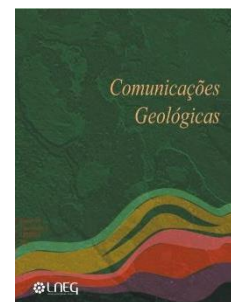


Earliest Pleistocene European hippos: a review

Primeiros hipopótamos europeus do Pleistocénico: uma revisão

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Resumo: A dispersão de hipopótamos de África para a Europa no Pleistocénico inferior tem sido amplamente discutida. A maioria dos autores propõe uma única entrada de formas semelhantes à espécie africana *Hippopotamus gorgops*, denominada *Hip. antiquus* ao entrar na Europa. No entanto, outros autores propõem uma primeira entrada de formas semelhantes ao táxon africano *Hip. kaisensis*, chamado *Hip. antiquus* ao entrar na Europa, e uma segunda entrada de formas semelhantes ao *Hip. gorgops*, chamado *Hip. tiberinus* ao entrar na Europa. Neste trabalho, avaliamos o estado da arte do debate, revisando o registo fóssil de hipopótamos e destacamos os últimos achados em locais da África Central à Europa e suas possíveis passagens.

Palavras-chave: *Hippopotamus*, Quaternário, África, Biogeografia, Pleistocénico inferior

Abstract: The dispersal of the genus *Hippopotamus* from Africa to Europe in the Early Pleistocene has been widely discussed in the last decades. Most authors propose a single entry of forms similar to the African species *Hippopotamus gorgops*, named *H. antiquus* upon entering Europe. However, other authors propose a first entry of forms similar to the African taxon *H. kaisensis*, named *H. antiquus* upon entering Europe, and an Early Pleistocene second entry of forms similar to *H. gorgops*, named *H. tiberinus* upon entering Europe. In this work we evaluated the current state of the debate reviewing the fossil record of genus *Hippopotamus* highlighting the last findings in sites from central Africa to Europe and their possible passageways.

Keywords: *Hippopotamus*, Quaternary, Africa, Biogeography, Early Pleistocene

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1. Introduction

Hippos (Artiodactyla, Hippopotamidae) are large mammals with ecological peculiarities associated with their close relationship to the continental aquatic environment. This apparent dependence on permanent bodies of water makes them especially interesting when

carrying out palaeoenvironmental reconstructions (Palmqvist *et al.*, 2003). The ecological characteristics of hippos also condition their dispersal capacity, making their distribution highly related to the connectivity of the habitats (Stoffel *et al.*, 2015). Reconstructing the palaeobiogeography of hippopotamuses is highly valuable for understanding the possible connections between geographic areas at critical moments in human evolution, such as the Early Pleistocene (O'Regan, 2008).

Knowing the distribution routes of these animals is not an easy task. There is no consensus among specialists on the phylogenetic relationships, the systematics, and the diagnostic characteristics of the different species. An example of this controversy is the diversity of hypotheses regarding the validity and relationships of European taxa (see Faure, 1985; Petronio, 1995; Mazza and Bertini, 2013). Each of the proposals entails a different interpretation of the biogeography of these animals and a different number of intercontinental movements.

Two dispersals of African hippos into Europe have generally been considered during the Quaternary. A first entry of forms compatible with *H. gorgops* that would give rise to the European *H. antiquus* in the Early Pleistocene; and a second entry from *H. amphibius* in the Middle Pleistocene (Petronio, 1995; Martínez-Navarro *et al.*, 2015).

However, Made *et al.* (2017) consider three different entries. A first entry of forms compatible with *H. kaisensis*, which would give rise to *H. antiquus* (synonym of *H. major*) recorded at Coste San Giacomo and Upper Valdarno, and would become extinct rapidly around 1.8 Ma; a second entry shortly before 1.2 Ma with forms similar to the African *H. gorgops* from the Levant, which would give rise to the debated taxon *H. tiberinus* / *georgicus* that would spread across Europe to at least the late Middle Pleistocene; and a last entry of *H. amphibius* / *incognitus* / *icosicensis* during the late Middle Pleistocene that would persist in Europe until the Late Pleistocene.

This work aims to review the evidence in the fossil record of hippos of genus *Hippopotamus* from the Plio-Pleistocene to the middle of the Early Pleistocene (from 2.6 to 1.6 Ma) from central Africa to Europe and their possible passageways in order to address the discussion of the Early Pleistocene entries of hippos to Europe.

2. Methodology

In order to compile the known fossil record, we carried out a rigorous compilation and update of the sites with the presence of hippos dated between the beginning of the Pleistocene and 1.6 Ma in Europe, Anatolia, the Levant, the Caucasus, and Africa. Each entry registered in the database has been georeferenced, allowing the analysis and visualization of the data graphically in Geographic Information Systems (GIS) software. The information on the sites has been obtained both from The Paleobiology Database (Peters and McClennen, 2016) and from specific bibliography. All the data associated with the findings are kept together with the locality reference. Appendix 1 summarizes the information on the fossil sites considered, the hippo taxa present, the chronology of the presence of each taxon and the references from which the data were obtained.

3. Results

3.1. Record in East Africa

Most of the world's hippo record from the Early Pleistocene comes from East Africa. This record has been continuous since the Pliocene in areas such as the Omo Valley or West Turkana (Coryndon and Coppens, 1973; Harris, 1991). The diversity of taxa in this area is wide and there is a large amount of material pending revision. Seven species of hippopotamus are cited between the beginning of the Pleistocene and 1.6 Ma ago. Within the genus *Hippopotamus* we find references to *H. karumensis* (West Turkana and East Turkana), *H. aethiopicus* (West Turkana and East Turkana), *H. protamphibius* (West Turkana and Omo Valley), *H. kaisiensis* (Kaiso Village), *H. gorgops* (East Turkana, West Turkana and Olduvai), and *H. amphibius* (Omo Valley, Chesowanja and Lusso Beds) (Coryndon & Coppens, 1973; Growlett *et al.*, 1981; Harris *et al.*, 1988; Pavlakis, 1990; Harris, 1991). In the Upper Maka locality Boisserie & White (2004) defined *Hexaprotodon bruneti*. In the sites around Lusso Beds several fossils have been attributed to *Hex. ?imaguncula* (Pavlakis, 1990). Boisserie (2005) has questioned the validity of this latter species, stating that it probably represents several small hippo taxa (Fig. 1).

3.2. Record in North Africa

Hippo records in North Africa were reviewed by Made *et al.* (2017). The oldest site within our timeframe is Lac Ichkeul, in Tunisia, with a chronology older than 2.5 Ma and the presence of *H. kaisiensis* (Arambourg, 1970). There are several later sites in Algeria with chronologies between 2.4 and 1.7 Ma. In the sites of Ain el Bey and Ain Boucherit the presence of *H. kaisiensis* has been determined, while *H. sirensis* and *H. gorgops* have been determined at the Ain Hanech / El Kherba and Mansoura sites (Chaid-Saoudi *et al.*, 2006). *H. sirensis* is considered a junior subjective synonym of *H. gorgops* (Geraads, 1980) (Fig. 1).

3.3. Record in Europe

Currently, the first confirmed presence of hippos in the Pleistocene in Europe is disputed between the Chiuse Basin and Coste San Giacomo sites in Italy (Bellucci *et al.*, 2012; Pandolfi & Petronio, 2015), and Elis in Greece (Reimann & Strauch, 2008), with chronologies between 2.1 and 2 Ma. Some authors indicate the first presence of hippos in the Late Pliocene deposits of Valea Graunceanului (Romania; Bolomey, 1965) or Moldavian

Roussillion (Moldova; Vangengeim *et al.*, 1998), although the validity of the determinations and the stratigraphic position of the materials have been discussed (O'Regan, 2008). Subsequently, there are references to hippo specimens in sites around the Upper Valdarno area (Italy, ca. 2.0-1.8 Ma; Gliozzi *et al.*, 1997), Mencil-9 (Spain, ca. 1.7 Ma; Pla-Pueyo *et al.*, 2011; Arribas, Pers. Comm.) and Livakos (Greece, ca. 1.6 Ma; Koufos, 2001). Following Mazza (1991), all hippo presences in the Early Pleistocene in Europe would be determined as *H. antiquus*. Made *et al.* (2017) propose to differentiate between *H. antiquus* for those sites with chronologies older than 1.7 Ma and *H. tiberinus* for those with chronologies after 1.4 Ma, recovering the disputed taxon *H. tiberinus* described by Mazza (1991) on the basis of Middle Pleistocene remains from the Italian peninsula (Fig. 1).



Figure 1. Geographic map that includes the sets of fossil sites with the presence of hippos with a chronology between 2.6 and 1.6 million years from central Africa to southern Europe. DKI: Douglas Korongo I; FLMI: Frida Leakey Korongo West I.

Figura 1. Mapa geográfico que inclui os conjuntos de sítios fósseis com a presença de hipopótamos com uma cronologia entre 2,6 e 1,6 milhões de anos da África Central ao sul da Europa. DKI: Douglas Korongo I; FLMI: Frida Leakey Korongo West I.

3.4. Record in the Levant, the Caucasus and Anatolia

There are few records of hippos in the area encompassing the Levant, the Caucasus, and Anatolia. In the Caucasus we found specimens of hippopotamuses at the Akhalkalaki site (Georgia), with an estimated maximum age of 0.98 Ma. These specimens were determined as belonging to the new species *H. georgicus* (Vekua, 1986), which has been assimilated to *H. antiquus* (Kalkhe, 1987) or *H. tiberinus* (Made *et al.*, 2017). In Turkey, specimens determined as Hippopotamidae have been found, in the Kocakir-2 site, with a proposed chronology between 1.9 and 1.6 Ma (Demirel *et al.*, 2016). The first record of hippos in the Pleistocene in the Levant is approximately 1.4 Ma at the Ubeidiya site (Israel; Martínez-Navarro, 2004).

4. Discussion

Of the East African hippo taxa only *H. kaisensis*, *H. gorgops*, and *H. amphibius* are recorded at higher latitudes during the Pleistocene. So far, no African specimen has been assigned to *H. antiquus*, probably as a consequence of their similarities with *H. gorgops*.

After reviewing the geographical and temporal distribution of the known fossil record and evaluating the models with one and two entries of hippopotamuses in Europe from Africa in the Early Pleistocene, the possibility of a single entry of hippos appears more plausible. Even though the fossil record of hippos between 2.1 Ma and 1.6 Ma in Europe is scarce, the data presented here contrast with the model of Made *et al.* (2017; Fig. 2a). This record seems to be more or less widely distributed with specimens from Greece (Elis) to Spain (Mencal-9). The appearance of specimens in Turkey (Kocakır-2) in chronologies that overlap with the first appearances in the Levantine corridor of the forms considered by Made *et al.* (2017) as *H. gorgops* / *sirensis* reinforce this geographical and chronological continuity of the European hippos from the Early Pleistocene (Fig. 2b).

The possibility of the presence of three species of hippos in Europe during the Pleistocene was exposed by Mazza (1991), although later works ruled out this possibility due to the absence of significant differences in the morphology among these taxa (Petronio, 1995). In turn, the similarities between *H. antiquus* (in the broad sense) and *H. gorgops* have been highlighted, raising the possibility of considering *H. gorgops* a junior subjective synonym of *H. antiquus* (Martínez-Navarro *et al.*, 2015; Pandolfi *et al.*, 2020).

5. Conclusions

The review of the record of fossil sites from the beginning of the Pleistocene to 1.6 Ma with the presence of hippos from central Africa to Europe allowed us to re-evaluate the possible hypotheses of hippo entry to Europe in the Early Pleistocene. As previously mentioned, the oldest hippo specimens located in Europe are found in Greece (Elis) and Italy (Chiusi Basin and Coste San Giacomo) about 2.1 Ma. These populations apparently persist during the Early Pleistocene with a wide geographic distribution range from the Caucasus (Akhalkalaki) to the Iberian Peninsula (Mencal-9). In light of the findings with early chronologies in Europe, Turkey and North Africa, a reassessment of the available specimens seems necessary, characterizing their anatomy accurately and analysing their relative position to the previous European and African record.

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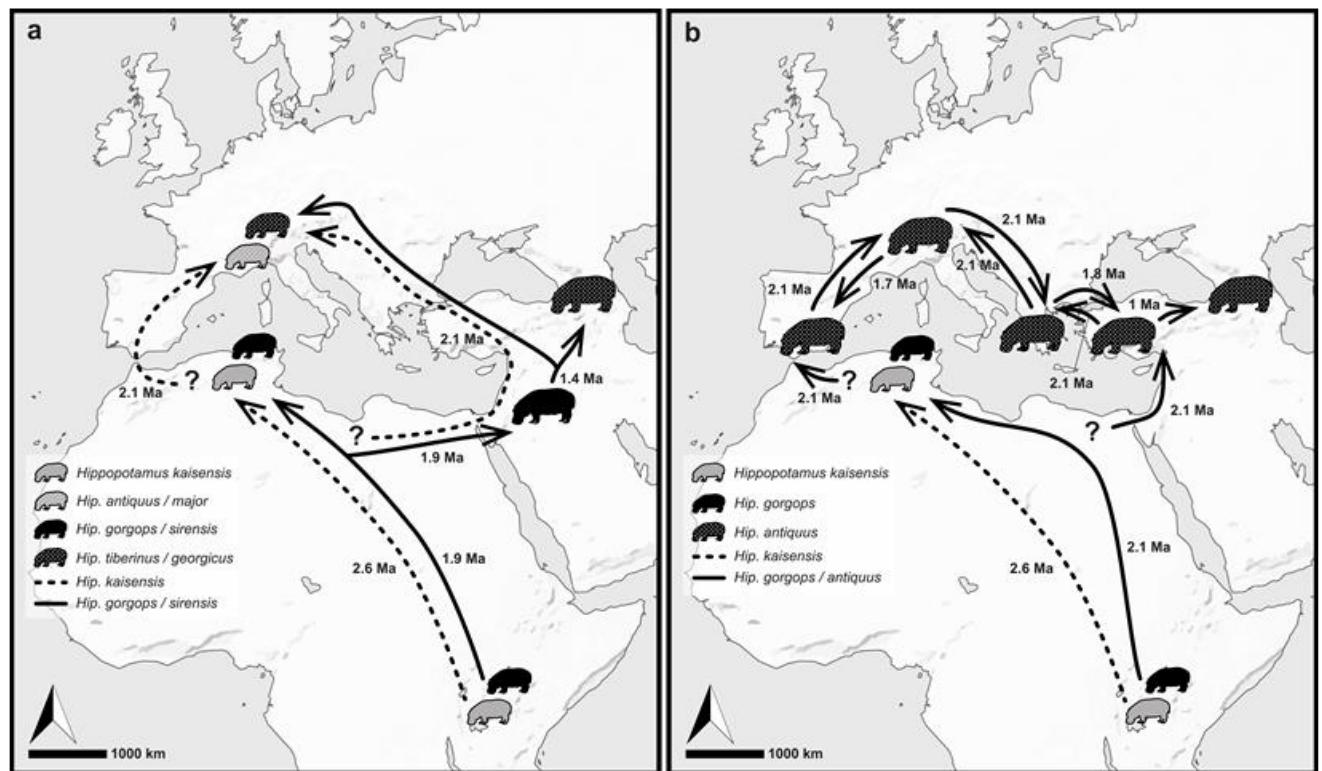


Figure 2. Explanatory maps of proposed entry of hippos to Europe during the early Pleistocene. a) Proposal made by Made *et al.* (2017); b) alternative that includes the proposals of Martínez-Navarro *et al.* (2015) and Petronio (1995), among others, and the findings not included in previously published proposals.

Figure 2. Mapas explicativos da proposta de entrada de hipopótamos na Europa durante o início do Pleistoceno. a) Proposta feita por Made *et al.* (2017); b) alternativa que inclui as propostas de Martínez-Navarro *et al.* (2015) e Petronio (1995), entre outros, e os achados não incluídos em propostas publicadas anteriormente.

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Annex 1. Summary table with the information on the fossil sites considered in this paper, the hippopotamus taxa present, the chronology of the presence of each taxon and the references from which the data were obtained. *H.* = *Hippopotamus*; *Hex.* = *Hexaprotodon*; Chron. = Chronology (Ma).

Anexo 1. Quadro-resumo com as informações sobre os sítios fósseis considerados neste trabalho, os taxa de hipopótamo presentes, a cronologia da presença de cada táxon e as referências das quais os dados foram obtidos. *H.* = *Hippopotamus*; *Hex.* = *Hexaprotodon*; Chron. = Cronologia (Ma).

Area	Site	Country	Taxa	ca. Chron.	Reference
East Africa	East Turkana (Various localities)	Kenya	<i>H. karumensis</i>	2.6-1.6	Harris, 1991
			<i>H. aethiopicus</i>	2.6-1.8	
			<i>H. gorgops</i>	2.6-1.6	
	Omo Valley (Various localities)	Ethiopia	<i>H. protamphibius</i>	2.6-1.8	Coryndon & Coppens, 1973
			<i>H. gorgops</i>	2.6-1.8	
			<i>H. amphibus</i>	2.6-1.8	
			<i>H. karumensis</i>	1.9-1.6	
	West Turkana (Various localities)	Kenya	<i>H. aethiopicus</i>	1.9-1.6	Harris <i>et al.</i> , 1988
			<i>H. protamphibius</i>	2.6-1.9	
			<i>H. gorgops</i>	1.9-1.6	
Chesowanja	Kenya	<i>H. amphibus</i>	2.5	Gowlett <i>et al.</i> , 1981	
Upper Maka	Ethiopia	<i>Hex. bruneti</i>	2.5	Boisserie & White, 2004	
Lusso Beds (Various localities)	D. R. Congo	<i>H. amphibus</i>	2.35-2	Pavlakis, 1990	
		<i>Hex. ?maguncula</i>	2.35-2		
North africa	Lac Ichkeul	Tunisia	<i>H. kaisensis</i>	>2.5	Arambourg, 1970; Made <i>et al.</i> , 2017
	Ain el Bey	Algeria	<i>H. kaisensis</i>	2.5-2.4	Chaid-Saoudi <i>et al.</i> , 2006; Made <i>et al.</i> , 2017
	Ain Boucherit	Algeria	<i>H. kaisensis</i>	2.1-2	Chaid-Saoudi <i>et al.</i> , 2006; Made <i>et al.</i> , 2017
	Ain Hanech / El Kherba	Algeria	<i>H. gorgops / sirensis</i>	1.9-1.8	Chaid-Saoudi <i>et al.</i> , 2006; Made <i>et al.</i> , 2017
	Mansoura	Algeria	<i>H. gorgops / sirensis</i>	1.7	Chaid-Saoudi <i>et al.</i> , 2006; Made <i>et al.</i> , 2017
	Coste San Giacomo	Italy	<i>Hippopotamus</i> sp.	2.1	Bellucci <i>et al.</i> , 2012
	Chiusi Basin	Italy	<i>H. antiquus</i>	2	Pandolfi & Petronio, 2015
	Ellis	Greece	<i>H. antiquus</i>	2	Reimann & Strauch, 2008
	Upper Valdarno (Various localities)	Italy	<i>H. antiquus</i>	2-1.8	Giozzi <i>et al.</i> , 1997
	Monte Riccio	Italy	<i>H. antiquus</i>	1.8	
Poggio ai Venti	Italy	<i>H. antiquus</i>	1.8	Martino & Pandolfi, 2021	
Torrente il Crostolo	Italy	<i>H. antiquus</i>	1.7	Martino & Pandolfi, 2021	
San Lorenzo	Italy	<i>H. antiquus</i>	1.7	Martino & Pandolfi, 2021	
Mencal-9	Spain	<i>Hippopotamus</i> sp.	1.7	Pla-Pueyo <i>et al.</i> , 2011; Arribas, Pers. Comm.	
Bacino di Travernelle	Italy	<i>H. antiquus</i>	1.7	Martino & Pandolfi, 2021	
Montecastrilli	Italy	<i>H. antiquus</i>	1.6	Martino & Pandolfi, 2021	
Livakos	Greece	<i>H. antiquus</i>	1.6	Koufos, 2001	
Kocakir-2	Turkey	<i>Hippopotamus</i> sp.	1.9-1.6	Demirel <i>et al.</i> , 2016	