



ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 183 (2002) 103–133

**PALAEO**

www.elsevier.com/locate/palaeo

# Circum-Mediterranean Oligo–Miocene biogeographic evolution – the gastropods’ point of view

Mathias Harzhauser<sup>a</sup>, Werner E. Piller<sup>b,\*</sup>, Fritz F. Steininger<sup>c</sup>

<sup>a</sup> *Naturhistorisches Museum Wien, Geologisch-Paläontologische Abteilung, Burgring 7, A-1014 Vienna, Austria*

<sup>b</sup> *Institut für Geologie und Paläontologie, Universität Graz, Heinrichstrasse 26, A-8010 Graz, Austria*

<sup>c</sup> *Naturmuseum Senckenberg, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany*

Received 2 April 2001; accepted 24 October 2001

## Abstract

Based on studies in Iran (Qom Basin, Esfahan–Sirjan Basin, Zagros Mountains), in Turkey (Mut and Sivas basins), in the Mesohellenic Basin, and in northeastern Egypt, a new palaeobiogeographic concept for the Oligocene and Miocene in the circum-Mediterranean area with special emphasis on the distribution patterns of gastropod faunas is presented. A very strict biogeographic terminology is proposed to avoid the common fusion of geographic, faunistic and geodynamic terms in the palaeontologists’ jargon. Our main interest focuses on the affinities and the faunistic interactions between the early ‘Mediterranean’ and the early ‘Indo-Pacific’ regions during the Oligo–Miocene. Especially the role of the early Indo-Pacific faunas as the mythic centre of origination of Early Neogene European mollusc faunas, as often vaguely indicated in the literature, is critically evaluated. This leads to the establishment of a Mediterranean–Iranian Province and a Western Indian–Eastern African Province as palaeobiogeographic subunits of the Western Tethys Region during the Oligocene. Due to major geodynamic and related biogeographic changes in the Early Miocene the Western Tethys Region no longer existed and was replaced by the Proto-Mediterranean–Atlantic Region. For the area of the Paratethys the palaeobiogeographic unit Danubian Province, which includes the Proto-Caspian Subprovince, is proposed. Furthermore, the underrated transatlantic communication of the Oligo–Miocene nearshore mollusc faunas is demonstrated. Altogether this paper is a contribution to the discussion on the biogeographic concepts, classification and nomenclature in palaeontology as initiated by Westermann [Palaeogeogr. Palaeoclimatol. Palaeobiogeogr. 158 (2000) 1–13; 163 (2000) 49–68]. © 2002 Elsevier Science B.V. All rights reserved.

**Keywords:** biogeography; gastropods; Indo-Pacific; Mediterranean; Paratethys; Atlantic

## 1. Introduction

During the 19th and 20th centuries a large dataset for Cenozoic gastropods from the Western Mediterranean, the European Atlantic and Cen-

tral Europe has been produced (e.g. Hörnes, 1856; Bellardi, 1872–1890; Hörnes and Auinger, 1879–1891; Sacco, 1890–1904; Cossmann and Peyrot, 1909–1934). This led to an early understanding of Eocene to Miocene biogeography of this area. In an eastern direction, however, information concerning the Eastern Mediterranean and the Middle East was scanty. Gastropods were documented as rare byproducts during inves-

\* Corresponding author.

E-mail address: werner.piller@uni-graz.at (W.E. Piller).

tigations of regional geology. Due to the strong preservational bias related to the predominantly studied calcareous facies, the mollusc studies focused mainly on oysters and pectinids (Douglas, 1927, 1928). On the other hand, scattered and inhomogeneous data on Eocene to Miocene gastropod faunas from Pakistan, Somalia, Kenya, Madagascar, Southern India, Burma, and Java (Noetling, 1901; Martin, 1914–1915, 1916–1917, 1921–1922; Davies, 1923; Vredenburg, 1925–1928; Collignon and Cottreau, 1927; Cox, 1930a; Azzaroli, 1958) allowed a glance at the composition and evolution of the early Indo-West Pacific faunas. The comparison of Mediterranean and Asian faunas, representing two major

biogeographic entities, was thus severely hampered by a palaeontological no man's land spanning the entire eastern Mediterranean and the connecting Tethyan seaway. Therefore, modern palaeobiogeographic interpretations of late Tethyan mollusc faunas (Piccoli, 1984; Piccoli et al., 1986, 1991) were usually based on the well-studied Northern Italian and Pakistanian faunas. The vast area in-between was taken into consideration only cursorily since their poorly documented and low diversity faunas were considered to be of little palaeobiogeographic value.

To close this gap we focused on this poorly studied area. Detailed investigations of Oligocene and Early Miocene sections in the Greek Meso-

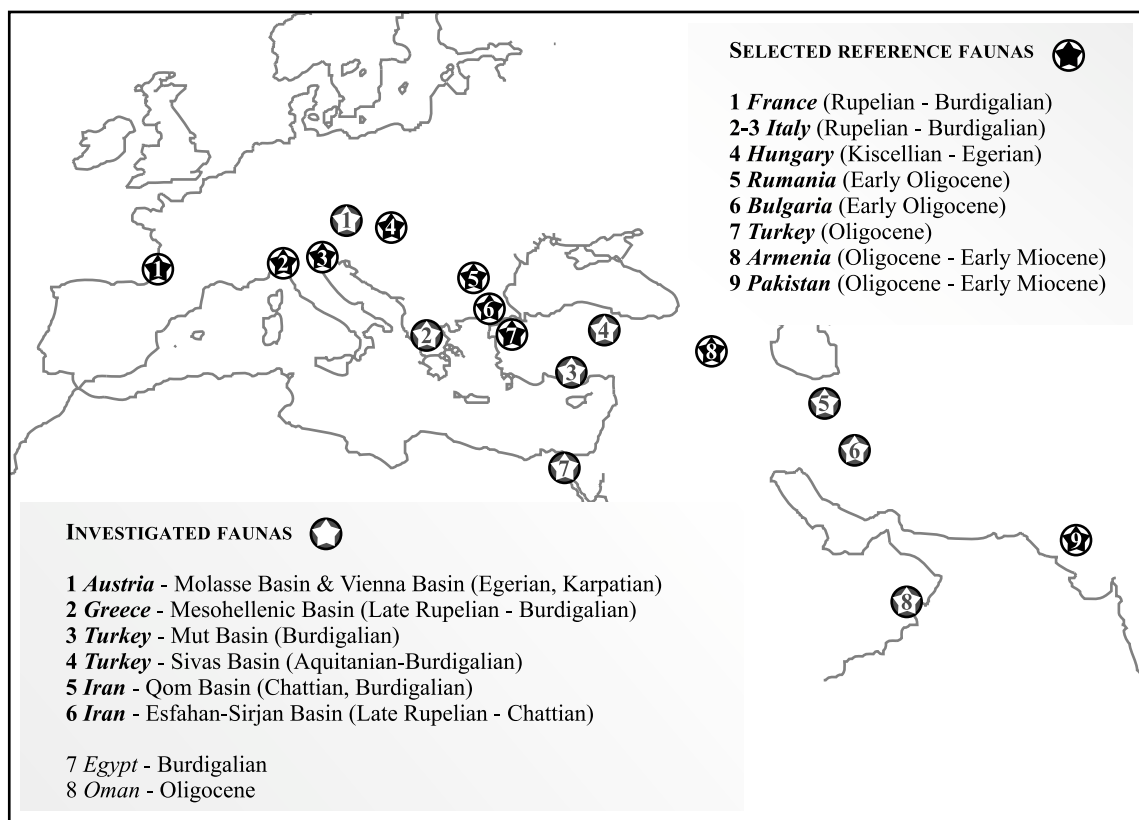


Fig. 1. Geographic location of the herein reported Oligocene and Early Miocene gastropod faunas. The faunas from Iran, Turkey and Greece form the base for the present study, whereas the low diversity and poorly preserved faunas from Egypt and Oman are only supplementary. Additionally, the position of some selected European and Asian reference faunas is indicated. Among these, the Italian and Pakistanian gastropod faunas turned out to represent the cornerstones for biogeographic considerations in the circum-Mediterranean area.

hellenic Basin, the Turkish Mut and Sivas basins and especially the Iranian Qom and Esfahan–Sirjan basins (Fig. 1) yielded a high number of shallow marine gastropod faunas. Hence, the faunistic gap in the Eastern Mediterranean was filled and data from Iran, which is identified as key area between Mediterranean and Pacific faunas, are available for the first time. Based on these data a new concept of the palaeobiogeography of the Oligocene and Early Miocene Western Tethys can be developed.

The main interest focussed on the dawn of the fauna of the Mediterranean–Iranian Province. Its birth from the Oligocene faunal-stock of the vast Tethys Realm is outlined, and the influence of the Proto-Indo-West Pacific Region on the Early Miocene gastropod faunas of the Iranian Qom Basin and the faunas of the Mediterranean area is evaluated.

## 2. Biogeographic basics

A summary of the various concepts and hierarchies in biogeography is given in Sedlag and Weinert (1987), who recommend a terminology corresponding to Lattin (1967). According to these authors the usually rather vaguely used term ‘province’ should be confined to a part of a subregion. The latter term corresponds largely to the term ‘province’ as used by Woodward (1856) and Hedgpeth (1957). Finally, the subregions are united into large biogeographic units – the regions.

A strict definition of the various biogeographic units based on percentages of endemisms is presented by Kauffmann (1973) and Kauffmann and Scott (1976). According to this definition a realm is characterised by more than 75% endemism, a region comprises 50–75%, a province 25–50%, a subprovince 10–25% and finally an endemic centre reaches 5–10% endemism.

Generally, the term province as proposed by Sedlag and Weinert (1987) is accepted by modern biogeographers including Briggs (1995), Longhurst (1998), and Westermann (2000a,b). Nonetheless the classification of higher ranks is in a state of flux. Briggs uses ‘region’ as a synonym

to Lattin’s subregion whilst the subrealm of Westermann (2000b) seems to be more or less synonymous to ‘region’ of most biogeographers. Longhurst (1998) unites the provinces in biomes. However, the geographic and biogeographic boundaries of the modern shallow-water subdivisions are more or less the same for all authors.

Recently, biogeographic principles and the denomination of units and their hierarchical ranking were discussed by Westermann (2000a,b). In his ‘Rules of Biogeographic Nomenclature’, Westermann (2000a) proposes a strict use of biogeographic terms, with emphasis on homonyms and synonyms as well as stability throughout geological time. Westermann (2000a) tries to establish the general term ‘biochore’ for all biogeographic units. The term ‘biochore’ is, however, highly controversially used: for many neontologists ‘biochore’ has a strong ecological component without geographic restrictions (e.g. biochores are grassland, forest, and desert) and even for palaeontologists such as Lehmann (1996) ‘Biochorion’ is a small area within a biotope (e.g. a tree trunk or a carcass). Thus a biochore in modern biology – especially in botany – is a subdivision of the biocycle which contains a group of biotopes that resemble one another. This diverging use of ‘biochore’ is based on the unclear translation of the Greek bio-‘ $\chi\omega\rho\sigma$ ’ as living-‘space’ instead of living-‘place’. Therefore, not to prolong the confusions, we prefer ‘biogeographic unit’ instead of the term biochore.

Westermann (2000a,b) recommends the ranks *Superrealm*, *Realm*, *Subrealm*, *Province*, and *Subprovince* as valid hierarchical categories for the definition of his biochores. The term region is for informal use only. We believe, however, that the well-established and widely used term ‘region’ should be obligatory and not replaced by an optional term as ‘Subrealm’. Therefore, in this paper the terms province and region are mainly used *sensu* Briggs (1995). In contrast, we follow Westermann (2000a) in his proposed rule, that the replacement of names is acceptable under certain conditions, e.g. extreme biochore expansion or contraction, exceptional geologic change at regional or global scale, and at mass extinction events.

The hierarchical categories of biogeographic ranks used in this paper are:

*Realm – Region – Province.*

For refinement these biogeographic core-units can be subdivided by adding the prefixes Super- or Sub- respectively.

### 3. Materials and methods

The shallow marine Late Oligocene Chattian faunas from Mesolouri, Doutsiko and Kipourio in the Mesohellenic Trough (Greece) (Fig. 1) yielded more than 90 taxa, representing about 50 species. An equal number of species was recorded from Abadeh in Iran. The Early Miocene nearshore faunas from Turkey, Greece and Iran are documented by 145 taxa composed of 46, 50 and 58 gastropod species respectively (Appendix 1). These faunas were compared and coincidence or differences between the faunas on species level were determined. Due to the partly rather small faunas, only presence/absence data are used for the analysis, yielding percentages of taxa occurring in two or more investigated faunas.

Finally, the Iranian and Eastern Mediterranean faunas were compared with those of the Western Mediterranean, the Atlantic, the Paratethys and especially with those from Pakistan. Our knowledge of these reference faunas is rather inhomogeneous. The small Eastern Mediterranean and Iranian faunas consisting of approximately 50–60 species each are in contrast to the extremely rich French and Italian faunas. For example, Cossmann and Peyrot (1909–1932) describe more than 600 Burdigalian and more than 500 Aquitanian gastropods. Bellardi (1872–1904) report even more than 980 Early Miocene species. The Oligocene gastropod faunas of northern Italy consist of at least 300 species, estimated from the various monographs of Fuchs (1870), Oppenheim (1900) and Bellardi (1872–1904). From the Late Oligocene of the Western Paratethys approximately 250 species are recorded by Wolff (1896–1897), Baldi (1973) and Hölzl (1962), and more than 300 species are described from the Early Miocene Paratethys by Steininger and Senes (1971), Hölzl in

Papp et al. (1973) and Harzhauser (2002). In contrast, the Pakistanian faunas with 77 Oligocene and 81 Early Miocene species described by Vredenburg (1925–1928) are considerably smaller. The discrepancy is even more obvious when eastern African and southern Indian gastropod faunas are considered. Thus, only 23 species are described from the Oligocene and Early Miocene of Somalia (Azzaroli, 1958), 28 from the Miocene of Ceylon (Cox, 1930a), 13 from the Miocene of Madagascar (Collignon and Cottreau, 1927), and only eight from the Miocene of Kenya (Davies, 1923).

The palaeobiogeographic interpretation of these inhomogeneous faunas based on statistical methods seems to be inappropriate. On the one hand, for many of the mentioned reference faunas modern revisions are completely missing. Therefore a reliable comparison of literature-based faunas is difficult, a fact that is obvious to every taxonomist after a short look at the usually long and manifold synonymy lists in modern revisions. This is not restricted to ‘difficult’ groups, such as the nassariids or conids, but can also be documented for ‘simple’ taxa such as the melongenids or strombids. E.g., the characteristic Oligocene *Melongena semseyiana* (Erdős) – a seemingly endemic Paratethyan species (Baldi, 1973) – was described at least under three synonyms (see Mikuz, 1999). Now the ‘endemic’ Hungarian species turned up in Austrian, Croatian, Hungarian, Slovenian, Greek and maybe also in Turkish faunas.

Similarly, the endemism-index should not be overemphasised, since endemism may partly depend on the quality of research. Recently, Lozouet (1998, 1999) and Valdés and Lozouet (2000) described 170 new species from the Oligocene and Lower Miocene of the Aquitaine Basin, indicating high endemism from the armchair. However, this high number of ‘endemic’ species seems mainly related to the lack of equivalent, elaborate studies in the Mediterranean area. The insufficient study of Mediterranean faunas was also stressed by Studencka et al. (1998) for Middle Miocene bivalve faunas. Thus, the lack of modern revisions caused a higher percentage of bivalves common to the Atlantic and the Paratethys (60%) than of species common to the directly

[illegible]

Fig. 2. Late Eocene to Late Miocene geochronology and biostratigraphy after Rögl (1996, 1998), Rögl et al. (1993), Steininger (1999) (mammal zones), Cahuzac and Poignant (1997) (larger foraminifera), and Hardenbol et al. (1998) (magnetostratigraphy).

connected Mediterranean and the Paratethys (47%).

Furthermore, the taxonomic overcompleteness of some faunas, caused by the tendency of older

workers such as H $\ddot{o}$ rn $\ddot{e}$ s and Auinger (1879–1891) to split ‘good’ species into morphs, is hard to handle in statistics. These so-called subspecies or variations tend to ‘evolve’ into species in subse-

quent studies, resulting in several local ‘species’ which mask palaeobiogeographic relations. Finally, open nomenclature is hard to adapt to statistics. This can be demonstrated very impressively by the otherwise highly valuable lists of Early Oligocene Paratethys faunas from Hungary by Baldi (1986), which comprise about 37% of taxa in open nomenclature. Within the eastern African gastropod faunas this percentage may even reach 61% (see Azzaroli, 1958).

Hence, in this paper the authors try to focus on the qualitative and semiquantitative composition of typical nearshore assemblages, which are suggested to characterise the biogeographic units in various time slices. For biostratigraphic and geochronologic correlation see Fig. 2.

#### 4. Circum-Mediterranean biogeography

Woodward (1856) was one of the first who tried to divide the marine mollusc faunas in bioprovinces with characteristic compositions. He proposed the rule that 50% of the species within a province should be peculiar (endemic) to it. Physical factors such as geographic barriers and climate were recognised by Woodward as dividing lines between distinct provinces. He additionally takes historical factors into account such as ‘different distribution of land and water over the surface of the globe’. Woodward’s mollusc-provinces are still accepted by some authors working on molluscs such as Sabelli (1980). Nonetheless, the bioprovince concept was improved during the 20<sup>th</sup> century by authors such as Ekman (1953) or Hedgpeth (1957), who attempted to integrate the littoral fauna as a whole.

In the following the authors provide a brief review of selected recent and historical bioprovinces and their geographic pattern within the circum-Mediterranean area.

##### 4.1. Modern bioprovinces

###### 4.1.1. Mediterranean–Atlantic Region

According to Briggs (1995) this region comprises the *Lusitania*, *Black Sea*, *Caspian*, and *Aral* provinces. Among them the *Lusitania* Prov-

*ince* is the most extensive, including the entire Mediterranean Sea but also parts of the Atlantic coast. Its westernmost extension are the Azores; in the north it includes the Bay of Biscay, and it reaches as far south as Madeira and the Canaries. It is bordered in the south by the Cape Verde Islands, which are part of the *Eastern Atlantic Province* (= *Senegalese Province* sensu Woodward) and the English Channel in the north.

The term *Lusitanian Region* as used by Ekman (1953) has a quite different meaning. He confines the term to the Atlantic part north of the Straits of Gibraltar. Consequently, he separates the southern part as *Mauretanian Region*. The *Mediterranean Sea–Black Sea Province* introduced by Longhurst (1998) corresponds partly to the *Lusitania Province* of Briggs (1995). A clear difference is only that Longhurst treats the Bay of Biscay as part of the *Northeast Atlantic Shelves Province*. The concept of Briggs (1995) concerns the shallow-water fauna whereas the provinces introduced by Longhurst (1998) are based on pelagic organisms.

In contrast to Briggs (1995), who maintains that the Recent *Caspian* and the *Aral Sea provinces* have derived their biotas from the Mediterranean, these provinces are considered herein as biogeographic and geologic descendants of the Paratethys Sea. This is strongly supported by the data given in Ekman (1953), who describes the Caspian fauna to be ‘practically a pure Sarmatic fauna’. Ekman (1953) even emphasised the small percentage of species common to the Mediterranean Sea and regards the Caspian fauna to be of Paratethyan (= Sarmatic sensu Ekman) origin.

Similarly, the Black Sea Basin was part of the Paratethys, but became part of the *Mediterranean–Atlantic Region* during the Pleistocene and the Holocene by its connection to the Aegean Sea via the Marmara Sea.

###### 4.1.2. Eastern Atlantic–Boreal Region

The Region extends from the British Channel north via the North Sea to the Baltic Sea and reaches from the Celtic Shelf as far north as the Hebrides. It is limited to the south and the southwest by the *Lusitania Province* and to the north

and the north-east by the *Arctic Region* (Briggs, 1995). In contrast to Woodward's *Celtic Province*, the *Eastern Atlantic–Boreal Region* includes also Iceland, the Norwegian coast and extends as far north as Murmansk.

Several terms are used in the literature as rough synonyms for this Region. Especially European palaeontologists usually called the geographic ancestor of this Region the '*Boreal Province*' (Kautsky, 1925; Baldi, 1973), the '*Scandic Region*' (Hözl, 1962), or simply the '*northern province*' (Senes, 1958), while Rögl and Steininger (1983, 1984) introduced the modern term '*Atlantic–Boreal Bioprovince*'.

#### 4.1.3. Indo-West Pacific Region

The term '*Indo-West Pacific*' was introduced by Ekman (1934), who united the Indo-Pacific, the Western Pacific, and parts of the Central Pacific in his biogeographic unit. Later, Briggs (1995) demonstrated that the Region has to be extended to the Easter Islands, thus introducing an area that nearly extends to the coasts of America. This vast Region is divided into the *Indo-Polynesian*, the *Western Indian Ocean*, the *Red Sea*, the *North-western Australian*, the *Hawaiian*, the *Easter Island*, and the *Marquesas provinces*. The modern *Western Indian Ocean Province* extends from the Persian Gulf along the eastern African shelf – including the Seychelles, Madagascar and the Mascarene Islands – as far south as Kwa Zulu north of Natal in South Africa (Kilburn and Rippey, 1982). The Red Sea is excluded from this Province, but forms a distinct Province due to the high percentage of endemics (Briggs, 1995). In an easterly direction the *Western Indian Ocean Province* is bordered by the larger *Indo-Polynesian Province*. This Province extends from the entrance of the Persian Gulf, via the Arabian Sea, along the Indian shelf to Sri Lanka and the Bay of Bengal and includes Malaysia, Indonesia and Eastern Australia. To the north it reaches as far as the Japanese Amami Islands.

The border between these two provinces is not unequivocal. Even the definition given in Briggs (1995) markedly differs from his drawing since the sketch includes also the Iranian and Pakistanian coasts of the Arabian Sea in the *Western Indian*

*Ocean Province*, while in the text the *Indo-Polynesian Province* reaches as far west as the entrance of the Persian Gulf. Other limits of the *Western Indian Ocean Province* are given by Macnae (1968), who includes the entire coasts of the northern Arabian Sea as far as the Gulf of Khambhat in north-western India. Additionally, the *Western Indian Ocean Province* as defined by Por (1989) would reach to southern India, to the coast between Mangalore and Calicut.

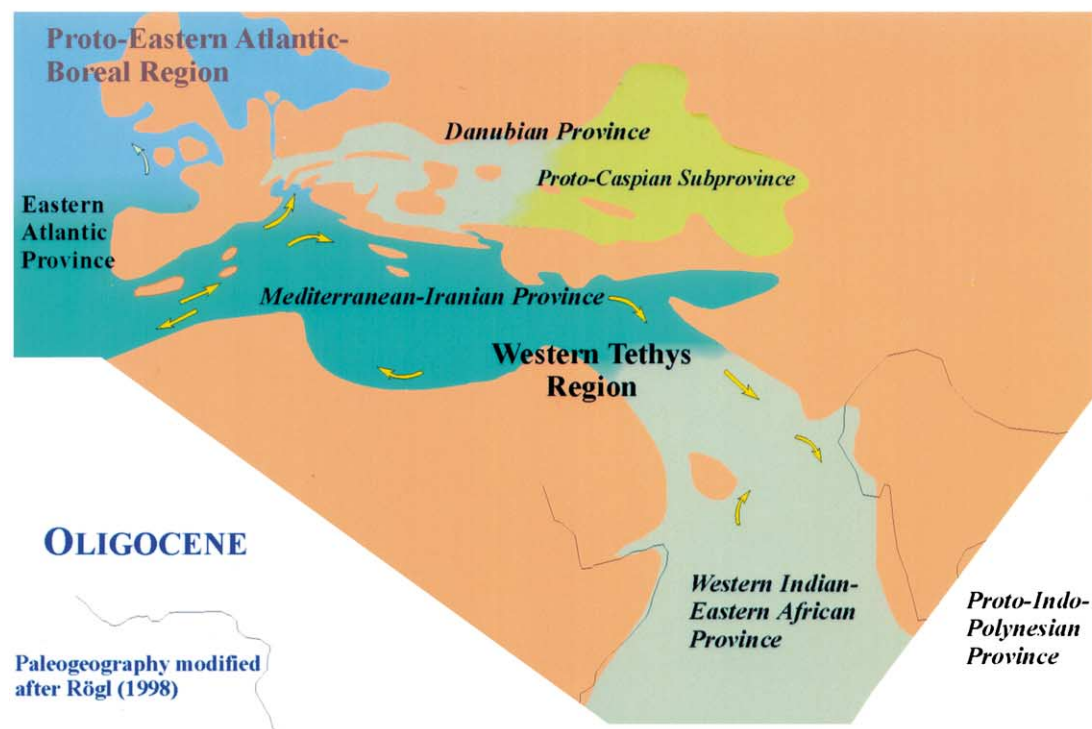
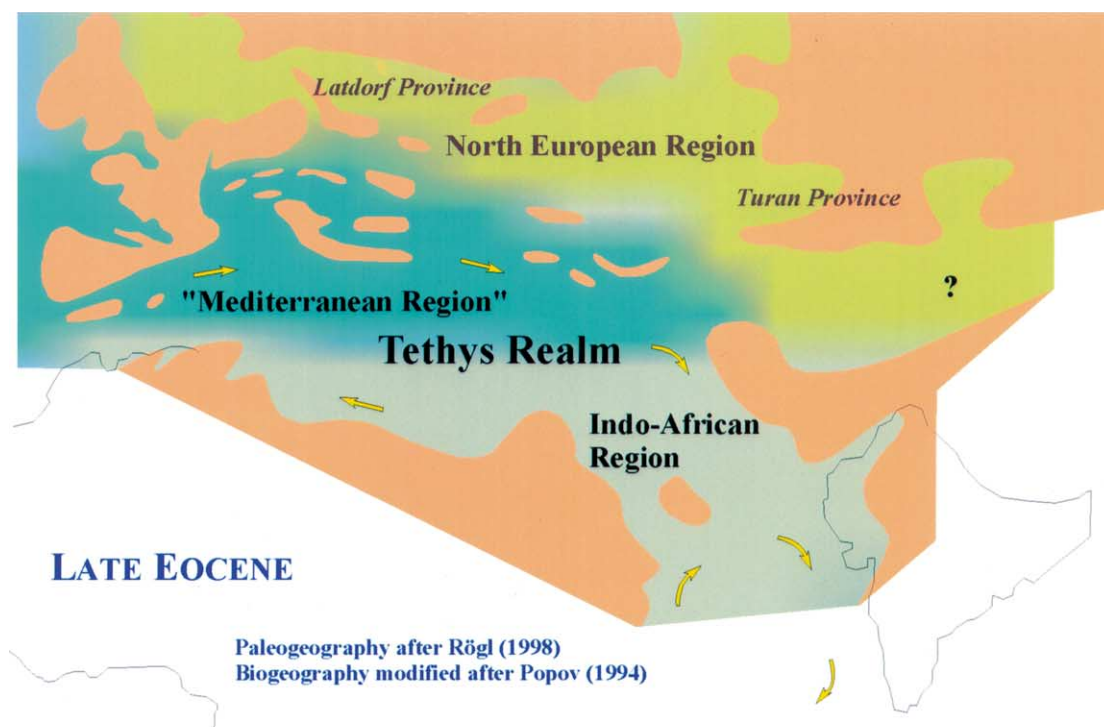
## 4.2. Historical biogeographic units

### 4.2.1. Tethys Realm

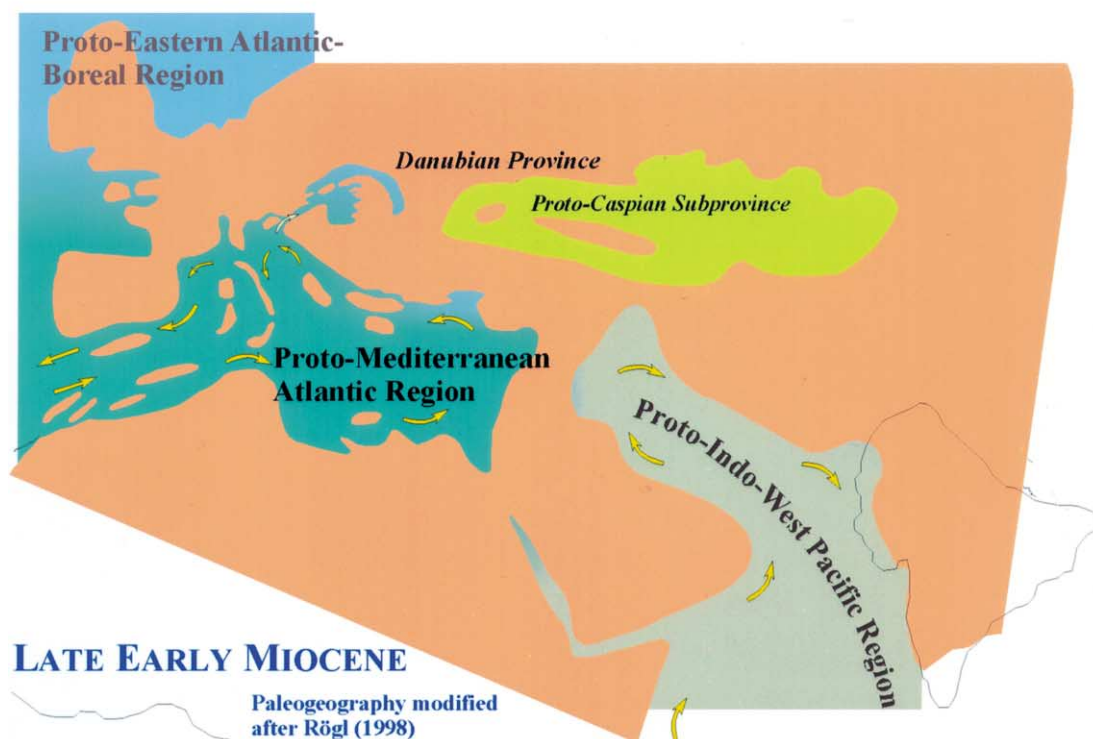
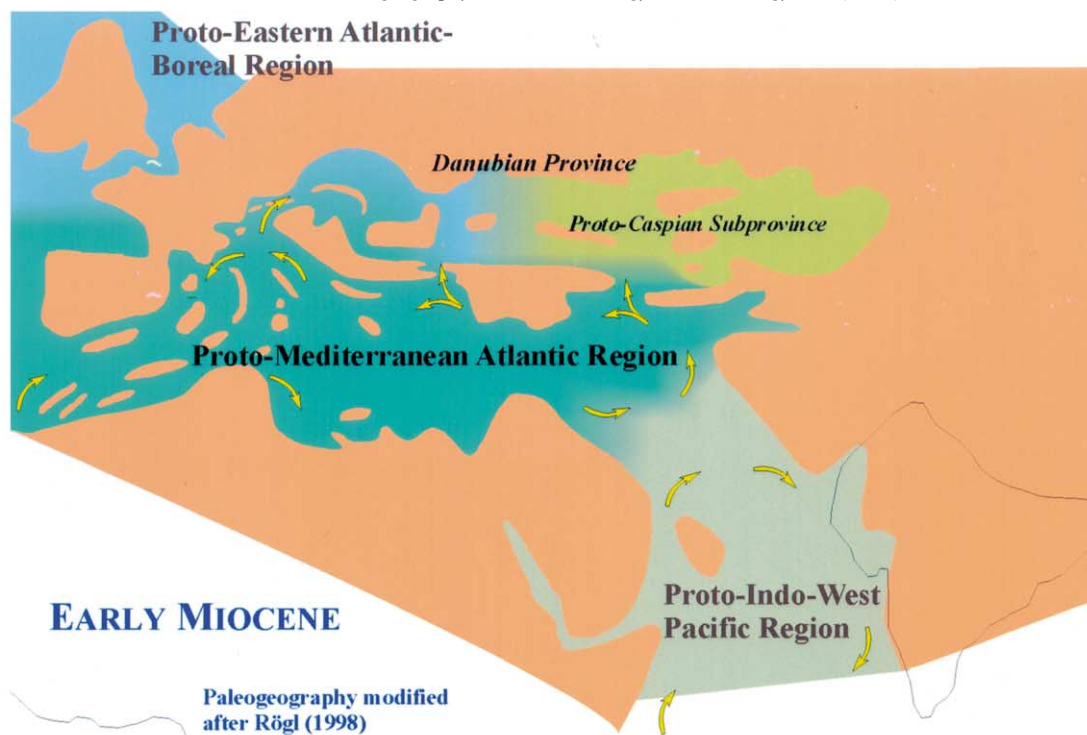
The term '*Tethys*' was introduced by the Austrian geologist E. Suess (1893) as a palaeogeographic entity. Herein '*Tethys Realm*' is used in a strict biogeographic sense and must not be intermingled with the geographic term '*Tethys*' as described by Hsü and Bernoulli (1978) and Sengör (1998). This is of great importance, since the geographic Tethys (sensu Hsü and Bernoulli, 1978) or the tectonically defined Tethys (sensu Sengör, 1998) vanished during the Eocene when India collided with Laurasia.

Originally, the biogeographic *Tethys Realm*, as defined by Kauffmann (1973), was applied to 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* is still used by Popov (1993) when defining zoogeographic units for Late Eocene bivalves. This *Tethys Region* sensu Popov is modified herein with respect to hierarchy and enlarged as *Tethys Realm* (Fig. 3(left, top)). According to Popov, the Late Eocene Tethys of western Eurasia can be divided into an *Indo-African Region* and a *Mediterranean Region* (subregions sensu Popov, 1993). At that time the southern Tethyan faunas of Egypt, Somalia and India displayed highest resemblance, but differed clearly from the northern Tethyan ones from Italy and southeastern France.

Simultaneously, with the narrowing of the Tethys in the north of the Indian shield, the 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. With respect to the divergent meaning of Tethys Ocean and Tethys Realm, it might be more correct to name the biogeographic unit the '*Proto-Mediterranean–Indo-African–Western Pacific Realm*' – an obviously unwieldy term. Thus the term *Tethys Realm* is favoured in this paper.

The post-Eocene *Tethys Realm* existed during the entire Oligocene and during the very Early Miocene without major interruption. The biogeographic unit vanishes during the Burdigalian and with the formation of the *Gomphotherium* landbridge between Eurasia and the Arabian plate in the Late Burdigalian (Rögl, 1998). The final breakdown of the *Tethys Realm* is also evident from a geographical viewpoint. However, as mentioned above, the Tethys Sea vanished much earlier during the Eocene.

During the Oligocene and the Early Miocene, the *Tethys Realm* covered an extraordinarily large area. Its main territory was an area, which coincides more or less with the modern *Indo-West Pacific Region*, but in western direction it also included the area of the modern Mediterranean Sea. A broad connection between the Iranian

and the African/Arabian plates enabled a fair exchange of shallow-water faunas between these areas. In the eastern direction, the Indonesian seaway acted as a marine connection between the 'Indo-Pacific' and the western Pacific areas which lasted until the early Middle Miocene (Ogasawara and Noda, 1996; Nishimura and Suparka, 1997). A tropical, equatorial current flowed through this Pacific–Indian Ocean gateway in a westerly direction (Tsuchi, 1997). Tethyan gastropods, such as *Tibia*, *Telescopium*, *Terebralia*, or *Vicarya*, however, were spread as far north as Southern Japan during the Early and early Middle Miocene (Ogasawara and Noda, 1996; Noda and Watanabe, 1996).

Corresponding to the modern *Indo-West Pacific Region*, a separation of this vast marine sphere into several biogeographic units is to be expected. Due to inadequate data it is currently impossible to designate any of these boundaries exactly. Nevertheless the representative Oligocene and Miocene faunas of Italy (Bellardi, 1872–1904; Fuchs, 1870), Greece, Central Iran, Pakistan (Vredenburg, 1925–1928; Iqbal, 1969a,b, 1980), Burma (Noetling, 1901), Java (Martin, 1916–1917, 1921–1922), Celebes (Beets, 1942, 1943), and the Sunda Islands (Vlerk, 1931) reflect clear shifts in

---

Fig. 3. Marine biogeography of the circum-Mediterranean area in four time slices. Different colours represent separate biogeographic units on the hierarchy of a *Region* or a *Province*. Arrows indicate hypothetical direction of surface currents. (Left, top) Late Eocene: The biogeographic pattern is based on bivalve genera as outlined by Popov (1993). At that time the Eurasian marine sphere displays a distinct S–N trend expressed by a northern entity united in the *North European Region* and a southern entity, the *Tethys Realm*. The *Tethys Realm* can be divided into two *Regions*, which were named the 'Mediterranean' *Region* and the 'Indo-African' *Region* by Popov (1993). (Left, bottom) Oligocene: The *Western Tethys Region* is divided into the *Mediterranean–Iranian Province* and the *Western Indian–Eastern African Province*. W–E oriented surface currents along the northern shores of the Tethys facilitated the distribution of 'European' gastropods as far southeast as Pakistan. However, a distinct N–S gradient is indicated by the characteristic faunistic composition in the *Western Indian–Eastern African Province*. In the Paratethys Sea, the *Danubian Province* and the *Proto-Caspian Subprovince* formed as a result of the reduced connections to the Tethys. The complex biogeographic development of these units is triggered by immigrations from the north and/or south as well as by local evolution. (Right, top) Early Miocene: The *Western Tethys Region* vanished as the *Western Indian–Eastern African Province* ceased to exist. Hence, in this area the gastropod fauna of the *Proto-Indo-West Pacific Region* developed and the 'European' influence was lost. In contrast, the newly formed *Proto-Mediterranean–Atlantic Region* is a pure descendant of the Oligocene *Mediterranean–Iranian Province*. Simultaneously, the *Danubian Province*, which now lacks the northern influence, contains southern species of the *Proto-Mediterranean–Atlantic Region*, and should probably be treated as part of this *Region*. (Right, bottom) Late Early Miocene: The separation of the *Proto-Mediterranean–Atlantic Region* from the *Proto-Indo-West Pacific Region* is completed by the formation of the so-called '*Gomphotherium* landbridge', which connected Arabia with Eurasia in the Late Burdigalian (Rögl, 1998). The *Proto-Mediterranean–Atlantic Region* displays a rather homogeneous gastropod fauna, which nearly takes over the *Danubian Province*. In the west, the *Proto-Mediterranean–Atlantic* gastropod fauna spread along the Atlantic coast.

compositions, which prove the existence of distinctive regions and provinces. Some of them will be proposed in the following.

#### 4.2.1.1. *Western Tethys Region*

*Paleogene*: During the Oligocene, the *Western Tethys Region* (=Indo-European sensu Ekman, 1953) represents part of the *Tethys Realm*. It covered the area of the modern Mediterranean but probably included also the European Atlantic coast up to the Bay of Biscay in the west and reached to Pakistan, Somalia and Zanzibar in the east and the south (Fig. 3(left, bottom)). Most characteristic for the *Western Tethys Region* are the faunas of Northern Italy. The *Mediterranean–Iranian Province* (see below) is designated herein as the type unit for the *Western Tethys Region* (=chorotype sensu Westermann, 2000a).

Its eastern border seems to have been located somewhere along the coast of Southern India, since the south-eastern Asian faunas display no similarities either with those of Pakistan (Vlerk, 1931) or with those of Europe. Such faunistic demarcation lines have also been documented for the Eocene by Cotter (1923) for the bivalves. He stated that Burma, Sumatra, Java, and Borneo constituted a distinct bioprovince, different from the Sind–Baluchistan and Egypt faunas. Some years later Cox (1930b, 1936) concluded that the affinities of the Bahrain and southern Iranian faunas with those of north-western India, Somalia and Egypt hint at an Indo-African biogeographic entity (=Indo-African fauna sensu Cox, 1930b). Correspondingly, Martin (1931) proposed an Indo-Malayian bioprovince based on the homogeneity of Late Eocene faunas from eastern India to Java and Burma, and on their marked difference from that of western India–Pakistan. This biogeographic pattern fits well the simulations of Barron and Peterson (1991) who demonstrated that Burma and Java were separated from north-western India during the Eocene by a strong western boundary current, while the Indian Ocean circulation pattern and the Somali current are evident only from ‘middle’ Oligocene onwards (Barron and Peterson, 1991). Hence, in the east the Paleogene *Western Tethys Region* is bordered by a major adjacent biogeographic unit inhabited by these

Indo-Malayian faunas, called herein informally the Proto-Indo-Polynesian Province of the Proto-Indo-West Pacific Region. The fauna of this Proto-Indo-West Pacific Region displays hardly any resemblance with the Oligocene gastropod fauna of the *Western Indian–Eastern African Province*. Neither the Pakistanian nor the eastern African faunas have species in common with the Oligocene gastropod faunas of the Proto-Indo-Polynesian Province (e.g. Buton-fauna described by Martin (1933, 1935) and Beets (1942, 1943)).

During the Oligocene a separation within the *Western Tethys Region* in at least two provinces is obvious.

(1) *Mediterranean–Iranian Province*. The herein proposed *Mediterranean–Iranian Province* became established in the area of the modern Mediterranean Sea and had its south-easternmost known extension in Central Iran (Fig. 3(left, bottom)). The new term is introduced instead of ‘Mediterranean’ Province, because of the different geographic extension and moreover because of the synonymous use of the term for Mesozoic and Cenozoic biogeographic units with different biotic characteristics. Characteristic gastropod faunas of this province are those of Northern Italy (Fuchs, 1870; Bellardi, 1872–1890; Sacco, 1890–1904), the fauna of the Mesohellenic Trough in Greece (Brunn, 1956; Harzhauser, 2000), and the fauna of the Esfahan–Sirjan Basin in Central Iran (Harzhauser, 2000; Fig. 4a,c). It is best characterised by its rich strombid fauna which seems to be a heritage of the highly diverse, blooming Eocene strombid fauna. None of the giant species of *Oostrombus* or *Dilatilabrum* is known from any Oligocene section southeast of Iran. Characteristic gastropods of the *Mediterranean–Iranian Province* are, among many others, *Tectus lucasianus* (Brongniart), *Angaria scobina* (Brongniart), *Turritella asperula* Brongniart, *Turritella conofasciata* (Sacco), *Peyrotia strangulata* (Grateloup), *Campanile charpentieri* (Basterot), *Granulolabium plicatum* (Bruguière), *Tympanotonos stroppus* (Brongniart), *Clava ampullosa* (Brongniart), *Clava voglioi* (Michelotti), *Cerithium calculosum* Defrance, *Gourmya romeo* (Bayan), *Diastoma costellatum elongatum* (Brongniart), *Proadusta parvitala* (Sacco), *Ampullinopsis crassatina* (Lamarck), *Globu-*

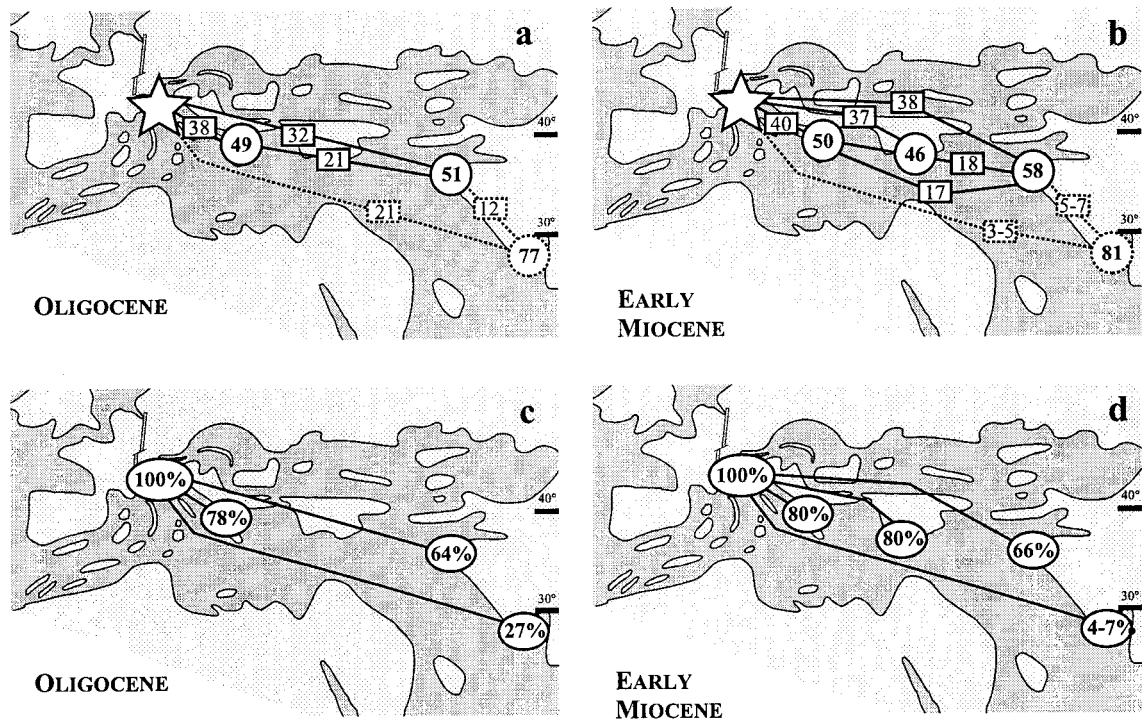


Fig. 4. (a,b) Species level similarities within gastropod faunas. Numbers in circles represent total numbers of species of basin; numbers in squares represent numbers of co-occurring species; the asterisk indicates reference faunas in Northern Italy. (c,d) Percentages of N-Mediterranean species represented in the Greek, Turkish, Iranian, and Pakistanian gastropod faunas. The sketches (a) and (c) demonstrate the high faunistic similarities in the Western Tethys Region during the Oligocene and document the homogeneity within the Mediterranean–Iranian Province. During the Early Miocene (b,d) this homogeneity is strongly indicated within the Proto-Mediterranean–Atlantic Region. In contrast, the Pakistanian gastropod faunas lost the similarities and have only 4–7% of species, which are typical of the Proto-Mediterranean Region, thus pointing to the beginning development of the Proto-Indo-West Pacific Region. The very significant drop in similarity between the Iranian and the Pakistanian faunas during the Early Miocene clearly witness the formation of a major biogeographic boundary between  $\sim 30^\circ$  and  $35^\circ$  N.

*laria gibberosa* (Grateloup), *Sinum aquensis* (Recluz), *Bayania semidecussata* (Lamarck), *Oostrombus auriculatus* (Grateloup), *Oostrombus irregularis* (Fuchs), *Strombus radix* (Brongniart), *Strombus (Dilatilabrum) roegli* Harzhauser, *Xenophora cumulans* (Brongniart), *Cassis mamillaris* Grateloup, *Cassis vialensis* Fuchs, *Turbinella episoma* (Michelotti), *Volutilithes subambigua* d'Orbigny, *Lyria anceps* (Michelotti), *Conus (Leptoconus) diversiformis* Deshayes, and *Terebra subtesellata* d'Orbigny.

(2) Western Indian–Eastern African Province. Towards the southeast the Mediterranean–Iranian Province is bordered by a very distinct biogeographic unit, which is introduced herein as the Western Indian–Eastern African Province (Fig.

3(left, bottom)). The term 'Indo-African' should be avoided, because of its quite different use in the literature, e.g. Popov (1993) versus Cox (1930b). It is represented by the fauna of the Pakistanian Nari Formation, which has at least 40 species in common with those of Northern Italy (Vlerk, 1931) (Fig. 4). However, the high number of species unknown from European localities (about 50–60 species) reflects a rather independent development in this south-eastern termination of the Western Tethys Region. This Western Indian–Eastern African Province is documented by the Pakistanian faunas (Vredenburg, 1925–1928; Iqbal, 1969a,b, 1980), but can also be traced along the coast of Eastern Africa as confirmed by the faunas of Somalia described by Azzaroli (1958)

and Kenya (Davies, 1923). The *Western Indian–Eastern African Province* includes also the area of Oman (Fig. 3(left, bottom)) as documented by a small reefal gastropod fauna kindly donated by M. Bernecker (Erlangen). Characteristic gastropods of the *Western Indian–Eastern African Province* are ‘*Turbo (Senectus) naricus* Vredenburg, ‘*Turbo (Olearia) protocepoides* Vredenburg, *Protoma retrodilatum* Vredenburg, *Turritella narica* Vredenburg, *Semicassis oligocalantica* (Vredenburg), *Harpa (Eocithara) narica* Vredenburg, *Bel-latara narica* (Vredenburg), or *Cerithium sindiense* Vredenburg.

Widespread species which are recorded from both provinces and are therefore diagnostic (typical) of the entire *Western Tethys Region* are: *Tectus lucasianus* (Brongniart), *Campanile charpentieri* (Basterot), *Granulolabium plicatum* (Bruguère), *Tympanotonos stropus* (Brongniart), *Cerithium ighinai* (Michelotti), *Turritella magnaspe- rula* Sacco, *Turritella asperula* Brongniart, *Turritella conofasciata* (Sacco), *Peyrotia desmarestina* Basterot, *Peyrotia strangulata* (Grateloup), *Strombus radix* (Brongniart), *Cassis mamillaris* Grateloup, *Cassis retusa* Michelotti, *Cassis nummuliti- phila* (Sacco), *Sconsia beyrichi* (Michelotti), *Proadusta parvitala* (Sacco), *Globularia gibberosa* (Grateloup), *Ampullinopsis crassatina* (Lamarck), *Amaurellina oweni* (Archiac and Haime), *Sinum aquensis* (Recluz), *Xenophora cumulans* (Brongniart), *Ficus condita* (Brongniart), *Turbinella episoma* (Michelotti), *Conus diversiformis* Deshayes, *Conus carcarenensis* Sacco, *Lyria anceps* (Michelotti), and *Terebra subtessellata* d’Orbigny. Along with these gastropods the remarkable bivalve *Avicularium carinatum* (Bronn) may be regarded as a characteristic element of the *Western Tethys Region*.

The southeasternmost known gastropod fauna of the *Mediterranean–Iranian Province* occurs in the Late Rupelian and Early Chattian of the Esfahan–Sirjan Basin in Central Iran. The Oligocene section of Lordegan in the Iranian Zagros Mountains, located still further south, bears a strombid of the *Mediterranean–Iranian Province*. In contrast, the northwesternmost fauna of the *Western Indian–Eastern African Province* is actually represented by the Pakistanian assemblages. Therefore

the boundary between these biogeographic areas along the northern Tethys shores is located somewhere between Central Iran and the Sind–Baluchistan Region. Along the southern shores, the faunas of Libya, Palestine and Egypt are considered part of the *Mediterranean–Iranian Province* (Fig. 3(left, bottom)), while the faunas of Oman represent the northern known extension of the *Western Indian–Eastern African Province* (Fig. 3(left, bottom)). Similarities between the two provinces are high within the potamidids, turritellids and naticids but low amongst the volutids, turrids and other neogastropods, documenting the peculiar character of the fauna. Only very few of these species, such as *Ampullinopsis crassatina*, *Globularia gibberosa* or *Granulolabium plicatum* managed to colonise adjacent bioprovinces in high numbers. Others such as *Turbinella episoma*, *Cassis mamillaris* or *Angaria scobina*, which are very common in Western Tethyan assemblages, are rare faunal elements within their northernmost distribution area in the Early Oligocene of the Paratethys. The connection between these biogeographic entities was supported by a distinct easterly current along the northern shores of the Tethys (Fig. 3(left, bottom); Barron and Peterson, 1991). According to Barron and Peterson (1991) a westward-directed Eocene to Oligocene Tethyan current system along the northern shores as suggested by Berggren and Hollister (1974) has to be rejected.

A third province in the western part might be based on differences in the composition of the Oligocene faunas from southwestern France (Grateloup, 1840; d’Orbigny, 1852; Lozouet, 1998, 1999) and the Italian and Greek localities. This is additionally supported by the northern influence in the French faunas as suggested by Welle (1998) and by numerous muricids, buccinids, nassariids, or conids described only from France (Lozouet, 1999).

*Early Neogene:* During the Early Miocene the *Western Tethys Region* shrank drastically from the gastropods’ point of view. Still, the area from the Bay of Biscay to the Mediterranean basins as far east as Central Iran display a rather similar fauna (Fig. 4). However, the Early Miocene brings about a drastic change for the *West-*

ern Indian–Eastern African Province, which vanishes as a distinct unit probably even before the closure of the Tethyan corridor in the Late Burdigalian. The data on Pakistanian molluscs from the Early Miocene Gaj Formation given by Vredenburg (1925–1928) reflect a strongly increasing influence by the fauna of South-East Asia, and a rapid decrease of elements of the *Western Tethys Region*. Correspondingly, Azzaroli (1958) noticed in the Miocene faunas of Somalia some influence from Indonesia, although his fauna still has some species in common with Italian localities. Hence, the separation of the gastropod faunas of the eastern African and the western Indian coastal areas from those of the *Western Tethys Region* already took place during the Early Miocene (Burdigalian?). 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*, which should be termed the *Proto-Western Indian Ocean Province*.

With the disconnection of the Indo-African fauna and the take-over by elements of the *Proto-Indo-West Pacific Region* in the area of the former *Western Indian–Eastern African Province* during the Early Miocene the *Mediterranean–Iranian Province* lost its southeastern counterpart. Finally, the point-of-no-return was reached by the closure of the Eastern Mediterranean seaway between the Anatolian and the Arabian/African plates during the Late Burdigalian (Jones, 1999). Based on the dramatic geodynamic and biogeographic changes and especially due to the evolution of the advanced Miocene Mediterranean gastropod fauna, the term *Western Tethys Region* seems hardly acceptable for the Early Miocene at least for the Burdigalian (see also Westermann’s rules for replacement of names, Westermann, 2000a). Therefore, we propose the term *Proto-Mediterranean–Atlantic Region* (Fig. 3 (right, top and bottom)) for the descendant of the strongly reduced Paleogene *Western Tethys Region*.

#### 4.2.1.2. *Proto-Mediterranean–Atlantic Region*

As discussed above a marine faunal exchange between the southeastern and the ‘Mediterranean’

faunas was strongly prevented during the Early Miocene. Therefore in the area of the Recent Mediterranean Sea a biogeographic unit formed which might best be named *Proto-Mediterranean–Atlantic Region* (Fig. 3(right, top)). According to the palaeogeographic situation as drawn by Rögl (1998) this area roughly corresponds to the limits of the modern *Mediterranean–Atlantic Region* except for the *Black Sea Province*, which was not in existence. This area was part of the Paratethys at that time.

The southwestern extension of the *Proto-Mediterranean–Atlantic Region* is not well defined due to the lack of available data on shallow marine faunas along the shores of northwestern Africa. However, the limits along the European Atlantic coast in northern direction were more or less equivalent to those of the Recent *Mediterranean–Atlantic Region* (sensu Briggs, 1995). The Artois axis formed a landbridge, which repeatedly separated the fauna from that of the North Sea Basin (Pomerol, 1982; Ziegler, 1990).

Unequivocal evidence for direct marine connections to adjacent provinces exists for the Central Paratethys, which is strongly influenced by the fauna of the *Proto-Mediterranean–Atlantic Region* during that time (Rögl, 1998, 1999; Harzhauser, 2002).

Within this area the data on gastropod faunas from France (Cossmann and Peyrot, 1917–1922), Italy (Bellardi, 1872–1904) and Iran (Harzhauser, 2000) show good correspondence during the Burdigalian, although a slight northwest-southeast shift in the composition is evident. However, the eastern Mediterranean faunas have 80% of species in common with Northern Italy and France, thus indicating a rather homogeneous distribution of taxa within this area during the Burdigalian (Fig. 4d). A slight drop in resemblance is recorded in the Iranian fauna, which still contains 66% (38 species) of ‘Mediterranean’ species (Fig. 4d). To obtain a better understanding of the similarities and differences between the Iranian and the Mediterranean faunas it is necessary to focus on the family level, because the degree of resemblance strongly fluctuates in the various families. In general the melongenids, cerithiids, strombids, and to some extent also the naticids show highest affin-

ities to the Mediterranean faunas. In contrast, the conids and the turrids display a considerable number of taxa which are known only from the Qom Basin (10–15%); due to the poor information it is unclear whether these species are also distributed in the Indo-Pacific or if they represent endemic forms, thus hinting at a distinct Iranian subprovince. Some of the most characteristic taxa within the *Proto-Mediterranean–Atlantic Region* are: *Turritella* (*Turritella*) *terebralis* Lamarck, *Protoma quadriplicata* (Basterot), *Peyrotia desmarestina* (Basterot), *Protoma cathedralis* (Brongniart), *Terebralia bidentata* (Defrance), *Cerithium vulgatum* Bruguière, *Granulolabium bicinctum* (Brocchi), *Granulolabium plicatum* (Bruguière), *Tibia dentata* (Grateloup), *Strombus* (*Lentigo*) *bonelli* (Brongniart), *Xenophora deshayesi* (Michelotti), *Sconsia striata miocenica* Sacco, *Melongena lainei* (Basterot), *Tudicla rusticula* (Basterot), *Athleta ficulina* (Lamarck), and *Conus* (*Conolithus*) *dujardini* Deshayes.

Aside from this core-area, the *Danubian Province* (see below) – spanning the western and eastern part of the Paratethys Sea – is considered to represent a distinct province of the *Proto-Mediterranean–Atlantic Region* at least during the late Early Miocene and the early Middle Miocene (see below).

This palaeogeographic framework of the *Proto-Mediterranean–Atlantic Region* based on gastropod data corresponds largely to the ‘Mediterranean Province’ as introduced by Jones (1999) based on larger benthic foraminifera. His province unites the entire Mediterranean area, the Qom Basin, and the Atlantic coasts of the Aquitaine Basin and of West Africa. Similarly, Rögl and Steininger (1983, 1984) recognised this biogeographic entity and called it the ‘Mediterranean (or Tethyan) bioprovince’.

The mollusc fauna of the *Proto-Mediterranean–Atlantic Region* suffered two major incisions. The first one took place in the early Middle Miocene when a short-lived connection to the Indo-Pacific – coinciding with a marked global warming (Miller et al., 1991; Rögl, 1998; Nishimura and Suparka, 1997; Tsuchi, 1997) – gave rise to a highly diverse Middle Miocene mollusc fauna. Until now the role of immigration of Indo-West Pacific

gastropods during the early Middle Miocene is somewhat dubious. Instead of the usually advocated immigrations, the autochthonous evolution in a phase of climatic optimum seems to be underrated. Anyway, the short-lived connections of the *Proto-Mediterranean–Atlantic Region* to the *Indo-West Pacific Region* did not change the equilibrium gastropod faunas of the *Proto-Mediterranean–Atlantic Region* markedly. During the Miocene and Pliocene various reconnections are discussed (Grecchi, 1978; Lozouet, 1992; Rögl, 1998; Jones, 1999), however, the biogeographic boundaries between the Indo-Pacific and ‘Mediterranean’ remained stable.

A second impact on *Proto-Mediterranean–Atlantic* mollusc faunas was the Messinian salinity crisis in the Late 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 – except for some supposed shelters such as the ‘Andalusian sanctuary’ (see Demarcq, 1987) – due to desiccation throughout the Mediterranean. The fauna of the Eastern Atlantic coasts was less affected. After the salinity crisis the deep-water fauna was distinctly impoverished (Raffi and Taviani, 1984), but it had not such a catastrophic effect on shallow marine molluscs (Sabelli and Taviani, 1984), which recolonised the Mediterranean basins from the Atlantic. Nevertheless, the Messinian salinity crises caused a turnover in composition of the nearshore fauna. Post-Messinian gastropod faunas lack characteristic Miocene taxa, such as *Terebralia bidentata* (Defrance), *Melongena cornuta* (Agassiz), *Polinices redempta* (Michelotti) or *Perrona jouanetti* (Desmoulin). In fact, many of the conids, turrids and turritellids of the *Proto-Mediterranean–Atlantic Region* became extinct (cf. Dermitzakis and Georgiades-Dikeoulia, 1987). Hence, the post-Messinian gastropod fauna represents rather the ancestral, warm-water stock of the modern *Mediterranean–Atlantic Region*.

During the Late Pliocene and Pleistocene the change from the *Proto-Mediterranean–Atlantic Region* to the modern *Mediterranean–Atlantic Region* was accelerated by distinct cooling events (Rögl and Steininger, 1983). Consequently, trop-

ical/subtropical taxa which contribute to the fauna of the *Proto-Mediterranean–Atlantic Region* are missing in the modern region (e.g. Olividae as demonstrated by Davoli, 1989, or Strombidae as emphasised by Abbott, 1960).

#### 4.3. Biogeographic position of the Paratethys Sea

The Paratethys, as a distinct palaeogeographic and palaeobiogeographic unit, formed around the Eocene/Oligocene boundary (Fig. 2) and lasted until the Pliocene. In fact, even the modern *Aral* and *Caspian provinces* are a heritage of the huge Paratethys, based on its peculiar fauna and endemism. During its maximum extent the Paratethys Sea spread from the Rhone Basin in France towards Inner Asia. Its geographic subdivisions are the Western Paratethys, comprising the Rhone Basin and the Molasse Basin of Switzerland and western Bavaria, the Central Paratethys, reaching from Bavaria in the west to the Carpathian Mountains in the east, and the Eastern Paratethys. Recently, the stratigraphy and geodynamics of the latter area were studied by Popov et al. (1993) and Jones and Simmons (1996). A critical up-to-date overview on palaeogeographic data has been given and discussed by Rögl (1998, 1999) and summarised in several palaeogeographic sketches.

This region underwent an outstanding history of total or partial isolation, reflected in a high percentage of endemics, alternating with various connections to the adjacent northern and/or southern seas.

The term Paratethys was introduced as early as 1924 by Laskarev (1924). During the last decades and especially due to the edition of the 'Chronostratigraphie und Neostatotypen' volumes the palaeobiotic framework was distinctly improved (Cicha et al., 1967; Steininger and Senes, 1971; Baldi and Senes, 1975; Papp et al., 1973, 1974, 1978, 1985; Stevanovic et al., 1990). Its geodynamic history was described by Senes and Marinescu (1974) and Rusu (1988), who divided the geodynamic development of the Paratethys into four stages: the Proto-Paratethys formed in the Late Eocene to Early Oligocene, caused by first isolation from the open oceans. This stage is fol-

lowed by the Late Oligocene and Early Miocene Eo-Paratethys, the late Early Miocene to early Middle Miocene Meso-Paratethys and the Middle to Late Miocene Neo-Paratethys (see also Steininger and Wessely, 2000).

To avoid an intermingling of geographic and biogeographic terms, we reject the terms Western, Central and Eastern Paratethys for biogeographic use in this paper. Instead we propose the new terms *Danubian Province* and *Proto-Caspian Subprovince* (Fig. 3(left, top; right, top and bottom)). Hence, the *Danubian Province* is characterised by the total fauna of the Western, Central, and Eastern Paratethys. The peculiar faunistic inventory of the Eastern Paratethys allows a further segregation of a *Proto-Caspian Subprovince*. (A further differentiation of these biogeographic units and a detailed description of their evolution and expansion will be published elsewhere.)

##### 4.3.1. Danubian Province and Proto-Caspian Subprovince

The first endemic Paratethys fauna developed during the Early Oligocene Solenovian, when the first nearly complete closure of the Paratethys occurred. This event peaked in the blooming and rapid evolution of a highly endemic brackish water bivalve fauna with genera such as *Janschinella*, *Korobkoviella* or *Ergenica* (Voronina and Popov, 1984; Popov et al., 1985; Nevesskaja et al., 1987; Rögl, 1998). By this event the Paratethys was united in a single, very distinct biogeographic entity – the *Proto-Caspian Subprovince* – as far as bivalves are concerned (Popov et al., 1993). Nonetheless, as shown by Popov et al. (1985) and Popov and Titova (1982), this endemism is much lower within the gastropods. Brackish or estuarine gastropods which are at that time widespread in the entire *Western Tethys Region* inhabited the coasts of the Paratethys; *Melanopsis impressa* Krauss, *Granulolabium plicatum* (Bruguière), *Theodoxus crenulatus* (Klein), and *Tympanotonos margaritaceus* (Brocchi) give evidence of reduced marine conditions within this interval, but do not justify a separation of a biogeographic unit at the level of a region.

Aside from this short-lived extreme western extension of the *Proto-Caspian Subprovince*, the



western part of the Paratethys was characterised by the quite different fauna of the *Danubian Province* (Fig. 3(left, bottom)). In times of open seaways, the Early Oligocene *Danubian Province* consists of northern species accompanied by a surprisingly large number of Western Tethyan elements, giving evidence of the earliest stage of separation of these biogeographic entities. Amongst these the most characteristic Western Tethyan species are *Turritella conofasciata* Sacco, *Turritella asperula* Brongniart, *Ficus oligoficoides* Sacco, *Athleta italica* Fuchs, *Turbinella episoma* (Michelotti), *Cassis mamillaris* Grateloup, *Angaria scobina* (Brongniart), and *Babylonia caronis* Brongniart (Baldi, 1986). Thus the later Early Oligocene, as documented by Baldi (1986) for the gastropod faunas of the Hungarian Kiscell Clay, displays about 31–35% endemic gastropods but also more than 20% Western Tethyan taxa and approximately 16% northern species.

During the Late Oligocene Egerian the southern flair decreased. The *Danubian Province* hosts a mixture of northern elements, which made their way from the North Sea Basin during the Rupelian, such as *Cassidaria megacephala* (Philippi), *Drepanocheilus (Arrhoges) speciosus* (Schlotheim), *Ficus concinnus* (Beyrich), ‘cosmopolitan’ Tethyan species such as *Granulolabium plicatum* (Bruguière), *Tympanotonos margaritaceus* (Brocchi) and *Melanopsis impressa* Krauss, and a fair number of endemics, such as *Melongenella incornuta* (Hözl), *Bullia hungarica* (Gábor), *Chicoreus trigonalis* (Gábor), *Pisanella doboi* (Noszky), and *Egerea collectiva* (Gábor). These considerable number of endemics grow distinctly smaller during the Early Miocene Eggenburgian, when faunistic ingressions from the west and south led to a turnover in composition.

The heavy influx of species from the northern bioprovince – herein called the *Proto-Eastern Atlantic–Boreal Region* (Fig. 3(left, bottom; right, top and bottom)) – characterises also the Oligocene gastropod fauna of the *Proto-Caspian Subprovince*. Northern elements such as *Drepanocheilus (Arrhoges) speciosa*, *Cassidaria buchildepressa*, *Ficus crassistria*, *Turritella planispira*, *Cancellaria evulsa*, and *Typhis pungens* reach the Aral and Caucasus basins (Oveckin, 1956; Alizade, 1968),

and northern turrids such as *Orthosurcula regularis* contribute to the fauna of the Ustjurt area (Amitrov, 1973). Endemism, however, is much stronger in the *Proto-Caspian Subprovince* throughout the Oligocene.

The second phase of a rather uniform Paratethys fauna, coinciding with the westward extension of the *Proto-Caspian Subprovince*, developed during the Early Miocene Kotsakhurian (corresponding to the Ottnangian). Again, the separation of the Eastern Paratethyan Sea coinciding with brackish water conditions is followed by a sudden evolutionary peak in bivalves, resulting in a large number of endemic genera such as *Limnopageta*, *Rzehakia*, *Lenticorbula*, or *Eoprosodacna* (Kvaliashvili, 1962; Voronina and Popov, 1985). This peculiar, so-called ‘*Rzehakia* fauna’ reaches even the Western and Central Paratethys Sea in the Late Ottnangian. Corresponding to the first isolation stage in the Early Oligocene, the Early Miocene *Proto-Caspian Subprovince* is more distinctly characterised by the bivalves than by the gastropod fauna (see also Ctyroky, 1972).

A complete disconnection of the Western/Central Paratethys and Eastern Paratethys began in the latest Early Miocene (Fig. 3(right, bottom)) and early Middle Miocene (Nevesskaja et al., 1987; Rögl, 1998). Good marine connections of the Western/Central Paratethys with the southern sea allowed immigration of ‘Mediterranean–Atlantic’ gastropods. At times of high immigration rates such as the late Early Miocene Karpatian or the early Middle Miocene Badenian the ‘Mediterranean’ character became overwhelming. The Karpatian gastropod fauna of Austria (Harzhauser, 2002) has only 25–30% Western Paratethys endemics – a percentage which is probably even too high, since several of the ‘endemic’ species are probably hidden in poorly described Mediterranean species groups. Anyway, the remaining 70–75% of these latest Early Miocene gastropods are typical inhabitants of the *Proto-Mediterranean–Atlantic Region*. In respect to biogeography this take-over by ‘Mediterranean–Atlantic’ gastropods within the *Danubian Province* and the low endemism requires an integration of the *Danubian Province* into the *Proto-Mediterranean–Atlantic Region* which thus consists of the *Mediterranean–Iranian*

*Province* at its core and the *Danubian Province*. This development was reversed during the late Middle Miocene Sarmatian when the isolation of the Central Paratethys from the adjacent seas may have caused a dramatic change of the water chemistry (Pisera, 1996) leading to a severe impoverishment of the marine fauna. Simultaneously, its reconnection with the Eastern Paratethys allowed the establishment of a rather uniform Sarmatian brackish gastropod fauna, being typical for the entire Paratethys Sea. During the latest Middle Miocene and earliest Late Miocene the marine cycle ended within the Paratethys and a brackish to freshwater lake system became installed.

#### 4.4. Transatlantic communication – witnessing an extensive *Tethys Realm*?

The Caribbean and adjacent tropical areas display a characteristic faunistic composition at least from the Late Cretaceous onwards (Kauffmann, 1973). During the Paleogene this is expressed in the formation of a distinct large Central American biogeographic unit, which roughly covers the geographic area of the modern Eastern Pacific and the Western Atlantic regions sensu Briggs (1995). However, within the Central American bioprovinces a surprising flair of familiarity with the *Western Tethys Region* is perceptible from the Eocene up to the Miocene.

Especially during the Paleogene, the Tethyan heritage is obvious, since genera such as *Ampullinopsis*, *Globularia*, *Terebralia*, or *Strombus* indicate immigration from the Tethyan bioprovince. The faunistic exchange between the amphiatlantic bioprovinces was a two-way story for sure, but due to the gaps in the fossil record, it is often unclear whether a taxon migrated from the Old World to the New World or vice versa. Although the amphiatlantic relations were discussed several times in the literature (e.g. Maury, 1902; Cooke, 1924; Gardner, 1924; Woodring, 1924a,b, 1928; Kautsky, 1925; Vokes, 1964–1986; Savazzi, 1989; Lozouet et al., 1994), this important migration pattern is yet hardly embodied in palaeobiogeographic concepts.

Especially during the Eocene some major mi-

grations across the Atlantic took place. Amongst the naticids the genera *Ampullinopsis* and *Globularia*, which both can be traced back to the Western Tethyan Eocene, reached the Americas during the Eocene. *Ampullinopsis* and the archaeogastropod *Velates* may be regarded as some of the most successful Tethyan gastropods during the Paleogene, since they are recorded from the eastern Pacific in the west to as far east as Pakistan or Burma. Tethyan affinities in the Eocene with the Americas are documented by a large number of taxa, usually on the generic level and rarely on species level. Palmer (1967) united some of those taxa of proposed Tethyan origin, e.g. the genera *Velates*, *Eovasum*, *Gisortia*, and *Terebellum*, in the so-called '*Velates perversus* Group'. This small list can be easily enlarged by data of Clarke and Vokes (1936), Givens (1978, 1989), Jung (1974), and Squires and Advocate (1986) to include the genera *Agaronia*, *Akera*, *Amaurellina*, *Ampullella*, *Ampullinopsis*, *Athleta*, *Buccinorbis*, *Calyptrophorus*, *Campanilopa*, *Chedevillia*, *Clavilithes*, *Cornulina*, *Crommium*, *Cryptochorda*, *Caricella*, *Ectinochilus*, *Eocithara*, *Eocypraea*, *Eopleurotoma*, *Galeodea*, *Gilbertina*, *Hipponix*, *Keilostoma*, *Laevityphis*, *Lyria*, *Mazzalina*, *Muricopsis*, *Paraseraphs*, *Pleurofusua*, *Sassia*, *Semicassis*, *Seraphs*, *Strepsidura*, *Streptochetus*, *Surculites* and *Volutilithes* – a list which is far from being complete. Another Middle Eocene similarity is documented by the endemic American *Dirocerithium*, which shows closest resemblance with the Tethyan genus *Bellatara* hinting at a common Tethyan ancestry (Woodring, 1959).

An excellent example for the intensive transatlantic relationship during the Paleogene are the strombids. The family arises during the Eocene when it develops a fair number of new taxa such as *Dilatilabrum*, *Orthaulax* and *Oostrombus*. The genus *Oostrombus*, well established in the Tethyan Eocene by species such as *Oostrombus auriculatus*, displays one of the most striking disjunct patterns. The genus has been recorded by Olsson (1931) as *Oostrombus chiraensis* from the Late Eocene Chira Formation of Peru, by Clarke and Durham (1946) as *Oostrombus cedroensis* from the Eocene of Colombia, and by Woodring (1959) as *Oostrombus* aff. *chiraensis* from the Mid-

dle or Late Eocene Gatuncillo Formation of Panama. From the Eocene onwards, the New World–Old World route can also be documented for the two seemingly typical Western Tethyan genera *Turbinella* and *Vasum*. *Turbinella* first appeared in the Late Eocene of Peru with *Turbinella peruviana* (Olsson). Thereafter, two lineages developed separately in the New and the Old World (Vokes, 1964). The latter is rooted in the earliest Old World species *Turbinella episoma* (Michelotti), which appears in the Western Tethyan Oligocene. Similarly, the genus *Vasum* developed in the New World where it is recorded from the Eocene of Louisiana. During the Oligocene the genus managed to pass the Atlantic barrier and, with *Vasum subpugillare* (d'Orbigny), is documented from the Oligocene of France. According to Vokes (1966) all Early Miocene Old World representatives of *Vasum* are very close to the ancestral Eocene New World species *Vasum humerosum* Vaughan. Correspondingly, the genus *Deromurex* appears in the Early Oligocene of the Mississippi Region, whilst its European counterpart is known only from the Late Oligocene of western France (Vokes, 1975a). The vicariating species pair is represented by the New World *Deromurex cookei* (Vokes) and the Old World *Deromurex cotteavi* (Meunier).

The opposite route was taken by some western Atlantic species of *Cheilea*. According to Vokes (1975b) the New World species *Cheilea equestris* (L.), which is first known from the Chipola Formation (NW Florida), is a descendent of the Eocene Old World *Cheila boutillieri* (Cossman). Correspondingly, *Cheila uncinata* (Reeve) can be traced to the European Eocene where *Cheila bernayi* (Cossman) is considered to be the ancestral form. Another amphiatlantic connection of a strombid taxon has been documented by Savazzi (1989) for the genus *Orthaulax*. It first appeared with *Orthaulax dainelli* in the early Middle Eocene of northern Italy but thereafter was ubiquitous in the Oligocene and Early Miocene of Central America. Correspondingly, the genus *Strombus* appeared in Tethyan Paleogene and crossed the Atlantic barrier during the Oligocene. Notice that, according to Woodring (1959), the genus – formerly mentioned from Eocene sediments in

Alabama as *Strombus albirupianus* by Dall (1890–1903) – has been only documented from the Late Oligocene of Georgia!

Correspondingly, the Western Atlantic representatives of *Aspella* originated in the European Oligocene (Vokes, 1975a) and '*Cerithium*' *halense* of Dall (1917) has its closest relatives amongst the Tethyan Oligocene potamidids usually assigned to '*Telescopium*' *charpentieri* or *Tympanotonos stropus*. This Oligocene migration from the Tethys into the tropical Americas is obviously not restricted to the gastropods but can also be documented for other molluscs. For example, the strange bivalve *Kuphus* is very common in the entire Mediterranean Oligocene and gained a foothold in the Mid-American area at least in the Late Oligocene (Mansfield, 1940). A cosmopolitan transatlantic character has been also reported for reef coral assemblages of the Eocene–Oligocene (Budd, 2000).

Beside these Eocene/Oligocene migrations, a remarkable and well-documented cross-Atlantic migration took place during the Burdigalian and probably early Middle Miocene. As far as can be judged from the fossil record the main route was from the Western Tethyan Region to the Western Atlantic, since many of the amphiatlantic taxa have their earliest record in the European Cenozoic.

The most convincing evidence for those migrations are amphiatlantic occurrences at the species level. Some of these species have been recognised in the Chipola Formation of northwestern Florida. E.g., *Eudolium* (*Galeodolium*) *subfasciatum* Sacco appears in the Burdigalian and early Middle Miocene of the Mediterranean area and in the Early Badenian of the Western Paratethys. In the Burdigalian the species also appears in the Cantare Formation of Venezuela and Chipola Formation of northwestern Florida (Vokes, 1986; Gibson-Smith and Gibson-Smith, 1988). Others, such as *Lindapterys*, are documented by highly similar species at both sides of the Atlantic (Lozouet et al., 1994). Similarly, *Calyptraea* (*Trochita*) *ornata* Basterot and *Calyptraea* (*Trochita*) *costaria* Grateloup have been recorded from the Chipola Formation and the European Aquitanian and Burdigalian (Vokes, 1975b). High similarities

between European Atlantic Burdigalian faunas and the Chipola fauna was also recognised by Dolin (1991) within the cypraeids. *Trona leporina calhounensis* Dolin has its origin in the Old World and emigrated to the Western Atlantic coast. The same has been suggested by Dolin (1991) for *Talparia dominicensis* (Gabb) and *Mauritia campbelliana* (Pilsbry).

However, the New World–Old World route is also documented. Following Dolin (1991) the Burdigalian Chipola species *Siphocypraea chilona* Dall seems to derive from a Caribbean stock and entered the Old World in the Early Miocene. Similarly, a migration from west to east is also supported by Bernasconi and Robba (1982) based on pteropods. According to Bernasconi and Robba (1982) the faunistic interchange of pteropods between the Caribbean and the Western Tethyan area occurred mainly from the Oligocene up to the Middle Miocene.

Less obvious at first sight, but very important as indicators of transatlantic faunal relations are some pairs that probably represent vicariating species. Worth mentioning and recently studied are pairs such as *Bursa* (*Bufronariella*) *pelouatensis* (Cossmann and Peyrot) from the Early Miocene of the Aquitaine Basin and *Bursa* (*Bufronariella*) *chipolana* Schmelz from the Burdigalian of Florida (Schmelz, 1997). The similarities are so striking that Vokes (1973) erroneously even considered the Florida species to be synonymous with the Old World gastropod. Vokes (1965a,b) also discussed the high similarities between the Florida and the European representatives of *Chicoreus* s.s. during the Late Burdigalian and the early Middle Miocene. According to her, the genus originated in the Tethyan area, having its roots in Eocene Old World muricids, such as '*Murex*' *tricarinatus* Lamarck. Vicariating or at least very similar amphiatlantic species pairs are *Chicoreus folioides* (Gardner), *Chicoreus lepidotus* (Vokes) and *Chicoreus dujardinioides* (Vokes) from the New World and *Chicoreus aquitanicus* (Grateloup), *Chicoreus bourgoisi* (Tournouer) and *Chicoreus dujardini* (Tournouer) from the early Middle Miocene of Europe. Similarly, Vokes (1974) mentioned *Pterotypis wenzelidesi* from the Badenian stage (early Middle Miocene) of the Vienna Basin and *Pterot-*

*typis vokesae* Gertman from the Chipola Formation as closely related species. Two further species with a European ancestry are mentioned by Vokes (1966, 1979) from the Early Miocene (Burdigalian?) of the Dominican Republic. Especially the Burdigalian *Vasum tuberculatum* Gabb can hardly be distinguished from the Aquitanian *Vasum aquitanicum* Peyrot from France and might even be conspecific (Vokes, 1966). Similarly, *Vasum pugnus* Pilsbry and Johnson seems to be a descendent of the French *Vasum stephanense* Peyrot, although a close relationship as discussed by Vokes (1966, 1979) seems to be unlikely due to the large stratigraphic gap between the Late Oligocene French occurrence and the alleged Burdigalian occurrence in the Americas (*Vasum stephanense* from St.-Etienne-d'Orthe is, according to Lozouet (1998), of Chattian age, whilst Peyrot (1928) formerly assigned the species to the Aquitanian).

The latest but subordinate Miocene transatlantic migration seems to be documented for the Late Miocene. A remarkable example of this event is the genus *Vittularia*, which is an Old World genus, appearing in the Oligocene of France. During the Early and Middle Miocene the genus, represented by *Vittularia linguabovis* (Basterot), becomes ubiquitous in the Mediterranean as well as in the Paratethys. In the New World it first appears during the Late Miocene (Vokes, 1967, 1977). Therefore, if a transatlantic migration is considered, some minor, occasional faunal exchange occurred even as late as the Late Miocene. Generally, the Miocene transatlantic exchange of biota is still insufficiently studied. For reef corals, for example, dispersal across the Atlantic from the Mediterranean to the Caribbean is considered to have ceased at the end of the Oligocene (Frost, 1977; Budd, 2000). Contrary, Riegl and Piller (in press) reported the genus *Mussismilia*, which was recorded from the Late Miocene as a mere Caribbean element (Budd, 2000), from the Middle Miocene of the Styrian Basin (*Danubian Province*).

However, the similarities between the Western Atlantic and the European faunas are too poor at any time to allow a comparison on a hierarchy lower than a biogeographic region. The Miocene

fauna of the ‘central’ part of this western *Region* has been very well studied, allowing a chiefly gastropod-based conception of the Miocene Mid-American bioprovinces as proposed by Woodring (1974). He defines a Miocene *Caribbean Region* (= province sensu Woodring, 1974), which is characterised by the bivalve *Clementia darienna* (Woodring) and a large number of gastropods, such as *Orthaulax*, *Strombina*, *Metula*, *Potamides suprasulcatus*, and *Stigmaulax guppiana*. This bioprovince falls apart into the *Mexican*, *West Indian*, *Central American–northern South American*, *Columbian–Venezuelan–Trinidad*, *Brazilian*, and *Ecuadorian–Peruvian provinces* (=subprovinces sensu Woodring, 1974). It is worth mentioning that Woodring’s Brazilian Province is based on the absence of taxa rather than on endemisms.

Despite the amphiatlantic similarities, which document some communication between two major biogeographic units, the Atlantic was a barrier for many Tethyan genera, such as *Pyrazus*, *Tibia* s.s., *Sulcogladius*, *Tudicla*, and *Amalda*. With respect to the large total gastropod faunas the percentage of shared species is rather small and requires a distinct separation of both biogeographic units on the level of a region. Many of the amphiatlantic taxa are only erratics within an otherwise independent Western Atlantic Region. Therefore, most authors studying the amphiatlantic distribution of tropical/subtropical molluscs in the Cenozoic considered a more or less occasional and accidental rafting of larvae as most probable mode of transportation, representing sweepstakes routes in terms of modern biogeography. However, there seem to be some distinct peaks of similarity between Western Tethyan and American gastropod faunas, e.g. during the Middle Eocene or the Burdigalian. Such peaks, if not an artefact due to lack of investigations or adequate faunas in the intervening intervals, might indicate changes in the Atlantic current systems, which repeatedly supported or suppressed the migration of larvae. Correspondingly, the amphiatlantic similarities are explained by Berggren and Hollister (1974) and Barron and Peterson (1991) by an early gyre-like Gulf Stream with limited poleward extension. According to the simulations of Barron

and Peterson (1991) this early Gulf Stream in the North Atlantic is evident even during the Eocene and Oligocene. In contrast, a ‘nearshore-hopping’ along the northern coasts as documented for some species in the Pleistocene can be excluded for all the amphiatlantic Eocene to Miocene taxa due to the strict climatic requirements of the warm-water faunas. Additionally, both faunas, especially the Mediterranean one, obviously reached a stage of equilibrium during the Miocene (Demarcq, 1987). Therefore, most of the intruders probably had little chance to gain a foothold. Despite the broad marine connections all these taxa rarely made their way in eastern direction into the Pacific. The distribution via the Atlantic strait is the only satisfying explanation, since evidence for a Pacific route is missing. The transatlantic migration route during the Eocene was also emphasised by Clarke and Vokes (1936), who stated that the similarities between the faunas of the American west coast and those of India are low, thus excluding an arrival via a Pacific migration route, which was even at that time probably obstructed by the East Pacific Barrier.

## 5. Conclusions

Several phases of major transatlantic faunal exchange can be deduced from the gastropod data on both sides. The first phase comprises the Eocene to Oligocene with an Eocene peak. It could probably be separated in several distinct migration waves, if stratigraphic resolution would be better. A first westward migration wave is documented for Early Eocene or even Late Paleocene times (Squires and Advocate, 1986). The second phase spans the Burdigalian and the early Middle Miocene. This phase is very well documented and again might be composed of two minor waves. The first being characterised by migrations from the Old World into the Western Atlantic coastal faunas mainly during the Burdigalian. The second took place somewhat later in the early Middle Miocene, when American species or their closely related forms suddenly appeared in European sections. Finally, a third phase may be suggested for the Late Miocene. However, data documenting

this phase are scanty and the impact on the faunas on both sides of the Atlantic was very low.

The western Atlantic coast – similar to the Indo-Pacific in late Early Miocene times for genera such as *Tibia* and *Tudicla* – obviously acted as refuge for several Tethyan genera such as *Ampullinopsis* and *Orthaulax*, which managed to pass the Paleogene/Neogene boundary in the Americas but became extinct in the European bioprovinces.

Altogether the data furnish evidence for a circum-equatorial, Paleogene *Tethys Realm* which extended from Peru (Eastern Pacific!) through the early *Caribbean Region* across the Atlantic and the entire Mediterranean basins at least as far east as Indonesia in the Eocene. During the Oligocene this biogeographic unit still extended from the Mid-Americas via Pakistan and eastern Africa to Indonesia with at least one centre of origin in the Mediterranean basins. In contrast, an equivalent centre of origin is missing at that time in the Proto-Indo-Polynesian Province.

The similarities of the Mediterranean, the Iranian, the Pakistanian and the eastern African gastropod faunas during the Oligocene requires to unite them in a *Western Tethyan Region*, which otherwise can be split into a *Mediterranean–Iranian Province* (Western and Eastern Mediterranean, Cyrenaica, Armenia, Libya, Syria, Palestine, Central Iran), and a *Western Indian–Eastern African Province* (Oman, Pakistan, Somalia, Zanzibar, Kenya, Madagascar). A third province was probably established along the shores of the Eastern Atlantic (France).

The gastropod fauna of the *Proto-Indo-West Pacific Region* developed in an area, which is similar to the geographic extension of the modern *Indo-Polynesian Province* but did not dominate the Oligocene faunas of the *Western Indian–Eastern African Province*. Therefore, the often advocated ‘Indo-Pacific’ influence on Oligocene and Early Miocene Central European faunas seems to be a myth. However, with the Early Miocene the Indo-Pacific gastropod fauna established itself within the area of the former *Western Indian–Eastern African Province* and replaced the ‘Indo-European’ fauna completely.

The Paratethys Sea represents a distinct biogeographic

entity – the *Danubian Province*. At least at the subprovince level a separation of the eastern *Proto-Caspian Subprovince* is necessary. The *Danubian Province* was always influenced by high immigration rates from the adjacent northern (Oligocene) and/or the southern (Oligocene–Miocene) bioprovinces. During phases of restricted marine connections and salinity crises the *Danubian Province* was repeatedly threatened by the expansion of the *Proto-Caspian Subprovince*.

In the Early Miocene a rather homogeneous *Proto-Mediterranean–Atlantic Region* formed (France, entire Mediterranean, Central Iran). During times of high emigration into the adjacent Paratethys Sea, the *Danubian Province* has to be treated as part of the *Proto-Mediterranean–Atlantic Region* (latest Early Miocene through early Middle Miocene). The biogeographic affiliation and hierarchical position of the *Proto-Caspian Subprovince*, however, is obscure with respect to the poor data on gastropods from the Eastern Paratethys.

Generally, endemism in the Paratethyan gastropod fauna is low compared to that of bivalves until the beginning isolation in the Sarmatian (late Middle Miocene). In contrast to bivalves, the composition of the gastropod fauna was often massively influenced by immigrants rather than by local evolution.

## Acknowledgements

The authors thank Fred Rögl and Ortwin Schultz (Museum of Natural History, Vienna) for fruitful discussions and for helpful comments on an earlier draft of this paper. We are also grateful to Oleg Mandic (Institute for Palaeontology, Vienna) for information on bivalve distribution. Our special thanks go to the members of the research projects on Late Oligocene–Early Miocene circum-Mediterranean palaeobiological relations, A. Kroh (Graz), F. Schuster (Tübingen), and U. Wielandt-Schuster (Frankfurt). This work was supported by the Austrian FWF (P11886-GEO) and the Deutsche Forschungsgemeinschaft (STE 857/1-1).

## Appendix 1

Observed occurrences of gastropod taxa in studied basins: 1 Greece – Mesohellenic Trough (Oligocene); 2: Iran – Esfahan–Sirjan Basin (Oligocene); 3: Iran – Esfahan–Sirjan Basin (Early

Miocene, Aquitanian); 4: Greece – Mesohellenic Trough (Early Miocene, Aquitanian); 5: Iran – Qom Basin (Early Miocene, Burdigalian); 6: Greece – Mesohellenic Trough (Early Miocene, Burdigalian); 7: Turkey – Mut Basin (Early Miocene, Burdigalian)

Gastropod taxa	1	2	3	4	5	6	7
<i>Nerita (Theliostyla) plutonis</i> Basterot	o				o		o
<i>Nerita (Theliostyla) asperata</i> Dujardin					o		
<i>Nerita caronis</i> Brongniart		o					
<i>Agapilia picta</i> (Férussac)		o		o	o		o
<i>Theodoxus? grateloupianus</i> (Férussac)				o			
<i>Gibbula buchi</i> (Dubois)					o		
<i>Gibbula affinis</i> (Eichwald)					o		
<i>Clanculus (Clanculopsis) araeonis</i> (Basterot)					o		
<i>Clanculus cerberi</i> (Brongniart)		o					
<i>Paroxystele amedei</i> (Brongniart)						o	o
<i>Jujubinus</i> aff. <i>bucklandi</i> (Basterot)			o				
<i>Jujubinus</i> aff. <i>subcarinatus</i> (Lamarck)	o	o					
<i>Jujubinus</i> sp.					o		
<i>Angaria scobina</i> (Brongniart)	o	o					
<i>Tectus</i> nov. sp. 1		o					
<i>Tectus?</i> nov. sp. 2		o					
<i>Tectus</i> sp.			o				
<i>Tectus</i> cf. <i>rugosus</i> (Grateloup)			o				
<i>Tectus lucasianus</i> (Brongniart)	o	o					
<i>Turbo</i> nov. sp.	o						
<i>Turbo</i> cf. nov. sp.		o					
Turbinidae Operculum indet.		o					
<i>Littorina?</i> sp.		o					
<i>Peasiella</i> cf. <i>girondica</i> Benoist		o					
<i>Grevenilla mesohellenica</i> Harzhauser and Kowalke				o			
<i>Protoma cathedralis</i> (Basterot)			o			o	
<i>Protoma quadriplicata</i> (Basterot)			o		o		
<i>Peyrotia tauroperiturrus</i> (Sacco)					o		
<i>Peyrotia strangulata</i> (Grateloup)	o		o		o		
<i>Peyrotia desmarestina</i> (Basterot)		o	o		o	o	
<i>Turritella (Turritella) terebralis</i> Lamarck					o	o	o
<i>Turritella (Turritella) gradata</i> Menke						o	o
<i>Turritella (Haustator) venus</i> d'Orbigny	o	o		o			
<i>Turritella (Haustator) asperula</i> Brongniart	o	o					
<i>Turritella (Haustator) conofasciata</i> (Sacco)	o						
<i>Turritella (Haustator) vermicularis</i> Brocchi						o	o
<i>Turritella (Haustator) eryna</i> d'Orbigny						o	o
<i>Turritella (Zaria) angulata</i> Sowerby			o				
<i>Turritella</i> cf. <i>subtriplicata</i> d'Orbigny							o
<i>Tenagodus</i> cf. <i>anguinus</i> Linné		o					
<i>Melanopsis impressa</i> Krauss	o			o			
<i>Bellatara palaeochroma</i> nov. ssp.	o						
<i>Campanile charpentieri</i> (Basterot)	o						
<i>Campanile</i> sp.			o				
<i>Terebralia bidentata lignitarum</i> (Eichwald)					o		o
<i>Terebralia bidentata</i> (Defrance)	o			o	o		
<i>Terebralia</i> aff. <i>subcorrugata</i> (d'Orbigny)		o					

Gastropod taxa	1	2	3	4	5	6	7
<i>Terebralia</i> aff. <i>subcorrugata subinterrupta</i> (d'Orbigny)		o					
<i>Granulolabium plicatum</i> (Bruguiere)	o	o		o			
<i>Granulolabium</i> ( <i>Tiaracerithium</i> ) <i>pseudotiarella</i> (d'Orbigny)				o			
<i>Granulolabium</i> ( <i>Tiaracerithium</i> ) nov. sp.		o					
<i>Granulolabium</i> ( <i>Tiaracerithium</i> ) cf. nov. sp.			o				
<i>Granulolabium pictum mitralis</i> (Eichwald)							o
<i>Tympanotonos margaritacus</i> (Brocchi)	o			o			
<i>Tympanotonos stropus</i> (Brongniart)	o	o					
<i>Pyrazus daemon</i> (Oppenheim)	o						
<i>Gourmya romeo</i> (Bayan)	o						
<i>Clava ampullosa</i> (Brongniart)	o						
<i>Clava voglinoi</i> (Michelotti)	o						
<i>Cerithium calculosum</i> Defrance	o	o		o			
<i>Cerithium vulgatum</i> Bruguière					o		o
<i>Cerithium globulosum</i> Deshayes	o						
<i>Cerithium</i> ex gr. <i>granulinum</i> (Bellardi and Michelotti)		o					
<i>Cerithium</i> ( <i>Ptychocerithium</i> ) <i>bronni turritoplicatum</i> Sacco					o		
<i>Cerithiidae</i> indet. 1		o					
<i>Cerithiidae</i> indet. 2		o					
<i>Hemicerithium?</i> sp.		o					
<i>Diastoma costellatum elongatum</i> (Brongniart)	o	o					
<i>Diastoma</i> cf. <i>alpinum</i> (Tournouer)		o					
<i>Agapibittium grevenienae</i> Harzhauser and Kowalke				o			
<i>Bayania semidecussata</i> (Lamarck) nov. ssp.		o					
<i>Aporrhais meridionalis</i> (Basterot)					o		
<i>Aporrhais uttingerianus</i> (Risso)				o			o
<i>Tibia dentata</i> (Grateloup)					o		o
<i>Rimella</i> ( <i>Dientomochilus</i> ) <i>decussata</i> (Defrance)				o			
<i>Rimella subrimosa</i> d'Orbigny		o					
<i>Oostrombus auriculatus</i> (Grateloup)		o					
<i>Oostrombus irregularis</i> (Fuchs)		o					
<i>Strombus</i> ( <i>Dilatilabrum</i> ) <i>roegli</i> Harzhauser	o	o	o				
<i>Strombus radix</i> (Brongniart)	o	o					
<i>Strombus bonelli</i> (Brongniart)			o		o	o	o
<i>Strombus</i> sp.			o				
<i>Xenophora cumulans</i> (Brongniart)	o	o					
<i>Xenophora deshayesi</i> (Michelotti)					o	o	o
<i>Xenophora</i> cf. <i>deshayesi</i> (Michelotti)			o				
<i>Xenophora</i> nov. sp.			o				
<i>Calyptraea</i> cf. <i>chinensis</i> (Linné)			o				
<i>Hipponix</i> cf. <i>interruptus</i> Michelotti		o					
<i>Cypraea</i> cf. <i>globosa</i> (Dujardin)	o						
<i>Cypraea</i> cf. <i>subovum</i> (d'Orbigny)			o				
<i>Cypraea</i> ( <i>Zonaria</i> ) cf. <i>fabagina</i> Lamarck							o
<i>Cypraea</i> sp. 1		o					
<i>Cypraea</i> sp. 2			o				
<i>Cypraea</i> sp. 3			o				
<i>Cypraea</i> sp. 4			o				
<i>Cypraea</i> sp. 5					o		
<i>Cypraea</i> sp. 6					o		
<i>Cypraea</i> sp. 7					o		
<i>Proadusta inquitens inaequilabiata</i> (Sacco)	o						
<i>Proadusta parvitala</i> (Sacco)	o	o					
<i>Trivia?</i> sp.		o					
<i>Ampullinopsis crassatina</i> (Lamarck)	o	o					



Gastropod taxa	1	2	3	4	5	6	7
<i>Globularia gibberosa</i> (Grateloup)	o	o					
<i>Globularia</i> cf. <i>callosa</i> (Sowerby)			o				
<i>Natica</i> sp.			o				
<i>Natica tigrina</i> (Defrance)					o	o	o
<i>Natica</i> cf. <i>subepiglottina</i> d'Orbigny				o	o		
<i>Polinices</i> cf. <i>redemptus</i> (Michelotti)					o		
<i>Euspira catena helicina</i> Brocchi				o			o
<i>Natica burdigalensis</i> Mayer							o
<i>Neverita olla</i> (De Serres)	o				o	o	o
<i>Amaurellina</i> ( <i>Euspirocrommium</i> ) <i>oweni</i> (Archiac and Haime)					o		
<i>Amaurellina</i> ( <i>E.</i> ) aff. <i>sindiensis</i> (Cossmann and Pissarro)					o		
<i>Amaurellina</i> sp. 1			o				
<i>Amaurellina</i> sp. 2		o					
<i>Sinum michaudi</i> (Michelotti)				o			
<i>Sinum aquensis</i> (Recluz)		o					
<i>Sinum</i> cf. <i>striatum</i> (De Serres)						o	
<i>Sinum</i> sp.	o						
<i>Cassis mamillaris</i> Grateloup	o	o				o	
<i>Cassis vialensis</i> Fuchs		o					
<i>Cassis</i> sp.		o					
Cassididae indet.			o				
<i>Galeodea</i> ? sp.						o	
<i>Semicassis</i> cf. <i>rondeleti apenninica</i> (Sacco)	o						
<i>Semicassis grateloupi</i> (Deshayes)						o	
<i>Sconsia striata miocenica</i> Sacco					o		o
<i>Eudolium subfasciatum</i> Sacco				o			
<i>Cassidaria</i> cf. <i>tauropomum</i> Sacco					o		
<i>Sassia apenninica</i> (Sassi)					o		
<i>Sassia</i> cf. <i>flandrica</i> (De Koninck)	o						
<i>Charonia</i> sp.		o					
Cymatiidae indet.					o		
<i>Cymatium</i> ? sp. 1					o		
<i>Cymatium</i> ? sp. 2					o		
<i>Ficus condita</i> (Brongniart)			o	o	o	o	o
<i>Ficus cingulata</i> (Bronn)							o
<i>Ficus oligoficoides</i> (Sacco)	o						
<i>Ficus</i> sp.					o		
<i>Ficopsis</i> ( <i>Fulguroficus</i> ) <i>burdigalensis</i> (Sowerby)							o
<i>Cerithiopsis</i> sp.		o					
<i>Murex partschi</i> ssp.							o
<i>Murex</i> ( <i>Haustellum</i> ) <i>tchihatcheffi</i> Archiac and Haime					o		
<i>Pterynopsis</i> cf. <i>tristichus</i> (Beyrich)	o						
<i>Editharus polygonus</i> (Lamarck)		o					
<i>Cymia hellenica</i> Harzhauser and Kowalke				o			
<i>Euthriofusus burdigalensis</i> (Defrance)							o
<i>Dorsanum</i> ( <i>Dorsanum</i> ) <i>haueri excellens</i> (Schaffer)				o			
<i>Nassarius</i> ( <i>Hinia</i> ) nov. sp.				o			
<i>Nassarius</i> sp. 1					o		
<i>Nassarius</i> sp. 2					o		
<i>Nassarius</i> cf. <i>semistriata</i> (Brocchi)							o
<i>Nassarius</i> cf. <i>restitutianus</i> (Fontannes)							o
<i>Nassarius</i> sp. cf. <i>limatus</i> Chemnitz							o
<i>Melongena lainei</i> (Basterot)				o	o		o
<i>Melongena semseyiana</i> (Erdős)	o						
<i>Melongena</i> cf. <i>semseyiana</i> (Erdős)		o					

Gastropod taxa	1	2	3	4	5	6	7
<i>Melongena cornuta</i> (Agassiz)						o	
<i>Melongena subcarinata</i> (Lamarck)	o						
<i>Melongena</i> aff. <i>basilica</i> (Bellardi)			o				
<i>Melongena</i> sp.			o				
<i>Pleuroploca tarbelliana</i> (Grateloup)							o
<i>Latirulus</i> sp.			o				
<i>Fusinus</i> cf. <i>costellatus</i> (Grateloup)	o						
<i>Streptodictyon</i> cf. <i>subelongatus</i> (d'Orbigny)	o						
<i>Mitrella</i> ( <i>Atilia</i> ) <i>fallax</i> (Hörnes and Auinger)							o
<i>Acamptochetus submitraeformis</i> (d'Orbigny)							o
<i>Siphonalia</i> sp.					o		
<i>Tudicla rusticola</i> (Basterot)			o		o		o
<i>Turbinella episoma</i> (Michelotti)		o					
<i>Mitra</i> sp.					o		
<i>Amalda</i> ( <i>Baryspira</i> ) <i>glandiformis</i> Lamarck				o		o	o
<i>Amalda</i> ( <i>Baryspira</i> ) <i>glandiformis anomala</i> (Schlotheim)	o						
<i>Oliva</i> ( <i>Anazola</i> ) cf. <i>clavula</i> (Lamarck)	o	o					
<i>Oliva</i> ( <i>Strephona</i> ) <i>dufresnei</i> Basterot				o			
<i>Olivella</i> cf. <i>longispira</i> Bellardi					o		
<i>Athleta</i> ( <i>Athleta</i> ) <i>consanguinea</i> (Bellardi)	o						
<i>Athleta</i> ( <i>Athleta</i> ) <i>ficulina</i> (Lamarck)				o	o	o	o
<i>Volutilithes subambigua</i> d'Orbigny							
<i>Lyria magorum angustolonga</i> Sacco			o				
<i>Lyria anceps</i> (Michelotti)	o	o					
<i>Lyria</i> cf. <i>anceps</i> (Michelotti)							
<i>Sveltia</i> sp.						o	
<i>Terebra subtessellata</i> d'Orbigny		o					
<i>Terebra pertusa</i> Basterot						o	
<i>Terebra</i> cf. <i>pertusa subacuminata</i> Peyrot				o			
<i>Conus</i> ( <i>Conolithus</i> ) <i>antediluvianus</i> Bruguière						o	o
<i>Conus</i> ( <i>Conolithus</i> ) <i>dujardini</i> Deshayes				o	o	o	o
<i>Conus</i> ( <i>Lithoconus</i> ) <i>antiquus</i> Lamarck						o	o
<i>Conus</i> ( <i>Lithoconus</i> ) cf. <i>mercati</i> (Brocchi)					o		o
<i>Conus</i> ( <i>Lithoconus</i> ) nov. sp.					o		
<i>Conus</i> ( <i>Stephanoconus</i> ) cf. <i>carcarensis</i> (Sacco)			o				
<i>Conus</i> ( <i>Leptoconus</i> ) <i>diversiformis</i> Deshayes	o	o					
<i>Conus</i> sp. 1			o				
<i>Conus</i> sp. 2			o				
<i>Conus</i> sp. 3					o		
<i>Genota ramosa</i> (Basterot)				o	o	o	
<i>Acamptogenotia intorta</i> Brocchi							o
<i>Bathytoma cataphracta</i> (Brocchi)						o	
<i>Clavatula asperulata</i> (Lamarck)					o	o	o
<i>Clavatula</i> cf. <i>glaberrima</i> (Grateloup)					o		
<i>Clavatula</i> cf. <i>carinifera</i> Grateloup							o
<i>Clavatula calcarata</i> Grateloup ssp.				o			
<i>Clavatula</i> sp. 1		o					
<i>Clavatula</i> sp. 2			o				
<i>Clavus</i> sp.					o		
<i>Raphitoma</i> sp. 1					o		
<i>Raphitoma</i> sp. 2					o		
<i>Turris</i> cf. <i>monilis</i> (Brocchi)					o		
<i>Turris</i> sp. 1					o		
<i>Turris</i> sp. 2	o						
<i>Turridae</i> indet. 1						o	

Gastropod taxa	1	2	3	4	5	6	7
<i>Turridae</i> indet. 2						o	
<i>Stenodrillia obeliscus</i> (Desmoulins)				o			
<i>Scaphander lignarius grateloupi</i> (Michelotti)					o	o	
<i>Sabatia</i> aff. <i>utriculus</i> (Brocchi)					o		
<i>Bulla</i> ? sp.					o		
<i>Architectonica</i> cf. <i>umbrosa</i> (Brongniart)		o					
<i>Architectonica carocollata</i> (Lamarck)				o			
<i>Architectonica</i> sp.						o	
<i>Otopleura mitrula</i> (Basterot)				o			
<i>Ringicula auriculata paulucciae</i> Morlet							o
<i>Limacina mirostralis</i> (Kautsky)							o
<i>Vaginella depressa</i> Daudin							o

## References

- Abbott, R.T., 1960. The genus *Strombus* in the Indo-Pacific. Indo-Pac. Mollusca 1 (2), 33–146.
- Alizade, K.A., 1968. The Oligocene Deposits of the Maly Caucasus. Baku, pp. 1–120 (in Russian).
- Amitrov, O.V., 1973. Late Eocene-Early Miocene turrids from South of the USSR. Trans. Palaeontol. Inst. NAUKA 135, 1–212.
- Azzaroli, A., 1958. L'Oligocene e il Miocene della Somalia: Stratigrafia, tettonica, paleontologia (Macroforaminiferi, Coralli, Molluschi). Paleontol. Ital. 57, 1–143.
- Baldi, T., 1973. Mollusc Fauna of Hungarian Upper Oligocene (Egerian). Akad. Kiado, Budapest, pp. 1–511.
- Baldi, T., 1986. Mid-Tertiary Stratigraphy and Paleogeographic Evolution of Hungary. Akad. Kiado, Budapest, pp. 1–201.
- Baldi, T., Senes, J., 1975. OM, Egerien. Die Egerer, Pouzdraner, Puchkirchener Schichtgruppe und die Breikaer Formation. Chronostratigraphie und Neostatotypen 5. Veda, Bratislava, pp. 1–577.
- Barron, E.J., Peterson, W.H., 1991. The Cenozoic ocean circulation based in ocean General Circulation Model results. Palaeogeogr. Palaeoclimatol. Palaeoecol. 83, 1–28.
- Beets, C., 1942. Beiträge zur Kenntnis der angeblich oberoligozoenen Mollusken-Fauna der Insel Buton, Niederländisch-Ostindien. Leid. Geol. Meded. 13, 255–328.
- Beets, C., 1943. Weitere Verwandtschaftsbeziehungen zwischen den oberoligozoenen Mollusken von Buton (S.E. Celebes) und den Neogenfaunen des Ostindischen Archipels. Leid. Geol. Meded. 13, 348–355.
- Bellardi, L., 1872–1890. I Molluschi dei terreni terziari del Piemonte e della Liguria. R. Accad. Sci. Torino, pp. 1–6.
- Berggren, W., Hollister, C., 1974. Paleogeography, paleobiogeography and the history of the circulation in the Atlantic Ocean. In: Hay, W.W. (Ed.), Studies in Paleo-Oceanography. Soc. Econ. Paleontol. Miner. Spec. Publ. 20, 126–186.
- Bernasconi, M.P., Robba, E., 1982. The Thecosomatous Pteropods: A contribution toward the Cenozoic Tethyan paleobiogeography. Boll. Soc. Paleontol. Ital. 21, 211–222.
- Briggs, J.C., 1995. Global Biogeography. In: Developments in Palaeontology and Stratigraphy 14. Elsevier, Amsterdam, 452 pp.
- Brunn, J.H., 1956. Contribution à l'étude géologique du Pinde septentrionale et d'une partie de la Macédonie occidentale. Ann. Géol. Pays Hellén. 7, 1–358.
- Budd, F.A., 2000. Diversity and extinction in the Cenozoic history of Caribbean reefs. Coral Reefs 19, 25–35.
- Cahuzac, B., Poignant, A., 1997. Essai de biozonation de l'Oligo-Miocène dans les bassins européens à l'aide des grands foraminifères néritiques. Bull. Soc. Géol. France 168, 155–169.
- Cicha, I., Senes, J., Tejkal, J., 1967. M3 (Karpatischen). Die Karpatische Serie und ihr Stratotypus. Chronostratigraphie und Neostatotypen, Miozän der Zentralen Paratethys 1. Bratislava.
- Clarke, B.L., Vokes, H.E., 1936. Summary of marine Eocene sequence of Western North America. Bull. Geol. Soc. Am. 47, 851–878.
- Clarke, B.L., Durham, J.W., 1946. Eocene faunas from the Department of Bolivar, Colombia. Geol. Soc. Am. Mem. 16, 126 pp.
- Collignon, M., Cottreau, J., 1927. Paléontologie de Madagascar. XIV. Fossiles du Miocène marin. Ann. Paléont. 16, 135–170.
- Cooke, C.W., 1924. American and European Eocene and Oligocene mollusks. Bull. Geol. Soc. Am. 35, 851–856.
- Cossmann, M., Peyrot, A., 1909–1934. Conchologie Néogène de l'Aquitaine. Act. Soc. Linnée de Bordeaux.
- Cotter, G.P., 1923. The Lamellibranchiata of the Eocene of Burma. Mem. Geol. Surv. India, Palaeontol. Ind. N.S. 7, Mem. 2, 1–38.
- Cox, L.R., 1930a. Miocene Mollusca. In: McKinnon Wood, M. (Ed.), Reports on geological collections from the coastlands of Kenya Colony. Monographs of the Geological Department of the Hunterian Museum. Glasgow University, Glasgow 4, 103–112.
- Cox, L.R., 1930b. The fossil fauna of the Samana Range and

- some neighbouring areas: Part VIII. The mollusca of the Hangu Shales. Mem. Geol. Surv. India, Palaeontol. Ind. N.S. 15, 129–222.
- Cox, L.R., 1936. Fossil mollusca from southern Persia (Iran) and Bahrein Island. Mem. Geol. Surv. India, Palaeontol. Ind. N.S. 22, Mem. 2, 1–69.
- Ctyroký, S., 1972. Die Molluskenfauna der *Rzehakia* (*Onco-phora*) Schichten Mährens. Ann. Naturhist. Mus. Wien 76, 41–141.
- Dall, W.H., 1890–1903. Contributions to the Tertiary fauna of Florida. Wagner Free Inst. Sci. Trans. 3–6, 1654 pp.
- Dall, W.H., 1917. A contribution to the invertebrate fauna of the Oligocene beds of Flint River, Georgia. Proc. US Natl. Mus. 51, 487–523.
- Davies, A.M., 1923. The fauna of the Miocene of Ceylon. Q. J. Geol. Soc. 79, 584–602.
- Davoli, F., 1989. Olividae (Gastropoda) miocenici: Ultima testimonianza nell'area mediterranea di un clima intertropicale. Boll. Soc. Paleontol. Ital. 28, 101–132.
- de Grateloup, J.S.S., 1840. Conchyliologie Fossile des Terrains Tertiaires du Bassin de l'Adour (Environs de Dax). I. Univalves (Atlas). Bordeaux.
- de Lattin, G., 1967. Grundzüge der Zoogeographie. Fischer, Jena.
- Demarcq, G., 1987. Palaeothermic evolution during the Neogene in Mediterranean through the marine megafauna. Ann. Inst. Geol. Publ. Hung. 70, 371–375.
- Dermitzakis, M., Georgiades-Dikeoulia, E., 1987. Biozonation of the Neogene invertebrate megafauna of the Hellenic area. Ann. Inst. Geol. Publ. Hung. 70, 125–136.
- Dolin, L., 1991. Cypraeoidea and lamellarioidea (Mollusca: Gastropoda) from the Chipola Formation (Late Early Miocene) of northwestern Florida. Tulane Stud. Geol. Paleontol. 24, 1–60.
- d'Orbigny, A., 1852. Prodrome de Paléontologie stratigraphique universelle des Animaux Mollusques et Rayonnés 3. Victor Masson, Paris, pp. 1–189.
- Douglas, J.A., 1927. Contributions to Persian Palaeontology. I. 1–15, Anglo-Persian Oil Company. Holywell Press, London.
- Douglas, J.A., 1928. Contributions to Persian Palaeontology. III. 1–19, Anglo-Persian Oil Company. Holywell Press, London.
- Ekman, S., 1934. Indo-Westpazifik und Atlanto-Ostpazifik, eine tiergeographische Studie. Zoogeography 2.
- Ekman, S., 1953. Zoogeography of the Sea. A Comprehensive Marine Animal Geography which is Invaluable in its Field. Sidgwick and Jackson, London.
- Frost, S.H., 1977. Oligocene reef coral biogeography, Caribbean and western Tethys. Mém. Bur. Rech. Géol. Min. 89, 342–352.
- Fuchs, T., 1870. Beitrag zur Kenntnis der Conchylienfauna des Vicentinischen Tertiärgebirges. Denkschr. Math. Nat.-Wiss. Classe Kais. Akad. Wiss. 30, 137–216.
- Gardner, J., 1924. Coastal plain and European and Oligocene mollusks. Bull. Geol. Soc. Am. 35, 857–866.
- Gibson-Smith, J., Gibson-Smith, W., 1988. Further notes on *Eudolium* (*Galeodolium*) *subfasciatum*. Tulane Stud. Geol. Paleontol. 21, 119.
- Givens, C.R., 1978. An occurrence of the Tethyan genus *Volutilithes* (Gastropoda: Volutidae) in the Eocene of California. J. Paleontol. 62, 104–108.
- Givens, C.R., 1989. First record of the Tethyan genus *Volutilithes* (Gastropoda: Volutidae) in the Paleogene of the Gulf coastal plain with a discussion of Tethyan molluscan assemblages in the Gulf coastal plain and Florida. J. Paleontol. 63, 852–856.
- Grecchi, G., 1978. Problems connected with the recorded occurrence of some Mollusks of Indo-Pacific affinity in the Pliocene of the Mediterranean area. Ist. Geol. Paleontol. Univ. Milano, N.S. 275 84, 797–812.
- Hardenbol, J., Jacquin, T., Vail, P.R. (Eds.), 1998. Mesozoic and Cenozoic Sequence Stratigraphy of European basins. SEPM Spec. Publ. 60, 1–786.
- Harzhauser, M., 2000. Paleobiogeography and Paleocology of Oligocene and Lower Miocene Gastropods in the Eastern Mediterranean and the Western Indo-Pacific. Unpubl. PhD Thesis, University Vienna, Vienna, 284 pp.
- Harzhauser, M., 2002. Marine and brachyhaline Gastropoden aus dem Karpatium des Korneuburger Beckens und der Kreuzstettener Bucht (Österreich, Untermiozän). Beitr. Paläontol. 27, 61–159.
- Hedgpeth, J.W., 1957. Marine biogeography. In: Treatise on Marine Ecology and Paleocology, 1. Mem. Geol. Soc. Am. 67, 359–382.
- Hözl, O., 1962. Die Molluskenfauna der oberbayrischen marinen Oligocänmolasse zwischen Isar und Inn und ihre stratigraphische Auswertung. Geol. Bavarica 50, 1–143.
- Hörnes, M., 1856. Die fossilen Mollusken des Tertiär Beckens von Wien, 1. Gastropoden. Abh. Geol. Reichsanst. 3 (1870), 1–404.
- Hörnes, R., Auinger, M., 1879–1891. Die Gastropoden der Meeresablagerungen der ersten und zweiten Miozänen Mediterranstufe in der österreichischen- ungarischen Monarchie. Abh. K.K. Geol. Reichsanst. 12, 1–382.
- Hsü, K.J., Bernoulli, D., 1978. Genesis of the Tethys and the Mediterranean. Init. Rep. DSDP 42, 943–949.
- Hsü, K.J., Montadert, L., Bernoulli, D., Cita, M.B., Erickson, A., Garrison, R.E., Kidd, R.B., Mélières, F., Müller, C., Wright, R., 1978. History of the Mediterranean salinity crisis. Init. Rep. DSDP 42, 1053–1078.
- Iqbal, M.W.A., 1969a. Bibliography of Tertiary pelecypod and gastropod species of West Pakistan. Rec. Geol. Surv. Pakistan 18, 1–63.
- Iqbal, M.W.A., 1969b. The Tertiary pelecypod and gastropod fauna from Drug, Zindapir, Vidor (district D.G. Khan), Jhalar and Chharat (district Campbellpore), West Pakistan. Mem. Geol. Surv. Pak. Palaeontol. Pak. 6, 1–77.
- Iqbal, M.W.A., 1980. Oligo-Miocene bivalves and gastropods from Kithar province, Lower Indus Basin, Pakistan. Rec. Geol. Surv. Pak. 51, 1–59.
- Jones, R.W., 1999. Marine invertebrate (chiefly foraminiferal) evidence for the palaeogeography of the Oligocene-Miocene of western Eurasia, and consequences for terrestrial verte-

- brate migration. In: Agusti, J., Rook, L., Andrews, P. (Eds.), *Hominid Evolution and Environmental Change in the Neogene of Europe*. Cambridge Univ. Press, Cambridge, pp. 274–308.
- Jones, R.W., Simmons, M.D., 1996. A review of the stratigraphy of eastern Paratethys (Oligocene-Holocene). *Bull. Nat. Hist. Mus. Lond. (Geol.)* 52, 25–49.
- Jung, P., 1974. A revision of the family Seraphsidae (Gastropoda): Strombacea. *Palaeontogr. Am.* 8, 72 pp.
- Kauffmann, E.G., 1973. Cretaceous bivalvia. In: Hallam, A. (Ed.), *Atlas of Palaeobiogeography*. Elsevier, Amsterdam, pp. 353–383.
- Kauffmann, E.G., Scott, R.W., 1976. Basic concepts of community ecology and paleocology. In: Scott, R.W., West, R.R. (Eds.), *Structure and Classification of Paleocommunities*. Dowden, Hutchinson and Ross, Stroudsburg, pp. 1–28.
- Kautsky, F., 1925. Die boreale und mediterrane Provinz des europäischen Miozäns und ihre Beziehungen zu den gleichaltrigen Ablagerungen Amerikas. *Mitt. Geol. Ges. Wien* 18, 28–67.
- Kilburn, R., Rippey, E., 1982. *Sea Shells of Southern Africa*. Macmillan, Johannesburg, pp. 1–240.
- Kvaliashvili, G.A., 1962. The oncophora (Rzehakia) formation of Eurasia. *Acad. Nauk Gruzinskoi SSR, Tbilisi*, pp. 1–231 (in Russian with English abstract).
- Laskarev, V.N., 1924. Sur les équivalents du Sarmatien supérieur en Serbie. *Zborn. Cvijic* 73–85.
- Lehmann, U., 1996. *Paläontologisches Wörterbuch*. Ferdinand Enke, Stuttgart.
- Longhurst, A., 1998. *Ecological Geography of the Sea*. Academic Press, San Diego, 398 pp.
- Lozouet, P., 1992. New Pliocene and Oligocene Olividae (Mollusca, Gastropoda) from France and the Mediterranean area. *Contrib. Tert. Q. Geol.* 29, 27–34.
- Lozouet, P., 1998. Nouvelles espèces de gastéropodes (Mollusca: Gastropoda) de l'Oligocène et du Miocène inférieur de l'Aquitaine (Sud-Ouest de la France). *Cossmanniana* 5, 61–102.
- Lozouet, P., 1999. Nouvelles espèces de gastéropodes (Mollusca: Gastropoda) de l'Oligocène et du Miocène inférieur de l'Aquitaine (Sud-Ouest de la France). *Partie 2. Cossmanniana* 6, 1–68.
- Lozouet, P., Ledon, D., Lesport, J.-F., 1994. The genus *Lindapterys* (Neogastropoda, Muricidae): An example of range disjunction in tropical marine area. *Geobios* 27, 39–50.
- Macnae, W., 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. *Adv. Mar. Biol.* 6, 73–270.
- Mansfield, W.C., 1940. Mollusks of the Chickassawhay Marl. *J. Paleontol.* 14, 171–226.
- Martin, K., 1914–1915. Die Fauna des Obereocäns von Nanggulan, auf Java. *Samml. Geol. Reichs-Mus. Leiden*, n.s. 2. Brill, Leiden, pp. 1–222.
- Martin, K., 1916–1917. Die Altmiozäne Fauna des West-Progogebirges auf Java. *Samml. Geol. Reichs-Mus. Leiden*, n.s. 2. Brill, Leiden, pp. 223–296.
- Martin, K., 1921–1922. Die Mollusken der Njalindungschichten. *Samml. Geol. Reichs-Mus. Leiden*, n.s. 1. Brill, Leiden, pp. 446–496.
- Martin, K., 1931. Wann löste sich das Gebiet des Indischen Archipels von der Tethys. *Leidsche Geol. Meded.* 4, 1–8.
- Martin, K., 1933. Eine neue tertiäre Molluskenfauna aus dem Indischen Archipel. *Leidsche Geol. Meded.* 6, 7–32.
- Martin, K., 1935. Oligocäne Gastropoden von Buton. *Leidsche Geol. Meded.* 7, 111–118.
- Maury, C.J., 1902. A comparison of the Oligocene of Western Europe and the Southern United States. *Bull. Am. Paleontol.* 15. New York.
- Mikuz, V., 1999. Revision of Lower Miocene Gastropoda *Melongena deschmanni* Hoernes, 1906 from Sotska near Moravce, Central Slovenia. *Razpr. Razreda Sazu* 40, 27–45.
- Miller, K.G., Wright, J.D., Fairbanks, R.G., 1991. Unlocking the ice house: Oligocene-Miocene oxygen isotopes, eustasy, and margin erosion. *J. Geophys. Res.* 96 (B4), 6829–6848.
- Nevesskaja, L.A., Goncharova, I.A., Iljina, L.B., Paramonova, N.P., Popov, S.V., Voronina, A.A., Chepalyga, A.L., Babak, E.V., 1987. History of Paratethys. *Ann. Inst. Geol. Publ. Hung.* 70, 337–342.
- Nishimura, S., Suparka, S., 1997. Tectonic approach to the Neogene evolution of Pacific-Indian Ocean seaways. *Tectonophysics* 281, 1–16.
- Noda, H., Watanabe, R., 1996. Subtropical gastropod *Tibia* from the Miocene Sunakozaka Formation in Kanazawa, Ishikawa Prefecture, Japan Sea Borderland. *Ann. Rep. Inst. Geosci. Univ. Tsukuba* 22, 29–35.
- Noetling, F., 1901. The Miocene of Burma. *Verh. K. Akad. Wetensch.* 7, 1–129.
- Ogasawara, K., Noda, H., 1996. Miocene *Hataiarca* (Mollusca, Bivalvia) invasion event in the Japanese Islands from a viewpoint of Indo-Pacific connection. *Prof. H. Igo Commem. Vol.*, pp. 133–139.
- Olsson, A.A., 1931. Contributions to the Tertiary paleontology of northern Peru, IV. The Peruvian Oligocene. *Bull. Am. Paleontol.* 17, 164 pp.
- Oppenheim, P., 1900. Beiträge zur Kenntnis des Oligozäns und seiner Fauna in den venetischen Voralpen. *Z. Dtsch. Geol. Ges.* 52, 243–326.
- Oveckin, N.N., 1956. The Middle Paleogene of the Turgai basin and the northern Aral region. *VSEGEI (1954), Trudy*, pp. 1–140 (in Russian).
- Palmer, K.V.W., 1967. A comparison of certain Eocene molluscs of the Americas with those of the western Tethys. In: Adams, C.G., Ager, D.V. (Eds.), *Aspects of Tethyan Biogeography*. Systemat. Assoc. Publ. 7, pp. 183–193.
- Papp, A., Rögl, F., Senes, J., 1973. M2 Ottnangien. Die Innviertler, Salgótarján, Bántapusztaer Schichtengruppe und die Rzehakia Formation. *Chronostratigraphie und Neostatotypen, Miozän der Zentralen Paratethys* 3. VEDA, Bratislava.
- Papp, A., Marinescu, F., Senes, J., 1974. M5 Sarmatien. Die Sarmatische Schichtengruppe und ihr Statotypus. *Chronostratigraphie und Neostatotypen, Miozän der Zentralen Paratethys* 4. VEDA, Bratislava.
- Papp, A., Cicha, I., Senes, J., Steininger, F., 1978. M4 Bade-

- nien (Moravien, Wielicien, Kosovien). Chronostratigraphie und Neostatotypen, Miozän der Zentralen Paratethys 6. VEDA, Bratislava.
- Papp, A., Jambor, A., Steininger, F., 1985. M6 Pannonien (Slavonien und Serbien). Chronostratigraphie und Neostatotypen, Miozän der Zentralen Paratethys 7. VEDA, Bratislava.
- Piccoli, G., 1984. Cenozoic molluscan associations of Mediterranean and South-East Asia: A comparison. *Mem. Sci. Geol. Miner. Univ. Padova* 36, 499–521.
- Piccoli, G., Sartori, S., Franchino, A., 1986. Mathematical model of the migration of Cenozoic benthic molluscs in the Tethyan belt. *Mem. Sci. Geol. Padova* 38, 207–244.
- Piccoli, G., Sartori, S., Franchino, A., Pedron, R., Claudio, L., Natale, A.R., 1991. Mathematical model of faunal spreading in benthic palaeobiogeography (applied to Cenozoic Tethyan molluscs). *Palaeogeogr. Palaeoclimat. Palaeoecol.* 86, 139–196.
- Pisera, A., 1996. Miocene reefs of the Paratethys: A review. *SEPM Concepts Sedimentol. Paleontol.* 5, 97–104.
- Pomerol, C.H., 1982. The Cenozoic era. Tertiary and Quaternary. Ellis Horwood Series in Geology. Ellis Horwood, Chichester, 272 pp.
- Popov, S.V., 1993. Zoogeography of the Late Eocene basins of Western Eurasia based on bivalve mollusks. *Stratigr. Geol. Correl.* 2, 103–118.
- Popov, S.V., Titova, L.V., 1982. Bivalve molluscs from the analogs of the Solenovian Horizon in Georgia. *Paleontol. J.* 4, 36–48.
- Popov, S.V., Ilyina, L.B., Nikolaeva, I.A., 1985. Molluscs and ostracods from the Solenovian Horizon of the Eastern Paratethys. *Paleontol. J.* 1, 28–41.
- Popov, S.V., Akhmet, M.A., Zaporozhets, N.I., Voronina, A.A., Stolyarov, A.S., 1993. Evolution of the Eastern Paratethys in the Late Eocene–Early Miocene. *Stratigr. Geol. Correl.* 1, 10–39.
- Por, F.D., 1989. The Legacy of Tethys, An Aquatic Biogeography of the Levant. *Monogr. Biol.* 63. Dordrecht.
- Raffi, S., Taviani, M., 1984. An outline of the Tertiary to Recent history of the Mediterranean deep-sea mollusk faunas. *Ann. Géol. Pays Hellen.* 32, 257–261.
- Riegl, B., Piller, W.E., in press. Reefs and coral carpets in the Miocene Leitha Limestone (Austria). *Proc. Coral Reef Symp.*, Bali.
- Rögl, F., 1996. Stratigraphic correlation of the Paratethys Oligocene and Miocene. *Mitt. Geol. Bergbaustud. Österr.* 41, 65–73.
- Rögl, F., 1998. Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Ann. Naturhist. Mus. Wien* 99A, 279–310.
- Rögl, F., 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geol. Carpath.* 50, 339–349.
- Rögl, F., Steininger, F.F., 1983. Vom Zerfall der Paratethys zu Mediterran und Paratethys. Die neogene Paläogeographie und Palinspastik des zirkum-mediterranen Raumes. *Ann. Naturhist. Mus. Wien* 85/A, 135–163.
- Rögl, F., Steininger, F.F., 1984. Neogene Paratethys, Mediterranean and Indo-Pacific seaways. Implications for the paleobiogeography of marine and terrestrial biotas. In: Brenchley, P.J. (Ed.), *Fossils and Climate*. Wiley, Chichester, pp. 171–200.
- Rögl, F., Zapfe, H., Bernor, R.L., Brzobohaty, L., Daxner-Höck, G., Draxler, I., Fejfar, O., Gaudant, J., Hermann, P., Rabeder, G., Schultz, O., Zetter, R., 1993. Die Primatenfundstelle Götzendorf an der Leitha (Obermiozän des Wiener Beckens Niederösterreich). *Jahrb. Geol. Bundesanst.* 136, 503–526.
- Rusu, A., 1988. Oligocene events in Transylvania (Romania) and the first separation of Paratethys. *Dari Seama Inst. Geol. Geofiz.* 72/73, 207–223.
- Sabelli, B., 1980. Guide to Shells. In: Feinberg, H.S. (Ed.), *Simon and Schuster*, New York, 512 p.
- Sabelli, B., Taviani, M., 1984. The paleobiogeographic distribution of the Mediterranean benthic mollusks and the Messinian salinity crisis or where did the mollusks go? *Ann. Geol. Pays Hellen.* 32, 263–269.
- Sacco, F., 1890. I molluschi dei terreni terziarii del Piemonte e della Liguria. *R. Accad. Sci. Torino* 7–30.
- Savazzi, E., 1989. *Orthaulax dainellii* n.sp. (Gastropoda, Strombidae) from the Lower Eocene of NE Italy. *Neues Jahrb. Geol. Paläontol. Mon. heft* 1, 30–36.
- Schmelz, G.W., 1997. Notes on the fauna of the Chipola Formation. XLI. A reexamination of *Bursa* (Mollusca: Gastropoda) from the Chipola Formation, with the description of a new species. *Tulane Stud. Geol. Paleontol.* 30, 105–108.
- Sedlag, U., Weinert, E., 1987. Biogeographie, Artbildung, Evolution. *Wörterbücher der Biologie*. Fischer, Jena.
- Senes, J., 1958. Pectunculus-Sande und Egerer Faunentypus im Tertiär von Kovacov im Karpatenbecken. *Geol. Práce Monogr. Ser.* 1, 1–332.
- Senes, J., Marinescu, F., 1974. Cartes paléogéographiques du Néogène de la Paratethys Centrale. *Mem. BRGM* 78, 785–792.
- Sengör, A.M.C., 1998. Die Tethys: Vor hundert Jahren und heute. Ein Festvortrag gehalten am 18. November 1993 im Kleinen Festsaal des Hauptgebäudes der Universität Wien. *Mitt. Österr. Geol. Ges.* 89, 5–178.
- Squires, R.L., Advocate, D.M., 1986. New Early Eocene mollusks from the Orocopia Mountains, Southern California. *J. Paleontol.* 60, 851–864.
- Steininger, F.F., 1999. Chronostratigraphy, geochronology and biochronology of the ‘European Land Mammal Mega-Zones’ (ELMMZ) and the Miocene ‘Mammal-Zones’ (MN-Zones). In: Rössner, G.E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Dr. Friedrich Pfeil, Munich, pp. 9–24.
- Steininger, F., Senes, J., 1971. M1 – Eggenburgien. Die Eggenburger Schichtengruppe und ihr Statotypus. Chronostratigraphie und Neostatotypen 2. Veda, Bratislava, pp. 1–827.
- Steininger, F.F., Wessely, G., 2000. From the Tethyan Ocean to the Paratethys Sea: Oligocene to Neogene stratigraphy, paleogeography and paleobiogeography of the circum-Med-

- iterranean region and the Oligocene to Neogene Basin evolution in Austria. *Mitt. Österr. Geol. Ges.* 92, 95–116.
- Stevanovic, P., Neveeskaja, L.A., Marinescu, F., Sokac, A., Jambor, A., 1990. Pl1 Pontien (sensu Le Play, F., Barbot de Marny, N.P., Andrussov, N.I.), Chronostratigraphie und Neostatotypen, Neogen der Westlichen ('Zentralen') Paratethys 8. Jugos. Akad. Wiss. Künste, Zagreb.
- Studencka, B., Gontsharova, I.A., Popov, S.V., 1998. The bivalve faunas as a basis for reconstruction of the Middle Miocene history of the Paratethys. *Acta Geol. Pol.* 48, 285–342.
- Suess, E., 1893. Are great ocean depths permanent? *Nat. Sci.* 2, 180–187.
- Tsuchi, R., 1997. Marine climatic responses to Neogene tectonics of the Pacific Ocean seaways. *Tectonophysics* 281, 113–124.
- Valdés, A., Lozouet, P., 2000. Opisthobranch molluscs from the Tertiary of the Aquitaine Basin (South-Western France), with descriptions of seven new species and a genus. *Palaeontology* 43, 457–497.
- Vlcek, M., 1931. Caenozoic Amphineura, Gastropoda, Lamellibranchiata, Scaphopoda. *Leidsche Geol. Meded.* 5, 206–296.
- Vokes, E.H., 1964. The genus *Turbinella* (Mollusca, Gastropoda) in the New World. *Tulane Stud. Geol.* 2, 39–68.
- Vokes, E.H., 1965a. Cenozoic Muricidae of the Western Atlantic Region. Part II. *Chicoreus* sensu stricto and *Chicoreus* (*Siratus*). *Tulane Stud. Geol.* 3, 181–204.
- Vokes, E.H., 1965b. Note on the age of the Chipola Formation (Miocene) of Northwestern Florida. *Tulane Stud. Geol.* 3, 205–208.
- Vokes, E.H., 1966. The genus *Vasum* (Mollusca: Gastropoda) in the New World. *Tulane Stud. Geol.* 5, 1–36.
- Vokes, E.H., 1967. The genus *Vittularia* (Mollusca: Gastropoda) discovered in the Miocene of Southern Florida. *Tulane Stud. Geol.* 5, 90–92.
- Vokes, E.H., 1973. Notes on the fauna of the Chipola Formation. XIV. On the occurrence of *Bursa* (Mollusca, Gastropoda), with comments on the genus. *Tulane Stud. Geol. Paleontol.* 10, 97–101.
- Vokes, E.H., 1974. Notes on the fauna of the Chipola Formation. XV. On the occurrence of '*Ranella*' *poppelacki* Hörnes. A gastropod of uncertain affinities. *Tulane Stud. Geol. Paleontol.* 11, 96–98.
- Vokes, E.H., 1975a. Cenozoic Muricidae of the Western Atlantic Region. Part VI. *Aspella* and *Deromurex*. *Tulane Stud. Geol. Paleontol.* 11, 121–162.
- Vokes, E.H., 1975b. Notes on the fauna of the Chipola Formation. XVIII. Some new or otherwise interesting members of the Calyptraeidae (Mollusca: Gastropoda). *Tulane Stud. Geol. Paleontol.* 11, 163–172.
- Vokes, E.H., 1977. A second western Atlantic species of *Vittularia* (Mollusca: Gastropoda). *Tulane Stud. Geol. Paleontol.* 13, 192–194.
- Vokes, E.H., 1979. The age of the Baitoa Formation, Dominican Republic, using Mollusca for correlation. *Tulane Stud. Geol. Paleontol.* 15, 105–116.
- Vokes, E.H., 1986. Notes on the fauna of the Chipola Formation. XXX. On the presence of *Eudolium* (*Galeodolium*) *subfasciatum* Sacco (Gastropoda: Tonnidae). *Tulane Stud. Geol. Paleontol.* 19, 177–180.
- Voronina, A.A., Popov, S.V., 1985. Main features of the evolution of the Eastern Paratethys in the Oligocene and lower Miocene. *Ann. Univ. Sci. Budapest. Sect. Geol.* 25, 87–95.
- Vredenburg, E., 1925. Description of Mollusca from the Post-Eocene Tertiary formations of North-Western India. 1 and 2. *Mem. Geol. Surv. India* 50, 1–463.
- Welle, J., 1998. Oligozäne Mollusken aus dem Schacht 8 der Bergwerksgesellschaft Sophia Jacoba bei Erkelenz (Niederrheinische Bucht). Teil 3: Paläoökologie. *Münster. Forsch. Geol. Paläontol.* 85, 43–136.
- Westermann, G.E.G., 2000a. Biochore classification and nomenclature in paleobiogeography: An attempt at order. *Palaeogeogr. Palaeoclimatol. Palaeobiogeogr.* 158, 1–13.
- Westermann, G.E.G., 2000b. Marine faunal realms of the Mesozoic: Review and revision under the new guidelines for biogeographic classification and nomenclature. *Palaeogeogr. Palaeoclimatol. Palaeobiogeogr.* 163, 49–68.
- Wolff, W., 1896. Die Fauna der südbayerischen Oligozänmolasse. *Paleontography* 43, 223–320.
- Woodring, D.C., 1974. The Miocene Caribbean faunal province and its subprovinces. In: Jung, P. (Ed.), *Contributions to the Geology and Paleobiology of the Caribbean and Adjacent Areas*. *Verh. Naturforsch. Ges. Basel* 84, 209–213.
- Woodring, W.P., 1924a. Tertiary history of the North Atlantic Ocean. *Bull. Geol. Soc. Am.* 35, 3.
- Woodring, W.P., 1924b. West Indian, Central American, and European Miocene and Pliocene mollusks. *Bull. Geol. Soc. Am.* 35, 4.
- Woodring, W.P., 1928. Miocene Mollusks from Bowden, Jamaica. Part II. Gastropods and Discussion of Results. In: *Contributions to the Geology and Paleontology of the West Indies*. *Carnegie Inst. Washington* 385, 564 pp.
- Woodring, W.P., 1959. Geology and paleontology of Canal Zone and adjoining parts of Panama. *US Geol. Surv. Prof. Pap.* 306-B, 147–239.
- Woodward, S.P., 1856. *A Manual of the Mollusca; or a Rudimentary Treatise of Recent and Fossil Shells*. John Weale, London, 486 pp.
- Ziegler, P.A., 1990. *Geological Atlas of Western and Central Europe 1990*. 2nd edn. 1, 239 pp., 2, 56 encl. *Shell Int. Petroleum Maatschappij*, Den Haag.