

15. HIPPOPOTAMIDAE FROM THE LATE MIOCENE BAYNUNAH FORMATION

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Abstract: The Baynunah hippopotamid material provides further evidence for the Hippopotamine Event, which marked the spread and increased ecological impact of the Hippopotaminae into wet habitats across Africa and Eurasia at around 8 Ma. The Baynunah Formation hippopotamid belongs to a hippopotamine species 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*. A phylogenetic analysis suggests that this hippopotamine is so far the most primitive for which the mandibular morphology is well known. The morphological affinities of the Baynunah species confirm biogeographic links with Africa and indicate no connection between Afro-Arabian and southern Asia hippopotamids at this time, between 8 and 6 Ma.

Keywords: Baynunah Formation, Abu Dhabi; eastern Arabo-African landmass;
Hippopotamidae; Hippopotamine event; paleobiogeography; phylogeny; systematics

Running head: Hippopotamidae

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 is key to 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 and Hill 1999), which was initially described as *Hexaprotodon* aff. *sahabiensis* by Gentry (1999), later revised to *Archaeopotamus* aff. *lothagamensis* by Boisserie (2005), and recently attributed to a new species, *Archaeopotamus qeshta*, by Boisserie et al. (2017a). 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 since 2002 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 confirms its attribution to a new species of the genus *Archaeopotamus*.

Material and methods

The material described here was collected between 1982 and 1995 during surveys led by Peter Whybrow and Andrew Hill (Whybrow and Hill 1999), as well as from 2002 onward during surveys led by Andrew Hill, Faysal Bibi, and Mark J. Beech. 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 compared with direct observations of other Miocene hippopotamids: the middle to late Miocene *Kenyapotamus* spp. (Boisserie et al. 2010; Tsubamoto et al. 2016; Boisserie et al. 2017b); the new hippopotamine material from Chorora (Suwa et al. 2015; Katoh et al. 2016; Boisserie et al. 2017c); *Archaeopotamus* spp. from the Nawata Formation at Lothagam, Kenya (Weston 2000; Weston 2003; Boisserie 2005); *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 and 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 follows the recommendations of Bengston (1988).

Site and Institutional 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 are: *WM* Adu Asa Formation (‘Western Margin’ of the Middle Awash, Ethiopia), *LT* Lothagam (Kenya), *NP* Napudet (Turkana, Kenya), *SH* Samburu Hills (Kenya), *TM* Toros-Ménalla (Djourab, Chad). Main repository institutions are as follows: *CNRD* Centre National de la Recherche pour le Développement (N’Djaména, Chad), *KNM* Kenyan National Museums (Nairobi, Kenya); *NHM* Natural History Museum (London, England), *NML* National Museum of Libya; *MNHN* Muséum National d’Histoire Naturelle (Paris, France); *TBI* Turkana Basin Institute (Turkwel, Kenya).

Systematic Paleontology

CETARTIODACTYLA Montgelard, Catzeflis, & Douzery, 1997

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

HIPPOPOTAMOIDEA sensu Gentry & Hooker, 1988

HIPPOPOTAMIDAE Gray, 1821

HIPPOPOTAMINAE Gray, 1821

ARCHAEOPOTAMUS Boisserie, 2005

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

Other representatives. *Archaeopotamus harvardi* (Coryndon, 1977); *A. aff. harvardi* from Rawi (“pigmy hippo mandible, possibly *Hexaprotodon imagunculus*” in [Ditchfield et al. 1999: 131]; see Boisserie 2005); *A. qeshta* Boisserie, Schuster, Beech, Hill & Bibi, 2017.

Spatiotemporal distribution. Late Miocene to late Pliocene/early Pleistocene of Arabia and eastern Africa. Known from the Baynunah Formation, United Arab Emirates; Lothagam and Rawi in Kenya (Boisserie 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 fewer 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 Boisserie, 2005).

ARCHAEOPOTAMUS QESHTA Boisserie, Schuster, Beech, Hill & Bibi, 2017

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

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

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 (P/2-P/4) less than 10% shorter than the

molar row (M/1-M/3). Further differs from other late Miocene hippopotamines by the largest lower incisor being I/2. Further differs from larger late Miocene hippopotamines in: I1/ and I2/ being subequal in size and larger than I3/; I2/ being labiolingually compressed; and in lower premolar rows (P/1 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 (from Boisserie et al., 2017a).

Distribution. Currently known only from the Baynunah Formation. Faunal comparisons with African faunas suggest an age between 8 Ma and 6 Ma, possibly 7.5 Ma to 6.5 Ma (Hill 1999; Bibi et al. 2006; Bibi et al. 2013).

Material. Hamra: AUH 2, incisor fragment (HMR 1); AUH 5, left astragalus, fragmentary (HMR 1); AUH 44, right astragalus (HMR 5); AUH 154, right metacarpal V (HMR 1); AUH 369, left P/1 (HMR 1); AUH 457, partial mandible with eroded symphysis, left & right I/1-C/1 roots, broken right P/2, M/1-M/3, roots of other teeth (HMR 1); AUH 1241, left metacarpal II (HMR 1); AUH 1793, left M/1 (HMR 6). Jebel Dhanna: AUH 36, right M³/ (JDH 5); AUH 664, left P/1, germ (JDH 5); AUH 420, right metatarsal III, fragment (JDH 4); AUH 421, P⁴/, fragmentary (JDH 4). Shuwaihat: AUH 53, right metacarpal III (SHU 1); AUH 83, proximal phalanx III or IV (SHU 1); AUH 96-97, right metacarpal III (SHU 1); AUH 247, left metatarsal III (SHU 4); AUH 481, juvenile mandible with partial symphysis, most of right corpus and fragment of left corpus, right I/1-I/2, left I/2-I/3, left & right C/1, left P/2-P/4, right P/2-P/3, and dP/4 (SHU 4). Thumayriya: AUH 243, right metatarsal III (THM 1). Kihal: AUH 262, P⁴/, fragmentary (KIH 1); AUH 1252 right astragalus, eroded (KIH 4). Harmiyah: AUH 359, two

enamel fragments from left upper premolar and right upper canine (HAR 1). Jebel Barakah: AUH 368, left astragalus (JBR 1); NHM M49464, holotype collected by Peter J. Whybrow in 1982, mandible with eroded symphysis, left P₃-M₃, right P₄ and fragmentary M₃ (JBR 2); NHM M49465, right P³/ (JBR 2). Gerain al-Aysh: AUH 1532, right M²/ (GAA 2); AUH 1561, right metacarpal IV (GAA 3); AUH 1564, left P¹/ (GAA 3); AUH 1794, proximal phalanx III or IV (GAA 2); AUH 1795, proximal phalanx III or IV (GAA 2). Baynunah North: AUH 1614, right premaxilla with I³/ and roots of I¹/-I²/, broken (BYN 1). Ruwais Central: AUH 1731, left I²/ (RUW C); AUH 1736, left astragalus, fragmentary (RUW C).

Some additional specimens are referred to *Archaeopotamus* cf. *qeshta*. Shuwaihat: AUH 29, canine, fragment (SHU 1); AUH 84, central metapodial, fragment (SHU 1); AUH 110, lower molar, fragment (SHU 1); AUH 248, lateral metapodial, distal fragment (SHU 4); AUH 795, right dP₃ (SHU 2). Hamra: AUH 150, right tibia, distal fragment (HMR 3); AUH 339, intermediate phalanx II or V (HMR 5); AUH 1242, metapodial, fragmentary and eroded (HMR 1); AUH 1714, tooth, fragmentary and distorted (HMR 5). Jebel Dhanna: AUH 288, right fibula, distal fragment (JDH 3); AUH 292, upper incisor, apical fragment (JDH 3). Ras al Qal'a: AUH 429, axis (RAQ 1). Jebel Barakah: AUH 446, left C/1, fragment (JBR 2). Thumayriya: AUH 478, intermediate phalanx II or V (THM 1). Jebel Mimiya: AUH 1278, lower incisor, fragmentary (MIM 1). Baynunah North: AUH 1619, left radius-ulna (BYN 3). Ruwais Central: AUH 1730, left hamate (RUW C); AUH 1741, proximal phalanx II or V (RUW C).

PLACE FIGURE 15.1 ABOUT HERE; WIDTH = 2 COLUMNS

Some of the material reported by Gentry (1999) cannot be attributed with certainty to *Archaeopotamus qeshta* and is treated here as Hippopotamidae indet. or cf. Hippopotamidae.

Hippopotamidae indet.: AUH 31, tooth fragments (SHU 1); AUH 49, right scapula, proximal fragment (HMR 5); AUH 57, incisor fragment; AUH 59, left femur, distal fragment (SHU 1); AUH 60, tooth fragments (SHU 1); AUH 66, cervical vertebra, fragment (SHU 1); AUH 68, left humerus, distal fragment (SHU 1); AUH 92, tooth fragments (SHU 1); AUH 98, right radius, distal fragment (SHU 1); AUH 99, maxilla with M³/ frag (SHU 1); AUH 103, ilium fragment (SHU 1); AUH 105, thoracic vertebra, fragments (SHU 1); AUH 118, right scapula, proximal fragment (SHU 1); AUH 133, ischium fragment (SHU 2); AUH 170, right lunate (HMR 1); AUH 224, cervical vertebra, fragment (SHU 4); AUH 235, mandible fragments (SHU 4); AUH 252, right cuneiform (SHU 4); AUH 253, right radius, proximal fragment (SHU 4); AUH 293, left rib, dorsal fragment (JDH 3); AUH 431, atlas, fragmentary (RAQ 1); AUH 443, right scapula, fragment (JBR 2); AUH 497, right humerus, fragmentary (JDH 3); AUH 498-499, right tibia, proximal fragments (JDH 3); AUH 637, right astragalus, fragment (BJW 1, Bin Jawabi); AUH 828, left tibia, slightly eroded (SHU 3); AUH 844, left metacarpal V, fragmentary and eroded (SHU 4); AUH 861, axis corpus, fragmentary (SHU 9); AUH 863, upper molar, fragmentary and very worn (SHU 9); AUH 870, right metatarsal V, fragmentary (SHU 10); AUH 1041, juvenile left calcaneum, fragmentary and eroded (SHU 3). cf. Hippopotamidae: AUH 37, incisor, fragment (JDH 5); AUH 312: incisor, fragment (KIH 1).

Comparative Description

Mandible

The two best-preserved mandibular specimens of *Archaeopotamus qeshta* are the holotype mandible M49464 and the fragmentary mandible AUH 457 (Fig. 15.1). The latter displays a damaged symphysis, lacks most of the ascending rami, and retains a broken right P₂ and partial

right M₁-M₃. Both specimens are adult, displaying M₃s with advanced wear. The two specimens differ mostly in that AUH 457 is more robust (with notably greater corpus thickness), has a longer symphysis and canine processes that project slightly more laterally (Fig. 15.1, Table 15.1). These moderate differences are compatible with sexual dimorphism in the living species *Hippopotamus amphibius* and *Choeropsis liberiensis* (see Weston 1997, Boisserie 2002). 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 P₂-P₃ erupting and dP₄ in advanced wear. It is only slightly smaller in size than the two adult mandibles, but markedly narrower (Fig. 15.2, Table 15.1).

PLACE TABLE 15.1 ABOUT HERE

These three mandibles are characterized by symphyses that are greatly elongated relative to their width, *A. qeshta* displaying the longest mandibular symphysis relative to the width within the Hippopotaminae (Table 15.3a). Only *Kenyapotamus ternani* Pickford, 1983 displays a relatively more elongate symphysis, documented by specimen KNM-NP 64505 from Napudet (Boisserie et al. 2017b). The Baynunah symphyses are also relatively shallow compared to the symphysis of *Hexaprotodon garyam* (Fig. 15.3a). This higher symphysis is related to the greater robustness of the nuchal part of the symphysis combined with the greater inclination of the incisive alveolar process in *Hex. garyam* (Fig. 15.4).

PLACE FIGURE 15.2 ABOUT HERE; WIDTH = 1 COLUMN

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, and *K. ternani*, differing from *Hex. garyam*, *Hex. sivalensis*, and *A. harvardi* in which a ventral shift in curvature clearly differentiate the process from the nuchal portion of the symphysis (Fig. 15.4). 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. 15.4). 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 the thinness and of the incisive alveolar process (Fig. 15.4).

PLACE FIGURE 15.3 ABOUT HERE; WIDTH = 2 COLUMNS

The incisive alveolar process of *A. qeshta* also displays a more or less marked sagittal depression on its ventral side (Fig. 15.1c). 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. 15.1), 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. 15.2a), as in KNM-NP 64505 attributed to *Kenyapotamus*. The rostral border in *A. harvardi* and *Hex. garyam* is more or less straight.

PLACE FIGURE 15.4 ABOUT HERE; WIDTH = 2 COLUMNS

In rostral view, the incisor alveolar plane in *A. qeshta* is displaced, the I_1 being set more ventrally than the I_3 , and the I_2 more dorsally than the two others (Fig. 15.1c). 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 that is 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 the same horizontal level. The most similar arrangement 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*. *Hex. 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. This is not the case in M49464, in which the canine processes are in continuity with the corpus (Fig. 15.1). 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 cheek teeth that diverge laterally. *Hexaprotodon 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.

In rostral view, the canine alveoli of *A. qeshta* are subparallel to the line joining the right and left I₃. 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.

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. 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. A relatively shallow 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 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. 15.1a,e), whereas AUH 481 displays a U shape (Fig. 15.2a). 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 in the extant species (Boisserie 2002).

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 flatter ventral surfaces. More caudally, the three specimens of *A. qeshta* also display large depressions for genioglossal insertions extending onto 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. 15.1d,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 *A. qeshta* is thin and oriented in the same plane as the corpus (Fig. 15.1a,e), as in *A. harvardi*, and unlike the everted process observed in *Hex. garyam*.

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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 onto the mesial and distal sides on the I²/, and restricted to the labial side of I³/. I¹/ and I²/ are subequal in cross-sectional 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 reduced compared to the I¹/, or similar in cross-sectional size (Table 15.2). The lingual side of these incisors is more or less flat, the I²/ having a longitudinal groove between two crests. I²/ is labiolingually compressed unlike in *A. harvardi*, *Hex. garyam*, and Hippopotamidae indet. from WM (Table 15.2). I¹/ and I³/ have close linguolabial and mesiodistal diameters (Table 15.3). I³/ presents an apical, beveled wear facet that extends to the distal side, the edge of the facet being smoothed by this distal wear.

PLACE TABLE 15.2 ABOUT HERE

AUH 1731 (Fig. 15.5a) is an isolated, complete I²/ that is similar to the AUH 1614 I²/ in being strongly compressed labiolingually, 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 tapers markedly from crown to base, suggesting that this tooth may not have been 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 that is usually observed in late Miocene hippopotamine canines.

PLACE TABLE 15.3 ABOUT HERE

Within the lower incisors of *Archaeopotamus qeshta*, I₂ displays the largest cross-section, as in *K. ternani* and *A. lothagamensis* (Tables 15.2 and 15.4). 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, *Hex. garyam*, and *Hexaprotodon sahabiensis*, I₁ is the largest lower incisor (Table 15.2). In AUH 481 (Fig. 15.2), 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).

PLACE TABLE 15.4 ABOUT HERE

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.

Postcanine Dentition

Premolar and molar dimensions are provided in Tables 15.5, 15.6, 15.7, and 15.8. The postcanine dentition of *Archaeopotamus qeshta* appears close in size to that 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* and *Hex. garyam*, as shown for M₃ on Fig. 15.3b, as well as with the lower range of Hippopotamidae indet. from WM in most cases (see Tables 15.5 to 15.8) .

PLACE TABLES 15.5, 15.6, 15.7, AND 15.8 ABOUT HERE

P¹/ of *Archaeopotamus qeshta* 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/ with advanced wear and missing a fragment of its apex (Fig. 15.5b). 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 Boisserie 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 (Boisserie et al. 2017c), 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. 15.5c), 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*. Similarly to *Kenyapotamus* and some specimens of *Hex. garyam*, the paracone does not present a well-developed endoparacrista,. This contrasts with the strong endoparacrista observed in *A. harvardi* and most representatives of *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. 15.5e). This tooth is square-shaped, as in most hippopotamines. Its cingula 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, or cristyles.

The other upper molar is an unworn, isolated right M³/ (AUH 36, Fig. 15.5f). This tooth has a strongly crenulated cingulum that attenuates only on the labial side of the paracone. The cristae are long and sharp, with the preparacristae and postmetacristae 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 postprotocrista 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 reaching 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 15.7. 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.

P₁ is known from two isolated specimens. AUH 369 is a moderately worn, single-rooted left P₁. The paraconid is fang-like with a minute conulid on the base of the postparacristid. A cingulid is present only on the mesial side. The root has a single lobe and it is large compared to the crown. AUH 664 is a crown of another left P₁ (Fig. 15.5d). It is unworn and probably unerupted. It is more labiolingually compressed 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 P₁ alveoli on M49464 and AUH 457 also indicate single rooted teeth (Fig. 15.1a,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 P₂-P₄ row is long relative to the molar row (Table 15.9). This is notably marked compared to *Hex. garyam*, but also true compared to other species of *Archaeopotamus*. Only *Kenyapotamus* displays a somewhat longer P₂-P₄ row. These teeth display a morphological gradient that is typical for early hippopotamines: the metaconid is incipient and distally shifted in P₂; large, high, and lingual on the P₄; intermediate or as in P₂ in the P₃. The mesial and distal cingulids are low and thin in P₂ and become larger and higher in the distal premolars. P₄ displays both well-expressed entoconid and hypoconid (Fig. 15.1b), whereas the former can be missing on P₂ and P₃ (AUH 481). A distal fragment of a lower premolar associated with M494646 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.

PLACE TABLE 15.9 ABOUT HERE

The lower molars of *A. qeshta* (Fig. 15.1b) have a trigonid organization typical of Hippopotaminae, observable on the M/3 of M49464 and on AUH 1793 (left M/1) preserved 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 prehypocristid, which is inflated into a prehyoconulid.

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* in this contribution. The astragali of *A. qeshta* are morphologically similar to those of hippopotamids. Their general proportions fit the ranges observed in *Kenyapotamus*, *A. harvardi*, *Hex. garyam*, and Hippopotamidae indet. from WM (Table 15.10), but the Baynunah specimens are on average somewhat narrower, especially compared with *A. harvardi* and the Adu Asa hippopotamid. Astragalar dimensions are a good proxy for body mass in artiodactyls (Martínez and Sudre 1995), and this element was used to provide a body mass estimate for *A. qeshta* (Table 15.10). 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 twice the mass of *Kenyapotamus*.

PLACE TABLE 15.10 ABOUT HERE

The relatively small dimensions of the Baynunah hippopotamid compared to *Hex. garyam*, *A. harvardi* and Hippopotamidae indet. from WM are confirmed by metapodial and phalangeal dimensions (Tables 15.11, 15.12, 15.13, and 15.14). A metacarpal V attributed to *A. lothagamensis* is smaller than that of *A. qeshta* (Table 15.13), 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 15.11). 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 wider relative to their length than in the Baynunah species (Table 15.14).

PLACE TABLES 15.11, 15.12, 15.13, AND 15.14 ABOUT HERE

Phylogenetic Analysis

A morphological character matrix was initially assembled by Boisserie et al. (2010), refined by Orliac et al. (2010) and further extended by Alloing-Séguier et al. (2014) and Lihoreau et al. (2015) in order to test the phylogenetic relationships between Hippopotamidae, anthracotheres, Suina, and other cetartiodactyls. This matrix so far combines the largest number of fossil hippopotamoids and other cetartiodactyls in a phylogenetic investigation to date (164 craniodental characters for 58 taxa; outgroups: *Homacodon*, *Gujaratia*, and *Bunophorus*). Here we include *Archaeopotamus qeshta* as well as new hippopotamid material of *Kenyapotamus* from the middle Miocene of Napudet (Boisserie et al. 2017b) and from the middle and upper beds at Chorora (Suwa et al. 2015; Katoh et al. 2016; Boisserie et al. 2017c). The matrix was additionally

modified from that of Lihoreau et al. (2015) by changing the coding of one character (character 120: connection of premetacrista and postprotocrista). The matrix and tree nexus files are available at <http://purl.org/phylo/treebase/phylows/study/TB2:S21683>.

PLACE TABLE 15.15 ABOUT HERE; LANDSCAPE FORMAT, WIDTH = 9.2 INCHES

A parsimony analysis was performed using PAUP 4.0a150 (Swofford 2002). The search was heuristic, treated multistate characters as polymorphisms, and was run for 1,000 replicates with random addition sequence. The analysis resulted in 33 trees of 1091 steps. The resulting consensus tree (Fig. 15.6) resolves the relationships of Hippopotamidae by anchoring this family within the archaic bothriodontine group that mostly evolved in Africa and that includes *Bothriogenys* and *Brachyodus*. This agrees with the general interpretation of the position of *Epirigenys* as sister-group of the clade Hippopotamidae (Lihoreau et al. 2015). Within this clade, the relationships between kenypotamines are not resolved. In contrast, the Hippopotaminae form a clade (Fig. 15.6D) supported by multiple dental features including the presence of more than two postparaconules (character 80), the low cingula on the upper molars (character 101) and the organization of the trigonid (notably character 39). *Archaeopotamus* is paraphyletic, with *A. qeshta* being the sister-group of *A. harvardi* + *Hexaprotodon garyam*. The latter two species are united only by the I_1 being the largest lower incisor, while in *A. qeshta* it is the I_2 (character 4).

PLACE FIGURE 15.6 ABOUT HERE; WIDTH = 1 COLUMN

Discussion and Conclusions

The Baynunah Hippopotamid and its Relationships with Hexaprotodon? sahabiensis

In summary, the Baynunah hippopotamid material belongs to a small-sized species intermediate in size between *Archaeopotamus lothagamensis* and *Archaeopotamus harvardi*. There is no evidence for the presence of more than one hippopotamid species in the Baynunah Formation. The main differences of the Baynunah hippopotamid from other hippopotamines with known mandibular morphology are that it displays a symphysis more elongate relative to its width and a premolar row (P₂-P₄) less than 10% shorter than the molar row (M₁-M₃). The rostral dentition is also quite distinctive. I₂ is the largest lower incisor, whereas in other late Miocene hippopotamines it is I₁ or I₃. Unlike other species of *Archaeopotamus*, I₁ and I₂ are the most ventral and dorsal lower incisors, respectively, and the lower incisors are less procumbent than in *A. harvardi*. Unlike the larger late Miocene hippopotamines (notably *Hexaprotodon garyam* and *A. harvardi*), I²/₁ is labiolingually compressed, and I¹/₁ and I²/₁ are subequal in size and larger than I³/₁. The Baynunah material further differs from these large hippopotamines in displaying almost no rostral divergence between its left and right lower premolar rows (P₁ included).

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 and of the reexamination of the older material (Gentry 1999), Boisserie et al. (2017a) formally recognized the Baynunah hippopotamid as a distinct species, *Archaeopotamus qeshta*.

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 I₂. Its approximate symphyseal cross-section (see Fig. 15.4) 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 P₄-M₃ (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. 15.3a 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 15.1 and 15.8).

Phylogenetic Placement

Archaeopotamus can 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 shallower symphysis (Fig. 15.3a) and a relatively longer premolar row (Table 15.9), *Archaeopotamus qeshta* is more like the earlier *Kenyapotamus* than *A. lothagamensis*. Following our phylogenetic analysis, in which *Kenyapotamus* is basal to a paraphyletic *Archaeopotamus* (in agreement with

Boisserie et al. 2010; Lihoreau et al. 2015) and *A. qeshta* is the sister-group of a clade comprising *A. harvardi* and *Hexaprotodon garyam* from central Africa (Fig. 15.6), the mandibular morphology of the Baynunah species could be interpreted (contra Boisserie 2005) as the most archaic 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* (see 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) have more derived mandibular morphology but combine relatively short symphyses with some cranial traits seemingly more primitive than those of *A. harvardi* and *Hex. garyam*, indicating that their lineage may root even deeper within the Hippopotamine Event than *Archaeopotamus*.

Our analysis relied on craniodental characters and did not consider a large number of hippopotamine taxa. Further analyses of the relationships among these different hippopotamine lineages can continue to expand the array of skeletal characters and hippopotamid taxa considered. The full description of *A. qeshta* was an additional step in this regard.

Paleobiogeography and Paleoecology

Another interesting aspect of our growing understanding of Miocene hippopotamines is that the material attributed to *Archaeopotamus* is known only from the northeastern parts of the Arabo-African landmass (Kenya and Abu Dhabi). Whether these species actually formed a clade within

Hippopotaminae or not, they are morphologically poor candidates for the late Miocene expansion of Hippopotamidae to southern Asia. The Siwalik forms, and notably *Hex. sivalensis* (Falconer and 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 the most archaic representative of the latest Miocene hippopotamines known suggest that, for hippopotamids, the Arabian Peninsula was not a pathway for dispersal toward southern Asia at this time period.

Finally, relative to their ecology, species of the Hippopotamine Event are distinct from earlier hippopotamids in being very abundant and in incorporating a greater proportion of C₄ 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. At these latter two sites, hippopotamines 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 C₄ plants in tropical areas, is an important element of the Hippopotamine Event to the point that coevolution was suggested between hippopotamines and grass communities (Boisserie et al. 2011; Boisserie and Merceron 2011). Notably, *Archaeopotamus harvardi* and *Hex. garyam* had diets in which C₄ plants occupied a significant to predominant proportion (Boisserie et al. 2005b; Cerling et al. 2003; Harris et al. 2008). The stable isotopic content of Baynunah hippopotamid (Kingston, 1999; Uno, this volume) tooth enamel indicates a diet dominated by C₄ plants, while $\delta^{18}\text{O}$ values are among

the lowest obtained for the whole fauna and support an interpretation of semi-aquatic habits (Bocherens et al. 1996; Cerling et al. 2003; Clementz and Koch 2001). These isotopic ecological features of the Baynunah hippopotamids therefore do not depart from those observed in other late Miocene hippopotamines, corroborating the scenario proposed for the Hippopotamine Event (Boisserie et al. 2011; Boisserie and Merceron 2011).

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Tables

Table 15.1 Measurements (min.-max. in mm; mean; N) for mandibles of *Archaeopotamus qeshta* (in *italics*) compared to those of other hippopotamids

	M1	M2	M3	M4	M5	M6
<i>AAH 457</i>	~355	~192	117	52	~96	97
<i>M49464</i>	~356	~165	113	42	87	~88
<i>AAH 481</i>		165	~87		~82	
KT		104	47		53	
AL	~302	~139	101	44	92	80
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
AR	328	155	126			
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
HS		127	112		83	

Taxa: *AL Archaeopotamus lothagamensis* from Lothagam, *AH Archaeopotamus harvardi* from Lothagam, *AR Archaeopotamus aff. harvardi* from Rawi, *HG Hexaprotodon garyam* from Toros-Ménalla, *HS Hexaprotodon? sahabiensis* from Sahabi (data from Pavlakis 2008), *KT Kenyapotamus ternani* from Napudet (data from Boisserie et al. submitted-a)

Measurements: *M1* length from mid-point between right and left I_1 to distal M_3 , *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 $M/1$, *M5* corpus height at mesial $P/2$, *M6* corpus height at mesial $M/3$

Table 15.2 Proportions of $I^2/$ (min.-max.; mean; N) and interincisive ratios (min.-max.; mean; N) in *Archaeopotamus qeshta* (in *italics*) compared to those of other hippopotamids

	I^2/S	$I^2/1$	$I^3/1$	$I_2/1$	$I_3/1$
<i>AQ</i>	<i>70.5-76.7;</i> <i>73.42; 3</i>	<i>98.2</i>	<i>62.9</i>	<i>108.4-140.6;</i> <i>126.29; 3</i>	<i>90.9-123.5;</i> <i>107.20; 2</i>
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
HS				53.8	93.4
WM	99.6	107.2	81.3		

Taxa: *AQ* *Archaeopotamus qeshta*, *AL* *Archaeopotamus lothagamensis* from Lothagam, *AH* *Archaeopotamus harvardi* from Lothagam, *AR* *Archaeopotamus* aff. *harvardi* from Rawi, *HG* *Hexaprotodon garyam* from Toros-Ménalla, *HS* *Hexaprotodon? sahabiensis* from Sahabi (data

from Gaziry 1987), *KT Kenyapotamus ternani* from Napudet (data from Boisserie et al. submitted-a), *WM* Hippopotaminae indet. from Adu Asa Formation

Measurements: I^2/S : shape ratio of the $I^2/$ cross-section, $100 \times (LL / MD)$ in which LL is the linguolabial diameter and MD the mesiodistal diameter. I^2/I^1 ratio $100 \times (I^2/ MD \times I^2/ LL) / (I^1/ MD \times I^1/ LL)$, I^3/I^1 ratio $100 \times (I^3/ MD \times I^3/ LL) / (I^1/ MD \times I^1/ LL)$, $I_{2/1}$ ratio $100 \times (I_2 MD \times I_2 LL) / (I_1 MD \times I_1 LL)$, $I_{3/1}$ ratio $100 \times (I_3 MD \times I_3 LL) / (I_1 MD \times I_1 LL)$. These values are calculated from measurements summarized in Tables 15.3 and 15.4

Table 15.3 Measurements (min.-max. in mm; mean; N) for rostral upper dentition of *Archaeopotamus qeshta* (in italics) compared to those of other hippopotamids

	$I^1/$		$I^2/$		$I^3/$	
	MD	LL	MD	LL	MD	LL
<i>AQ</i>	18.3	17.6	20.8-21.7; 21.17; 3	15.2-16.1; 15.53; 3	15.0	13.5
AH	24.0	22.6	25.5	23.2	20.9	22.7
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

Taxa: *AQ* *Archaeopotamus qeshta*, *AH* *Archaeopotamus harvardi* from Lothagam, *HG* *Hexaprotodon garyam* from Toros-Ménalla

Measurements: *MD* mesiodistal diameter, *LL* labiolingual diameter, *MAX* maximum diameter, *MIN* minimum diameter

Table 15.4 Measurements (min.-max. in mm; mean; N) for rostral lower dentition of *Archaeopotamus qeshta* (in italics) compared to those of other hippopotamids

	I ₁		I ₂		I ₃		C ₁	
	MD	LL	MD	LL	MD	LL	MAX	MIN
<i>AQ</i>	<i>10.4-14.8;</i> <i>12.60; 2</i>	<i>16.2-18.6;</i> <i>17.40; 2</i>	<i>15.2-18.2;</i> <i>16.70; 2</i>	<i>13.8-17.1;</i> <i>15.45; 2</i>	<i>11.8-16.1;</i> <i>13.95; 2</i>	<i>14.9</i>	<i>42.6-44.6;</i> <i>43.60; 2</i>	<i>24.0-27.9;</i> <i>25.95; 2</i>
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	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	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

Taxa: *AQ* *Archaeopotamus qeshta*, *AL* *Archaeopotamus lothagamensis* from Lothagam, *AH* *Archaeopotamus harvardi* from Lothagam, *AR* *Archaeopotamus* aff. *harvardi* from Rawi, *HG* *Hexaprotodon garyam* from Toros-Ménalla, *HS* *Hexaprotodon? sahabiensis* from Sahabi (data from Pavlakis 2008), *KT* *Kenyapotamus ternani* from Napudet (data from Boisserie et al. submitted-a)

Measurements: *MD* mesiodistal diameter, *LL* labiolingual diameter, *MAX* maximum diameter, *MIN* minimum diameter

Table 15.5 Measurements (min.-max. in mm; mean; N) for upper third premolar of *Archaeopotamus qeshta* (in *italics*) compared to those of other hippopotamids

	P ³ /	
	L	W
<i>AQ</i>	37.8	~30.6
KE	25.0-29.4; 27.20; 2	19.7-20.3; 20.00; 2
AH	35.4-48.2; 40.35; 10	27.4-35.1; 31.70; 9
HG	35.6-47.0; 41.22; 31	28.2-43.0; 34.15; 31
HS	36.0	26.0
WM	38.6	26.2

Taxa: *AQ* *Archaeopotamus qeshta*, *AH* *Archaeopotamus harvardi* from Lothagam, *HG* *Hexaprotodon garyam* from Toros-Ménalla, *HS* *Hexaprotodon? sahabiensis* from Sahabi (data from Gaziry 1987), *KE* middle and late Miocene *Kenyapotamus* from Kenya, *WM* Hippopotaminae indet. from Adu Asa Formation

Measurements: *L* mesiodistal length, *W* maximal width

Table 15.6 Measurements (min.-max. in mm; mean; N) for lower premolars of *Archaeopotamus qeshta* (in *italics*) compared to those of other hippopotamids

	P/1		P/2		P/3		P/4	
	L	W	L	W	L	W	L	W
<i>AQ</i>	<i>17.3-18.7;</i> <i>17.55; 2</i>	<i>11.4-13.4;</i> <i>12.40; 2</i>	<i>29.2-40.2;</i> <i>34.70; 2</i>	<i>18.2-19.7;</i> <i>18.95; 2</i>	<i>35.7-39.1;</i> <i>37.40; 2</i>	<i>19.6-23.1;</i> <i>21.35; 2</i>	<i>33.9-34.5;</i> <i>34.20; 2</i>	<i>22.4-23.8;</i> <i>23.10; 2</i>
KE			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			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	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	25.0
WM	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

Taxa: *AQ* *Archaeopotamus qeshta*, *AL* *Archaeopotamus lothagamensis* from Lothagam, *AH* *Archaeopotamus harvardi* from Lothagam, *AR* *Archaeopotamus* aff. *harvardi* from Rawi, *HG* *Hexaprotodon garyam* from Toros-Ménalla, *HS* *Hexaprotodon? sahabiensis* from Sahabi (data

from Gaziry 1987), *KE* middle and late Miocene *Kenyapotamus* from Kenya and Tunisia, *WM* Hippopotaminae indet. from Adu Asa Formation

Measurements: *L* mesiodistal length, *W* maximal width

Table 15.7 Measurements (min.-max. in mm; mean; N) for upper molars of *Archaeopotamus qeshta* (in *italics*) compared to those of other hippopotamids

	M ² /		L	M ³ /		
	L	W		W	h	H
<i>AQ</i>	<i>46.0</i>	<i>44.6</i>	<i>42.6</i>	<i>44.4</i>	<i>34.0</i>	<i>76.6</i>
KE	22.6-29.0; <i>25.92</i> ; 4	24.6-25.7; <i>26.05</i> ; 2	20.0-29.7; <i>24.85</i> ; 2	23.0-29.4; <i>25.63</i> ; 3	18.8	66.6
AH	37.2-50.0; <i>44.58</i> ; 16	39.7-55.6; <i>45.99</i> ; 16	44.0-51.7; <i>47.17</i> ; 13	41.4-56.2; <i>46.48</i> ; 13	32.1	76.6
HG	42.4-54.3; <i>48.37</i> ; 35	41.2-53.5; <i>47.38</i> ; 30	37.8-57.4; <i>47.74</i> ; 49	40.8-52.2; <i>46.54</i> ; 48	34.6-40.0; <i>36.41</i> ; 8	73.7-81.4; <i>78.49</i> ; 8
HS			39.0	42.0		
WM	45.4-46.2; <i>45.80</i> ; 2	44.4-45.5; <i>44.95</i> ; 2	43.4-49.2; <i>46.68</i> ; 4	39.1-45.9; <i>42.77</i> ; 4	36.4	107.2

Taxa: *AQ* *Archaeopotamus qeshta*, *AH* *Archaeopotamus harvardi* from Lothagam, *HG* *Hexaprotodon garyam* from Toros-Ménalla, *HS* *Hexaprotodon? sahabiensis* from Sahabi (data

from Gaziry 1987), *KE* middle and late Miocene *Kenyapotamus* from Kenya and Tunisia, *WM* Hippopotaminae indet. from Adu Asa Formation

Measurements: *L* mesiodistal length, *W* maximal width, *h* paracone height from cervix to apex, *H* hypsodonty index $100 \times h / W$

Table 15.8 Measurements (min.-max. in mm; mean; N) for lower molars of *Archaeopotamus geshta* (in *italics*) compared to those of other hippopotamids

	M ₁	M ₂		M ₃	
	W	L	W	L	W
<i>AQ</i>	25.2-25.7; <i>25.45; 2</i>	41.5-44.8; <i>43.15; 2</i>	31.8-33.7; <i>32.75; 2</i>	54.9- ~62.9; 58.9; <i>2</i>	<i>31.5</i>
KE	17.7	28.5-33.1; <i>30.8; 2</i>	26.4	41.1-42.9; 42.00; 2	23.9-24.1; <i>24.00; 2</i>
AL	22.9-28.6; <i>25.75; 2</i>	41.1-42.7; <i>41.90; 2</i>	27.8-34.0; <i>30.90; 2</i>	49.8-51.1; 50.45; 2	28.3-29.2; <i>28.75; 2</i>
AH	26.1-35.0; <i>31.34; 9</i>	41.2-51.3; <i>47.44; 11</i>	33.0-38.4; <i>36.16; 10</i>	58.3-68.0; 63.10; <i>16</i>	32.0-40.2; <i>35.88; 15</i>
AR	24.1	41.3	27.3	54.4	31.0
HG	26.8-39.0; <i>30.99; 23</i>	41.6-54.0; <i>49.28; 31</i>	30.8-45.2; <i>37.53; 26</i>	59.1-70.7; 63.26; <i>31</i>	31.9-45.2; <i>38.12; 31</i>

HS		39.0	34.0	59.0	33.0
WM	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

Taxa: *AQ Archaeopotamus qeshta*, *AL Archaeopotamus lothagamensis* from Lothagam, *AH Archaeopotamus harvardi* from Lothagam, *AR Archaeopotamus aff. harvardi* from Rawi, *HG Hexaprotodon garyam* from Toros-Ménalla, *HS Hexaprotodon? sahabiensis* from Sahabi (data from Gaziry 1987), *KE* middle and late Miocene *Kenyapotamus* from Kenya and Tunisia, *WM* Hippopotaminae indet. from Adu Asa Formation

Measurements: *L* mesiodistal length, *W* maximal width

Table 15.9 Measurements (min.-max. in mm; mean; N) and proportions of lower dental rows (min.-max. in mm; mean; N) in *Archaeopotamus qeshta* (in *italics*) compared to those of other hippopotamids

	P	M	$100 \times (P / M)$
<i>AAH 457</i>	<i>126</i>	<i>127</i>	<i>99.2</i>
<i>M49464</i>	<i>131</i>	<i>~142</i>	<i>92.3</i>
KE	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

Taxa: *AL Archaeopotamus lothagamensis* from Lothagam, *AH Archaeopotamus harvardi* from Lothagam, *AR Archaeopotamus aff. harvardi* from Rawi, *HG Hexaprotodon garyam* from Toros-Ménalla, *HS Hexaprotodon? sahabiensis* from Sahabi (data from Pavlakis 2008), *KE* middle and late Miocene *Kenyapotamus* from Kenya and Tunisia

Measurements: *P* length from mesial P₂ to distal P₄, *M* length from mesial M₁ to distal M₃

Table 15.10 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 hippopotamines (in *italics*) and other late Miocene hippopotamids

	H	W	100 × W / H	EM
<i>BF</i>	77.7-90.7; 83.9; 3	44.5-46.9; 46.0; 3	55.9-57.3; 56.6; 2	555-655; 605; 2
KC	58.0-61.5; 59.8; 2	33.2-36.0; 2	54.0-62.1; 58.0; 2	254-263; 259; 2
LTH	80.2-117.9; 97.6; 14	49.0-71.0; 58.1; 14	51.8-65.5; 59.6; 14	671-2,055; 1,202; 14
TM	100.2-121.8; 109.5; 10	56.2-70.4; 63.0; 10	55.7-59.7; 57.7; 10	1,230-2,132; 1,612; 8
WM	101.3-123.9; 111.9; 9	61.6-73.9; 66.8; 8	55.9-63.0; 59.8; 8	1,397-2,279; 1,753; 8

Taxa: *BF* Baynunah Formation, Abu Dhabi, *KC Kenyapotamus cf. coryndonae* from the Nakali Formation and Ngeringerowa (data for Ngeringerowa from Pickford 1983, data for Nakali from Tsubamoto et al. 2016), *LTH* Nawata Formation at Lothagam (data for *A. harvardi* from Weston 2003), *TM* Toros-Ménalla in the Djourab, *WM* Adu Asa Formation in Middle Awash

Measurements: *H* maximal proximodistal length, *W* proximal trochlea transversal width, *EM* estimated mass using Martinez & Sudre (1995)'s allometry equation $3.16 \times (H \times W)^{1.482}$

Table 15.11 Proportions (min.-max.; mean; N) for metapodials in Baynunah hippopotamines (in *italics*) and other late Miocene hippopotamines

	Mc III	Mc IV	Mc V	Mt II	Mt III
<i>BF</i>	<i>23.1</i>	<i>24.4</i>	<i>30.2</i>	<i>22.9</i>	<i>23.1-26.1;</i> <i>24.6; 2</i>
LTL			27.6		
LTH	17.3-18.1; 17.8; 3	20.8-22.2; 21.5; 2	25.7-28.0; 26.5; 3	17.0-24.3; 20.7; 2	20.5-24.5; 22.5; 5
TM	21.9-29.9; 25.9; 2	22.8-25.1; 23.7; 5	25.6		23.7-24.9; 24.5; 4

Taxa: *BF* Baynunah Formation in Abu Dhabi, *LTL* Nawata Formation at Lothagam (data for *A. lothagamensis* from Weston 2003), *LTH* Nawata Formation at Lothagam (data for *A. harvardi* from Weston 2003), *TM* Toros-Ménalla in the Djourab

Measurements: *Mc* metacarpal, *Mt* metatarsal. These values are calculated from measurements summarized in Tables 15.12 and 15.13 as following: $100 \times L / W$

Table 15.12 Measurements (min.-max. in mm; mean; N) for metacarpals in Baynunah hippopotamines (in *italics*) and other late Miocene hippopotamines

	Mc III		Mc IV		Mc V	
	L	W	L	W	L	W
<i>BF</i>	<i>140-142;</i> <i>40.9; 2</i>	<i>33</i>	<i>122</i>	<i>30</i>	<i>91</i>	<i>28</i>
LTL					76	21
LTH	177-185; 180.3; 3	32-32; 32.0; 3	154-162; 158.0; 2	32-36; 34.0; 2	101-125; 111.7; 3	26-35; 29.7; 3
TM	154-187; 170.6; 2	41-46; 43.6; 2	145-158; 153.5; 5	35-38; 36.4; 5	109.9	28.1

Taxa: *BF* Baynunah Formation in Abu Dhabi, *LTL* Nawata Formation at Lothagam (data for *A. lothagamensis* from Weston 2003), *LTH* Nawata Formation at Lothagam (data for *A. harvardi* from Weston 2003), *TM* Toros-Ménalla in the Djourab

Measurements: *Mc* metacarpal, *L* proximodistal length, *W* mid-diaphysis transversal width

Table 15.13 Measurements (min.-max. in mm; mean; N) for metatarsals in Baynunah hippopotamines (in *italics*) and other late Miocene hippopotamines

	Mt II	Mt III
--	-------	--------

	L	W	L	W
<i>BF</i>	96	22	110-119; 114.5; 2	28-29; 28.1; 2
LTH	106-111; 108.5; 2	18-27; 22.5; 2	134-166; 148.8; 5	29-37; 33.4; 5
TM			146-167; 159.0; 4	36-49; 38.9; 4

Taxa: *BF* Baynunah Formation in Abu Dhabi, *LTH* Nawata Formation at Lothagam (data for *A. harvardi* from Weston 2003), *TM* Toros-Ménalla in the Djourab

Measurements: *Mt* metatarsal, *L* proximodistal length, *W* mid-diaphysis transversal width

Table 15.14 Measurements (min.-max. in mm; mean; N) and proportion (min.-max.; mean; N) for proximal phalanges III or IV in Baynunah hippopotamines (in *italics*) and other late Miocene hippopotamines

	L	W	100 × W / L
<i>BF</i>	<i>58.6-64.5; 60.8; 3</i>	<i>34.2-38.5; 36.3; 3</i>	<i>56.0-62.9; 59.7; 3</i>
TM	70.6-73.7; 72.5; 3	40.2-42.0; 41.3; 3	56.5-57.4; 56.9; 3
WM	66.3-79.4; 73.2; 6	42.5-51.6; 46.7; 6	61.4-65.0; 63.8; 6

Taxa: *BF* Baynunah Formation in Abu Dhabi, *TM* Toros-Ménalla in the Djourab, *WM* Adu Asa Formation in Middle Awash

Measurements: *L* proximodistal length, *W* mid-diaphysis transversal width

Table 15.15 Character-taxon matrix used for the phylogenetic analysis (adapted from Boisserie et al.

2017b)

Taxa	Character states
<i>Aepinacodon</i>	0?10?0???? ?00100000 1000110100 2001100111 0100001110 1220010112 00011??1?? 0002000100 0100?11100 0111000000 0110000000 0000220112 0101011A?1 1
<i>Afromeryx</i>	G??????1? ?00100001 1010120100 1?01100011 0100000110 1220010000 00011?0110 0?0?110001 1000?11110 0100000000 0110000000 101--10112 0201011102 11
<i>Amphimeryx</i>	0011000110 ?002001110 1020000001 -000001011 0100301001 1201110131 0000000110 0??2???100 0?21000122 0111000000 2100200001 -000220112 0111011020 1
<i>Amphiragatherium</i>	????????1? ????2001110 0000000011 2101101101 0000001011 1000011000 1012002000 ???????001 0121010110 0100101100 1210201100 0001110F1D 0001010021 1
<i>Anthracokeryx tenuis</i>	000-00001? 1000000100 0000000100 1000000001 0100000110 1010010000 1000002000 0001H?0100 0100?10??? ?10???0000 0010111000 1001110102 02010110?? 1
<i>Anthracokeryx thailandicus</i>	?????????? ????000000 0000000100 1000100001 0000000110 1210010000 0001002000 ?????????? ?00?10100 0100000000 ?00021F000 1001210102 0101011101 111
<i>Anthracotherium chaimanei</i>	?0100101?? ??????0?00 0000000100 0010101001 0011000110 1010101001 1110001001 ????10100 0110?11110 11000?0000 0010111010 1101210102 0101011102 1
<i>Anthracotherium magnum</i>	0010010000 0000100000 0000000100 0010101001 0011000110 102010100A 1100002001 00001?1100 0110111111 1?00000000 0010111010 A101210102 0201011102
<i>Archaeomeryx</i>	000-?0?1? ?002001110 1020000101 0000001001 0000301001 1201010130 00000001?0 00010?0120 012F?01102 0100000000 0101200001 -01--10102 02111111?1 11
<i>Archaeopotamus harvardi</i>	001212011? 0010200000 112110-111 2101101111 0111311100 1201A11030 0112112000 000031010D 0020120110 0110110011 0200200100 A0A--0F10C 000101000
<i>Archaeopotamus qeshta</i>	001012011? 0010200?00 112110-111 2101101111 0111311?00 1201111030 ?11211?000 00103??0? 0?201??110 011?1?0??1 0200200100 A011-00110 00010A00?2
<i>Brachyodus aequatorialis</i>	11110?1?1? 0??1000000 1110110200 11A0100011 0100001011 11200000A2 0001111100 1212000000 F000?11101 0100000001 0111001000 1001210102 0201011101
<i>Brachyodus depereti</i>	21110?--?? ????1000000 0000110200 1100100011 0100001011 1220010112 0000110100 ???????00? ????0?11110 0100000000 0100000F00 1001210102 02010111?1 1?1
<i>Brachyodus onoideus</i>	1111001112 0001000000 0100110200 1010100011 0100001011 1121010112 0000110100 1212000000 1000?11101 0100000001 0111000000 1001210102 0201011101
<i>Bothriodon</i>	0010000012 0001000000 1000120100 0000100011 0000000110 1220010012 0001?00110 0002000100 0100?11110 0101000000 0110011000 0000220112 0101012001
<i>Bothriogenys andrewsi</i>	?????????? ?????????? ?????????? ??????????01 0100001000 1121010012 0001110?00 ?????????? ?????????? ?????????? 0?????00? ?00?1?102 ?2??1111?1 ??????????

Bothriogenys fraasi ?????????? 0????00000 1020111200 1?10100011 000000110 1110110001 1001110100 ?????00000 1000?11100 010000000? 0010111000 1001210102 02010111?1 11

Bothriogenys gorringei F00?001112 0001000000 1100121200 1010100011 0000001A10 122001000D 0111110100 000??????? ?????11101 0100000000 1110D11000 1001110102 0201011101

Bothriogenys orientalis ?????????? ?????00000 1120121100 1010100001 0000010110 1110110001 0102101100 ?????00000 A000?11100 0110100000 00101110?0 0001110102 0101011001 11

Bunophorus ?????????? ?????1000 000000000? 2000000010 1100001011 0-00110000 0001000000 ?????????? ?????000-- 0010000000 0200300000 1001000011 000010-021 0002?

Cebochoerus 000-000?10 ?002010000 0000000001 0000001001 0001010000 0-10010000 0102002000 ???2000100 0020010110 0001000000 0200200100 0001010001 020100-000 1

Choeropotamus 000-????? ?002000100 0000010100 0000100001 0000100000 0-00100000 0012000000 ???0????00 0100?00110 0101001000 0100201110 0001100102 01010111?1 11

Chorora (middle) ?????????12 0?02?0?0 ????-?? ????11 0101?11100 1201?110?? 01???1G?00 ?????????2 0?101?110 011?1?0011 ?200200100 A00110110B 0001010002 1???0

Chorora (upper) ?0?1??12 00102?0?0 ?????-1?? ?10?101111 0101311100 1D01111030 01121?0?0 ????3????2 0?20120110 011111?011 0200200100 A0???0010B 0001010002 1??

Dacrytherium 0???00?12 1002000100 0000110201 2100101001 1100000001 0-11010120 0010000100 0??20?1000 00201110-2 0101100001 0100000001 -001020112 0211011120 11

Dichobune 000-00?12 ?001001000 0010020000 0000001000 1000000001 0-00010000 1002000000 ??????100 0?1?0000-0 0011000000 0001000000 000100011 020010-020 010

Diplobune 0010000112 1001000110 0000110211 0100001010 0100001011 0-11011122 0000000100 0212001000 0120111122 0101000000 2100000001 -001020012 0111011120

Elomeryx borbonicus 0010001012 0001000001 1010120100 1110100011 0000001A11 1220010112 0002110110 0001110000 0000?111A0 0100000000 01A0100100 1001220112 010101110

Elomeryx crispus 0010001012 000100000A 1010100100 1110100001 0000000110 1020010112 10011101FA 0001110000 0000?11110 0100000000 0110111100 1001220112 020101110

Entelodon 001A000100 0000110100 0000000000 0000001010 1100101101 1000110000 10000000-0 0000?1100 012010010- 0001000000 12010-0000 0001001010 000010-011 0

Epirigenys ???0111?? ?????0?00 010111-100 2A11111001 00AA000110 1210001000 0112?1?100 ?????????? ?????11110 0110110001 1010D11010 0101200102 01010110?1 11

Gobiohyus ?????????? ?????1000 0000100100 2001001000 1000000011 1000010000 1001001000 ?????????? ??2?010110 0101000000 1001000001 -001010111 020100-021 1111

Gujaratia 000-000?12 1001001000 0000000000 0000000010 1100001001 0-00110000 0001001000 00011?1100 0120?00112 0001000100 0000300000 1001101011 100010-020 1

Hallebune ?????????? ?????01110 1020000011 ?10?001010 0100001011 1000010000 1001002000 ?????????? 0?21?10110 0100001?00 1210300000 0001110111 000A10-0?1 0F0

Heptacodon 000-????11 0000100000 0020000100 0000101011 0000000110 1011110001 1000000000 0?00111000 0110?11110 1100000000 0010101000 1101110102 02010121?2 1

Hexaprotodon 001212011? 0010200000 112110-111 2101101111 0111311100 1D01A11030 A112112000 0000310A0D 0020120110 0110110011 0200200100 A0A-0F10C2 0001010

Homacodon ?????????? ?????????? ?????????? ??????????10 0100001001 1000010000 1002000000 ?????????? 0?10000110 0011000000 0010300000 0000010001 020000-021 01020?

Indohyus ?????????? ??????0?0 00????01?? 0000001011 1000001011 1000010200 1000001200 ??????????0 0?001000-- 0000000110 0200201001 -001101011 100110-021 1?100

Kenyapotamus coryndonae ?0??12011? 00102?000? 112110-111 21011A1101 00A1E101A0 1210111000 0112112000 ??????????1 0?10110110 0110110011 12A020A100 A10110110B 000101000

Kenyapotamus ternani 00101????? ?010200?00 ?12?10-??0 ??????????01 00A1E?01A0 1210111000 011?1?2000 ??????????A 0?10?20110 01101?0011 1210201100 A10110110B 0001010002 1?

Kenyasus 001B010013 0100210000 000000-000 -000001011 0001200100 0-11110010 1001000000 01102?0100 0?00?10110 0101001000 2201001100 0101001010 100100-010 1

Khirtaria ?????????? ??????0000 0000000100 0000101011 1001-01111 1000110200 1000001G0F ?????????? ?????????? ?????????? 0200001010 0001101011 100110-021 10021

Libycosaurus anisae A012100A11 0100210001 1010120100 1000101011 0100001011 1210010120 0002110110 ???020?012 1000?11110 0111000000 0100002000 101--20112 010101111?

Libycosaurus bahri 2012100111 0100210001 1010120100 1000101011 0100001011 1210010120 0002110110 00102?0012 1000111110 0101000000 0100002000 101--20112 0101011111 1

Lophiomeryx 001200??1? ???2001110 0020000101 -000001011 0100301001 1201010130 0002000110 ---2?00120 0110001122 0111000000 0100200001 -01--20112 01110111?1 111

Merycoidodon ??????????01 0000100000 0020110111 0010101001 0100-00001 1221010132 00120001?? 00001?0000 1000001122 0100000000 2000200001 -01--20012 02110111?2 11

Merycopotamus dissimilis 000-0????11 0100210001 1010120100 1000101011 0100001011 1210010120 0002110110 ???0110001 1000111110 0101000000 0100002000 101--20112 0101011112 1

Merycopotamus nanus 000-0????11 0100110001 1010120100 1000101011 0100001011 121A010120 0002110110 00001?0001 1000111110 0101000000 0100000000 101--20112 0101011112 1

Microbunodon 000-000011 1000000100 0010000100 1000000001 0000000110 1211010000 0001002000 0001311000 0100?11100 0101000000 0100200000 1001210102 0101011101

Mixtotherium ??????????12 0000101110 0020000111 -?00001000 1000011011 0-10110001 0102000100 ???01?1000 0?21011110 0100001000 0100200001 -001020002 0201111122 11

Morotochoerus ?????????? ??????0??? 01????-1?? 2?0F1?101 0111110110 1F10011000 0112102000 ?????????? ?????????? ?????????? A200201100 000110010B 00010100?1 11100?

Myaingtherium 000-000?0? ???110000 0000000100 ?000101001 0011000011 1010010000 1000002001 ?????????? ??????10100 1100000000 ?210111000 0001100111 0001010012 111

Palaeochoerus 001B010013 0110200000 000000-000 -000001011 0011000011 0-10011010 0001000000 0?1021A000 00101000-0 0011011000 2201001110 0001000010 100100-010 1

Paroxacron 000-000?1? ???2?11110 1020000201 0000001001 1000001001 0-01010120 00000001-1 ???????000 0121011112 0101000100 2101000001 -000020012 0110111120 111

Perchoerus 001B0?0013 0110200000 00?0??-0?0 ?000001011 0011000010 0-?1?10010 1001000000 0?02?A100 0?00?000-0 0001001000 2201001000 ?001000011 000100-0?0 11

Siamotherium 0???00?00 00?0000000 0000000100 0000100101 0000000000 1010010000 1100002000 00001?0?00 01A01100-0 0001000000 1000210000 1001110101 0001010001 1

Sivameryx 000-????11 0?00110001 1010120100 1000100001 0000010110 122001012B 0101110110 ??????00?1 1000?11100 0100000000 0110000000 1001120112 01010111?2 1

Xiphodon ?????????? ??????1110 1020000211 0100001011 0100001011 0-20010110 0001000110 ???????001 0101111112 0101000000 2100000001 -000220012 0111011022 111

Polymorphic states: A (01), B (02), C (012), D (12), E (13); variable states: F {01}, G {02}, H {23}

Figure Captions

Fig. 15.1 Adult mandibles of *Archaeopotamus qeshta* from the Baynunah Formation, Abu Dhabi, United Arab Emirates. **(a–d)** NHM M49464, holotype mandible of *A. qeshta*. **(a)** dorsal view. **(b)** dentition: top left, occlusal view of right P₄; top right, lingual view of right P₄; middle, occlusal view of left M₂; bottom left, occlusal view of left M₃; bottom right, occlusal of right M₃. **(c)** rostradorsal view. **(d)** left lateral view. **(e–f)** AUH 457. **(e)** dorsal view. **(f)** left lateral view.

Fig. 15.2 AUH 481, juvenile mandible of *Archaeopotamus qeshta* from the Baynunah Formation, Abu Dhabi, United Arab Emirates. **(a)** dorsal view. **(b)** rostradorsal view. **(c)** right lateral view.

Fig. 15.3 Measurements and proportions of *Archaeopotamus qeshta* compared with those of other hippopotamids. **(a)** plot of mandibular symphysis proportions: *M2* maximal length from mid-point between right and left I₁ 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.

Fig. 15.4 Cross-sections of mandibular symphyses attributed to *Archaeopotamus qeshta* compared with those of other hippopotamids. All sections are direct observations, except *Hexaprotodon? sahabiensis* (Pavlakis 2008: fig. 3).

Fig. 15.5 Dentition of *Archaeopotamus qeshta* from the Baynunah Formation, Abu Dhabi, United Arab Emirates. **(a)** AUH 1731, left I²/₁ in mesial view on left and in lingual view on right. **(b)**

NHM M49465, right P³/ in occlusal view on left and in labial view on right. **(c)** AUH 262, ?right P⁴/ in occlusal view on top and in distal view on bottom. **(d)** AUH 664, left P₁/ in lingual view on top and in distal view on bottom. **(e)** AUH 1532 (right M²/ in occlusal view on left and in labial view on right). **(f)** AUH 36, right M³/ in occlusal view on left and in lingual view on right.

Fig. 15.6 Consensus of 33 most parsimonious trees (1091 steps, consistency index = 0.293, retention index = 0.636). **(a)** clade Hippopotamoidea, **(b)** clade (Hippopotamidae, Bothriodontinae), **(c)** clade Hippopotamidae, **(d)** clade Hippopotaminae. Abbreviations: *A. Archaeopotamus*, *Akx. Anthracokeryx*, *Ant.*, *Antracotherium*, *Bot. Bothriogenys*, *Bra. Brachyodus*, *Elo. Elomeryx*, *Ken. Kenyapotamus*, *Lib. Libycosaurus*, *Mer. Merycopotamus*.

Fig. 15.1

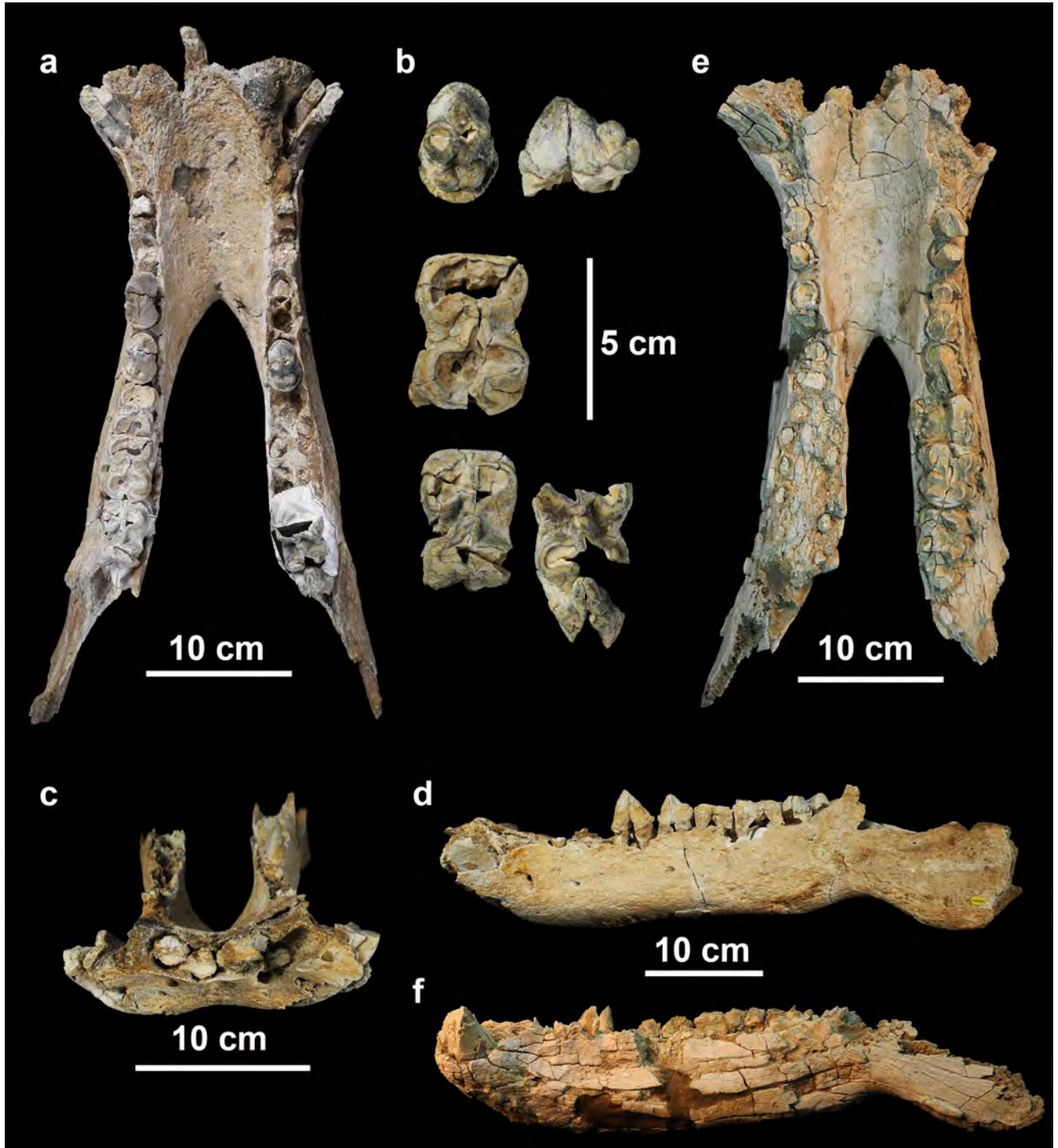


Fig. 15.2

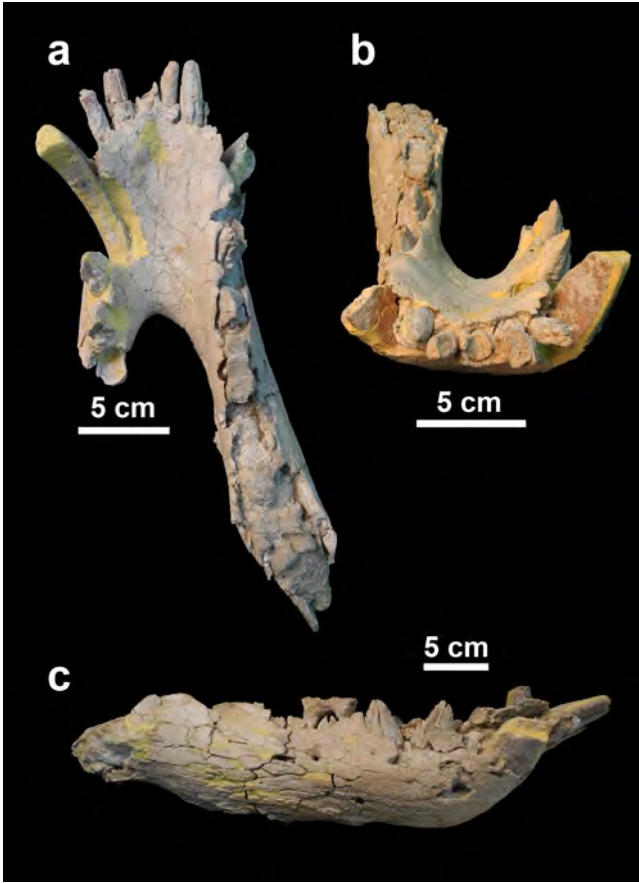


Fig. 15.3

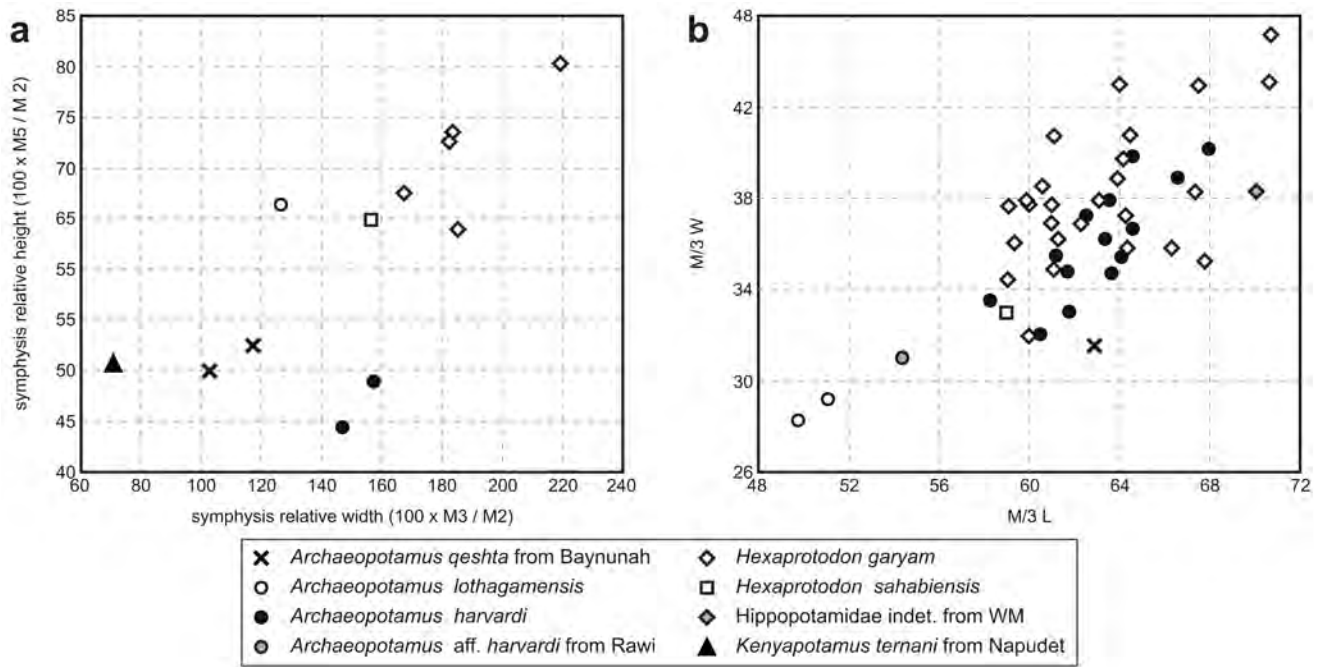


Fig. 15.4

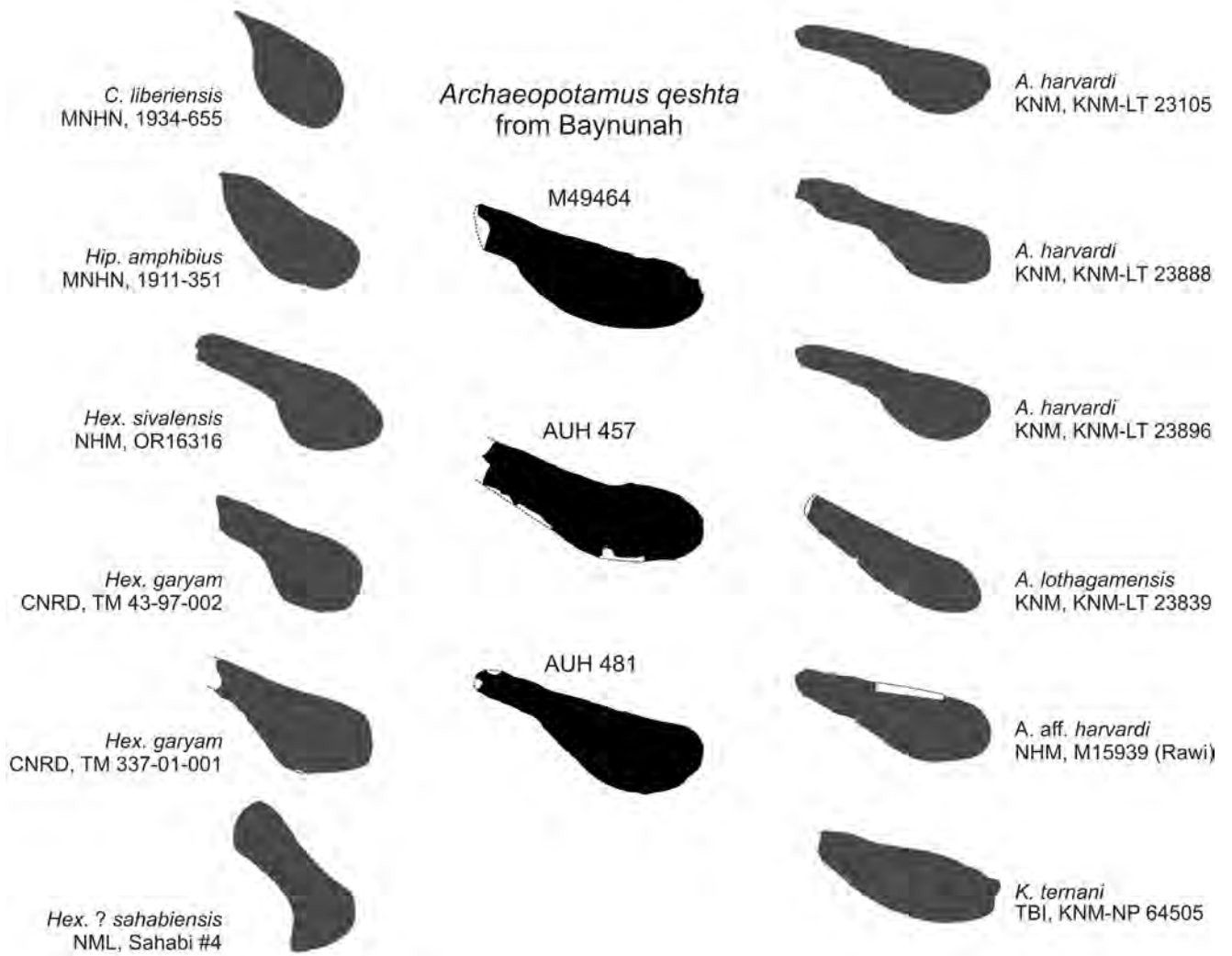


Fig. 15.5

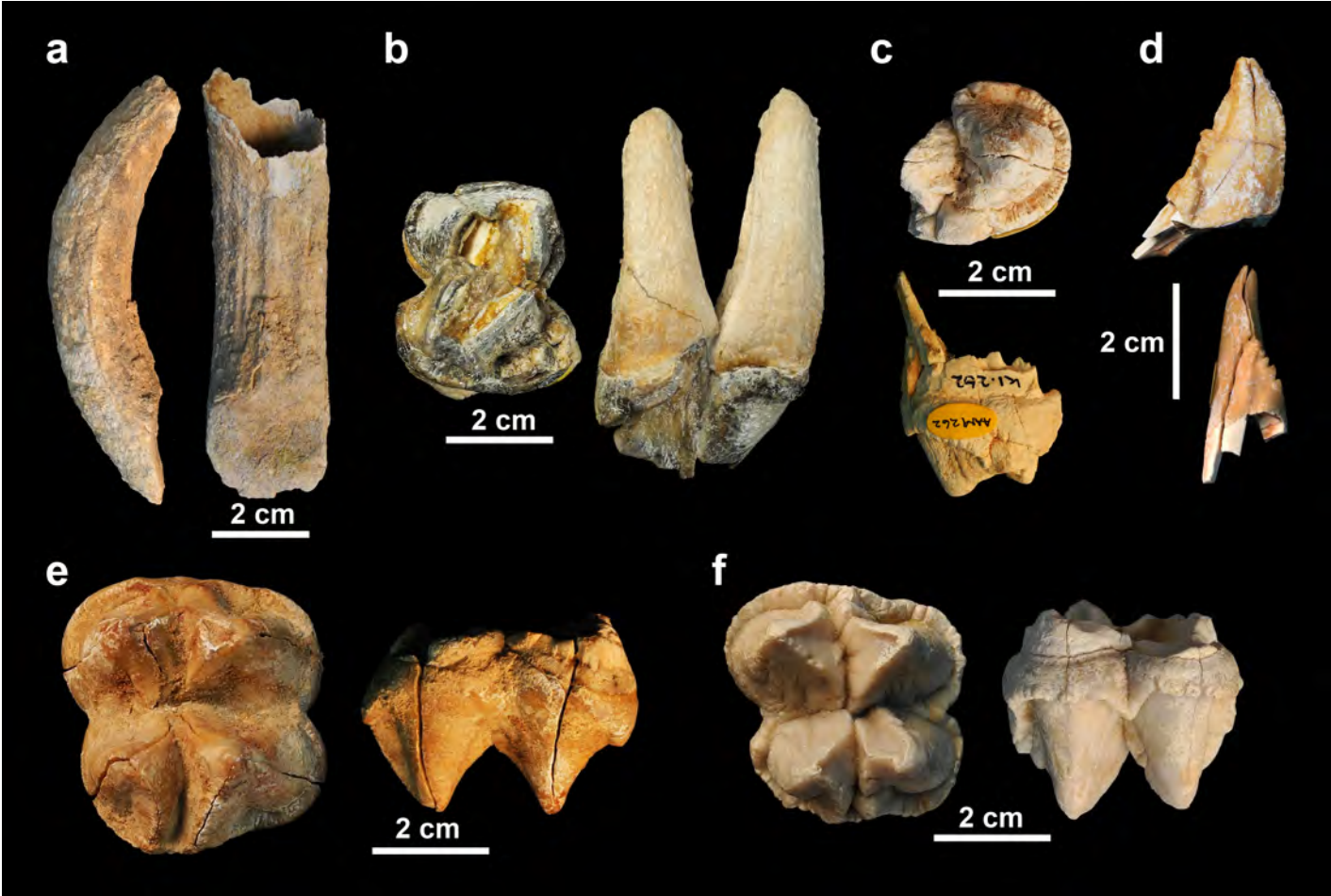


Fig. 15.6

