The giant tortoise, *Aldabrachelys*, and its bearing on the biogeography and dispersal of terrestrial biota in the Western Indian Ocean

Colin J. R. Braithwaite

School of Geographical and Earth Sciences, the University of Glasgow, Glasgow G12 8QQ
UK

ABSTRACT

The evolution of species of giant tortoises and the nature of processes governing their dispersal in the Western Indian Ocean have been matters of interest for some time. Historical records indicate that these animals were once widely distributed in the region, from Madagascar to the Seychelles in the north and to the Mascarene islands in the south. New data on the status of *Aldabrachelys* and related or supposed species, and controversies regarding genetic diversity and distribution have prompted an evaluation of the islands and submerged Banks in the region that, during the later Cenozoic, might have provided refuges and/or stepping-stones for the spread of populations in what is now open ocean. Given the apparent stability of the crust in much of the area for at least the Quaternary Period, sea-level, driven by climatic change, and transport by ocean currents, appear to be the principle factors controlling the access not only of populations of giant tortoises but also other terrestrial biota to potential refuge areas in the Region. The distributions of living and fossil tortoise communities are discussed. Four types of terrestrial oceanic refuges for migrants have been identified. At the present day, with the exception of Aldabra, high limestone islands offer only relatively small areas for colonization and all would have been drowned during interglacial sea-level high-stands. Although they have the potential for some increases in land area during the early stages of transitions to low-stand, as sea-level fell significantly they would have become waterless pinnacles, only generally accessible to organisms capable of flight. Volcanic islands have the same general limitations, but may have remained as smaller entities when sea-level was higher than at present, but providing only limited land access and restricted vegetation. Low islands and sand cays, typically of more recent origin, could not have existed during periods of high sea-levels, but many are situated on extensive submerged Banks that would have formed relatively large land areas when sea-level was low. Major Banks, most of which are regarded as fragments of continental crust, are currently submerged but, during glacial periods would together have offered land areas in excess of 130,000 km²,

providing a diverse range of terrestrial environments and vegetation. Access to all of these was nevertheless restricted by the distribution of ocean currents, the only plausible natural means of dispersal, which probably varied during glacial interludes, but also by the abilities of the animals to survive long periods adrift in the ocean. The distribution of these tortoises, in both the fossil record and historical data, provides a model for the dispersal of other terrestrial biota in the region, although the present distribution and genetic characteristics of the tortoises probably reflects recent human intervention.

Keywords: Biogeography, Indian Ocean, Giant Tortoises

1. Introduction

The remarkable endemism of terrestrial biotas of the Western Indian Ocean, including tortoises, has been known for many years (see Stoddart, 1984a), and has been supported and reinforced by more recent work (Agnarsson & Kuntner, 2012). The biogeographical region centred on Madagascar, and including high limestone islands and low-lying islands north of these, the Seychelles to the north-east, and the Mascarene Islands to the south and east, hosts the most diverse fauna of living large and giant tortoises in the world (J.G. Frazier pers comm.). Although recent genetic evidence suggests a Malagasy origin for these (Palkovacs et al., 2002) the period it provides for radiation of the species is only ~15 Ma. Genetic and morphological evidence implies an older, African, ancestral area, although suggested origins in the early Oligocene deposits of the Fayum of Egypt (~33 Ma old) are simply speculation. Dispersal and radiation events followed well after the break-up of Gondwana and do not reflect vicariance. Recent studies of the distribution of fossil and living populations of the giant tortoise (Fig. 1), now *Aldabrachelys gigantea* (Frazier, 2009), in this region have suggested that there have been at least three distinct phases of dispersal. The first wave came from eastern Africa, to Madagascar, where tortoises are thought to have radiated into several different lineages and species. Subsequently, some species are believed to have dispersed to smaller islands to the north, as far as the granitic Seychelles, and south and eastwards to the Mascarene Islands. However, genetic studies by Karanth et al. (2005) seem to indicate that there is now very little variation in the giant tortoises dispersed in the region, and that all are likely to have been derived from Aldabran populations where recent work by Balmer et al. (2010) found no genetic variation.

The dispersal of these animals has depended in part on their ability to float but also, critically, on their capacity to survive without food or fresh water for many weeks, or months. This trait was widely exploited by European mariners in the area over a considerable period

in the 17th and 18th centuries, when chelonians were routinely taken on board ship as a source of fresh meat (Stoddart et al., 1979; Chambers, 2006). As a result, by around 1800, they were effectively extinct in many areas where they had once been common (Karanth et al., 2005). The transmarine distances involved in their dispersal from supposed sources to inferred destinations are immense, and led some workers to conclude that human intervention must have been responsible for the oceanic distribution of living forms (e.g. Wilme et al. 2016). However, historical records and the discovery of fossil remains on Madagascar, Aldabra, Astove, Assumption (Stoddart and Peake, 1979) and Mauritius (Rijsdijk et al., 2009) in deposits representing several distinct pre-human periods, argue for natural causes. The temporary (Mid-Eocene to early Miocene) ‘Land Bridges’ invoked by McCall, (1997), to explain the distribution of mammalian species to Madagascar, never had any firm scientific basis. Such ideas were superseded in the early 1960s by Plate Tectonics, the then new paradigm explaining both the structures and movements of continents and oceans. First suggested as early as 1596 by the Dutch map maker Abraham Ortelius, who described the lateral spreading of continents bordering the Atlantic, the ‘modern’ development of the theory is attributed to Alfred Wegener (1929, 1966), modified by du Toit (1937). It reached its present form following studies of the paleomagnetism of the floor of the eastern Pacific Ocean in the 1950s and ‘60s (see Vine, 1966). However, as Press and Siever (1974) observed, the pattern that first emerged from the Indian Ocean was so complex that the whole theory might have foundered if it had depended on such data. Recent work by Ali and Aitchison (2008) and Torsvik et al. (2013) has clarified and thrown new light on a number of geological and tectonic features of the Indian Ocean. These have a bearing on the past and present distributions of land areas of the region, but also on the potential effects of vicariance on the biogeography of tortoises and other terrestrial organisms discussed below. However, there is an additional factor that has also changed views on how the dispersal of flightless terrestrial organisms might have occurred. Deep-sea research has provided an accurate isotopic time-scale of climate change that can be translated into cycles of variation in sea-level. Whereas models of the 1960s and earlier had described four major ‘ice ages,’ this new evidence has shown a regular 100 ka (thousand year) cyclicity of climate extending over 500 ka, with more frequent (~41 ka) cycles for a considerable time before (Lisiecki and Raymo, 2005). Superimposed on these are minor variations in both climate and sea-level on time-scales of a few thousand years (Sosdian and Rosenthal, 2009; McClymont et al. 2013). Like the theory of plate tectonics, this model, invoking hundreds of thousands of years of climate

cycles, was based on ideas first put forward over a century ago (Croll, 1867) and subsequently developed by Milankovich (1941). An important corollary, with regard to the dispersal of terrestrial organisms, was the realization that during glacial periods the sequestration of water in the polar ice caps caused sea-level to fall globally, at times by as much as 120–135 m (Lambeck et al. 2014, Yokoyama et al. 2000). These figures are important in moderating speculation regarding when and where refuges for a migrating terrestrial biota might have existed. The chronology to which these events are referred is defined by isotopic analysis of Arctic and Antarctic ice cores and cores of deep ocean sediments (Lisiecki and Raymo, 2005). The principal events recorded are described in terms of Marine Isotope Stages (MISs), numbered backwards from the present (Fig. 2). Even numbers represent cooler (typically glacial) periods when sea-level was relatively ‘low’, odd numbers are warmer intervals when sea-level was ‘high’.

2. Record of the Indian Ocean Giant tortoise: *Aldabrachelys*

The western Indian Ocean today hosts the most diverse fauna of large and giant tortoises (J. G. Frazier, pers com.). These are centered on three genera, *Cylindraspis*, *Astrochelys* and *Aldabrachelys*. The most confusing genus is *Aldabrachelys*, which includes several disputed species, assumed species, and an enigmatic absence of records. Evidence from fossils found on Madagascar (Bour, 1994), the Comoros, Assumption, Astove, Cosmoledo, Denis, and Glorioso (Stoddart et al., 1979) and Aldabra (Arnold 1976; Taylor et al. 1979) shows that giant tortoises were once widespread in the Indian Ocean. However, populations that historical records indicate had reached the Seychelles Mauritius, Reunion, and Rodrigues (Stoddart et al. 1979) were effectively extinct by the late 19th century and the only surviving wild population today is on Aldabra. Genetic sequencing of mitochondrial DNA (Palkovacs et al. 2000) indicates that all living forms are genetically the same species and were probably derived from a Malagasy ancestor. Only one sub-fossil specimen has been described from the African mainland, from Pliocene deposits in northern Tanzania. Meylan & Auffenberg (1987) referred to this as “*Geochelone*” (*Aldabrachelys*) *laetoliensis* but this attribution has not been widely accepted (J.G. Frazier, pers com.).

The taxonomy of this group has long been contentious and will only be summarized. First described by Schweigger (1812) as a single species, *Testudo gigantea* was referred to by Rothschild (1915) and later Arnold (1979) as “variable”. The sub-genus *Aldabrachelys* was

created by Loveridge & Williams (1957) to describe the giant tortoises of Aldabra and their allies on other western Indian Ocean islands, including Madagascar. Arnold (1979) renamed the Aldabra species *Geochelone gigantea*, in the subgenus *Aldabrachelys* and placed five extinct species from the Mascarene Islands in the subgenus *Cylindraspis*. Bour (1984) thought that *Aldabrachelys* was a junior synonym of *Cylindraspis* and proposed the alternative name of *Dipsochelys*, which he regarded as a genus. An additional problem lay in the species name as ‘*gigantea*’ appears to have been used in error. Schweigger’s (1812) holotype, was of uncertain origin, but is now lost. Subsequently, Gerlach and Canning (1996) redescribed six species of giant tortoise within the genus *Dipsochelys*. Only one of these, *Dipsochelys dussumieri* is living in the wild. *D. daudinii* is known from only two museum specimens, the holotype lacks collection data and the second specimen is a juvenile. Two species, *D. abrupta* and *D. grandidieri* are known only from subfossil remains in Madagascar. Arnold (1979) thought that *D. abrupta* (which he regarded as *Geochelone*) might be conspecific with *G. gigantea*. However, molecular analysis by Pedrono and Smith (2013) suggests that both species were closely related to *A. gigantea*. Of the three remaining species, two may be of Seychelles origin (*D. arnoldi* and *D. hololissa*) but are said to exist only in captivity. Only the Aldabran tortoise, *Aldabrachelys gigantea* is currently living in the wild. Subsequent work by Palkovacs et al. (2003) Austin et al. (2003) and Balmer et al. (2010) sequencing mitochondrial DNA showed that notwithstanding the morphological variation described by Arnold (1979) only a single lineage of Indian Ocean tortoises survives. In an attempt to clarify the obvious problems with names, a petition was submitted to the International Commission on Zoological Nomenclature (ICZN) to conserve prevailing usage (Frazier 2009). Issues were resolved by publication in 2013 by Opinion 2316 (case 3463) of the ICZN. The Commission conserved the specific name *Testudo gigantea* Schweigger, 1812 (family TESTUDINIDAE) in its use for the giant tortoise on Aldabra, by affirmation of the neotype designated in 2006 (USNM 2269962 in the Smithsonian Museum) and suppression of *T. dussumieri* Gray, 1831. The ruling placed *Aldabrachelys* on the Official List of Generic names in Zoology.

The earliest land tortoises date from the late Palaeocene, 60-55.5 Ma (Holroyd & Parham 2003), some time after the major fragmentation of Gondwana. However, the record of colonization of Madagascar, based on molecular clock models, varies between different authors but centres around 22-14 Ma (Palkovacs et al. 2002), during the early Miocene. The extent to which there was genetic radiation is not clear but there is little doubt that successive waves of colonization carried their descendents northwards to the Seychelles and,

subsequently, southwards to the Mascarene Islands. Fossil evidence on Aldabra (Braithwaite et al. 1973) points to three periods of colonization at times when sea-level was relatively high. However, from the preceding discussion, it is clear that the intervening periods, when sea-level was relatively low, provided much greater opportunities for dispersal to extensive refuges such as the Seychelles and other Banks to the East. It could be argued that a variety of animals and plants were continuously shed from the Madagascar coastline but their chances of a successful landfall and survival were far greater during some periods than others. The exceptionally high sea levels of the Last Glacial Maximum (26 ka) wiped out the population on Aldabra and elsewhere, and no doubt also severely reduced numbers in areas such as the Mascarene islands where some diversity may have been preserved. However, the final chapters in the record are fairly certainly the result of human intervention, first by the destruction one might say consumption, of extant residents, and second by re-population by individuals from a single source, Aldabra.

3. The Geology of the Western Indian Ocean

During the late Precambrian >600 Ma (million years) ago, present-day Madagascar, the Seychelles and India together formed parts of the eastern edge of the Gondwana supercontinent, adhering to what is now east Africa (Fig. 3). These crustal blocks remained closely linked until the late-Cretaceous (~85 Ma ago) when, after eastward separation from Africa, both India and the Seychelles, moving northeastwards, also detached from Madagascar, the latter probably moving slightly southwards (Anon. 1971). The Seychelles are believed to have separated from India at around the Cretaceous-Tertiary boundary ~65 Ma ago (Storey et al., 1995; Plummer and Belle, 1995; Torsvik et al., 1998; Ali and Aitchison 2008), close to the time when the Earth was struck, first by the Chixulub meteorite in Yucatan, Mexico, and second (less certainly), some 40 ka later, by the Shiva meteorite, striking southern India and what was to become the northern margin of the Seychelles Bank (Lerbekmo, 2014). The granitic rocks of the Seychelles, principally on Mahé and Praslin Islands, yield Rb-Sr ages of 570–713 Ma, but more recent U-Pb zircon dating suggests that they may be older, 748–764 Ma (Torsvik et al., 2001). Basaltic dykes intruding these granites include some that are clearly also of Precambrian age (~750 Ma), but others that are Cretaceous or Tertiary. The youngest igneous rocks from the Seychelles include syenites (on Silhouette Island), alkaline granites and trachytic tuffs, that apparently

formed part of an early Tertiary alkaline ring complex with an Rb-Sr age of 63.2 Ma (Dickin et al., 1986). They broadly correspond with the age of chemically similar alkaline ring intrusions in East Africa, but also with the age of mantle plume activity peripheral to the flood basalts of the Deccan Traps (Owen-Smith et al., 2013).

There are no surface exposures of basaltic rocks on Assumption, Astove, Cosmoledo or the Amirantes, but Udintsev (1975) described gravity anomalies around these islands that probably signify the presence of basic rocks beneath. Magnetic profiles across the arc-like ridge of the Amirantes, run by HMS Owen (Anon., 1963) suggested that basalts lie less than a kilometre beneath the present sea surface (Matthews and Davies, 1966). A Scripps Institute Expedition later dredged fragments of tholeiitic basalt from the flanks of the Amirantes Ridge that provided a whole-rock K-Ar age of ~82 Ma (Fisher et al., 1967). The Mascarene Plateau, the Chagos Bank and the Maldivé and Laccadive chains form parts of a volcanic suite that has been interpreted as a sequence of volcanic build-ups, reflecting movement of the crust over a stationary hotspot that may still be active (Fisk et al., 1989). Morgan (1981) suggested that volcanic activity on Reunion represents the most recent of a series of eruptions that may have begun with the formation of the flood basalts of the Deccan Traps in India (Morgan, 1981; Courtillot et al., 1986; Duncan et al., 1989), reflecting first, the northerly motion of the Indian Plate, followed by the north-eastern movement of the African Plate (Duncan and Hargraves, 1990). The oldest rocks exposed on Reunion are ~2 Ma old (McDougall, 1971; Fisk et al., 1989). On Mauritius the most voluminous eruptive phase, building the shield volcano, is dated at 7–8 Ma (Duncan and Hargraves, 1990), with later stages of activity extending up to 200 ka ago (McDougall, 1971). Basaltic rocks from Rodrigues have been dated at 1.58–1.3 Ma (McDougall, 1971, Duncan and Hargraves, 1990). Basalts have also been recovered (drilling for oil exploration) on the Saya de Malha and Nazareth Banks, beneath some 2400 m of Tertiary and Quaternary carbonate deposits (Meyerhoff and Kamen-Kaye, 1981). Although these are somewhat weathered, they suggest a late Oligocene age of ~25 Ma. However, basalts are closer to the surface on the Maldivé Ridge and some of these appear to have been erupted subaerially or at least under only shallow marine conditions (Duncan and Hargraves, 1990). The important conclusion here is that although the historical movements of many of the islands are spectacular they can have little bearing on the distribution of the present land fauna. Nevertheless, the most recent (principally volcanic) events in the Comoros and the Mascarene Islands may have been contemporary with the early stages of migrations of both tortoises and other biota.

4. Potential refuges

Madagascar has probably been a significant land area since its separation from Africa, and it appears to have formed a key centre for the dispersals discussed. It is now separated from Africa by some 430 km of open ocean, representing a considerable barrier to migration. However, as Krause (2010) has pointed out, although endemic terrestrial mammals on Madagascar are very diverse, “Unfortunately, the record of identifiable Malagasy terrestrial mammals from the entire Cenozoic era, the past 65 Myr, is virtually non-existent; it dates back only a few thousand years”. If correct, this statement leads to the conclusion that the ancestral stocks not only of mammals but also other terrestrial biota must have overcome this barrier.

Islands off the African coast, Pemba, Zanzibar and Mafia are too small to be seen as refuges and dispersal to them would not represent a significant step forward. Island groups in the Mozambique Channel, Juan de Nova, Europa and Bassas de India, with areas of only 40, 30 and 80 km² respectively, are mostly sand or gravel cays with little relief, although Europa (Stoddart, 1984b) and Bassas de India both have rocky shores, presumably of limestone, 2–3 m high. Their pyramidal gross morphology means that they would have had only slight increases in area during periods of lowered sea-level and thus, notwithstanding their likely steep shorelines, might have acted as stepping stones, but they are unlikely to have supported a diverse terrestrial biota.

The remaining islands of the western Indian Ocean can be conveniently divided into four morphological groups (cf. Braithwaite, 1984a). High limestone islands, like Aldabra, Astove, Assumption and Cosmoledo; high volcanic islands, including the Comores and the Mascarene islands; low islands, including the Amirantes, the Maldives and Chagos; and high ‘granitic islands’, like Mahé, Praslin, and Silhouette. However, to regard this inventory as representing the sum of potential refuges is to overlook the cumulative effects of the tectonic and climatic processes referred to above.

Krause (2010), using data modelling Eocene and more recent currents in the Mozambique Channel provided by Ali and Huber (2010), pointed out that “large rafts of matter vegetation torn from the banks of East African rivers” and capable of carrying a variety of passengers, could have reached Madagascar in as little as 25–30 days at speeds of up to 20 cm.sec⁻¹. As will be shown, tortoises would not have required any assistance in transport, other than their own tenacity, to make the same journey. Observations, like those

of Krause (2010) and Samonds et al. (2012), reporting sightings of floating islands up to 100 m diameter suggest that these played an additional critical part in dispersal of other biota. The present floras of the western Indian Ocean are not uniform and although they have been impacted by centuries of human intervention distinctive patterns of dispersal remain. These suggest relative ages of colonization, particularly in the Mascarene Islands (Cheke and Hume, 2007) and illustrate passive dispersal, aided no doubt by the greater tenacity of plant propagules. But they have an additional significance. There is no doubt that only islands that had acquired a diverse flora would have been able to sustain any terrestrial animal community. There may, however, have been a positive feedback as Hnatiuk, (1978) recorded the germination of 28 species of grasses, herbs and woody plants from faeces of the Aldabran giant tortoise.

4.1. High Limestone Islands

High Limestone Islands, as defined by Baker (1963), provide a useful starting point, and Aldabra, the best studied (Braithwaite et al., 1973), with a naturally derived thriving population of giant tortoises in addition to other unusual and endemic biota including two flightless birds, the Rail and the Coucal offers an appropriate model. Four main islands rise a little over 8 m above present sea-level, forming the atoll-like rim to a central lagoon that is typically less than 5 m deep. The main islands vary from 0.25–5.0 km wide and the total length of the ‘atoll’ is ~34 km, giving a present land area of ~155 km². The entire edifice rises from ocean depths of 4–5 km and geophysical evidence (gravity anomalies, Udintsev, 1975) suggests that the limestones form the cap to a volcanic core that may be as little as 320 m beneath the surface (Williams, 1971). However, bathymetric surveys by Barnes et al. (1971) showed that within 30–100 m of the present ocean shoreline, at a depth of little more than 30 m, there is a sharp increase in slope, indicating that although the lagoon would have drained as sea-level fell, the land area would not have increased significantly and what land there was would have been bounded by steep cliffs.

The stratigraphy of Aldabra has been described by Braithwaite et al., (1973). The Pleistocene limestones that form the islands comprise at least four distinct marine sequences. These are separated by erosion surfaces mantled by thin terrestrial deposits; two intervals of which contain fossils of tortoises (Taylor et al. 1979) and evidence of a terrestrial flora (Braithwaite, 1975). The earliest limestones represent a shallowing-upwards sequence of quiet-water deposits that imply a sea-level higher, perhaps 6–8 m higher, than the present.

This might reflect deposition in MIS 9, some 300 ka ago, but no reliable dates are available. Presaging the fall in sea-level of MIS 8, the limestones were subaerially eroded and during the period of exposure phosphorites (Braithwaite, 1980), found on the island of Esprit in the Aldabra Lagoon, were deposited.

However, there is no evidence of the area of any land that may have been present prior to phosphorite formation, or of any terrestrial biota, although the most likely source of the phosphates is in ‘guano’ from ground-nesting sea-birds. Phosphorites on the nearby island of Assumption that are apparently younger (Korotky et al., 1992) are reported to have been over 15 m thick. On Aldabra the overlying deposits reflect a sea-level similar to the present datum, and argue for a substantial interval before their deposition that may have occurred during MIS 7e. A subsequent fall in sea-level would once more have subjected the accumulated limestones to subaerial erosion, resulting in the local formation of dissolution pits and caves of karst and the accumulation of further terrestrial deposits. The land area at this time would have been at least of the order of 20 km², partly vegetated, and with a fauna including tortoises, a crocodile, an iguana, birds and land snails with freshwater ostracodes (Taylor et al., 1979). Sea-level rose again, this time ending slightly above its present position, and forming extensive deposits of carbonate muds characterized by a prolific flora of red calcareous algae with few corals. There was probably no land at this time and thus no terrestrial fauna. This period could correspond to MIS 7c, approximately 200 ka ago. In the following interval sea level remained a little below its present position before rising again to MIS 7a. This would account for the formation of additional local terrestrial deposits and the generation of marine erosion surfaces, including low cliffs preserved in the present stratigraphy. The land area at this time is uncertain and the only terrestrial fossils recovered so far are land snails. After minor fluctuations, sea-level then fell again, to ultimately reach more than 120 m below its present position. The most recent marine deposits, reflecting a sea-level rise to 8–10 m above the present datum, have been dated at ~125 ka (Thomson and Walton, 1972), equivalent to Marine Isotope Stage 5e. There is no hard evidence of the interval between these two events but we can conclude, from the characteristic saw-tooth profiles of plots of global isotopic data (Fig. 2), that cooling was protracted, with a net fall in sea-level taking place over 50–60 ka. The emergence of the island would therefore have been gradual, but would have resulted in a progressive increase in height of the surrounding slopes that probably also became steeper. By contrast, the rise in sea-level, when it came, would have been on a millennial scale. Subsequent sea-level fluctuations, around 80 ka ago, resulted in the formation of an island or islands of some 50 km² that enlarged as sea-level

began another descent. It was during this period that terraces formed, at 8 m and 4 m above present sea-level, during periods of relative sea-level stasis. Younger terrestrial deposits, found particularly in dissolution pits, include the remains of giant tortoises, a crocodile, an iguana, and six species of lizards (geckos and a skink), together with bones of the flightless Rail, several other birds, and terrestrial snails (Arnold, 1976; Taylor, et al., 1979). The rise in sea-level since the last glacial maximum began approximately 20 ka ago, but has only been close to its present position within the last 10 ka. It is only in this latter period, and perhaps only in the last 5 ka, that it has again been possible for tortoises and other terrestrial fauna to clamber ashore and re-colonize Aldabra, following an absence of probably around 100 ka.

This history serves as a model for that of other high limestone islands in the region. Few age dates have been obtained but the most extensive depositional units that have been dated, including those in Kenya (Braithwaite, 1984b), on Madagascar (Battistini, 1969, 1976), on Mahé, in the Seychelles and on Mauritius (Montaggioni, 1982). All include deposits relating to MIS 5 (Stoddart, 1984a). Similar limestones are seen on the islands of Praslin and La Digue in the Seychelles, on Assumption, Astove, Cosmoledo, Europa, St. Pierre and Glorieuse. Terrestrial deposits on Assumption have provided fossil tortoise bones (Fryer, 1910) and fossil eggs (Honegger, 1966), and Fryer (1911) also reported large fossil bones from Astove and fossil eggs on Cosmoledo, although the precise ages of the latter are not known. It is probable that all of these fossils were recovered from terrestrial deposits filling dissolution pits in the Pleistocene limestones, resembling those on Aldabra (Braithwaite et al., 1973) and on Glorieuse (Battistini and Cremers, 1972). The added significance of these observations is that, notwithstanding the complex earlier geological history, during the Quaternary the western part of the Indian Ocean appears to have been relatively tectonically stable and sea-level histories have been essentially similar in all of these areas (Camoin et al., 2004). With sea-level close to its present position, the island areas available for colonization by terrestrial faunas and floras appear to have been relatively small, although the fossils indicate that some were colonized nevertheless. However, on Aldabra at least, and elsewhere by extrapolation, although falls in sea-level of 10–30 m might have resulted in larger land areas, intervening (glacial) periods would have left the islands as steep-walled rocky pinnacles rising more than 100 m above the sea surface. The only water supply on these would have been rain and on karst surfaces this would have drained rapidly, limiting vegetation. It is difficult to see how tortoises in particular could have survived in such places or colonized them *de novo*. During the high sea-levels of interglacial periods, when the major marine limestone sequences were being deposited, most islands would have been

entirely submerged beneath the waves, with only continental East Africa and large islands like Madagascar, the Seychelles, and the volcanic islands of the Comores and Mascarenes providing any refuge.

4.2. *High Volcanic Islands*

High Volcanic Islands include the Comores and the Mascarene islands of Mauritius and Reunion, and retain substantial relief. Like Aldabra, the islands of the Comores archipelago rest on the remnants of relatively isolated volcanic pinnacles. However, the presence of sandstone inclusions within the lavas (Flower and Strong, 1969) implies that the northern part of the Mozambique Channel may consist of non-oceanic crust. Hajash and Armstrong (1972) suggested, on the basis of palaeomagnetic data and K/Ar ages, that the group represents the products of a hotspot that migrated to the NW. Ages range from 8 Ma on Mayotte to 0 Ma on Grande Comoro (Nougier et al. 1986), with the largely submerged pinnacle of Bank du Geyser undated. Most of the islands in this group would have remained as smaller islands during the last interglacial, when sea-level was higher, and would have become progressively larger as sea-level fell. However, no tortoise remains have been recorded and such islands would again have been flanked by relatively steep slopes. Thus, although they may have provided temporary refuges or stepping stones for a few individuals, they are unlikely to have supported substantial colonies.

The volcanic islands of Mauritius and Reunion are broadly similar in their general characteristics but also have raised limestone deposits dated to the last interglacial (MIS 5e). Both islands, together with Rodrigues, supported abundant giant tortoises when first visited by Europeans in the 17th and early 18th centuries, but thereafter the animals were exploited to extinction (Stoddart and Peake, 1979). The remains of giant tortoises were recovered in the 2006–2008 excavations at Mare aux Songes on Mauritius, described by Rijdsdijk et al. (2009) and Meijer et al. (2012). Tortoise bones have also been recovered from caves on Rodrigues (Burney, 2011) but the species identity and age of these is not known. Burleigh and Arnold (1986) recorded fossils of two species of giant tortoise from Mauritius, but the radiocarbon ages obtained from these give dates of 1490 and 1580 (relative to A.D. 1950) that may pre-date any human occupation, but certainly imply a relatively recent colonization or introduction.

4.3. *Low Islands*

Low Islands include those on the arc-like Amirantes Ridge, together with Farquhar, Coetivy and the Maldivian islands. The Amirantes Ridge is approximately 155 km long, bearing a chain of small islands and shoals from African Banks, Remire and D'Arros in the north to, Desroches, Poive and Desnœufs in the south. The Ridge is currently some 70 m deep at the centre with a raised rim at 11–27 m depth. None of the Amirantes islands is now more than 2–3 m above sea-level and, with the exception of some phosphatic beach-rocks on Remire (Braithwaite, 1968), most of the sediments on them appear to be unconsolidated. Fossil tortoise eggs have been reported from the Amirantes (Stoddart and Peake, 1979) but the specimens have been lost and the locality where they were originally found was not recorded. Dredging by the Scripps expedition recovered fragments of basalts and calcareous sandstones on the flanks of the Amirantes Ridge (Fisher et al., 1968), but although their presence might be inferred, there is no surface evidence of the Pleistocene limestones that have been recorded from the High Islands. It has been suggested that the raised rim of the Amirantes Ridge might reflect failed reef growth during a lower sea-level, but there is no evidence to support this view, and it is equally likely that the topography reflects residual karst pinnacles formed by subaerial dissolution of older limestones when sea-level was lower, as described on Aldabra by Barnes et al. (1971). The critical feature here is that the shallower parts of the Amirantes Ridge represent an area of some 6,300 km², much of which would have been available as a terrestrial refuge for would-be colonizers during periods leading up to the culmination of the last glacial interval (~20 ka ago) and probably during earlier low sea-level interludes as well.

The Farquhar Group consists of one small island, two atolls and a submerged reef. Farquhar itself is a relatively large atoll with a central lagoon occupying an area of some 170 km² (Stoddart and Poore, 1970), surrounded by a number of small sand and coralline gravel islets. Although shallow waters extend up to 2.5 km from the eastern shore, depth beyond this increases to “hundreds of metres”. Providence Atoll is smaller but is also low-lying, whereas the island of St Pierre has low rocky (limestone?) cliffs. Given the strategic position of the group between northern Madagascar and the Seychelles these islets may appear as potential refuges but they are relatively small and no evidence has been found of either recent or former occupation.

The Maldivian islands formed on an early Paleogene (60–50 Ma) volcanic basement, that is overlain by ~3 km of shallow-water carbonate deposits. Multibeam surveys by Fürstenau *et al.* (2010) identified several terraces between 97 and 55 m below sea-level that reflect

relative still-stands of sea-level that would have left substantial areas exposed. However, there is again no evidence of occupation by tortoises or any other terrestrial biota.

Bird and Denis islands on the northern rim of the Seychelles Bank are also low islands (sand cays). Tortoise egg shell has been recorded from Denis, associated with phosphate deposits, and has been radiocarbon dated at 1308 yr BP (corrected to 680 A.D.) by Burleigh (in Stoddart et al., 1979). This date is well before any recorded entry into the Indian Ocean by European mariners, but islands that appear to be the Seychelles are present on Arab documents published in AD 851 and Chinese ships are reported to have sailed into the Indian Ocean from the late 2nd century BC (Sun, 1989). Whether Arabic or Chinese sailors were partial to tortoise meat is a moot point, but otherwise the Denis discovery indicates that at least one egg-laying tortoise got to the Seychelles without the help of humans.

4.4. *Granitic Islands and Microcontinental Plateaux*

A remarkable feature of the Indian Ocean, setting it apart from others, is the presence of a large number of elevated banks and submarine plateaux scattered throughout the basin. The granites of the Seychelles are of Precambrian age and represent a fragment of the break-up of the Gondwana supercontinent and, as Torsvik et al. (2013) have shown, it is likely that the major plateaux are all of similar origin. Even areas like the Mascarene Plateau, dominated by evidence of relatively recent volcanic activity, probably also have Precambrian rocks as their foundations. The substructures of the Laccadive Islands, Chagos, Saya de Malha and the Mascarene group have been regarded as allied to Mesoproterozoic rocks (~1000–2500 Ma) now in southern India, whereas the Seychelles, dated at 700–800 Ma show closer affinities to Neoproterozoic arc-volcanic rocks, now linked with Madagascar. These microcontinental areas would all have been closely linked before about 83.5 Ma (Torsvik et al. 2013).

Although initial geophysical and borehole studies on the Chagos Bank (Duncan and Hargraves, 1990) suggested that it rests on a volcanic foundation, recent work by Torsvik et al. (2013) indicates that again this probably overlies continental rocks. The Grand Bank of Chagos has an area of 12,642 km², whereas the present land only occupies ~5.6 km². It has a central basin about 70 m deep with a rim 1.6 km wide 10–18 m below sea-level, and a terrace 8–20 km wide at 30 m depth. There may therefore have been substantial periods, when sea-level was lower, when it would have provided a significant land area. However, like the Maldives, there is no evidence to support any claim to occupation by a terrestrial fauna and flora.

The Saya de Malha, Nazareth, and Cargados Carajos Banks, to the south, are also regarded as microcontinents (Torsvik et al. 2013), with areas of approximately 40,808 km², 11,000 km² and 800 km² respectively and with present depths ranging from 8–150 m. Large areas of the Saya de Malha Bank are less than 35 m deep (Stoddart, 1971), and typical maximum depths of other Indian Ocean Platforms are 33–90 metres below sea-level. Most have shallower rims around their margins. These microcontinental Banks are of particular biogeographical significance because they would have been emergent for substantial periods during successive glacial intervals, creating land areas totalling in excess of 90,000 km² in the western Indian Ocean. This is important because, although there is no evidence of occupation, at a minimum, all could potentially have provided way-stations in migratory routes to sites in the Mascarene islands that were formerly colonized by giant tortoises.

The Seychelles Bank, with an area of approximately 43,000 km², is known in much greater detail that lends credence to this suggestion. As indicated, the islands of Mahé, Praslin, and La Digue that rest on it include Neoproterozoic granites. However, seismic investigations by Davies and Francis (1964) and Francis et al. (1966) suggested that the Bank also has a cover, albeit relatively thin (~500 m), of sedimentary rocks. These have since been shown (by boreholes during oil exploration) to include Triassic, Jurassic and Cretaceous deposits (Plummer and Belle, 1995) that may be correlated with deposits on Madagascar and in East Africa, predating the break-up of the eastern margin of the Gondwana supercontinent. Most of the Seychelles Bank lies between 44 and 65 metres below present sea-level, but around the outer edge, facing deeper water, a prominent discontinuous rim rises to within 14–20 m depth. Samples dredged from the surface of the rim indicate that it consists of coralline algae (including branching *Archaeolithothamnion*, and encrusting *Lithophyllum*) with branching bryozoans and encrusting foraminiferan *Homotrema* (Lewis and Taylor, 1966). Nevertheless, like the Amirantes and other Banks, it is uncertain whether these shallower areas represent a failed reef, formed during a period of lowered sea-level, an erosional karst remnant, generated by subaerial dissolution of limestone during low sea-level, or some combination of these.

Dredging of the surface sediments of the Seychelles Bank by HMS Owen and RSS Discovery (Fisher et al., 1967) recorded a variety of marine deposits blanketing much of the surface that become coarser-grained towards the shallower rim. However, investigations by Udintsev (1975) and Badyukov et al. (1989) recorded a diverse surface relief, including karst topography, alluvial plains, lacustrine and marshy depressions and river valleys, some of the

last-named ending in canyons on the outer slope of the Bank. Peat recovered on the Bank, some 62 m below present sea-level, has been dated (^{14}C) at 9.84 ± 0.25 ka BP (Badyukov et al., 1989), only slightly older than the reef-related deposits. This date sets an important limit on the time of flooding of the outer edges of the Bank and thus, indirectly, of the areas within the bank presently occupied by reefs. Taken at face value it implies flooding of the Bank, in what may have been only a few hundred years, to a depth that allowed the present reefs to become established, and indicates rapidly rising sea-level in response to a rapidly warming climate.

It is important to note that attention has only been drawn to the larger islands and Banks in the western Indian Ocean that might have been expected to have formed, at times, land areas capable of supporting viable populations of tortoises and other terrestrial biota. Smaller islands have been omitted because they are unlikely to have made such a contribution to dispersal. It is difficult to arrive at a realistic total land area but during the more dramatic glacial intervals it may have exceeded $130,000 \text{ km}^2$, equivalent to a country the size of Greece.

5. Ocean Currents and Dispersal

Although it is certain that giant tortoises spread to many areas in the Western Indian Ocean, the question of how they were able to achieve this seems difficult to answer. Postulated “landbridges”, even small ones, can be dismissed because the water depths between the islands discussed are far too great for any significant land extensions to be achieved. One alternative, that they were distributed by human hand, also falls. The fossil record indicates that tortoises were present on remote islands long before European, Arab, Chinese or Austronesian mariners existed. It has been argued (Wilme et al., 2016) in support of human intervention, that distribution by ocean currents can be ruled out because the principal current vectors oppose the supposed distribution directions, but this to ignore fossil evidence and also to take a very simplistic view of ocean currents.

The ability of giant tortoises to float is well established and graphic illustrations of their aptitude to swim are available at [http://www.arkive.org/aldabra-giant-tortoise/geochelone-gigantea/video-06b.html?offset=opx\[hr\]](http://www.arkive.org/aldabra-giant-tortoise/geochelone-gigantea/video-06b.html?offset=opx[hr]). Coupled with their capacity to survive without food or fresh-water for long periods; their known practical limits are of the order of 6–7 weeks (quoted by Gerlach et al., 2006, but may be more), and thus it seems likely that they would

have been able to drift to and colonize areas of exposed platforms during lowered sea-levels. However, this analysis ignores an important detail relating to surface currents in the Western Indian Ocean, and in particular, the South Equatorial Current. Principal flow directions at the present day are indicated on Fig. 4. It is not known whether similar features would have existed during the Pleistocene but analysis of present conditions highlights potential difficulties and suggests a solution. As indicated, it is thought that Madagascar was probably the principal point of departure. Voyagers leaving the west coast of this island would have faced entrainment in the Mozambique Current whereas those leaving the east coast would have joined the Madagascar Current. Both of these flow southwards, away from potential refuges and known remains. The South Equatorial Current dominates this part of the ocean, flowing westwards towards the east coast of Madagascar between about 10° and 20° south (New et al., 2005) and currently delivering plastic and other anthropogenic debris from the East Indies, to many islands and East African shores. Flow rates of 25–50 cm.s⁻¹ imply that floating objects will have difficulty in escaping from this. However, currents sweeping the northern tip of Madagascar divide, veering to both the south and north. Northerly flows are entrained in gyres that merge with the Equatorial Counter Current, between 2° and 10° S. The position of this current varies during the year in response to monsoonal cycles, lying further south during the SW monsoon but, importantly, flows in this are predominantly eastwards. A narrow (500 km) eastward-flowing Equatorial Jet is sometimes established during transitions between the monsoon seasons, strong in April/May and somewhat weaker in September/October, but locally reaching speeds of 64 cm.s⁻¹ (Wyrski, 1973), with local flows of 215 cm.s⁻¹ reported between 60° and 90° E. What this means is that floating tortoises, or vegetation, could have been carried on an indirect route north of Madagascar and arrived at more southerly destinations to the east in eddies that were essentially random.

It is important to note here that large (several metres diameter) rafts of vegetation, including stands of bamboo) have been observed arriving on the shores of Aldabra. It is not known whether these are derived from eastern or western sources but similar rafts would be able to support a variety of small animals for a substantial period. Samonds et al. (2012) report sightings of floating islands up to 100 m across more than 240 km from their supposed place of origin, and an unconfirmed report published by Powers (1911) describes an island in the Atlantic first seen in July 1892 at latitude 39.5° N., longitude 65° W, 400 km off Cape Cod. This was estimated to have an area of 836 m², with trees ~9 m high. It was last seen in September of that year at latitude 45° 29' N, longitude 42° 39' W, 600 km off Newfoundland, having travelled over 1,850 km (Powers, 1911). Thus, the conclusions drawn from what is

assumed to be the passive transport of tortoises can certainly also be applied to other elements of the biota. Evidence from molecular studies of 52 taxa of Chameleons (Raxworthy et al. 2002) supports the view that present distribution implies over-sea distribution from Madagascar to Africa, and to the Seychelles, Comoros, and probably Reunion and does not reflect vicariance. These animals would have to have relied on passive rafting. More dramatically, Vences et al. (2003), analysing mitochondrial DNA, have been able to map the dispersal of at least two species of frogs (traditionally regarded as unable to tolerate contact with seawater); from Africa to Madagascar 19-30 Ma ago, from Madagascar to the Comoros (Mayotte) <8.7 Ma ago, and to the Seychelles 11-21 Ma ago.

Ali and Huber (2010) described enigmatic results to explain the dispersal of mammalian populations from Africa to Madagascar, noting the piecemeal arrival of individual species (that included tortoises) that argues strongly for a water-borne dispersal. However, they also identified the issues of present-day southwards-flowing currents that militate against such a process. Their solution to this problem was to model past ocean circulation, based on a Climate System Model of the US National Center for Atmospheric Research, with supposed Eocene boundary conditions. During the Eocene, both Africa and Madagascar were more than 10° further south, placing them in the convergence zone of the subtropical gyre. Models indicate that this intermittently generated an eddy within the Mozambique Channel that directed much of the flow eastwards, with velocities of 10–20 cm.s⁻¹, resulting in a time for swimmers (or rafters) crossing the channel of 25–30 days. Although they are infrequent, present-day eddies in the channel may occasionally reach flows of 100 cm.s⁻¹ (de Ruijter et al. 2005). However, as the continental masses drifted further north this mechanism would shut down, making further colonization of Madagascar “more difficult, if not impossible” (Ali and Huber, 2010). It is not known when this change would have occurred.

These models do not explain more recent conditions further east. New et al. (2005) discuss present-day perturbations that only seem to emerge from relatively high resolution models of sparse data. The Mascarene Plateau presently provides a significant barrier to the South Equatorial Current. East of these shoals this forms a broad westwards-directed flow of approximately 25 cm.s⁻¹ between 9° and 16° S. It divides between the various Banks on the Plateau with the dominant flow in the deep channel between the Saya de Malha and Nazareth Banks, where it reaches speeds approaching 50 cm.s⁻¹. West of the Banks, it partially reforms, to give two cores, from 10–15° S and from 17–20° S. However, during Pleistocene glacial (low sea-level) intervals the only access would have been via the channel between Saya de Malha and Nazareth Banks and flow overall would therefore have been significantly

interrupted by the emergence of the Mascarene Plateau. This would have formed a barrier extending from the Seychelles in the north to Reunion in the south that may well have entirely disrupted flow of the South Equatorial Current.

The possibly circuitous route(s) that tortoises must have travelled (and survived) in order to colonize emergent platforms imply large distances. The distance from Madagascar to Aldabra is 425 km. The flow rates recorded in this area range between 25 and 50 cm.s⁻¹ and suggest the most favourable estimates for time in the water of from 1.5 to 3 weeks. The distance from Aldabra to the Seychelles Bank is of the order of 1,150 km and this would require a journey time ranging from a month to 7–8 weeks, or more at the lower end of the flow estimates. However, if entrained in flows equivalent to the Equatorial Jet they could manage the same journey in as little as a week! The total distance from the Seychelles to Reunion is 1,829 km. At the slower rates this translates into nearly 3 months in the water for an uninterrupted journey. The Pleistocene palaeocurrents around the Mascarene Ridge are unknown, but the South Equatorial Current may be expected to have been weak to the west of the ridge and may have involved a series of eddies. The Saya de Malha and Nazareth Banks could have acted as stepping stones and these seem the best way to have extended colonization to the south. The key issue that remains is whether the travel times indicated, that would have been shortened in any equivalent of the Equatorial Jet (moving at up to 160 km per day; Wyrski, 1973) were within the survival capabilities of the tortoises. Gerlach et al. (2006) described the arrival of a giant tortoise on the coast of East Africa. This was presumed to have come from Aldabra, 740 km away and, from estimates based on the sizes of encrusting barnacles on its legs, to have been in the water for 6–7 weeks.

6. Conclusions

- The biogeography of the western Indian Ocean reflects dramatic climatically driven changes in sea-level and thus also changes in the palaeogeography of the region.
- Four groups of islands can be identified, with varying and distinctive contributions to the present and past distributions of the terrestrial biota, and in particular that of the giant tortoises.
- High limestone islands, like Aldabra, provide present-day refuges for terrestrial organisms and would have offered larger land areas when sea-level lay below but close to its present position. However, during maximum glacial withdrawals of the

sea they would have stood as steep-sided columns. Although these probably had relatively flat tops they would nevertheless have generally been inaccessible to larger animals, and water and thus also vegetation were probably limited. At times of high sea-level, like the last and other interglacial periods, land-living organisms of all sizes would have been wiped out.

- High volcanic islands, like Mauritius and the Comores are presently capable of supporting substantial colonies of giant tortoises but, as a result of human predation, no longer have viable natural populations. However, they differ from high limestone islands in that, notwithstanding subsidence, their naturally high pyramidal profiles ensured that they remained above water during times of high sea-level. The same profiles were reflected in increased land areas when sea-level was lower, with the proviso that slopes were locally benign enough to allow access and continued to support a diverse vegetation.
- Low island groups, like those of the Amirantes and Cargados Carajos, are currently too small to provide refuges for significant populations and would also have been submerged at times of higher sea-level. However, the platforms on which they rest are substantial areas that would have been exposed for long periods during low-sea-level interludes, and may have supported significant terrestrial populations at these times.
- There is no doubt that the Granitic islands of the Seychelles had an indigenous population of giant tortoises well before humans had the capacity to navigate freely in these waters. However, the granite slopes are steep and although the flat so-called 'plateau' areas around the margins currently offer suitable habitat they are probably of post-glacial origin. Things were different when sea-level was lower but we do not know the precise age(s) of the fossils. Higher sea-levels, reflected in raised Pleistocene limestones present around the shores, would have reduced these opportunities. The Seychelles Bank and similar continental fragments scattered across the ocean are a different matter. There is ample evidence, in the Seychelles at least, that these Banks were exposed and provided relatively flat surfaces that supported a diverse range of environments. These can be presumed to have been reflected in a diverse ecology. There is no direct evidence that giant tortoises colonized these areas, but any that did can be expected to have thrived.

- Present ocean currents do not provide direct routes for the known dispersals. If these are a reflection of former conditions it is likely that floating tortoises would have had to have travelled northwards from Madagascar before their entrainment in the Equatorial Counter-Current that would then have carried them to the east. Local gyres on the margins of this flow may have carried some south along the Mascarene Ridge but the details of Pleistocene flows are not known. Given travel times at the lower rates of flow, individuals would have needed to survive as long as two months in order to reach some refuges, but this seems to have been within their capabilities.
- Although floating (and swimming) tortoises are able to travel independently it is clear that floating rafts of vegetation would necessarily have followed similar paths and could have contributed to the passive distribution of a more varied fauna and flora. As the tortoise records indicate, this process probably occurred on a number of occasions. However, genetic evidence that present tortoise populations belong to a single species suggests that their current distribution reflects human influence.

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Plate Fig. 1

Figure 2

Figure 3

Figure 4

Captions to Figures

Fig. 1. *Aldabrachelys* on Aldabra.

Fig. 2. Plot of stacked $\delta^{18}\text{O}$ data from benthic organisms derived from globally distributed ODP records, based on the work of Lisiecki and Raymo (2005). Numbered Marine Isotopic Stages are marked by broadly, warmer (interglacial) temperatures that act as proxies for relatively high sea-levels, as at present and ~100 ka ago. These reflect melting of ice caps and thermal expansion of ocean waters. Cooler (glacial) intervals are characterized by sequestration of water in ice caps and result in relatively low sea-levels. Recent differences between high and low levels have been of the order of 130 m. Whereas cooling is generally protracted, warming is typically rapid. Although global calculations of sea-level do not correlate precisely with local responses, that may incorporate isostatic adjustments, differences in temperature, and hydroisostasy, their effects on the areas of land available for colonization have been critical to animal and plant dispersal.

Fig. 3. Palaeogeography of the Western Indian Ocean, illustrating the sequential movements of continental microplates, based on the work of Torsvik et al. (2013) and others. At ~750 Ma global continents were grouped together with elements relating to the Western Indian Ocean, Madagascar and the Seychelles, in close proximity. By 83 Ma the supercontinent had broken apart, with Madagascar and India separating from the African mainland and carrying with them many of the microplates discussed. By 41 Ma these had substantially dispersed. The arrows mark approximate points of origin, directions and distances of travel. The final diagram shows their present positions with arrows again indicating former positions (at 41 Ma), directions and distances of travel.

Fig. 4. Illustrates the present position of shallow platforms (<120 m) in the Western Indian Ocean. Brown areas are land and lighter yellow areas currently submerged platforms that would have become land as a result of falls in sea-level. Note that although most of these carry islands these are generally too small to be shown at this scale. Blue arrows indicate the paths of present ocean currents discussed, with stronger currents represented by larger arrows.