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Evolutionary mechanisms and diversity in a western Indian Ocean center of diversity

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Abstract. The biogeography and evolutionary history of the shallow marine fauna in the western Indian Ocean (WIO) is poorly known, as are the consequences of ancient and recent biodiversity-generating processes. In-water surveys of scleractinian corals show maximum diversity in a core region centered on the northern Mozambique Channel. Maximum species richness is at ≈300 with a threshold of ≈250 that differentiates this core region from lower-diversity zones in northern Tanzania and Kenya, the Seychelles and small islands in the Mozambique channel, and the Mascarene islands. Species distributions show significant clustering of sites within this high diversity core region, distinguished from peripheral regions. A heritage of ancient Tethyan lineages is suggested by the distinctive WIO endemic fauna of monospecific genera, basal *Acropora* clades, and cryptic phylogenetic patterns in *Stylophora* and *Siderastrea*. Their presence in the WIO is likely associated with the closure of the Tethys Sea in the Miocene and little radiation subsequently. The dominance (90%) of Indo-West Pacific species in the extant WIO coral fauna reflects invasion during the Mio-Pliocene of the younger and more diversified fauna from the West Pacific during the same period. Various lines of evidence suggest the northern Mozambique Channel may have been a refuge for shallow tropical species throughout its history, particularly during the Cenozoic. This deep evolutionary history suggests a unique biodiversity across multiple taxonomic levels in this second peak of tropical marine biodiversity.

Key words: Western Indian Ocean, Tethys Sea, Scleractinian corals, Mozambique channel, Endemics

Introduction

The marine biodiversity of the Western Indian Ocean (WIO) is one of the least known globally, with major gaps in species distribution records of even well known taxonomic groups (Wafar 2011). Until recently, regional coral distribution analyses (Sheppard 1987, Veron 2000) found that coral species diversity across the Indo-Pacific declines approximately linearly in all directions from the high-diversity center in the southeast Asian region. However Obura (in review) shows evidence of a second high diversity region for scleractinian corals in the northern Mozambique channel and relates this to the principal currents of the WIO, suggesting these patterns may also hold for other shallow marine taxa.

Understanding the evolutionary history behind major biomes or realms, and the influence of tectonic events, is essential to understanding extant patterns of biodiversity and ecosystem processes. Over geological time, hotspots have shifted geographically, with 3 main centers of diversity for shallow marine species through the Cenozoic having been identified (Renema et al. 2008): the West Tethys in the Eocene, the East African-Arabian Province (EAAP) in the Oligocene (Harzhauser et al. 2008), and the Indo-Australian Archipelago (IAA, Miocene-present) from the Miocene to the present (Hoeksma 2007). Investigations of species origination and extinction of tropical marine taxa in relation to plate tectonics have been investigated, e.g. for pyrgomatid barnacles globally (Ross & Newman 2000), a variety of taxa (including *Acropora* and fungiid corals) within specific locations such as the Togian islands straddling the Wallace line (Wallace et al. 2000), tridacnid clams (Newman & Gomez 2000, Harzhauser et al. 2008) and corals in general (Wilson and Rosen 1998). Veron (1995) makes the point that corals show complex patterns of 'reticulate evolution' such that species should be interpreted cautiously as a particular time-space slice of genetic 'packaging'. This claim makes the broader point that evolutionary time and geographic space must be interpreted simultaneously in trying to understand the biogeography of what we now label as coral 'species'.

This paper explores various lines of evidence in reef building corals to propose an evolutionary hypothesis for the extant biogeographic pattern of species in the Western Indian Ocean.

Methods

The biogeography of reef-building corals in the Western Indian Ocean as reported in Obura (in review) is interpreted here in the light of Cenozoic tectonic history. This includes plate tectonic and hotspot activity across the ocean basin, the closure of the Tethys and Paratethys Seas in the Eocene-Oligocene and formation of the IAA in the Miocene. In Obura (in review), species richness of 21 locations in the WIO was estimated from species accumulation curves (Michaelis-Menten equation). In total, 369 species were included in the dataset. Cluster analysis of presence/absence data was conducted, using the Bray-Curtis similarity coefficient.

Results

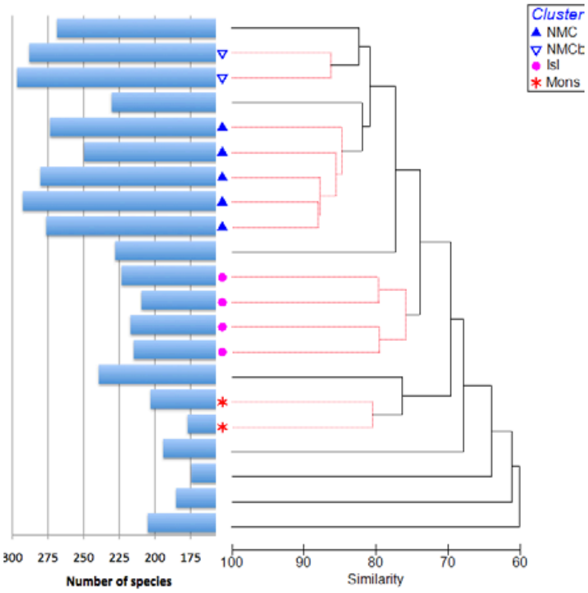

Figure 1. Estimated maximum number of species (left panel, bar chart) and cluster analysis (right panel) for 19 locations in the Western Indian Ocean plus Djibouti and Chagos (from Obura in review). Symbols and light branch lines show statistically significant clusters (SIMPER test, $p < 0.05$) in the Northern Mozambique Channel (NMC and NMCb), islands in the western Seychelles and the NMC (Isl), and northern Kenya (Mons).

The maximum location-specific diversity was estimated at almost 300 species, in a center of diversity covering the northern Mozambique Channel (Fig. 1). Diversity declined to about 200 in northern Kenya and 175 in the remote islands eastwards in the central Indian Ocean. The coral assemblages of sites in the high-diversity center were also the most similar reflecting a core regional fauna. Comparison of these results with field records of 324 coral species at a site in NW Madagascar (Veron & Turak 2005) suggested that with multiple detailed taxonomic surveys (i.e. with comparable effort as in other regions such as the Great Barrier Reef, or northern Red Sea) actual maximum species richness for a location in the WIO center of diversity could reach 350-400 species.

Table 1. Phylogenetic, fossil and distribution evidence of Tethyan origins in extant Western Indian Ocean corals.

Acropora - the oldest fossil of the genus is recorded from Somalia in late Paleocene desposits, and 9 of the 20 extant species groups are present in Eocene fossils from European locations. Species with restricted distributions in the west side of the IO (*A. roseni, hemprichii, austera, variolosa, rudis*) belong to the basal clade(s) of the genus, while many of the endemic/restricted range species in the IAA and West Pacific are from terminal (recent) clades (Carbone et al. 1994, Wallace 2000, Wallace & Rosen 2006).
Siderastrea - the phylogeny of the genus suggests the single Indo-Pacific species should be differentiated into two species, from Oman/Kenya and the W. Pacific, with the former being ancestral and more closely related to the more diverse Atlantic species group (5 species) (Chuang 2006, Obura et al. 2007).
Stylophora - the WIO contains higher genetic diversity than the Pacific, the ancestral species to the genus is found in the Red Sea (Flot et al. 2011, Stefani et al. 2011, Chen et al., in prep).
Endemic IO species – *Horastrea indica, Anomastrea irregularis, Craterastrea laevis, Parasimplastrea sheppardi, Gyrosmilia interrupta* and *Ctenella chagius*. Six of the endemic species of the western and northern IO are in monospecific genera with simple and small morphologies, a range of geographic extents from narrow to regional, suggesting relict rather than neoendemic lineages. Two of these (*Gyrosmilia, Ctenella*) are in a mainly Atlantic family (Meandrinidae) with similarly low species diversity. By contrast, endemic species in the West Pacific region tend to be recent, and in more speciose higher taxa, reflecting speciation and radiation since migration of the hotspot in the Miocene.

Of the 369 species in the database, 90% had broad Indo-Pacific distributions, and 10% were restricted to the Indian Ocean from Sri Lanka/South India westwards (Obura in review). Of these 37 species: 26 (7% of the total) are found throughout this region, though 13 were previously reported as endemic to northern locations only (Red Sea, Arabian Sea and Gulfs). The remaining 11 species are endemic to the WIO.

Discussion

The conventional view of coral diversity in the Indian Ocean, of declining species richness from east to west, is contradicted by Obura (in review), in which a high diversity center for Indian Ocean corals in the northern Mozambique channel is demonstrated (Fig. 1). Five hypotheses relating oceanographic conditions to the origin these patterns can be formulated: a) gene flow and immigration of species from the IAA in the South Equatorial Current (SEC) and accumulation of these in the WIO (90% Indo-Pacific species); b) complex eddies in the Mozambique Channel result in high retention of larval material, high connectivity and high species richness within the channel; c) declining diversity north (and south) are a result of both dispersal and reduced water and habitat quality for corals associated with the Somali and Agulhas current systems (north and south, respectively); d) the main flow of the SEC and counter current/gyre systems result in isolation and low diversity of islands north (Seychelles) and south (Mascarene islands) of the SEC; and e) exchange with the northern Indian Ocean is due to current reversals and monsoon fluctuations in the Somali Current system.

Table 2. Major events during the Cenozoic hypothesized to affect the coral reef and shallow marine biota of the Western Indian Ocean. The most important influences are highlighted in shading. Date units are millions of years before present. See main text for abbreviations.

			Dates	Plate Tectonics	Tethys Sea	Hotspot	Climate	Currents	Species
Quarternary		**Holocene**	present		No exchange between Indian and Atlantic Oceans		Glacial cycles - rapid sea level and temperature fluctuations		Dominance of I-P diversity patterns by IAA and West Pacific species
		Pleistocene	0.02-1.6						
Tertiary	Neogene	**Pliocene**	1.6-5.3	Current configuration reached.		Reunion (2 mya)		Likely establishment of E-W connectivity	
		Miocene	5.4-23	Full development of IAA	Closure of Tethys Sea, by 15 mya	Mauritius (7-8 mya)	Low pCO_2, increase in glaciation/cooler temps		Diversity hotpot developing in IAA
	Paleogene	**Oligocene**	23-36	Collision of Asian and Australian plates (25 mya) Collision of India with Asia (35 mya)	Progressive narrowing and blockage of Tethys Sea	WIO/central IO banks (30-45 mya)	Oligocene cooling, start of Antarctic ice caps	E-W flow obstructed by India & Mascarene plateau	Diversity hotspot in Arabian region (EAAP)
		Eocene	36-55	Period of rapid northward migration of India			Hot, high CO_2, no polar ice caps		Diversity hotspot in West Tethys.
		Paleocene	55-64			Lakshadweep and Maldives			‘Paleogene gap’ in fossil record
Cretacious-Tertiary (K-T) boundary			64-67	India in mid-position NE of Madagascar	End of dominance of Tethys	Deccan Traps Large Igneous Province	Rapid climate changes		Extinction of up to 30% of marine genera

The paraphyletic nature of many coral genera and families (Fukami et al. 2008), and unclear species boundaries within seemingly well-known species and genera (see Veron 1995) are opening up new questions of phylogeography among corals (Table 1). Of interest here is an apparent phylogenetic relatedness between Atlantic and IO corals in contrast to the Indo-Pacific relationship that is dominant in the literature. The genera *Siderastrea* and *Stylophora* point to Atlantic-Indian Ocean relatedness that is ancestral to Indo-Pacific ties. The family Meandrinidae is predominantly Atlantic in distribution, except for the monospecific endemic genera *Ctenella* and *Gyrosmilia* in the WIO and a poorly known species from NW Australia..

Historical speciation and extinction associated with the Tethys Sea has been discussed for the genus *Acropora* (Wallace 2000), with significant parallels with the history of the clam subfamily Tridacninae (Harzhauser et al 2008). The earliest *Acropora* fossil is from the EAAP of the Eocene (Somalia, Carbone et al. 1994) followed by radiation of 9 of the 20 currently recognized species groups in the West Tethys in the Eocene (Wallace and Rosen 2006), and subsequent eastward migration and further diversification during the Miocene in the IAA and surrounding regions. The Tridacninae had a diverse fauna in the Eocene with 5 genera and 15 species in the West Tethys, compared to 2/9 in the Indo-West Pacific today (Newman & Gomez 2000). The West Tethyan populations suffered local extinction as the Tethys closed (see Rögl 1998) but established a foothold in the EAAP in the Oligocene, then as this also closed, migrated to the IAA center of diversity in the Miocene and Quaternary (Harzhauser et al. 2008). Unlike the acroporids, however, they did not diversify in the IAA.

The monospecific genera of corals in the IO appear to have followed the same fate as the Tridacninae. The WIO endemics show a range of geographic extents from highly restricted (e.g. *Ctenella chagius*, *Craterastrea laevis*) to wide-ranging but rare (e.g. *Gyrosmilia interrupta*, *Horastrea indica*), variation consistent with relict species rather than neo-endemics (Bellwood and Meijer 2008), or late stages in the ‘taxon cycle’ (Ricklefs 2011) where species persist in isolated pockets of once-larger distributions, applied in this case at the scale of an ocean basin and tens of millions of years. In this interpretation, like the Tridacninae, these coral lineages apparently ‘stalled’ in the EAAP in the Oligocene, failing to take advantage of new evolutionary opportunities available in the subsequent center of diversity in the IAA, and/or lacking genes or adaptive traits enabling such radiation.

Stages in the geological and oceanographic history of the WIO of relevance to this thesis are presented in Table 2. At the beginning of the Cenozoic, the K-T extinction drove an estimated 30% of marine genera to extinction. Following this, during the Eocene the shallow margins of the West Tethys Sea contained the largest buildup of carbonate platforms (though largely of benthic foraminifera) and highest diversity of shallow marine species, in what is now North Africa and Europe. During the Oligocene, as the Tethys progressively closed (Rögl 1998), the center of diversity and carbonate platform development migrated east (Renema et al. 2008) to the Arabian/Middle Eastern region (the EAAP in Harzhauser et al. 2008), though little fossil evidence from this period has so far been reported from East Africa. At this time, though substantial shallow banks were being formed by plate collisions in the IAA region, conditions for reef corals were poor, and they were predominantly foraminiferal (Wilson and Rosen 1998). Finally, during the Miocene, the shallow seas in the Arabian region were obliterated as continental collision progressed, erasing this center of diversity as diversification in the IAA began and the current diversity hotspot now referred to as the Coral Triangle (Hoeksma 2007) emerged.

The above patterns suggest the following major steps in faunal origins of the WIO, illustrated in fig. 2. First, as the Tethys Sea closed, the EAAP (and eventually just the East African/WIO part of it) was the main refuge for Tethyan species on its eastern side, and subsequently formed the main global diversity hotspot of the time (Renema et al. 2008). Further, during the migration of India northwards, and with the formation of the central Indian Ocean banks produced by the Mascarene hotspot, the WIO was likely more isolated than it is today from the eastern Indian Ocean and West Pacific (WP). Thus, with the extinction of the Arabian shallow seas following the Oligocene, the WIO may have played the role of a 'museum', preserving relict Tethyan lineages that disappeared from both the West Tethys and EAAP as these seas disappeared as a result of tectonic processes. Second, in the late stage of geological formation of the IAA (mid-late Miocene), it is likely that the present configuration of ocean currents became established, with the SEC conveying species from the IAA westwards to East Africa. This is reflected in the overarching faunal similarity in Indo-Pacific coral reef fauna that has established the biogeographic paradigm to date (e.g. Wells 1956, Veron 2000), and the 90% of coral species in the WIO with broad Indo-Pacific distributions (Obura in review).

Present patterns in reef fish and molluscan diversity broadly mirror this pattern of a dominant Indo-Pacific fauna, and a subordinate distinct west Indian Ocean one. For reef fish approximately 25% of species in the Indian Ocean (and West Pacific) are endemic (Allen 2000), with the rest being widespread in the Indo-Pacific. Among molluscs, the Red Sea is strongly differentiated from the Indian Ocean, having the highest number of endemics (51), followed closely by the West Pacific (49) and then the WIO (44) (Wells 2000).

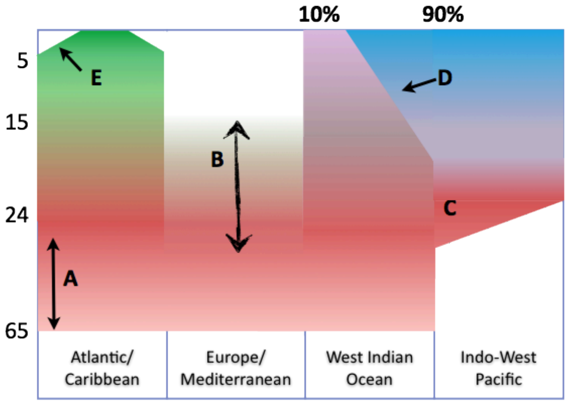

Figure 2: Schematic of evolutionary phases affecting the Western Indian Ocean. The y axis shows an approximate timeline in millions of years before present. Note that the y axis is not to scale, and vertical alignments of features in the figure are approximate. Annotations in the figure: A-evolutionary change in the Tethys Sea (West Tethys and EAAP) during the Paleogene; B- progressive closure of the Tethys Sea during the Miocene (25-15 mya); C- eastward invasion of species from the Tethys/EAAP to the newly forming IAA before and during the Miocene (≈24 mya); D- westward invasion of the WIO by West Pacific species in the South Equatorial Current; and E- closure of the isthmus of Panama at the start of the Pliocene (5 mya). The numbers at the top illustrate the composition of IO and Indo-Pacific species recorded in Obura (in review). Figure adapted from Wallace and Rosen 2006.

This focus on older (tens of millions of years) evolutionary history contrasts with recent work that has focused on Plio-Pleistocene drivers of diversification (e.g. Potts 1985), and genetic studies that emphasize more recent evolutionary change (e.g. Carpenter et al. 2011). Further, this provides some corroboration to earlier findings suggesting a second center of dispersion for Indian Ocean corals due to the presence of genera not found more broadly in the Indo-Pacific (Rosen 1971, Pichon 1978).

In contrast to the dynamism of diversity hotspots in tectonically active regions, the WIO shows interesting contrasts suggesting long-term stability. First, it is tectonically relatively inactive, with crustal ages as old as 180 mya in the Mozambique channel, and no plate collisions. Second, the East African and Madagascar coasts are relatively steep, so sea level fluctuations over the course of the Cenozoic and in the Plio-Pleistocene would have had relatively minor effects on habitat migration, connectivity and speciation/extinction processes. There is also no evidence of large carbonate platforms in the WIO during the Cenozoic, emphasizing the lack of extensive shallow seas associated with active tectonic margins and their association with hotspots (Renema et al. 2008). Third, the Africa/Madagscar region has migrated northwards about 15° during the Cenozoic, potentially tracking the narrowing tropical belt during Oligocene cooling, thereby providing an unusually stable climate for shallow marine species for a large part of the Cenozoic. Finally, activity of the Mascarene hotspot during the Cenozoic, throwing up a string of emergent islands and banks separating the east and west sides of the Indian Ocean may have reduced connectivity, resulting in genetic isolation of the WIO, effectively impeding the invasion of species from the east. The combined effect of all of these factors may be that the northern Mozambique channel in particular, and the WIO in general, may have presented a constant refuge environment throughout the Cenozoic, serving as a museum for Tethyan species as diversity hotspots hopped from the West Tethys to the EAAP and thence to the IAA.

Two corollaries of this thesis are: a) whether existing high connectivity across the IO will lead to full homogenization of the Indo-Pacific fauna and extinction of the WIO Tethyan relicts, a corollary of the hypothesis presented here, or if obliteration of the IAA by continued continental collision will happen first. Whichever of these occurs, b) will the WIO continue to be a museum for older lineages while the IAA disappears and the next biodiversity hotspot establishes in a new region of tectonic collision?

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