

A new species of hippopotamine (Cetartiodactyla, Hippopotamidae) from the late Miocene Baynunah Formation, Abu Dhabi, United Arab Emirates

JEAN-RENAUD BOISSERIE^{a,b*}, MATHIEU SCHUSTER^c, MARK J. BEECH^d, ANDREW HILL[†] & FAYSAL BIBI^e

a Centre Français des Études Éthiopiennes, USR 3137 CNRS, Ambassade de France en Éthiopie, P.O. BOX 5554 Addis Abeba, Éthiopie

b Institut de paléoprimatologie, Paléontologie Humaine : Évolution et Paléoenvironnements, UMR 7262 CNRS, Université de Poitiers, 6 rue Michel Brunet 86000 Poitiers, France

c Institut de Physique du Globe de Strasbourg, UMR 7516 CNRS, École et Observatoire des Sciences de la Terre (EOST), Université de Strasbourg, 1 rue Blessig, 67084 Strasbourg, France

d Coastal Heritage and Palaeontology Section, Historic Environment Department, Abu Dhabi Tourism and Culture Authority (TCA Abu Dhabi), 12th Floor – Tower B – Nation Towers Corniche, P.O. Box 94000, Abu Dhabi, United Arab Emirates

e Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43, 10115 Berlin, Germany

* Corresponding author: jean.renaud.boisserie@univ-poitiers.fr

Abstract: The discovery of new hippopotamid material from the late Miocene Baynunah Formation (Abu Dhabi, United Arab Emirates) has prompted the revision of the existing material of this as yet unnamed fossil taxon. The Baynunah hippopotamid appears to be distinct from all other contemporary and later species in having a relatively more elongate symphysis, a feature similar to the earlier (and more primitive) *Kenyapotamus*. Yet, the Baynunah hippopotamid presents a dentition typical of the Hippopotaminae. It is therefore a distinct species attributed to the later subfamily, described and named in this contribution. This species provides further evidence for a ca. 8 Ma evolutionary event (termed “Hippopotamine Event”) that initiated the spread and ecological significance of the Hippopotaminae into wet habitats across Africa and Eurasia. The morphological affinities of the new species from Abu Dhabi suggest that the Arabian Peninsula was not a dispersal route from Africa toward southern Asia for the Hippopotamidae at ca. 7.5 Ma to 6.5 Ma.

Keywords: Hippopotamidae, Hippopotamine event, systematics, Arab Peninsula

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INTRODUCTION

The evolutionary history of the Hippopotamidae was marked around 8 Ma by the abrupt appearance in the fossil record of large hippopotamine forms with relatively high and simple molars. This Hippopotamine Event (Boisserie *et al.*, 2011) marks the shift of hippopotamids from large herbivores rare in fossil faunas to megaherbivores very abundant in wet habitats. The Hippopotamine Event was also characterized by a dramatic increase in specific diversity, from a single non-hippopotamine species known across eastern and northern Africa during the early late Miocene (*Kenyapotamus coryndonae* Pickford, 1983) to almost a dozen hippopotamine forms by the end of the Miocene (Boisserie *et al.*, 2011). The documentation and detailed understanding of the Hippopotamine Event therefore bears a great interest for understanding diversification dynamics of large herbivores during the late Miocene, a time when the core elements of modern biomes were being formed.

Some of the earliest hippopotamines that mark the Hippopotamine Event are poorly known. This is the case of the material from the Baynunah Formation, Abu Dhabi, United Arab Emirates (Whybrow & Hill, 1999), which was initially described as *Hexaprotodon* aff. *sahabiensis* by Gentry (1999) and later revised to *Archaeopotamus* aff. *lothagamensis* by Boisserie (2005). Outstanding questions remain, however, regarding this extinct Arabian hippopotamine’s taxonomic status, biogeographic affinities, and its implications for the

age of the biochronologically-dated Baynunah fauna (Bibi *et al.*, 2013). The discovery of new specimens in fieldwork conducted since 2003 has prompted the revision of all fossil material belonging to this hippopotamid and the clarification of its taxonomic status. This contribution describes in detail the mandibular and dental morphology of this material, and attributes it to a new species of the genus *Archaeopotamus*.

GEOLOGICAL CONTEXT

The Baynunah Formation, exposed as discontinuous patches distributed across the Al Gharbia region west of Abu Dhabi city (Fig. 1), has produced the only known upper Miocene terrestrial fossil-bearing deposits (vertebrates, invertebrates and plants) from the Arabian Peninsula. These fossils indicate a biochronological age of sometime between 8 Ma and 6 Ma (Bibi *et al.*, 2006; Whybrow & Hill, 1999), possibly 7.5 Ma–6.5 Ma (Bibi *et al.*, 2013). Both the geology and paleontology of the Baynunah Formation point to continental – terrestrial and aquatic – paleoenvironments (e.g., Hill & Whybrow, 1999).

The Baynunah Formation, late Miocene in age, was first described by Whybrow (1989) who defined its stratotype at Jebel Barakah. This was later complemented by Whybrow *et al.* (1999) who also introduced the Shuwaihat Formation, underlying the Baynunah Formation (Bristow, 1999; Whybrow *et al.*, 1999).

Exposures of the Baynunah Formation are often several tens of meters thick, exceeding 50 m at the stratotype section (Jebel Barakah). These are often covered by recent eolian sands, and in some places unconformably overlain by Quaternary carbonated eolian dunes. The Baynunah Formation clearly differs from the immediately underlying Shuwaihat Formation, which is mainly made up of eolian dune, sabkha (salt flat), and playa lake deposits (e.g., Bristow, 1999). The Baynunah Formation is best identified in the field from typical fluvial conglomerate beds, from well-developed paleosols (rhizoliths and insect nests), from its fossiliferous content (notably terrestrial vertebrate remains), as well as from whitish carbonate beds that mark the upper part of the formation. A cap-rock complex (sandstone and carbonate with displacive gypsum-anhydrite and chert veins) forms the tabular resistant top of most coastal exposures (Ditchfield, 1999; Whybrow *et al.*, 1999).

The most representative schematic section of the Baynunah Formation was proposed by Ditchfield (1999). It reflects well the fining-upward vertical lithological evolution, from conglomerates and coarse sandstones in its lower part, to sandstones and limestones in its upper part. It also shows the ideal case of an erosive contact between the Baynunah Formation and the underlying Shuwaihat Formation. The synthetic section presented herein (Fig. 2) compiles various observations made on some key-outcrops. Due to development activities, exposure conditions are worse than they were when the pioneering work occurred, and the existing sections (Bristow, 1999; Ditchfield, 1999; Whybrow *et al.*, 1999) helped control this synthetic log. Limited spatial extent and rapid lateral facies changes are typical in these continental deposits.

The main sedimentary features of the Baynunah Formation are the fluvial deposits from the lower part of the formation, the associated paleosols, and the whitish carbonates which appear in the upper part of the formation. Gravels and sands from the lower part of the Baynunah Formation, where most of the fossils come from, have been deposited by rivers as evidenced

by primary sedimentary structures (Friend, 1999). Thick (up to several meters), broad (up to several tens of meters) and upwardly thinning lenses of cross-stratified conglomerates are typical of the lower part of the Baynunah Formation (Fig. 2). These are notable for clasts that are intraformational in origin and are reworked from paleosols (Ditchfield, 1999; Friend, 1999). Many have irregular nodular shapes, but some display a typical root-like morphology. These clasts are mainly made of sandstone cemented by carbonate and range in size from granules to cobbles. The cross-stratified conglomerate beds of the Baynunah Formation are fluvial in origin. The Baynunah rivers, with a local flow directions towards the ESE, have been proposed to be part of an ancestral Tigris-Euphrates river system (Friend, 1999).

Paleosols are well-developed in the Baynunah Formation whereas only sparse rhizoliths and insect galleries and nests can be observed in the Shuwaihat Formation. Paleosols can thus be considered typical of the Baynunah Formation, though they received only scant attention that mainly outlined the presence of root related sedimentary structures (Friend, 1999; Glennie & Evamy, 1968; Whybrow & McClure, 1981). Rhizoliths are extremely well-represented in sandstones in the form of root molds, root casts, root tubules and rhizoconcretions. They are associated with galleries and nests of termites and possibly dung beetle brood-balls, the presence of termite, bee, and ant nests being already reported from the Miocene of Abu Dhabi (Bown & Genise, 1993; Genise & Bown, 1996). The importance and the preservation of some paleosol beds as well as the presence of soil-derived clasts within the fluvial conglomerates suggests that parts of the landscape (e.g., emerged fluvial bars, the distal floodplain, and abandoned channels) were only partly and temporarily impacted by fluvial reworking.

MATERIAL AND METHODS

The material described here was collected during surveys led between 1988 and 1995 by Peter Whybrow and Andrew Hill (Whybrow & Hill, 1999), as well as from 2003 onward during surveys led by FB, AH, and MJB. This material is curated by the Historic Environment Department at the Abu Dhabi Tourism and Culture Authority (formerly the Abu Dhabi Authority for Culture and Heritage) in Abu Dhabi city and the Al Ain National Museum, with the exception of a few specimens housed at the Paleontology Department of the Natural History Museum in London.

The Baynunah specimens were directly compared with other Miocene hippopotamids: the middle to late Miocene *Kenyapotamus* spp. (Boisserie *et al.*, 2010; Boisserie *et al.*, 2017; Tsubamoto *et al.*, 2016); the new hippopotamine material from Chorora (Kato *et al.*, 2016; Suwa *et al.*, 2015); *Archaeopotamus* spp. from the Nawata Formation at Lothagam, Kenya (Boisserie, 2005; Weston, 2000, 2003); *Hexaprotodon garyam* from the Anthracotheriid Unit at Toros-Ménalla, Chad (Boisserie *et al.*, 2005a); and the hippopotamine remains from the Adu Asa Formation in the Middle Awash Valley (western margin), Ethiopia (Boisserie & Haile-Selassie, 2009). All measurements were taken by JRB, unless mentioned otherwise. Other comparisons were conducted using published data, notably for the material from Sahabi, Libya (*Hexaprotodon? sahabiensis* Gaziry, 1987). All descriptions follow the nomenclature proposed by Boisserie *et al.* (2010), and open nomenclature use follows the recommendations by Bengston (1988).

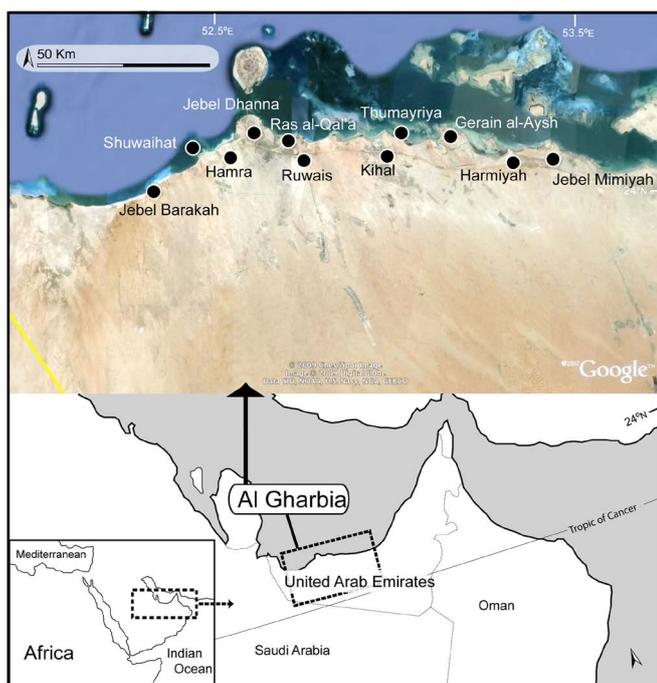


Figure 1. General location of the Baynunah Formation and of the localities with hippopotamid material described in the text.

Site Abbreviations. Baynunah Formation specimens numbered with the prefix **AUH** are curated by the Abu Dhabi Tourism and Culture Authority, while those with the prefix **NHM M** (abbreviated **M** in the text below) are curated by the Natural History Museum, London. Other mentioned sites: **WM**, Adu

Asa Formation ('Western Margin'), Ethiopia; **LT**, Lothagam, Kenya; **NP**, Napudet, Kenya; **SH**, Samburu Hills, Kenya; **TM**, Toros-Ménalla, Chad.

Institutional abbreviations. **CNRD**, Centre National de la Recherche pour le Développement (N'Djaména); **KNM**,

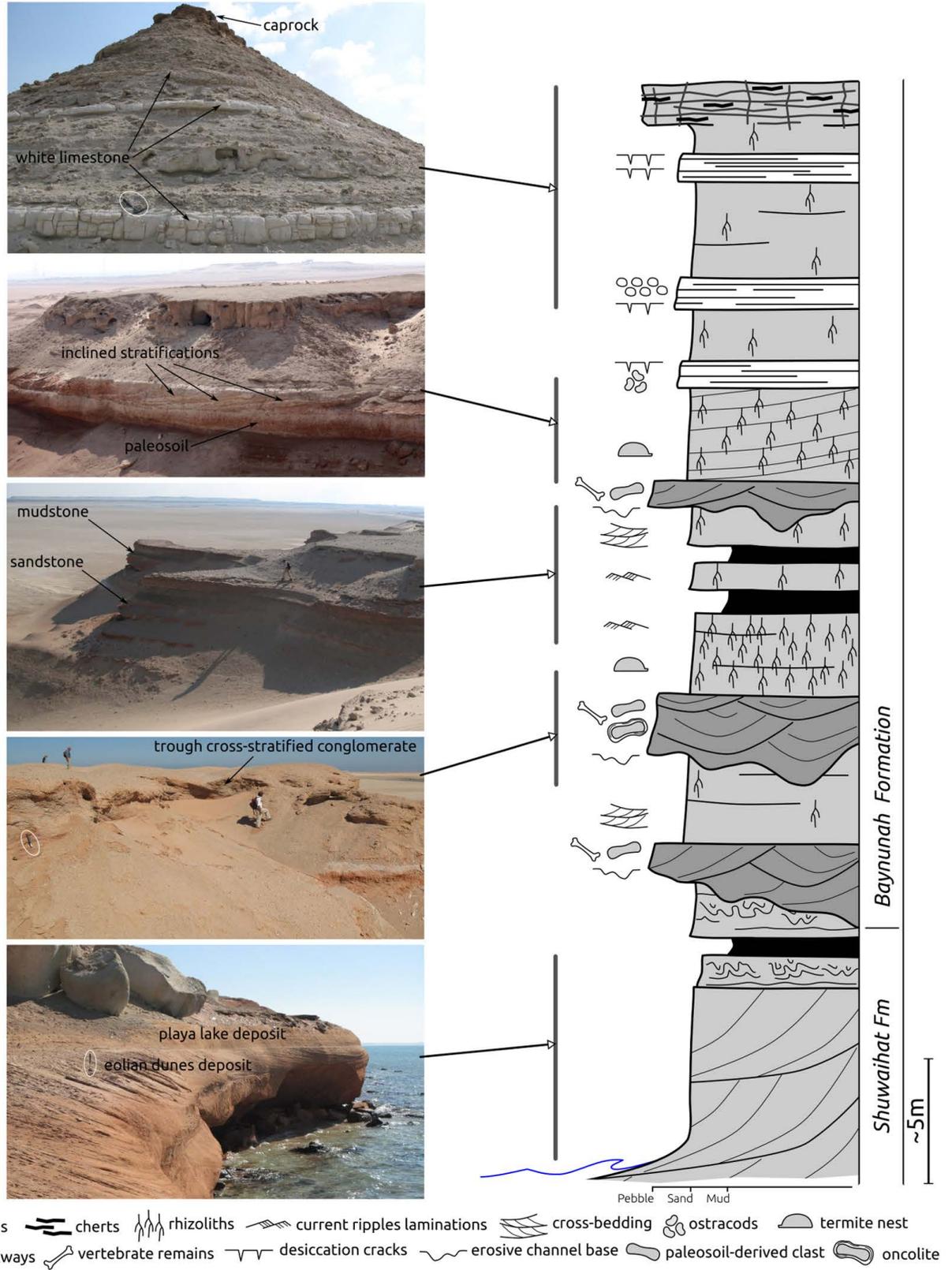


Figure 2. Synthetic log of the Baynunah Formation supported by general field views of the main sedimentological components of the section.

National Museums of Kenya (Nairobi); **NHM**, Natural History Museum (London); **NML**, National Museum of Libya; **MNHN**, Muséum National d'Histoire Naturelle (Paris); **TBI**, Turkana Basin Institute (Turkwel).

SYSTEMATIC PALEONTOLOGY

CETARTIODACTYLA Montgelard, Catzeflis & Douzery, 1997

CETANCODONTA Arnason, Gullberg, Solweig Ursing, & Janke, 2000

HIPPOPOTAMOIDEA Gray, 1821 (sensu Gentry & Hooker, 1988)

HIPPOPOTAMIDAE Gray, 1821

HIPPOPOTAMINAE Gray, 1821

Archaeopotamus Boissérie, 2005

Type species. *Archaeopotamus lothagamensis* (Weston, 2000).

Other representatives. *Archaeopotamus harvardi* (Coryndon, 1977); *A. aff. harvardi* from Rawi (M15939, “pigmy hippo mandible, possibly *Hexaprotodon imagunculus*” in Ditchfield *et al.*, 1999: 131; see Boissérie, 2005); new species defined below.

Spatiotemporal distribution. Late Miocene to early Pleistocene of Arabia and eastern Africa. Known from Baynunah, United Arab Emirates; Lothagam and Rawi in Kenya (Boissérie, 2005); and possibly Manonga in Tanzania (Harrison, 1997).

Emended diagnosis. Hexaprotodont hippopotamids differing from *Kenyapotamus* and earlier genera in displaying the trigonid pattern typical of the Hippopotaminae (i.e. lacking a developed metacristid, having an enlarged endometacristid and a postprotocristid reduced in comparison to the postparacristid). Differ from *Kenyapotamus* and the early hippopotamine material from Beticha (Chorora) by P³ having distolingual cusps distinct from the cingulum, relatively deeper fossae and longer cristae, a smaller paraconule, and less conules/-ids. Differ from other hippopotamine genera in having: a mandibular symphysis more elongate relative to its width; an incisive alveolar process projected rostrally relative to the canine processes; less lateral extension of the canine processes; a greater length of the lower premolar row relative to the length of the molar row; and gonial angle of the ascending ramus not laterally everted (modified from Boissérie, 2005).

Archaeopotamus qeshta nov. sp.

1999 *Hexaprotodon* aff. *sahabiensis*; Gentry: 277.

2005 *Archaeopotamus* aff. *lothagamensis*; Boissérie: 18.

lsid:zoobank.org:act:3D2365AC-E01F-4A5C-AF79-D522215A985F

Holotype. NHM M49464, mandible with eroded symphysis bearing complete and fragmentary teeth including left P₃-M₃ and right P₄ and M₃ (Fig. 3A-D).

Material. Hamra (see Fig. 1 for locality location): AUH 2 (incisor fragment); AUH 5 (left astragalus, fragmentary); AUH 44 (right astragalus); AUH 154 (right metacarpal V); AUH 369 (left P₁); AUH 457 (partial mandible with eroded symphysis,

left & right I₁-C₁ roots, broken right P₂, M₁-M₃, roots of other teeth); AUH 1241 (left metacarpal II); AUH 1793 (left M₁). Jebel Dhanna: AUH 36 (right M³); AUH 420 (right metatarsal III, fragment); AUH 421 (P⁴, fragmentary). Shuwaihat: AUH 53 (right metacarpal III); AUH 83 (proximal phalanx III or IV); AUH 96-97 (right metacarpal III); AUH 247 (left metatarsal III); AUH 481 (juvenile mandible with partial symphysis, most of right corpus and fragment of left corpus, right I₁-I₂, left I₂-I₃, left & right C₁, left P₂-P₄, right P₂-P₃, and dP₄); AUH 664 (left P₁, germ). Thumayriya: AUH 243 (right metatarsal III). Kihal: AUH 262 (P⁴, fragmentary); AUH 1252 (right astragalus, eroded). Harmiyah: AUH 359 (two enamel fragments from left upper premolar and right upper canine). Jebel Barakah: AUH 368 (left astragalus); NHM M49464 (mandible with eroded symphysis, left P₃-M₃, right P₄ and fragmentary M₃); NHM M49465 (right P³). Gerain al-Aysh: AUH 1532 (right M²); AUH 1561 (right metacarpal IV); AUH 1564 (left P¹); AUH 1794 (proximal phalanx III or IV); AUH 1795 (proximal phalanx III or IV). Baynunah North: AUH 1614 (right premaxilla with I³ and roots of I¹-I², broken). Ruwais Central: AUH 1731 (left I²); AUH 1736 (left astragalus, fragmentary).

Some additional specimens are referred to *Archaeopotamus* cf. *qeshta*. Shuwaihat: AUH 29 (canine, fragment); AUH 84 (central metapodial, fragment); AUH 110 (lower molar, fragment); AUH 248 (lateral metapodial, distal fragment). Hamra: AUH 150 (right tibia, distal fragment); AUH 339 (intermediate phalanx II or V); AUH 1242 (metapodial, fragmentary and eroded); AUH 1714 (tooth, fragmentary and distorted). Jebel Dhanna: AUH 288 (right fibula, distal fragment); AUH 292 (upper incisor, apical fragment). Ras al Qal'a: AUH 429 (axis). Jebel Barakah: AUH 446 (left C₁, fragment). Thumayriya: AUH 478 (intermediate phalanx II or V). Jebel Mimiyah: AUH 1278 (lower incisor, fragmentary). Baynunah North: AUH 1619 (left radioulna). Ruwais Central: AUH 1730 (left hamatum); AUH 1741 (proximal phalanx II or V).

Type locality and age. Jebel Barakah, one of the westernmost localities of the Baynunah Formation outcrops, ca. 50 km west of Ruwais, Al Gharbia, western part of Abu Dhabi Emirate. Faunal comparisons with African faunas suggest an age between 8 Ma and 6 Ma, possibly 7.5 Ma to 6.5 Ma (Bibi *et al.*, 2006; Bibi *et al.*, 2013; Hill, 1999).

Distribution. Currently known only from the Baynunah Formation.

Etymology. From the Arabic for cream, قشطة, the common hippopotamus being known affectionately as “Mr. Cream” (سيد قشطة) in the Egyptian dialect. The full species name *Archaeopotamus qeshta* means “Cream of the Ancient River.”

Differential diagnosis. Small-sized hippopotamid, intermediate in size between *Archaeopotamus lothagamensis* and *Archaeopotamus harvardi*. Differs from other hippopotamines with known mandibular morphology in having a symphysis more elongate relative to its width, and in having a lower premolar row (P₂-P₄) less than 10% shorter than the molar row (M₁-M₃). Further differs from other late Miocene hippopotamines by the largest lower incisor being I₂. Further differs from larger late Miocene hippopotamines in: I¹ and I² being subequal in size and larger than I³; I² being linguolabially compressed; and in lower premolar rows (P₁ included) displaying almost no rostral divergence from each

other. Further differs from other species of *Archaeopotamus* in I_1 and I_2 being the ventralmost and dorsalmost lower incisors, respectively (observed in rostral view). Further differs from *A. harvardi* in having less procumbent lower incisors.

Comparative description

Mandible. The two best-preserved mandibular specimens of *Archaeopotamus qeshta* nov. sp. are the holotype mandible M49464 and the fragmentary mandible AUH 457 (Fig. 3). The latter displays a damaged symphysis, lacks most of the ascending

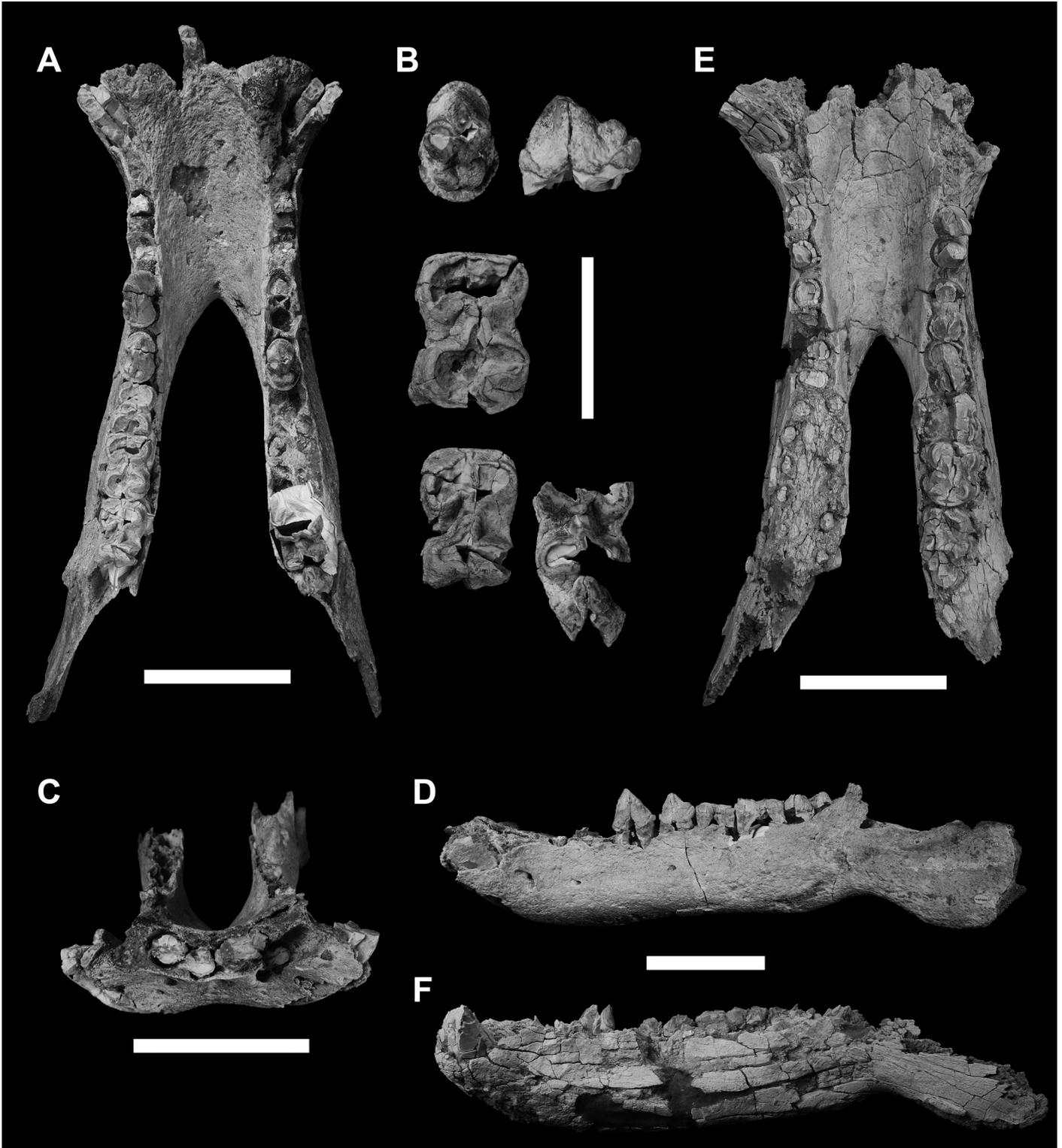


Figure 3. Adult mandibles of *Archaeopotamus qeshta* nov. sp. from the Baynunah Formation, Abu Dhabi, United Arab Emirates. NHM M49464, holotype mandible of *A. qeshta*: **A**, dorsal view; **B**, dentition (top left, occlusal view of right P_4 ; top right, lingual view of right P_4 ; middle, occlusal view of left M_2 ; bottom left, occlusal view of left M_3 ; bottom right, occlusal of right M_3); **C**, rostradorsal view; **D**, left lateral view. AUH 457: **E**, dorsal view; **F**, left lateral view. Scale bars for A and C-F are 100 mm; scale bar for B is 50 mm.

rami, and retains a broken right P_2 and partial right M_1 - M_3 . Both specimens are adult, displaying M_3 s with advanced wear. The two specimens differ mostly in that AUH 457 is more robust (notably a greater corpus thickness), has a longer symphysis and canine processes that project slightly more laterally (Fig. 3, Table 1). These moderate differences are compatible with sexual dimorphism in the living species *Hippopotamus amphibius* and *Choeropsis liberiensis*. Following this interpretation, AUH 457 and M49464 would represent the male and female morphotypes, respectively. AUH 481 is a juvenile symphysis preserving a damaged symphysis and most of the right corpus with P_2 - P_3 erupting and dP_4 in advanced wear. It is only slightly smaller in size than the two adult mandibles, but markedly narrower (Fig. 4, Table 1).

These three mandibles are characterized by symphyses that are greatly elongated relative to their width, *A. qeshta* displaying the longest mandibular symphysis within the Hippopotaminae (Fig. 5A). Only *Kenyapotamus ternani* Pickford, 1983 displays a relatively more elongate symphysis, documented by specimen KNM-NP 64505 from Napudet (Boisserie *et al.*, 2017). The Baynunah symphyses are also relatively shallow compared to the symphysis of *A. lothagamensis* and to those of *Hexaprotodon garyam* (Fig. 5A). This higher symphysis is related to the general incline of the symphysis in *A. lothagamensis*, and to the greater robustness of the nuchal part of the symphysis combined with the incline of the incisive alveolar process in *Hex. garyam* (Fig. 6).

In sagittal cross-section, the incisive alveolar process of AUH 457 displays a continuous ventral slope as in *A. lothagamensis*, *A. aff. harvardi* from Rawi (M15939), and *K. ternani*, differing from *Hex. garyam* and *A. harvardi* in which a ventral shift in curvature clearly differentiates the process from the nuchal portion of the symphysis (Fig. 6). M49464 displays such a ventral shift in curvature, but this lies closer to the rostral extremity of the symphysis and is less marked than in *A. harvardi* and *Hex. garyam* (Fig. 6). Overall, the thickness of the symphysis in sagittal cross-sections in M49464 and AUH 457 is relatively greater than that of *A. lothagamensis* and *A. harvardi*. AUH 481 is more similar to *A. harvardi* in its thinness and differentiation of the incisive alveolar process (Fig. 6).

The incisive alveolar process of *A. qeshta* also displays a more or less marked sagittal depression on its ventral side. This is wide in AUH 457, narrow and well-marked in M49464, and narrow and shallow in AUH 481. Such a depression is not found in other specimens attributed to *Archaeopotamus* or in *Hex. garyam*.

In dorsal view, the incisive alveolar process projects rostrally to the canine alveoli, as in other species of *Archaeopotamus*. The two adults are damaged in this area (Fig. 3), M49464 suggesting a more or less straight rostral border of this process. However, AUH 481, better preserved, has a rostral border that is curved in dorsal view (Fig. 4A), as in KNM-NP 64505 attributed to *Kenyapotamus*. The rostral border in *Archaeopotamus harvardi* and *Hex. garyam* is more or less straight.

In rostral view, the incisor alveoli of *A. qeshta* form a broken line, the I_1 being set more ventrally than the I_3 , and the I_2 more dorsally than the two others (in rostral view: Fig. 3C). This differs from *A. lothagamensis*, in which the alveoli are more or less aligned with a slighter dorsal shift of the I_2 , and from *A. harvardi*, in which the alveoli form a shallow arc dorsally convex. *Hexaprotodon garyam* is similar to *A. qeshta* in retaining a more dorsal I_2 , but the I_1 and the I_3 tend to be aligned

on a same horizontal level. The most similar organization to that seen in *A. qeshta* is observed in *K. ternani* from Napudet, the I_3 being even more dorsally-shifted, close to the level of the I_2 .

In lateral view, the incisors of M49464 emerge upward from the incisive alveolar process at an angle of about 36° to the cheek tooth alveolar plane. This angle is smaller for the flatter symphysis of AUH 481 (about 24°). In *A. harvardi*, the incisors are more procumbent, with the same angle being less than 10° . The condition in *A. lothagamensis* is uncertain because the main specimen (holotype KNM-LT 23839) is missing its incisors; the alveoli and the inclination of the symphysis suggest a condition closer to that of *A. qeshta* than to *A. harvardi*. *Hexaprotodon garyam* has angle values close to those of *A. qeshta*, ranging between 20° and 30° .

The canine processes of AUH 457 are slightly inflated laterally, bulging out of the corpus lateral sides. This is not the case in M49464, in which the canine processes are in continuity with the corpus (Fig. 3). The postcanine constriction of the mandible is not very marked. This morphology again recalls *K. ternani* from Napudet and *A. lothagamensis*. Yet, in dorsal view, the main axis of the canine alveoli forms a greater angle with the parallel cheek tooth rows in *A. qeshta* (ca. 43° to 45°) than in *A. lothagamensis* (ca. 31°). In *A. harvardi* and *Hex. garyam*, the canine processes extend more laterally than in *A. qeshta* and define a more marked postcanine constriction, but this extension concerns also the corpus and the mesial

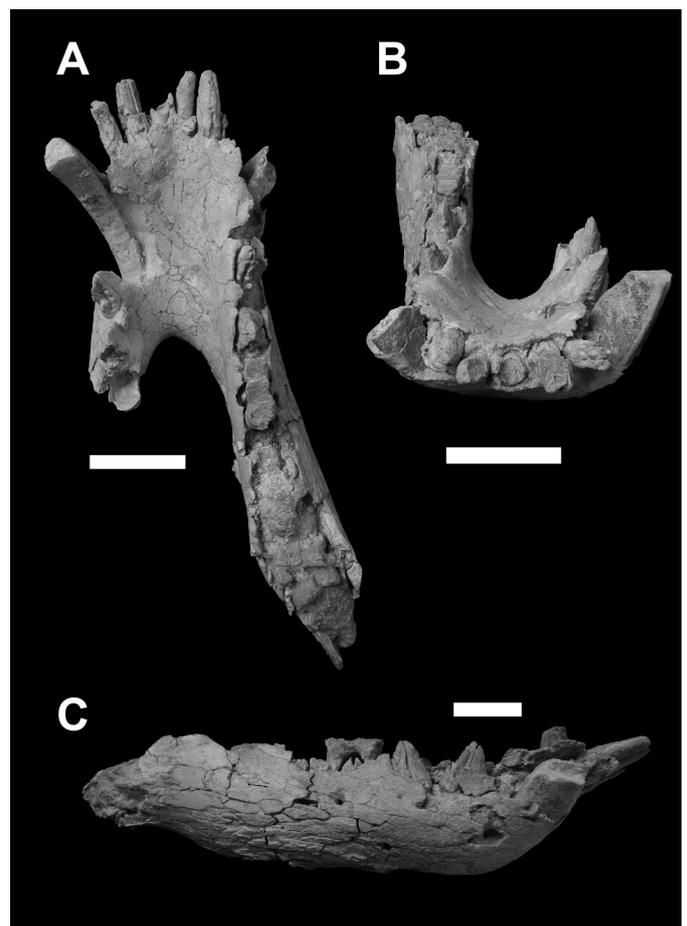


Figure 4. AUH 481, juvenile mandible of *Archaeopotamus qeshta* nov. sp. from the Baynunah Formation, Abu Dhabi, United Arab Emirates. **A**, dorsal view; **B**, rostradorsal view; **C**, right lateral view. Scale bars are 50 mm.

cheek teeth that diverge laterally. *Hex. garyam* also displays a moderate rostral extension of the canine processes, but this is not the case in *A. qeshta* and in other representatives of *Archaeopotamus*, except *A. aff. harvardi* from Rawi (M15939).

In rostral view, the canine alveoli of *A. qeshta* are subparallel to the line joining the right and left I_3 . In *Hex. garyam*, the canine alveoli are rostro-laterally oriented, forming an angle of ca. 40° with the incisor line. *Archaeopotamus harvardi* presents an intermediate condition.

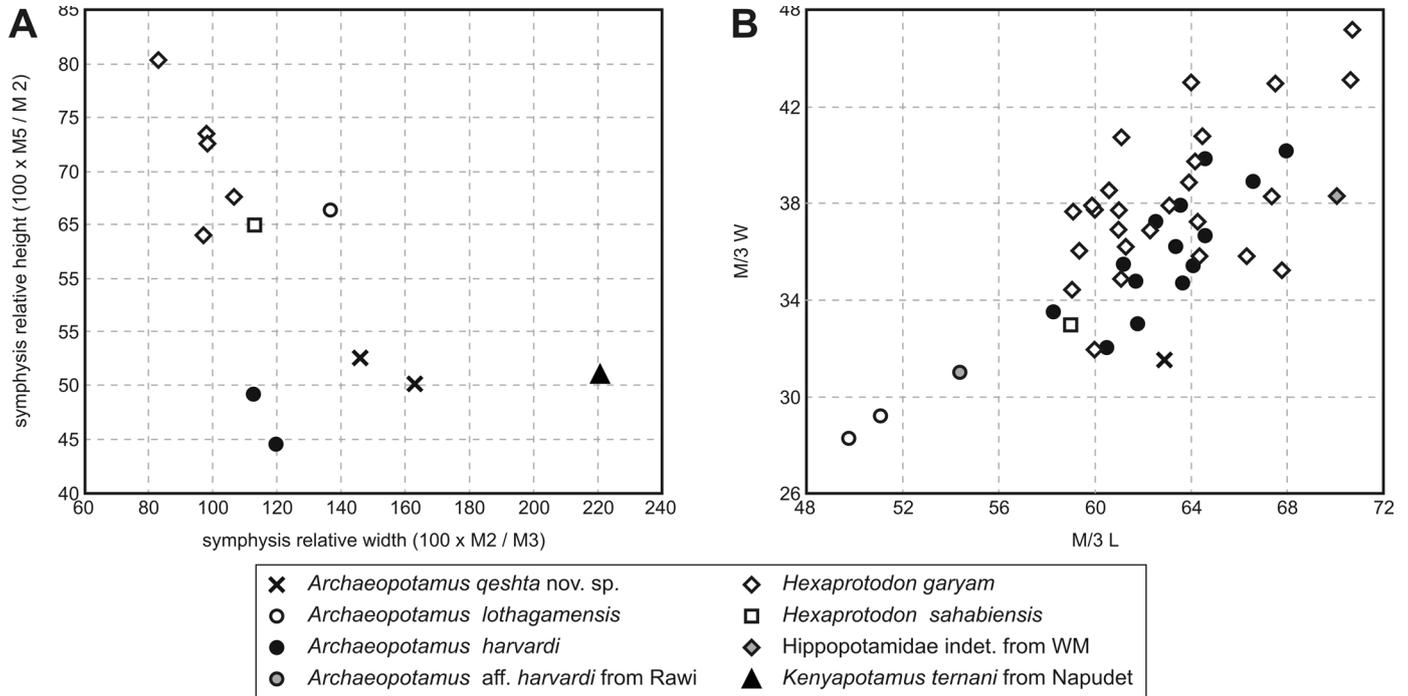


Figure 5. Measurements and proportions of *Archaeopotamus qeshta* nov. sp. compared with those of other hippopotamids. **A**, plot of mandibular symphysis proportions (M2, maximal length from mid-point between right and left I_1 and nuchal symphysis; M3, width between right and left canines; M5, corpus height at mesial P₂); **B**, plot of M₃ dimensions (L, mesiodistal length; W, mesial width).

	M1	M2	M3	M4	M5	M6	M7	M8
AAH 457	~355	~192	117	52	~96	97	126	127
M49464	~356	~165	113	42	87	~88	131	~142
AAH 481		165	~87		~82		~114	
Kt		104	47		53		72	
Al	≈302	≈139	101	44	92	80	105	123
Ah	356-402; 380.8; 3	183-211; 191.8; 4	152-187; 168.8; 3	40-63; 48.9; 7	81-124; 102.0; 4	99-124; 108.4; 6	104-130; 118.9; 7	134-152; 144.9; 8
AR	328	155	126				118	133
Hg	375-410; 389.7; 3	126-197; 159.3; 9	123-188; 156.4; 10	51-70; 59.7; 9	104-127; 116.7; 7	103-126; 116.3; 15	90-132; 116.4; 8	133-163; 148.2; 13
Hs		127	112		83			

Table 1. Measurements (min.-max. in mm; mean; N) for mandibles of *Archaeopotamus qeshta* nov. sp. compared to those of other hippopotamids. **Al**: *A. lothagamensis* from Lothagam; **Ah**: *A. harvardi* from Lothagam; **AR**: *A. aff. harvardi* from Rawi; **Hg**: *Hexaprotodon garyam* from Toros-Ménalla; **Hs**: *Hex. ? sahabiensis* from Sahabi (data from Pavlakis, 2008); **Kt**: *K. ternani* from Napudet; **M1**: length from mid-point between right and left I_1 to distal M₃; **M2**: symphysis length (maximal length from mid-point between right and left I_1 and nuchal symphysis); **M3**: width between right and left canines; **M4**: corpus mediolateral thickness below M₁; **M5**: corpus height at mesial P₂; **M6**: corpus height at mesial M₃; **M7**: length from mesial P₂ to distal P₄; **M8**: length from mesial M₁ to distal M₃.

The symphyseal dorsal plane of *A. qeshta* is narrow as in *A. lothagamensis* and *K. ternani* and does not present a rostral widening as in *A. harvardi*, *Hex. garyam*, and *A. aff. harvardi* from Rawi (M15939). Also unlike *A. harvardi* and *Hex. garyam*, the symphyseal dorsal plane is transversely curved between the canines, this curvature increasing nuchally between the premolars. It is very deep in the adults, but shallower in AUH 481. Relative shallowness of the symphysis was also described in a large juvenile from Lothagam (indeterminate level), tentatively attributed to a species larger than *A. harvardi* (KNM-LT 79: Weston, 2003). The occurrence of similar morphology in a juvenile from Baynunah, as well as in another juvenile of similar biological age from the lower Pliocene of Kossom Bougoudi in Chad (KB 3-97-201: Boisserie *et al.*, 2003), suggests that the depth/flattening of the symphysis may be subject to ontogenetic variation in early hippopotamines.

In adult specimens of *A. qeshta*, the nuchal portion of the symphysis is shallow and forms a V with the corpora in dorsal and ventral views (Fig. 3A,E), whereas AUH 481 displays

a U shape (Fig. 4A). This feature also tends to be related to ontogenetic stage as well as to the extension of the canines within the symphysis, which is usually more marked in males.

Ventrally, the symphysis of *A. qeshta* is markedly convex, as in *K. ternani* from Napudet and *A. lothagamensis*. *Archaeopotamus harvardi* and some specimens of *Hex. garyam* have more flat ventral surfaces. More caudally, the three specimens of *A. qeshta* also display large depressions for genioglossal insertions extending on the ventral side of the symphysis.

In *A. qeshta*, the mandibular corpus is about the same height below the premolars as below the molars, differing from *A. harvardi* in which the corpus is deeper under the molars, and from most specimens of *Hex. garyam* that display a greater depth under the premolars. In lateral view, the ventral transition with the ascending ramus is marked by a deep vascular incisure (Fig. 3D,F), as in *A. lothagamensis* and some representatives of *A. harvardi*. This contrasts with the rectilinear ventral edge of the corpus in *Hex. garyam*. Caudally, the angular process of

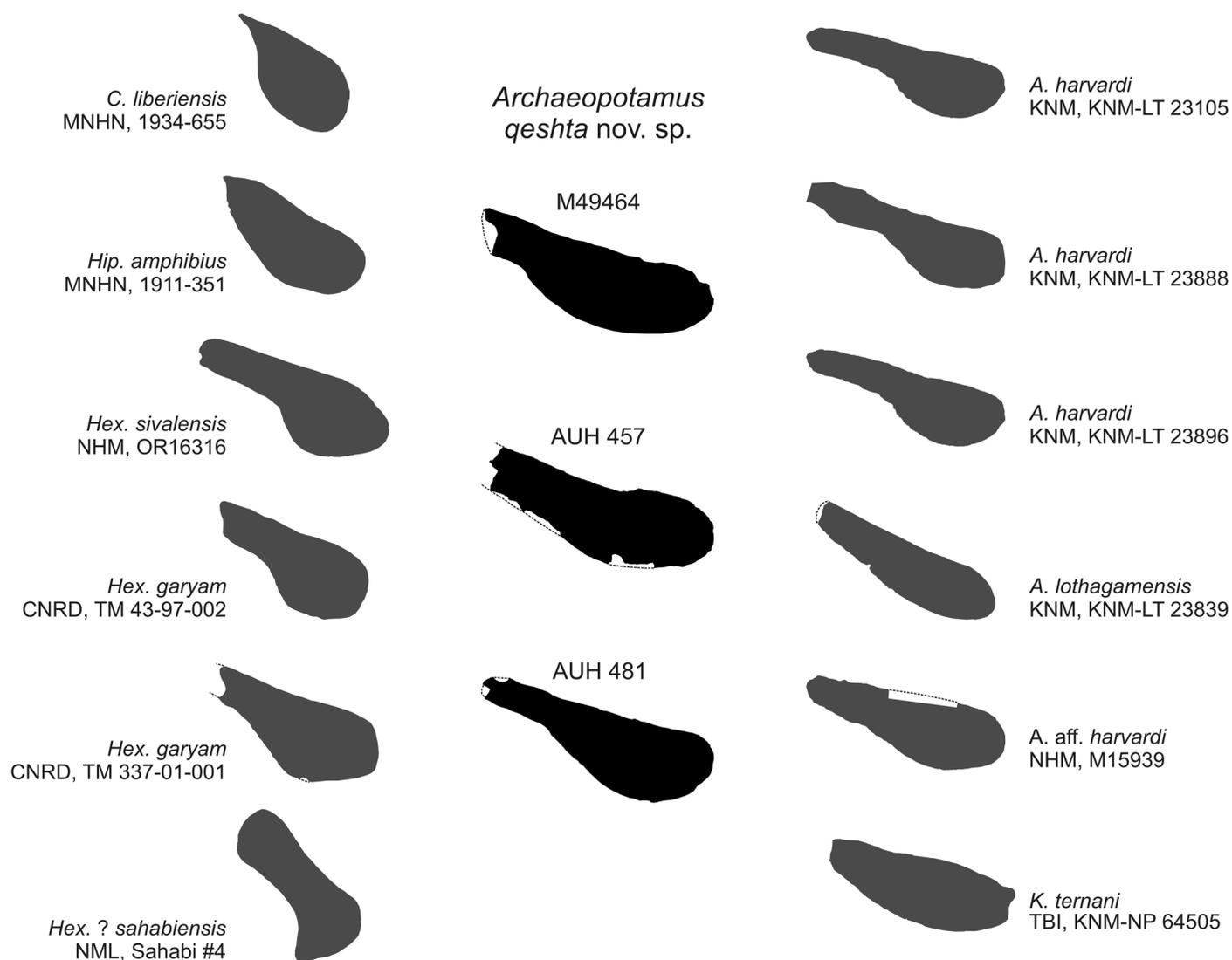


Figure 6. Cross-sections of mandibular symphyses attributed to *Archaeopotamus qeshta* nov. sp. compared with those of other hippopotamids. All sections are direct observations, except *Hexaprotodon? sahabiensis* (Pavlaklis, 2008: fig. 3). **Black tone**, *A. qeshta*; **grey tone**, other hippopotamids.

A. qeshta is thin and oriented in the same plane as the corpus (Fig. 3A,E), as in *A. harvardi*, and unlike the everted process observed in *Hex. garyam*.

Rostral dentition. Upper incisors are documented by AUH 1614, an eroded, fragmentary premaxilla that is actually the only hippopotamid cranial remain from the Baynunah Formation. It includes broken I¹ and I² and a complete I³. The three incisors present a continuous band of thick, striated enamel. This band is mesiolabial on I¹, covering the labial side and extending on the mesial and distal sides on the I², and restricted to the labial side of I³. I¹ and I² are subequal in cross-section size and about 56 % larger than I³, whereas in *A. harvardi*, *Hex. garyam*, and Hippopotamidae indet. from WM, I² is on average larger than I¹ and I³ is less or not reduced (Table 2). The lingual side of these incisors is more or less flat, the I² having a longitudinal groove between two crests. I² is linguolabially compressed unlike in *A. harvardi*, *Hex. garyam*, and Hippopotamidae indet. from WM (Table 2). I¹ and I³ have close linguolabial and mesiodistal diameters (Table 3). I³ presents an apical, beveled wear that extends to the distal side, the edge of the facet being smoothed by this distal wear.

AUH 1731 (Fig. 7A) is an isolated, complete I² that is similar to the AUH 1614 I² in being strongly compressed linguolabially, in possessing a labial band of enamel extending along the entire tooth length, and in displaying a lingual longitudinal groove. This tooth presents an apical, undulating wear facet cutting the main axis of the tooth at a 45° angle. The base is open, but the linguolabial diameter markedly tapers from crown to base, suggesting that this tooth may have been not ever-growing as in the extant *Hippopotamus amphibius*. AUH 2

is an apical fragment of another I² with the exact same features.

The upper canine is known only by a ca. 6 cm-long enamel fragment (included in AUH 359). This fragment displays the curvature usually observed in late Miocene hippopotamine canines.

Within the lower incisors of *Archaeopotamus qeshta* nov. sp., I₂ displays the largest cross-section, as in *K. ternani* and *A. lothagamensis* (Table 2). Yet, the difference is less marked between I₁ and I₂ than in those latter species, and in *A. lothagamensis*, the I₃ is by far the largest lower incisor. In *A. harvardi*, *A. aff. harvardi* from Rawi (M15939), *Hex. garyam*, and *Hexaprotodon? sahabiensis*, I₁ is the largest lower incisor (Table 2). This is also true for the material collected in Algeria (in Annaba – formerly Bône) and attributed to *Hexaprotodon? hipponensis* Gaudry, 1876 (see Table 2 and Arambourg, 1944). In AUH 481 (Fig. 4), the preserved incisors present an enamel cap that has a long lingual extension, as seen in the second specimen attributed to *A. lothagamensis* (KNM-LT 23879, see Weston, 2000).

The lower canine morphology of *A. qeshta* does not depart significantly from that of the other late Miocene hippopotamines: the canine is ever-growing, extending within the symphysis from alveolus to the nuchal part; its cross-section is bean-shaped with the flat-to-concave side being mesial; its lingual side (with contact facet for the upper canine) is not covered by enamel. The enamel is smooth to finely wrinkled. On the distal surface, the enamel is relatively thick compared to the canine dimensions. Relatively thick distal enamel, accounting for approximately 6 % to 8 % of the mesiodistal width of the section, is found in other species of *Archaeopotamus*, whereas in *Hex. garyam* the enamel is thinner.

	I ² S	I ² vs. I ¹	I ³ vs. I ¹	I ₂ vs. I ₁	I ₃ vs. I ₁
Aq	70.5-76.7; 73.42; 3	98.2	62.9	108.4-140.6; 126.29; 3	90.9-123.5; 107.20; 2
Kt				146.2	103.2
Al				153.3	205.5
Ah	91.0	109.3	87.7	62.7-79.6; 71.14; 2	69.1
AR				43.2	71.3
Hg	90.0-123.5; 110.12; 7	81.1-126.5; 104.04; 4	89.4-111.7; 99.88; 3	54.4-90.8; 69.69; 10	64.2-100.1; 83.4; 10
Hh				69.2	57.8
Hs				53.8	93.4
WM	99.6	107.2	81.3		

Table 2. Proportions of I² (min.-max.; mean; N) and interincisive ratios (min.-max.; mean; N) in *Archaeopotamus qeshta* nov. sp. compared to those of other hippopotamids. These values are calculated from measurements summarized in Table S1. **Aq:** *A. qeshta* nov. sp.; **Al:** *A. lothagamensis* from Lothagam; **Ah:** *A. harvardi* from Lothagam; **AR:** *A. aff. harvardi* from Rawi; **Hg:** *Hexaprotodon garyam* from Toros-Ménalla; **Hh:** *Hexaprotodon hipponensis* from Algeria (data from Arambourg, 1944); **Hs:** *Hex. ? sahabiensis* from Sahabi (data from Gaziry, 1987); **Kt:** *K. ternani* from Napudet; **WM:** Hippopotaminae indet. from Adu Asa Formation; **I² S:** shape ratio of the cross-section 100 × (LL / MD), in which LL is the linguolabial diameter, and MD the mesiodistal diameter; **I² vs. I¹:** 100 × (I² MD × I² LL) / (I¹ MD × I¹ LL) – applying similarly for I³ vs. I¹, I₂ vs. I₁, and I₃ vs. I₁.

Postcanine dentition. Premolar and molar dimensions are provided in Tables 4 and 5, respectively. The dentition of *Archaeopotamus qeshta* nov. sp. appears close in size to the dentition of *Hexaprotodon sahabiensis*. It is larger in size than that of *K. ternani*, *A. lothagamensis*, and *A. aff. harvardi* from Rawi (except for P⁴ length in the latter). It overlaps with the lower range of the larger *A. harvardi*, *Hex. garyam*, and Hippopotamidae indet. from WM, as shown for M₃ on Fig. 6B.

P¹ of *Archaeopotamus qeshta* nov. sp. is known through a fragmentary left specimen, AUH 1564. This is a robust, permanent tooth with thick, strongly pustulate enamel on its mesial wall. It has two roots that are fused by a thin wall of dentine labially. This morphology is also observed in other late Miocene hippopotamines such as *A. harvardi* and *Hex. garyam*. P² is not known.

M49465 is an isolated right P³ in advanced wear and missing a fragment of its apex (Fig. 7B). In occlusal view, this tooth forms two lobes separated by a marked constriction. It is wide, with a strong cingulum present on all sides but attenuating at the labial indentation of the cervix. The massive paracone is flanked by four distolingual accessory cusps in a position equivalent to a ‘protocone’ (see definition by Boissérie *et al.*, 2010), a condition frequently observed in *A. harvardi* and *Hex. garyam*. These conules are distinct from the well-expressed distolingual cingulum, a condition differing from that observed in *Kenyapotamus* and typical of most hippopotamines. The valley separating the paracone and the distolingual cusps is narrow, as in *Kenyapotamus* and some of the hippopotamine material from the late Miocene of Chorora (Boissérie *et al.*, in press), but unlike any other hippopotamines. At least one strong basal postparaconule is present on the postparacrista, and wear may have obliterated more apical postparaconules. The roots are massive.

P⁴ is documented by two fragmentary specimens. The most complete one, AUH 262 (Fig. 7C), is the lingual half of a P⁴, tentatively sided as from the right side. It displays a strong and high crenulated cingulum. The protocone is crescentic; it does not display deep fossae, as in *Kenyapotamus* and some

specimens of *A. harvardi*, and unlike in *Hex. garyam*. The paracone does not present a well-developed endoparacrista, as in *Kenyapotamus* and some specimens of *Hex. garyam*, and unlike in *A. harvardi* and *Hex. garyam*.

Two upper molars are known for *A. qeshta*. The first one is an isolated right M² with incipient wear on the mesial cusps (AUH 1532, Fig. 7E). This tooth is square-shaped, as in most hippopotamines. Its cinguli are well-developed mesially and distally, but reduced on the lateral sides. The cusps display a crest pattern similar to that observed in *A. harvardi* and *Hex. garyam*. The preprotocrista is inflated, the bulging recalling an incipient paraconule. There are no ecto- or endostyles, and no cristyles.

The other upper molar is an unworn, isolated right M³ (AUH 36, Fig. 7F). This tooth has a strongly crenulated cingulum that attenuates only on the labial side of the paracone. The cristae are long and sharp, the prepara- and postmetacristae being strongly curved labially. The preprotocrista joins a small paraconule, as seen in some specimens of *A. harvardi* and *Hex. garyam*, but rarely in later taxa. A similar conule is adjacent to the distostyle. There is an entostyle and an ectostyle unusually shifted distally to the labial valley. The most remarkable feature of this tooth is the organization of the metaconule cristae. The premetacristule is relatively short and straight. Mesially, it joins the postprotocristae on its lingual wall. Distally, it forms an apical loop with a crista in labial position as an endometacristule. This endometacristule bifurcates in two long branches before to reach the lingual wall of the metacone. The mesial branch is straight and directed toward the extremity of the postprotocrista. Its distal branch is thicker and shorter and joins the distal conule near the distostyle. To our knowledge, such a bifid morphology of a molar crest is only found in a pre-entocristid of a specimen from the latest Miocene of Chorora, which is identified as an indeterminate hippopotamine.

This M³ displays a full crown height, and its hypsodonty index H (100 × paracone height / mesial width) is reported in Table 5. This tooth is higher-crowned than in *Kenyapotamus*, and has a crown height equivalent to those of *A. harvardi* and *Hex. garyam*. One M³ from WM is markedly higher-crowned.

	I ¹		I ²		I ³		I ₁		I ₂		I ₃		C ₁	
	MD	LL	MAX	MIN										
Aq	18.3	17.6	20.8-21.7; 21.17; 3	15.2-16.1; 15.53; 3	15.0	13.5	10.4-14.8; 12.60; 2	16.2-18.6; 17.40; 2	15.2-18.2; 16.70; 2	13.8-17.1; 15.45; 2	11.8-16.1; 13.95; 2	14.9	42.6-44.6; 43.60; 2	24.0-27.9; 25.95; 2
Kt							7.4	9.9	9.0	11.9	6.3	12.0	20.1-32.4; 26.25; 2	13.1-19.5; 16.30; 2
Al							10.7	11.1	15.6	11.7	18.4	13.3	32.1	17.8
Ah	24.0	22.6	25.5	23.2	20.9	22.7	23.1-26.7; 24.90; 2	28.5-23.2; 25.85; 2	17.4-25.2; 21.30; 2	19.3-24.0; 21.65; 2	19.0	19.5-21.7; 20.60; 2	34.6-58.2; 45.03; 6	23.1-35.7; 27.51; 7
AR							23.8	20.0	12.3	16.7	17.4	19.5	45.0	27.2
Hg	13.9-21.9; 18.42; 3	13.2-23.3; 19.31; 4	18.3-22.6; 20.55; 6	18.8-25.3; 22.80; 6	12.1-19.3; 15.93; 6	13.5-22.4; 19.26; 5	21.3-31.7; 27.23; 9	18.5-37.4; 28.74; 9	16.1-32.0; 22.62; 9	18.8-30.4; 24.04; 9	18.4-31.8; 26.36; 8	19.3-33.0; 26.36; 9	39.7-68.5; 55.23; 9	25.7-39.7; 34.21; 9
Hs							23.8	20.0	12.3	16.7	17.4	19.5	45.0	27.2

Table 3. Measurements (min.-max. in mm; mean; N) for rostral dentition of *Archaeopotamus qeshta* nov. sp. compared to those of other hippopotamids. **Aq:** *A. qeshta* nov. sp.; **Al:** *A. lothagamensis* from Lothagam; **Ah:** *A. harvardi* from Lothagam; **AR:** *A. aff. harvardi* from Rawi; **Hg:** *Hexaprotodon garyam* from Toros-Ménalla; **Hs:** *Hex. ? sahabiensis* from Sahabi (data from Pavlakakis, 2008); **Kt:** *K. ternani* from Napudet; **MD:** mesiodistal diameter; **LL:** labiolingual diameter; **MAX:** maximum diameter; **MIN:** minimum diameter.

P_1 is known from two isolated specimen. AUH 369 is a moderately worn, single-rooted left P_1 . The paraconid is fang-like with a minute conulid on the base of the postparaconid. Cingulid is present only on the mesial side. The root is not bilobed and large compared to the crown. AUH 664 is a crown of another left P_1 (Fig. 7D). It is unworn and probably unerupted. It is more compressed linguolabially than AUH 369. It displays a higher distolingual conulid with four marked triangular indentations, a morphology also observed in *A. lothagamensis* (KNM-LT 23879). The P_1 alveoli on M49464 and AUH 457 also indicate single rooted teeth (Fig. 3A,E). In the latter specimen the alveoli are very shallow, suggesting that these teeth may be lost in advanced age.

Compared to other hippopotamines, in *A. qeshta* the P_2 - P_4 row is long relative to the molar row (Table 6). This is notably marked compared to *Hex. garyam*, but also true compared to other species of *Archaeopotamus*. Only *Kenyapotamus* displays a somewhat longer P_2 - P_4 row. These teeth display a morphological gradient usual for early hippopotamines: the metaconid is incipient and distally shifted in P_2 ; large, high, and lingual on the P_4 ; intermediate or as in P_2 in the P_3 . The mesial and distal cingulids are low and thin in P_2 and become larger and higher in the distal premolars. P_4 displays both well-expressed ento- and hypoconids (Fig. 3B), whereas the former can be missing on P_2 and P_3 (AUH 481). A distal fragment of a lower premolar associated with M49464 is unusual in having a marked

entoconid, a labially shifted hypoconid and, in addition, a conulid basal to the entoconid looking like a cingulid. It differs from P_4 in this morphology and in being more slender, and is better interpreted as the right P_2 or P_3 .

The lower molars of *A. qeshta* (Fig. 3B) have a trigonid organization typical of Hippopotaminae, observable on the M_3 of M49464 and on an isolated unnumbered molar at NHM: the preprotocristid directed toward the mesiostylid and the endometacristid joining the lingual wall of the preprotocristid. The postprotocristid is short and joins the labial wall of the long postmetacristid that connects to the prehypocristid. The entoconid is reduced. On the M_3 , the hypoconulid has relatively short cristids, as in *A. lothagamensis*, except the prehypocristulid, which is inflated into a prehypoconulid.

Autopodium. Hippopotamid postcranial elements from the Baynunah Formation were described in detail by Gentry (1999), and the present account focuses on the relative dimensions of astragali, metapodials, and phalanges attributed to *Archaeopotamus qeshta* nov. sp. in this contribution. The astragali of *A. qeshta* are morphologically similar to those of other hippopotamids. Their general proportions fit the ranges observed in *Kenyapotamus*, *A. harvardi*, *Hexaprotodon garyam*, and Hippopotamidae indet. from WM (Table 7), but the Baynunah specimens are on average somewhat narrower,

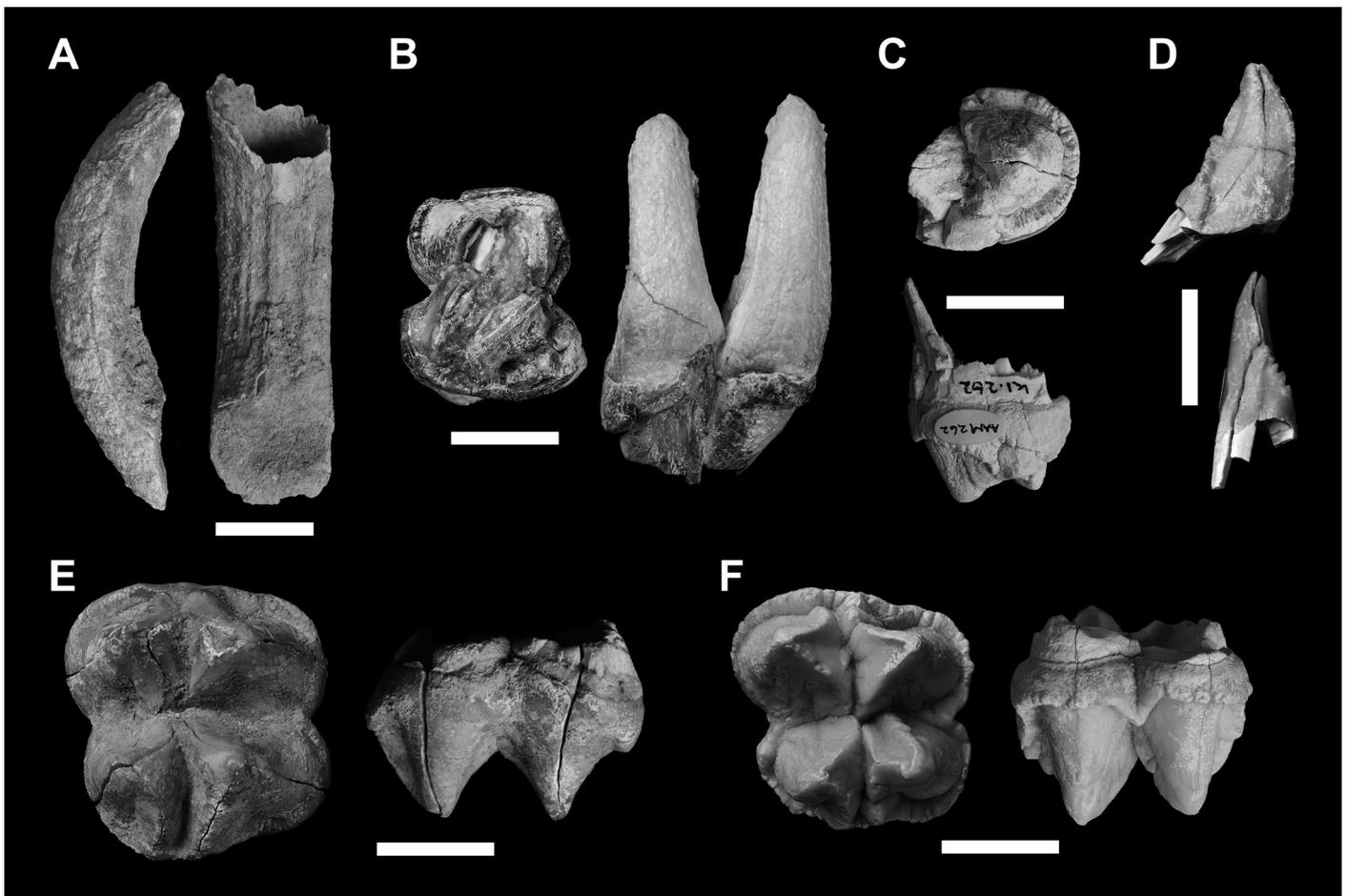


Figure 7. Dentition of *Archaeopotamus qeshta* nov. sp. from the Baynunah Formation, Abu Dhabi, United Arab Emirates. **A**, AUH 1731 (left I^2 in mesial view on left and in lingual view on right); **B**, NHM M49465 (right P_3 in occlusal view on left and in labial view on right); **C**, AUH 262 (right ? P_4 in occlusal view on top and in distal view on bottom); **D**, AUH 664 (left P_1 in lingual view on top and in distal view on bottom); **E**, AUH 1532 (right M^2 in occlusal view on left and in labial view on right); **F**, AUH 36 (right M^3 in occlusal view on left and in lingual view on right). Scale bars are 20 mm.

	P ³		P ₁		P ₂		P ₃		P ₄	
	L	W	L	W	L	W	L	W	L	W
Aq	37.8	~30.6	17.3-18.7; 17.55; 2	11.4-13.4; 12.40; 2	29.2-40.2; 34.70; 2	18.2-19.7; 18.95; 2	35.7-39.1; 37.40; 2	19.6-23.1; 21.35; 2	33.9-34.5; 34.20; 2	22.4-23.8; 23.10; 2
K	25.0-29.4; 27.20; 2	19.7-20.3; 20.00; 2			18.8	11.0	24.5-31.2; 27.85; 2	15.5-17.1; 16.30; 2	25.6-26.2; 25.90; 2	18.2-18.9; 18.55; 2
Al									30.7-33.6; 32.15; 2	20.5-23.8; 22.15; 2
Ah	35.4-48.2; 40.35; 10	27.4-35.1; 31.70; 9			31.3-41.0; 36.27; 6	21.4-24.7; 22.85; 5	36.5-45.1; 40.04; 6	22.5-26.6; 24.62; 6	36.4-41.6; 38.66; 8	24.9-30.6; 27.41; 8
AR									36.9	22.3
Hg	35.6-47.0; 41.22; 31	28.2-43.0; 34.15; 31	16.3-33.1; 24.7; 2	11.2-40.7; 25.95; 2	29.8-47.1; 35.99; 17	19.0-27.6; 22.12; 17	31.7-48.0; 39.42; 20	18.0-32.9; 24.17; 19	33.4-43.1; 39.10; 19	21.7-32.5; 27.81; 18
Hs	36.0	26.0							36.0	25.0
WM	38.6	26.2	17.4-18.5; 17.95; 2	13.3-14.5; 13.90; 2			37.5-40.1; 38.60; 3	23.1-26.8; 25.07; 3	38.1-43.9; 41.43; 3	25.8-31.0; 28.73; 3

Table 4. Measurements (min.-max. in mm; mean; N) for premolars of *Archaeopotamus qeshta* nov. sp. compared to those of other hippopotamids. **Aq:** *A. qeshta* nov. sp.; **Al:** *A. lothagamensis* from Lothagam; **Ah:** *A. harvardi* from Lothagam; **AR:** *A. aff. harvardi* from Rawi; **Hg:** *Hexaprotodon garyam* from Toros-Ménalla; **Hs:** *Hex. ? sahabiensis* from Sahabi (data from Gaziry, 1987); **K:** middle and late Miocene *Kenyapotamus* from Kenya and Tunisia; **WM:** Hippopotaminae indet. from Adu Asa Formation; **L:** mesiodistal length; **W:** maximal width.

	M ²		M ³			M ₁	M ₂		M ₃		
	L	W	L	W	h	H	W	L	W	L	W
Aq	46.0	44.6	42.6	44.4	34.0	76.6	25.2-25.7; 25.45; 2	41.5-44.8; 43.15; 2	31.8-33.7; 32.75; 2	54.9-~62.9; 58.9; 2	31.5
K	22.6-29.0; 25.92; 4	24.6-25.7; 26.05; 2	20.0-29.7; 24.85; 2	23.0-29.4; 25.63; 3	18.8	66.6	17.7	28.5-33.1; 30.8; 2	26.4	41.1-42.9; 42.00; 2	23.9-24.1; 24.00; 2
Al							22.9-28.6; 25.75; 2	41.1-42.7; 41.90; 2	27.8-34.0; 30.90; 2	49.8-51.1; 50.45; 2	28.3-29.2; 28.75; 2
Ah	37.2-50.0; 44.58; 16	39.7-55.6; 45.99; 16	44.0-51.7; 47.17; 13	41.4-56.2; 46.48; 13	32.1	76.6	26.1-35.0; 31.34; 9	41.2-51.3; 47.44; 11	33.0-38.4; 36.16; 10	58.3-68.0; 63.10; 16	32.0-40.2; 35.88; 15
AR							24.1	41.3	27.3	54.4	31.0
Hg	42.4-54.3; 48.37; 35	41.2-53.5; 47.38; 30	37.8-57.4; 47.74; 49	40.8-52.2; 46.54; 48	34.6-40.0; 36.41; 8	73.7-81.4; 78.49; 8	26.8-39.0; 30.99; 23	41.6-54.0; 49.28; 31	30.8-45.2; 37.53; 26	59.1-70.7; 63.26; 31	31.9-45.2; 38.12; 31
Hs			39.0	42.0				39.0	34.0	59.0	33.0
WM	45.4-46.2; 45.80; 2	44.4-45.5; 44.95; 2	43.4-49.2; 46.68; 4	39.1-45.9; 42.77; 4	36.4	107.2	31.0	41.1-49.5; 45.83; 3	31.0-31.2; 31.10; 2	62.0-70.1; 66.05; 2	36.4-38.3; 37.35; 2

Table 5. Measurements (min.-max. in mm; mean; N) for molars of *Archaeopotamus qeshta* nov. sp. compared to those of other hippopotamids. **Aq:** *A. qeshta* nov. sp.; **Al:** *A. lothagamensis* from Lothagam; **Ah:** *A. harvardi* from Lothagam; **AR:** *A. aff. harvardi* from Rawi; **Hg:** *Hexaprotodon garyam* from Toros-Ménalla; **Hs:** *Hex. ? sahabiensis* from Sahabi (data from Gaziry, 1987); **K:** middle and late Miocene *Kenyapotamus* from Kenya and Tunisia; **WM:** Hippopotaminae indet. from Adu Asa Formation; **L:** mesiodistal length; **W:** mesial width; **h:** paracone height from cervix to apex; **H:** hypsodonty index 100 × h / W.

	P	M	100 × (P / M)
AAH 457	126	127	99.2
M49464	131	~142	92.3
K	72-104; 87.9; 2	95-103; 99.0; 2	101.0
Al	105	123	85.4
Ah	104-130; 118.9; 7	134-152; 144.9; 8	70.2-90.2; 81.94; 5
AR	118	134	88.1
Hg	90-132; 116.4; 8	133-163; 148.2; 13	67.7-84.9; 74.9; 6

Table 6. Measurements (min.-max. in mm; mean; N) and proportions of lower dental rows (min.-max. in mm; mean; N) in *Archaeopotamus qeshta* nov. sp. compared to those of other hippopotamids. **Al:** *A. lothagamensis* from Lothagam; **Ah:** *A. harvardi* from Lothagam; **AR:** *A. aff. harvardi* from Rawi; **Hg:** *Hexaprotodon garyam* from Toros-Ménalla; **Hs:** *Hex. ? sahabiensis* from Sahabi (data from Pavlakis, 2008); **K:** middle and late Miocene *Kenyapotamus* from Kenya and Tunisia; **P:** length from mesial P₂ to distal P₄; **M:** length from mesial M₁ to distal M₃.

	H	W	100 × W / H	estimated mass
BF	78-91; 83.9; 3	45-47; 46.0; 3	56-57; 56.5; 2	555-655; 605; 2
Kc	58-62; 60; 2	33-36; 34.5; 2	54-62; 58; 2	254-263; 259; 2
LTh	80-118; 97.6; 14	49-71; 58.1; 14	51.8-65.5; 59.6; 14	671-2,055; 1,202; 14
TM	100-122; 109.5; 10	56-70; 63.0; 10	56-60; 57.7; 10	1,230-2,132; 1,612; 8
WM	101-124; 111.9; 9	62-74; 66.8; 8	56-63; 59.8; 8	1,397-2,279; 1,753; 8

Table 7. Measurements (min.-max. in mm; mean; N), proportion (min.-max.; mean; N), and estimated weight (min.-max. in kg; mean; N) for astragali in Baynunah hippopotamids and other late Miocene hippopotamids. **BF:** Baynunah Formation, Abu Dhabi; **Kc:** *Kenyapotamus* from Nakali Formation and Ngeringerowa (data for Ngeringerowa from Pickford, 1983; data for Nakali from Tsubamoto et al., 2016); **LTh:** Nawata Formation, Lothagam (data for *A. harvardi* from Weston, 2003); **TM:** Toros-Ménalla, Djourab; **WM:** Adu Asa Formation, Middle Awash; **H:** maximal proximodistal length; **W:** proximal trochlea transversal width; **estimated mass:** using Martínez & Sudre (1995)'s allometry equation $3.16 \times (H \times W)^{1.482}$.

especially compared with *A. harvardi* and the Adu Asa hippopotamid. Astragalar dimensions are a good proxy for body mass in artiodactyls (Martínez & Sudre, 1995) and this element was used to provide a body mass estimate for *A. qeshta* (Table 7). This species appears to be of moderate size for a hippopotamid, ca. 600 kg, i.e. on average half to one third the mass of the common species from Lothagam (*A. harvardi*), TM (*Hex. garyam*), and WM. It is however more than twice the mass of *Kenyapotamus*.

The relatively small dimensions of the Baynunah hippopotamid compared to *Hex. garyam*, *A. harvardi* and Hippopotamidae indet. from WM are confirmed by metapodial and/or phalangeal dimensions (Tables S1, S2, and S3). A metacarpal V attributed to *A. lothagamensis* is smaller than that of *A. qeshta* (Table S2), again supporting a smaller size of the former species compared to *A. qeshta*. Interestingly, the metapodials of *A. qeshta* are more robust than those of *A. harvardi*, although the later species is larger (Table S1). Compared with *A. harvardi*, the lateral metapodials are also

slightly more elongated relatively to the central ones. With regard to these proportions, *A. qeshta* is more similar to *Hex. garyam*. Both *Hex. garyam* and Hippopotamidae indet. from WM have larger phalanges than in *A. qeshta*, but in the WM they are wide relative to their length compared to the Baynunah species (Table S3).

DISCUSSION AND CONCLUSIONS

In his initial description of the hippopotamid material from the Baynunah Formation, Gentry (1999) observed that this material exhibited fewer morphological differences with *Hexaprotodon? sahabiensis* from Sahabi (Libya) than other species, and attributed it to '*Hexaprotodon* aff. *sahabiensis*'. In describing '*Hexaprotodon*' *lothagamensis*, Weston (2000) recognized more affinities between this new species and the Baynunah hippopotamid. Consequently, in a general revision of the phylogeny and systematics of the Hippopotamidae (Boisserie, 2005), the demonstration that *Hexaprotodon* was

a paraphyletic wastebasket taxon led to the establishment of the genus *Archaeopotamus* for hippopotamines displaying a relatively long symphysis, and to the proposition that the Baynunah hippopotamid should be referred to *Archaeopotamus* aff. *lothagamensis*. In light of the above description of the new material found in the Baynunah Formation following the first account by Gentry (1999) and of the reexamination of the older material, we here formally describe the Baynunah hippopotamid as a distinct species, *Archaeopotamus qeshta* nov. sp.

The lack of direct affinities between *A. qeshta* and *Hex. sahabiensis* is confirmed thanks to the recovery in the NML of additional Sahabi material described by Pavlakis (2008): the Libyan form has a clearly shorter symphysis and a more reduced I_2 . Its approximate symphyseal cross-section (see Fig. 6) is also quite distinct from any other late Miocene hippopotamids, but the pictures published by Pavlakis (2008) suggest that it could be somewhat distorted. The affinities of *Hex.?* *sahabiensis* remain obscure. Unfortunately, its holotype specimen is a partial corpus with P_4 - M_3 (Gaziry, 1987), i.e. a part of the mandible bearing few diagnostic features, and the original diagnosis does not present features that distinguish it from other late Miocene forms. The NML symphysis may have some morphological affinities with *Hex. garyam* from Chad (Fig. 5A and see illustrations provided by Pavlakis, 2008), but dimensions available for various specimens of *Hex.?* *sahabiensis* suggest that it could be a smaller species (see Tables 1 and 5).

Other material from northern Africa, from Annaba in Algeria and Wadi-Natron in Egypt, also differs from *A. qeshta*: the former display a greater difference between lower incisors, whereas the latter seems tetraprotodont (see Harrison, 1997) and somewhat smaller than *A. qeshta* according to the dimensions reported by Andrews (1902) and Stromer (1914).

Archaeopotamus can itself be described as a genus combining a *Kenyapotamus*-like mandibular morphology with a dental morphology similar to that of late Miocene-early Pliocene hippopotamines. It is therefore tempting to identify the late Miocene representatives of *Archaeopotamus*, and notably its somewhat more derived, larger species *A. harvardi*, as the stem group of latter hippopotamines (Harrison, 1997; Weston, 2000, 2003). In having a flatter symphysis and a relatively longer premolar row, *Archaeopotamus qeshta* is more like the earlier *Kenyapotamus* than *A. lothagamensis*. According to phylogenetic relationships within Hippopotamidae indicating that *Kenyapotamus* is basal to the Hippopotaminae (see, e.g., Boisserie *et al.*, 2010; Boisserie *et al.*, 2017; Lihoreau *et al.*, 2015), the Baynunah species would display the most archaic mandibular morphology within *Archaeopotamus* and all hippopotamines for which mandibular morphology is known.

However, the situation may be more complex as a result of the diversity generated during the Hippopotamine Event, not restricted to *Archaeopotamus* (Boisserie *et al.*, 2011). Other late Miocene species roughly contemporary with *A. qeshta* display more derived mandibular morphologies, such as *Hex. garyam* from central Africa (Boisserie *et al.*, 2005a) and the tetraprotodont *Hex.?* *crusafonti* (Aguirre, 1963) from southern Europe (Lacombe *et al.*, 1986). In addition, the early Pliocene *Saotherium mingoz* (Boisserie *et al.*, 2003) and the extant *Choeropsis liberiensis* (Morton, 1849) combine relatively short symphyses with some cranial traits seemingly more primitive than those of *A. harvardi* and *Hex. garyam*, indicating that another lineage may root even deeper within the Hippopotamine Event than *Archaeopotamus*. Future phylogenetic

analyses including *A. qeshta* should help unravel the relationships among these different hippopotamine lineages.

Another interesting aspect is that the material attributed to *Archaeopotamus* is known only from the northeastern parts of the Arabo-African landmass (Kenya and Abu Dhabi, and possibly Tanzania). Whether these species actually formed a clade within Hippopotaminae or not, they figure in any case as poor candidates for the late Miocene expansion of Hippopotamidae to southern Asia: the Siwalik forms, and notably *Hex. sivalensis* (Falconer & Cautley, 1836), have derived crania and relatively short, deep and robust symphyses that are much more similar to the morphology observed in *Hex. garyam* from central Africa (Boisserie *et al.*, 2005a). This and the fact that *A. qeshta* is so far the most archaic representative of the latest Miocene hippopotamines suggest that, for hippopotamids, the most parsimonious biogeographical scenario seems to be that the Arabian Peninsula was not a pathway for dispersal toward southern Asia at this time period, but instead an area of endemism.

Finally, relative to their ecology, species of the Hippopotamine Event are distinct from earlier hippopotamids in being very abundant and in incorporating a higher amount of C_4 plants (presumably grasses) in their diet. The family Hippopotamidae is an abundant taxon in the Baynunah Formation, comprising almost 20% of all collected large herbivore specimens (including equids, bovids, giraffids, suids, and proboscideans), a figure that compares with the relative frequency of hippopotamids in the Nawata Formation at Lothagam and in the Anthracotheriid Unit at Toros-Ménalla. In these two sites, the most common hippopotamine species are also the most abundant mammalian species. In the Baynunah Formation, fragmentary hippopotamid remains are very common on outcrop surfaces, and *A. qeshta* is certainly among the most abundant identified large mammal species.

The consumption of grasses, accounting for most of the C_4 plants in tropical areas, is an important element of the Hippopotamine Event, to the point that a coevolution was suggested between hippopotamines and grass communities (Boisserie *et al.*, 2011; Boisserie & Merceron, 2011). Notably, *Archaeopotamus harvardi* and *Hex. garyam* had diets in which C_4 plants occupied a significant to predominant proportion (Boisserie *et al.*, 2005b; Cerling *et al.*, 2003; Harris *et al.*, 2008). The enamel stable isotopic content of three specimens of Baynunah hippopotamids was analyzed by Kingston (1999), and this showed that these specimens had a diet dominated by C_4 plants (with $\delta^{13}C$ ranging between -5.6 ‰ and -0.3 ‰, mean -2.53 ‰). It can also be noted that the four $\delta^{18}O$ values obtained by Kingston (1999) for the Baynunah hippopotamids are among the five lowest obtained for the whole fauna, i.e. supportive of semi-aquatic habits (Bocherens *et al.*, 1996; Cerling *et al.*, 2003; Clementz & Koch, 2001). These isotopic ecological features of the Baynunah hippopotamids therefore do not depart from those observed in other late Miocene hippopotamines, fitting well the scenario proposed for the Hippopotamine Event (Boisserie *et al.*, 2011; Boisserie & Merceron, 2011).

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