CORRESPONDENCE

Giant tortoises spread to western Indian Ocean islands by sea drift in pre-Holocene times, not by later human agency – response to Wilmé *et al.* (2016a)

ABSTRACT

Evidence from DNA phylogeny, Plio-Pleistocene ocean currents, giant tortoise dispersal, evolution of plant defences, radiocarbon dates and archaeology indicates that the endemic giant tortoises on the Mascarenes and Seychelles colonized naturally and were not translocated there by humans.

Keywords Aldabra, Austronesian, giant tortoise, heterophylly, Mascarenes, radiocarbon dating, sea drift, Seychelles

Giant tortoises have fascinated Indian Ocean travellers since their first discovery on Mauritius by the Dutch in 1598 (Cheke & Bour, 2014), and a Réunion tortoise was among the earliest biological specimens to reach Europe from the Malagasy region (in 1671: Bour, 2004), but Wilmé *et al.* (2016a) are the first to suggest that humans introduced them, their main arguments being that:

1. Sea drift is too rare, uncertain and contrary to currents to account for the presence of tortoises on so many western Indian Ocean islands.

2. The existing phylogeny, with dating considered uncertain, does not rule out rapid evolution in recent millenia as some tortoise mtDNA is known to mutate very rapidly.

3. Hence, they imply that it is more likely that humans populated the Mascarene and Seychelles islands with tortoises.

Specifically, they propose that Austronesian transoceanic colonists, with implied identity to settlers on Madagascar *c.* 4000 yr BP, distributed tortoises from Madagascar or Africa to Aldabra and the Mascarenes (Mauritius, Réunion, Rodrigues) as a food resource; the granitic Seychelles, oddly, are unmentioned.

There are numerous reasons to reject this hypothesis. While Austronesians may have taken chickens and various crops from the Sunda Islands to East Africa and Madagascar (e.g. Boivin *et al.*, 2013; but see Anderson *et al.*, in press), there is no archaeological evidence that they discovered or visited the Mascarenes, granitic Seychelles or the Aldabra group atolls (Blench, 2010; Anderson *et al.*, in press). In addition, the phylogeographical, ecological, evolutionary, palaeontological and archaeological evidence all strongly indicates the contrary.

PHYLOGEOGRAPHY

mtDNA analysis indicates that the endemic Mascarene genus *Cylindraspis* dates from the Miocene and pre-dates the emergence of the existing islands (Cheke & Hume, 2008; Gerlach & Rioux Paquette, 2014). Sister to the Malagasy clade (Austin & Arnold, 2001), itself of African origin (Le *et al.*, 2006), the genus evolved from an East African or Malagasy ancestor probably on one of the former volcanic islands, now submerged banks, formed by the Réunion hotspot north of the Mascarenes. The prevailing sea currents *c.* 14 Ma (Gourlan *et al.*, 2008) favoured later drift from St. Brandon and/or Nazareth Bank to Rodrigues, the likely first landfall for the subsequent evolution of the genus and spread to Mauritius and Réunion (Cheke & Hume, 2008; Gerlach & Rioux Paquette, 2014). A generic origin around 23–17 Ma, estimated from the divergence levels in Austin & Arnold (2001), and subsequent radiation into five species, gives a rather rapid mtDNA evolution rate for an ectothermic vertebrate of 0.7–1% per Myr. For this to happen in *c.* 4000 years as proposed by Wilmé *et al.* (2016a) would require a rate 250 times faster, an unprecedented rate for vertebrates. Their claim of possible ultra-rapid mtDNA evolution is based on a misinterpretation of Caccone *et al.*'s (2004) finding that Galapagos tortoise *Chelonoidis nigra* mtDNA evolved 30 times faster than the nuclear DNA – but the Galapagos mtDNA rate (1% per my) is similar to that for *Cylindraspis*; it is just that the nuclear DNA rate is very slow.

For Aldabra, Wilmé *et al.* (2016a) acknowledged the presence of subfossil tortoise material from Pleistocene interglacial periods (e.g. Taylor *et al.*, 1979), but nevertheless claimed that the current population originates from Austronesian translocation. Given favourable currents, it is unclear why Wilmé *et al.* (2016a) considered sea drift an acceptable process in the mid-Pleistocene but not viable at its end.

Wilmé *et al.* (2016a) did not discuss the granitic Seychelles. The giant tortoises there are conspecific with those on Aldabra, with minor differences (Austin *et al.*, 2003; Gerlach, 2011). Intensive recent searches (Anderson *et al.*, in press) have discovered no archaeological evidence of pre-European landings. Europeans found giant tortoises on all visited granitics, whatever their size (Malavois, 1787), while outlying sand cays, bar one (Denis; Cheke & Bour, 2014), had none. The tortoises were surely marooned on the numerous islands formed when the large glacial-period Seychelles bank island contracted as sea levels rose in the late Pleistocene (e.g. Rocha, 2010) – would Austronesians have bothered to distribute tortoises to every granitic island and islet?

DISPERSAL BY SEA DRIFT

Although Wilmé *et al.* (2016a) acknowledged that a living tortoise drifted from Aldabra to Tanzania in 2004 (Gerlach *et al.*, 2006), they dismissed sea drift as responsible for tortoises reaching the Mascarenes or leaving Madagascar, arguing that ocean currents are unfavourable. Although true at present for the Mascarenes, prevailing currents in the Miocene would have favoured such movements, and they remain favourable for Aldabra

(Gourlan *et al.*, 2008; Gerlach & Rioux Paquette, 2014). Giant tortoises, with extensive fat deposits and slow metabolism, can survive for months without food or water, a fact widely exploited by European mariners in the 17th/18th centuries (e.g. Luillier, 1705). That, and their buoyancy, floating with their head well above water, noted long ago (Ohier de Grandpré, 1801) and frequently observed in the large Aldabra lagoon, whence they are occasionally swept out to sea (e.g. Coe, 1995), made long marine drifting possible, and thus survival to found new populations (Cheke & Hume, 2008). Wilmé *et al.* (2016a) mention the Galapagos, 965 km from South America, but do not suggest that humans translocated tortoises there, although they differ less from South American congeners (*Chelonoidis* spp.; Caccone *et al.*, 2002; Poulakakis *et al.*, 2012) than Mascarene tortoises did from all others (Bour *et al.*, 2014). The genus *Chelonoidis* itself is thought to have originated by sea drift from Africa (Le *et al.*, 2006). In the Pacific, there were giant spiny tortoises (*Meiolania* spp.) in Fiji, Vanuatu and New Caledonia which pre-date Polynesian colonization (e.g. White *et al.*, 2010). Sea drift is a perfectly viable, and indeed the most likely, method of transmarine dispersal in giant tortoises.

Although Wilmé *et al.*'s (2016a) case against sea drift only discussed giant tortoises, much less seaworthy taxa (six lizard lineages and two of snakes) have over millions of years sea drifted to the Mascarenes (reviewed, with references, in Cheke & Hume, 2008) and yet others to the granitic Seychelles (e.g. Townsend *et al.*, 2011; Maddock *et al.*, 2014); indeed most of Madagascar's vertebrate fauna is now believed to have done so, well after the separation from Africa and India (Samonds *et al.*, 2012). Sea drift, albeit infrequent, is now seen in geological time as a major driver of distributions worldwide (de Queiroz, 2005).

CO-EVOLUTION

In the Mascarenes, several woody plant families show marked heterophylly – modified juvenile leaves, often narrow with red veins, contrasting with 'normal'-looking adult leaves. Introduced Aldabra giant tortoises *Aldabrachelys gigantea* avoid the anomalous juvenile leaves (Eskildsen *et al.*, 2004). The transition height (around 1.2 m) is consistent with the maximum browsing height of large *Cylindraspis* tortoises, the only large native herbivores, which were abundant and thus likely to have been the selective agent (Cheke & Hume, 2008). Such anti-browsing defences could not have evolved in just 4000 years.

PALAEONTOLOGY

In Réunion, Maillard (1862) reported tortoise fossils under a *c.* 435 ka lava bed (Bour *et al.*, 2014), and in Mauritius, Freycinet (1825) reported fossil tortoise bones and eggs found buried in tuff; the last eruption in Mauritius occurred *c.* 31 ka (Moore *et al.*, 2011). In Mauritius, radiocarbon dates from tortoises (and other biota) in the Mare aux Songes bone beds indicate a mass mortality event 4300–4000 yr BP, centred on 4200 (Rijsdijk *et al.*, 2011); anthropogenic indications and animal introductions only appear much later in the profile (Hume *et al.*, 2014). Pollen cores in Mauritius show no human influence before the 17th century (van der Plas *et al.*, 2011; de Boer *et al.*, 2013), nor has any earlier archaeology been detected (Anderson *et al.*, in press). A *c.* 4000 yr BP or later tortoise arrival would show up the pollen profile, given their ability to modify vegetation at the high densities formerly present (e.g. Griffiths, 2014). In the granitic Seychelles, subfossil tortoises from North Island have been carbon dated to 764–395 BCE (= 2714–2345 yr BP) (Karanth *et al.*, 2005), outside the generally accepted range for Austronesians, but not Wilmé's dates.

ARCHAEOLOGY

We acknowledge likely transfer of plants and domestic animals from the Sunda area to East Africa and Madagascar (Boivin *et al.*, 2013), but the only confirmed early tortoise translocations are between Africa, Madagascar and the Comoros. Ploughshare and Spider Tortoises *Astrochelys yniphora* and *Pyxis* sp. were taken from Madagascar to the Comoros from the 8th century CE onwards (Allibert *et al.*, 1989). *Kinixys zombensis* tortoises and possibly *Pelusios castanoides*, *P. subniger* and *Pelomedusa subrufa* terrapins were introduced to Madagascar from Africa by humans (Pedrono, 2008), but when or by which ethnic group is unknown, though *K. zombensis* dates back at least 600–900 years (Cheke & Bour, 2014). The native *Aldabrachelys grandidieri* and *A. abrupta* are found in Malagasy middens (Cheke & Bour, 2014) prior to their extinction by 1200–500 yr BP (Burleigh & Arnold, 1986), but the absence of Aldabra/Seychelles tortoises (*A. gigantea*) in later middens in Madagascar (or the Comoros) suggests that the Austronesians/Malagasy were unaware of these sources, otherwise they would surely have made use of them.

Furthermore, most authors consider voyages by Austronesians across the Indian Ocean began only around 2000 yr BP (e.g. Wright & Rakotoarisoa, 2003; Blench, 2010), more recent research suggesting they began later, *c.* 1300 yr BP (Dewar *et al.*, 2013; Anderson *et al.*, in press). Claims of earlier *c.* 4000 yr BP human settlers on Madagascar (from Africa, not Austronesians; Blench, 2010; Dewar *et al.*, 2013) are considered by Anderson *et al.* (in press) to be the result of erroneous dating. Computer simulations of putative transoceanic Austronesian voyages (Fitzpatrick & Callaghan, 2008) suggest that Aldabra and the granitic Seychelles (but not the Mascarenes) would have been encountered, though European mariners later mapped the islands to steer clear of their dangerous reefs (Cheke & Bour, 2014), and Austronesians may have been equally cautious about landings. Anderson *et al.* (in press) argue that Malay sail technology, even by the mid-first millennium CE, would not have supported transoceanic journeys, only more coastal routes within the monsoon zone.

NO REASON TO TRANSLOCATE

Blench (2010) suggested possible settlement of Indian Ocean islands, then abandonment through lack of food and/or water, but admitted archaeological evidence was lacking. In fact, aside from tortoises, all these islands had ample resources: i.e. abundant nesting sea turtles when discovered by Europeans (Cheke & Bour, 2014), which Wilmé *et al.* (2016b) accepted as pre-existing, as well as plentiful water (except on Aldabra), abundant fish and other edible animals (dugongs and large flightless birds on the Mascarenes, and seals and flying-foxes on many islands; e.g. Cheke & Hume, 2008; Cheke & Bour, 2014). Horridge (1995) considered that the survival into European times of the flightless Dodo *Raphus cucullatus* in Mauritius indicated that Austronesians had *not* visited. Furthermore, on Pacific islands Austronesians/Polynesians notoriously overexploited pre-existing animal resources causing extensive extinctions (e.g. Steadman, 2006), and would surely have done so equally on

Indian Ocean islands. Only on Aldabra, never fully settled, did such species survive. On neighbouring Astove and Assumption, there are subfossil tortoise remains dated to 1570–1140 yr BP (Burleigh & Arnold, 1986); the absence of living tortoises when Europeans first landed may indicate visits by early second millennium mariners who eliminated the tortoises (rather than introducing them). In any case, the 30-year generation time for giant tortoises and extremely slow population recruitment (Swingland & Coe, 1979) means that mariners could not have reaped any benefit from introductions during their lifetime.

CONCLUSION

In conclusion, there is no case for considering that Austronesians or any other humans were involved in the original distribution of giant tortoises to the Mascarene or Seychelles in the western Indian Ocean. We anticipate that future more detailed genetic analyses of modern and ancient DNA will further confirm our arguments, as well as provide more precise ageing of tortoise movements to and between islands, as has been done in the Galapagos (Poulakakis *et al.*, 2012).

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