Palaeogeography, Palaeoclimatology, Palaeoecology 461 (2016) 449–459

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

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

ARTICLE INFO

Article history:
Received 16 December 2015
Received in revised form 3 August 2016
Accepted 4 August 2016
Available online 8 August 2016

Keywords:
Biogeography
Indian Ocean
Giant tortoises

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 km^2, 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.

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http://dx.doi.org/10.1016/j.palaeo.2016.08.010
0031-0182/

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 and 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 and Peake, 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 Milankovitch (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'.

Fig. 1. *Aldabrachelys* on Aldabra.

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 and Peake, 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