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Human translocation as an alternative hypothesis to explain the presence of giant tortoises on remote islands in the south-western Indian Ocean

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Abstract

Giant tortoises are known from several remote islands in the Indian Ocean (IO). Our present understanding of ocean circulation patterns, the age of the islands, and the life history traits of giant tortoises makes it difficult to comprehend how these animals arrived on such small, remote and geologically young (8–1.5 Ma) landmasses. For colonization to have occurred by dispersal, giant tortoises must either have originated in Madagascar or Africa and swum for hundreds of km against the ocean currents, or have launched themselves from the eastern IO margin and drifted with the currents over several thousands of km of open ocean. After these navigational feats, the tortoises would have needed to found new, viable populations on potentially inhospitable volcanic or coral outcrops. Geologically recent sea level changes are likely to have eliminated terrestrial life from islands like Aldabra, complicating the scenario. We reviewed information relating to IO geology, the evolution and ecology of giant tortoises, and the spread of humans within the region, and propose an alternative explanation: we posit that giant tortoises were introduced to the IO islands by early Austronesian sailors, possibly to establish provisioning stations for their journeys, just as European sailors did in more recent historical times.

Keywords

Austronesians, giant land tortoises, Madagascar, Mascarene Islands, ocean currents, volcanic islands

Introduction

Large land tortoises had a cosmopolitan distribution until relatively recently; as many as 36 large and giant land tortoise species became extinct after the Pleistocene. Today only two species survive, Chelonia nigra (Quoy & Gaimard, 1824) in the Galápagos, north-eastern Pacific Ocean, and Aldabrachelys gigantea (Schweigger, 1812) on Aldabra, south-western Indian Ocean (SWIO). Aldabra, a coral reef 400 km NW of Madagascar and 600 km W of Africa, is the only island in the SWIO sustaining a natural population of extant giant land tortoises today (Hansen et al., 2010).

Both historical records and in situ remains testify that Madagascar harboured two subfossil giant land tortoise species, while in the Mascarene Islands, Mauritius and Rodrigues were home to two species each, and Réunion, to one species (van Dijk et al., 2014). The two Malagasy species went extinct 750 ± 37 and 1250 ± 50 years ago respectively (Burleigh & Arnold, 1986). The Aldabra giant tortoise is the only SWIO giant tortoise which had a wide range historically, whereas the extinct Mascarene tortoises were endemic to their islands (Fig. 1; Karanth et al., 2005; Pedrono et al., 2013).

Although the demise of the extinct species is well documented, the biogeographical evolution of the IO giant tortoises is not well understood, despite the great leaps that our knowledge of IO geology and continental drift, SWIO ocean currents, palaeontology, the phylogeny and ecology of land tortoises and of human history has taken in recent decades. The enigma of the arrival of giant land tortoises on the SWIO islands is complicated by several facts: (1) the islands are magnitudes smaller and much more remote than Madagascar, the colonization of which has fuelled much debate; (2) they emerged only a few million years ago and (3) that are located even further east of Africa than Madagascar. If ocean currents prohibited repeated colonization of Madagascar from Africa during the last few million years, it seems highly unlikely that the small, remote SWIO islands could have been colonized by giant tortoises during this period. We aim, therefore, to evaluate the commonly accepted
theory of the colonization of SWIO islands by tortoises against an alternative hypothesis that humans transported giant tortoises to some of these islands. This evaluation is based on an analysis of more than 700 peer-reviewed publications from several pertinent fields (see Appendices S1 & S2 in Supporting Information).

MODERN HISTORY

Giant land tortoises were present on the Mascarene Islands when they were first encountered by European sailors between 1511 and 1638, and became extinct between 1735 and 1840 (Stuckas et al., 2013; Bour et al., 2014). The dates recorded for the European discoveries of the small SWIO islands are 1511 for Mauritius, 1512 for Réunion, 1638 for Rodrigues and 1609 for the granitic Seychelles (Stoddart et al., 1979). Madagascar, with a total area of some 587,000 km², is almost 130 times larger than the three Mascarene Islands combined. Archaeological sites in the northwest have Arabic affinities (Dewar et al., 2013), but linguistic ties clearly link earlier settlement with Austronesians (Greenhill et al., 2010; Forster & Renfrew, 2011). Humans first colonized Madagascar 4000 years ago, according to carbon dated artefacts from two unrelated sites (Fig. 1). A site in western Madagascar yielded a subfossil dwarf hippopotamus (Hippopotamus sp.) bone bearing a mark made by a metal implement (Gommery et al., 2011), while artefacts have been recovered from two localities in the north-east of the island (Dewar et al., 2013). These traces were left by people of unknown origin who exploited the forest and coastal resources. Archaeological evidence from different regions in Southeast Asia shows that people have been making transoceanic journeys since 45,000 years bp (Balter, 2007).

OCEANIC DISPERSAL AND ISLAND COLONIZATION BY ANCESTRAL LAND TORTOISES

Current consensus holds that Madagascar’s extant terrestrial mammal fauna can be explained by four successful transoceanic dispersals over the approximately 500 km that separate Africa and Madagascar. The events occurred between the Early Eocene and Early Miocene (60–20 Ma), when ocean currents were more favourable (Ali & Huber, 2010; Krause, 2010). Malagasy land tortoises are also generally viewed as originating from Africa (Le et al., 2006; Samonds et al., 2012, 2013), although other authors have proposed an island origin (Jaffe et al., 2011). Nevertheless, Aldabra land tortoises could not have benefitted from the vagaries of Eocene circulation as the island only formed in the Pleistocene. Since at
least the Early Miocene, well before the surfacing of the Mascarenes, SWIO currents have flowed from east to west. Based on tortoise subfossil material collected on Aldabra and given that Aldabra has been completely submerged several times during the Quaternary, it has been proposed that Aldabra’s subfossil and extant giant tortoises colonized Aldabra three times during the Late Pleistocene and Holocene (Taylor et al., 1979; Pedrono et al., 2013), although even when sea level was at its lowest stand, as during the Last Glacial Maximum, the minimum distance between emergent landmasses would still have been 150 km (Fig. 1).

Current opinion envisages ancestral land tortoises as having been washed offshore from Madagascar or Africa, and having drifted passively (against the surface currents) towards the various SWIO islands which they colonized. Giant tortoises float well in the ocean and can survive harsh conditions for several months (Migaud, 2011). In 2004 an Aldabra giant land tortoise was washed ashore south of Dar es Salaam, Tanzania; the tortoise was emaciated, and its legs and lower part of the carapace were covered with goose barnacles, indicating that it had drifted in the ocean for several weeks. The tortoise was thought to have come from Aldabra, some 740 km away (Gerlach et al., 2006). Theoretically, one female tortoise that successfully reaches an island is capable of founding a new population, as they have the capacity to store sperm for several years (Pearse et al., 2001). The ability of physiologically stressed individuals who have been afloat for extended periods without any food intake to reproduce, however, has not been established. Hence, long-distance dispersal by floating remains an option for colonization of remote islands by tortoises, but the boundary conditions for successful colonization need to be established, and are potentially restricting.

**OCEAN CURRENTS**

With the closure of the Tethys Sea, the IO surface currents and gyres reached their modern configuration, with the South Equatorial Current flowing strongly westward (Ali & Huber, 2010; Lutjeharms & Bornman, 2010) (Fig. 1). This pattern was established well in advance of the emergence of the Mascarenes. Hence, even if colonization of the island of Mauritius was achieved by chance dispersal over millions of years, the probability of a subsequent colonization from Mauritius to Rodrigues seems highly unlikely. Alternatively, colonization could have occurred from Asia using stepping stones (sensu MacArthur & Wilson, 1967) such as Saya de Malha, Nazareth and St Brandon as intermediate stopovers (Fig. 1). While this trajectory complies with the ocean current direction, it invokes very long distances between potential stepping stones, as well as between them and the Mascarenes.

Ocean currents are more favourable for over-water dispersal by passive drifting between Madagascar and Aldabra, but mainly from the northern tip of Madagascar towards Aldabra, and still involving a distance of at least 400 km (Fig. 1).

The probability of covering such distances between landfalls is low and requires travelling along a precise route and an extended period of time. Additionally, Aldabra was fully submerged as recently as 80,000 years ago (Taylor et al., 1979), limiting the period available for successful colonization.

**GEOLOGY**

Madagascar and some of the Seychelles are continental in origin, fragments of the Gondwana supercontinent set adrift from Africa and India 140 and 83 Ma ago respectively (de Wit, 2003). In addition to Gondwanan granite, the Seychelles consist of more recent volcanic rocks and coral reefs. To the east of Madagascar lies La Réunion, the oldest outcrops of which are dated at 2.2–2 Ma (Quidelleur et al., 2010). La Réunion marks the present position of the Réunion hotspot that formed Mauritius approximately 8.9 Ma ago (Moore et al., 2011). A long hiatus in volcanism allowed erosion to reduce the surface of Mauritius before a renewal of volcanism 3.5–1.9 Ma ago. The oldest outcrops on the island of Rodrigues are 1.5–1.3 Ma old, although some authors have estimated the island’s age as 15 Ma (e.g. Bour et al., 2014). Machida et al. (2014) have interpreted this discordance as the result of interactions between the Réunion hotspot and the nearby Central Indian Ridge. Rodrigues is located in a tectonically undisturbed area some 900 km north-east of the Rodrigues Triple Junction (Machida et al., 2014), and the older estimate is actually the age of the tectonic evolution of the Rodrigues Triple Junction (Mendel et al., 2000). Other SWIO volcanic islands include the Comoros, and Aldabra, an 8 m high coral atoll of Pleistocene age. Madagascar, Aldabra and the Mascarenes are several hundred km apart; even during Pleistocene sea level lowstands the islands would have been separated by several hundred km (Lambeck et al., 2014) (Fig. 1).

**PHYLOGEOGRAPHICAL EVOLUTION OF SWIO GIANT TORTOISES**

All giant tortoises of the SWIO islands are thought to have originated in Africa and Madagascar (Austin & Arnold, 2001; Palkovacs et al., 2002; Austin et al., 2003; Le et al., 2006; Bour et al., 2014). The species from Madagascar and the Seychelles (including Aldabra) are considered to form a clade (Aldabrachelys spp.) distinct from the species of the Mascarenes (Cylindraspis spp.). An African origin has been supported for Aldabrachelys (Le et al., 2006), but a similar origin for Cylindraspis has been postulated not on molecular evidence but rather on the assumption that the distance between Asia and the Mascarenes is too far to allow dispersal by drifting (Austin & Arnold, 2001). Cylindraspis is proposed to have colonized Mauritius initially, and then dispersed to Rodrigues and Réunion (Austin & Arnold, 2001; Bour et al., 2014). This scenario would require a non-swimming animal to drift passively, against the prevailing surface currents, over a minimal distance of 800–860 km depending on the sea...
Austronesian sailors (Wilmshurst, 2011). The land tortoises found on the small islands in the Indian Ocean, as well as in coastal sites in Chile (Razafindraibe et al., 2004; Wilmshurst et al., 2008; Blench, 2009; Boivin et al., 2013). Bones of domestic fowls are common in archaeological sites on islands in both the Pacific and the Indian Oceans, as well as in coastal sites in Chile (Razafindraibe et al., 2008; Chambers, 2013; Mwacharo et al., 2013), as are sea turtle remains (Dye, 1990; Frazier, 2003, 2004). Although archaeological sites confirming the presence of Austronesians on the Mascarenes have not been found (possible due to a rise in sea level), the presence of early sailors may be inferred indirectly, as has been done for the Pacific islands (e.g. Wilmshurst et al., 2011). If giant tortoises were present and numerous on the SWIO islands at the time of the discovery of the islands by European sailors, it is possible that they had been introduced by earlier sailors, probably Austronesians. The land tortoises found on the small islands in the SWIO could have been translocated from Madagascar by Austronesian sailors (Wilmé et al., 2016).

Our human translocation hypothesis encounters a possible contradiction in the morphological peculiarities (e.g. reduced shells and small body size; Austin & Arnold, 2001) of the giant tortoises on the three Mascarene islands: pronounced morphological changes are assumed to require long-term evolution, perhaps longer than humans have been seafarers. Nevertheless, it is known that under certain circumstances, evolutionary change can be unexpectedly fast, and one instance of this rapid change involves the phenomenon of “island dwarfing” – rapid body size reduction in large animals that become trapped on islands (Lomolino, 2010). During the Quaternary, European hippopotamuses became increasingly isolated in habitat fragments, acting as islands, and responded by becoming smaller between late Early Pleistocene and Middle Pleistocene (Mazza & Bertini, 2013). More recently, during the Holocene, a 10% reduction in skull size has been documented in island-dwelling sloths, even on poorly isolated islands with maintained predation pressure off the coast of Panama, within less than 4000 years (Anderson & Handley, 2002). Given that giant tortoises produce four to ten times more progeny than sloths, their potential for morphological adaptation may be higher than that of sloths (MacDonald, 1984; Ende, 2012). Further, dietary peculiarities have pronounced effects of the shape of tortoise shells, which could represent phenotypic rather than genotypic variation (e.g. Gerlach, 2004; Taylor et al., 2011). Molecular estimates of the dates of species divergence in giant tortoises have been difficult in the absence of independent calibration measures, and vary substantially according to the method and markers used (e.g. Hippsley & Müller, 2014; Ho & Duchêne, 2014); for example, in the giant tortoises of Galápagos, the divergence rate of mitochondrial DNA was estimated to be 30 times faster than that of nuclear DNA, and much faster than any previous estimates (Caccione et al., 2004). This result calls for comparative studies with other taxa.

In making our argument, we do not question the validity of the established phylogenetic and phylogeographical methods. However, we are calling for critical thinking in biogeographical models that identifies and challenges inconsistencies and allows for the generation of alternative hypotheses. With this in mind, we wish to extend the set of processes viewed as having contributed to the protohistoric movements of various plants and animals by including human-assisted dispersal in the SWIO (Collerson & Weisler, 2007). If the first European sailors were able to translocate land tortoises (Migaud, 2011), then it is not far-fetched to assume that earlier sailors could have done the same.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Systematics of the Testudines.

**Appendix S2** List of references compiled.
BIOSKETCHES

Lucienne Wilmé is Research Associate of Missouri Botanical Garden in Madagascar, Editor in Chief of the peer-reviewed journal Madagascar Conservation & Development (www.journalmcd.com), and a lecturer at University of Antananarivo. Her main interests are in biodiversity, biogeography and geomorphology of south-western Indian Ocean.

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