



Absence of post-Miocene Red Sea land bridges: biogeographic implications

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ABSTRACT

In a large number of studies concerned with species movements between Africa and Eurasia, including the migrations of hominids out of Africa, a frequently-cited dispersal route is across a hypothetical land bridge in the southern Red Sea, which is suggested to have emerged during glacial sea-level lowstands. This paper, however, unequivocally demonstrates that palaeoceanographic and palaeoecological data are incompatible with the existence of Red Sea land bridges since the Miocene. The case is made by presenting the first quantitative history of water depth above the Red Sea sill for the last 470,000 years, a time period that includes the four most recent glacial–interglacial cycles, and by discussing the predictable consequences of any land bridge formation on the Red Sea sedimentary and microfossil records. The absence of post-Miocene Red Sea land bridges has extensive implications for biogeographic models in the Afro-Arabian region. Genetic, morphometric and palaeontological patterns reported in the literature cannot be related to dispersals over a land bridge, or in the case of marine organisms, separation of the Red Sea from the Indian Ocean by a land bridge. If such patterns in terrestrial species are only congruent with a southern Red Sea dispersal route, then they need to be considered in terms of sweepstake rafting, anthropogenic introduction, or in the particular case of the Out-of-Africa migration by modern humans, seafaring. The constraints imposed by our palaeoenvironmental record on biogeographic reconstructions within and around the Red Sea will hopefully encourage both the review of previous works and the preference for multidisciplinary approaches in future studies.

Keywords

Afro-Arabian biogeography, dispersal, land bridges, Out-of-Africa, palaeoceanography, palaeoecology, Plio-Pleistocene, rafting, Red Sea, seafaring.

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INTRODUCTION

The Red Sea region plays a central role in the history of species movements between Africa and Eurasia, including migrations of modern humans and earlier *Homo* species. Species dispersal models for this region have been suggested based on both palaeontological and archaeological data, and morphometric or genetic comparisons between populations in (northeastern) Africa and (southwestern) Asia. The two main routes proposed (Tchernov, 1992; Cavalli-Sforza *et al.*, 1993; Lahr & Foley, 1994) are: (1) through the Sinai Peninsula, or (2) across the Bab-el-Mandeb Strait in the southern Red Sea (Fig. 1). The second is commonly equated with a land bridge that would have emerged during Pleistocene sea-level lowstands (Delany,

1989; Robinson & Matthee, 1999; Walter *et al.*, 2000; Mithen & Reed, 2002; Wildman *et al.*, 2004; Winney *et al.*, 2004). The land bridge hypothesis has also been discussed in relation to patterns of genetic differentiation between Red Sea and Indian Ocean populations of marine species (Shefer *et al.*, 2004). Alternatively, as in the case of the Out-of-Africa migration of modern humans for which models involving a single, or at least major, dispersal event along the ‘southern route’ are increasingly supported by genetic evidence (Quintana-Murci *et al.*, 1999; Maca-Meyer *et al.*, 2001; Underhill *et al.*, 2001; Forster, 2004; Lovell *et al.*, 2005; Macaulay *et al.*, 2005); the precise nature of the dispersal mechanism across the southern Red Sea is usually left unspecified (e.g. across a land bridge or using watercraft).

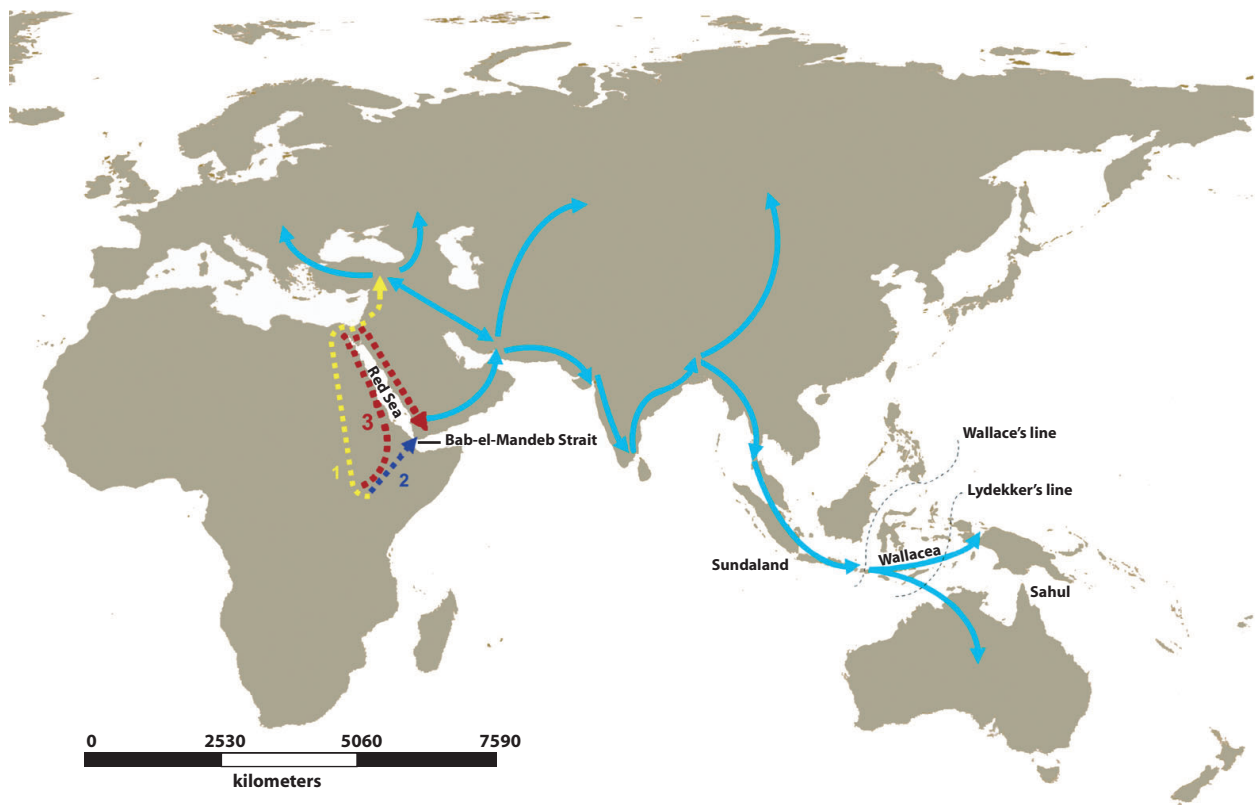


Figure 1 Biogeographic map showing the three possible dispersal routes connecting Africa and Asia that are available to terrestrial animals: (1) through the Levantine corridor (in yellow), (2) across the southern Red Sea (in blue), and (3) around the Red Sea coastline (in red). Although the pathways are represented as stemming from Africa into Eurasia, because the Out-of-Africa migration by modern humans is used as the main example to discuss the biogeographic implications of our palaeoenvironmental record, the biotic movements along them can obviously be in any of the two directions. Based on our data we conclude that post-Miocene dispersals through route 2 could not have been across land bridges, but instead they involved sweepstake rafting, anthropogenic transport, or in the case of modern humans, seafaring. Also depicted in the map is the hypothetical peopling of Eurasia (in cyan), including the ‘southern route’ from Arabia to Australasia, as well as the geographic places and biogeographic features that are mentioned in the text.

EVAPORITES, MICROFOSSILS AND WATER DEPTH HISTORY IN THE RED SEA

The only place where a hypothetical land bridge might develop is in the southernmost Red Sea, at the Hanish Sill, with a present-day maximum water depth of 137 m (Werner & Lange, 1975). Emergence of that sill would isolate the Red Sea from the Indian Ocean. The high net evaporation over the Red Sea would then rapidly draw down the basin level, at a rate of approximately 2 m year^{-1} (Smeed, 2004). The resultant concentration of salt within the basin would cause dramatic deterioration of the Red Sea environment. Without doubt such deterioration would be registered in the Red Sea sedimentary and fossil record. Essentially, the basin would become sterilized within about 200 years, except for a small number of hypersalinity-tolerant species, and formation of evaporite deposits would start within about 600 years. Neither is observed in marine sediment cores covering the last 470,000 years – there are no basin-wide evaporite deposits, and marine faunas and floras that are unable to survive hypersaline conditions continue throughout (Rohling *et al.*, 1998; Siddall *et al.*, 2003).

Using the model of Siddall *et al.* (2003), we calculate that sea level must at all times during the last 470,000 years have remained more than 15 m above the level of the sill (Fig. 2). Note also that the strait would have remained at least 5 km wide during even the most severe sea-level lowstands. The most recent phase of basin-wide evaporite deposition occurred in the Red Sea during the middle to late Miocene around 12–6 Ma (Orszag-Sperber *et al.*, 2001). Realistically this was the most recent period for which a land bridge can have separated the (proto-)Red Sea from the open ocean.

IMPLICATIONS FOR AFRO-ARABIAN BIOGEOGRAPHY AND OUT-OF-AFRICA MODELS OF *HOMO* DISPERSAL

Given this seemingly incontrovertible evidence against the emergence of land bridges in the southern Red Sea, we conclude that models of Plio-Pleistocene movements of terrestrial fauna between Africa and Arabia should only consider the hypotheses of dispersal via the Sinai route, ‘sweepstake’ rafting and/or anthropogenic introduction.

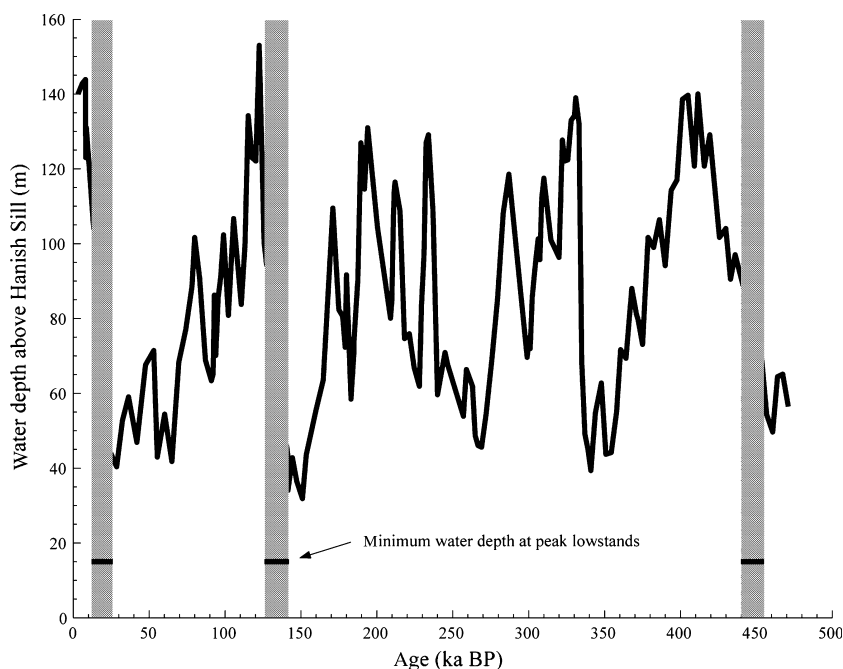


Figure 2 Record for the last 470,000 years of minimum water depth above Hanish Sill in the southern Red Sea. In the Red Sea evaporation strongly alters the levels of salt and stable oxygen isotope ratios compared to the open ocean. The refreshment of Red Sea waters depends on the exchange of water over Hanish Sill. The exchange of water between the Red Sea and Indian Ocean depends strongly on the depth of Hanish Sill – this leads in turn to high sensitivity of the stable oxygen isotope ratio in the basin to the depth of Hanish Sill. A combined model of Red Sea exchange over Hanish Sill and stable oxygen isotope fractionation in the basin (Siddall *et al.*, 2003) can be used to calculate the relationship between Red Sea stable oxygen isotope ratios and water depth above Hanish Sill. This relationship can then be used to establish a curve of Hanish Sill depth over time based on the stable oxygen isotope ratios analysed using microfossils from sediment cores in the basin. Because this is effectively a sea-level curve relative to Hanish Sill no account needs to be made for uplift of the sill due to tectonic or glacial-loading (isostatic) effects (Siddall *et al.*, 2004). The refreshment rate similarly affects salinity in the basin. At low sea level the low refreshment rate generates very high salinities ($S > 50$ practical salinity units (p.s.u.), approximately $S > 50\text{‰}$). At these high salinities the Red Sea planktonic foraminifera become extinct for a period, indicated in the Red Sea sediment cores by aplanktonic zones (grey bars). Throughout the aplanktonic zones intervals, pteropod and diverse benthic foraminiferal faunas continue (Rohling *et al.*, 1998), indicating that S was less than 70 p.s.u., which requires a minimum water depth above the sill of 15 m. The 1 sigma error margin applicable to this record is around 6 m (Siddall *et al.*, 2003).

Rafting is recognized to have played a role in several transmarine colonizations across distances that far exceed the width of the Red Sea, not only by invertebrates and small vertebrates but also by medium to large-sized mammals (de Queiroz, 2005).

Likewise, biogeographic studies of marine organisms in the Red Sea should not simply ascribe genetic differentiation across the strait to a land bridge separating the Red Sea from the Indian Ocean during past sea-level lowstands (Shefer *et al.*, 2004). Alternative explanations may include strongly enhanced environmental (salinity) gradients and diminished water mass exchange through the strait at those times (Fenton *et al.*, 2000).

The question of the origin of *Homo sapiens* has been for decades a hotly debated subject in palaeoanthropology, but the weight of anatomical, genetic and archaeological evidence increasingly supports an African dawn (Stringer, 2002; Lewin & Foley, 2004; Ray *et al.*, 2005), going back at least 160,000 years (White *et al.*, 2003). Its emergence was followed by demographic fluctuations and multiple dispersals

within and out of Africa, such as the one into the Levant 130,000–100,000 years ago attested by the Skhul and Qafzeh burials (Grün *et al.*, 2005), mostly determined by glacial–interglacial environmental instability and local appearance of behavioural novelties (Lahr & Foley, 1998; Harpending & Rogers, 2000; McBrearty & Brooks, 2000). However, the issue of how many dispersals are at the root of all living non-Africans, and of whether the Levantine corridor (the ‘northern route’) had a role in the appearance of the first modern humans in Europe, is still currently under dispute (Quintana-Murci *et al.*, 1999; Maca-Meyer *et al.*, 2001; Underhill *et al.*, 2001; Forster, 2004). Some recent mitochondrial DNA studies (Macauley *et al.*, 2005; Thangaraj *et al.*, 2005) indicate a single Out-of-Africa migration that only started *c.* 70,000 years ago, spreading first to Asia along the ‘southern route’, and later into Europe during the frequent interstadials around 45,000–35,000 years ago (Allen *et al.*, 2000; Sánchez-Goñi *et al.*, 2000; Guiter *et al.*, 2003; Mellars, 2004). Conversely, the results of some nuclear DNA surveys (Eswaran *et al.*, 2005; Garrigan *et al.*, 2005) have been

interpreted as suggesting significant admixture, instead of simple replacement, between anatomically modern humans expanding from Africa and archaic populations in Eurasia.

Regardless of the evolutionary scenarios for its later stages, our record of minimum water depth above the Red Sea sill offers new constraints to the nature of the first step in the global colonization by our species (Fig. 1). If the Out-of-Africa migration entailed the crossing of the southern Red Sea, then the use of watercraft must be invoked in what would possibly be the earliest instance of seafaring in *Homo sapiens* (Straus, 2001; Bednarik, 2003).

In this context it is interesting that as early as 840,000 years ago (Morwood *et al.*, 1998, 2004) *Homo erectus*, a species with lower cognitive capabilities, was able to colonize Flores, an Indonesian island on the eastern side of the Wallace's Line – a major biogeographic boundary associated with the permanent deep-water barrier that prevented dispersals from Sundaland into Wallacea by most other land mammals, even during glacial periods of lowered sea level (van den Bergh *et al.*, 2001). Nevertheless, the absence of *H. erectus* remains in Australia and New Guinea, coupled with doubts about the presence in this species of the cultural and technological complexity needed for seafaring (Erlandson, 2001), raises the question of whether the colonization of Flores might have been the result of mostly passive accidental rafting(s) on vegetation mats (Diamond, 2004).

Because suggestions of planned maritime voyaging in *H. sapiens* before the colonization of Australasia also remain controversial (Erlandson, 2001), the hypothesis of a coastal dispersal around the Red Sea basin (Stringer, 2000) needs to be evaluated. Movement along the coasts would have provided a buffer against prevailing cool and dry conditions and could have been particularly fast if taking place during interstadials in southern Asia (Schulz *et al.*, 1998), making this model also compatible with recent estimates of the coalescence time for all extant non-African human populations (Macaulay *et al.*, 2005). Furthermore, this is a scenario that fits better with the apparently absent, or at least limited, role of the southern Red Sea passageway in later human migrations during the Upper Palaeolithic and Mesolithic (Luis *et al.*, 2004).

Unfortunately, no modern human fossils confidently dated between 85,000 and 65,000 years ago have been found from Arabia, northeastern Africa and the Levant, yet such a find would help to identify the most likely route for the Out-of-Africa dispersal (Vermeersch *et al.*, 1998; Shea, 2003). Similarly, data on the lithic industries from the Red Sea margins and environs that could be potentially relevant for the same issue are so far undated (Rose, 2004a) or remain unable to provide an unambiguous picture, due both to their paucity (Rose, 2004b) and regional incomparability; the latter a product of the diversity of how lithic assemblages have been described and analysed in separate localities and by different archaeologists (Vermeersch, 2001).

It is therefore clear that we need more data (genetic, palaeontological, archaeological and palaeoenvironmental) to resolve competing reconstructions of species dispersals

through the Red Sea region. We hope that the far-reaching implications of the record here presented might stimulate such future investigations.

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