

**Palaeoenvironmental drivers of ostracod
biodiversity change in Pontocaspian Basins**

By

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Abstract

The present-day, partially landlocked basins of the Pontocaspian region (Black Sea, Caspian Sea and Aral Sea) are the relicts of the ancient Paratethys Sea that once covered broad parts of central Eurasia. Ongoing tectonics resulted in the creation of ephemeral gateways, connecting basins to each other and the open ocean, which in turn had regional climatic and profound environmental impacts. It is these impacts and the response of the ecosystem that this thesis aims to understand.

Ostracods, small crustacean arthropods, preserved in the sedimentary archives of Pontocaspian basins are the focus of this research. They provide the means to study the biotic response to past environmental changes and may further contribute towards understanding how similar changes will affect ecosystems in the near future.

Ostracods are among one of the most abundant and ubiquitous calcareous microfossils in the fossil record, with different species occurring in a wide range of environments from fully marine to freshwater and hypersaline habitats. The diversity of these organisms can be utilized to reconstruct past environments, mainly constrained by salinity and water depth, often located at stage boundaries, which additionally allows to utilize ostracods for integrated stratigraphy.

This study adds new data from Miocene – Pleistocene deposits of the Pontocaspian domain and has advanced our understanding of past biotic changes that occurred in the region. Considerable improvements of the Quaternary time scale for the Pontocaspian domain have been made through a high-resolution ostracod-based biochronology that was integrated with magnetostratigraphy and resulted in a stratigraphic framework that facilitated a coherent correlation to the international geological timescale. This permits the identification of major interbasinal connectivity events that facilitated faunal migration between Paratethyan subbasins and surrounding satellite regions. One of those neighbouring areas and subject to this research is the Denizli Basin in SW Anatolia (Turkey). It harboured an isolated long-lived lake environment that permits to study the impact of long-term natural biotic drivers and biotic response to perturbations. Detailed taxonomic analysis of the ostracod assemblage has further led to the conclusion that the encountered assemblage is Paratethys-derived, inferring that the area was once a connected paleobay of the Paratethys.

Throughout the study of fossil material in this thesis, it has been demonstrated that the rate at which changes occur are an important factor for ecosystem stability and that naturally

driven processes alone have resulted in quick enough changes for faunal turnovers to occur. In the context of understanding the biotic echo to anthropogenic activities, ostracods have the potential to become established bioindicators for estimating biodiversity and environmental change.

1 Introduction

The most outstanding feature on this planet is the existence of life and the most extraordinary feature of life is its diversity (Cardinale et al., 2012). While the “big five” mass extinction events in the geological past each occurred over a time span of hundreds of thousands to millions of years, the current biodiversity loss came into existence within the short period of about 200 years, associated with the activities of human expansion (Naeem et al., 1994; Singh, 2002). Conservative estimates indicate that only 1,76 million out of the 13,6 million species are described, revealing a remarkably incomplete knowledge of Earth’s biota (Singh, 2002). Studies indicate that humankind has altered roughly half of the habitable surface of the earth, degrading and destroying ecosystems, leading to a species extinction rate that is 1000-10,000 times higher than the background rate inferred from the fossil record (May, 1988; Singh, 2002). It is the sheer finality of extinction that makes it so heartbreaking and avoiding irreversible damage will be crucial for future generations. Apart from ethical values, biodiversity underpins the functioning of the ecosystem, which provides humanity with enormous direct economic benefits such as the availability of food and freshwater (Hirsch, 2010; Pereira et al., 2010).

Reducing the rate of biodiversity loss will further critically contribute mitigating the scale of climate change and its negative impacts on ecosystems and therefore human societies (Hirsch, 2010). For example, the conservation of carbon-storing ecosystems, such as tropical rainforests or salt marshes, will be essential in limiting the accumulation of more greenhouse gases in the atmosphere. Ecosystems at the same time will become more resilient and therefore less vulnerable towards climate change, providing them with the opportunity to continue to nurture humanity (Leadley, 2010).

The tipping points of ecosystems and their accompanied loss in biodiversity occurs due to a complex interplay of key processes including speciation, endemism and a variety of drivers, for example habitat loss and/or fragmentation (Singh, 2002; Leadley, 2010; Dakos et al., 2019). The interaction between those mechanisms is, however not adequately understood yet, and restoring biodiversity demands addressing the underlying causes in order to understand the nature of the undeniable and globally occurring decline.

The current Pontocaspian species downfall is a textbook example of an emerging biodiversity crisis. Although the region looks back to a dynamic history shaped by rapid and profound geological and environmental changes, human activities may pose a profound

threat to the regions unique ecosystem (Dumont, 2000; Krijgsman et al., 2019; Lattuada et al., 2019; Wesselingh et al., 2019). The Pontocaspian faunas are at their minimum, both spatially, where they are almost entirely restricted to the Caspian Sea and deltaic and estuarine systems of the northern Black Sea (e.g., Grigorovich et al., 2003; Yanina, 2012), and in terms of species numbers as shown by observational time series such as those of the environmental monitoring programme (2005-2016) of the North Caspian Operating Company (NCOC; Kosarev and Yablonskaya, 1994). Their inventory shows that 49% of mollusc biodiversity mass is nowadays dominated by highly adaptive and competitive marine invasive species, which in part were introduced as food source for fish stock (Karpinsky, 2010; NCOC, 2018). In comparison, snapshots of pre-20th century assemblages still contained 100% Pontocaspian communities, indicating the loss of many endemic species since then (Velde et al., 2019). The extreme example in Lake Aral, which almost entirely disappeared within the past five decades, exemplifies the ecocide that resulted from the excessive extraction of river water for agricultural use, causing the extirpation of most of the Pontocaspian species in this location (Dumont, 1995; Boomer et al., 2000; Krijgsman et al., 2019). It is for that reason that the expansion of interest in understanding palaeoenvironments is, that those environments serve as the context of evolution of today's biota (Faith and Lyman, 2019). Understanding long-term natural biotic and abiotic drivers of sea/lake level change and biotic response to perturbations in the past five million years – i.e., gradual, rapid and/or threshold responses – is absolutely necessary to assess the current response of Pontocaspian biota to rising natural and human-induced perturbations.

A major part of the Earth's continental surface is represented by landlocked (endorheic) seas, large bodies of water that have a limited or no connection to the open ocean (Hostetler, 1995; Wang et al., 2018). Environmental variations, related to climate or basin connectivity, can have a potentially rapid (in geological terms) impact on these ecosystem, as the reduced connection with the open ocean limits the oceans buffering effect which acts to minimize demise associated differences. Marginal basins therefore provide a convenient ambience to study faunal turnover events and associated biotic adaptability and ecosystem stability (Kawecki, 2008).

Endorheic basins can either be semi-isolated like the present day Black Sea or like the world's largest lake, the Caspian Sea, completely isolated (Fig. 1). The present-day, partially landlocked basins of the Pontocaspian region are the relicts of the ancient Paratethys Sea (Black Sea, Caspian Sea and Aral Sea), which formed as a result of the

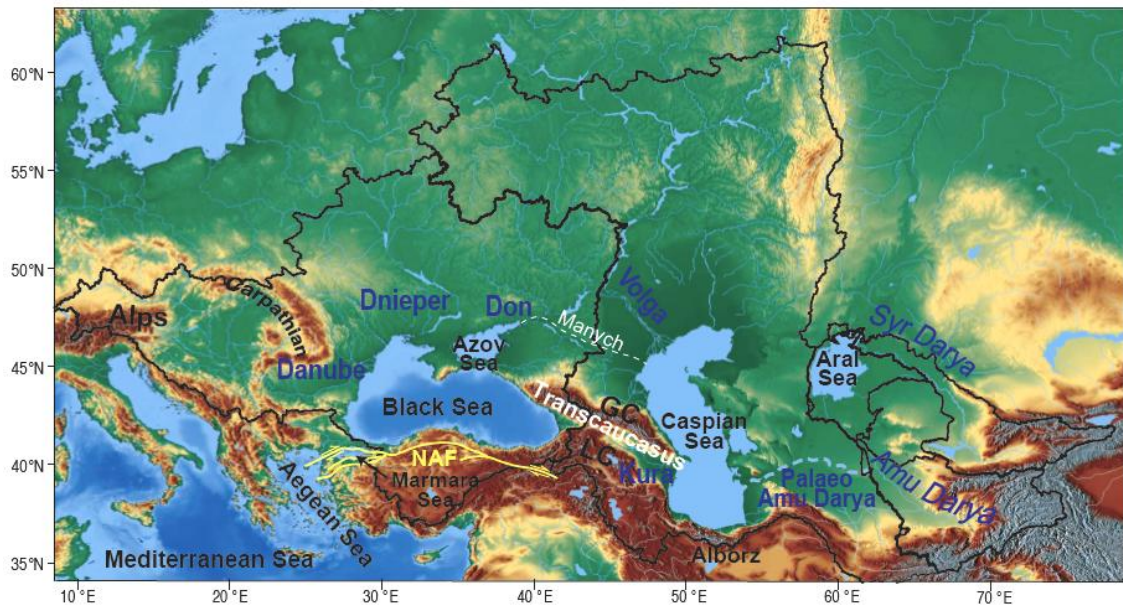


Figure 1. Topographic map of the present day Pontocaspian region with the Black and Caspian seas drainage area, indicated by the solid black line. GC: Greater Caucasus and LC: Lesser Caucasus (adapted from Bista, 2019).

collision of the African continent with Asia during Eocene-Oligocene times (Rögl, 1998; Popov et al., 2006; Van Baak et al., 2017). Ongoing tectonics resulted in the creation of ephemeral gateways, connecting basins to each other and the open ocean, which in turn had regional climatic and partly quite profound environmental impacts (e.g., Popov et al., 2006; Palcu et al., 2017). These high-amplitude environmental changes led to faunal assemblages (e.g., ostracods, molluscs and dinoflagellates) that are endemic to the region (e.g., Harzhauser et al., 2002; Wesselingh, 2008; Cziczter et al., 2009; Stoica et al., 2013; Krijgsman et al., 2019). For example, estimated species diversity comprises approximately 400 endemic species in the Caspian Sea (Dumont, 1995) of which ostracods, i.e., small crustacean arthropods, show extraordinary adaptations to the unique environmental setting of the study area, expressed in an outstanding morphological exuberance (Gofman, 1966; Boomer et al., 2005). Ostracods (Fig. 2), preserved in the sedimentary archives of Pontocaspian basins, provide the means to study the biotic response to past environmental changes and further contribute towards understanding and predicting the biotic echo to anthropogenic activities. They are among one of the most abundant and ubiquitous calcareous microfossils in the fossil record, with different species occurring in a wide range of environments from fully marine to freshwater and hypersaline habitats (Lister, 1988). The diversity of these organisms can be utilized to reconstruct past

environments, mainly constrained by salinity and water depth, often located at stage boundaries, which additionally allows to utilize ostracods for integrated stratigraphy.

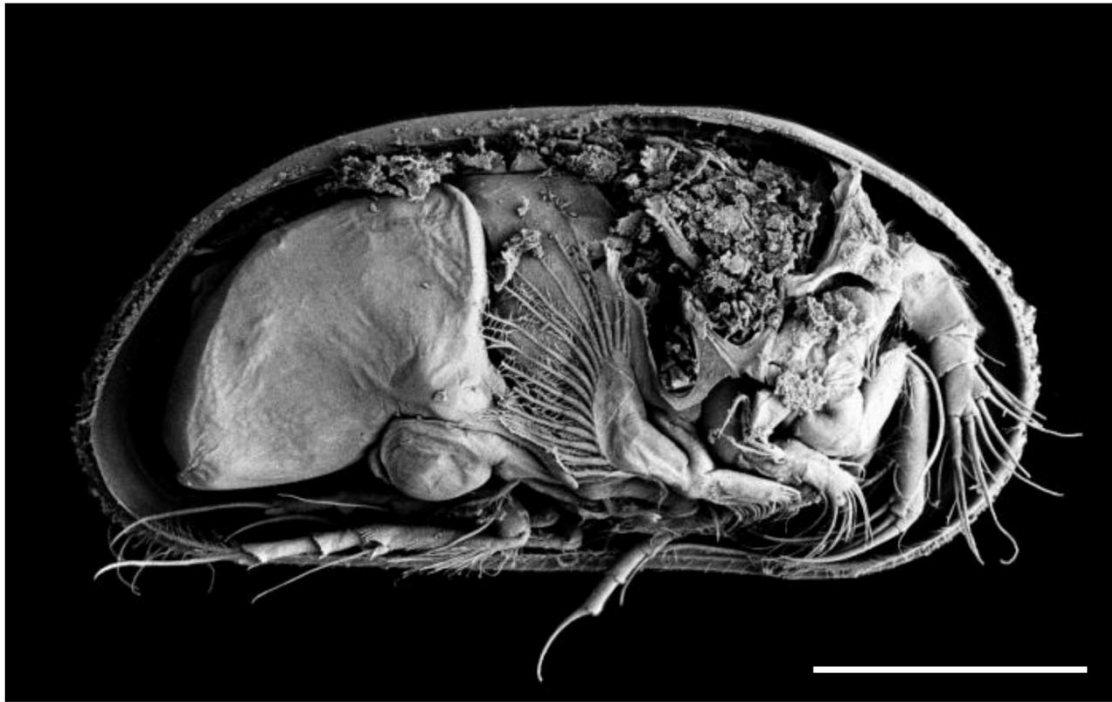


Figure 2. Lateral view of a dissected male specimen of *Cyprideis torosa* showing the arrangement of the appendages (left valve removed) with soft parts and appendages. Scale bar 300 μm (SEM picture by Dietmar Keyser).

1.1 Disentangling chronologies

Ostracods and other groups endemic to the Paratethys region allow a comprehensive view into the evolutionary history of the area dating back to the earliest Oligocene (e.g., Molostovsky, 1997; Rögl, 1999; Popov et al., 2006; Krijgsman et al., 2019). The presence of mainly endemic and localised faunas combined with the near total absence of open marine faunal assemblages normally used for biostratigraphy and correlation to the standard geological time scale, has resulted in regional time schemes for the different Paratethyan subbasins, which are mainly based on characteristic faunal assemblages from these individual subbasins (e.g., Hilgen et al., 2012; Nevesskaya et al., 2003; Popov et al., 2004; Krijgsman et al., 2019). As a result, stratigraphic cross-correlation between different subbasins as well as to the current geological time scale is problematic in many instances (Krijgsman et al., 2019). Besides the taxonomic study of ostracods, this study aims to give a comprehensive overview of the existing ostracod stratigraphy and distribution patterns in

order to partly revise the Pontocaspian Quaternary time scale. This permits the identification of major interbasinal connectivity events that facilitated faunal migration between the Pontocaspian subbasins.

Epoch GTS (2012, 2004)	Med. Stages	Pannon Basin	Dacian Basin	W' Georgia	Caspain Sea	Timeframes covered in this thesis by chapter			
Pleistocene	Pleistocene	Ionian	Pleistocene	Pleistocene	N. Euxinian	Novocaspian	<i>Isolated, (endoheric) Caspian Basin with minor marine incursions and connection to the Black Sea</i> Chapter 3		
					Karangatian	Khvalinian			
					Uzunlarian	Khazarian			
					O. Euxinian				
					Chaudian	Bakunian			
	Calabrian	Gurian	Apsheronian	Chapter 6					
	Pliocene	Pliocene	Gelasian 2.59	Romanian	Romanian	Kuialnician		Akchagilian	Chapter 4 Chapter 5 5.3 Ma Zanclean flooding Chapter 6 6.1 Ma Pontian flooding Chapter 5 <i>Isolated, (endoheric) Paratethys</i> 11.6 Ma Isolation of Pannonian Basin
			Piacenzian 3.60		Dacian	4.8 Dacian		Kimmerian	
		Zanclean 5.33	Pontian	Pontian		Pontian		Pontian	
		Messinian		?		6.1		Maeotian	
Miocene			Miocene	Tortonian	Pannnonian	7.5	Sarmatian s.l.	Sarmatian s.l.	
	11.6 Sarmatian s.str.	Sarmatian s.l.			Sarmatian s.l.	Sarmatian s.l.			

Figure 3. Summarized overview of the stratigraphic concepts used inside the Central and Eastern Paratethys in combination with the ages of the geological time scale after Hilgen et al. (2004, 2012). Mediterranean stages after Berggren et al. (1995), Pannonian Basin after Rögl (1998), Dacian Basin after Van Baak et al. (2017), the Black Sea (W' Georgia) after Shatilova et al. (2009) and the Caspian Sea after Adamia et al. (2002). The dashed yellow lines indicate the assumed stratigraphic position of the studied sections of Chapter 5 whos age has proven difficult to constrain. The dashed red lines on Chapter 6 indicate the assigned stratigraphic position of the studied section by previous authors (Kirscher et al.,

2017). Below, indicated in solid red, is the newly proposed stratigraphic range of the same section (Chapter 6).

1.2 Elucidate the role of satellite basins

Biodiversity is unevenly distributed across the earth (Singh, 2002). The spatial distribution and the reasoning behind why some areas display an extraordinary diversity has intrigued naturalists over centuries and makes the core of biogeography (Gaston, 2000). Biodiversity hotspots, such as the Anatolian region, provide the means to understand processes responsible for creating and maintaining diversity (Ricklefs, 1987; Sands et al., 2019). At the same time these regions are critically prone to environmental change and particularly threatened by human activities in recent years. The Denizli Basin in SW Anatolia (Turkey), located in one of the most active extensional regions in the world (e.g., Alçiçek 2010; Alçiçek et al., 2015), harboured an isolated long-lived lake environment during the late Neogene (Wesselingh et al., 2008; Van Baak et al., 2016). Long-lived lake environments commonly host ecosystems that are isolated from the “outside” world often containing endemic ecospecies, tied to specific local biotopes (Martens, 1994; Wesselingh, 2007; Hauffe et al., 2015). This has been observed in Pannonian strata of the Pannonian Basin (Krstić, 1985; Olteanu, 2011). With the advance of molecular techniques it has been shown that high endemic biodiversity in long-lived lake environments is predominantly the result of intra-lacustrine diversification (“cradle function”; e.g., Martens, 1997; Schön and Martens, 2004; Salzburger et al., 2005). However, the rates of diversification remain little understood. Diversification may happen after a lake first comes into existence or after the occurrence of major environmental events such as flooding events. For these reasons, long-lived lakes have become model systems in understanding the impact of long-term natural biotic drivers and biotic response to perturbations (Belmercheri et al., 2009; Jovanovska, 2016).

Previous investigations on the sedimentary strata and biota of the Denizli late Miocene – early Pliocene lake successions have shown a clear resemblance between ostracod and mollusc species (Freels, 1980; Wesselingh et al., 2008; Şafak, 2010) known from Lake Pannon, inevitably raising the question of the existence of a temporary connection and so far unknown gateway between SW Anatolia and the Paratethys (Freels, 1980; Wesselingh et al., 2008; Şafak, 2010). Such a scenario could *explain* why Anatolia is the biodiversity hotspot it is today (Alçiçek, 2010; Sands et al., 2019). Another aim of this work is to

elucidate the role of the Denizli region as a source/sink-area of Paratethyan-like ostracod taxa and to discuss the origin and link between the geological and biological evolution of the faunal community and investigate the processes driving potential faunal turnovers by assessing the taxonomy of the ostracod assemblages preserved in the fossil record.

1.3 Thesis outline

The thesis is organized in seven chapters. The first chapter (Introduction) contains the general background information of the study area and puts special emphasis on the age control, ecological and geographical distribution of the endemic Paratethyan ostracod assemblages. It further describes the research question and highlights the motivation behind this study. As the vast majority of the encountered ostracods are of Paratethyan origin, special attention is drawn towards the challenges ostracodologists face while working in late Miocene to Pleistocene strata of the Pontocaspian area. In Chapter 2, information regarding the methods used and the taxonomic concept applied are provided. The chapter further explores the morphological diversity displayed in the ostracods carapace. Chapter 3 gives a comprehensive overview of the available stratigraphic and geochronologic data for the Caspian Sea, the Black Sea and adjacent continental domains and incorporates my contribution that focuses on the faunal indicators of basin isolation and connectivity. The fourth chapter is composed of the synthesis of two publications that highlight the value of ostracods as important contributors in reconstructing the palaeoecological framework required in a palaeoanthropological setting of Pleistocene age. Besides taxonomically describing the encountered ostracod assemblage, the chapter further introduces the Denizli Basin in SW Anatolia (Turkey) as the central study area of this thesis. In the following Chapter 5, the ostracod assemblage of a late Miocene to early Pliocene long-lived lake environment in the Denizli Basin is taxonomically described, illustrated and discussed with the goal of understanding mechanisms responsible for faunal diversification. The chapter concentrates on the biogeographic resemblance of ostracod taxa and gives implications on their palaeogeographic distribution. Chapter 6 is dedicated to the enigmatic Khvarbeti section in Guria, Georgia. In this chapter I focus on the biostratigraphic constraints on the late Miocene/Pliocene connection between the Black and Caspian seas. Chapter 7 summarizes the key findings from this thesis.

1.4 Peer reviewed publications included in this thesis

For a complete review of each chapter the reader is encouraged to read the published papers that are included in this thesis.

Chapter 3: Krijgsman W., Tesakov A., Yanina T., Lazarev S., Danukalova G., Van Baak C., Agustí J., Alçiçek M., Aliyeva E., Bista D., Bruch A., Büyükmeriç Y., Bukhsianidze M., Flecker R., Frolov P., Hoyle T., Jorissen E., Kirscher U., Koriche S., Kroonenberg S., Lordkipanidze D., Oms O., **Rausch L.**, Singarayer J., Stoica M., van de Velde S., Titov V., Wesselingh F., 2019, **Quaternary time scales for the Pontocaspian domain: Interbasinal connectivity and faunal evolution**, *Earth-Science Reviews*, 188 (1- 40).

Chapter 4: **Lea Rausch**, Marius Stoica; **An early Pleistocene anomalohaline water ostracod fauna from lake deposits of the Homo erectus-bearing Kocabaş locality (SW Turkey)**, *Acta palaeontologica Romaniaae*, 15(2), 41-69.

Chapter 4: **Lea Rausch**, Hülya Alçiçek, Amélie Vialet, Nicolas Boulbes, Serdar Mayda, Vadim V. Titov, Marius Stoica, Sylvain Charbonnier, Hemmo A. Abels, Alexey S. Tesakov, Anne-Marie Moigne, Valerie Andrieu-Ponel, Dario De Franceschi, Thomas A. Neubauer, Frank P. Wesselingh, M. Cihat Alçiçek; **An integrated reconstruction of the early Pleistocene palaeoenvironment of Homo erectus in the Denizli Basin (SW Turkey)**, *Geobios*, 57, p. 77-95.

Peer reviewed publications in prep.

Chapter 5: **Lea Rausch**, Marius Stoica, Sergei Lazarev. A late Miocene – early Pliocene Paratethyan type ostracod fauna from the Denizli Basin (SW Anatolia) and its palaeogeographic implications, accepted in *Acta palaeontologica Romaniaae*.

2 Methodology

All samples were predominantly derived from fine grained clay or silt intervals and processed using standard micropalaeontological methods following procedures outlined in

Stoica et al., (2013). To improve disaggregation, samples were boiled with sodium carbonate before being subsequently washed and sieved over a battery of three sieves (500 – 125 – 63 µm). The dried residue was handpicked using a ZEISS - GSZ light microscope. All analyses were semi quantitative. For high resolution images the ZEISS MERLIN GEMINI 2 Scanning Electron Microscope (SEM) of the Geological Institute of Romania (Microcosmos Laboratory) was used. For illustrating the ostracods in Chapter 6 a ZEISS – Stemi SV11 microscope with a NIKON digital camera mounted onto it was used. The material is housed in the Faculty of Geology and Geophysics, Department of Geology at Bucharest University (Romania).

The Class Ostracoda is subdivided into two subclasses, the Podocopa and the Myodocopa (Horne et al., 2002). The vast majority of the later subclass are marine species. The podocopans are divided into following three orders: Platycopida (exclusively marine); Podocopida (most diverse and found in marine, brackish and non-marine waters); Palaeocopida (diverse and widespread in Palaeozoic sediments).

All ostracods in the encountered assemblages of this study are podocopids. For the suprageneric classification I used Meisch (2000) and Horne et al. (2002). For describing the morphology, I followed the taxonomic concept of the previously published work by Moore (1961), Van Morkhoven (1962) and Hartmann (1966).

3 Interbasinal connectivity and faunal evolution of the Pliocene – early Pleistocene of the Caspian Sea

The Pontocaspian (Black Sea – Caspian Sea) region has a very dynamic history of basin development and biotic evolution. The region is the remnant of a once vast Paratethys Sea. It contains some of the best Eurasian geological records of tectonic, climatic and palaeoenvironmental change. The Pliocene-Quaternary co-evolution of the Black Sea-Caspian Sea is dominated by major changes in water (lake and sea) levels resulting in a pulsating system of connected and isolated basins. Understanding the history of the region, including the drivers of lake level and faunal evolution, is hampered by indistinct stratigraphic nomenclature and contradicting time constraints for regional sedimentary successions. In this chapter we review the stratigraphic framework of the late Pliocene-early Pleistocene Caspian Sea.

The Caspian Basin has experienced a long and dynamic history of lake/sea level evolution that resulted in the unfolding of a unique fauna that adapted to unusual salinities. Ostracod occurrences (Fig. 4) in the Caspian Sea reflect the evolution of the region since the Pliocene and provide important evidence in disentangling the contribution of the drivers behind lake/sea level change through time. For a complete review of the stratigraphy of the entire Pontocaspian region, the reader is encouraged to read Krijgsman et al. (2019).

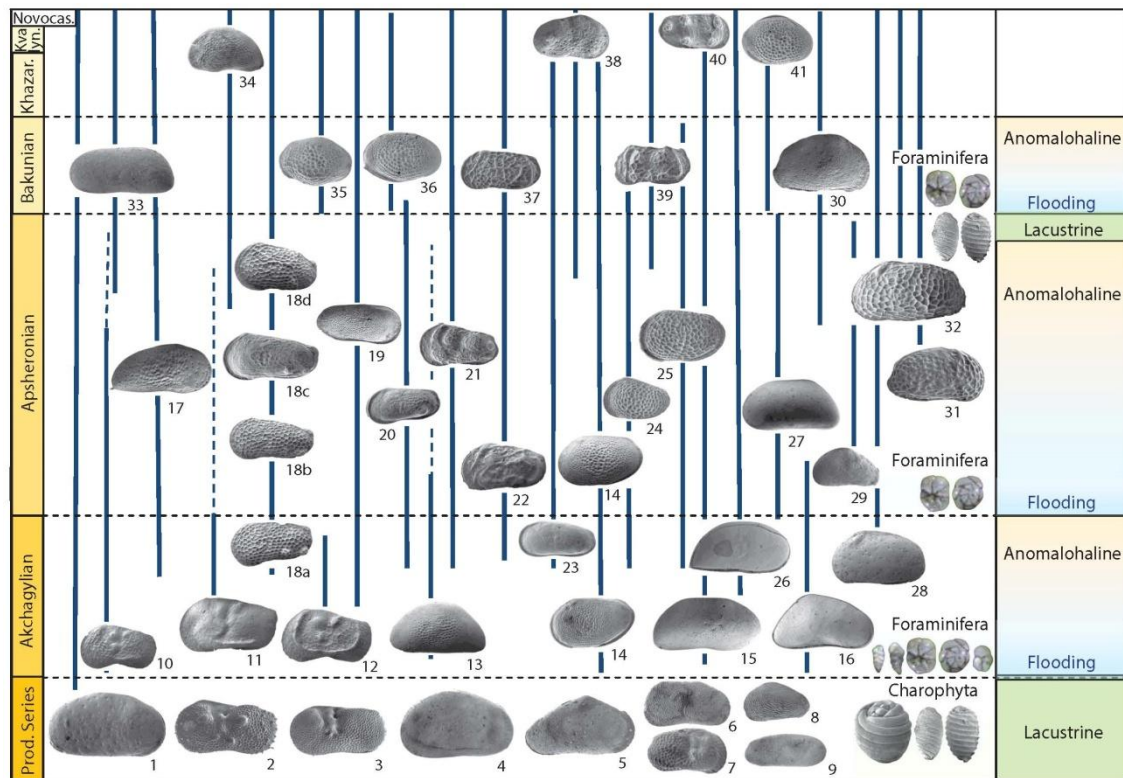


Figure 4. Distribution of the main ostracod species, foraminifera and charophyta in the Caspian Basin during the Plio-Pleistocene. 1) *Cyprideis torosa*; 2) *Ilyocypris gibba*; 3) *I. bradyi*; 4) *Cyprinotus salinus*; 5) *Eucypris* sp.; 6) *Pseudocandona compressa* (juvenile); 7) *Limnocythere aralensis*; 8) *Zonocypris membranae*; 9) *Darwinula stevensoni*; 10) *Limnocythere alveolata*; 11) *L. luculenta*; 12) *L. tschaplyinae*; 13) *Typhlocypris gracilis*; 14) *Loxoconcha eichwaldi* (different stages of evolution); 15) *Candona candida*; 16) *C. combibo*; 17) *Eucythere naphhtatscholana*; 18a) *Amnicythere andrussovi*; 18b) *A. palimpsesta*; 18c) *A. normalis*; 18d) *A. saljanica*; 19) *Amnicythere nata*; 20) *Leptocythere gubkini*; 21) *A. multituberculata*; 22) *Euxinocythere praebosqueti*; 23) *A. cymbula*; 24) *Loxoconcha babazanica*; 25) *L. petasa*; 26) *Camptocypris acronasuta*; 27) *Caspiocypris filona*; 28) *Tyrrhenocythere bailovi*; 29) *Xestoleberis chanakovi*; 30) *T. annicola donetziensis*; 31) *T. azerbaijanica*; 32) *T. papillosa*; 33) *Camptocypris acronasuta*; 34) *Bakunella dorsoarcuata*; 35) *Loxoconcha gibboides*; 36) *L. lepida*; 37) *Euxinocythere bosqueti*; 38) *Cytherissa bogatschovi*; 39) *Euxinocythere bacuana*; 40) *A. quinquetuberculata*; 41) *Loxoconcha endocarpus*.

4 An integrated reconstruction of the early Pleistocene palaeoenvironment of *Homo erectus* in the Denizli Basin (SW Turkey) with special emphasis on the anomalohaline water ostracod fauna from lake deposits of the *Homo erectus*-bearing Kocabaş locality

The early Pleistocene travertines from Kocabaş in the Denizli Basin (SW Turkey), from which the only known *Homo erectus* from Anatolia derives, are covered by a succession of lake deposits. So far, the taphonomic history of the site has precluded a detailed palaeoecological analysis. This paper details the sedimentary succession and palaeoenvironmental conditions by analysing the micro- and macropalaentological species compositions. These data provide direct evidence of the opportunities and limiting factors of the environs inhabited by hominins during the early Pleistocene. Four distinctive lithostratigraphic units are recognized in the Quaternary succession, consisting of: Lower Travertine, Lower Conglomerates, Upper Travertine and Upper Conglomerates. These units are corresponding to an alternation of lacustrine limestone, fluvial-lacustrine siliciclastic deposits and sub-aerially precipitated travertine accumulations. The age of the succession is constrained by cosmogenic nuclide concentration, palaeomagnetic measurements and large mammal biostratigraphy which suggest deposition occurred between ~ 1,6 and 1,2 Ma. The travertine succession contains a moderately diverse macromammal fauna, including *Homo erectus*, decapod crustaceans and leaf imprints. The herbivore association likely dwelled in a mixed landscape during temperate and humid climatic conditions, supported by negative $\delta^{18}\text{O}$ values from analysed gastropod and bivalve shells. The presence of an anomalohaline lake is indicated by an abundant and well-preserved ostracod community, consisting of alkaline tolerant taxa and freshwater genera further supported by the presence of cardiid bivalves.

The early Pleistocene palaeoenvironment evident in the Kocabaş succession, characterized by alternating travertine-and fluvial-lacustrine carbonate deposits, can be associated to the presence of i) travertine springs and streams, ii) high energy lacustrine sedimentation linked to lateral migration of channels and iii) fine-grained sediment accumulation inside an anomalohaline lake environment (Fig. 5).

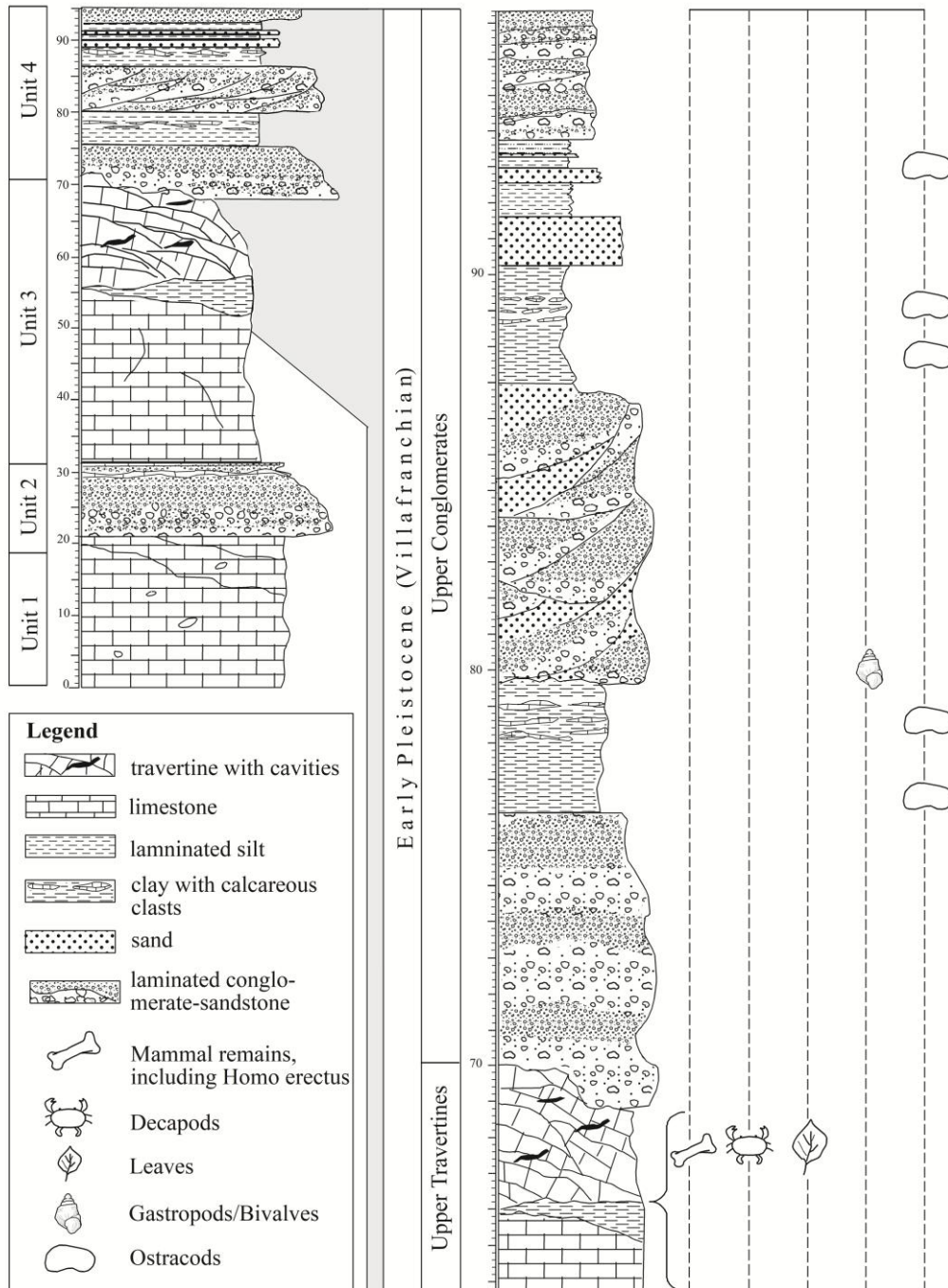


Figure 5. Stratigraphy of the Kocabas succession, locating the studied fossil assemblages and detailing Unit 4 (Upper Conglomerates).

The ostracod assemblage is lacking a higher diversity, typical for freshwater or marine water environments. Low diversity assemblages are characteristic for transitional habitats, supporting our assumption of a restricted water body. The diversity remains equal along the

entire succession and a total of sixteen species have been recorded, shedding light on the palaeoecological conditions. The co-occurrence of anomalohaline (oligohaline to mesohaline) water taxa and mainly freshwater cypridoid ostracods suggest a shallow water lake environment with a salinity no greater than lower mesohaline (~18‰; Fig. 6). The input of calcium-rich water from nearby travertine springs is assumed to have had a major impact on the faunal diversity development.

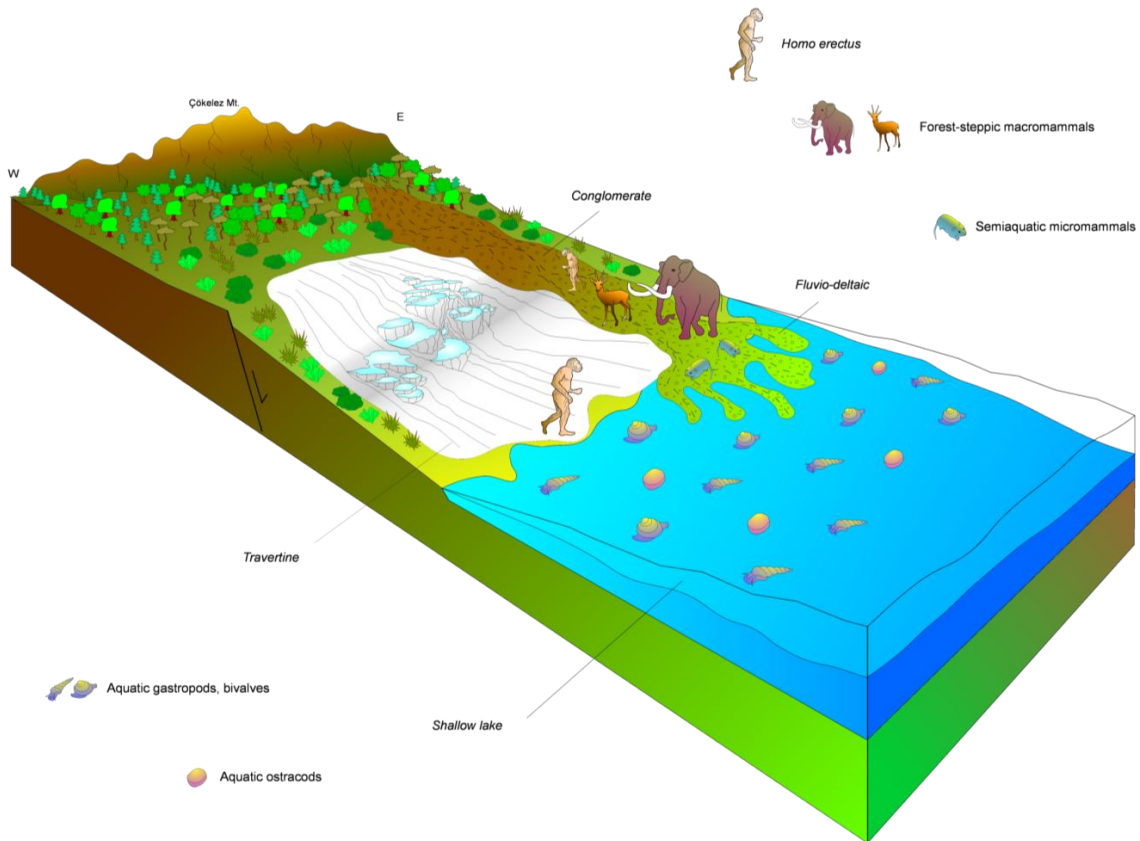


Figure 6. Depositional model of the Kocabaş palaeolake.

5 A late Miocene – early Pliocene Paratethyan type ostracod fauna from the Denizli Basin (SW Anatolia) and its palaeogeographic implications

The late Miocene – early Pliocene sedimentary succession of the Denizli Basin (SW Anatolia) displays a unique record of undisturbed stratigraphy and provides an excellent

opportunity to study long-term palaeoecological changes. This paper documents the ostracod assemblages of two sections of the Neogene Kolankaya Formation, resulting in the following taxonomic, palaeobiogeographic and ecological interpretations.

The Denizli Basin is a WNW-ESE trending extensional depression (Fig. 7) that is approximately 50 km wide and 70 km long (Şimşek, 1984; Alçiçek et al., 2007). It contains a unique stratigraphic record, displaying a complex Miocene to Quaternary basin-fill that is reaching up to 1300 m in thickness, consisting of alluvial-fan, fluvial and lacustrine deposits

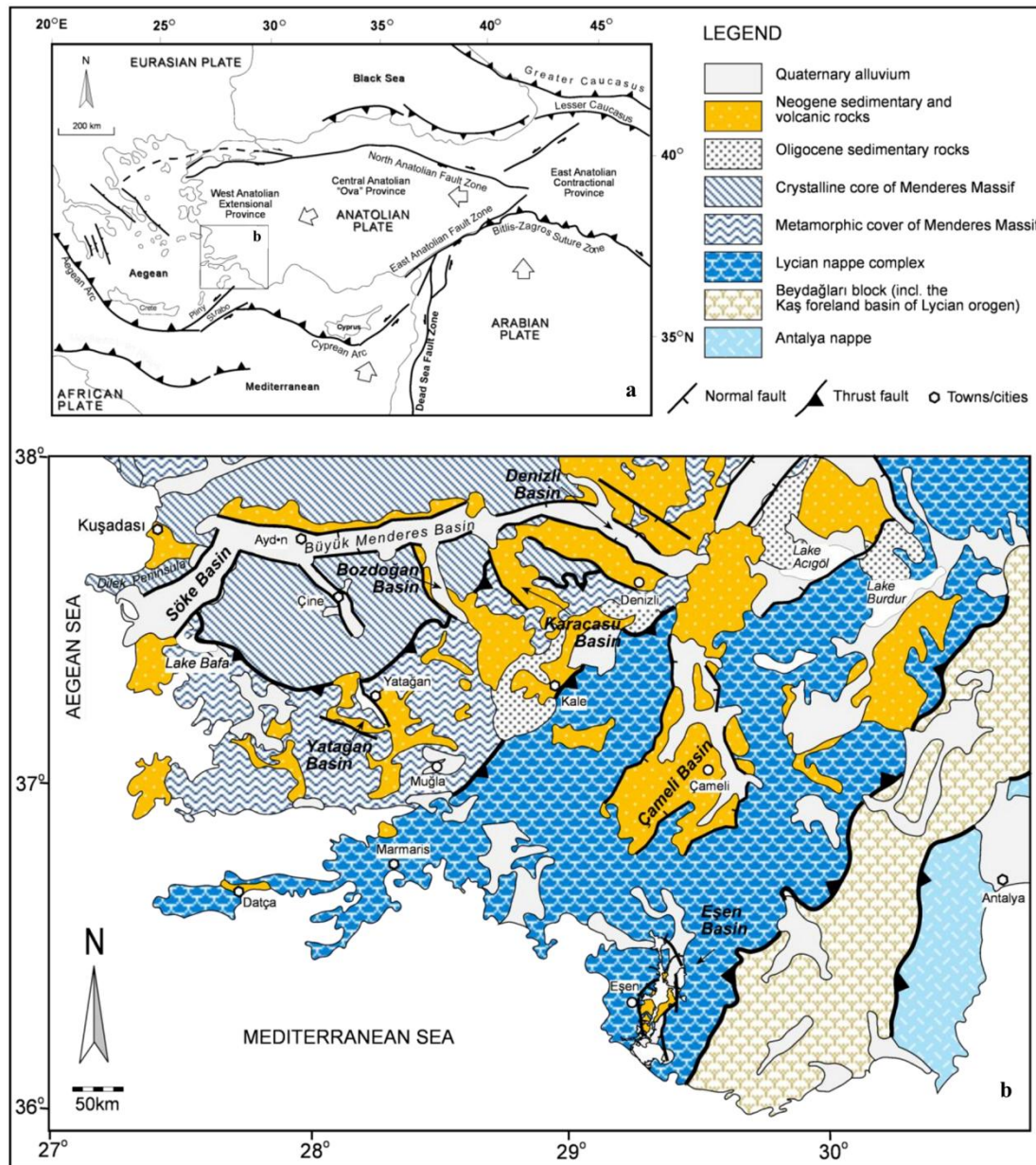


Figure 7. a. Tectonic map of the Aegean Sea and western Turkey showing the main tectonic structures; b. Simplified geological map of southwestern Anatolia, Turkey (after Alçiçek, 2010).

(Şimşek, 1984; Alçiçek et al., 2007, 2015; Sun, 1990; Kaymakçı, 2006). The sedimentary succession has developed on a pre-Neogene bedrock, that consists of Paleozoic-Mesozoic metamorphic rocks of the autochthonous Menderes Massif and the Lycian Nappes, which are mainly made of a ophiolitic melange with intercalated allochthonous units that are composed of carbonates of middle Eocene age (e.g., Sun, 1990; Bozkurt, 2001; Alçiçek et al., 2015). Neogene deposits are relatively well exposed and have been affected by an ongoing regional extension that started during the late early Miocene (Alçiçek et al., 2007, 2015). The basin- fill, referred to as Denizli Group (Sun, 1990), consists of siliciclastic deposits, associated with occasionally occurring carbonates and evaporites (Alçiçek et al., 2007). The sediments unconformably overlie the metamorphic bedrock and are divided into four formations (Şimşek, 1984; Sun, 1990; Alçiçek et al., 2007): the Kızılburun Formation (early – early middle Miocene), the Sazak Formation (middle – early late Miocene), the Kolankaya Formation (late Miocene – late Pliocene), the Tosunlar Formation (Early Pleistocene) and alluvial deposits of middle Pleistocene age. The ostracod fauna described herein is obtained from the Kolankaya Formation that can reach up to 500 m in thickness and is subdivided into four subunits following the classification of Wesselingh et al. (2008; Fig. 8):

(1): a unit that is approximately 100 m thick and consists of laminated mudstones - siltstone and marls. It is interpreted to represent a shallow water and low energy environment.

(2): a unit 200 m thick, consisting of alternating marl,- clay-and sandstones, clayey limestone and black shales. Oxygen isotope measurements indicate the presence of an anomalohaline open lacustrine environment deposited under a gradually shallowing setting (Alçiçek et al., 2007) which is further supported by the presence of a brackish water mollusc fauna of late Miocene age (Nebert, 1958; Taner, 2001; Wesselingh et al., 2008). Based on mammal remains, the unit could be assigned to MN 11-12 biozone (Late Tortonian: Sickenberg and Tobin, 1971; Saraç, 2003).

(3): a unit that consist of thinly bedded and well-sorted, coarse – to very fine-grained sandstones, that additionally shows ripple cross-lamination. The sandstones are overlain by planar crossed-stratified conglomerates and sandstones as well as ripple cross-laminated and massive fine – to coarse grained sandstones. In some layers an abundant mollusc and ostracod fauna, suggesting a Pliocene age and fresh water conditions were found (Nebert, 1958; Taner, 1974a, b, 1975; Freels, 1980; Yalçınlar, 1983). Mammal remains, recovered from the upper part of the unit, suggest

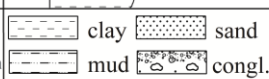
Period	Epochs		Mediterranean stages	Central Paratethyan stages	Dacian Basin stages	Mammal zones	Formation	Unit	Depositional environment	Synthetic Log		
	Holoc.	Ionian				MNQ 20-24	Tonsular Fm. 50 m					
	Pleist.	Calabrian				MNQ 19						
	Pliocene											
N e o g e n e	Late		Gelasian				MN 18	Unit 4 (80 m)		Alluvial fan		
			2.59					MN 17				
	Middle		Piacenzian		Romanian	Romanian		MN 16	Unit 3 (120 m)		Foreshore (beach)	
			3.60									
	Early		Zanelean		Dacian	Dacian		MN 15				
			5.33									
	Late		Messinian		Pontian	Pontian		MN 14	Unit 2 (150 - 200 m)		Shoreface	
Late				Pontian	Pontian		MN 13			Brackish lake		
Late				Maeotian	Maeotian		MN 12					
Late				Pannonian	Sarmatian s.l		MN 11	Unit 1 (100 m)		Ephemeral shallow lake		
Late												
Sazak Fm. 300 m												

Figure 8. Stratigraphic framework of the Denizli Basin and the lithology of the Kolankaya Formation (modified after Wesselingh et al., 2008).

the presence of the the Late Piacenzian – Early Gelasian biozone MN 17 (Yalçınlar, 1983; Kaymakçı, 2006). The shoreface and foreshore deposits of this unit represent a wave-dominated freshwater lake.

(4): a unit that is approximately 80 m thick and consists of alternating cross-stratified conglomerates, sandstones and mudstones with few mudstone dominated intercalations. This unit is representing fluvial to alluvial fan deposits.

The ostracod assemblages from the two sections consist of a mixture of oligohaline to mesohaline tolerant taxa but expose fundamental differences in their composition. This is reflected by the fact that out of 32 determined species, both sections only have 3 in common. In the stratigraphic older succession the diverse ostracod fauna resembles taxa known from the Paratethys. Faunal relations to the brackish lake habitats of the Euxinic and Pannonian basins are apparent and the palaeobiogeographic significance of the fauna is discussed. The ostracod association of the younger section indicates a low brackish water habitat with fluctuating salinities, most likely in the oligohaline range. The ostracod assemblage of the Kolankaya Formation only permits a broad age assignment to the late Miocene – early Pliocene.

6 New age constraints on the Transcaucasian basin: implications for its palaeogeographic and palaeoenvironmental evolution

The Paratethys, the unified precursor of the Black and Caspian seas, has a dynamic history of basin development and biotic evolution. The largely isolated evolution of fauna and flora resulted in highly endemic assemblages, forming the base for complex regional stratigraphic frameworks. Accurate age correlations between these regional stratigraphic schemes are still hampered in many places by the lack of proper age constraints. Here, we present an updated biostratigraphic framework based on high-resolution ostracod analyses for the Gurian region in the Transcaucasian Basin (Western Georgia). Khvarbeti is the type section for the Gurian regional stage, previously magnetostratigraphically correlated to the early Pleistocene (1,8 – 0,8 Ma). The ostracod assemblages, however contain several species elsewhere in the region not exceeding a temporal range higher than late Miocene – early Pliocene (6,1 – 5,5 Ma) corresponding to the Pontian/Kimmerian regional stages of

Epoche		Age (2012, 2004)	Stage	Dacian Basin	W' Georgia	Caspian Sea
Pleistocene	Pleistocene	0.17 0.22 0.35 0.70	Ionian	Pleistocene	N. Euxinian	Novocaspian
					Karangatian	Khvalinian
					Uzunlarian	Khazarian
					O. Euxinian	
					Chaudian	Bakunian
Pliocene	Pliocene	0.78 1.81	Calabrian	Romanian	Gurian	Apsheronian
					Gelasian	Kuialnician
Miocene	Miocene	2.59 3.60 3.80 4.70	Piacenzian	Dacian	Kimmerian	Kimmerian
			Zanclean			
			Messinian	Pontian	Pontian	Pontian
				Maeotian	Maeotian	Maeotian
Tortonian	Sarmatian	Sarmatian	Sarmatian			

Figure 9. Stages of the geological time scale after Hilgen et al. (2004, 2012) in combination with the regional stages of the Dacian Basin (Van Baak et al., 2017), the Black Sea (Shatilova et al., 2009) and the Caspian Sea (Adamia et al., 2002). The previously assigned Gurian substage is indicated in light grey and the in this study newly designated Pontian to Kimmerian age in darker grey.

the Black Sea basin. We also measured the Sr isotopic ratio on ostracods collected from the Khvarbeti section to examine the connectivity of the Black Sea with the Caspian Sea. In the light of the biostratigraphy based late Miocene age, we show that the Black and Caspian seas have similar Sr isotopic values indicating that the two basins were hydrologically connected during the time.

The biostratigraphic study of the Gurian sections provide new age constraints and insights into the paleogeographic and paleoenvironmental evolution of the Rioni bay. Our ostracod based results cast doubt onto the previously assigned early Pleistocene age and instead

suggest that the deposition of the successions occurred during the late Miocene – early Pliocene.

The newly determined age makes the Guria sequence coeval to the Black Sea Zheleznyi Rog section and the Caspian Sea Adzheveli section. Similarities in Sr isotopic values in all three sections, indicates that the Black and Caspian Seas were part of a single Pontocaspian basin at that time. Undergoing taxonomic investigations on molluscs however indicate that the uppermost part of the Khvarbeti section contains faunal evidence that is pointing towards an early Pleistocene age and is therefore in agreement with the age model of previous authors. However, the spatial relationship between the basal part of the section and the upper part is not clear due to adverse outcrop conditions and a hiatus cannot be excluded. Our new and to some extent contradicting findings call for further investigations in order to constrain the age of the Gurian regional stage.

7 Conclusion

Biodiversity change has many metrics and the need and opportunity for improving our knowledge have inspired this thesis. It presents new data from Miocene – Pleistocene deposits of the Pontocaspian domain and has advanced our understanding of past biotic changes that occurred in the region.

7.1 Updating the Quaternary time scale for the Pontocaspian region

The highly integrated approach this project has pursued yielded considerable improvements of the Quaternary time scale for the Pontocaspian domain. Changes in marine gateway configurations along with climate fluctuations, altering the bathymetry and salinity of Paratethyan basins, resulted in the unfolding of a unique and endemic fauna. The analysis of ostracod assemblages that adapted to these unusual salinities provided valuable data that advanced our understanding of the biotic response to past environmental changes. Tracing faunal turnovers allowed the identification of sequence boundaries, providing a high-resolution ostracod-based biochronology of regional Paratethys stages. The integration with magnetostratigraphy resulted in a stratigraphic framework that facilitated a coherent correlation to the international geological timescale. The near total absence of open-marine

faunal assemblages normally used for biostratigraphy showed that ostracods, the primary tool used in this thesis, embody an excellent alternative that allowed a comprehensive view into the evolutionary history of the Pontocaspian area.

7.2 Role of satellite basins

The Denizli Basin is considered a major landmark in terms of hominin evolution, being situated on the cross-roads between Africa, Asia and Europe. While the dispersal of our ancestors out of Africa has received a considerable amount of attention, this thesis highlights the use of ostracods as palaeoecological indicators in palaeoanthropology related studies. The detailed taxonomic study of the Pleistocene assemblage showed that some of the observed genera from the Kocabaş *Homo erectus* site most likely originated in the Paratethys. This indicates that the Pleistocene fauna might be the relict of the long-lived lake environment that has prevailed inside the Denizli Basin since the late Neogene. The taxonomic analysis of the ostracod assemblage from the late Miocene – early Pliocene sedimentary succession near Babadağ village documents a faunal turnover and reflects two distinct types of faunas that we relate to the paleogeographic and associated palaeoenvironmental evolution of the basin, i) migration of a Paratethys-derived fauna and ii) the diversification of an endemic community. The close affinity of the observed fauna of presumably late Miocene age to assemblages known from the Euxinic and Pannonian Basin let us conclude that the Denizli Basin was once a temporarily connected paleobay of the Paratethys and might have functioned as a sink for the Pontocaspian biota. We assume that the changes in faunal composition is the result of the organisms' response to the changing hydrodynamic conditions in the basin, e.g. salinity fluctuations or episodes of shoreline progradation.

7.3 Outstanding issues

For reconstructing the connectivity history of the Black and the Caspian seas, well dated successions are required. The Gurian region in Georgia in the Western Transcaucasian Basin is a key area for tackling that issue. However, despite considerable work in the region, proper age constraints are still partially lacking, hindering accurate correlations of regional stages with each other and to the standard geological time scale. Faunal evidence that resulted from this thesis disagrees with the previously published age model, which

lacked a detailed integrated biostratigraphic framework. This particular case shows that the geochronological correlation between some of the basins and their regional stages still contains large uncertainties. With the integrated stratigraphic approach used in this thesis we suggest carefully approaching and if necessary re-investigate key sections. The lack of an independent absolutely dated age model also presents the most pressing issue regarding the connectivity history of the Denizli Basin. Improvements in dating and correlation however might be difficult to achieve due to difficult outcrop conditions and the highly active tectonics in the region. The encountered ostracod assemblage further calls for an increasing number of sampling locations along the SW Anatolian drainage system towards the Aegean Sea in order to redraw the pathway of the temporary connection that is assumed to have enabled faunal migration.

7.4 Future perspectives

The ecosystem has an intrinsic value that goes beyond its utility as a resource, and there is no doubt that humanity is now destroying its diversity at an alarming rate. A crucial question at this stage is how badly this loss affects the ecosystem functioning.

Throughout this thesis it was noted that the rate at which change occurs is an important factor for ecosystem stability. Naturally driven processes in the Pontocaspian domain alone have caused quick enough changes to drive faunal turnovers. The tragic destiny of Lake Aral for example has shown that human impacts on the Pontocaspian system within the last five decades have already resulted in devastating consequences. We are approaching a point where human intervention will soon be needed to create sanctuaries in order to sustain ecosystems, not only in the Pontocaspian domain but globally. In this context, ostracods might not present poster organisms for extinction studies, yet they have become an established indicator for estimating biodiversity and environmental change and undoubtedly will help explore the complexity of the Anthropocene.

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