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Biogeographic responses to geodynamics:
A key study all around the Oligo–Miocene Tethyan Seaway ☆

Mathias Harzhauser[a],[*], Andreas Kroh[a], Oleg Mandic[a], Werner E. Piller[b],
Ursula Göhlich[a], Markus Reuter[b], Björn Berning[b]

[a]Natural History Museum Vienna, Burgring 7, A-1010 Vienna, Austria
[b]Institute for Earth Sciences, Geology and Palaeontology, Graz University, Heinrichstrasse 26, A-8010 Graz, Austria

Abstract

Extensive terrestrial exchanges were initiated by the closure of the Tethyan Seaway during the Early Miocene. Proboscideans are among the most prominent African immigrants, which arrived in Eurasia about 19 Ma ago via the "*Gomphotherium* Landbridge". Several distinct waves of continental migrations, however, document that the formation of this landbridge was a multiphase process. Until the closure, a marine faunal exchange was enabled via the Mesopotamian Trough and the Zagros Basin, as reflected by contributions of Indonesian corals in the Iranian basins and by the occurrence of "western" gastropods in Pakistan and India. Nevertheless, the emergence of the landbridge was preceded in the marine biosphere by first biogeographic divergences on both sides of the seaway already during Oligocene times (e.g. within the tridacnines and strombids). Around the closure event, the breakdown of biogeographic relations was near-complete and the Proto-Mediterranean faunas bear little in common with those of the Indo-West Pacific Region (IWPR). Some of the discussed examples suggest that the Western Tethys Region (WTR) had acted as centre of origin and diversity during Oligocene and Early Miocene times. After the closure of the seaway, this centre had shifted to the southeast, heralding the enormous biodiversity of the modern IWPR. Some originally WTR elements managed to follow this shift and formed the Miocene stock for the modern IWPR faunas. In contrast, the marine fauna in the Mediterranean cul-de-sac suffered strong impoverishment due to the Miocene cooling, the Messinian Salinity Crisis and the late Pliocene and Pleistocene glacials – a fact which might explain the receptivity of the Mediterranean Sea for Lessepsian migrants.

This synthesis tries to document the practical problem of recognising biogeographic patterns despite the heterochronous developments in different systematic groups, which, in addition, are often obscured by a stratigraphically incomplete and geographically patchy fossil record.
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1. Introduction

The Cenozoic history of the circum-Mediterranean area was strongly influenced by the Alpidic orogenies, which caused tectonic compression and fusion of numerous microplates between Europe and Africa. As a consequence of this compressive tectonic regime, Eurasia moved northwards and experienced considerable uplift (e.g. Tibetan Plateau, Alpine-Carpathian Chain, Anatolian Plate; see Kuhlemann (2003) for an extensive review). Simultaneously, the Eurasian ecosystems and landscapes were impacted by a complex pattern of changing seaways and landbridges between the Paratethys Sea, the North Sea and the Proto-Mediterranean Sea as well as the western Indo-Pacific (e.g. Rögl 1998; Popov et al. 2004). The geodynamic changes in landscapes and environments were further amplified by drastic climate changes during the Cenozoic (Fig. 1). The warm Cretaceous climate continued into the early Paleogene with a distinct optimum during the Late Paleocene and the Early Eocene. A gradual decrease in temperature during the later Eocene culminated in the formation of the first ice-sheets in Antarctica around the Eocene/Oligocene boundary (Zachos et al. 2001). A renewed warming trend that began during the Late Oligocene continued into the Middle Miocene with a climax at the Middle Miocene Climatic Optimum. The turning-point at around 14.2 Ma led to the onset of the Middle Miocene Climate Transition indicated by the cooling of surface waters and the expansion of the East-Antarctic ice-sheet (Shevenell et al. 2004). A final trend reversal during the Early Pliocene is reflected by a gentle warming until 3.2 Ma (Zachos et al. 2001) when the onset of permanent Arctic glaciation heralded the Pleistocene ice-ages.

During Oligocene and Early Miocene times, the Tethys connected two major oceanic areas, the Atlantic and the Pacific. Hydrogeographically, this seaway existed until the geodynamically induced closure of the Tethyan Seaway during the Burdigalian (Rögl 1998). Throughout the latest Cretaceous to the Early Eocene marine benthic invertebrate faunas in this area were characterised by a large number of taxa showing a wide geographic distribution (e.g. Harzhauser et al. (2002) for gastropods; Roman et al. (1989) and Kroh (2003a, b) for echinoids). Affinities between eastern and western coasts were even larger than between the northern and southern coasts (Popov 1993). The "Terminal Tethyan Event" (TTE, Adams et al. 1983), which resulted in the disconnection of these two oceanic realms and brought about the "birth" of the Indian Ocean and the Mediterranean Sea, changed this situation. From the Late Eocene to Early Oligocene onwards affinities between European/North African and West Indian/East African faunas began to decline (e.g. Roman et al. 1989). Although the precise dating of the disconnection and when it started to affect faunal migration is still under discussion (Jones 1999; Harzhauser et al. 2002 and references therein), most authors agree that with the beginning of the Middle Miocene each region had developed its own distinct biota. While the evolution of the marine biota of the Mediterranean Sea and its palaeobiogeography are well known, and has been in the focus of scientific studies since the early 19th century, marine biota of the "other" side, the Western Indian Ocean, are comparatively poorly known (Fig. 2). Taxonomic studies were mainly based on material collected occasionally during mapping or oil exploration. Indeed, recent attempts to date precisely the TTE have been severely hampered by the lack of well-dated marine invertebrate faunas of this region (Adams et al. 1983; Jones 1999; Harzhauser et al. 2002). The persistence of Mediterranean biotic elements on the Arabian Peninsula and along the East African coast during the Late Oligocene and Early Miocene (Ali 1983a, b; Ali and Cherif 1987; Harzhauser 2007) and the relation of faunas of East Africa to those of Western India/Pakistan is an important topic in this context. New biostratigraphic data on Greek (Wielandt-Schuster et al. 2004), Turkish (Mandic et al. 2004), Egyptian (Abdelghany and Piller 1999; Mandic and Piller 2001; Schuster 2002a, c), Iranian (Schuster and Wielandt 1999; Reuter et al. submitted), Pakistani (Müller 2002), Omanian (Harzhauser 2007) and Javanese faunas (van den Hoek Ostende et al. 2002) now allow a more precise evaluation of the biogeographic responses to the closure of the Tethyan Seaway. Herein, we aim at demonstrating how marine faunas of adjacent biogeographic areas may develop around gradually emerging landbridges. Biogeographic divergence in marine communities is discussed to herald the final establishment of geographic barriers.

2. Mollusc-based Tethyan Biogeography in the Oligocene and Miocene

The term "Tethys" was introduced by the Austrian geologist Suess in 1893 as a palaeogeographic entity. The geographically and tectonically defined Tethys was subsequently divided into a mainly Paleozoic Palaeo-Tethys, and a Mesozoic to Cenozoic Neo-Tethys (Hsü and Bernoulli 1978; Sengör 1998). The latter was initiated during the Permian as a narrow ocean basin on the eastern part of Gondwana. During the Triassic and Jurassic it widened significantly and achieved the typical triangular outline, limited by the European, Anatolian, Iranian and Tibetan plates in the North, by the Arabian Plate, the Zagros shelf, and India in the west and southwest, and by Australia in the south (Sengör 1998). This tectonically defined Tethys, however, vanished already during the Eocene when India collided with Laurasia. Herein, as we focus on biogeography, we refer
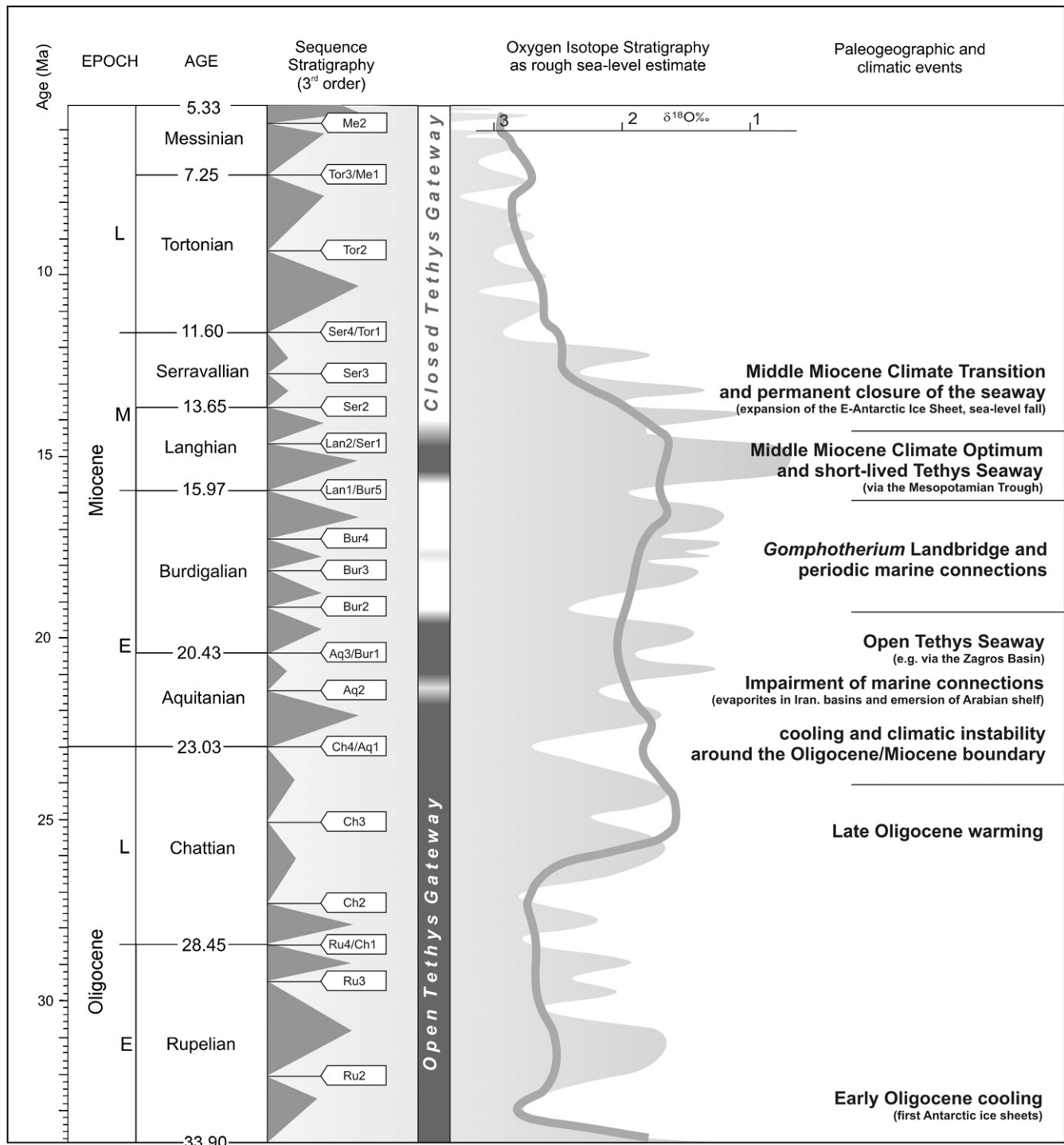
Fig. 1. Oligocene and Miocene stratigraphy after Gradstein et al. (2004) with 3rd-order sequence stratigraphy after Hardenbol et al. (1998) and oxygen isotope stratigraphy after Abreu and Haddad (1998). The grey line represents the smoothed isotope curve of Zachos et al. (2001). These isotope records are a rough reflection of temperature and the sea level. The column on open Tethyan Seaway versus closure phases is based on Rögl (1998) and own results. Palaeogeographic and climatic events are summarised from Shevenell et al. (2004), Zachos et al. (2001), Rögl (1998), Spezzaferri (1995), and Harzhauser et al. (2002).

to the biogeographic Tethys Realm as introduced by Kauffman (1973) for Mesozoic faunas. Kauffman's Tethys Realm is based on Cretaceous bivalves and represents a vast, circum-equatorial area. For the

Cenozoic era the biogeographic term Tethys Realm was defined by Popov (1993) and Harzhauser et al. (2002), and was divided in two regions: Indo-African Region and Mediterranean Region. At that time (Paleocene–Eocene)

1 France (Oligocene, Early Miocene) - E Atlantic
2 N-Italy (Oligocene, Early Miocene) - N Tethys
3 Austria & Hungary (Oligocene, Early Miocene) - Paratethys*
4 Romania (Oligocene) - N Tethys/Paratethys transition
5 Bulgaria (Oligocene) - N Tethys
6 Greece (Oligocene, Early Miocene) - N Tethys*
7 Maltese Islands (Oligocene, Early Miocene) - S Tethys*
8 Turkey, Sivas Basin (Early Miocene) - N Tethys*
9 Turkey, Mut Basin - N Tethys*
10 Armenia (Oligocene) - N Tethys
11 Egypt, Gineifa-Gharra Basin (Early Miocene) - S Tethys*
12 Iran, Qom Basin (Oligocene, Early Miocene) - NE Tethys*
13 Iran, Esfahan-Sirjan Basin (Oligocene, Early Miocene - NE Tethys*)
14 Oman (Oligocene, Early Miocene) - SE Tethys*
15 Pakistan (Oligocene, Early Miocene) - NE Tethys
16 Somalia (Oligocene, Early Miocene) - SE Tethys
17 Java, Borneo (Early to Late Miocene) - Pacific

* these faunas have been investigated in own projects

Fig. 2. Important sections and areas with shallow marine Oligocene and Miocene faunas of the Tethys and Indo-West Pacific (for details see Harzhauser et al. 2002; Schuster 2002a; Kroh 2005). The distribution of localities, following roughly the northern and southern coasts of Tethys, shows the considerable lack in information concerning such crucial areas such as the Mesopotamian Trough, Arabia, eastern Africa and western India. Aside from political reasons, which complicate fieldwork in some of these areas, the fact that Oligocene and/or Lower Miocene deposits are simply missing in many regions reveals the basic problem in historical biogeography.

the southern Tethyan faunas of Egypt, Somalia and India displayed highest resemblance, but differed clearly from the northern Tethyan ones from Italy and south-eastern France. Despite the narrowing of the Tethys Ocean north of the Indian shield, a new southern seaway and the ancestral Indian Ocean widened. This seaway warranted a continuous connection of the western and eastern tropical Tethyan faunas, hence allowing to extend the biogeographic term Tethys Realm also for Oligocene and Early Miocene times. This biogeographic unit vanishes irretrievably with the formation of the *Gomphotherium* Land-bridge between Eurasia and the Arabian Plate in the late Burdigalian at approximately 19 Ma (Rögl 1998).

2.1. The open Tethyan Seaway (>approx. 19 Ma)

Based on the shallow marine gastropod faunas, Harzhauser et al. (2002) and Harzhauser (2007)

proposed a detailed biogeographic scheme for the Oligocene and Miocene Tethys Realm (Fig. 3). According to their concept, the Tethys Realm was composed of two major biogeographic compartments, namely the Western Tethys Region (WTR) and the Proto-Indo-West Pacific Region (PIWPR), during the Oligocene and Early Miocene. The WTR was composed of the Mediterranean-Iranian Province (MIP) in its core area. In the West, the Eastern Atlantic Province (EAP) was already forming a transitional zone to faunas in the North Sea. For the eastern part of the WTR, Harzhauser (2007) proposed two provinces, which are termed the Western Indian Province (WIP), comprising marine faunas in Pakistan and N and SW India, and the Eastern African-Arabian Province (EAAP), represented by faunas on the Arabian shelf and in eastern Africa. Thus, the WTR reached to Pakistan, Somalia and Zanzibar in the east and south, respectively, and was bordered at its eastern margin by a major biogeographic
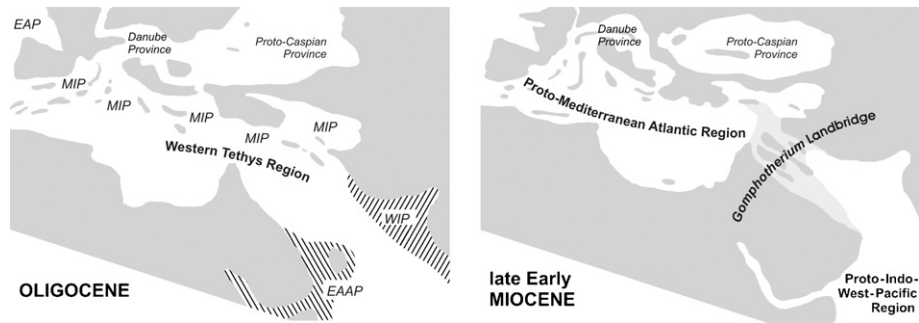
Fig. 3. Palaeogeography and mollusc-based biogeography of the Western Tethys during the Oligocene and Early Miocene (geography modified from Rögl (1998), Popov et al. (2004) and Harzhauser and Piller (2007); biogeography after Harzhauser et al. (2002) and Harzhauser (2007)). Note that the selected time slices are only snapshots from a much more complex palaeogeographic development as reflected by the numerous maps presented by Rögl (1998) and Popov et al. (2004). *Abbreviations*: MIP – Mediterranean-Iranian Province, EAP – Eastern Atlantic Province, WIP – Western Indian Province, EAAP – Eastern African-Arabian Province.
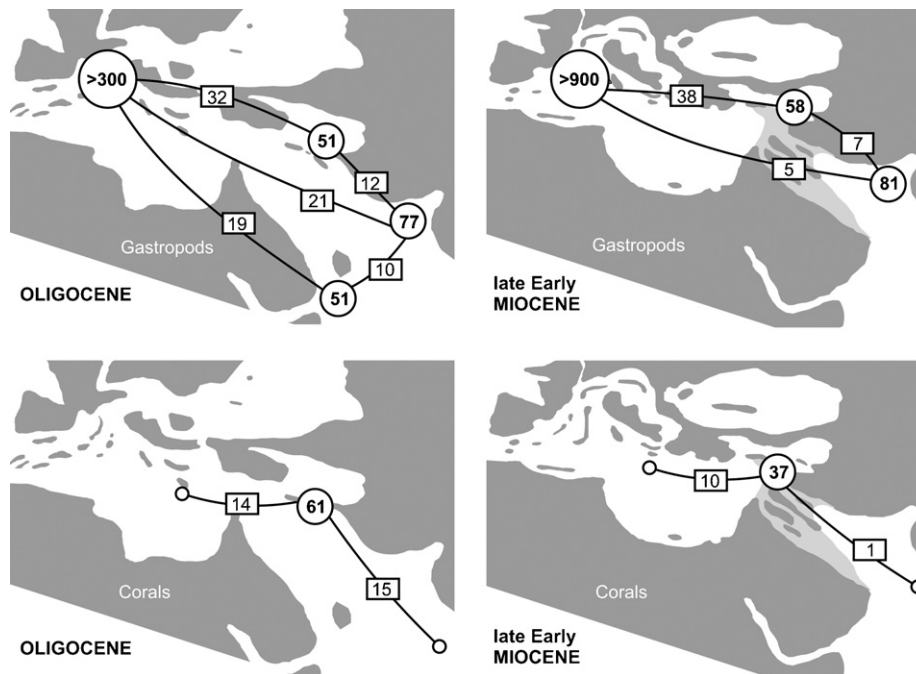

Fig. 4. Species level relations of selected Western Tethys faunas (gastropods from Harzhauser et al. (2002a) and Harzhauser (2007); scleractininan corals from Schuster 2002a–e). Circles indicate total numbers of species, rectangles represent the number of species occurring in both faunas. During the Oligocene, the broad Tethyan Seaway enables a good faunal exchange. The gastropod faunas of the WIP and EAAP have 30–40% of their stock in common with the MIP. The coral reefs in the Iranian basins are contributed in equal amounts by western and eastern faunas. With the rise of the *Gomphotherium* Landbridge the eastern part became disconnected and the take-over by elements from the Indo-West-Pacific Region is reflected by a decline of species that occur also in the Proto-Mediterranean Sea.

unit inhabited by early Indo-Malayan faunas, which represent members of the Proto-Indo-Polynesian Province (PIPP) of the PIWPR (Fig. 3).

Despite the open Tethyan Seaway, the gastropod faunas of the Arabian shelf (EAAP) demonstrate the gradual biogeographic shift from Oligocene to Early Miocene times and are an example for biogeographic divergence that predates the development of a fully

emerged landbridge (Fig. 4). During the Oligocene, the EAAP faunas, settling on the southern Tethys shelf, are characterised by a frequency of 40% of western Tethyan elements. This contingent is even higher than on the north-eastern Tethyan coast where the WIP faunas have 27% common taxa with the MIP faunas. During the Aquitanian, the mollusc faunas of the Arabian shelf witnessed a takeover by PIPP elements and a strong

decline of western Tethyan elements down to 16%. At that time, the Zagros fault zone still formed a deep trench, which connected the MIP faunas in the west with those of the WIP and EAAP in the east. The biogeographic re-organisation is thus rather related to changes in current systems and to a beginning deterioration of migration potential across a very shallow and partly evaporitic shelf of the Mesopotamian Trough.

2.2. After the closure of the Tethyan Seaway (< approx. 19 Ma)

The pre-landbridge pattern vanishes completely during the Early Miocene, when faunistic similarities between the Pakistani faunas and those from the Proto-Mediterranean Sea crash to about 5% (Harzhauser et al. 2002; Fig. 4). In the west, a rather homogenous fauna of the Proto-Mediterranean-Atlantic Region (PMAR) develops. Within this area the data on gastropod faunas from France, Italy, Greece and Turkey show good correspondence during the Burdigalian, with about 80% of species in common (Harzhauser et al. 2002). At its eastern margin, in the central Iranian basins, 66% of the fauna are still composed of PMAR ubiquists. This homogeneity was also confirmed for larger benthic foraminifera (Jones 1999). Geographically, the extension of the PMAR corresponds largely to the limits of the modern Mediterranean-Atlantic Region (MAR) (see Briggs 1995), except for the Black Sea Province, which was not existent yet. The latter area was part of the Paratethys at that time, forming an own biogeographic unit (Danube Province) (Harzhauser et al. 2002).

The Early Miocene brought about drastic changes for the EAAP and WIP, which vanished as distinct units probably even before the closure of the Tethyan Seaway. The data on Pakistani molluscs from the Early Miocene Gaj Formation given by Vredenburg (1925–1928) reflect a strongly increasing influence by the fauna of SE Asia, and a rapid decrease of the WTR elements. Correspondingly, Azzaroli (1958) and Harzhauser (2007) mentioned in the Early Miocene faunas of Somalia and Oman some influence from Indonesia, although this fauna still had some species in common with Italian localities. Hence, the separation of gastropod faunas of the eastern African and the western Indian coastal areas from those of the WTR core already took place during the Early Miocene. Since the faunas of this area have a clear "Indo-Pacific" character and bear high percentages of Indonesian species, they may be treated as western part of an early stage of the Indo-West Pacific Region (IWPR) (sensu Briggs 1995). The biogeographic separation between the Mediterranean-Atlantic and the IWPRs remained stable since the late Early Miocene despite a short-lived marine connection during the

Langhian. This revival of the Tethyan Seaway was probably related to a sea-level rise during the Middle Miocene Climate Optimum (Fig. 1; Zachos et al. 2001).

A second impact on Proto-Mediterranean-Atlantic mollusc faunas was the Messinian Salinity Crisis in the latest Miocene, when the marine fauna of the Mediterranean basins was strongly impoverished (Hsü et al. 1978). The gastropod fauna of the Mediterranean basins probably vanished completely because there are no indications that any fully marine fauna survived this event. All studies that suggest refuges for certain taxa within the Mediterranean neglect the fact that these faunas occurred in the eastern Atlantic as well (e.g. Berning 2006). After the salinity crisis the Mediterranean basins were re-colonised from the Atlantic but already lacked several Tethyan relics (see Harzhauser et al. (2002) for details). Hence, the post-Messinian fauna seems to represent rather the ancestral, warm-water stock of the modern MAR. Finally, the cooling events during the Late Pliocene and Pleistocene caused the final transformation into the modern MAR.

3. Biogeographic patterns and trends around the Tethyan Seaway

Within this biogeographic framework, we have chosen several exemplary terrestrial and marine groups in order to document biogeographic traits and processes, which are related to the emerging biogeographic barriers such as the *Gomphotherium* Landbridge.

3.1. The *Gomphotherium* Landbridge – African-Eurasian faunal exchange

Until the Early Miocene, the open Tethyan Seaway hindered land mammals to migrate between Africa and Eurasia to a large extent (but see Lange-Badré and Böhme (2005) for pre-Miocene migrations). The collision of the Afro-Arabian plates with Eurasia during the mid-Burdigalian caused the emergence of a terrestrial corridor, called the "*Gomphotherium* Landbridge" (Rögl 1998, 1999). This landbridge allowed a faunal exchange between Africa and Eurasia. Because the palaeontological terrestrial index-fossils of this event were proboscideans, the dispersal was also called the "Proboscidean Datum Event" (Madden and van Couvering 1976). Subsequently, this event was recognised to be composed of multiple immigration events (Tassy 1989, 1996; Koufos et al. 2003). Proboscideans were supposed to be endemic to Africa during the Paleogene. Primitive elephantoids reached the Indo-Pakistani subcontinent during the earliest Miocene about 21–22 Ma (Tassy 1989; Lukas and Bendukidze 1997) – or perhaps earlier, as recently scanty evidence for the presence of

elephantoids was also found from the Late Oligocene of Pakistan (Antoine et al. 2003). This implies that the first, short-lasting migration corridors evolved already during the Aquitanian. The main wave of migration, however, started during the late Burdigalian. The first arrivals in Europe are gomphotheres (*Gomphotherium* Burmeister, 1837), deinotheres (*Prodeinotherium* Ehik, 1930) and mammutids (*Zygolophodon* Vacek, 1877) at the end of the Mammal Neogene Zone MN3 (Mein 1975, 1999; Tassy 1989; Koufos et al. 2003) dated at 19–18.5 Ma (Steininger 1999). Just shortly after, during the Mammal Neogene Zone MN4, amebelodontids (*Archaeobelodon* Tassy, 1984) appeared in Europe. This second wave of proboscidean immigration took place between 18 and 17.5 Ma (Steininger 1999).

Geographic and temporal data of migrations of other land mammals are presented by van der Made (1999). At the beginning of the MN3 several taxa dispersed from Africa into the Indian subcontinent and vice versa. Simultaneously with the first proboscideans, at the MN3/MN4 boundary, the creodont *Hyainailouros*, of African origin, and the rodent *Democricetodon*, of Anatolian origin, dispersed into Europe. A second wave of African emigrants during MN4 brought the chalicothere *Chalicotherium*, the suid *Bunolistriodon*, and the tragulid *Dorcatherium* to Europe (van der Made 1999).

3.2. Go east! – The shift of the Tethyan centre of origin illustrated by the tridacnine experiment

The tridacnine bivalves appear in the Eocene, represented by about 10 species of the genera *Goniocardium* Vasseur, 1880, *Avicularium* Gray, 1853 and *Byssocardium* Munier-Chalmas in Fischer, 1882 (see Schneider (2002) and Harzhauser et al (2007) for reviews and references). This species diversity is roughly equivalent to that of extant tridacnines (Fig. 5). It is noteworthy, however, that these Paleogene tridacnines evolved in the eastern Atlantic (Normandy) and only subsequently started to establish their centre of diversity in the western part of the Western Tethys (France, Italy, Bulgaria). Nevertheless, already during the Oligocene the diversity collapsed in this region and only a single species of *Avicularium* is recorded in the WTR (Harzhauser et al. 2007), being a common element of the EAP and the MIP. Simultaneously, the tridacnines managed to expand their range towards the east for the first time, documented by the first occurrence of *Omanidacna eos* Harzhauser and Mandic, 2007 (in Harzhauser et al. 2007) in the Oligocene of the Arabian shelf. Despite that distributional pulse, however, they never managed to colonise the Proto-Eastern Atlantic-Boreal Region in the northwest or the Danubian Province of the Parathethys Sea in the northeast. The Early Miocene brought about the biggest crisis of
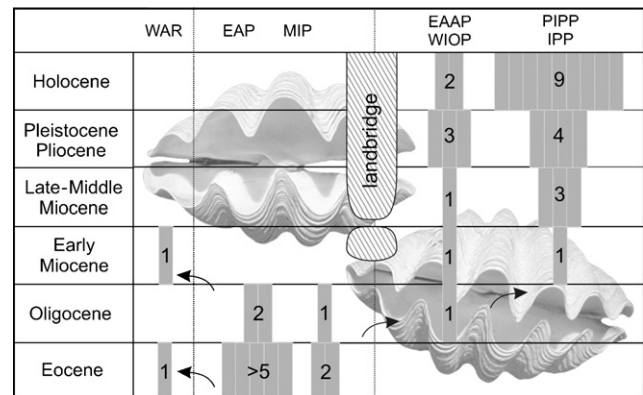

Fig. 5. Biogeographic evolution of the tridacnines (based on Schneider 2002; Harzhauser et al. 2007). Within the Western Tethys Region, an Eocene maximum of diversity is recorded from the Eastern Atlantic Province. During the Oligocene, the diversity declines and the first species appears in the East African-Arabian Province (EAAP). During the Miocene, a buildup phase starts and the centre of diversity shifts from the EAAP to the Proto-Indo-Polynesian Province (PIPP). After the Miocene, the centre moves further from the Western Indian Ocean Province (WIOP) into the Indo-Polynesian Province (IPP). The tridacnines managed to extend their range even across the Atlantic and appear at least twice in the Western Atlantic Region (WAR).

tridacnine evolution, as the group became extinct in the EAP and the MIP. Only the Arabian shelf, where the first *Tridacna* is recorded from the Early Miocene, acted as refuge, while they do not appear in the Oligocene and Early Miocene of the WIP (e.g. Pakistani and Indian faunas in Vredenburg (1925–1928) and Dey (1961)) or in coeval deposits of the PIPP (Martin 1899, 1905, 1906, 1916, 1921; Fig. 5). Only during the Middle Miocene the centre of tridacnine diversity gradually moved eastwards and seems to be established in the PIWPR not before the Late Miocene when first modern *Tridacna* and *Hippopus* species are known from Java and Borneo (Beets 1986). A modern pattern of distribution is not developed before the Pliocene and Pleistocene, reflecting the final shift of the centre of diversity into the western Pacific (Harzhauser et al. 2007). The fossil record of the tridacnines is thus a good example for the gradual eastward migration of an originally Tethyan group, arriving in the IWPR during the late Neogene.

The clear vector of migration towards southeast was most probably stimulated by the post-Eocene climate deterioration (Zachos et al. 2001), accentuated by the simultaneous tectonic northward shift of Europe and Africa (Marton et al. 2003). The latest Oligocene cooling (Spezzaferri 1995; Zachos et al. 2001) might have been the deathblow for the tropical tridacnines in large parts of the WTR. Later, when the global Middle Miocene Climatic Optimum would have enabled the re-conquest of the former distribution area, theses bivalves did not

manage to re-immigrate into this region. The reason why this short-lived connection was not passable for the tridacnines is not understood.

3.3. Go east! – Tethyan migrants that failed in the IWPR

One reason for the successful establishment of tridacnines in the PIWPR was probably owing to their exceptional symbiosis with photosynthetic algae, which allowed them to explore a new ecological niche. In contrast to these very successful invaders, the Tethyan strombids may have had to compete for the same ecological niche with already established PIPP strombids when extending their area. Again, the fate of these immigrants seems to be linked with the development of the Tethyan Seaway (Fig. 6). An example for an ultimately unsuccessful invasion is the huge strombid *Dilatilabrum sublatissimus roegli* (Harzhauser, 2001). This taxon forms large populations in the MIP during the Late Oligocene and was also established as *Dilatilabrum sublatissimus sublatissimus* (d'Orbigny, 1852) in the EAP. At that time, the warming allowed the formation of diverse reef systems along the northern coast of the Tethys (Schuster 2002a, b, d) and tropical mollusc faunas to flourish. The latest Oligocene cooling

Fig. 6. The *Strombus radix-bonellii-coronatus* species complex is the most successful strombid in the Western Tethys. It managed to invade the Western Atlantic Region (WAR) during the Miocene where it is represented today by *Strombus granulatus* (Lozouet and Maestrati 1986). After the permanent closure of the Tethyan Seaway, it was exposed to the Pliocene-Pleistocene cooling events but survived by repeated retreats into the Eastern Atlantic Region (EAR), where the lineage is represented since the Pleistocene by *Strombus latus* (Meco 1977). Like the tridacnines, this strombid group appears in the EAAP during the Oligocene and subsequently invade the Proto-Indo-Polynesian Province during the Miocene. Despite the less severe impact of climate changes in the vast Indo-West-Pacific Region, the eastern offshoot became extinct already during the Miocene. A reason for the extinction of that Tethyan element might have been the evolutionary pressure by modern strombids.

forced *Dilatilabrum* to retreat to a refuge in the SE Western Tethys (Qom Basin and Esfahan-Sirjan Basin) where it managed to persist into the Early Miocene. At that time it even reached the EAAP (Harzhauser 2004, 2007). *Dilatilabrum* became extinct soon after and is unknown from the Burdigalian. Like the tridacnines, this strombid reached the EAAP but could not use this bioprovince as stepping stone into the PIPP, where its potential ecological niche seems to have been already occupied by several modern strombid genera (Abbott 1960; van den Hoek Ostende et al. 2002).

One Tethyan strombid lineage, which did manage to spread into the PIPP, is represented by the *Strombus radix-bonellii* group (Fig. 6). This species complex appeared during the Oligocene in the Western Tethys (MIP and EAP) and gave rise to a Late Oligocene to Early Miocene offshoot lineage in the EAAP (*Strombus bernielandaui* Harzhauser, 2007; *Strombus gijskronenbergi* Harzhauser, 2007). The descendant *Strombus preoccupatus* (Finlay, 1926) represents the next step towards the east and appeared in the Java-Borneo archipelago during the Middle and Late Miocene but became extinct thereafter. An ad hoc explanation for its disappearance may be that at that time the centre of origin was already established in the PIWPR (as indicated by the rich faunas described by Martin 1899, 1905, 1906, 1916, 1921). Therefore, like in *Dilatilabrum*, this Tethyan strombid lineage may have faced active competition with an array of modern strombids.
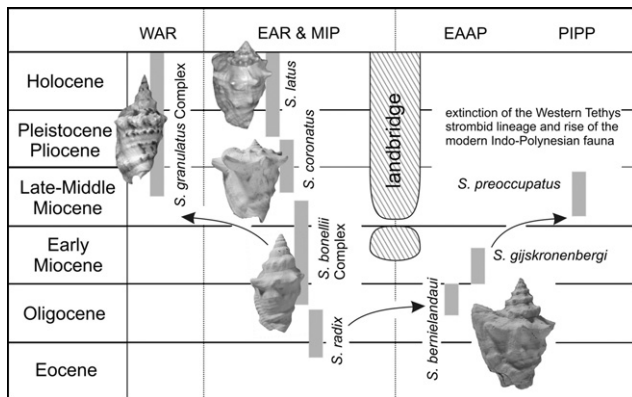
3.4. Pectinids around the Tethys Seaway – shifting diversities and parallel evolution

Pectinid bivalves are among the most frequent fossils in the late Cenozoic near-shore deposits, due to their diagenetically robust calcitic shell structure. In consequence to the major extinction event around the Cretaceous/Paleogene boundary (Waller 1991), the Paleogene pectinids went through a phase of a worldwide crisis and their diversity was low. Thereafter, the Neogene pectinid record reflects a drastic renewal and a complete recovery of the family lasting up to the present day (Raines and Poppe 2006).

The Oligocene pectinids still indicate reduced species richness (Fig. 7) in the entire Western Tethys. Despite extensive field collections only few taxa are known from the WIP (Vredenburg 1925–1928) and EAAP (Azzaroli 1958). Of these about 50% are widespread species in the WTR. The misbalance in species richness between the diverse MIP in the west and the low diverse faunas of the WIP and EAAP in the east suggests that the MIP acted as an early Cenozoic centre of origin for these shallow marine benthic bivalves.

Among several speciation and radiation pulses, particularly the Early Miocene one was essential for
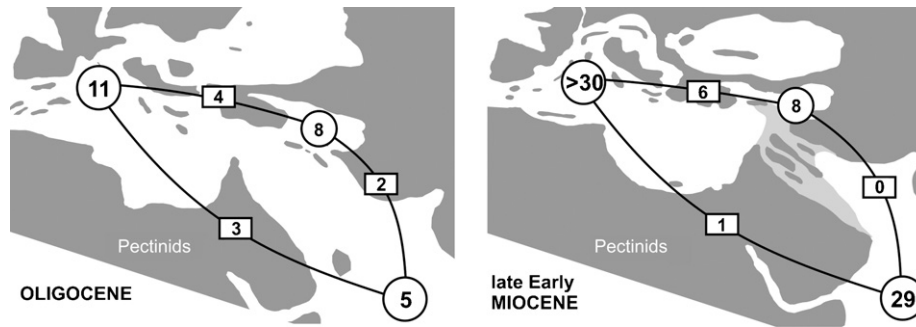
Fig. 7. Distributional patterns for pectinid bivalves based on Sacco (1897), Depéret and Roman (1902–1928), and Roger (1939) (see Fig. 4 for explanation and text for details).

the Neogene Western Tethys assemblage. That particular radiation resulted in taxonomically rich but disjunctive pectinid assemblages at the opposite flanks of the *Gomphotherium* Landbridge (Fig. 7). The only shared Early Miocene taxon between the MIP and the EAAP was *Crassadoma multistriata* (Poli, 1795), present in the region already before the closure of the Tethys Seaway (Eames and Cox 1956) and still living in the MIP and EAP. The pectinid bivalves, being highly sensitive to environmental perturbations, comprise mainly short-living species and such ancient, conservative taxa are exceptions.

In the easternmost tip of the MIP, in the Central Iranian basins, the pectinid fauna clearly indicates the existence of a physical barrier preventing any faunal exchange with the EAAP already in the middle Burdigalian (Reuter et al. submitted) (Fig. 7). Except for few endemic taxa, the assemblage comprises exclusively Mediterranean-NE Atlantic and Paratethys taxa (Mandic 2000). The giant Burdigalian taxa such as *Gigantopecten holgeri* (Geinitz, 1837) or *Amussiopecten expansus* (Sowerby, 1847) are widely distributed throughout the area (e.g. Mandic and Piller 2001; Mandic and Steininger 2003; Mandic et al. 2004) and represent the products of the MIP autochthonous evolutionary processes, additionally characterised by an overall body size and mass increase within the family. *Gigantopecten* Rovereto, 1899, in particular, with maximal disc length exceeding 200 mm, originated in the Early Burdigalian (Bongrain 1988) and never managed to reach the PIWPR. In contrast, *Amussiopecten* (Sacco 1897), showing circum-equatorial distribution already during the Oligocene (Waller 2006), went through a distinctive radiation at the southern side of the *Gomphotherium* Landbridge. Hence, solely the East African Early Miocene fauna comprises as many as six new species (Cox 1927, 1936; Eames and Cox 1956). Representatives of *Amussiopecten* are mobile active swimmers. To optimise the adaptation to this mode of life, at least two *Amussiopecten*-lineages independently reduced their exterior macrosculpture during the

Oligocene and Miocene (Waller 1991, 2006). This iterative evolutionary tendency in *Amussiopecten* resulted in the Miocene or Pliocene with the rise of *Amusium* Röding, 1798 as its direct and only offshoot (Mandic 2000; Beu and Darragh 2001; Waller 2006). *Amusium*, a true Indo-Pacific endemic genus, never managed to reach the MIP or EAP. In the MIP, however, the ecologic niche was filled during the Miocene and Pliocene by the *Amusium*-look-a-like pectinid *Costellamussiopecten cristatus* (Bronn, 1827), which evolved from *Aequipecten* Fischer, 1886 (Bongrain and Cahuzac 2004; Mandic 2004).

3.5. Echinoderms – indicators for a semi-permeable marine seaway?

From the few palaeobiogeographical studies (Roman et al. 1989; Smith 1992) on this group it becomes apparent that in the Late Cretaceous the fauna of the SW Arabian Peninsula was closely related to that of the Mediterranean area and belonged to the same biogeographic entity. In the Middle Eocene, however, affinities to the Pakistani/Western Indian echinoid fauna increased, while affinities to the Mediterranean faunas decreased. This is especially true for spatangoids, which have only one species in common between Dhofar (southern Oman) and the Mediterranean. In the Early Oligocene, affinities with Pakistan/Western India prevailed, whereas affinities to the Mediterranean greatly diminished. This indicates that the migration between the WTR and the PIWPR was becoming difficult well before the interruption of the Tethyan Seaway (Roman et al. 1989). Generally, at species level the Late Oligocene to Middle Miocene echinoid faunas of the Persian Gulf area display affinities to those of Pakistan/ Western India and more rarely to those of Indonesia (compare data presented in Douglas 1928; Clegg 1933; Kier 1972; Roman 1976), whereas at generic level affinities with the Mediterranean prevail (Rosen and Smith 1988). Still, the Early to Middle Miocene echinoid

faunas from East Africa (Somalia: Stefanini 1931; Socin 1956; Zanzibar: Stockley 1927; NE South Africa: King 1953) were reported to include species characteristic for the Mediterranean region, such as *Schizaster eurynotus*, *S. desori*, *S. parkinsoni*, *Pericosmus latus*, *Clypeaster martini*, and *C. latirostris* (see also Ali 1983a, b; Ali and Cherif 1987). If correct, these faunistic affinities might point to the possibility for echinoderms to have used the temporary connection between the Proto-Mediterranean and the Indian Ocean during the Middle Miocene Climatic Optimum (Fig. 1). This shallow marine and partly evaporitic connection via the Mesopotamian Trough (as indicated by Jones and Racey 1994; Jones 1999), however, seems to have been of little importance for the migration of mollusc faunas (Harzhauser et al. 2002).

The absence of Persian Gulf species along the East African coast points to a further biogeographic fragmentation in the EAAP. An explanation might have been a counter-clockwise circulation pattern in the early NW Indian Ocean, which would have prevented a successful northward larval dispersal. Current models for this region, however, suggest a clockwise circulation pattern (Barron and Peterson 1991). Moreover, the influence of temperature gradients, playing a major role in the distribution of mollusc and echinoderm taxa along the African coast today (molluscs: Kilburn and Rippey 1982; echinoderms: Samyn and Thandar 2003), is completely unknown for the Oligo–Miocene of East Africa. Thus, the still very poor database for this area (partly due to the absence of sediments) is a major problem for a detailed analysis.
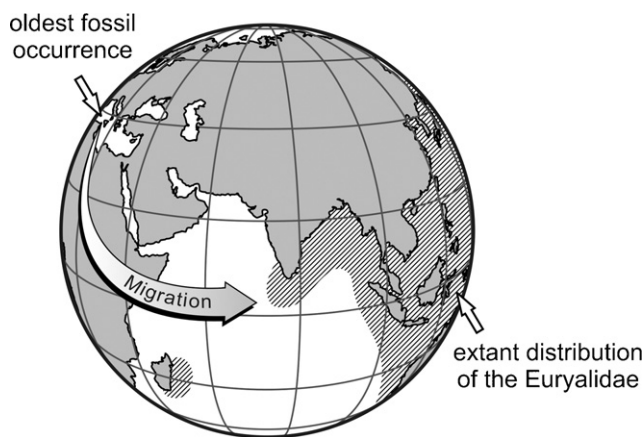

Fig. 8. The "snake stars" (Ophiuroidea: Euryalidae) are widespread in the Indo-Malayan Region and around Australia today. The earliest fossil representatives of this group are found in the Western Tethys region, from where they have migrated to the Indo-West-Pacific prior to the TTE. While they survived in the latter region, they went extinct in the Mediterranean and Atlantic. Modified from Kroh (2004, Fig. 4).

As observed for the molluscs, the WTR seems to have acted as centre of diversity in the Late Cretaceous and early Cenozoic also for echinoderms. This pattern might be partially attributed to various biases, in particular the long tradition of palaeontological research in Europe (see for instance Kowalewski et al. (2002) for the effects of intense study on palaeontological interpretation). Data from numerous unrelated echinoderm lineages (Fig. 8), however, suggests that the WTR acted as centre of origin for numerous taxa in the Eocene (e.g. many scutelline sand dollars: Seilacher 1979; Smith 1984; Roman 1990; loveniids: Kroh, 2007; clypeasteroids: Ali 1983b; echinolampadids: Roman 1977; gorgonocephalid basket stars and euryaline snake stars: Kroh 2003b, 2004; Kroh and Jagt 2006).

3.6. Scleractinian corals – contradicting the mollusc-based biogeography

The coral fauna of the Western Tethys and the Proto-Mediterranean has been revised in detail by Schuster and Wielandt (1999) and Schuster (2002a–e). According to these data, the Oligocene centre of diversity developed in the Iranian basins, where reef formation is contributed by 61 species of 39 genera (Schuster 2002b), whereas the western faunas (e.g. Greece) are less diverse and comprise about 31 species of 25 genera (Schuster 2002d; Fig. 4). Moreover, the Iranian fauna is considered by Schuster (2002b, p. 11) as an "experimental fauna consisting of old-fashioned Mediterranean Tethyan species and modern (Miocene) species from the Indo-West Pacific Region." The contribution of species from the Indonesian, East African and Pakistani faunas is about 30%. This pattern is different from that shown by the mollusc faunas, which display their Oligocene centre of diversity in the western part of the Western Tethys (e.g. France, Italy, see Harzhauser et al. 2002). However, selected taxa, such as *Acropora*, fit well to the "go-east" scenario of the molluscs and support the interpretation of the Western Tethys as Paleogene centre of origin (Wallace 1999, 2002; White et al. 2006). Nevertheless, the relatively high proportion of old-fashioned Western Tethyan scleractinian corals can be seen in accordance with molecular data pointing at a relatively great genetic distance between many modern scleractinian corals of the Indo-West Pacific and their Atlantic "cogeners" (Fukami et al. 2004).

During the Early Miocene, the biogeographic pattern of scleractinian corals became nearly identical to that displayed by molluscs. The diversity in the Iranian basins declined drastically (37 species, 25 genera; Schuster 2002e) and the composition of the Iranian fauna is comparable with other reef faunas in the PMAR (e.g. France, Turkey, Egypt, Libya, Algeria;

Schuster 2002a). Simultaneously, any relation with the IWPR vanishes completely.

3.7. Bryozoans – faunal turnover in the Mediterranean region

Even more than for other taxa, information on fossil bryozoan faunas is extremely sparse from regions east of the Mediterranean area, and from the Oligocene in general. Therefore, any interpretation of past biodiversity and biogeographic patterns as well as of relationships between Mediterranean taxa and those of the Western Indo-Pacific and SE Asia needs to be considered with great caution. Sampling has been very spotty in time and space, and described faunas usually consist of only a handful of taxa (e.g. Furon and Balavoine 1959; Tewari and Srivastava 1967; Braga and Bahr 2003; Guha and Gopikrishna 2005). Furthermore, as most modern genera have their first appearance in the Paleocene or Eocene, a great number of taxa was already widely distributed by the end of the Paleogene and especially so in the Neogene (e.g. Lagaaij 1968). At the species level, where such information could potentially be retrieved, the data are still too few and poor to be of any significance.

New findings of fossil faunas do, however, have significant impact on our knowledge of evolutionary and biogeographic patterns through time, and aid in interpreting modern distribution and genetic heritage. An example is provided by *Herentia* and *Therenia*, two closely related cheilostome genera, which today exclusively occur in the tropical to warm temperate Atlantic Ocean and Mediterranean Sea. As the first occurrence of *Therenia* was hitherto believed to be in the Late Eocene of western North America (David and Pouyet 1978), and because all other fossils were recorded from Atlantic and Mediterranean sites as well, these taxa were, until recently, thought to be restricted to this region throughout their history. However, Guha and Gopikrishna (2005) reported *Therenia indica* from the Middle Eocene of India, which shows several primitive traits and which may therefore be a possible ancestor, thus shifting the centre of origination from the western Atlantic towards the PIWPR. The widespread distribution of both *Therenia* and *Herentia* during the late Paleogene is furthermore confirmed by the presence of *Herentia* in the Late Oligocene of Germany (David and Pouyet 1978), and by the occurrence of both taxa in the MIP during the same time interval (B. Berning, own observation). Yet, after closure of the Tethyan Seaway, *Herentia* and *Therenia* became, for whatever reason, probably extinct in the Indo-Pacific Region and restricted to their present range of geographic distribution in the Atlantic and Mediterranean Sea.

A much clearer picture of a stepwise extinction of tropical taxa due to climate change is observed in the PMAR, paralleling the trend in scleractinian corals. Several genera of presumed Indo-Pacific origin (e.g. *Hiantopora*, *Thalamoporella*, *Emballotheca*), which remained in the area after closure of the Tethyan Seaway, were not only decimated by the Messinian Salinity Crisis but also declined in numbers and/or disappeared during the Late Pliocene and Pleistocene cooling trend (e.g. Moissette and Pouyet 1987; Taylor 2000; Berning et al. 2005; Berning 2006). Nevertheless, the successful establishment of Lessepsian elements in the eastern Mediterranean Sea, migrating through the Suez Canal from the Red Sea (Powell 1969), shows that for some tropical taxa the local environmental conditions are still suitable during interglacial stages.

4. Conclusions

Two major processes can be deduced for the Oligocene and Early Miocene around the Tethyan Seaway:

1. There is evidence that the centre of marine diversity, situated in the Western Tethys during the Oligocene, shifted towards the Indo-West Pacific during the Miocene. The establishment of high diversity levels in the Western Tethys during the Late Oligocene was supported by tropical conditions related to the Late Oligocene warming (Fig. 1). This centre, however, was geographically widespread and not uniform for all marine groups; e.g. the highest diversities for the mollusc faunas are documented in the west (France, Italy), whereas the scleractinian corals developed a maximum of diversity further to the east (Central Iran). This centre of diversity might have acted also as a centre of origin (sensu Briggs 1995) for several mollusc taxa such as the tridacnines and certain strombid lineages, several taxa of which even reached the Western Atlantic Region (WAR). Coral and echinoderm data suggest that this centre of diversity had shifted towards the south-east already during the Early Miocene (Roman et al. 1989; Schuster 2002a), when also a considerable increase of mollusc diversity is obvious in the IWPR (cf. Martin 1899, 1905, 1906, 1916, 1921). With the narrowing of the Tethyan Seaway and the reorganisation of biogeographic patterns during the Early Miocene, coral diversity was cut down to 50% and the faunal exchange between the IWPR and the PMAR became negligible. This is probably related to changes in current systems but possibly also to the development of rather hostile conditions along the shallow marine, evaporitic shelf areas. Among the echinoderms, however, some species seem to have used the short-lived passage during the early Middle Miocene and settled along the East African coast. In contrast to the low diverse

coral fauna, mollusc diversity in the PMAR achieved a last climax during the Middle Miocene Climate Optimum (e.g. more than 800 gastropod species are recorded from the Paratethys Sea by Harzhauser and Piller 2007). Thereafter, the Middle Miocene Climate Transition (Shevenell et al. 2004; Fig. 1) and the Pliocene to Pleistocene cooling events caused a gradual decline of diversities. These were replenished and maintained from the Eastern Atlantic Region after a complete community collapse caused by the Messinian Salinity Crisis (e.g. Raffi and Taviani 1984; Sabelli and Taviani 1984; Lauriat-Rage et al. 1999; Berning 2006) and during interglacial cycles henceforth. Therefore, the re-colonisation and faunistic enrichment of the impoverished MAR from the IWPR was successfully blocked for more than 15 Ma. The success of anthropogenic-induced Lessepsian migrants since 1869 (Por 1978; Zenetos et al. 2004) may thus also be a result from the unbalanced composition of the faunas in the Mediterranean Sea.

2. A gradual decline of faunistic similarities between the Western Tethys and the PIWPRs predates the final formation of the *Gomphotherium* Landbridge, which is reflected in the near complete loss of shared species thereafter. The faunistic differentiation on both sides of the Tethyan Seaway is already recognisable during the Late Oligocene, predating the landbridge by at least 5 Ma. Especially in the East African-Arabian Province an early take-over by PIPP molluscs is recognisable. In the same way, scleractinian corals and echinoderms display a discrete development east of the seaway despite the wide oceanic connection (Roman et al. 1989; Schuster 2002a). Some elements with evolutionary roots in the MIP, such as *Tridacna*, are already restricted to the EAAP in the Aquitanian and did not re-occupy the western seas. In reverse, the impact on terrestrial faunas is indicated by faunal exchange simultaneously with the emersion of the *Gomphotherium* Landbridge. Nevertheless, the initial exchange is followed by a series of "delayed" immigrations, which post-date the formation of the landbridge by up to 3 Ma.

Both "deviations" – the predating of biogeographic differentiation of marine faunas and the delayed exchange of terrestrial faunas due to successive migrations – call for attention in modern phylogenetic analyses when molecular clocks are simply calibrated against geodynamic data without acknowledging a heterochronous response of fossil faunas.

Acknowledgements

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