

On the cranial anatomy of the smallest insular hippopotamus (Cyprus, Pleistocene)

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ABSTRACT - The Pleistocene Cyprus dwarf hippopotamus (c. 132 kg) is the smallest insular hippopotamus known thus far. This species was part of an extremely depauperate fauna, in which the only other large herbivore was represented by a dwarf elephant, in agreement with a high degree of geographic isolation. Here we describe for the first time its cranial anatomy and reconstruct a virtual model of its skull. Unique characters of this taxon are the lack of upper fourth premolar in adult specimens and lophodont teeth. All other cranial phylogenetically relevant characters firmly place the Cyprus dwarf hippo within the genus *Hippopotamus*. The increased frontation of its orbits and the elevated neutral position of its head are derived features in respect to its hypothetical ancestor, *H. antiquus*. These features are here explained as correlated to a higher degree of terrestriality and deviation from a grazing lifestyle. The peculiarities of its dentition indicate a wider dietary niche than in other hippopotamids, probably containing a higher percentage of browse intake compared to mainland *Hippopotamus*. Wear facets on the incisors point to an increased lateral component during chewing, which results in more efficient chewing, probably to cope with potential (seasonal) resource limitations on the island. The mandible is either anteriorly broad with large canines, or narrower with small canines, probably due to sexual dimorphism which was retained from its ancestor. The combination of extreme body size shift, a higher degree of terrestriality, and a change in dietary niche is here hypothesised as an evolutionary adaptation to this island environment, facilitated by ecological release from competition and predation that allowed the species to survive for hundreds of thousands of years.

INTRODUCTION

Cyprus is known for its unique, extremely depleted Pleistocene mammal fauna, which was limited to dwarf elephants and dwarf hippopotamuses. Later, at the end of the Pleistocene or the Early Holocene, also mice, genets, and bats arrived (van der Geer et al., 2017). The nature of this depauperate fauna and the size reduction of its megafauna are likely an indirect consequence of the isolated nature of the island, similar to what is observed on other palaeo-islands worldwide (Lomolino et al., 2013, 2017). Cyprus has a long history of isolation since the Miocene, when the island emerged from the sea, starting with the main mountainous areas (Robertson, 1990). Therefore, the only way vertebrate species could have colonised the island was via overseas dispersal either by rafting, swimming or flying. The most likely way the ancestor of the Cyprus dwarf hippo, *Hippopotamus minor* (Boekschoten & Sondaar, 1972) reached the island was by swimming (Sondaar, 1977; van der Geer et al., 2015). However, when exactly it arrived on Cyprus and which species arrived, remain unknown. Fossils of the dwarf hippo have been found only at Late Pleistocene sites, based on stratigraphy only, but the (larger) elephant dates back to the late Middle Pleistocene (MIS7, 243-191 kya; Athanassiou et al., 2015), indicating an arrival of the fauna in the preceding glacial period, which started around 300 kya, or any other earlier glacial period, when the sea level dropped and the crossing distance decreased. Regarding the ancestral species, this remains unknown. Ancestry

from *H. antiquus* Desmarest, 1822 would mean that it was stranded on the island since at least ca. 0.4 Ma, when the former was replaced in Europe by *H. amphibius* Linnaeus, 1758 (Fidalgo et al., 2023). The youngest remains in southern Europe date after all to approximately 450-380 kya (Martino et al., 2023, 2024b), which date is close to the oldest remains of the Cyprus Pleistocene fauna. Skeletal morphology seems to confirm this, although with uncertainty (Georgitsis et al., 2022a, b).

The Cyprus dwarf hippo was recognised as an endemic species based on features of its dentition that are unique among hippopotamids, justifying the establishment of a new genus, *Phanourios* Boekschoten & Sondaar, 1972. Based on the shape of the lacrimal bone, the latter authors recognised a phylogenetic relationship closer to *Hippopotamus* Linnaeus, 1758 rather than *Choeropsis* Leidy, 1853, despite its small body size. The lacrimal bone in *Hippopotamus*, including in the Cyprus dwarf hippo, is oblong and borders the nasal bone, whereas it is small, triangular and separated from the nasal bone by the frontal bone in *Choeropsis*. Morphological data (Boisserie, 2005; Georgitsis et al., 2022a, b) and molecular data (Psonis et al., 2022) point to a close affinity to *Hippopotamus* as well, with an estimated divergence time of about 1.36-1.58 Mya from the common hippo (*H. amphibius*), which falls in the range of *H. antiquus*. Nevertheless, the generic name *Phanourios* is still in use by some authors (e.g., Hadjisterkotis & Reese, 2008; van der Geer et al., 2010; Bethune et al., 2019; Georgitsis et al., 2022a, b; Nakasi et al., 2023; Bradshaw Corey et al., 2024). Other

authors, however, assign it to the genus *Hippopotamus* instead (e.g., Lomolino et al., 2013; van der Geer et al., 2018, 2021), which usage we follow here.

The island provides sufficient resources with its surface area of almost 10 thousand km² to allow for the fauna to survive long enough to evolve unique features. For the Cyprus dwarf hippo (*Hippopotamus minor* Desmarest, 1822), the most striking and unique feature is the remarkable reduction in body size, which decreased to approximately 4% of the mass of its ancestor, with an estimated weight of only 132 kg based on the analysis of long bones (Lomolino et al., 2013). This minute size makes the Cyprus hippopotamus the smallest hippopotamus ever. Also, its extreme size reduction indicates a long time in isolation, since the degree of evolutionary body mass shifts on islands correlates with time (Lomolino et al., 2013; van der Geer et al., 2017), which is more in line with ancestry from *H. antiquus* than from *H. amphibius*. Apart from this body size decrease, the species is characterised by a derived dentition to accommodate a higher percentage of browse intake in its diet (Boekschoten & Sondaar, 1972b; Sondaar, 1977), a more digitigrade stance and a higher degree of cursoriality (Houtekamer & Sondaar, 1979), modifications to its feet for better mobility in the sagittal plane (Georgitsis et al., 2022a, b), higher encephalisation (Lyras, 2019), more forward-looking eyes (van der Geer, 2014), a proportionally shorter muzzle (van der Geer et al., 2018), slower ontogenetic growth (Kolb et al., 2015; van Heteren & Sander, 2016), and a rapid bone turnover rate (Miszkiwicz et al., 2023). Some of these trait shifts are probably directly related to its body mass reduction through allometric constraints, e.g., the shorter snout. The latter feature agrees with the general and widespread pattern in mammals of shortening of the muzzle when skull size decreases, referred to as cranial evolutionary allometry (Radinsky, 1985; Cardini & Polly, 2013; Cardini, 2019). Fossils of the Cyprus dwarf hippo are known for centuries, mostly as remains of saints or dragons (e.g., Bordone, 1528; Machairas, 1555), and were first described scientifically only in the early 1900s (Bate, 1906). After Dorothea's Bate expeditions to Cyprus, several other expeditions to collect hippo fossils were undertaken, including those by Dreghorn in the late 1960s or early 1970s, Sondaar and Boekschoten in 1969, Malatesta and Girotti in 1970-1971, Nienhuis, Reymont, Richards, and White, all independently in 1971, Reese in 1973-1974, and Theodorou from 2001 onwards (for a review of the history of discoveries, see van der Geer et al., 2021).

Despite collecting efforts and number of papers published on this insular species, the skull of the Cyprus dwarf hippo has never been described in detail. Here we describe for the first time key anatomical features of *Hippopotamus minor* skull. The objective of this contribution is to present new data that can shed further light on the phylogeny, functional morphology and ecology of this unique hippopotamus.

MATERIALS AND METHODS

Material

The material here presented, and used as base to a full virtual reconstruction of the skull of *H. minor* (Fig. 1;

Supplementary Online Material [SOM] 1-3) are partially fragmented crania and mandibles (Figs 2-3; Tab. 1). The Cypriot hippo material used in this study was collected by Dorothea Bate in 1901-1902 (Bate, 1906) and in April/June 1969 by Bert Boekschoten and Paul Yves Sondaar (Boekschoten & Sondaar, 1972a), curated respectively at the Natural History Museum of London (UK), and (currently) at the Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Greece (previously at the Department of Geosciences, University of Utrecht, the Netherlands).

Acquisition of digital models and skull reconstruction

This is not the first attempt to model a complete skull of *H. minor*. An earlier effort was undertaken at the Natural History Museum in London in the early 1900s. Frank Barlow (1880-1951), who worked as a workshop attendant and later as a museum preparator, used material collected by Dorothea Bate between 1901 and 1902 to mount a complete skeleton (Bate, 1906). Since no complete skull was available to him, Barlow sculpted one (SOM 1), with one notable misinterpretation: he added a fourth premolar to the model, which we now know is absent in the Cypriot hippo (Fig. 4).

For our virtual reconstruction (SOM 2-3), we used twenty-five isolated cranial specimens (Tab. 1). Nine of these isolated parts served as the basis for our virtual reconstruction. The material in the Museum of Palaeontology and Geology of the University of Athens was scanned using a NextEngine 3D ULTRA HD scanning imaging system with a resolution of 0.1 mm. Scans were then processed using the software ScanStudio CORE 1.7.3

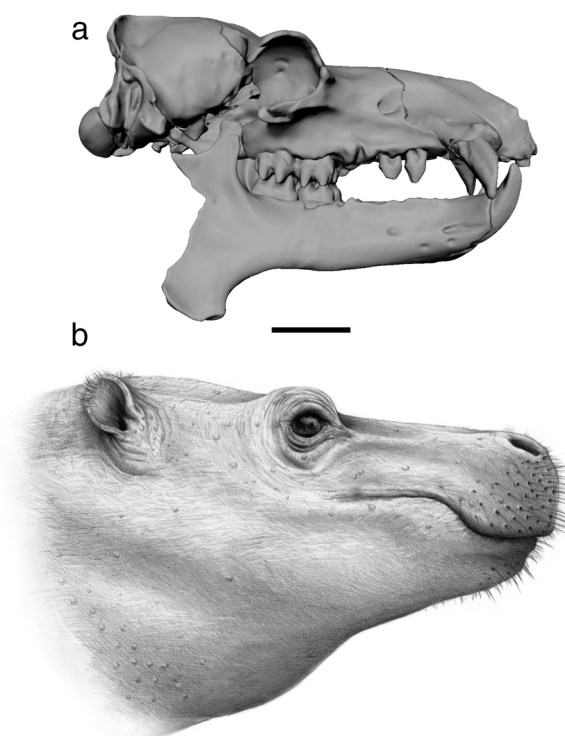


Fig. 1 - The head of the Cyprus dwarf hippopotamus. a) Virtual reconstruction of its skull and mandible in lateral view. b) In vivo reconstruction. Scale bar is 5 cm.

to generate a 3D virtual model. The original material in the Natural History Museum of London was digitised using photogrammetry. The photos were taken without moving the specimen, using the “walk-around” technique. The photos were imported in Agisoft Metashape version 1.7.0 to generate a digital model.

The digital models were post-processed using MeshLab v.2023.12 (Cignoni et al., 2008) and Blender v. 3.4.0 (Blender Foundation, 2002). MeshLab is a free, open-source software for managing and processing unstructured large meshes. It is widely used in palaeontological research (e.g., Sellers et al., 2012; Díez Díaz et al., 2021; Garza et al., 2021). Similarly, Blender, a free and open-source 3D computer graphics and animation software, is also commonly applied in palaeontological studies (e.g., DeVries et al., 2022; Herbst et al., 2022; Gerakakis & Makris, 2024; Martino et al., 2024a).

For building the final model, we combined parts of the individual 3D meshes. Since the fossils were not deformed, digital retro-deformation was unnecessary. However, most meshes were minimally scaled, either uniformly or non-uniformly, to ensure the best fit. Specimen CDKM was used as a reference for the relevant proportions between the maxilla and the basicranium. Specimen NHMUK M 8316 was scaled up non-uniformly, with scaling factors of 1.02 along the X-axis, 1.05 along the Y-axis, and 1.14 along the Z-axis. The incisor, M2-M3, and part of the left maxillary bone were mirrored to the right side. The premolars from CAK 675 and the canine from CAK 265 were used to complete the dental battery. The basicranium from CAK 1260 was uniformly scaled down by a factor of 0.95 to fit with the posterior part of the neurocranium from AYII 115. Specimens NHMUK M 9279 and CAK 1262 were used to construct the frontal part of the neurocranium. For the mandible, the left part of the mandibular symphysis from specimen CAK 491 was mirrored from the right, and the right vertical ramus was mirrored from the left.

Orbit orientation

Two angles were measured on each skull: convergence (angle β) and frontation (angle α). Convergence is the dihedral angle between the orbital margin plane and the midsagittal plane, serving as a proxy for the degree of binocular visual field overlap (Heesy, 2004, 2007). Frontation is defined as the angle between the nasion-inion chord and the orbital plane at its intersection with the sagittal plane (Heesy, 2007). Following Heesy's (2004, 2007) definitions, the orbital margin plane was determined using 3D coordinate data from three landmarks: the point on the orbital margin furthest from the toothrow, the point on the bony orbital margin closest to the toothrow, and the point on the bony margin farthest from the inion. The sagittal plane was defined using 3D coordinates of the inion, nasion, and opisthion. All landmark data were collected using MorphoDig v.1.6.5 (Lebrun, 2018).

Taxonomic background of the material

The confusion around the taxonomic history of the Cyprus dwarf hippopotamus (*Hippopotamus minor*) originates at the beginning of the 19th Century. The renowned French anatomist and palaeontologist Georges Cuvier described three fossilised hippopotamuses of

differing sizes in 1804 and 1824, assigning provisional names based on their characteristics. Among these were 26 elements that Cuvier (1804, p. 112) referred to as the “petit hippopotame fossile” (literally, small fossil hippopotamus), possibly originating from the region between Dax and Tartas in southern France based on the fossil's matrix and apparent degree of fossilisation. The specimens, curated at the Muséum national d'Histoire naturelle in Paris, remained largely overlooked until the 20th Century. In 1901, Dorothea Bate excavated fossil hippopotamus remains in Cyprus and sent them to Charles Forsyth Major, describing them as possibly belonging to a fossil pig species (Bate, 1906). Upon examining Bate's material, Forsyth Major noted its striking resemblance to Cuvier's earlier descriptions and illustrations of the “petit hippopotame fossile”. Forsyth Major (1902a, b) concluded that the Paris fossils described by Cuvier, and subsequently named *Hippopotamus minor* by Desmarest (1822), actually originated from Cyprus instead of southern France. Based on the presence of unique features (see Introduction), Boekschoten & Sondaar (1972b) moved the species to the new genus *Phanourios*, endemic to Cyprus. Faure et al. (1983) suggested considering the specific name *minor* as a junior synonym of *minutus*, because Desmarest (1822) had simply copied the original description by Cuvier, translating the French epithet *petit* into Latin as *minor*. Two years later, Cuvier (1824) renamed *minor* into *minutus* in an attempt to reclaim his new species (Faure et al., 1983), probably also because the Latin equivalent of the French *petit* (small) should be either *parvus* or *minutus*. The Latin *minor*, used by Desmarest (1822), is the comparative of *parvus*, so a translation of the French *plus petit*. From a linguistic point of view, the correct species name should thus be Cuvier's (1824) *minutus* as also proposed by Faure et al. (1983). However, the rules of zoological nomenclature prescribe priority, in which case *minor* has priority over *minutus* even if wrongly translated.

Abbreviations

For dental elements, we use I, C, P, M and i, c, p, and m for respectively the upper (in upper case) and lower (in lower case) incisors, canines, premolars and molars.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Family HIPPOPOTAMIDAE Linnaeus, 1758

Hippopotamus minor Desmarest, 1822
(Figs 2-3)

CRANIUM - *Hippopotamus minor* has a short muzzle and a globular brain case. The lateral profile of the skull makes an angle (stop) of about 130° between the forehead and the muzzle (Fig. 5). The sagittal crest is weakly developed (Fig. 2f2 and 2b1) and slightly slopes down posteriorly. In lateral view, the occipital profile is nearly vertical. The occipital condyles protrude posteriorly. The orbits are large relative to the head. The orbital summit is

Number	Locality in Cyprus	Element
NHMuK M 8316*	Cape Pyla	Partial skull with M2-M3 on right maxilla
NHMuK M 9335	Dikomo Mandra	Part of neurocranium
NHMuK M 9282	Dikomo Mandra	Part of neurocranium
NHMuK M9279*	Dikomo Mandra	Posterior part of skull
NHMuK M 9329	Dikomo Mandra	Maxilla with M1-M3
NHMuK M n.n.	Cyprus	Anterior part of skull
CDKM n.n. 1*	Dikomo Mandra	Maxilla and posterior part of skull
CDKM n.n. 2*	Dikomo Mandra	Frontal part of neurocranium
CAK 596	Akanthou	Maxilla with M2-M3
CAK 580	Akanthou	Maxilla with M1-M3
CAK 492	Akanthou	Anterior part of mandible
CAK 491*	Akanthou	Nearly complete mandible
CAK 512	Akanthou	Left mandible
CAK 677	Akanthou	Maxilla with C, M2-M3
CAK 675*	Akanthou	Maxilla with M1-M3
CAK 375	Akanthou	Lower canine
CAK 265*	Akanthou	Upper canine
CAK 1259	Akanthou	Part of skull
CAK 1299	Akanthou	Nasals
CAK 1262*	Akanthou	Frontal part of neurocranium
CAK 508	Akanthou	Part of mandible
CAK 510	Akanthou	Part of mandible
AYII 126	Agia Irini	Part of neurocranium
AYII 115*	Agia Irini	Part of neurocranium
AYII 269	Agia Irini	Part of mandible with left c, m2-m3

Tab. 1 - List of specimens used in this study. Asterisks indicate the specimens used in the construction of the digital model. NHMuK: Natural History Museum, London, United Kingdom. CDKM, CAK, and AYII are specimens currently curated at the Museum of Palaeontology and Geology of the University of Athens, Greece.

only slightly elevated above the cranial roof. The anterior border of the orbit is at the level of the second molar and has a deep, narrow notch. The orbital tilt (frontation) is similar to that in the Madagascar dwarf hippo *H. lemerlei* Stuenes, 1989. It is instead different from the common hippopotamus and the African pygmy hippopotamus, which are more like suids in this respect (Fig. 6). The convergence of its orbits (angle 2β) is similar to that of the common hippo (Fig. 6).

From a dorsal view, the cranium exhibits a weak postorbital constriction. The frontal sinuses do not reach the fringe of the supraorbital margin. The orbits are forward-facing. The infraorbital foramen opens above the anterior end of the first molar. The zygomatic arch inserts at the level of the second molar (Fig. 2h1). The lacrimal bone has a quadrangular shape (Fig. 2g). Its medial side is in contact with the nasal bone, thus isolating the frontal and maxillary bones. The nasals extend posteriorly up to the level of the middle part of the orbit.

The maxillary bones represent the major part of the hard palate. The post-canine constriction of the muzzle is weak (Fig. 2a). The posterior palatine border extends beyond the posterior end of the third molar (Fig. 2h1). Anteromedially the maxillary bones form a V-shaped notch, bordered by the premaxillary bones (Fig. 2a2).

The inter-premaxillary suture is partly fused without a gap occurring between the premaxillae anteriorly. The glenoid articular surface is elongated, and its anterior and posterior borders are more or less rectilinear and laterally converging (Fig. 2e). The posterior border of the glenoid process diverges strongly forward relative to the exoccipital bone.

MANDIBLE - The mandible has a delicate structure (Fig. 3). Viewed from the side, the basal profile of the horizontal ramus is straight, with a low corpus. The gonial angle is well-developed but not hook-shaped. The mandibular symphysis extends posteriorly till the third premolar. The plane of the symphysis slopes anterodorsally and is less robust than *H. amphibius*.

UPPER DENTITION - The molars display the highest occlusal tooth relief within hippopotamids and have large compression basins (Fig. 2h2), as already observed by Bethune et al. (2019). The upper dental formula is 4I, 1C, 2P, 3M. The first upper incisor is larger than the second incisor. The upper canine has a triangular cross-section and a shallow groove on the lingual side of the tooth (Fig. 2). The first and fourth upper premolars are missing in adult specimens, as already observed by Boekschooten & Sondaar (1972b) and no alveoli are present for these elements (Fig. 4). The second and third adult upper

premolars have a distolingual heel. The first upper molar is usually the most worn molar.

LOWER DENTITION - The lower dental formula is 2i, 1c, 3p, 3m. The size of the alveolus of the second lower incisor is smaller than that of the first lower incisor. The diastema between the two first incisors from each hemimandible (i1

left-i1 right) is shorter than the width of each incisor (Fig. 3b). In frontal view, the alveoli of the lower incisors are not horizontally aligned, but the first incisor is positioned lower than the second incisor. The canine processes of the anterior part of the mandible in dorsal view are well developed in some specimens (presumably males) but

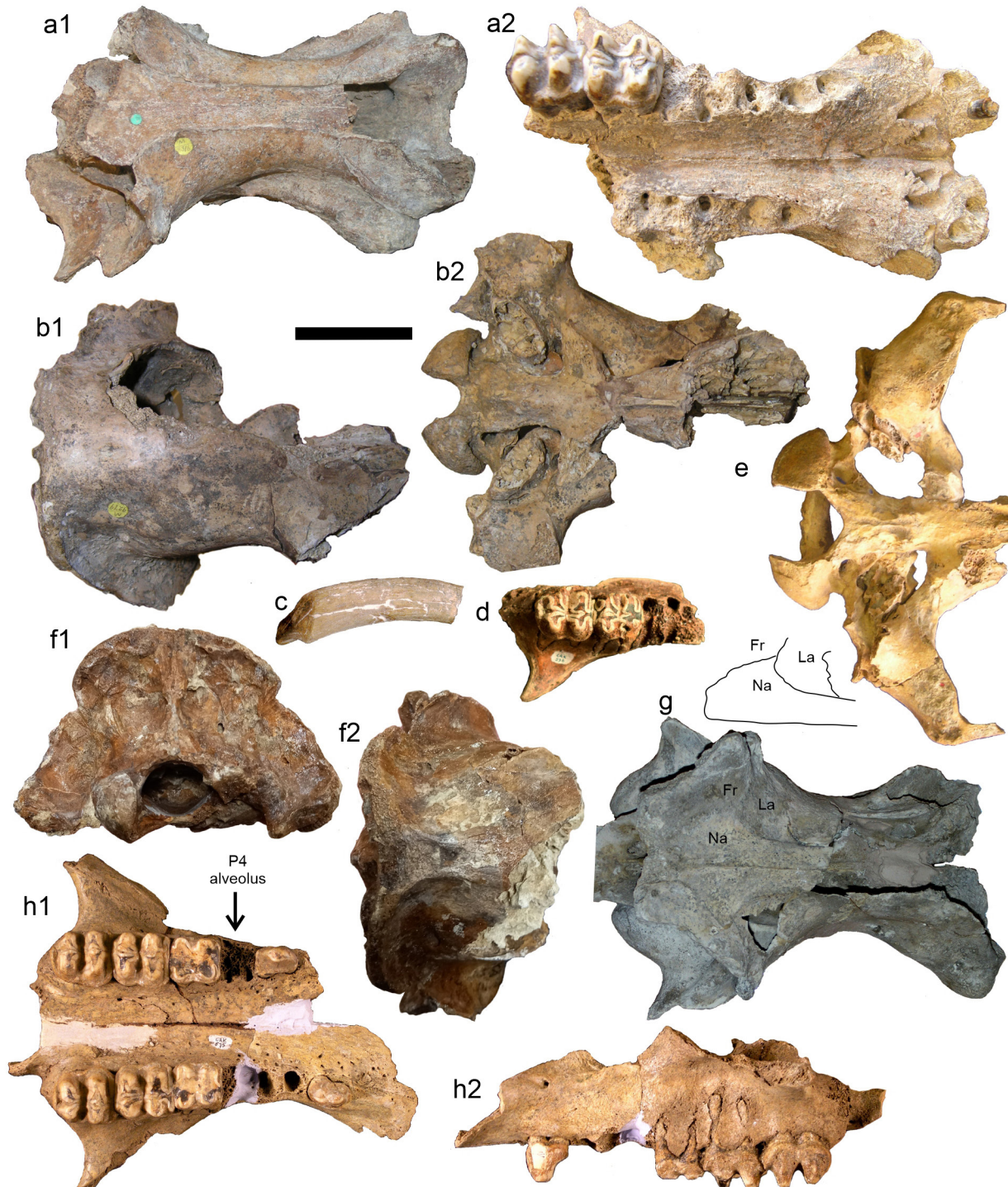


Fig. 2 - (color online) Cranial elements used in this study. a) NHMUK M 8316 partial cranium, in dorsal (a1) and palatal (a2) views. b) NHMUK M 9279 partial neurocranium in dorsal (b1) and palatal (b2) views. c) CAK 265 upper canine. d) CAK 596 left M2-M3 in occlusal view. e) CDKM partial basicranium in ventral view. f) AYII 115 posterior part of neurocranium in caudal (f1) and dorsal (f2) views. g) NHMUK M n.n. partial cranium in dorsal view. h) CAK 675, partial maxilla in palatal (h1) and lateral (h2) views. Fr: Frontal; Na: Nasal; La: Lacrimal. Scale bar is 5 cm.

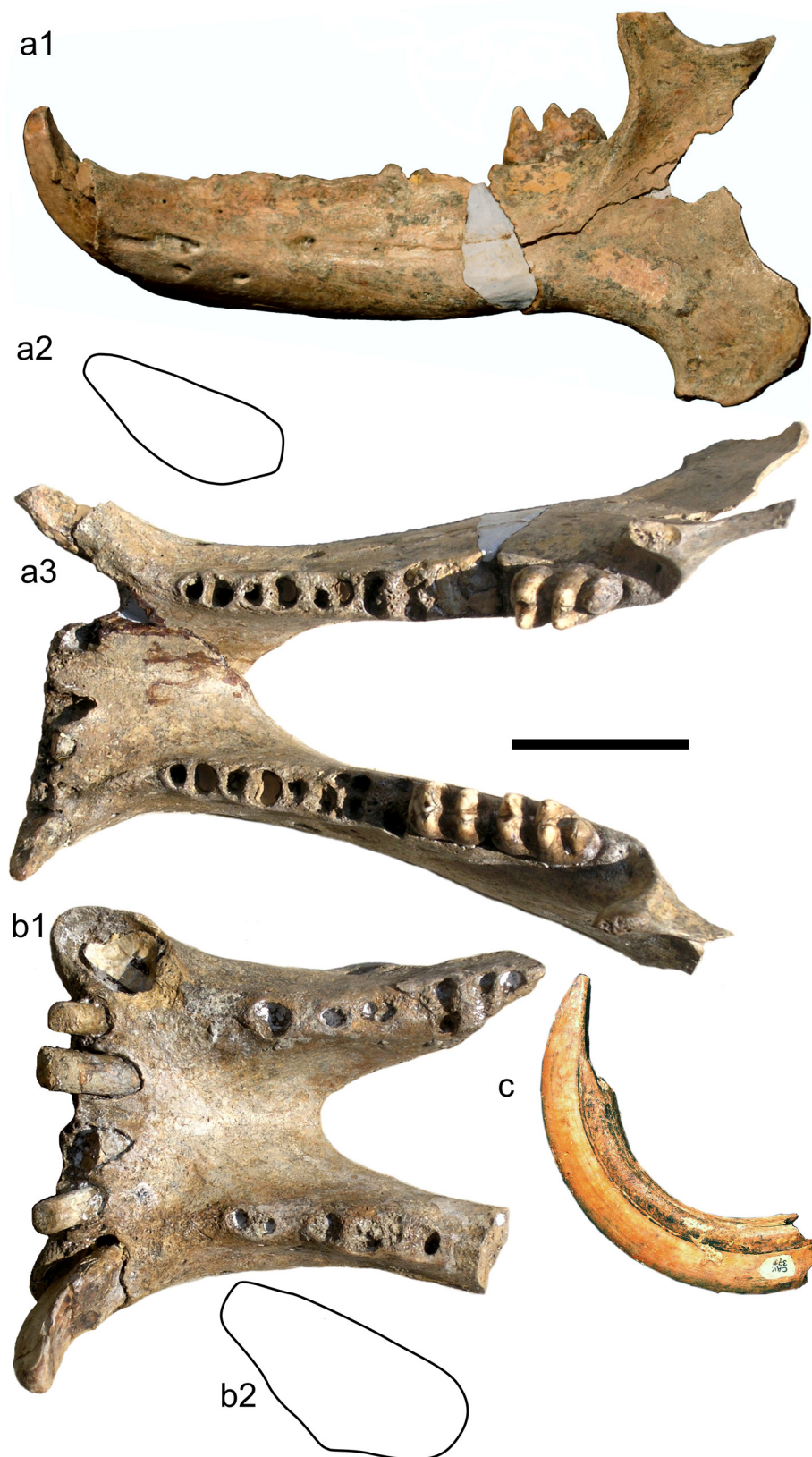


Fig. 3 - (color online) Mandibular elements used in this study. a) CAK 491 nearly complete mandible in lateral (a1) and occlusal (a3) views and outline of mandibular symphysis (a2). b) CAK 492 Rostral part of a mandible in occlusal (b1) view and outline of mandibular symphysis (b2). c) CAK 375 lower right canine. Scale bar is 5 cm.

poorly developed in others (presumably females; Fig. 3a-b); for scatter plots with canine sizes showing two distinct groups with minimal overlap, see Boekschooten & Sondaar (1972: fig. 10). The canines are triangular in cross-section. The enamel of the lower canine exhibits very small (low) ridges that converge towards the apex of the canine (Fig. 3c).

DISCUSSION

Remarks on systematics

Phylogenetic character states following Boissierie (2005) for morphological features of the crania, mandible, and teeth of hippopotamids confirm the placement of the Cyprus dwarf hippopotamus within the genus *Hippopotamus*. This applies to most characters that are observable in the analysed specimens at our disposal (see Results for trait descriptions). The only exception is character 17 (Fig. 4). This character 17 describes the posterior groove of the upper canines. In *Hippopotamus*, this groove is shallow and narrow, and the canine has an almost rounded cross-section, while in *Choeropsis* and Asian *Hexaprotodon* Falconer & Cautley, 1836 it is deep and the canine has a bilobate cross-section. In African *Hexaprotodon* on the contrary, the groove is usually shallow and wide (Boissierie, 2005). In the Cyprus dwarf hippopotamus, the groove is shallow and wide as in African *Hexaprotodon*, but the cross-section is bilobate, which is more in line with the Asian *Hexaprotodon* and *Choeropsis*. However, the upper canines of a *H. antiquus* specimen from Italy seem to show the same

configuration as *H. minor* (own observation based on only two specimens). This may either indicate that this character is ambiguous, or an ancestry from *H. antiquus* (as has been suggested by van der Geer et al., 2021, based on the degree of its size decrease). To claim this, however, a larger comparative study is needed, which is outside the scope of the present manuscript.

Orbit and head orientation

The common hippopotamus is characterised by an amphibious disposition of the sensory organs, nostrils, eyes, and ears, being characterised by their “periscope” eyes, their ears, and nostrils situated above the water level, and the mouth and throat below the water level (Orliac et al., 2023). In water, the common hippopotamus has its head tilted upward anteriorly to keep breathing above water level, whereas when it moves on land, it has a strongly anteriorly tilted neutral head posture (Benoit et al., 2020). Based on orbitation, or the level of its orbit, we argue that the Cyprus dwarf hippo had a higher neutral head posture (Fig. 7). If the Cyprus dwarf hippo had retained the neutral head posture of the common hippopotamus, then its orbits would have been oriented almost downwards. This option is the least likely head posture because the orbital tilt (or frontation, corresponding to angle alpha in Fig. 6) in *H. minor* is similar to that in the Madagascar dwarf hippo *H. lemerlei* Stuenes, 1989. The common hippopotamus and the African pygmy hippopotamus on the other hand are more like suids in this respect (Fig. 6). All these taxa carry their head downward following their feeding habits (grazing and rooting respectively). The Cyprus and Madagascar dwarf hippos both exhibit

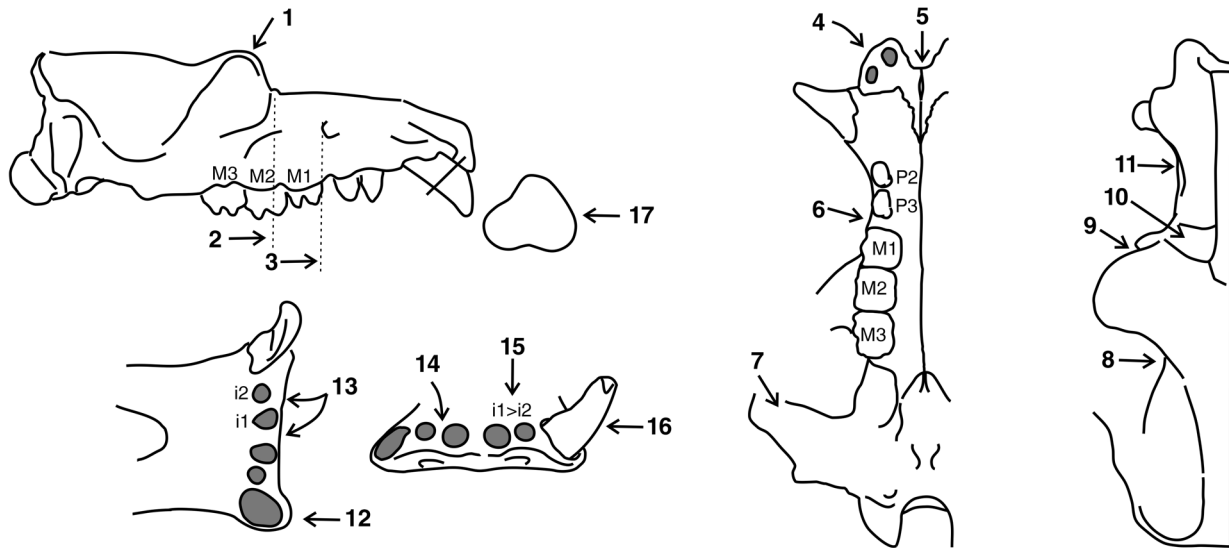


Fig. 4 - Overview of key anatomical features of *Hippopotamus minor* (Cyprus, Pleistocene). 1) The orbital summit is only slightly elevated above the cranial roof. 2) The anterior border of the orbit is at the level of the second molar. 3) The infraorbital foramen opens above the anterior end of the first molar. 4) Four upper incisors are present. 5) The inter-premaxillary suture is partly fused without a gap between the premaxillae anteriorly. 6) The fourth premolar is missing in adult individuals. 7) The glenoid articular surface is elongated and its anterior and posterior borders are more or less rectilinear and laterally converging. 8) The postorbital constriction is weak. 9) The anterior border of the orbit has a deep notch. 10) The lacrimal bone has a quadrangular shape, its medial side is in contact with the nasal bone, isolating the frontal and maxillary bones. 11) The post-canine constriction of the muzzle is weak. 12) Developed canine processes. 13) The diastema between the two first incisors of each hemimandible is shorter than the width of either first incisor. 14) The first lower incisor is positioned lower than the second incisor. 15) The alveolus of the second lower incisor is smaller than that of the first incisor. 16) The lower canine bears small ridges. 17) The upper canine has a bilobate cross-section due to the presence of a shallow groove.

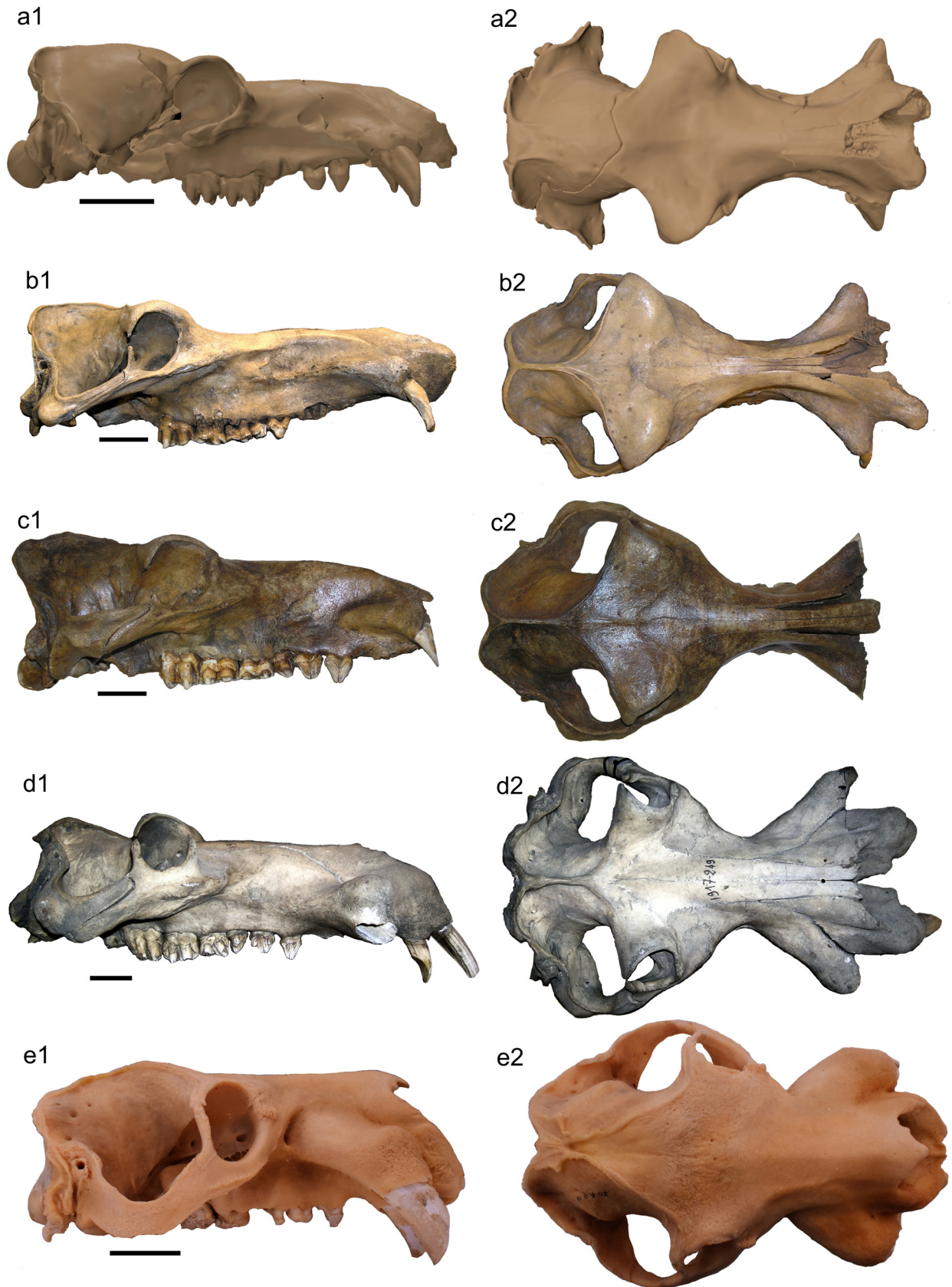


Fig. 5 - (color online) Virtual reconstruction of *H. minor* skull compared to other hippopotamids in right lateral (1) and cranial (2) views. a) *Hippopotamus minor*. b) *Hippopotamus lemerlei* NHMUK M8218. c) *Hippopotamus madagascariensis* MNHN MAD7352. d) *Hippopotamus amphibius* MNHN 1917-249. e) *Choeropsis liberiensis* RMNH MAM 20469. All specimens are scaled to the same condylobasal length. Scale bar is 5 cm.

a wide view angle (or convergence, corresponding to angle 2β) similar to the common hippo, whereas the African pygmy hippo has a wider angle, although not as wide as the horse. This contrasts with van der Geer (2014), who showed that the Cyprus dwarf hippo had a wider angle of view than the common hippo, which was explained as an adaptation to walking in a mountainous habitat, following the view of Sondaar (1977) in respect to the Cretan dwarf hippopotamus. The even wider angle in the African pygmy hippo agrees with its somewhat less aquatic lifestyle compared to the common hippo, as also inferred from the reduced webbing of its toes (Eltringham, 1999; Ramson et al., 2015). However, angle of view and the tilt or frontation of the orbits are not strongly correlated, and the frontation present in *H. minor* points to a more terrestrial way of life. A higher degree of terrestriality has been shown previously, based on the functional morphology of its limbs (Georgitsis et al., 2022a, b) and its browsing diet (Boekschoten & Sondaar, 1972b; Bethune et al., 2019). This may also apply to *H. lemerlei*, the smallest Madagascar dwarf hippopotamus species, which also shifted towards a diet with less grass (Godfrey & Crowley, 2016).

Remarks on dietary niche

The molars and premolars of the Cyprus dwarf hippopotamus have the highest occlusal tooth relief within hippopotamids in combination with large compression basins (Bethune et al., 2019). This is explained as a shift

towards lophodonty, compared to the more complex dental enamel pattern of all other hippopotamuses (Boekschoten & Sondaar, 1966, 1972b). A more lophodont dentition is typical for stratigraphically older hippopotamids (Osborn, 1921), hence the latter author mistakenly assumed that Cyprus was the oldest island of the Mediterranean Sea, harbouring the most primitive species of hippotamids. However, this ancestral feature is best explained as an adaptation to a different niche and thus secondarily derived instead of a retention of an ancestral character (van der Geer, 2014).

The shift towards a higher degree of browsing, evolving away from the grazing habits of the common hippopotamus aligns with the change in neutral head posture. The loss of the fourth upper premolar in adult Cyprus dwarf hippopotamuses was interpreted by Sondaar (1977) as correlated to a change in jaw movement towards a larger transversal component. In the common hippopotamus, this lateral component during chewing is limited by the size and position of the large lower incisors, resulting in a specific wear pattern of these incisors with wear aspects on the medial side of the upper incisors and the lateral one of the lower incisors (Avedik & Clauss, 2023). However, when looking at the erosion patterns of the lower incisors of the Cyprus dwarf hippopotamus, we see a different erosion pattern, with the lower incisors completely and evenly worn all around. As Avedik & Clauss (2023) have shown, hippopotamid teeth have the lowest chewing efficacy among mammals despite their

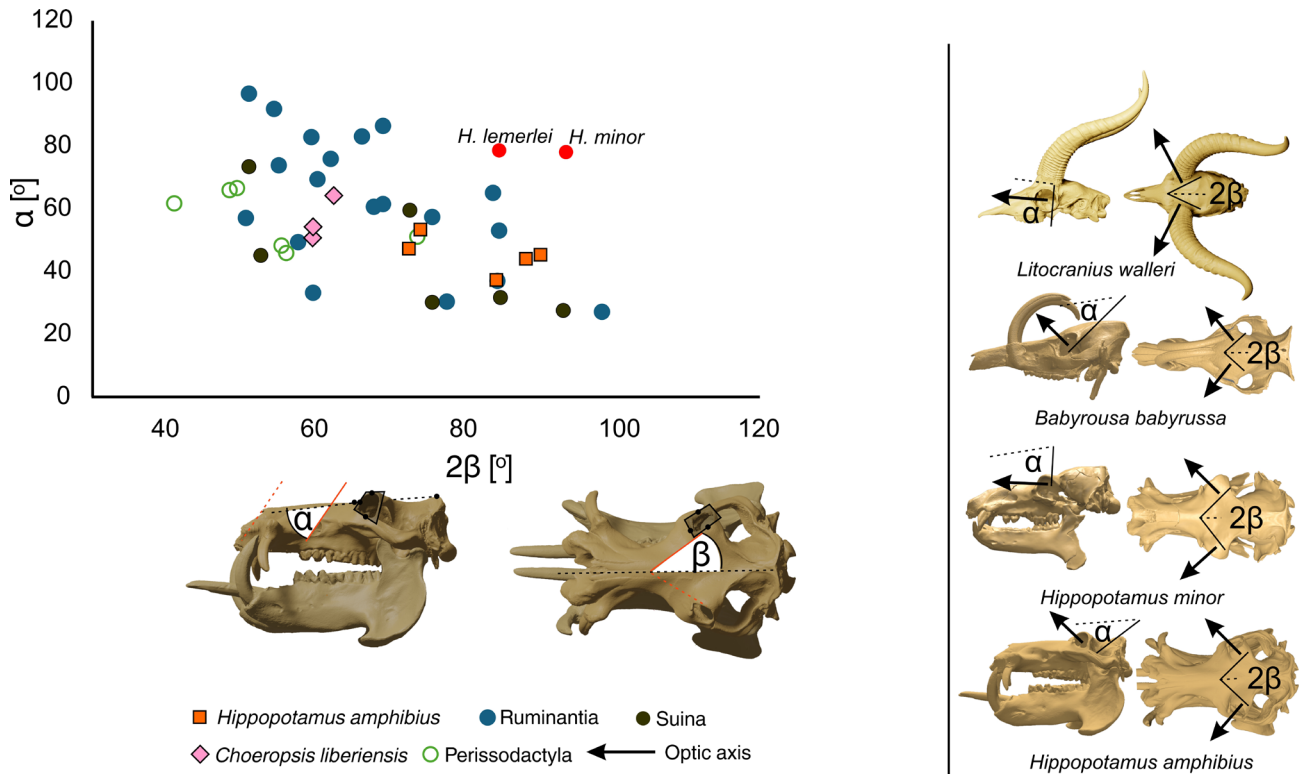


Fig. 6 - (color online) Scatter plot of orbit convergence (angle β) against frontation (angle α). Angle β is the dihedral angle between the orbital and sagittal plane. Angle α is the angle between the nasion-inion chord and the line formed by the intersection of the orbital and sagittal planes. Angle α represents orbit frontation and angle 2β represents orbit convergence. The latter is used as a surrogate variable for binocular visual field overlap (Heesy, 2007). Convergence and frontation angles of the comparative sample (Ruminantia, Suina and Perissodactyla) were taken from Gaillard et al. (2023). Images of skulls generated from models downloaded from Sketchfab (*Hippopotamus* and *Babyrousa*) and Morphosource (*Litocranius*; Blackburn et al., 2024).

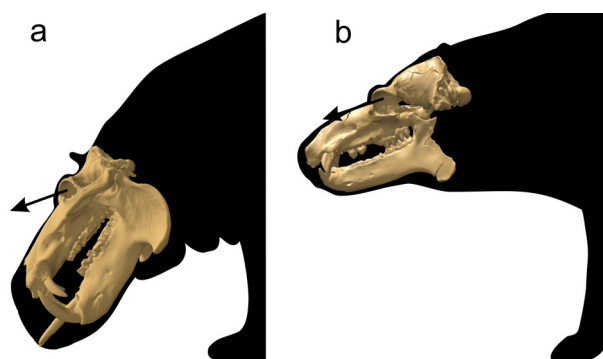


Fig. 7 - (color online) Neutral head posture in *Hippopotamus amphibius* (a) and *H. minor* (b). The arrow indicates the orbital axis. Head posture in *H. amphibius* is based on Benoit et al. (2002). The head of *H. minor* has been tilted here so that its orbital axis aligns with that of *H. amphibius*.

elaborate enamel folds. A substantial lateral component enhances chewing efficiency and was thus probably an advantage for the Cyprus dwarf hippopotamus, enabling it to increase its dietary niche width.

Sexual dimorphism

The mandibles of the Cyprus hippo roughly fall into two groups. One group is characterised by a considerably enlarged anterior part of the mandible and enlarged canines. The other group is characterised by narrow muzzles and smaller canines instead. In the common hippopotamus, the mandibles of males are on average 44% heavier and their canines are nearly twice the size as those of adult females (Shannon et al., 2021). This investment in weapon size is explained in the light of territoriality amongst males, but also as a tool in direct mating success. During mating, the male bites the neck or head of the female to hold on during mounting. Seen the dimorphism in jaw shape and canine size, the Cyprus dwarf hippopotamus likely retained this mating behaviour.

Ecological release

The lack of any other large mammal, except for an elephant, on Cyprus during the Pleistocene resulted in opening up evolutionary paths unavailable to mainland relatives of *H. minor*. In due time, it evolved a combination of traits that are unique to this endemic species. Probably body size reduction was the first evolutionary change, analogue to what has been observed in other insular megaherbivores, which evolved dwarfism (Lomolino et al., 2012). The highest degree of insular dwarfism among mammals was found in species with the longest time in isolation (Lomolino et al., 2013), indicating an arrival on Cyprus already in the Middle Pleistocene, despite the fact that *H. minor* fossils are found in Late Pleistocene sites. The extreme body mass shift in the Cyprus dwarf hippo probably reduced its dependency on fresh water for cooling, as its surface/volume ratio shifted significantly, opening up a change towards terrestriality as reflected in the anatomy of its feet, its head posture, and orbit orientation. Probably due to the absence of large river deltas with their grassy plains on this island, *H. minor* evolved a shift in its feeding ecology towards a browsing diet with a more efficient chewing, as reflected

in the anatomy of its teeth and dental wear patterns. This evolution towards this specialised ecology compared to its ancestor was probably the result of ecological release from competition and predation (Lomolino & van der Geer, 2024). The species survived for hundreds of thousands of years on the island, until it went extinct around the time of human arrival, as indicated by the occurrence of its youngest fossils at the archaeological site of Akrotiri Aetokremnos, dated to approximately 12,5 ka B.P. (Zazzo et al., 2015). Its tiny size may have accelerated its demise, because species that evolved the most extreme body size shifts, either towards dwarfism or gigantism, are most likely to go extinct when humans colonised the islands (Rozzi et al., 2023).

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data are available on the BSPI website at: <https://www.paleoitalia.it/bollettino-spi/bspi-vol-641/>

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