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If hippopotamuses cannot swim, how did they colonize islands?

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Owing to their aquatic lifestyle, hippopotamuses are normally believed to have reached islands by swimming. Yet, some studies suggest they cannot swim due to their relatively high density. If so, this raises the question of how hippopotamuses would have reached some islands. Their immigration into the British Isles, Sicily, Malta, Zanzibar and Mafia can be accounted for, because these islands sit on continental shelves and were often linked to the mainland during the Pleistocene glacio-eustatic sea-level falls. In contrast, their occurrence in Crete, Cyprus and Madagascar would be more difficult to explain. Available geological evidence does not seem to rule out that the latter islands might have been connected with the nearest mainland areas in very recent times. This study intends to consider possibilities about how hippopotamuses reached islands and to show that more effective collaboration is required among specialists involved with the study of insular evolution, colonization and speciation. ☐ *Dispersal events, extra-Mediterranean islands, glacio-eustatic sea-level excursions, Mediterranean islands, Pleistocene.*

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It is still an unsettled question whether or not *Hippopotamus amphibius* can swim. Yet, the biogeographical, and perhaps also geological, implications of this debate are not trivial. If they are non-swimmers, how did they reach and colonize islands?

Many researchers (e.g. Howell 1930; Schüle 1993; Sondaar & van der Geer 2002; Marra 2005; O'Regan *et al.* 2006; Ali & Huber 2010) believe hippopotamuses are excellent divers and swimmers. This belief, however, is based solely on their aquatic lifestyle. In fact, there is no published account, to the writer's knowledge, where hippopotamuses are demonstrably shown swimming or floating at the surface of any water body.

The only study that seems to demonstrate their supposed swimming skills is that published by Modha (1968), who worked on the basking behaviours of crocodiles on Central Island (Lake Turkana, Kenya). In that paper, Modha (1968) described an encounter of the crocodiles with a single hippopotamus. Central Island is almost 9 km off the nearest (western) coast of Lake Turkana, and the lake floor lies at −50 m of depth around it. The hippopotamus, therefore, could only have swum there. The report, however, is dubious. While Modha (1968) gave full accounts on when he observed crocodiles interacting with other species, such as birds and turtles, he failed to do so for the hippopotamus, writing generically that the animal 'had absolute right of way over basking crocodiles', except brooding females, which snapped at him as he passed by. The suspicion is that the author might have reported a behaviour which he did not directly observe on the island.

In fact, the case reported from Central Island is practically ignored by later authors. van der Geer *et al.* (2010) state that hippopotamuses cannot swim in freshwater, but only walk upon river or lake bottoms. The authors claim, however, that hippopotamuses can float in seawater. This is untested an opinion, based on Frädrich's (1967) belief, cited by Hadjisterkotis *et al.* (2000), that hippopotamuses must have swum to reach the islands of Zanzibar and Mafia. These two islands, however, rest on the continental shelf. Today, they are separated from the African mainland by extremely shallow sea straits. During past glacial sea-level lowstands, Zanzibar and Mafia were part of the African coast.

Recently, Coughlin and Fish (2009) conducted scientific investigations on the aquatic locomotor performances of hippopotamuses. The results imply that extant hippopotamuses cannot swim nor float. Their conclusion is supported by a number of studies (see below) that indicate that the hippopotamus body is denser than water. These conclusions confirm earlier opinions of several scholars (Howell 1930; Klingel 1991; Fish 1993; Eltringham 1999; Nowak 1999; Inuzuka 2000; Fisher *et al.* 2007) that they cannot swim. This opens a number of challenging problems. How did hippopotamuses manage to cross tens or even hundreds of kilometres of open

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ocean to islands? And what forced them to venture through stretches of salt water?

Hippopotamuses' aquatic locomotion and life habits

Hippopotamuses have poor streamlining and non-buoyant barrel-like bodies (Fish 2001; Coughlin & Fish 2009). Their feet are not modified enough for swimming (Howell 1930; Fish 1993; Eltringham 1999; Coughlin & Fish 2009). They were seldom observed losing contact with river and lake bottoms; instead, they preferentially walk underwater rather than swim (Klingel 1991; Eltringham 1999; Nowak 1999; Inuzuka 2000; Fisher *et al.* 2007; Coughlin & Fish 2009). When they lose contact with the bottom, they actually gallop short distances with brief unsupported intervals (they 'walk on the bottom… as astronauts on the moon': Estes 1992). To overcome buoyancy, hippopotamuses needed to increase their specific bone density (Wall 1983; Fish & Stein 1991; Thewissen *et al.* 2009). This was achieved by tightly packing cancellous bone into the medullary cavity (Wall 1983; Thewissen *et al.* 2009). Their high bone density and the control on their specific gravity allow them to keep their feet firmly on the bottom (Wall 1983; Nowak 1999; Thewissen *et al.* 2009). A solution comparable to the weighted boots of past deep-sea divers. When submerged, the counterbalance of the denser limb bones helps hippopotamuses stabilize their underwater walking by shifting the centre of mass under the centre of buoyancy. This prevents their barrel-shaped body from rolling and thus from unstable motions (Fish 2002; Coughlin & Fish 2009). The necessity to keep the feet firmly in contact with the bottom to control stability and avoid rolling over is even more imperative when hippopotamuses venture in salt water, where buoyancy is enhanced.

Adults need to resurface to breathe every 3–6 minutes, juveniles every two to three minutes (Eltringham 1999; Nowak 1999). They also resurface automatically while sleeping underwater. If they cannot swim, hippopotamuses would not like being out of their depth and thus cautiously keep away from deep water (Jackson & Gartlan 1965) where hydrostatic pressure would prevent their resurfacing.

Contrary to other large mammals, hippopotamuses have low metabolic energy requirements and can resist starvation longer than other mammals (Verheyen 1954; Field 1968; Owen-Smith 1988; Mapesa *et al.* 2007). Nonetheless, if they are not immersed in muddy wallows, which enables them to resist some time without any food, water, or shade, hippopotamuses need water to avoid diurnal desiccation (Luck & Wright 1964). By being evaporation-insensitive animals, they also need to drink water daily (Levin *et al.* 2006). A theoretic approach using the metabolic rate versus body mass relationship estimates that hippopotamuses have a water intake of 43–72 l per day (Calder 1984).

Hippopotamuses also have low birth rate (mean calving interval around two years, i.e. fecundity of 0.5–0.55: Laws & Clough 1966). Hence, to successfully colonize and durably settle on islands, a fair number of individuals need to be involved.

Hippoptamus antiquus, a Pleistocene species from which many endemic insular hippopotamuses derived (see below), differed from the present-day *H. amphibus* somewhat in size (it was generally 5–10% larger: Mazza & Bertini 2012, 2013), in the shape of the skull, as well as in the proportions of the limb bones (Mazza 1995; Kahlke 1997, 2001). *H. antiquus* also had relatively more graviportal limbs (Mazza 1995; Kahlke 1997). Worth mentioning is that like *H. amphibius*, also *H. antiquus* had increased limb bone density with analogous tight packing of cancellous bone in the medullary cavity (Fig. 1). The overall larger size, barrel-like, poorly streamlined body, and dense and graviportally built limb bones suggest that, quite like (or perhaps even more than) *H. amphibius*, also *H. antiquus* might have been a bottom walker, not a swimmer.

Insular hippopotamuses

In the course of the Pleistocene, hippopotamuses colonized numerous islands. In the Mediterranean, hippopotamuses reached Sicily, Malta, Cyprus, Crete and probably most other Mediterranean islands. Outside the Mediterranean, they arrived at the British Isles, Mafia, Zanzibar and Madagascar. The time of their dispersal to most of these islands is unknown or roughly inferred biochronologically from the accompanying faunas, and rarely referred to the marine isotope stages. These insular hippopotamuses derived from either the extinct *Hippopotamus antiquus* or the living *H. amphibius* (e.g. Marra 2005). Most of the Mediterranean pygmy hippopotamuses probably derived from *H. antiquus* (Caloi & Palombo 1983; Spaan 1996), whereas others, such as the ones from Cyprus (e.g. Marra 2005) and Madagascar (Weston & Lister 2009), originated from *H. amphibius*. Madagascar prehistorically supported up to three species.

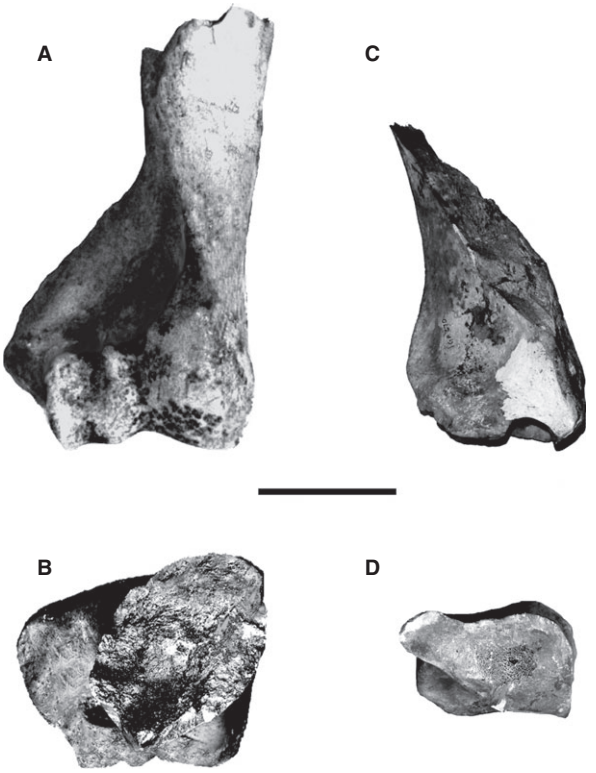


Fig. 1. Two limb bone fragments of *Hippopotamus antiquus* from the collections of the Geological and Palaeontological Section of the Museum of Natural History of the University of Florence, Italy. The broken diaphyses of the bones show the medullary cavities tightly packed with cancellous bone: A, distal half of right humerus (IGF 640), cranial view; B, distal half of right humerus (IGF 640), proximal view; C, distal half of right tibia (IGF 670), dorsal view; and D, distal half of right tibia (IGF 670), proximal view. The enlarged proximal views (B, D) show the medullary cavities of the diaphyses filled with cancellous bone. This solution, which can be observed also in modern *H. amphibius*, increases the specific bone density of the distal parts of the limb bones, enabling hippopotamuses to overcome buoyancy (Wall 1983; Fish & Stein 1991; Thewissen *et al.* 2009). Scale bar 10 cm.

The British Isles, Sicily, Malta, Zanzibar and Mafia are classified as land–bridge islands by biogeographers (e.g. van der Geer *et al.* 2010). The shortest distance across the English Channel is 34 km. All the Mediterranean islands but Sicily are presently several tens of kilometres off the nearest mainland areas. Zanzibar and Mafia are some 20 and 18 km off Tanzania's coastline, respectively. The favourable interplay between regional uplifts, glacio-isostatic rebounds and high-amplitude glacio-eustatic changes created temporary connections that enabled hippopotamuses to spread into these islands (e.g. Bridgland & Schreve 2004).

The cases of Cyprus, Crete and Madagascar are quite different. Cyprus is an oceanic island, and Crete and Madagascar are micro-continental islands (e.g. van der Geer *et al.* 2010). Cyprus is some 80 km off the nearest Turkish coastline, while Crete can be reached via two island stepping-stone connections, one from Greece, the other from Turkey, with a set of sea straits, about 30 to 40–50 km wide, among them. Madagascar and Africa are separated by the 430-km-wide Mozambique Channel. Even if hippopotamuses were good swimmers, these distances would anyhow be challenging, or impossible to cross. How could they get across?

Hippopotamus insular colonization

Several dispersal methods have been hypothesized to explain the presence of non-volant animals on islands. These include: (1) a two-way corridor, through which two regions freely interchange faunas; (2) filtered dispersal, which lets through only selected organisms; (3) the pendel route, a two-way connection for some animals, but an insurmountable barrier for others; and (4) a sweepstakes spread, which is a sporadic, accidental and highly selective one-way dispersal (Simpson 1940, 1952; van der Geer *et al.* 2010). Successful colonizers are generalist, broad-niched species, with high ecological tolerance (Lomolino *et al.* 2010). They must be, or must become, efficient in using limited resources. Hence, r-strategists, those with high fecundity to potentially ensure sufficient offspring, are normally favoured immigrants (Lomolino *et al.* 2010). Transition to K-strategy eventually leads to consolidated insular colonization and thus to the generation of endemic sub-species, or species (Lomolino *et al.* 2010).

Hippopotamuses are extreme K-selected animals (e.g. Eltringham 1999). They should therefore be quite unsuitable insular colonizers, unless islands are physically connected to mainland areas, and an appropriate number of individuals can immigrate in a reasonably short period of time. Owing to their stochastic nature, sweepstakes routes, such as natural rafting or tsunami-like transportation, would not assure the settlement of sufficient numbers of hippopotamuses. There are also physiological and eco-ethological characteristics of these animals that speak against sweepstakes.

Large terrestrial mammals are more effective thermoregulators than poikilotherm animals and smaller mammals, but need greater supplies of food and water. Some mammals lower their food and water requirements by going into a state of torpor or hibernation. Torpor or hibernation, however, are unimaginable in hippopotamuses.

Seawater rafting, however, in the case of hippopotamuses, would also raise other issues. How thick should a seaworthy craft of tangled mat of vegetation be to carry pachyderms weighing anywhere from 1 to 2 tons? And how long could a hippopotamus resist exposed to sunlight on floating mats of vegetation? The skin of these animals is very sensitive and will crack if exposed for a long time at direct sunlight. This is one of the reasons why they drink large amounts of water (Calder 1984) and stay submerged or wallow in mud during the day, grazing at night near their aquatic habitats (Luck & Wright 1964). When out of the water, to protect their skin, hippopotamuses secrete an oily red fluid produced by mucous glands.

If we exclude a few anecdotal reports (van Duzer 2004), there is only one account (Prescott 1959), to the writer's knowledge, where a mammal, a jackrabbit (*Lepus californicus*), was discovered perched on a pelagic raft of giant kelp, *Macrocystis pyrifera*, about 15 miles southeast of San Clemente, one of the three Channel islands. The animal was found in very poor condition. This example seems to argue against island colonization via natural rafting. In fact, no jackrabbits are reported inhabiting any of the Channel Islands, although *Lepus californicus* is reported in western North America since the Early Irvingtonian (Barnosky 2004). In over 1.5 million years, not one rafting jackrabbit ever colonized one of the three Channel Islands, which are located, at most, within a reach of 120 km off the Californian coast. And, leporids have far higher reproductive potential than hippopotamuses.

In the light of all this, overseas dispersal by rafting should be considered a rare (if possible) and fortuitous occurrence in animals that would suffer from prolonged lack of food, water and long-lasting contact with sea water, provided they possess the physiological ability to withstand periods passed drifting on the sea gripping to vegetation, and to successfully settle in the island habitat. Hippopotamuses do not seem to meet these requirements.

An option might be that hippopotamuses sometimes get caught up by particularly strong channels of flowing water. Drifting tens or even hundreds of kilometres across the sea to an island requires strong, sustained and favourably directed currents, and favourable vertical water movements to stay afloat long enough, or the ability to do so. All conditions that have never been verified in hippopotamuses, either experimentally and/or with field data. Strong, confined energetic jets flowing seaward from near the shore are rip currents (McKenzie 1958). Peak rip flow speeds may reach up to 1.3 m/s (Austin *et al.* 2010). A rip channel normally moves diagonally across the surf zone, but it may flow at right angles to the beach. In particularly heavy storms, rip currents may stretch as much as 1400 metres out to sea (McKenzie 1958; Dalrymple *et al.* 2011). Most of the islands colonized by hippopotamuses, however, are far beyond this range.

Implications of the presence of non-swimming insular hippopotamus

In the light of the above considerations, if hippopotamuses cannot swim, their occurrence on islands can be an important tell-tale sign. It may furnish useful evidence, but also chronological constraints, to geologists for a better comprehension of the dynamics of landmasses and of sea-level excursions. By revealing and possibly dating yet undetected physical connections with the nearest mainland, the presence of non-swimming hippopotamuses on islands can be used to test the strength and reliability of available geological reconstructions. The eventuality that hippopotamuses cannot swim may suggest some re-examination of available geological, paleogeographical and paleontological records. The careful examination of the seafloor around islands such as Cyprus or Madagascar, for example, shows the presence of positive structures blanketed by hitherto unexplored Quaternary sedimentary successions (e.g. see Deep Sea drilling Program: http://www.deepseadrilling.org/25/dsdp_toc.htm, where the Pleistocene deposits overlying the Davie Ridge which crosses the Mozambique Channel have been bypassed). From the literature we learn, for instance, that the Plio-Pleistocene terms of the stratigraphical sequences over the northeastern underwater extension of the Kyrenia Range, at Cyprus, are missing or largely condensed (Aksu *et al.* 2005), as happens when there is the surfacing of an originally submerged structure. The same sources inform us that those structures were also affected by active Quaternary tectonics and volcanism. Because the Quaternary is a time when the sea level fluctuated, sometimes dropping down 120–130 m, in response to cyclic climatic forcing, we can speculate that the interplay of tectonics and sea-level lowstands may have temporarily created the favourable conditions for the direct colonization of those islands from the nearest mainland, at least during the most severe glacial periods. Until more information is available and seafloor sediments are more carefully explored, we cannot be sure that sea-level changes and/or tectonics could have generated such connections.

Hippopotamuses offer new prospects in the study of insular colonization

If Coughlin & Fish's (2009) conclusion that hippopotamuses cannot swim is correct, then widely accepted models for the methods, patterns, and timing of the colonization and dispersal to several islands (e.g. Cyprus, Crete and Madagascar) must be reconsidered. Rather than swimming to the islands, they either walked on land bridges or 'bottom walked' in waters shallow enough to allow them to resurface every few minutes to breathe. Of the four dispersal methods proposed by Simpson (1940, 1952), sweepstake spread is the least probable for hypothetically non-swimming hippopotamuses, and for most terrestrial mammals. It is far too demanding and stressful physiologically for homoeotherm animals, and it cannot guarantee a critical number of individuals, and therefore a sufficiently varied genepool, to avoid the unsteadiness of genetic drift and extinction. Parsimony must always guide our choice among alternative options. This suggests Cyprus, Crete and Madagascar were likely connected to the mainland by land bridges, or very shallow water that would allow the hippopotamuses to periodically surface. Associated insular faunal components can make us discern whether the connection was a two-way or a filtered corridor, or maybe even a filtering stepping-stone connection, although selective extinction and within-island speciation may have profoundly altered the community's original composition.

The colonization of islands by hippopotamuses indicates that our knowledge of the many complex processes operative in insular systems, such as colonization, insular evolution and speciation, is far from complete. The resolution of such problems will require effective collaboration among biologists, palaeontologists, geologists and biogeographers.

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