## Hippopotamus gorgops from El Kherba (Algeria) and the context of its biogeography

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### ABSTRACT

Archaeological excavations at the site of El Kherba, an Early Pleistocene site in Algeria, have yielded *Hippopotamus* fossils, including a skull. El Kherba is a site known for producing Oldowan stone artifacts and cutmarked bones, dated to about 1.8 Ma. The elevated occipital and orbits of the skull, the short temporal fossa and the backward sloping nasal profile suggests that it belongs to *Hippopotamus gorgops*. The same species of *Hippopotamus* is present in the nearby locality of Ain Hanech, which is of the same age as El Kherba. The oldest known Hippopotamidae are from the Early Miocene of sub-Saharan Africa, where they reached their major diversity with five or six coeval species being common during the Plio-Pleistocene. From there they dispersed northwards to North Africa and Europe, and eastwards to the Indian subcontinent and SE Asia. The most likely origin of the European *Hippopotamus* is North Africa and it seems that in both areas the same three or very similar species appeared one after the other. The first *Hippopotamus* from North Africa is not well known, but it may have originated from the East African *H. kaisensis* and may have given rise to *H. antiquus*. This species, which lived from 2 till shortly after 1.8 Ma, is well documented in Europe. *Hippopotamus gorgops* dispersed around 1.8 Ma to North Africa and around 1.2 Ma to Europe, where it is known as *H. tiberinus*. During the late Middle or Late Pleistocene *Hippopotamus amphibius* dispersed to North Africa and Europe. The dispersal of *H. gorgops* across the Sahara towards North Africa around 1.8 Ma is well documented. The dispersal of the species which gave rise to *H. antiquus* may have occurred as early as 2.5 Ma, when lakes were extensive in East Africa. The same climatic circumstances, that caused more extensive lakes and rivers in East Africa, may have created similar environments in the Sahara, allowing hippos and other fauna, including humans, to spread northwards.

Keywords: Hippopotamus, dispersal, Sahara, Maghreb, environment

## RESUMEN

Las excavaciones arqueológicas en El Kherba, un vacimiento del Pleistoceno inferior de Argelia, han proporcionado fósiles de Hippopotamus, incluyendo un cráneo. El Kherba es un yacimiento conocido por haber revelado la presencia de artefactos líticos olduvayenses y huesos con huellas de corte datados hace unos 1.8 Ma. El elevado occipital y órbitas, la fosa temporal corta y los nasales inclinados hacia atrás sugieren que el cráneo pertenece a Hippopotamus gorgops. Esta misma especie de Hippopotamus está presente en el cercano vacimiento de Ain Hanech, contemporáneo a El Kherba. Los Hippopotamidae más antiguos conocidos son del Mioceno del África sub-sahariana, donde alcanzaron su mayor grado de diversidad con cinco o seis especies coetáneas durante el Plio-Pleistoceno. Desde aquí estas especies se dispersaron hacia el norte, alcanzando el norte de África y Europa, y hacia el este, hasta el subcontinente indio y el sureste de Asia. El origen más probable de los hipopótamos europeos es el norte de África, y parece que las mismas especies, o especies muy próximas, vivieron en ambas zonas. No se conoce bien la primera especie

de *Hippopotamus* del norte de África, pero pudo haberse originado del *H. kaisensis* del este de África, dando lugar a la especie Hipopotamus antiquus, que vivió en Europa entre unos 2 y 1,8 Ma. Hace unos 1,8 Ma, *H. gorgops* se dispersó hacia el norte de África y hace alrededor de 1,2 Ma a Europa, donde se conoce como *Hippopotamus tiberinus*. Durante el Pleistoceno Medio tardío o Superior, *Hippopotamus amphibius* se dispersó hacia el norte de África y Europa. La dispersión de los hipopótamos a través del Sahara hacia el Norte de África ocurrió probablemente hace alrededor de 1,8 y 2,5 Ma. En este tiempo existían extensos lagos en el este de África y las mismas circunstancias climáticas puedieron haber dado lugar a ambientes parecidos con lagos extensos y ríos en el norte de África. Estos ambientes pudieron haber permitido la dispersión hacia el norte de los hipopótamos y de otra fauna, incluyendo a los humanos.

## 1. INTRODUCTION

The Hippopotamidae have a remarkable biogeographical history. Hippos were more diverse in sub-Saharan Africa than in North Africa and dispersed several times into Europe and Southern Asia. Most probably these dispersals into Europe took place through North Africa.

Most researchers consider the initial dispersal of hippos into Europe as an important event of stratigraphic importance (e.g. Rook & Martínez Navarro, 2010), and consider this event to be related to climatic change and even to the first human dispersal to Europe (e.g. Martínez Navarro, 2010). The taxonomy (Caloi et al., 1980; Faure, 1985; Mazza, 1991; 1995; Guérin, 1996; Kahlke, 1997; 2001; 2006), the number of dispersals, and the timing of the first of these towards Europe (e.g. Faure, 1985; Mazza, 1991; 1995; Van der Made, 2005a; 2011; Martínez-Navarro, 2010, Rook & Martínez-Navarro, 2010; Bellucci et al., 2012; 2014) have been contentious issues in paleontology. A recent proposal is that there were three Pleistocene dispersals: 1) *Hippopotamus antiquus (= H. major)* at about 2 Ma; 2) *Hippopotamus tiberinus* shortly before 1.2 Ma; and 3) *Hippopotamus amphibius* in the late Middle or early Late Pleistocene (Van der Made et al., in press).

Most likely, the hippo species which reached Europe or their immediate ancestors passed through or at least reached the Maghreb. Pleistocene fossils of Hippos have been described or mentioned from North Africa (Pomel, 1890; 1896; Arambourg, 1970; 1979; Thomas, 1977; Geraads, 1980; 2002; Geraads et al., 1992; Chaid-Saoudi et al., 2006; Van der Made & Sahnouni, 2013).

Here we report on some morphological features of a hippo skull recovered from the El Kherba archaeological site (Algeria), and discuss their significance to systematics and the dispersal of hippo species from sub-Saharan Africa towards the north.

## 2. THE EL KHERBA ARCHAEOLOGICAL SITE

The El-Kherba site is situated on the edge of the north-eastern Algerian High Plateau, north of the city of El-Eulma (Province of Sétif). Discovered in 1992, it is a part of the Ain Hanech Plio-Pleistocene site complex, representing a lateral extension of the classic site of Ain Hanech. Both El Kherba and Ain Hanech are contemporary and belong to the Ain Hanech Formation. The Ain Hanech Formation is 30 m thick and formed of several cyclothemic units of fluvial origin (from O to T) (Sahnouni & de Heinzelin 1998). The stratigraphic profiles of the Ain Hanech and El-Kherba sites are correlated with the base of Unit T based on stratigraphic and altimetric evidence.

Paleomagnetic studies undertaken in the Ain Hanech Formation, including El Kherba, indicate a succession of magnetic polarities (R-N-R), beginning with reversed polarity in Units O, P, and Q, followed by normal polarity in Units R and S, and a reversed polarity in Unit T and the calcrete deposits sealing the sequence. The normal polarity at the bottom of the sequence, identified as the Olduvai subchron, is 6 m thick with the El Kherba and Ain Hanech archaeological sites situated near the top. Therefore, an age of 1.7 Ma is estimated for both localities (Parés et al., 2014), which is also corroborated by biostratigraphic data from East Africa (Sahnouni & Van der Made 2009). Thus, currently the El Kherba and Ain Hanech sites document the oldest archaeological occurrences known in North Africa.

The excavations at El Kherba (Figure 1) yielded a rich fauna associated with Oldowan stone tools. The fauna is savanna-like and comprises of Proboscidea, Equidae, small and large Bovidae, Girafidae, Suidae, Carnivora, Crocodilia, and Lagomorpha. The stone artifacts include unifacial and



Figure 1: A view of excavation at El Kherba in 2006. (Photo Jordi Mestre)

bifacial choppers, polyhedrons, subspheroids, spheroids, whole flakes, retouched pieces, and various fragments. The lithic industry and associated fauna are contained in three distinct levels (A, B, and C). However, the bulk of the archaeological materials, mainly accumulated in Level B including the *Hippopotamus* skull described in this study, were recovered within a floodplain setting consisting of silt and clay with gravel and calcic grains, deposited on top of a 20 cm thick conglomerate characterized by gravels of various sizes and shapes.

## 3. BIOGEOGRAPHIC HISTORY OF THE HIPPOPOTAMIDAE

The origin of Hippopotamidae has been under discussion since the nineteenth century (see reviews by Pickford, 2008; Orliac et al., 2010). In recent times, the Palaeochoeridae (Pickford, 1983; 2008; 2015) and An-thracotheriidae (Gentry & Hooker, 1988; Van der Made, 1999; Boisserie et al., 2005a; 2005b; Orliac et al., 2010; Lihoreau et al., 2015) have been proposed as their ancestors. If hippos originated from the Palaeochoe-ridae, they did so during the Early Miocene, either already in Eurasia or

shortly after their dispersal into Africa. If they originated from the Anthracotheriidae, they may have done so during the Late Eocene or Early Oligocene (Lihoreau et al., 2015). For a long time fossil teeth from the Early Miocene site of Rusinga (Kenya) were considered to represent the oldest evidence for hippo (Coryndon, 1978; Van der Made, 1999). Later, Pickford (2007) named those teeth Kulutherium and placed this genus in the Anthracotheriidae, but Orliac et al (2010) reaffirmed the identity of the teeth as hippo. The slightly younger Morotochoerus ugandensis was named on the basis of fossils from Moroto (Uganda) and four other localities and was placed in the Tayassuidae (Pickford, 1998). Later, it was recognized to be a gryphon taxon based on fossils of different taxa, which were identified as Albanohyus, Kenyasus, Lopholistriodon and prossibly Nguruwe (Van der Made, 2003; 2010). The holotype from Moroto was subsequently placed in the Hippopotamidae by Orliac et al. (2010) and in the Anthracotheriidae by Pickford (2011). However, there seems to be a consensus that by the Middle Miocene, Hippopotamidae occurred only in sub-Saharan Africa and that the Hippopotaminae and more specifically the genus *Hippopotamus* originated there.

Hippopotaminae spread out of Africa during the latest Miocene. *Hexaprotodon* reached the Middle East, the Indian subcontinent and as far away as Java in SE Asia (Falconer & Cautley, 1836; Colbert, 1938; Hooijer, 1950; Dubois, 1908; Van der Maarel, 1932; Faure, 1986; Gentry, 1999; Boisserie, 2005). At about the same time the hippo species *Hexaprotodon? pantanelli* reached Europe, where it is known from about nine latest Miocene and one early Pliocene locality. This species has simple molars like *Hexaprotodon* and only four lower incisors like *Hippopotamus* and its affinities have been disputed (see review by Van der Made, 1999 and the cited references). While *Hexaprotodon* has a long temporal range in southern Asia, the incursion in Europe was short-lived, from about 6 Ma till shortly after 5 Ma.

During the Plio-Pleistocene, Hippopotamidae diversified in sub-Saharan Africa, where at certain times existed six or more contemporaneous species (Figure 2) (Weston & Boisserie, 2010; Van der Made, 2014a, figure 19; 2014b, figure 21). By contrast, the diversity seems to have been much lower in North Africa. Several species were named on the basis of fossils from North African localities while still more fossils were described or mentioned from others.



Figure 2: The chronological distribution of the African Plio-Pleistocene Hippopotamidae (adapted from Van der Made, 2014 and ultimately based on Weston & Boisserie, 2010). Archaeopotamus harvardi reconstruction by Mauricio Antón; recent Choeropsis liberiensis (IVAU); "Trilobophorus" afarensis from Hadar (ARCCH AL109/319); Hexaprotodon protamphibius from Omo (MNHN 1933-9-777); recent Hippotamus amphibius (CNRPAH); Hippopotamus gorgops holotype from Olduvai (MNB).

Gaudry (1876) named a small species based on some teeth from Pont de Duvivier across the river Seybouse near Annaba (formerly Bône) in Algeria (the geographic positions of the localities are indicated in Figure 3 and the approximate ages in Figures 4 & 5). The specimens have a primitive morphology (Pomel, 1890), are believed to be of Pliocene age and currently placed in a different genus as *Hexaprotodon? hipponensis* (Weston & Boisserie, 2010).

The oldest North African localities where *Hippopotamus* has been reported are the following three localities. Arambourg (1970) mentioned *Hippopotamus* sp. from Ain el Bey and *Hippopotamus amphibius* from Ain Boucherit (pages 8, 131) and Lac Ichkeul (page 131), and described *Hippopotamus (Hexaprotodon) hipponensis* from Ain Boucherit (page 7), but indicated its presence a question mark in the summary table (page 131)



Figure 3: The geographic location of the hippopotamus localities mentioned in the text.

(Figure 4). One of us (J. van der Made) reviewed the fossils from these localities in the MNHN, but only nine teeth and two bones from Ain Boucherit were identified as hippos and none from Ichkeul. Our work at Ain Boucherit yielded few hippo specimens, which are too poor for an unequivocal species designation. Hippos were also reported from a group of slightly younger sites in North Africa (Figure 4). Arambourg (1979) reported *Hippopotamus amphibius* from Mansoura and Ain Hanech. Geraads (1980) considered the Early Pleistocene hippos to belong to the "group of *H. amphibius*", that many of them might be *H. gorgops*, which he suggested to be a junior synonym of *H. sirensis*. Chaid-Saoudi et al (2006) assigned the fossils from Mansoura to *Hippopotamus* cf. *sirensis*.

A group of still younger localities in North Africa includes Tighennif (formerly Ternifine, formerly Palikao). Pomel (1890) named the species *Hippopotamus sirensis* on the basis of fossils from this locality. Later he described the species in more detail (Pomel, 1896). Geraads (1980) reported poor material of *Hippopotamus* from Thomas Quarry 1 level L and hominid level, similar to the living species. Later, he assigned the material to *Hippopotamus* cf. *sirensis* (Geraads, 2002). Richer materials from Aïn Maarouf, but still lacking the relevant skull parts were assigned to *H. c.f. sirensis* (Geraads et al., 1992). The fossils assigned to *H. sirensis* (or *H. cf. sirensis*) cover a very long temporal range.

*Hippopotamus amphibius*, the living species, is reported from the youngest North African localities (Figure 4), including Tihodaine (Thomas, 1977) and Gisement des Phacochères (Hadjouis, 1990). The fossils from the cave of Pointe Pescade and Beni Saf (Algeria), described by Pomel (1896) as *Hippopotamus icosiensis*, probably belong to the living species of hippo.

The fossil evidence seems to point to two or three Pleistocene North African species of *Hippopotamus*, which appeared one after the other (Figure 4). North African hippo diversity seems to have been low, as was also the case in Europe. European hippos are likely to have come from or through North Africa, either crossing the Gibraltar or the Sicily Straits, or following the route around the eastern end of the Mediterranean.

Concerning the systematics and temporal distribution of European *Hippopotamus*, there are two main opinions, and recently a third has been published (Figure 5). Traditionally, two species or subspecies were recognized: the early Middle Pleistocene *Hippopotamus* antiquus (= *H. major* or *H. amphibius antiquus*), which is large, and *H. amphibius* from the early Middle to Late Pleistocene, which is smaller, but still larger than the living hippos (e.g. Hooijer, 1942; 1950; Kurtén, 1968; Blandamura & Azzaroli, 1977; Caloi et al., 1980). Faure (1984) named the latter *H. incognitus*.



Figure 4: The approximate chronological position of the North African localities with hippos (solid squares indicate presence, open squares indicate uncertainty: cf., aff., sp., ?), compared to the East African record (thick lines). Hippopotamus sp. from Ain Boucherit unit P/Q upper molar (MNHN 195A-13-94); H. gorgops skulls from El Kherba (KH06-G30-149), Ain Hanech (photograph from Arambourg, 1979) and Olduvai (Photographs from Mazza, 1991); H. amphibius (= H. icosiensis) from Pointe Pescade (Pomel, 1896).

The two species were supposed to have been sympatric virtually during the entire Middle Pleistocene (Figure 6) (Faure, 1985; Faure & Guérin, 1992; Guérin, 1996). Kahlke (1997; 2001; 2006) recognized the same taxa, but as subspecies of *H. amphibius*. Generally, it was believed that *H. antiquus* (= *H.* major) was closely related to, or evolved from, *Hippopotamus gorgops* (Coryndon, 1977; 1978; Blandamura & Azzaroli, 1977; Faure, 1985).

The second main opinion is from Mazza (1991; 1995; figure 6), who argued that there were two dispersals from Africa. First, *H. gorgops* dispersed to Europe, giving rise to *H. antiquus*. Subsequently, *Hippopotamus tiberinus* evolved from *H. antiquus*, but also coexisted with that species. Later, *H. amphibius* dispersed from Africa and coexisted with the latest populations of *H. tiberinus*. In this model, *H. incognitus* is just a large *H. amphibius*.

There is confusion on the species names *Hippopotamus major* and *H. antiquus*. For a discussion see Hooijer (1942), Blandamura and Azzaroli (1977), Caloi et al. (1980) and Faure (1985). The informal names "Grand hippopotame fossile" and "Ippopotamo maggiore" used by Cuvier in 1804 and Nesti in 1820, respectively, are not valid in a nomenclatorial sense, while Desmarest named *H. antiquus* in 1822 and Cuvier named *H. major* in 1824. The name given by Desmarest has thus priority and should be used. Both names are based on fossils from the Upper Valdarno, stored in the Muséum National d'Histoire Naturelle (MNHN) in Paris.

Not only the systematics and affinities of the European hippos were controversial, but also the date of their first arrival. Central in the debate is the age of the hippo fossils from Valdarno (Italy). Blandamura and Azzaroli (1977) believed that the fossils originate from the Tasso Faunal Unit and that their age is about 1.5 Ma, while Mazza (1991) believed their age to be 1.5-1.2 Ma. However, no other hippo occurrences were known from Europe that are this old, and Faure (1985) considered that these fossils come from higher up in the local sequence and have an age of close to 1 Ma, corresponding to the early Middle Pleistocene. At present the beginning of the Middle Pleistocene is taken at the beginning of the Brunhes at 0.78 Ma. Currently, the age of the Tasso Faunal Unit is estimated to be 1.8 till about 1.6 Ma (Gliozzi et al., 1997). Since Faure (1985), numerous Early Pleistocene Gaucino (Bellucci et al., 2012; 2014; also referred to as Costa San Giacomo by Gliozzi et al., 1997), dated to older than 2 Ma.

Considering these new data and the fact that, *H. antiquus* from Upper Valdarno has the morphology of the occipital, temporal fossa and orbits more like in *H. amphibius* than in *H. tiberinus* and *H. gorgops*, a third model of the systematics and temporal distribution of the European hippos was proposed (Figure 6) (Van der Made, in press). According to the new proposal, *H. antiquus* dispersed shortly before 2 Ma from Africa to Italy and went extinct shortly after 1.8 Ma, while at or shortly before 1.2 Ma *H. tiberinus* 

dispersed from Africa to Europe and during the late Middle Pleistocene *H. amphibious* did so.

With the currently available information, it seems that during the Pleistocene, both North Africa and Europe were colonized three times by different hippo species. In the case of Africa these are: *Hippopotamus* sp., *H. gorgops/H. sirensis*, and *H. amphibius*. In the case of Europe these are: *H. antiquus*, *H. tiberinus* and *H. amphibius*.



Figure 5: The chronological distribution of the European Pleistocene species of Hippopotamus (particularly the oldest localities) and the approximate age of the hippo localities (solid squares indicate presence, open squares indicate uncertainty: cf., aff., sp.?). Ranges and localities largely after Van der Made et al. (2015); ages of Tor di Quinto, Maglianella, Sant'Oreste very approximate. Dorsal and lateral views of Hippopotamus skulls: H. antiquus from Upper Valdarno (MNHN) and Figline (U Valdarno; IGF 1043, photograph from Mazza, 1991); H. tiberinus from Untermassfeld (IQW 1991/23909 Mei 23438, photographs from Kahlke, 2001) and from Maglianella (CC C601, photograph from Mazza, 1991); H. amphibius from Tor di Quinto (USR).



Figure 6: Three models of the origin, systematics, and temporal distribution of the European Hippopotamidae.

## 4. MATERIAL

Excavations at the site of El Kherba have yielded *Hippopotamus* fossils, including a skull, which is stored at the Musée Public National de Sétif (MPNS), Sétif in Algeria. In addition to the hippo skulls described and figured in the literature, the following specimens were used for comparison in this study:

*Choeropsis liberiensis*: A recent skull from the comparative collections of the Instituut voor Aardwetenschappen (IVAU) of the University of Utrecht, Netherlands.

*"Trilobophorus" afarensis*: Skull AL109/319 at the National Museum of Ethiopia, Addis Ababa, Ethiopia.

*Hippopotamus protamphibius*: Skulls 1933-9-777 and 1933-33-768 from the Omo (Ethiopia) in the Muséum National d'Histoire Naturelle (MNHN), Paris, France.

*Hippopotamus* antiquus: Two skulls from the Upper Valdarno (Italy) on display in the MNHN, and another one on display at the Museo di Storia Naturale in Florence, Italy (formerly Istituto di Geologia, IGF).

*Hippopotamus gorgops*: The holotype skull from Olduvai housed at the Museum für Naturkunde (MNB) in Berlin, Germany.

*Hippopotamus amphibius*: A fossil skull from Tor di Quinto in the Universitá La Sapienza in Rome, Italy (USR) and recent skulls in the Institut Català de Paleoecologia Humana i Evolució Social, (IPHES) Tarragona, Spain, and the Centre National de Recherches Préhistoriques Anthropologiques et Historiques (CNRPAH), Algiers, Algeria.

*Hippopotamus* sp.: Bones and teeth from Ain Boucherit in the MNHN, Paris, France.

## 5. DESCRIPTION AND COMPARISON

The skull from El Kherba is fairly complete, but even while embedded in the sediment it was in a bad state (Figure 7/1). The postero-dorsal part of the skull is preserved and shows several of the features that are of interest here. The orbits are much elevated with respect to the rest of the frontal bone. This is well seen in frontal view (Figure 8). If seen from the side, the orbit is well above the dorsal surface of the skull just before and behind the orbit. This feature is as in *Hippopotamus gorgops* and *H. tiberinus*, while in *H. amphibius* and *H. antiquus* the orbit tends to be lower, though occasionally there are individuals with a somewhat more elevated orbit (Figures 5 & 8). In more primitive or older African hippos the orbits tend to be less elevated (Figure 2).

When seen in side view and if the occlusal surface is taken as horizontal, the line along the dorsal surface of the nasals slopes backwards or is horizontal in *H. gorgops*, *H. tiberinus* and in the skull from El Kherba, while in *H. amphibius* and many older or primitive hippos it slopes anteriorly (Figures 5 & 8). This suggests that in *H. gorgops* and *H. tiberinus* the nostrils are more elevated than in *H. amphibius*. Still in side view, the dorsal profile of the parietals and occipital rises steeply backwards in *H. gorgops*, *H. tiberinus* and in the El Kherba skull (Figures 5 & 8). This profile also tends to be concave up in the El Kherba skull. In *H. amphibius* and many older or more primitive species, this profile is straight or convex up and does not rise as much as in the El Kherba skull.

In *H. amphibius*, the dorsal profiles of the nasals, parietals and occiput form nearly a straight line which passes through the middle of the orbit. In *H. gorgops*, *H. tiberinus* and the skull from El Kherba, the line along the dorsal surface of the nasals passes below the orbit and makes a marked angle with the dorsal profile of the parietals and occiput (Figures 5 & 8).



Figure 7: Hippopotamus gorgops from El Kherba. 1) KH06-G30-149 - skull still in the excavation (photograph by Z. Harichane). 2) KH08-E34-231 - left lower third molar: a) buccal, b) occlusal, and c) lingual views.

The dorsal surface of the nasals and brain case are flexed. In most hippos, including *H. amphibius*, the temporal fossa is long, while in *H. gorgops*, *H. tiberinus* and the skull from El Kherba it is short (Figures 2, 4, 5 & 8). This seems to be related to the forward movement of the occiput.

## 6. DISCUSSION

### 6.1. Taxonomic assignment

With the extremely elevated orbits, the skull from El Kherba differs from the more primitive or older species of hippos, including from the living *Choeropsis* and the fossil *Hippopotamus* prot*amphibius*. The orbits are also more elevated than in *Hippopotamus amphibius*. Other hippos with similarly elevated orbits include *Hippopotamus gorgops*, *Hippopotamus* karumensis and *Hexaprotodon* palaeindicus (Boisserie, 2005, figure 8). The latter is a *Hexaprotodon* Indian species, while *H*. karumensis is reported to have molars with lower crowns than *H. gorgops*. The hippo from El Kherba has high crowned molars (Figure 7b). It seems justified to assign the fossils from El Kherba to *Hippopotamus gorgops*.

Geraads (1980) suggested that *H. gorgops* could be a junior synonym of *H. sirensis*. This suggestion is interesting, but *H. sirensis* from the type locality at Tighenif, described and figured by Pomel (1890; 1896), does not include the relevant skull parts. The excavations by Arambourg have increased the collections from that locality greatly, but we had no access to the Algerian fossils stored in the MNHN, thus we cannot discuss the problem here.

The locality of Ain Hanech is located a very short distance from El Kherba, in the same stratigraphic unit and approximately at the same topographic height, the bedding being more or less horizontal. Therefore the age is the same. Arambourg (1979) mentioned or described and figured hippo fossils from Ain Hanech, including two skulls, which he assigned to *Hippopotamus amphibius*. If correct, this would be one of the oldest records of that species. However, the orbits are very elevated, and the dorsal profile of the nasals slopes backwards (Figure 8). This feature would rather suggest the presence of *H. gorgops*, not only in El Kherba, but also in Ain Hanech.



Figure 8: Morphological features that distinguish Hippopotamus amphibius and Hippopotamus gorgops (shown on the type skull from Olduvai in the MNB) and, as well as the state in skull KH06-G30-149 from El Kherba. The skull of H. amphibius is a recent skull in the IPHES and for H. gorgops the holotype skull from Olduvai in the MNB and NHM M14957 also from Olduvai (photograph from Mazza, 1991) are shown.

### 6.2. Functional morphology

Hippos have an *amphibious* life style, which is reflected in various morphological adaptations. Two of these are relevant here.

Firstly, extant *Hippopotamus*es have eyes which are elevated above the skull. This is a common adaptation of animals that live at or close to

the water surface, like frogs and crocodiles, but also in fishes that live near the bottom, like flounder and sole. The elevated eyes allow the *Hi-ppopotamus* to see above the water, while being largely submerged (Figure 9-1) and sole to see when hidden in the sand at the bottom. In the skull from El Kherba, this adaptation is seen in the orbits which are elevated above the dorsal surface of the skull. In hippos and anthracotheres, elevated orbits are considered to be an adaptation to an *amphibious* life style. The feature of elevated orbits has been used to link Anthracotheriidae to Hippopotamidae (Colbert, 1935), but today this is understood to be due to convergence (Boisserie, 2005). Within Hippopotamidae, this feature evolved in parallel in the south Asian *Hexaprotodon* and in *Hippopotamus*, but if current phylogenetic models are correct, *H. karumensis* and *H. gorgops* also acquired extremely elevated orbits in parallel. The more elevated orbits in *H. gorgops* are generally interpreted as a more extreme aquatic adaptation than in the living species of hippo.

Secondly, living hippos have nostrils and ears that can be closed while diving (Nowak, 1991). The nostrils are on top of the nose and, like the eyes, may be above water while most of the body and head is submerged (Figure 9-1). The position of the nostrils cannot be judged from the shape of the nasals. However, the anteriorly rising nasals in *H. gorgops*, suggest that the nostrils were more elevated than in the living species of *Hippopotamus*. It seems plausible that the greater degree of elevation of the anterior part of the nose in *H. gorgops* is another aquatic adaptation that is more developed than in *H. amphibius*.

Above, it has been observed that the temporal fossa of *H. gorgops* is shorter than in *H. amphibius* and, as a result, there is less distance between the very elevated orbits and occiput. It should be possible to establish whether this resulted from a simple forward displacement of the occiput or from a forward rotation of the brain case. Whatever the cause, the result is that, the temporal fossa is shorter and the posterior most place of attachment of the temporal muscles moved forwards. Hippopotami are known to open their jaws up to 150° in antagonistic display (Nowak, 1991). An extreme opening of the jaws could be facilitated by the change in skull architecture in *H. gorgops*. These morphological differences are clearly visible in the fossils. However, most probably they would not have resulted in a very different aspect in a living individual (see tentative reconstruction in Figure 9-3).



Figure 9: Hippopotamus amphibius in Bioparco, the zoological garden of Rome (1) and in the zoo of Zürich (2). Reconstruction of the appearance of Hippopotamus gorgops by: elevating the eyes, occiput and ears; shortening the distance between occiput and ears and the eyes; and a clockwise rotation of the dorsal surface of the nasals.

# 6.3. The Hippopotamus record from sub-Saharan and North Africa, and from Europe compared

Unlike sub-Saharan Africa, where there was a high diversity of hippos (Figure 2), North Africa (Figure 4) and Europe (Figure 5) may have had just one species of *Hippopotamus* at a time. As observed above, European hippos are likely to have come from or through North Africa, and being *amphibious* either crossed the Straits of Gibraltar or Sicily, or came around the eastern end of the Mediterranean. Thus, it would not be surprising if both areas shared the same species.

*Hippopotamus* antiquus may have arrived in Europe shortly before 2 Ma (Figure 5). It was a large hippo with relatively low orbits and occiput and a short temporal fossa. The European hippo differed from *H. gorgops* and *H. karumensis* in having less elevated orbits and occiput, but the orbits are clearly more elevated than in *H. protamphibius*, and it is much larger than *H. aethiopicus*. Of the sub-Saharan species (Figure 2), the one which is most similar to *H. antiquus* is *H. amphibius* and probably, because of its phylogenetic position, not the well known *H. kaisensis*. *Hippopotamus amphibius* seems to have originated from *H. kaisensis* after the arrival of *H. antiquus* in Italy. The *Hippopotamus* from Ain Boucherit is close in age to the earliest European *H. antiquus*, but its skull shape is not known. It is possible that *H. kaisensis*: 1) dispersed towards North Africa; 2) is the hippo documented in Ichkeul, Ain el Bey and Ain Boucherit; and 3) dispersed to Italy before 2 Ma, where it went extinct shortly after 1.8 Ma (Figure 10). The European *Hippopotamus tiberinus* appeared some time before 1.2 Ma (see discussion on the ages of the localities by Van der Made et al., In Press) and lived there well into the Middle Pleistocene (Figure 5). It is a very large hippo with elevated orbits and occiput, a short temporal fossa and nasals that anteriorly slope upwards. These features are shared with the sub-Saharan *H. gorgops*, which appeared at or shortly after 2 Ma ago and survived till well into the Middle Pleistocene (Figure 4). The North African hippo fossils with ages between roughly 2 and 0.5 Ma include the type material of *H. sirensis* and other specimens which have tentatively been assigned to *H. gorgops*. These two species might be synonymous (Geraads, 1980). In any case, on the basis of the skull from El Kherba, it is possible that *H. gorgops* dispersed shortly after 2 Ma to North Africa and much later, around 1.2 Ma, to Europe (Figure 10).

The latest record of *H. tiberinus* is controversial. Mazza (1991, plate 2, figure 2) assigned a skull fragment from the Rhine gravels at Eich to H. tibe*rinus*. But this skull has a convex up lateral profile of the parietal and occipital, as in *H. amphibius*. The fossils from these deposits are considered to be Eemian in age (early Late Pleistocene or about stage 5) (Von Koenigswald & Heinrich, 1999). Mazza and Bertini (2013, figure 1) indicated the age of the Rhine gravels at Eich as Late Pleistocene, but did not even discuss the hippo fossils from there. Instead, these authors (figure 2) marked the last occurrence of "H. gr. H. antiquus (= H. tiberinus)" as being in Isotope Stage 7 based on materials from the locality of Castel di Guido. Previously, the age of Castel di Guido was considered to be stage 9 by Mazza (1995), who also argued that "a possible attribution to *H. tiberinus* should not be ruled out". Despite this suggestion, these fossils are too poor for a secure attribution. Mazza (1995) also considered H. tiberinus to be present in Mosbach-2 and Jockgrim (500-600 ka, Germany). Pandolfi and Petronio (2015) considered the latest H. tiberinus to be from Maglianella (Italy) and another locality correlated to Stage 15. Stage 15 or 500 ka may well be the age of the latest occurrence of the species.

The first record of *H. amphibius* in Europe is also controversial. Mazza and Bertini (2013, figure 2) indicated the first appearance of *H. amphibius* to be in Stage 5, and in particular in Barrington (UK). This is the type locality of *H. incognitus* and is considered to be Late Pleistocene in age (Ipswichian or about Stage 5; Faure, 1985; Stuart, 1982). However, Pandolfi and Petronio (2015) considered the first record of *H. amphibius* to be in Cava

Nera Molinario and Fontana Ranuccio (both in Italy), correlated to Stage 11 or 13. Caloi et al, (1980) suggested a skull from Tor di Quinto (Italy) might be from Cave Nera Molinario. In this quarry, there are various units of different ages, the youngest being 432-422 ka (Di Stefano & Petronio, 1993). Mazza (1995) considered the age of this skull unknown, and Mazza and Bertini (2013), have not even discussed it. The skull has a dorsal profile as in *H. amphibius* (Figure 5) and may well be the oldest European record of this species, though its age is still problematic. The replacement of *H. tiberinus* by *H. amphibius* may have happened sometime between 500 and 420 ka. In North Africa, the timing of the replacement is more imprecisely known. *H. amphibius* arose much earlier in sub-Saharan Africa and seems to have dispersed during the late Middle Pleistocene to North Africa and subsequently to Europe (Figure 10).

It is peculiar that *H. gorgops*, or at least hippos with a similar morphology, have been replaced more or less simultaneously in Europe, North Africa and sub-Saharan Africa by *H. amphibius*, which remained as the dominant or only hippo (Figure 10). It seems difficult to explain this with climatic or environmental change. Possibly *H. amphibius* evolved a feature, which gave it an edge over *H. gorgops*, possibly it is the robusticity of its limb bones. *H. amphibius* (or *H. incognitus*) tends to have very short limb bones (Faure, 1985). It is not clear when this feature evolved in Africa. As yet, differences in the robusticity of the bones have not been studied relative to this question, and there are only a few localities that have yielded relevant skull materials.

The living *H. amphibius* is smaller than the fossil *H. amphibius* from Europe, but it is not known when the size decrease occurred in Africa. The European hippos might be recognized as a different subspecies as *H. a. incognitus*. However, it is possible that the North African *H. icosiensis* is identical to *H. a. incognitus*, and thus a senior synonym.

The last European *Hippopotamus* may have been from level G at Grotta Romanelli (Italy) and level C2 at Canale delle Acque Alte (Italy), corresponding to Isotope Stage 4 or even Stage 3 (Pandolfi & Petronio, 2015). Early Holocene (11-8 ka) hippo fossils are known from the southern half of what is today the Sahara, and even from the Nile delta (Drake et al., 2011). Rock art suggests even a presence in these areas after 4000 BP (Le Quellec, 1999). At present, the geographical distribution of *H. amphibius* is restricted to sub-Saharan Africa.



Figure 10: The chronological distribution of the Pleistocene species of Hippopotamus and the approximate age of the hippo localities (solid squares indicate presence, open squares indicate uncertainty: cf., aff., sp.?) in sub-Sharan Africa, North Africa, the Levantine Corridor and Europe. Arrows indicate possible dispersal events.

### 6.4. Hippos and human dispersal

That the dispersal of *Hippopotamus* into Europe is related to human dispersal has been suggested by various authors. An elaborate description is provided by Martínez Navarro (2010). He proposed that, humans, *H. an-tiquus* and other species including *Theropithecus*, dispersed into Europe at the Plio-Pleistocene transition (at about 1.8 Ma) which he argued was favoured by the northward expansion of African mixed habitats savannas and gallery forest. He also proposed that hippos could have been easily

hunted from the shores by throwing stones on them. However, there are some flaws in this model. First of all, hippos are not defenceless animals that can be easily killed. Hippos are among the most dangerous animals in Africa, killing hundreds of humans each year (Treves & Naughton-Treves, 1999; Le Bel et al., 2011; Chomba et al., 2012). Actually, the estimated number of humans killed annually by hippo vary from 300<sup>1</sup>, up to nearly 3000<sup>2</sup>. A hippo is reported to have killed 13 persons in a single attack<sup>3</sup>. Thus, it does not seem likely that hippos, with a possible body weight of some four tonnes, were easy to kill by throwing stones from the bank of a river. Another flaw is that all of these species did not disperse to Europe at the same time. At the time Martínez Navarro (2010) wrote this, some vertebras from Pirro Nord (Italy) were identified as *Theropithecus* (Rook et al., 2004; Rook & Martínez-Navarro, 2013), but now these fossils are recognized to belong to a porcupine (Alba et al., 2014). As a result the fossils from Cueva Victoria (Spain) remain the only known European *Theropithecus* (Gibert et al., 1995; Ferràndez-Cañadell et al., 2014). This locality is believed to be a little older than 0.78 Ma (Gibert & Scott, 2014). Human dispersal into Western Europe is much older than 0.78 Ma, though far less than 1.8 Ma. Given the current evidence, the dispersal of *H. tiberinus* into Europe is probably a little older than that of *Homo*, but the appearance of *H. antiquus* in Europe is certainly much earlier. The dispersals of all of these species and humans did not occur in a single, but in many events widely separated in time. Finally, there is no evidence for the expansion of African habitats to Europe.

The dispersal of *H. tiberinus* to Europe shortly before 1.2 Ma seems to be close in age to the arrival of the first humans there, but no likely causal link has been identified. *H. tiberinus* may have arrived a little earlier and its dispersal may have been favoured by different environmental conditions. Instead, the dispersal of hippos across the Sahara towards North Africa could prove to be related to periods of increased humidify, i.e. when lakes and rivers were much larger. Though human and hippo environmental requirements and ecology are fundamentally different, increased humidity may have also favoured the dispersal of humans across the Sahara.

<sup>1</sup> http://www.animaldanger.com/most-dangerous-animals.php

<sup>2</sup> https://www.youtube.com/watch?v=cvoEj1\_yOrU

<sup>3</sup> http://www.abc.net.au/news/2014-11-20/hippopotamus-attack-kills-13-in-boat-in-niger/5904646

The distribution of the two living species of hippo, and especially the common hippo, seems to depend on the vicinity of a permanent water body. While the pygmy hippo *Choeropsis liberiensis* lives in forested environments and eats a variety of food, including fruit, the common hippo *H. amphibius* is a grazer that lives in open habitats close to a lake or river. It spends the day in or near the water and submerges in water to regulate its body temperature, and during the night it forages at a distance of up to some 3 km from the water (Nowak, 1991). This implies that it needs a permanent body of water with a minimum depth of about 1.5 metre for survival. Judging from skull morphology, all of the species of the genera *Hippopotamus* and *Hexaprotodon* seem to be more adapted to an *amphibious* life style than *Choeropsis*, and probably all had similar environmental requirements as the common living hippo. In order to reach North Africa and Europe, hippos needed rivers or lakes to cross the Sahara and to disperse along the north coast.

There are indications that large rivers were flowing across the Sahara during the Eemian and the Early Holocene (Drake et al., 2011; Coulthard et al., 2013; Skonieczny et al., 2015). There may have been rearrangements of watersheds by river capture, allowing aquatic and *amphibious* fauna to enter extensive new river basins. In addition, there are Holocene fossils and rock art depicting hippos in several parts of the Sahara, dating from before and after 4 ka (Le Quellec, 1999). Large rivers and lakes and northward expansion of hippos may have occurred during some of the earlier interglacials, but maybe not during all of them. The extension of lakes has been studied in a long sedimentary sequence in the Rift Valley (Trauth et al., 2005), where extensive lakes occurred close to 2.5 Ma, and between about 1.9 and 1.7 Ma. The occurrence of extensive lakes in the Rift is believed to be related to global climatic events, such as the increasing importance of the 40 ka Milankovich cycle around 2.5 Ma and the development of the Walker Circulation from about 1.9 to 1.7 Ma. If global climate affected the extension of lakes in East Africa, it may have also been the case in North Africa. Extensive lakes and associated rivers are the preferred habitats of hippos and may have allowed *H. kaisensis* (around 2.5 Ma?) and later H. gorgops (around 1.9 Ma?) to cross the Sahara. Based on the above we could infer that hippos may have lived in the area of the present day Sahara during parts of at least some of the climatic cycles and may have spread in this way to the North. The subsequent dispersal of hippos from North Africa to Europe depended probably on quite different conditions, though we do not know exactly which conditions these were.

Human north ward expansion, as well as other faunal exchange across the Sahara, may have been permitted by the more humid climate and extensive lakes and rivers, which allowed hippos to disperse northward. Based on current evidence it seems unlikely for early humans to have crossed the Straits of Gibraltar or Sicily (Villa, 2001; Van der Made, 2005b). In addition, the human fossils or indications of human presence in South-West and Southern Asia are older than in Europe (e.g. Dennell et al., 1988; Bar-Yosef & Goren-Inbar, 1993; Gabunia & Vekua, 1995; Larick et al., 2001; Dennell & Roebroeks, 2005) (Gibert et al., 1999; Carbonell et al., 2008; Toro-Moyano et al., 2013). Therefore, it seems more likely that humans dispersed out of Africa through the Middle East (e.g. Sirakov et al., 2010; Van der Made, 2011; 2013; Bar-Yosef & Bellmaker, 2011). Primitive features of the humans in Dmanisi and Flores (Martinón-Torres et al., 2007; Lordkipanidze et al., 2007; Argue et al., 2009; Jungers et al., 2009) suggest the possibility of a dispersal from sub-Saharan Africa into Eurasia anterior to that of Homo erectus, which means one dispersal before and one around 1.8 Ma. It is of interest to note here that, human remains from Rabat and Tighennif, for which the name Homo mauritanicus is available, seem to be more primitive than H. erectus (Martinón-Torres et al., 2007). The human crossing of the Sahara might correspond to two north ward dispersal events. The first one before 1.8 and possibly around 2.5 Ma, when the hippo species present in Ain Boucherit reached the Maghreb and gave rise to *H. antiquus* of Europe. At the same time a primitive species of *Homo* dispersed to the Maghreb, giving rise to *H. mauritanicus*, and to the south of Asia, giving rise to the species present in Dmanisi and Flores. The second event around 1.8 Ma, when *H. gorgops* reached North Africa and *H. erectus* dispersed into southern Asia.

## 7. CONCLUSIONS

The following conclusions are drawn:

*H. gorgops* is present in El Kherba. It dispersed around 1.9 Ma into North Africa when lakes and rivers were more extensive. This may have coincided with the dispersal of *H. erectus* out of Africa.

- 2) *H. gorgops* gave rise to, or is identical with, the European *H. tiberinus* around 1.2-1.4 Ma.
- 3) Before 2 Ma, possibly around 2.5 Ma, a species of hippo, perhaps *H. kaisensis*, dispersed to North Africa.
- 4) The species *H. antiquus* may have originated from *H. kaisensis* or a similar form in North Africa when it dispersed to Italy shortly before 2 Ma.
- 5) *H. amphibius* dispersed during the Middle Pleistocene to North Africa and subsequently to Europe.
- 6) The dispersals of *Hippopotamus* to North Africa may have been possible due to the presence of extensive lakes and rivers in the area which presently is the Sahara. The same environmental conditions may have allowed human North-ward dispersal.

The following questions remain open:

- It is possible that *Hippopotamus sirensis*, *H. gorgops*, *H. georgicus* and *H. tiberinus* are synonyms.
- It is also possible that *H. antiquus* and *H. kaisensis* are synonyms.
- To document the evolution (and timing) of shorter limb bones in African *H. amphibius*.
- It is possible that *H. amphibius incognitus* and *H. icosiensis* may be synonyms for the early stage (large) of *H. amphibius*.
- To document the decrease in size (and timing) leading to the living *H. amphibius amphibius* in Africa.

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Photo Credit - Cover Rock art painting from «Ti-n-Aressou » rock shelter in Tassili-n-Ajjer (Algeria). Photo by Malika Hachid

KNM-ER 1813 skull. Photo from cast by CENIEH

Trihedron from the Acheulean hominin site of Tighennif (ex. Ternifine, Algeria). Photo by Jordi Mestre

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## Chapter 05

# Hippopotamus gorgops from El Kherba (Algeria) and the context of its biogeography



**Figure 1** Excavation at El Kherba (photograph J. Mestre).





H. georgicus / tiberinus

15 Libakos / Aliakhmon Q-Profil / Kapetianos

27 Venta Micena / Barranco León / Fuente Nueva 3

14 Akhalkalaki

16 Maglianella

17 Sant'Oreste

18 Colle Curti

20 Mosbach

22 Jockgrim

26 Atapuerca

24 Sainzelles

25 St. Privat

21 Mauer

19 Untermassfeld

### Hexaprotodon?

### 1 Bône

### H. antiquus / kaisensis

- 2 Lac Ichkeul
- 3 Ain el Bey
- 4 Ain Boucherit
- 5 Coste S Giacomo
- 6 Upper Valdarno

### H. gorgops / sirensis

- 7 Ain Hanech / El Kherba
- 8 Manssoura
- 9 Tighenif
- 10 Thomas Quary / Ain Maarouf

#### 11 Ubeidiyah

- 12 G. Benot Yaakov
- 13 Evron

### Figure 3

The geographic position of the hippopotamus localities mentioned in the text.

#### H. amphibius / icosiensis

26 Tihodaine 27 G. des Phacochères 28 Pointe Pescade 29 Ain Maarouf 30 Beni Saf

#### H. amphibius / incognitus

31 Latamne32 Tor di Quinto33 Castel di Guido34 Fontana Ranuccio35 Eich36 Barrington



The approximate chronological position of the North African localities with hippos (solid quares indicates presence, open squares indicate incertainty: cf., aff., sp., ?), compared to the East African record (thick lines). *Hippopotamus* sp. from Ain Boucherit unit P/Q upper molar (MNHN 195 $\Box$ -13-94); *H. gorgops* skulls from El Kherba (KH06-G30-149), Ain Hanech (photograph from Arambourg, 1979) and Olduvai (Photographs from Mazza, 1991); *H. amphibius* (= *H. icosiensis*) from Pointe Pescade (from Pomel, 1896).



The chronological distribution of the European Pleistocene species of *Hippopotamus* (particularly the oldest localities) and the approximate age of the hippo localities (solid squares indicates presence, open squares indicate uncertainty: cf., aff., sp., ?). Ranges and localities largely after Van der Made et al. (2015); ages of Tor di Quinto, Maglianella, Sant'Oreste very approximate. Dorsal and lateral views of *Hippopotamus* skulls: *H. antiquus* from Upper Valdarno (MNHN) and Figline (U Valdarno; IGF 1043, photograph from Mazza, 1991); *H. tiberinus* from Untermassfeld (IQW 1991/23909 Mei 23438, photographs from Kahlke, 2001) and from Maglianella (CC C601, photograph from Mazza, 1991); *H. amphibius* from Tor di Quinto (USR).







**Figure 7** *Hippopotamus gorgops* from El Kherba. 1) KH06-G30-149 - skull still in the excavation (photograph by Z. Harichane). 2) KH08-E34-231 - left lower third molar: a) buccal, b) occlusal, and c) lingual views.



Morphological features that distinguish *Hippopotamus amphibius* and *Hippopotamus gorgops* (shown on on the type skull from Olduvai in the MNB) and, as well as the state in skull KH06-G30-149 from El Kherba. The skull of *H. amphibius* is a recent skull in the IPHES and for *H. gorgops* the holotype skull from Olduvai in the MNB and NHM M14957 also from Olduvai (photograph from Mazza, 1991) are shown.



*Hippopotamus amphibius* in Bioparco, the zoological garden of Rome (1) and in the zoo of Zürich (2). Reconstruction of the appearance of *Hippopotamus gorgops* by: elevating the eyes, occiput and ears; shortening the distance between occiput and ears and the eyes; and a clockwise rotation of the dorsal surface of the nasals.



The chronological distribution of the Pleistocene species of *Hippopotamus* and the approximate age of the hippo localities (solid quares indicates presence, open squares indicate incertainty: cf., aff., sp., ?) in Subsharan Africa, North Africa, the Levantine Corridor and Europe. Arrows indicate possible dispersal events.