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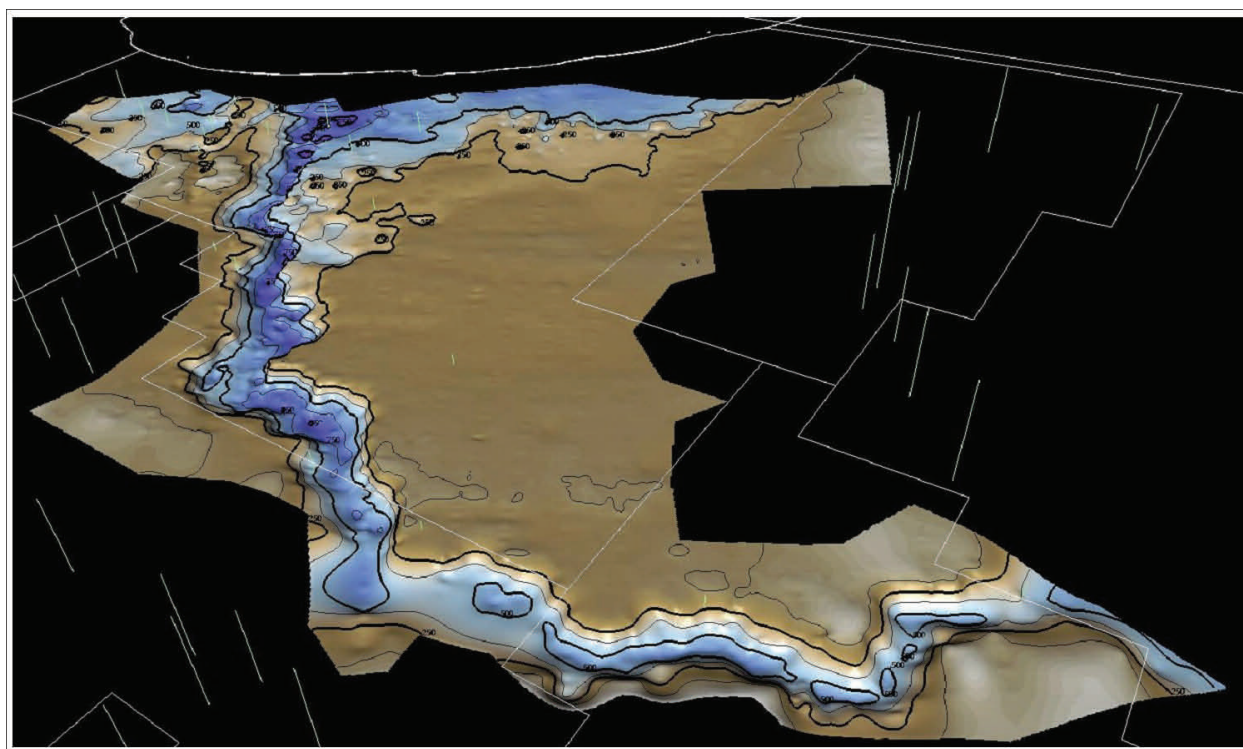


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Circum-Mediterranean Geology and Biotic Evolution During the Neogene Period: The Perspective from Libya

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University of Garyounis
Benghazi, G.S.P.L.A.J

Rediscovered Hippopotamid Remains from As Sahabi

PARIS PAVLAKIS

ABSTRACT

The anterior mandibular morphology of *Hexaprotodon sahabiensis* is evinced for the first time by previously undescribed mandibular fragments collected at As Sahabi by Petrocchi in the late 1930's, and housed since then in the National Museum of Libya, Tripoli. The sagittal cross-section of the mandibular symphysis shows a unique configuration for Neogene African Hippopotamidae species. The new *Hex. sahabiensis* morphological data permit a preliminary comparison with both *Saotherium* and *Archaeopotamus* (Boisserie, 2005). *Hex. sahabiensis* compares in overall mandibular shape with *Archaeopotamus*.

Paris Pavlakis, Department of Historical Geology – Paleontology, Faculty of Geology and Geoenvironment, University of Athens, Panepistimioupoli Zografou, 157 84 Athens, Greece, pavlakis@geol.uoa.gr

INTRODUCTION

Before the onset of palaeontological research in As Sahabi by the International Sahabi Research Project (I.S.R.P.) in 1974, and by the East Libya Neogene Research Project in 2004, fossil hippopotamid material collected from As Sahabi had been last reported in 1952 (Petrocchi, 1952:24, 26-27). Petrocchi reported four hippopotamid specimens (#13-16). They had been discovered during his 4th field campaign (Jan-March, 1939), in the area N-NW of the Qasr As Sahabi, at the “12th km pole of the road Sahabi-Ajdabya”. Their localities were noted on his map titled “Rilievo Topographico della Zona Fossilifera di Sahabi” (Petrocchi, 1952: Tav I). He gives no description or figure, however, other than the following information:

- a cranium in very bad state of preservation [#13], with only part of the maxilla being salvageable. It was found in Locality 55.
- a mandible, [#14] collected near #13, embedded in the sand. It had six incisors, and preserved the horizontal and the vertical rami. The molars were very worn and fragmented (Locality 56).
- 3 km north of the “campo di aviazione”, a complete skull was found immersed in the sand [#15]. The occipital, parietal and maxillary parts were in excellent condition, while the nasal was missing. The incisors were also missing, but the six alveoli revealed its hexaprotodonty. It was found in Locality 57. Finally,
- in the Locality 58, a badly damaged mandible was reported [#16].

These specimens were assigned by Petrocchi to *Hexaprotodon* based on the alveoli of the six incisors of the skull #15. The same referral was made by Coryndon (1978). The actual specimens, however, were considered lost.

The next hippopotamid sample from As Sahabi was discovered by I.S.R.P., during the field seasons 1977 to 1981. The recovered fossil hippopotamid sample consists of about 160 specimens. Of those, about 40% were craniodental material and they were described by Gaziry (1987). Gaziry (1987) erected a new hippopotamid species: *Hexaprotodon sahabiensis*. Hexaprotodonty was based on Petrocchi's reported observation, most probably that of the mandible (#14) and skull (#15), as well as on the three incisor alveoli on the right premaxilla 172P11A discovered by I.S.R.P. (Gaziry, 1987: Fig. 3, p. 306).

Here, I describe three previously undescribed hippopotamid specimens from As Sahabi (as labeled) located during a visit of Noel Boaz to the National Museum in Tripoli in 2004 and studied by me in October 2007. The most complete of the three specimens is a fairly complete anterior part of a mandible. Most probably it is the specimen #14 of Petrocchi's 1952 report of his 1939 palaeontological field season.

HIPPOPOTAMID MATERIAL

As Sahabi #4 (provisional Libya National Museum ID) anterior mandibular fragment with LI/1, LI/2, RI/2, RI/3, R/C

As Sahabi #1 Left mandibular fragment with LM/1, LM/2

As Sahabi #2 Right posterior mandibular body with M/3 germ.

Figure 1. *Hex. sahabiensis* anterior mandible with R/C, R/I₃, R/I₂, LI₁, LI₂, dorsal view. Scale unit 5 cm



DESCRIPTIONS

As *Sahabi* #4 is an anterior mandibular fragment (Figure 1) with complete symphyseal region. The right horizontal ramus is preserved up to the level mesially to M/3 alveolus, while the left ramus is missing posteriorly to about the M/1. The right anterior portion of the mandible is complete, with R/C, RI/3 and RI/2 intact. RI/1 is broken and the alveolar portion of the tooth was revealed after we removed glue and plastering material that blocked the incisor's alveolar opening (Figure 2a). The left anterior mandibular side is more damaged than the right. Only the LI/1 and LI/2, attached to it, are surviving. LI/3 and the L/C are broken (Figure 2b, 4b). The procumbent incisors

lay at the same general level of the dorsal symphyseal plane (inclined antero-dorsally). The incisors relative position is also roughly linear. The I/2s in both sides are attached to the 1st incisors (the RI/1 is documented by the tooth fragment revealed into the alveolus, Figure 2a). I/3's are about 6 cm high, while the I/2's about 3 cm. The incisors present close to horizontal occlusal wear facets (tilted lingually at an angle of about 45° to their long axis). The I/2s are considerably smaller than both I/1 and I/3s (Figure 2b). The I/1 is wider (horizontal diameter) than long (vertical diameter), while the opposite is true for I/3, which otherwise has similar size (Figure 2a). There is almost no inter-I/1 diastema. If we apply the same character states used by Boisserie (2005), in his recent

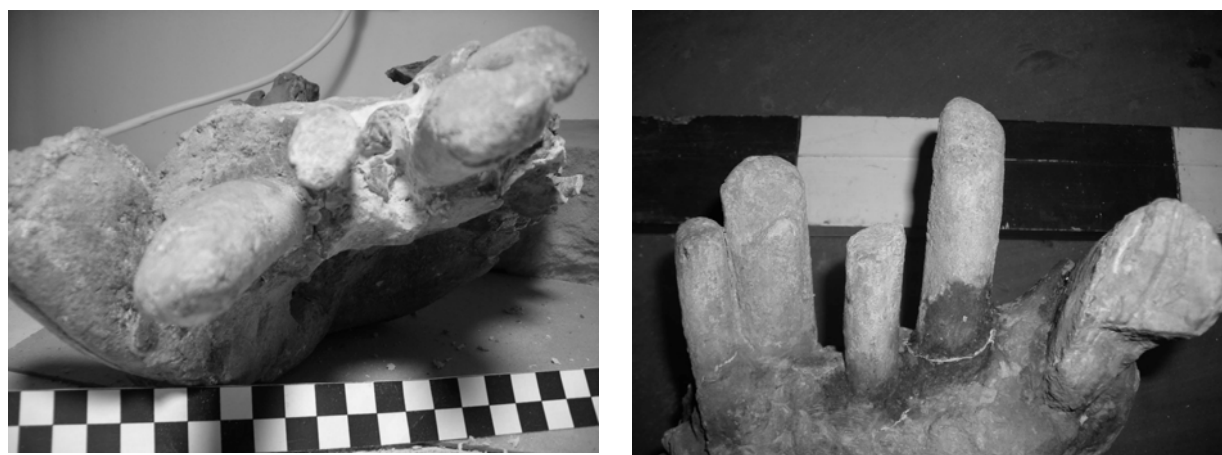


Figure 2. (a) Anterior view, and (b) dorsal close up view (b) of *Hex. sahabiensis* anterior dentition. R/I1 is broken, showing only the alveolar part, R/I2, R/I3, R/C, LI/1, LI2. Scale unit 1 cm.

comprehensive cladistic analysis of the family Hippopotamidae, *Sahabi #4* exhibits the character state 23(0): I/1-I/1 diastema shorter than the mesiodistal diameter of the I/1 (Boisserie 2005:26).

The canine is broken, preserving approximately 10 cm of its height. The lower part of the concave vertical wear facet with the upper canine is preserved. The mesial surface of the canine is flat, while the distal is quite rounded. No enamel morphology can be observed. The anterior border of the canine alveolus is located slightly posteriorly to the level of incisor alveoli. The canine process is poorly developed and does not diverge much laterally to the P-M tooth row.

Teeth length-width dimensions are reported in Table 1. Postcanine teeth do not survive.

The anterior mandibular fragment preserves the complete symphyseal area. The shape of the symphysis sagittal cross section is drawn in Figure 3. It is inclined upwards from the general level of both

horizontal rami at about 45° , [Character state 18(1) in Boisserie's (2005) analysis].

The anterior symphysis length is 127 mm and it is almost flat (Figure 1). The inferior configuration of the symphysis cross section presents an abrupt angle at the posterior part of the cross section, (approximately $72 \times 42 \text{ mm}^2$ anterior or frontal surface area, versus $55 \times 64 \text{ mm}^2$ posterior or ventral surface area (Figure 4a,

Table 1. Dimensions of anterior teeth in mm, of Sahabi #4 *Hex. sahabiensis* from As Sahabi.

	L	W
Sahabi # 4 LI/1	22.28	27.54
Sahabi # 4 LI/2	20.14	16.40
Sahabi # 4 RI/2	21.68	16.12
Sahabi # 4 RI/3	25.02	22.92
Sahabi # 4 R/C	60.48	34.20

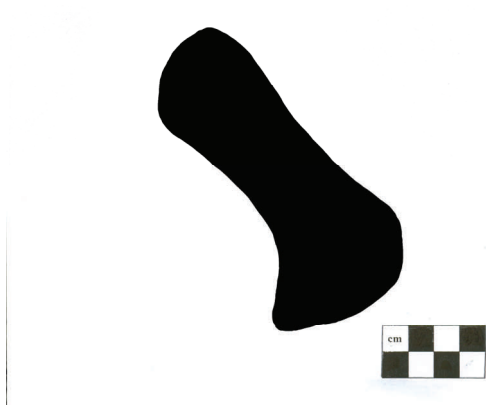


Figure 3. Schematic *Hex. sahabiensis* symphysis sagittal cross-section. Scale unit 1 cm.

4b). The incisor alveolar process is continuous between the two canines, and forms an overhang relative to the frontal face of the symphysis of about 48 mm thickness. The measured mandibular dimensions follow Pavlakis (1990) and the dentition dimensions follow Gaziry (1987). The measurements on the mandibular fragment that can be taken are:

Length of the mandibular symphysis = 127.00 mm

Minimum thickness of canine apophysis = 58.48 mm

Minimum thickness of mandibular body just mesial to right P/3 alveolus = 63.00 mm

Minimum width of the canine alveoli = 112.08 mm

Minimum width of the mandible taken at the buccal sides of both horizontal rami at the level of P/2s = 183.00 mm

Height of the right horizontal ramus taken vertically at the level mesially to right P/2 alveolus = 82.50 mm

Height of the right horizontal ramus taken vertically at the level mesially to right M/2 alveolus = 105.58 mm



Figure 4. *Hex. sahabiensis* anterior mandible, (a) right lateral view, (b) ventral view. Scale unit 5 cm.

Sahabi #1 is a left mandibular fragment with LM/1 and LM/2 (Figure 5a). M/1 shows considerable wear, while M/2 has moderate wear. It compares with *Hip. amphibious* age group XIV of Laws (1968). The left horizontal mandibular ramus preserves in length only the area from the of 4th premolar to the 3rd molar. This mandibular piece of the horizontal ramus is complete only for approximately



Figure 5. *Hex. sahabiensis* mandibular fragments #1 (a, buccal, b, occlusal view) and #2 (c, lingual view). Scale unit 5 cm.

the length of M/1. The height of the horizontal ramus, taken vertically to the occlusal surface at the level mesially to

Table 2. Dimensions of molar teeth (mm) of As Sahabi # 1 *Hex. sahabiensis*

	L	W _{ant}	W _{post}
Sahabi #1 LM/1	36.42	25.78	26.38
Sahabi #1 LM/ 2	22.92	11.48	18.02

M/2, measures 111.32 mm.

The molar measurements are shown in Table 2.

M/1 is worn almost to the bottom of the transverse valley. It is more worn on the buccal side. The protoconid and the metaconid are united. The hypoconid and entoconid show less wear exhibiting the typical hippotamid Ω enamel configuration (Figure 5b). The cingulum extends unevenly all around the occlusal surface, more mesially and distally. Interstitial wear is present. The M/2 occlusal surface presents the 4 cusps worn down to about half their height, as well as the transverse valley and the cingulum.

Sahabi #2 is a right posterior mandibular body fragment with an M/3 germ just raising from its alveolus (Figure 5c). The mandibular fragment extends in length at the buccal side, mesially from the small mental foramen to distally about half the ascending ramus. M/2 is missing, and the M/3 germ is in situ. The gonial angle area is missing, preserving only its origins.

The only mandibular body measurement that can be estimated is the height of the right horizontal ramus. Taken

vertically at the level mesial to the right M/2 alveolus, it measures 83.54 mm (comparing to 105.58 mm of *Sahabi #1*). No measurements can be taken on the molar germ. It exhibits the typical hippopotamid 3rd molar five-cuspid configuration.

DISCUSSION

As *Sahabi #4* anterior mandibular fragment provides the opportunity to document for the first time the general shape of the *Hexaprotodon sahabiensis* mandible. Specifically it demonstrates: 1) *Hex. sahabiensis* adult anterior dentition, 2) the degree of expansion of the mandibular canine processes, and 3) the relative length and sagittal cross-sectional configuration of its mandibular symphysis. These morphological characters are crucial, since they enable the *Hex. sahabiensis* sample to be included in studies to update the taxonomy of the Family Hippopotamidae.

Boisserie (2005), in a recent comprehensive cladistic analysis, attempts a revision within the Hippopotamidae of the last 8 ma of African and Asian species. In his proposed new phylogeny, *Hexaprotodon* is considered paraphyletic. He maintains this genus for the Asian mostly species and splits the rest of African *Hexaprotodon* species into two new genera, *Saotherium* (from Chad) and *Archaeopotamus* (mostly from Lothagam, including *Hex. harvardi* and *Hex. aff. sahabiensis* from Abu Dhabi). He reinstates *Choeropsis* for the extant pygmy hippo, and relates it to the *Saotherium* clade (Boisserie, 2005: Fig. 10, p. 14). He establishes new mandibular morphological criteria to support these clades. These include the

expansion of the canine processes, the relative length of the symphysis, the shape of the symphysis cross-section, and the length of the premolar row relative to molar row. *Hex. sahabiensis* was not included in this cladistic analysis because of the inadequate sample known from As Sahabi until 2003.

However premature it may be to accept this new phylogeny within the Hippopotamidae, nevertheless, it is so far the most recent and comprehensive attempt to establish new apomorphies in hippotamid phylogeny. The new mandibular *Hex. sahabiensis* data reported in this study provide the opportunity to make preliminary comparisons on the basis of this new phylogenetic hypothesis. For this reason, the new species nomenclature used in this phylogeny is followed.

The new material studied here verifies that *Hex. sahabiensis* is a hexaprotodont hippopotamid. Of the six lower incisors, both 2nd incisors are much smaller than the subequal 1st and 3rd lower incisors. The 1st is the largest, and presents a flatter cross-section than the more cylindrical 3rd. The 2nd lower incisors are almost attached to the 1st. All six incisors are aligned, with the 2nd being located slightly posteriorly and dorsally to the larger 1st.

The shape of the *Hex. sahabiensis* symphyseal sagittal cross-section, compared with the mandibular anatomy within the Hippopotamidae (Boisserie, 2005, Fig. 9, p. 13), presents a unique configuration among African Neogene hippopotamids. Specifically, unique morphological characteristics include: the quite thick anterior part of the symphyseal cross-section, and the acute angle the crest makes on the lower symphyseal surface,

between the frontal and ventral faces (character 19 in Boisserie's cladistic analysis).

The anterodorsal (upwards) orientation of the symphyseal plane and the linear position of the incisors characterise the new genus *Saotherium* (Boisserie, 2005). *Hex. sahabiensis* shares these characters with this new genus, and compares more closely to *Saotherium mingoz* (Boisserie *et al.*, 2003, Fig. 3, p. 18). This hippopotamid is of Early Pliocene age (from ca. 5 ma old strata of Kollé), and appears smaller than *Hex. sahabiensis* from As Sahabi and Abu Dhabi (Boisserie *et al.*, 2003). The hippopotamid material from the older Toros-Menalla fossiliferous area in Chad is still under study. Since, however, the anthracothere dental anatomy suggests a continuous Late Miocene Chado-Libyan bioprovince (Lihoreau *et al.*, 2006, also Pavlakis and Boaz, this volume), the hippopotamids from As Sahabi and Toros-Manella can be expected to be similar. It is not the purpose of this study, and we do not have yet the adequate hippopotamid sample from As Sahabi, to delineate true morphological relations between *Hex. sahabiensis* and *S. mingoz*.

On the other hand, the general shape of the mandible, in particular the small expansion of the canine process and the long symphysis, compares with *Archaeopotamus*, and more precisely with *Archaeopotamus* aff. *lothagamensis* (Boisserie, 2005, Fig 9, p. 13) and *A. lothagamensis* (Weston, 2000). We do not yet have, however, a mandibular specimen of *Hex. sahabiensis* to accurately estimate the P_{2-4} length relative to the molar row. This is necessary in order to clarify the relation of *Hex. sahabiensis* to *Saotherium*

or to *Archaeopotamus*. Based on the size of isolated premolars, *Hex. sahabiensis* seems to have a quite high P/M tooth row index and is, thus, closer to *Archaeopotamus* in that character than to *Saotherium*. This similarity is in addition to the similarity in overall shape of the anterior mandible (i.e., long symphysis and poorly developed canine processes). In fact there seems to be a size gradient from *A. lothagamensis* to *A. harvardi*, with *Hex. sahabiensis* being closer in size to *A. lothagamensis*. The same seems to be true with the lateral expansion of the anterior mandible. *Hex. sahabiensis* canines are close to the postcanine dental arcade line, like in *A. lothagamensis*, while the mandible of *A. harvardi* is the widest anteriorly, in addition to being the largest of the three species. This morphological size gradient poses the need of examining it under the light of the new *Hex. sahabiensis* sample, in order to reevaluate the relations between *A. lothagamensis* and *Hex. sahabiensis*. A crucial question is the validity of these two species names, and specifically whether the species name *sahabiensis* includes *lothagamensis* due to nomen priority.

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