casino Basin is morphologically closer to *Archaeopotamus* rather than Asian *Hexaprotodon* representatives.

Paleobiogeographic considerations

Besides the Casino Basin, Tuscany is characterised by further Late Miocene-earliest Pliocene localities, such as Borro Strolla, Baccinello V3 and Velona (Rook et al. 1999; Ghetti et al. 2002; Rook and Martínez-Navarro 2004; Abbazzi et al. 2008; Pandolfi et al. 2021a, 2021b) (See Supplementary material, Figure 1). However, no hippopotamids have ever been reported from these Tuscan localities, which nonetheless present a similar faunal assemblage to the one described from the Casino Basin. The faunal list from Velona Basin (base of MN 13, ca. 7–6 Ma) includes *Hipparion* sp., *Propotamochoerus* sp., several cervids, bovids and *Dipoides problematicus* (Ghetti et al. 2002), while Baccinello V3 (6.733–6.436 Ma) comprises *Pliorhinus megarhinus*, *Tapirus* cf. *arvernensis*, *Hippotherium malpassii*, *P. provincialis*, bovids, several cervids and carnivorans (Rook et al. 1999; Rook and Martínez-Navarro 2004; Pandolfi and Rook 2017; Pandolfi et al. 2021a, 2021b, 2021c). The youngest locality, Borro Strolla (5.55–5.33 Ma) has a mammal list characterised by the occurrence of bovids, cervids and giraffids (Abbazzi et al. 2008; Pandolfi et al. 2021a, 2021b). In addition to Borro Strolla, Baccinello V3 and Velona, there are further Italian sites ascribed to Late Miocene: Verduno (late MN 13, 5.55–5.33 Ma), Moncucco Torinese (MN 13), Monticino Quarry (late MN 13, 5.55–5.33 Ma), Cessaniti (7.2–8.1 Ma) and Gravitelli (late MN13) (Seguenza 1902, 1907; Alessio et al. 1982; Gallai and Rook 2006, 2011; Angelone et al. 2011; Colombero et al. 2011; Marra et al. 2011, 2014; Rook et al. 2015, 2017, 2017; Pandolfi and Rook 2017; Pandolfi et al. 2019; Rook 2021; Pandolfi et al. 2021a, 2021b) (See Supplementary material, Figure 1). Verduno (Piedmont, west-northern Italy) is characterised by a rich mammal list, which encompasses a proboscidean, giraffids, a rhinocerotid, bovids, cervids, an equid and several carnivorans (Colombero et al. 2014). Moncucco Torinese (Piedmont, west-northern Italy) faunal list comprises *Mesopithecus* sp., a rhinocerotid, *Tapirus arvernensis*, cervids, bovids and several carnivorans (Angelone et al. 2011; Colombero et al. 2017), while fossil mammals from Monticino Quarry (Emilia Romagna, central-northern Italy) include *M. pentelicus*, a proboscidean, *H. malpassii*, a rhinocerotid, *P. provincialis*, an aardvark, a honey badger, bovids, and several carnivorans (Rook et al. 2015; Rook 2021; Pandolfi et al. 2021a, 2021b). Cessaniti (Calabria, South Italy) has a faunal list, which comprises giraffids, a rhinocerotid, a proboscidean (Marra et al. 2011, 2017). Hippopotamid presence from this locality can be for now ruled out because most likely the specimens from Cessaniti (an incisor and a femur) belong to an anthracotheriid (Marra et al. 2017). Gravitelli (Sicily, South Italy) documented the presence of *Mesopithecus* sp., carnivorans, proboscideans, a rhinocerotid,

Table 3. Comparative dimensions of lower incisors (MD; LL) of Miocene hippopotamids (m–M dimensions in mm; mean in mm; N). Data for *Hex. ? siculus* from Seguenza (1902, 1907) and Hooijer (1946); *A. crusafonti* from Faure and Méon (1984) and Gentry and Hooker (1988); *Hex. ? sahabiensis* from Pavlakis (2008); *A. harvardi* from Boisserie et al. (2017a); *A. lothagamensis* from Boisserie et al. (2017a); *A. qeshta* from Boisserie et al. (2017a); *Hex. garyam* from Boisserie et al. (2017a); *Hex. sivalensis* from Hooijer (1950) and de Visser (2008); *Hex. bruneti* from Boisserie and White (2004).

	i1			i2			i3					
	MD (m-M) mm	Mean MD mm	N	LL (m-M) mm	Mean LL mm	N	MD (m-M) mm	Mean MD mm	N	LL (m-M) mm	Mean LL mm	N
Casino basin												
<i>A. harvardi</i>	23.1–26.7	24.5	1	18.3	23.7	2	17.4–25.2	18.46	1	19.3–24.0	19.4	1
<i>A. lothagamensis</i>		24.90	2	28.5–23.2	21.30	2		19.0	1	19.3–24.0	21.65	2
<i>A. qeshta</i>		10.7	1	11.1	15.6	1		18.4	1	13.8–17.1	11.7	1
<i>A. crusafonti</i>	10.4–14.8	12.60	2	16.2–18.6	16.70	2	15.2–18.2	13.95	2	11.8–16.1	15.45	2
<i>Hex. garyam</i>	16.6–19	17.8	2	19–23.6	15.5	3	15–16	26.36	8	14.3–16.2	15.25	3
<i>Hex. sivalensis</i>	21.3–31.7	27.23	9	18.5–37.4	22.62	9	16.1–32.0	23.4	10	18.4–31.8	24.04	9
<i>Hex. ? siculus</i>	18.8–27.8	23.3	10	20.7–33.9	19.95	10	16.2–24.1	25.02	1	19.3–33.0	20.15	10
<i>Hex. ? sahabiensis</i>		23	1	20	20.9	2	20.14–21.7	17	2	18.6–29.9	16.26	2
<i>Hex. ? hipponensis</i>		22.28	1	27.54	17.75	2	17.5–18	22.92	1	17.2–19	22.92	1
		23	1	22	17.75	2	17.5–18	18.1	2	17.2–19	18.1	2

P. provincialis. and several artiodactyls, including *Hex.? siculus* (Seguenza 1902; 1907; Gallai and Rook 2006; Pandolfi and Rook 2017; Martino et al. 2021; Pandolfi et al. 2019, 2021a, 2021b; Iannucci 2023). All the above-mentioned Italian localities display mammals' assemblages richer than the Casino Basin one including carnivorans, giraffids, different bovids and cervids species, proboscideans, equids and rhinocerotids. These large mammals were unearthed from different peri-Mediterranean localities in association with hippopotamids (Gravitelli, Venta del Moro, El Arquillo I, Las Casiones, As Sahabi, Wadi Natrun) (Seguenza 1902, 1907; Alcalá 1994; Alcalá and Montoya 1998; Bernor and Rook 2008; Morales et al. 2011; Pickford et al. 2022) (see Supplementary material). In particular, the absence of proboscideans and rhinoceros, as well as giraffids, probably suggests a 'barrier' to the dispersion of these mammals in the Casino Basin.

Among all the Late Miocene localities of the peri-Mediterranean area where hippopotamids occurred (Spanish sites, Gravitelli, As Sahabi, Point-De-Duvivier and Wadi Natrun all reported in Figure 4), the mammal assemblage of the Casino basin more closely resembles the fauna unearthed from Spain, in particular from Venta del Moro (Morales et al. 2011 and references therein) and El Arquillo I (Alcalá and Montoya 1998), which include *D. problematicus*, *P. provincialis*, *Thalassictis*, *Hipparion*, *Parabos* and *Eucyon*.

The peculiar mosaic characteristics of *Hex.? sahabiensis* should be better investigated in order to disclose if this species might be the ancestor of the Late Miocene European ones. As already pointed out by Weston (2000), some characters are close to *Archaeopotamus*. However, the sagittal section of the mandibular symphysis does not resemble the one of *Archaeopotamus* (Pavlakis 2008; Boisserie et al. 2017a). *Hexaprotodon? sahabiensis* should be therefore revised in order to disclose a possible massive event of dispersion of *Archaeopotamus* from the Central Africa-Arabian Peninsula to North Africa (As Sahabi and Wadi Natrun) and Europe (Casino Basin, Iberian Peninsula and France) (Gaziry 1987; Pavlakis 2008; Martino et al. 2021 and references therein; Pickford et al. 2022). The closeness of the Casino Basin fauna with the Spanish ones, where *A. crusafonti* is well documented, can support a dispersal event in the Tuscan area through the Iberian Peninsula. In that regard, Ghetti et al. (2002) argued for a full land connection between Tuscany and the European mainland during the Late Miocene, which may therefore have provided an easy dispersal way for mammals. The same connection between Central Italy and the European mainland around 6.3 Ma (M1-2 transition) is also highlighted by Van der Made et al. (2006) (Figure 4). Rögl (1999), Ferretti et al. (2003), Cirrinzione et al. (2015) and Broquet (2016) postulated that the areas of Sicily and Calabria were close to North Africa during the Tortonian. Van der Made et al. (2006) hypothesised two different scenarios regarding South Italy: (i) Calabria was part of the African land mass or (ii) it was temporarily connected during a regression. A dispersal from Calabria to North during the Messinian may have been therefore prevented due to different paleoenvironmental conditions inferred from the fauna or because Calabria was separated from northern areas. The other possible dispersal route, from North Africa through Sicily up to the Casino Basin, should be better investigated. Nevertheless, the partial isolation of the Tusco-Sardinian paleobioprovince with the Calabro-Sicilian paleobioprovince during the Late Miocene would not have probably allowed the dispersal of hippopotamids from Sicily, where *Hex.? siculus* is reported

(Rook et al. 2006). Hippopotamids are currently unknown from Late Miocene Eastern European sites, and their presence in Greece is doubtful, therefore a Balkan dispersal event can be discarded as well (Athanasidou 2022).

Conclusions

Most of the peri-Mediterranean hippopotamids are poorly known, and most of them are dubiously ascribed to the genus *Hexaprotodon*. *Hexaprotodon? sahabiensis*, *Hex.? siculus*, *Hex.? hipponensis*, *Archaeopotamus andrewsi* and *A. crusafonti* display characters that are not shared by the Casino Basin specimens, which is characterised by finely crenulated c enamel, with subtly transversal lines and a groove on the mesial side that is less defined than in other Late Miocene species. The c cross-section is D-shaped. The incisors are conical and straight and in cross-sections are mesial-laterally compressed. The m2 is simply built, cingulid is well developed on mesial, distal and labial sides, accessory cuspids are absent and the trefoil wear pattern is developed on the posterior cusps. In the light of these characters, the species erected by Joleaud (1920), originally named as *Hippopotamus pantanellii*, may be considered valid. The species collected from the Casino Basin is here reassigned, with caution due to their fragmentary nature, to *Archaeopotamus*.

The characters shared by Tuscan specimens in particular, the m2 without accessory cuspids and with cingulid on labial, mesial and distal sides, together with the i1 > i2 > i3 configuration, permit to exclude the genus *Hexaprotodon*. In *Hex. garyam* the i2 is always the smallest incisor, while in *A. pantanellii* is the i3. In the Asian lineage of *Hexaprotodon*, the m2 is fairly more complex than the one collected from the Casino basin. The c and m2 of *A. crusafonti*, poorly described in literature, should be better investigated to evaluate a possible synonymy with the Tuscan species. In case of synonymy with *A. crusafonti*, the Casino Basin species *A. pantanellii* would have the priority.

The occurrence of *Archaeopotamus* in the Casino Basin is very significant. The clear African affinity of this taxon testifies that the Late Miocene Hippopotamidae probably dispersed from the North Africa to Europe via the Iberian Peninsula. A dispersal event from Sicily does not seem likely, given the suggested palaeogeography of Italy during the Late Miocene, as well as a dispersion via the Balkans, because, hippopotamids have never been reported from that area.

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ORCID

R. Martino  <http://orcid.org/0000-0002-5749-3454>
 L. Rook  <http://orcid.org/0000-0001-8923-5428>
 O. Mateus  <http://orcid.org/0000-0003-1253-3616>
 L. Pandolfi  <http://orcid.org/0000-0002-4186-4126>

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