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A subfossil tooth of a dwarf *Hippopotamus* (Mammalia, Artiodactyla) from the Holocene of the Berivotra ouctrops (Mahajanga Basin, NW Madagascar), with remarks on the distribution of the genus in the island

Abstract - We report the presence of subfossil dwarf hippopotamuses from the neighbourhood of Berivotra (Mahajanga Basin, NW Madagascar), based on an isolated premolar of *Hippopotamus*, tentatively referred to *H. madagascariensis* Guldberg, 1882 or *H. lemerlei* Grandidier, 1868, two of the three species of the genus known in the Malagasy fossil record. Dwarf hippopotamuses from Madagascar are Holocenic, concentrated on the central upland and near the SW coast, with the exception of a single site on the East coast. Their presence and distribution in the N is poorly documented. The new finding, in a locality about 50 km E-SE to the city of Mahajanga, represents the innermost fossil site respect to the present coast line from the NW of the island, and increases the areal distribution of the genus in the Mahajanga Province.

Keywords: *Hippopotamus*, tooth, Holocene, NW Madagascar, distribution, palaeobiogeography.

Riassunto - Un dente subfossile di ippopotamo nano dell'Olocene dei depositi di Berivotra (Bacino di Mahajanga, Madagascar Nord-occidentale), con commenti sulla distribuzione del genere sull'isola.

Viene segnalata la presenza di ippopotami nani subfossili nei dintorni di Berivotra (Bacino di Mahajanga, NW Madagascar), sulla base del rinvenimento di un singolo premolare isolato. Il dente è attribuito ad *Hippopotamus*, e viene tentativamente riferito a *H. madagascariensis* Guldberg, 1882 o a *H. lemerlei* Grandidier, 1868, due delle tre specie appartenenti al genere note in Madagascar. I resti di ippopotami nani rinvenuti in Madagascar provengono da depositi esclusivamente Olocenici, concentrati nell'altopiano centrale e in prossimità della costa sud-occidentale dell'isola, ad eccezione di un unico sito sul versante orientale. La loro presenza e distribuzione nel nord, è invece (scarsamente) poco documentata. La nuova località, posta circa 50 km a est sud-est dalla città di Mahajanga, rappresenta il sito più interno rispetto all'attuale linea di costa sinora segnalato nel nord-ovest del Madagascar, ampliando l'areale di distribuzione del genere nella provincia.

Parole Chiave: *Hippopotamus*, dente, Olocene, Madagascar Nord occidentale, distribuzione, paleobiogeografia.

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Introduction

An isolated tooth of hippopotamus was collected as surface finds during October 2001 joint expedition conducted by palaeontologists from the Museo di Storia Naturale (Milano, Italy) and the Museo Civico dei Fossili di Besano (Varese, Italy), in agreement with the "Ministère de l'Énergie et des Mines" and "Direction des Mines et de la Géologie de Madagascar" (Antananarivo). The specimen MSNM V5310 comes from the right bank of a very small stream called Vavaranoniberivotra, SW to the Berivotra village (Fig. 1) at the foot of a cliff where the rill concentrates many and diverse fossils coming from the erosion of the overlying, exposed formations, belonging to differing geological times.

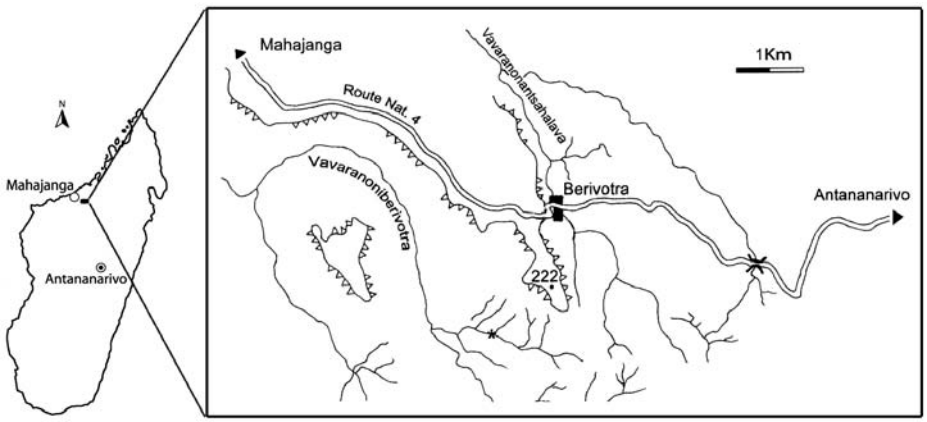

Fig. 1 - Map of the neighbourhood of the Berivotra village. The main localities and landscape elements cited in the text are shown in the map. The asterisk marks the site from where the specimen MSNM V5310 was collected. / Cartina geografica dei dintorni del villaggio di Berivotra, in cui sono evidenziati le principali località e i toponimi citati nel testo. L'asterisco indica la località da cui proviene l'esemplare MSNM V5310. (Modified from Garassino & Pasini, 2003: fig. 2; which is again based on the original drawing by Lavocat, 1955. / Rielaborata e semplificata a partire da Garassino & Pasini, 2003: fig. 2, basata sul disegno originale di Lavocat, 1955). Scale bar approximately equals 1 km. / La scala metrica equivale a circa 1 km.

Geological setting

The Berivotra Village is located in the Mahajanga Basin, NW Madagascar. This Basin is well known especially thanks to relevant findings occurred in the last decades, such as the Upper Cretaceous (Maastrichtian) dinosaurs (e.g., Krause, 2003; Sampson & Krause, 2007) and the coeval marine invertebrate fauna (e.g., decapod crustaceans; Garassino & Pasini, 2003).

The sedimentary record of the Mahajanga Basin includes strata dating from the upper Palaeozoic to Recent times. Cretaceous formations are in contact with Paleocene marls dated back to the Danian, in turn overlain by recent Quaternary deposits, which form a wide and scarcely vegetated plain extending from the E to the W, up to the surroundings of Mahajanga town. The stratigraphic section is well exposed along the sides of a cliff lowering to the SE, and to-date characterized by a system of small and ephemeral braided rivers which have eroded little and steep valleys. At both sides of these valleys, with typical flourishing vegetation and

sparse human sites, the recent fluvial deposits occur (Fig. 2). One of the Authors (G. P., 1989) heard local people telling about small autochthonous communities of crocodiles - *Crocodrylus niloticus ?madagascariensis* - still inhabiting those residual environments (see also Wermuth & Fuchs, 1978).

The fossil tooth has been recovered out of a clear geo-chronological context, in one of such allochtonous mounts mixed to small fragments of long bones gen et sp. indet. and two lateral teeth referable to the theropod dinosaur *Majungasaurus crenatissimus* (Depéret, 1896) Lavocat, 1955 (F. Fanti, Pers. Comm., 2005), the latter came down from the Upper Cretaceous Berivotra Formation (Sampson & Krause, 2007) strata of the overlying cliff, in turn covered by the recent Holocenic grounds.

As a consequence of the loose fossil finding, it is not know if pertained to the recent sediments deposed along the palaeoriver, or if it came down from the Quaternary deposits at the top of the cliff or if the transport occurred horizontally, vertically or in both ways.

Material and methods

The specimen is housed in the Vertebrate Palaeontological Collection of the Museo di Storia Naturale di Milano (acronym MSNM V). It consists of a single, isolated tooth, preserving a nearly complete crown, diagnostic at the genus level, and part of the worn root.

It was found isolated and exposed in loose sediments (see above). Measurements were taken with a digital caliper. Pictures were taken with a digital camera Panasonic Lumix DMC-LZ3. No particular specimen preparation was needed, thanks to the good preservation. The specimen was casted with silicon rubber for

Fig. 2 - Landscape in the neighbourhood of Berivotra (in N to SW view). / Aspetto attuale dei terreni nei dintorni di Berivotra (da nord verso sud ovest). (Photo/Foto G. Pasini).

comparison purpose. Although partly worn-out, the tooth crowns of the specimens MSNM Ma79, MSNM Ma4921, and MSNM unlabeled specimen, housed in the mammal collection of the Museo di Storia Naturale di Milano (MSNM Ma), and referred to *Hippopotamus amphibius*, were measured at the base of the cingulum for size comparisons. We adopted the terminology proposed by Smith and Dodson (2003) for anatomical notation and orientation in fossil vertebrate dentition.

Systematic Palaeontology

Mammalia Linnaeus,1758
Artiodactyla Owen, 1848
Hippopotamidae Gray, 1821
Genus *Hippopotamus* Linnaeus, 1758
Species *indet.*
(Fig. 3)

Specimen: MSNM V5310, one isolated tooth.

Age: recent Holocene.

Locality: Around Berivotra village, Mahajanga Basin, NW Madagascar, Vavaranoniberivotra River.

Description - Robust, well preserved, hypsodont tooth. The crown is subtriangular in shape, longer mesodistally than high apicobasally, with thick enamel. It mainly consists of a large central cusp, with a slightly worn tip. A well developed and asymmetric cingulum is present at the base of the crown. It is more developed, thicker, and rugose lingually, in particular in its distal portion where it bears small enamel crests and accessory enamel cusplets with vertical development. It is also well developed distally and mesially, whereas, although present, it is hardly evident labially. Although incomplete, the root was undoubtedly bifid, as indicated by the eight-shaped cross section, with the mesial portion forming the largest half of the eight. It shows traces of abrasion and sediment transport. The distolingual heel present in the P2 and P3 of some hippopotamids (Boisserie, 2005: fig. 5C) is absent. The tooth is considered an upper premolar based on the following features: the enamel is quite rugose, notably on the distal wall which includes a line of cusplets on a crest joining the lingual cingulum; there is no evidence of a lingual accessory cusp, generally occurring on lower premolars; the crown is distinctly curved lingually; and the mesial wall is marked by a triangular surface delimited lingually by a strong crest. Given the absence of distolingual accessory cusp is more frequent in P2, the tooth is considered a P2, although also P3s sometimes display a similar condition. This interpretation is supported by the ratio (61%) between the maximum labiolingual diameter, measured at the base of the cingulum, and the maximum mesodistal diameter (see Comparisons).

Comparisons - As pointed out by Boisserie (2005), “in mammal phylogeny, the cheek tooth rows often play a crucial role; this is not the case for the Hippopotamidae”. Moreover Coryndon (1977) noted “specially for the molars, that are very conservative in development and slight variations in enamel pattern often reflecting only slight differences in feeding habits rather than morphogenetic characters. In fact, hippo cheek teeth show only minor variations and are the least useful element for diagnosis”. Both size and morphology of the specimen MSNM V5310,

however, permit some comparisons with the three Malagasy species reported up to today. The mandible of the holotype of *H. laloumena*, housed at the Musée de l'Académie Malgache (Antananarivo), belongs to an adult individual lacking cheek teeth, and having three empty, closed molar alveoli, thus rendering impossible any comparisons (Faure et Guérin, 1990). The large body-size attained by the species *H. laloumena*, and the related size of the premolars, indicate that MSNM V5310 does not belong to an individual of this species. As a matter of fact, the upper premolars 2 and 3 of three individuals (see material and methods) of the extant species *H. amphibius*, recently considered a senior synonym of *H. laloumena* (Weston & Lister, 2009; see also below), have been measured, their diameters at the base of the cingulum resulting 129-179% larger than those of MSNM V5310.

Thus, the observed small size of the specimen MSNM V5310 limits its attribution to a dwarf *Hippopotamus* of the species *H. lemerlei* or *H. madagascariensis*.

According to Stuenes (1989), these species differ in cranial morphology, reflecting adaptations to two different habitats. As mentioned above, *H. madagascariensis* is larger in size than *H. lemerlei*, and had a more terrestrial lifestyle. The former has also a slightly smaller skull for its body size, this compensates for the larger body size, the skulls and the related teeth resulting comparable in size. *H. lemerlei* shows also a certain degree of sexual dimorphism in the general shape and morphology of the skull, not involving, however, cheek dentition (Stuenes, 1989). Stuenes (1989) briefly described some characters of the dentition of both species. In the upper dentition of *H. lemerlei* P2 and P3 are similar in shape, although P3 is slightly larger than P2; they are larger mesodistally than labiolingually, and they have a cingulum distinctly marked both lingually and distally, but not mesially and labially. Enamel nodules (or mamelons - see Hillson, 2005) are present on both sides, especially toward the mesial portion of the crown. As the premolar rows generally diverge rostrally, in most specimens P2 shows slight outward distorsion of the mesial part. The lower dentition has premolars similar to each other, surrounded by a cingulum developed mesially, distally, and lingually although hardly marked labially. In the upper dentition of *H. madagascariensis* P2 and P3 are similar in shape, but P3 is somewhat larger and sometimes bears a distal triangular structure; both P2 and P3 are surrounded by cingula of variable development, hardly marked mesially in some specimens. In the lower dentition, p2 and p3 are similar, surrounded by well developed cingula mesially, distally and lingually, whereas the labial cingulum may be incomplete; the enamel of the premolars often bears scattered or closely spaced nodules (or mamelons).

The specimen MSNM V5310 is well comparable with P2 (possibly P3) of *H. lemerlei* and. *H. madagascariensis* (Stuenes, 1989) in crown morphology, and it may pertain to the left maxilla of both species, which share a great intra- and interspecific variability and a similar premolar tooth morphology. MSNM V5310 has a maximum labiolingual diameter, measured at the base of the cingulum, of 14.5 mm, and a maximum mesodistal diameter, measured at the base of the cingulum, of 23.8 mm (Tab. 1), the ratio being 61%. The premolars of the specimens figured by Stuenes (1989: figs 4, 8, 9) are as large as MSNM V5310. For example, P2 of *Hippopotamus lemerlei* is about 16 mm long labiolingually and 22 mm long mesodistally (Stuenes, 1989: fig. 4), the ratio being 73%, whereas P2 and P3 of *Hippopotamus madagascariensis* are, respectively, 17 mm x 23 mm (ratio 74%) and 21 x 22 mm (ratio 96%). Based on these comparisons, MSNM V5310 is more similar to a P2. In conclusion, we consider our specimen as a left P2 or P3, more probably the former, of a dwarf *Hippopotamus* sp., referable in all likelihood to *H. lemerlei* or

H. madagascariensis, according to the crown morphology and the body-size (and the related tooth-size) attained by these species.

Tab. 1 – Measurements / Misure.

Maximum height of the tooth, root included	22.5 mm
Maximum tooth crown height	18.6 mm
Maximum mesodistal diameter, at the base of the cingulum	23.8 mm
Maximum mesodistal diameter, at the base of the root	21.5 mm
Maximum labiolingual diameter, at the base of the cingulum	14.5 mm
Maximum labiolingual diameter, at the base of the root	14.0 mm

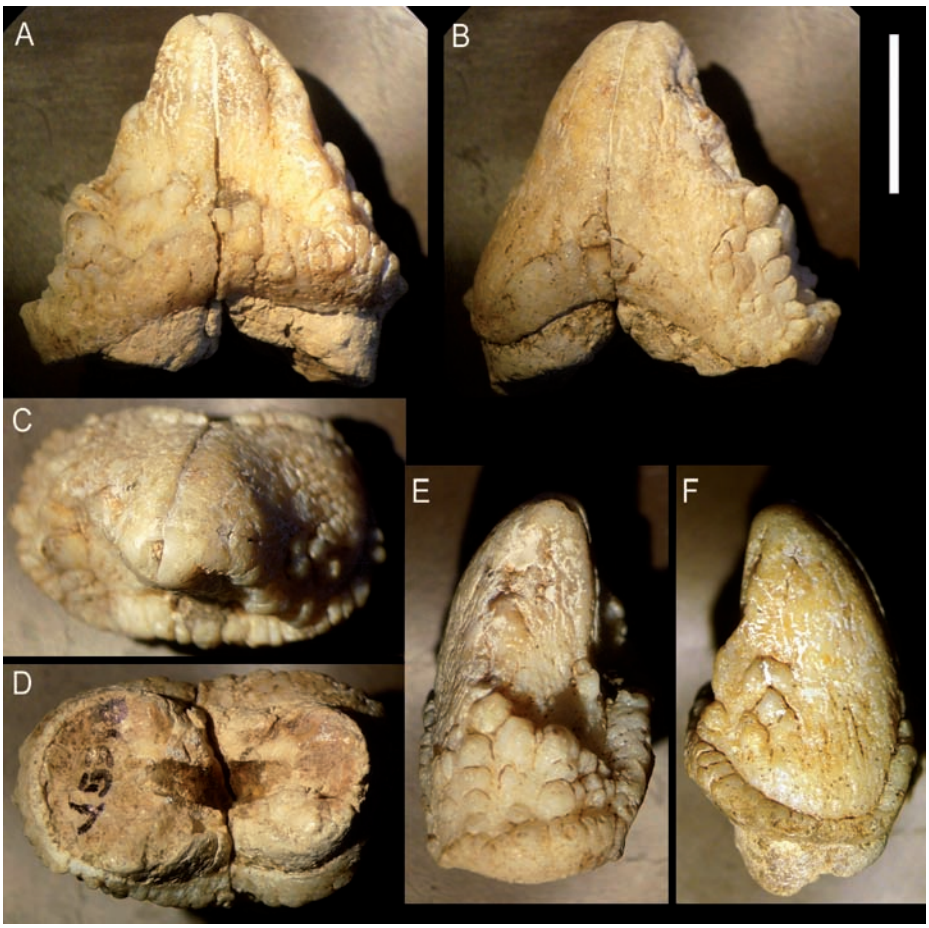

Fig. 3 - MSNM V5310. A) lingual view / vista linguale; B) labial view / vista labiale; C) occlusal (apical) view / vista occlusale (apicale); D) root apical view / vista apicale della radice; E) distal view / vista distale; F) mesial view / vista mesiale. Scale bar equals / barra pari a 10 mm. (Photo/Foto S. Maganuco).

Previous records and distribution of *Hippopotamus* in Madagascar

Hippopotamuses are known in the Malagasy fossil record as subfossil dwarf species referable to the genus *Hippopotamus*. The first subfossil dwarf hippopotamuses from Madagascar was reported by Grandidier, 1868 (in Milne Edwards, 1868), who published a note based on the remains of several individuals from the locality of Ambolisatra (SW coast of the island), referring the material to *Hippopotamus lemerlei*. Subsequently, Guldberg (1883) erected the new species *H. madagascariensis*, based on different remains coming from the upland plain (Antsirabe region) of the W-SW coast. Stuenes (1989) and Harris (1991) discussed the systematic position of the Malagasy species, recognizing as valid *H. lemerlei* and *H. madagascariensis.* They also discussed about the possible attribution of the latter species to the genus *Hexaprotodon*, genus finally adopted by Harris (1991). This attribution, however, is still highly debated among the specialists (Boisserie, 2005) and will not be followed here. Faure & Guérin (1990) described another species, *H. laloumena,* recorded in the south-central area of the East coast. According to Weston & Lister (2009), however, *H. laloumena* is morphologically indistinguishable from a young adult female *H. amphibius.* As for the N of the island, the occurrence had been vaguely reported in a short note by Perrier de la Bathie (1926); in a second note (see Lamberton, 1934), however, the same author stated: "Le seul gisement de subfossiles jusqu'a prèsent dans le N. e le N.-W. de l'Ile, celui ètudiè par Kaudern, dans un affluent de droite du Bemarivo (Anavilava)..." *,* signaling that it was the recent, even if not exactly dated, sediments infilling pothole inside the stream bed, without any mention either on the faunal assemblage or the presence of *Hippopotamus*. No subsequent mentions or studies are present in literature, neither information about the collection in which the material, if ever collected, is housed. As cited by Besairie (1972), the presence of *Hippopotamus* in the NW of the island was reported by Mahè (1965), who signaled the finding of an important deposit with subfossils at Amparihingidoro, a village located along the Route de l'Ouest (R.N. 4) towards Antananarivo, 7 km before the town of Mahajanga, on the right bank of the estuary of the Betsiboka River.

Apart from many fragments of diverse mammal species, Mahè (1965) reported the presence of *H. lemerlei,* remarking that this pile of fossils lies in a fluvial lowland or ephemeral swamp, periodically inundated during the wet season. More recently, Burney *et al*., (1997; 2004) reported the occurrence of the subfossil species *H.* cf. *lemerlei* in the northern areas of the island, along the West coast, NE to Mahajanga, Anjohibe cave complex.

Summing up, three species of subfossil dwarf hippopotamuses have been described in the Holocene in Madagascar:

H. laloumena Faure & Guérin, 1990 - or *H. amphibius*, according to Weston & Lister (2009) -, which was the largest one, had an amphibious lifestyle, and inhabited the South-East coast only;

H. lemerlei Grandidier, 1868, which was the smallest and slenderest species had an amphibious lifestyle and presented a marked sexual dimorfism (Stuenes,1989);

H. madagascariensis Guldberg, 1883, (syn. *Hexaprotodon madagascariensis* Harris, 1991), which was intermediate in size, and had a more terrestrial lifestyle.

The latter two species were both well distributed along the S-SW coast and the central upland, with few reports indicating also the sporadic presence of *H. lemerlei* or *H.* cf. *lemerlei* in the NW (Mahè, 1965; Burney *et al*., 1997; 2004). The distribution of the subfossil hippopotamuses is summarized in figure 4.

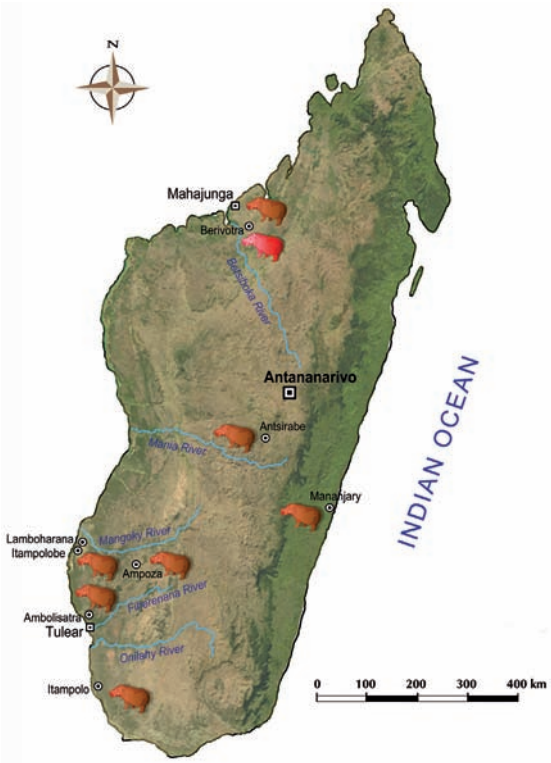

Fig. 4 - Geographical distribution of the subfossil remains of the genus *Hippopotamus* in the Holocene of Madagascar. The red silhouette indicates the new locality; each brown silhouette can refer to different, neighbouring localities. / Distribuzione geografica dei resti sub fossili del genere Hippopotamus nell'Olocene del Madagascar. La sagoma rossa indica la nuova località; le sagome in marrone possono indicare anche più località limitrofe. (Drawings by / Disegni di / D. Bonadonna, S. Maganuco & G. Pasini).

Conclusions

Despite of the allochtonous origin of the specimen, its preservation and the available geological data indicate that it undoubtedly dated back to the recent Holocene. This is consistent with the palaeontological data and zooarchaeological observations that documented the presence of dwarf hippopotamuses, at least for the S-SE of the Island, from 9th to 17th century - and up to 19th century (Rakotozafy & Goodman, 2005), when they became extinct probably due to climatic changes, human impact on the pre-existing ecosystem, and human hunting (MacPhee & Burney, 1991; Godfrey, 1986; Burney *et al*., 1997; 2004).

The large body size (and the related tooth size) of *H. laloumena / H. amphibius*, indicate that MSNM V5310 does not belong to an individual of this species. This attribution is ruled out also by the geographical distribution of *H. laloumena* / *H. amphibius*, limited to a small area along the SE coast. The specimen MSNM V5310 is well comparable with LP2 (or, less probably, LP3) of *H. lemerlei* and. *H. madagascariensis* (Stuenes, 1989) in both size and crown morphology. Sporadic remains of *H. lemerlei* and *H.* cf. *lemerlei*, the species with an amphibious lifestyle, was recovered in the NW, close to the town of Mahajanga (Mahè, 1965), and at Anjoibe

cave (Burney *et al*., 1997; 2004), around 60 km NE of the locality where the studied fossil were found. These remains, as well as the new finding described here, were found in recent Holocene sedimentary deposits showing no significant transport (Mahè, 1965; Burney *et al*., 1997), lying in the proximity of wide rivers, which in the past should have represented a larger deltaic fluvial system, surrounded by wide alluvial plains, favorable in some part to mostly amphibian species such as *H. lemerlei*, and possibly, in more internal and continental portions, to terrestrial breeding animals such as *H. madagascariensis*. In conclusion, our finding 1) in addition to the finding reported by Mahè (1965) and Burney *et al*. (1997; 2004), confirms the presence of a favorable environment for the dwarf *Hippopotamus* in the Mahajanga Province; 2) represents the inner most fossil site respect to the present coast line from the N of the island, increasing the up to today sporadic areal distribution of the genus; 3) supports the idea of a possible even more northern distribution of the hippopotamuses in similar behaviors (Sofia River Delta), perhaps up to the Mahavavy River Delta (Ambilobe Region, Diego Suarez Province), suggesting that the present knowledge about the distributional area of the Hippopotamidae in the N of the island during the recent part of the Holocene is more linked to the lack of data, rather than to an effective, really sporadic distribution of the genus.

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