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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, *Chelonoidis 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

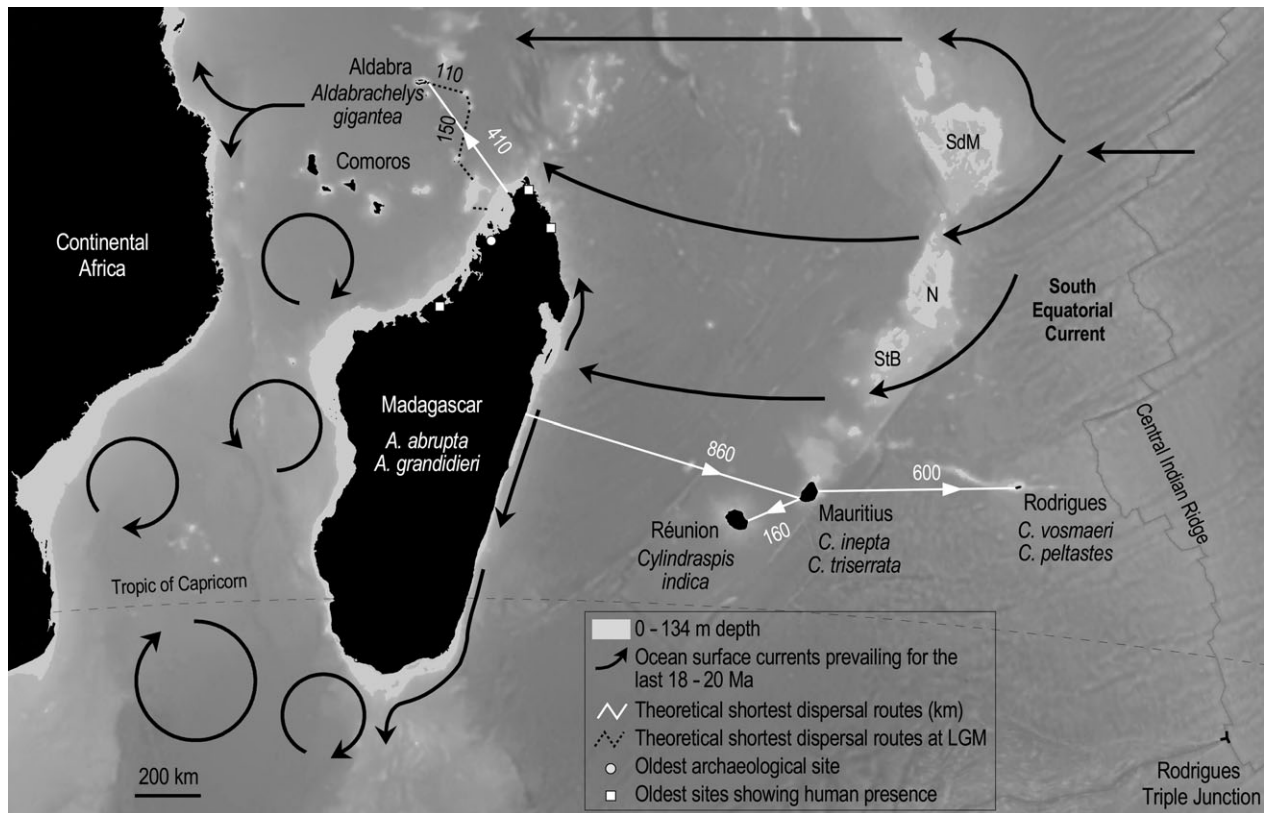


Figure 1 Giant land tortoises, geology, oceanography, archaeology of the south-western Indian Ocean, and distance between islands and ocean surface currents prevailing since the closure of the Tethys Ocean. (SdM = Saya de Malha; N = Nazareth; StB = St Brandon; LGM = Last Glacial Maximum).

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 north-west 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

level excursions, between Madagascar and Mauritius. While the probability of one such event over the course of a few million years is very low, the probability of several such events becomes vanishingly small. The colonization of Mauritius by this means has then been proposed to have been followed by speciation (Austin & Arnold, 2001; Bour *et al.*, 2014), and one of the resulting daughter species, *Cylindraspis triserrata*, to have subsequently dispersed to Rodrigues where a further speciation event generated the two species recorded from this island. The distance to Rodrigues is at least 600 km, and again, the tortoises would have had to swim against the prevailing current towards a geologically young island (Fig. 1). The unfavourable current directions, the youth of the islands and the long distances between them lead us to view this scenario as unlikely.

PROPOSING AN ALTERNATIVE HYPOTHESIS: TRANSLOCATION OF GIANT TORTOISES BY HUMANS

If dispersal by transoceanic drifting is an unlikely explanation for the biogeography of giant IO land tortoises, what constitutes a credible alternative? The Austronesian people who colonized Madagascar several thousand years ago were not only sailors; they were also farmers, and translocated plants and animals to the various islands they colonized. The list of human-introduced taxa includes the Pacific rat (*Rattus exulans*), domestic fowls (*Gallus gallus*), sweet potatoes (*Ipomea batatas*), taro (*Colocasia* sp.) and bananas (*Musa* sp.) (Kirch *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. Hipsley & 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 (Caccone *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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REFERENCES

- Ali, J.R. & Huber, M. (2010) Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature*, **463**, 653–656.
- Anderson, R.P. & Handley, C.O. (2002) Dwarfism in insular sloths: biogeography, selection, and evolutionary rate. *Evolution*, **56**, 1045–1058.
- Austin, J.J. & Arnold, E.N. (2001) Ancient mitochondrial DNA and morphology elucidate an extinct island radiation of Indian Ocean giant tortoises (*Cylindraspis*). *Philosophi-*

- cal Transactions of the Royal Society B: Biological Sciences*, **268**, 2515–2523.
- Austin, J.J., Arnold, E.N. & Bour, R. (2003) Was there a second adaptive radiation of giant tortoises in the Indian Ocean? Using mitochondrial DNA to investigate speciation and biogeography of *Aldabrachelys* (Reptilia, Testudinidae). *Molecular Ecology*, **12**, 1415–1424.
- Balter, M. (2007) In search of the world's most ancient mariners. *Science*, **318**, 388–389.
- Blench, R. (2009) Bananas and plantains in Africa: Re-interpreting the linguistic evidence. *Ethnobotany Research & Applications*, **7**, 363–380.
- Boivin, N., Crowther, A., Helm, R. & Fuller, D.Q. (2013) East Africa and Madagascar in the Indian Ocean world. *Journal of World Prehistory*, **26**, 213–281.
- Bour, R., Frétey, T. & Cheke, A.S. (2014) Philibert Marragon (1749–1826) and the Mémoire sur l'Isle de Rodrigue (1795). *Bibliotheca Herpetologica*, **10**, 5–32.
- Burleigh, R. & Arnold, E.N. (1986) Age and dietary differences of recently extinct Indian Ocean tortoises (*Geochelone* s. lat.) revealed by carbon isotope analysis. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **227**, 137–144.
- Caccone, A., Gentile, G., Burns, C.E., Sezzi, E., Bergman, W., Ruelle, M., Saltonstall, K. & Powell, J.R. (2004) Extreme difference in rate of mitochondrial and nuclear DNA evolution in a large ectotherm, Galápagos tortoises. *Molecular Phylogenetics and Evolution*, **31**, 794–798.
- Chambers, G.K. (2013) *Genetics and the origins of the Polynesians*. eLS. John Wiley & Sons Ltd, Chichester.
- Collerson, K.D. & Weisler, M.I. (2007) Stone adze compositions and the extent of ancient Polynesian voyaging and trade. *Science*, **317**, 1907–1911.
- Dewar, R.E., Radimilahy, C., Wright, H.T., Jacobs, Z., Kelly, G.O. & Berna, F. (2013) Stone tools and foraging in northern Madagascar challenge Holocene extinction models. *Proceedings of the National Academy of Sciences USA*, **110**, 12583–12588.
- van Dijk, P.P., Iverson, J.B., Rhodin, A.G.J., Shaffer, H.B. & Bour, R. (2014) Turtles of the world, 7th Edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. *Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. Chelonian Research Monographs 5 (ed. By A.G.J. Rhodin, P.C.H. Pritchard, P.P. van Dijk, R.A. Saumure, K.A. Buhlmann, J.B. Iverson, R.A. Mittermeier), pp 329–479. Chelonian Research Foundation, Lunenburg, Massachusetts.
- Dye, T.S. (1990) Marine turtle bones from an archaeological site in Polynesia yield reliable age determinations. *Radio-carbon*, **32**, 143–147.
- Ende, L. (2012) *Allometric relationships in tortoises: A comparative analysis of life-history traits in the Testudinidae*. BSc thesis, Dept. Biology. Hamburg University, Hamburg.
- Forster, P. & Renfrew, C. (2011) Mother tongue and Y chromosomes. *Science*, **333**, 1390–1391.
- Frazier, J. (2003) Prehistoric and ancient historic interactions between humans and marine turtles. *The biology of sea turtles*. Vol. 2 (ed. by P.L. Lutz, J.A. Musick and J. Wyneken), pp. 1–38. CRC Press, Boca Raton, Florida.
- Frazier, J. (2004) Marine turtles of the past: a vision for the future?. *The future from the past. Archaeozoology in wildlife conservation and heritage management* (ed. by R.C.G.M. Lauwerier and I. Plug), pp. 103–116. Proceedings of the 9th Conference of the International Council of Archaeozoology, Durham, August 2002, Oxbow Books.
- Gerlach, J. (2004) Effects of diet on the systematic utility of the tortoise carapace. *African Journal of Herpetology*, **53**, 77–85.
- Gerlach, J., Muir, C. & Richmond, M.D. (2006) The first substantiated case of trans-oceanic tortoise dispersal. *Journal of Natural History*, **40**, 2403–2408.
- Gommery, D., Ramanivosoa, B., Faure, M., Guérin, C., Kerloc'h, P., Sénégas, F. & Randrianantenaina, H. (2011) Les plus anciennes traces d'activités anthropiques de Madagascar sur des ossements d'hippopotames subfossiles d'Anjo-hibe (Province de Mahajanga). *Comptes Rendus Palevol*, **10**, 271–278.
- Greenhill, S.J., Drummond, A.J. & Gray, R.D. (2010) How accurate and robust are the phylogenetic estimates of Austronesian language relationships? *PLoS ONE*, **5**, e9573.
- Hansen, D.M., Donlan, C.J., Griffiths, C.J. & Campbell, K.J. (2010) Ecological history and latent conservation potential: large and giant tortoises as a model for taxon substitutions. *Ecography*, **33**, 272–284.
- Hipsley, C.A. & Müller, J. (2014) Beyond fossil calibrations: realities of molecular clock practices in evolutionary biology. *Frontiers in Genetics*, **5**, 138.
- Ho, S.Y.W. & Duchêne, S. (2014) Molecular-clock methods for estimating evolutionary rates and timescales. *Molecular Ecology*, **23**, 5947–5965.
- Jaffe, A.L., Slater, G.J. & Alfaro, M.E. (2011) The evolution of island gigantism and body size variation in tortoises and turtles. *Biology Letters*, **7**, 558–561.
- Karanth, K.P., Palkovacs, E., Gerlach, J., Glaberman, S., Hume, J.P., Caccone, A. & Yoder, A.D. (2005) Native Seychelles tortoises or Aldabran imports? The importance of radiocarbon dating for ancient DNA studies. *Amphibia-Reptilia*, **26**, 116–121.
- Kirch, P.V., Hartshorn, A.S., Chadwick, O.A., Vitousek, P.M., Sherrod, D.R., Coil, J., Holm, L. & Sharp, W.D. (2004) Environment, agriculture, and settlement patterns in a marginal Polynesian landscape. *Proceedings of the National Academy of Sciences USA*, **101**, 9936–9941.
- Krause, D.W. (2010) Washed up in Madagascar. *Nature*, **463**, 613–614.
- Lambeck, K., Rouby, H., Purcell, A., Sun, Y. & Sambridge, M. (2014) Sea level and global ice volumes from the Last Glacial Maximum to the Holocene. *Proceedings of the National Academy of Sciences USA*, **111**, 15296–15303.
- Le, M., Raxworthy, C.J., McCord, W.P. & Mertz, L. (2006) A molecular phylogeny of tortoises (Testudines: Testu-

- dinidae) based on mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution*, **40**, 517–531.
- Lomolino, M.V. (2010) Four Darwinian themes on the origin, evolution and preservation of islandlife. *Journal of Biogeography*, **37**, 985–994.
- Lutjeharms, J.R.E. & Bornman, T.G. (2010) The importance of the greater Agulhas Current is increasingly being recognised. *South African Journal of Science*, **106**, 160.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography* (Vol. 1). Princeton University Press, Princeton, New Jersey.
- Machida, S., Orihashi, Y., Magnani, M., Neo, N., Wilson, S., Tanimizu, M., Yoneda, S., Yasuda, A. & Tamaki, K. (2014) Regional mantle heterogeneity regulates melt production along the Réunion hotspot-influenced Central Indian Ridge. *Geochemical Journal*, **48**, 433–449.
- Mazza, P.P.A. & Bertini, A. (2013) Were Pleistocene hippopotamuses exposed to climate-driven body size changes? *Boreas*, **42**, 194–209.
- MacDonald, D. (1984) *The encyclopedia of mammals*. Facts on File Publications, New York.
- Mendel, V., Sauter, D., Patriat, P. & Munsch, M. (2000) Relationship of the Central Indian Ridge segmentation with the evolution of the Rodrigues Triple Junction for the past 8 Myr. *Journal of Geophysical Research: Solid Earth*, **105**, 16563–16575.
- Migaud, P. (2011) A first approach to links between animals and life on board sailing vessels (1500–1800). *The International Journal of Nautical Archaeology*, **40**, 283–292.
- Moore, J., White, W.M., Paul, D., Duncan, R.A., Abouchami, W. & Galer, S.J.G. (2011) Evolution of shield-building and rejuvenescent volcanism of Mauritius. *Journal of Volcanology and Geothermal Research*, **207**, 47–66.
- Mwacharo, J.M., Bjørnstad, G., Han, J.L. & Hanotte, O. (2013) The history of African village chickens: an archaeological and molecular perspective. *African Archaeological Review*, **30**, 97–114.
- Palkovacs, E.P., Gerlach, J. & Caccone, A. (2002) The evolutionary origin of Indian Ocean tortoises (*Dipsochelys*). *Molecular Phylogenetics and Evolution*, **24**, 216–227.
- Pearse, D.E., Janzen, F.J. & Avise, J.C. (2001) Genetic markers substantiate long-term storage and utilization of sperm by female painted turtles. *Heredity*, **86**, 378–384.
- Pedrono, M., Griffiths, O.L., Clausen, A., Smith, L.L., Wilmé, L. & Burney, D.A. (2013) Using a surviving lineage of Madagascar's vanished megafauna for ecological restoration. *Biological Conservation*, **159**, 501–506.
- Quidelleur, X., Holt, J.W., Salvany, T. & Bouquerel, H. (2010) New K-Ar ages from La Montagne massif, Réunion Island (Indian Ocean), supporting two geomagnetic events in the time period 2.2–2.0 Ma. *Geophysical Journal International*, **182**, 699–710.
- Razafindralaibe, H., Mobegi, V.A., Ommeh, S.C., Rakoton-dravao, J., Bjørnstad, G., Hanotte, O. & Jianlin, H. (2008) Mitochondrial DNA origin of indigenous Malagasy chicken: implications for a functional polymorphism at the Mx gene. *Annals of the New York Academy of Sciences*, **1149**, 77–79.
- Samonds, K.E., Godfrey, L.R., Ali, J.R., Goodman, S.M., Vences, M., Sutherland, M.R., Irwin, M.T. & Krause, D.W. (2012) Spatial and temporal arrival patterns of Madagascar's vertebrate fauna explained by distance, ocean currents, and ancestor type. *Proceedings of the National Academy of Sciences USA*, **109**, 5352–5357.
- Samonds, K.E., Godfrey, L.R., Ali, J.R., Goodman, S.M., Vences, M., Sutherland, M.R., Irwin, M.T. & Krause, D.W. (2013) Imperfect isolation: factors and filters shaping Madagascar's extant vertebrate fauna. *PLoS ONE*, **8**, e62086.
- Stoddart, D.R., Peake, J.F., Gordon, C. & Burleigh, R. (1979) Historical records of Indian Ocean giant tortoise populations. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **286**, 147–158.
- Stuckas, H., Gemel, R. & Fritz, U. (2013) One extinct turtle species less: *Pelusios seychellensis* is not extinct, it never existed. *PLoS ONE*, **8**, e57116.
- Taylor, J.D., Braithwaite, C.J.R., Peake, J.F. & Arnold, E.N. (1979) Terrestrial faunas and habitats of Aldabra during the late Pleistocene. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **286**, 47–66.
- Taylor, M.P., Hone, D.W.E., Wedel, M.J. & Naish, D. (2011) The long necks of sauropods did not evolve primarily through sexual selection. *Journal of Zoology*, **285**, 150–161.
- Wilmé, L., Waeber, P.O. & Ganzhorn, J.U. (2016) Marine turtles used to assist Austronesian sailors reaching new islands. *Comptes Rendus Biologies*, **339**, 78–82.
- Wilmshurst, J.M., Anderson, A.J., Higham, T.F.G. & Worthy, T.H. (2008) Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. *Proceedings of the National Academy of Sciences USA*, **105**, 7676–7680.
- Wilmshurst, J.M., Hunt, T.L., Lipo, C.P. & Anderson, A.J. (2011) High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. *Proceedings of the National Academy of Sciences USA*, **108**, 1815–1820.
- de Wit, M.J. (2003) Madagascar: heads it's a continent, tail it's an island. *Annual Review of Earth and Planetary Sciences*, **31**, 213–248.

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

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