ISSN 2079-0961, Arid Ecosystems, 2024, Vol. 14, No. 2, pp. 244–258. © Pleiades Publishing, Ltd., 2024.
Russian Text © The Author(s), 2024, published in Aridnye Ekosistemy, 2024, Vol. 30, No. 2(99), pp. 119–135.

WATER ECOSYSTEMS OF ARID TERRITORIES

Biodiversity of Malacofauna in the Caspian–Manych–Pont System in the Last Interglacial Era

T. A. Yanina[a], *, **D. V. Semikolennykh**[b], **, **and V. M. Sorokin**[a], ***

[a] *Moscow State University, Moscow, 119991 Russia*
[b] *University of the Witwatersrand, Johannesburg, 2050 South Africa*
**e-mail: didacna@mail.ru*
***e-mail: daria.semikolennykh@wits.ac.za*
****e-mail: vsorok@geol.msu.ru*

Received September 7, 2023; revised November 30, 2023; accepted December 1, 2023

Abstract—The conditions for the formation of biodiversity and their comparative analysis at individual stages of development of the Ponto-Caspian basins in the MIS 5 era have been identified. This work was carried out based on the results of studying materials from many years of field research in the Caspian Sea and Sea of Azov—Black Sea regions and the Manych Depression. The biodiversity of malacofauna in the Caspian–Manych–Pont system under the climatic conditions of the MIS 5 era is inextricably linked with the history of the development of the basins. In the Caspian Sea, two transgressive basins have been reconstructed: the Late Khazarian and Hyrcanian. The Late Khazarian malacofauna of the northern part of the paleo-Caspian Sea is represented by 26 species, the main part of which are Caspian endemics belonging to the Cardiidae family. The index species is *Didacna surachanica* Andrusov, 1910. The Hyrcanian malacofauna includes 22 species, the main part of which are also Caspian endemics. Characteristic types are *Didacna subcatillus* Andrusov, 1910 and *Didacna cristata* Bogachev, 1932. The composition of the malacofauna was determined by the main factors: the degree of inheritance from the previous basin, the salinity and temperature of the aquatic environment, and the introduction of freshwater fauna with river runoff. The influence of "random" catastrophic factors, such as the breakthrough of a periglacial lake and the flow of its waters into the Caspian Sea, which sharply changed the biodiversity of the Hyrcanian basin compared to the Late Khazarian basin, is significant. In the Pontian basin, the Karangatian transgression developed in three stages. The malacofaunal composition in the northeastern part of the Pontian basin is represented by 37 species, the main part of which are marine Mediterranean species, both euryhaline and stenohaline. Each stage is characterized by its own complex of malacofauna with varying degrees of development of euryhaline or stenohaline elements in them. The second complex, corresponding to the maximum stage of transgression, was characterized by the greatest diversity and the presence of the most halophilic elements. An important feature of the third complex is the presence of Caspian species characteristic of the Hyrcanian transgression of the Caspian Sea. In the Manych Depression, events closely related to the development of the Caspian and Pontian basins were reconstructed: the ingression gulf of the Karangatian transgression of the Pontian basin in the second stage of its development; reduction in the length of the bay, with the simultaneous advance of waters of the Hyrcanian transgression and their discharge into the bay; complete release of the depression from the Karangatian waters and the discharge of the waters of the Hyrcanian transgression into the Karangatian basin in the third stage of development. In the Pontian basin, species diversity was determined by the composition of the malacofauna that migrated to it from the Mediterranean Sea. At the final stages of the development of the Karangatian transgression, its faunal composition was influenced by Caspian invasive species that penetrated into the Pontian basin with the waters of the Hyrcanian transgression through the Manych Strait. In the Caspian Sea, the formation of the malacofauna composition was predominantly evolutionary in nature. There was no evolutionary component in the development of the Black Sea malacofauna; its formation was of a migration nature.

Keywords: Late Pleistocene, climate change, Late Khazarian transgression, Hyrcanian transgression, Karangatian transgression, evolution of species, migrations of malacofauna

DOI: 10.1134/S2079096124700148

The Caspian–Manych–Pont system includes inland reservoirs that differ in natural features and the history of paleogeographic development—relics of the Paratethys. The Caspian Sea is an isolated basin. The Sea of Azov—Black Sea basin (Pontian) through a system of straits and the Sea of Marmara had a connection with the World Ocean, and the Manych Depression periodically represented a strait between the Caspian and Pontian basin. The development of the natural environment in the links of the system in the Late Quaternary was characterized by complex dynamics caused mainly by global and regional climate changes. Identifying the dynamics of ecosystems in the region is an important aspect for creating a paleogeographic basis for predictive assessments of the state of the natural environment of basins under conditions of climate change.

Mollusks, which are an important component of ecosystems, are sensitive to changes in the physiographic and hydrological conditions of basins and serve as an important indicator of changes in the natural environment. The formation of malacofauna biodiversity in each basin of the system is determined by its geographical location, environmental parameters (primarily temperature and salinity of water, as well as the nature of the soil and associated geochemical processes), and the history of the development of the basin. An analysis of the malacofauna and its comparative analysis was carried out for the Northern Caspian and the Northeastern region of the Black Sea, since it was in these components of the complex Ponto–Caspian system that the impact of sea level fluctuations under the influence of climate change and the closely related functioning of the strait in the Manych Depression.

For paleogeographic analysis of the malacofauna, we chose the last interglacial epoch, the Quaternary, corresponding to marine isotope stage (MIS) 5e. The Mikulino interglacial (Eemian in the paleogeographical schemes of Western and Central Europe) is a well-studied time interval described in numerous scientific publications. However, its position in the geochronological scheme and its time interval remain a controversial issue in Pleistocene paleogeography (Helmens, 2014). Most experts admit that the interglacial corresponds to MIS 5e (Shackleton, 1969). Its duration is estimated at 13000 years, between 128000 and 115000 years ago (ka). This geochronological position of the interglacial was accepted by the International Stratigraphic Commission (Litt and Gibbard, 2008; Head, 2019). Many interglacial researchers include not only MIS 5e, but also 5d (Kukla et al., 2002; Brauer et al., 2007), and N.S. Bolikhovskaya and A.N. Molod'kov (2000; Bolikhovskaya, 2007) correlate the entire MIS 5 with the Mikulino interglacial, identifying endothermal cooling within the interglacial. Every year new material appears, providing numerous data, but not leading to a unity of opinions. In the work by Kukla et al. (1997), it was proposed to consider the warm period, identified according to the sections of Western Europe, as the Eemian interglacial sensu stricto (ss), and the interval of the existence of thermophilic forest vegetation in southwestern and southern Europe as the Eemian interglacial sensu lato (sl). For this reason, we consider the entire stage of MIS 5 in this article. The paleogeographic analysis of this Quaternary epoch is relevant because it is in it that most researchers see an analogue of the modern interglacial (MIS 1) and compare their development. Identification of the conditions for the formation of biodiversity and their comparative analysis at individual stages of development of the Ponto-Caspian basins in the MIS 5 era is the main objective of this article. Its solution is important for understanding the current state of biodiversity and its changes under a changing climate.

MATERIALS AND METHODS

This work was carried out based on the results of studying materials from long-term field research in the Caspian region, the Sea of Azov–Black Sea region, and the Manych Depression (Fig. 1). In the Caspian region, research has covered natural outcrops in the areas of the Caspian Lowland: Northwestern Caspian region, Lower and Middle Volga region, Volga–Ural interfluve, and the Ural River valley. The core of more than 20 wells from the Northern Caspian Sea was studied (drilling was carried out by OOO MorInzh-Geologiya, Riga). In the Black Sea region, we studied natural outcrops on the Kerch and Taman peninsulas and sediments from well cores in the northeastern sector of the Black Sea; in the Manych valley, natural sections and cores of wells drilled to identify the relationship between the Caspian and Pontian basins in certain epochs of the Late Pleistocene.

Both deposits of natural sections and well cores were studied using a complex of methods. We performed lithological and malacofaunal analyses. Lithological analysis makes it possible to assess the bottom sediments in which the mollusks lived, their facies, and the dynamics of the aquatic environment. Malacofaunal analysis includes the study of the taxonomic composition of shell material, taphonomic features of occurrence in sediments, biostratigraphic distribution along the section, historical development, phylogeny, and biogeography of mollusks. To control the results and obtain additional paleogeographic information about the habitat basins of malacofauna, the results of geomorphological, palynological, microfaunal, geochronological, and other analyses of sediments obtained by different researchers and published in the scientific literature were used. For areas not covered by our studies, other published data were used. All sources used are referenced in the text of the article.

RESULTS

Caspian. Late Khazarian basin. According to our previously published paleogeographic reconstructions (Yanina et al., 2014; Yanina et al., 2018; Sorokin et al., 2018), at the beginning of the Late Pleistocene, during the MIS 5 era, the Late Khazarian transgressive era took place in the Caspian Sea, in the development of which two transgressions (stages) have been identified: Late Khazarian and Hyrcanian. The Late Khazarian transgressive basin had a maximum level of about –10

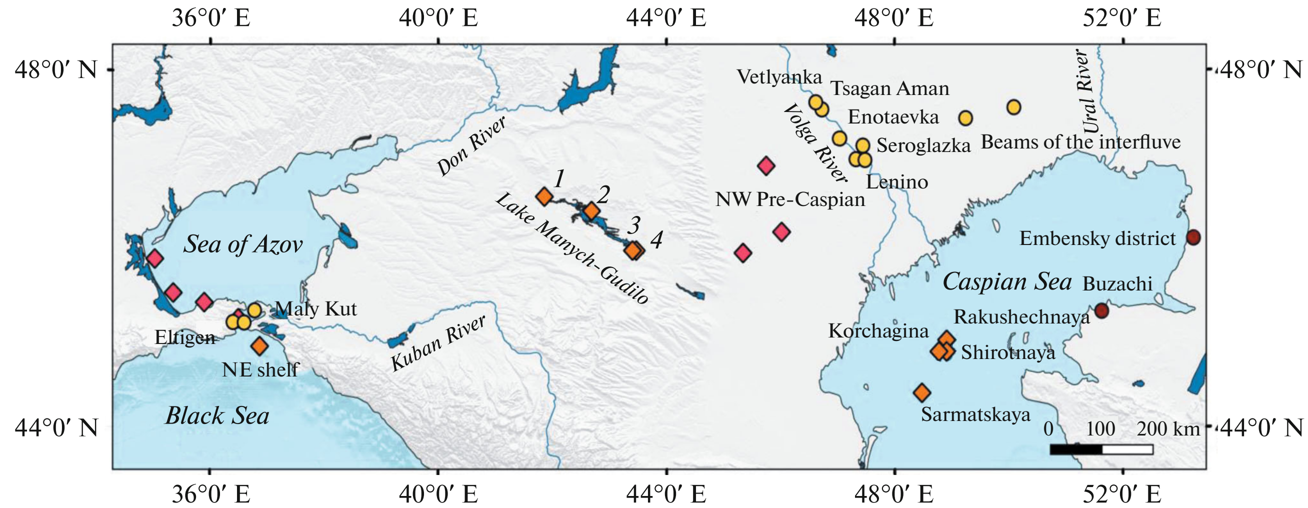

Fig. 1. Locations with Late Khazarian and Hyrcanian malacofauna. *Legend:* 1, natural sections studied by the authors; 2, natural sections borrowed from publications; 3, wells studied by the authors; 4, wells borrowed from publications.

m a.s.l. BS. The boundaries of the sea and the coast are described in the work of O.K. Leontieva et al. (1977). In the Northern Caspian region, we studied deposits of the Late Khazarian transgressive basin in natural outcrops in the Lower Volga region and in the Volga–Ural interfluve. In the Lower Volga region, Upper Khazarian deposits with fauna are exposed in the Seroglazka and Lenino sections (stratigraphic descriptions are given in other works (Svitoch and Yanina, 1997; Yanina, 2012)). The species composition of malacofauna is given in Table 1. In the Volga–Ural interfluve, outcrops of sediments from the Late Khazarian basin are rare. We encountered them in the valley of Gorkii Creek, where clays and sands with shells are revealed in the sands under Atelian continental loams of *Didacna nalivkini* Vassoevich, 1930, *Didacna surachanica* Andrusov, 1910, *Dreissena polymorpha* Pallas, 1771, and *Laevicaspia caspia* (Eichwald, 1838). Sediments with a similar didacna composition were found in a number of gullies. In addition to didacnas, they contain numerous *Monodacna caspia* (Eichwald, 1829), *Adacna laeviuscula* (Eichwald, 1829), *Adacna vitrea* (Eichwald, 1829), *Hypanis plicata* (Eichwald, 1829), and *Dreissena polymorpha*.

In the Ural River valley, we studied the malacofauna from a number of sections, the main ones being the Mergenevo, Kalmykovo, Kharkino, Inderborgskii, and Inder. Sediments with Late Khazarian fauna were not found in them, despite published data on the distribution of sediments of this age in the valley (Vasiliev, 1961; Yakhimovich et al., 1986). A revision of the malacofauna indicates the Early Khazarian age of the faunal communities described by the authors (Yanina, 2012).

East of the Urals, in the Embenskii region, P.V. Fedorov (1957) noted Late Khazarian fauna, including *Didacna surachanica* and *Didacna nalivkini*, in sediments exposed in natural outcrops beneath younger Khvalynian sediments that overlay the sediments of the Late Khazarian basin. Upper Khazarian sediments with fauna were described by this researcher north of the Tyup–Muyun–Chapke tract and in other areas of the Caspian Lowland on both sides of the Emba valley. On Buzachi Peninsula shell rocks with the Late Khazarian fauna *Didacna surachanica*, *Didacna* aff. *čelekenica* Fedorov, 1948, *Didacna* ex gr. *crassa* (Eichwald, 1829) (predominantly) developed under younger sediments at absolute levels up to –20 m a.s.l. BS.

In the northwestern part of the Caspian region, Late Khazarian fauna were recorded in deposits between the Volga delta, Sostinsky lakes and the lower reaches of the Kumas river valley (Geomorphology..., 1958; Popov, 1983). The Upper Khazarian sands here have been exposed only by wells. In the Northern Caspian, wells penetrated sediments of the Late Khazarian basin in the Rakushechnaya, Shirotnaya, and Korchagina drilling areas. The species composition of malacofauna from the sediments is given in Table 1.

Analysis of the species composition of the Late Khazarian malacofauna from sediments of the northern part of the paleo-Caspian Sea shows that it is represented by 26 species, the main part of which are Caspian endemic genera *Didacna*, *Monodacna*, *Hypanis*, and *Adacna*, belonging to the family Cardiidae. In the Quaternary period, they lived both in the Caspian Sea and in the Black Sea basin. Currently, mollusks of the genus *Didacna* live only in the Caspian Sea. Of the Caspian malacofauna, Didacnae are the most plastic mollusks, sensitive to changing environmental conditions. This is what made them the leading genus for the biostratigraphic division of sediments and for paleogeographic reconstructions. The Late Khazarian

Table 1. Composition of the Late Khazarian and Hyrcanian malacofauna in localities of the Caspian region

Species	Location																	
	Late Khazarian fauna									Hyrcanian fauna								
	NW Caspian Sea	Lenino	Grey-eye	Beams of the interfluve	Embensky district	Buzachi	Rakushechnaya	Latitudinal	Korchagina	NW Caspian Sea	Tsagan-Aman	Vetlyanka	Enotaevka	Selitrennoe	Shell	Latitudinal	Korchagina	Sarmatskaya
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Didacna surachanica Andrusov, 1910	R	R	N	R	R	R	R	P	P									
Didacna nalivkini Vassoevich, 1930			N	P			P	P	P									
Didacna ovatocrassa Pravoslavlev, 1939	R																	
Didacna subcrassa Pravoslavlev, 1939			N						R									
Didacna cf. pontocaspia Pavlov, 1925			N															
Didacna pallasi Pravoslavlev, 1939		P	R				R			R		R			R			
Didacna subcatillus Andrusov, 1910	R									R	R			P	R	P	P	
Didacna shuraosenica Svitoch, 1978			R															
Didacna aff. *čelekenica* Fedorov, 1948						R												
Didacna ex gr. *crassa* (Eichwald, 1829)						P												
Didacna subovalis Pravoslavlev, 1939	R																	
Didacna vulgaris Andrusov, 1910							R											
Didacna cristata Bogachev, 1932										R	P			R	R		R	
Didacna umbonata Ebersin, 1958										R		R						
Didacna ex gr. trigonoides (Pallas, 1771)												R		R				R
Didacna parallela Bogachev, 1932										R						S		
Didacna protracta (Eichwald, 1841)																S		
Didacna zhukovi Fedorov, 1953										R								
Didacna ebersini Fedorov, 1953										R								
Monodacna caspia (Eichwald, 1829)	R	P		P			R	R		P	P	P	P	R	R	R		
Hypanis plicata (Eichwald, 1829)			R	P			R			R	R							P
Adacna laeviuscula (Eichwald, 1829)	R			P						R	R			R				
Adacna vitrea (Eichwald, 1829)				P														
Dreissena caspia Eichwald, 1855			R				P	P	P	P					R			
Dreissena rostroformis (Deshayes, 1838)							P		R	P			R	R	R	R	R	P
Dreissena polymorpha Pallas, 1771	R	P	R	P				P	P	R		P	P	R		R	R	
Theodoxus pallasi Lindholm, 1924							R	R	R							R	R	
Laevicaspia caspia (Eichwald, 1838)			R	P			P	R	R					R	P	P	R	P
Clessiniola variabilis (Eichwald, 1838)			R				R			R				P	R	R		
Turricaspia spica (Eichwald, 1855)															S	R		
Turricaspia grimmi (Clessin & W. Dybowski, 1887)										R								
Ecrobia grimmi (Clessin, 1887)																R		
Lithoglyphus caspius (A. Mousson, 1863)										R						R		
Corbicula fluminalis (O.F. Müller, 1774)	R	R	R				P			P		R						
Sphaerium corneum Linne, 1758	R						S											
Viviparus duboisianus Mousson, 1863	R																	
Valvata piscinalis (O.F. Müller, 1774)							S			S								
Unio Philipson, 1788 sp.													S					

Letters in the cells indicate the relative occurrence of shells of species (P, predominant; N, numerous; R, rare; S, single).

fauna includes seven species of didacnes, noted in more ancient faunal communities of the region: *Didacna vulgaris* Andrusov, 1910, *Didacna pallasi* Pravoslavlev, 1939, *Didacna subcatillus* Andrusov, 1910, *Didacna nalivkini, Didacna ovatocrassa* Pravoslavlev, 1939, *Didacna* cf. *pontocaspia* Pavlov, 1925, *Didacna shuraosenica* Svitoch, 1978, and *Didacna subcrassa* Pravoslavlev, 1939 found as part of the early Khazarian fauna (Yanina, 2012). Of these species, only *Didacna nalivkini* became widespread (often dominant) in the Late Khazarian fauna; other species are rare or isolated. Only one species is new, leading for the Late Khazarian fauna and widely developed in the Northern Caspian Sea—*Didacna surachanica*.

The Late Khazarian fauna differs from the Early Khazarian fauna as a whole by the clear predominance in its composition of shells of two types, *Didacna surachanica* and *Didacna nalivkini*, related to crassoid didacnus, with weak distribution of catilloid forms and the absence of trigonoid ones and the massiveness of its main representatives, often with large shell sizes. Among all Caspian species, Crassoid didacnas prefer the highest salinity, up to 16‰. The presence of a relatively large number of species of genera in faunal communities of *Monodacna*, *Hypanis*, *Adacna*, and *Dreissena*, living in more desalinated conditions (belong to slightly brackish water species), and also, as a rule, freshwater species *Corbicula fluminalis* (OF Müller, 1774) and rare representatives of freshwater fauna (genera *Sphaerium*, *Viviparus*, *Valvata*, and *Unio*) indicates a significant influence of the Volga waters in the Northern Caspian. However, compared to the modern Northern Caspian Sea, the Late Khazarian basin was more saline, by 4–5‰.

The Late Khazarian basin was warm-water, as evidenced by the massiveness of the Caspian shells and the wide distribution of the thermophilic species *Corbicula fluminalis*, now living only in the southern regions of the Caspian region. The pollen spectra indicate a warm, dry climate of the era (Abramova, 1972; Yakhimovich et al., 1986). The formation of a cemented carbonate crust on the surface of shallow sediments (Yanina et al., 2014) also indicates warm climatic conditions.

Hyrcanian basin. The reality of the existence of this transgressive basin has remained controversial for decades. This transgression as an independent stage in the development of the Caspian Sea was established by G.I. Popov (1967) as a result of the analysis of drilling material in the Northwestern Caspian region and the Eastern Manych valley. Most researchers rejected its existence (Vasiliev and Fedorov, 1965; Fedorov, 1978; Svitoch et al., 1998; Shkatova, 2010). Analysis of drilling materials from the waters of the Northern Caspian allowed us to return to this problem and confirm the existence of the Hyrcanian basin (Yanina et al., 2014; Sorokin et al., 2018). In the structure of the Upper Pleistocene strata in the Northern Caspian, the sequence of Caspian sediments corresponding to this basin has been established. Sediments with Hyrcanian malacofauna were exposed by a number of wells in the Rakushechnaya, Shirotnaya, Korchagina, and Sarmatskaya areas (Table 1).

As for the Northern Caspian region, then, according to G.I. Popov (1983), Hyrcanian deposits in the southern part of the Sarpinsko-Prigergeninskii Caspian region overlie Upper Khazarian deposits with a break. The leading Upper Khazarian species *Didacna surachanica* is missing from them (Table 1). At the foot of the southern Ergeni, didacnae are dominated by *Didacna cristata* Bogachev, 1932, the less common *Didacna zhukovi* Fedorov, 1953, *Didacna* aff. *parallela* Bogachev, 1932, and *Didacna subcatillus*. Many freshwater shells appear in the pre-estuarine areas of the ravines. According to S.M. Ilyinskii (1947), in the Terek-Kuma Lowland, drill holes revealed sediments of the Upper Khazarian horizon with shells of *Didacna nalivkini* and *Didacna surachanica*. The horizon lying above represents in its fauna (*Didacna praetrigonoides* Nalivkin & Anisimov, 1914, *Didacna* aff. *parallela*, *Dreissensia*, *Corbicula fluminalis*) deposits transitional from the Khazarian stage to the Khvalynian; S.M. Ilyinskii conditionally attributed it to the lower Khvalynian stage. It was this fauna (and horizon) that G.I. Popov (1983) identified as Hyrcanian. He also described (Popov, 1967, 1983) the Hyrcanian fauna in outcrops along the right bank of the Volga (Vladimirovka, Enotaevka, Kopanovka, Tsagan-Aman, Vetlyanka). Monodacnae and zebra mussels predominate in its composition; among Didacnae there are *Didacna praetrigonoides abescunica* Popov, 1983, *Didacna cristata*, *Didacna subcatillus*, *Didacna zhukovi*, and *Didacna hyrcana* Popov, 1983. These sections were described by many researchers of the Volga valley (Fedorov, 1957; Vasiliev, 1961; Moskvitin, 1962; Vasiliev and Fedorov, 1965; Shkatova, 1973; Sedaikin, 1988), but none of them identified Hyrcanian deposits here; the age of the sediments was determined as either Early Khazarian or Late Khazarian (but with a more desalinated fauna).

We also studied the malacofauna from the localities listed. In the Enotaevka, Tsagan-Aman, Vetlyanka, and Selitrennoe sections, faunal communities are distinguished that are similar in taxonomic composition to the Hyrcanian malacofauna (Table 1). A feature of the distribution of this fauna is its occurrence outside the development of the Late Khazarian fauna with the leading species *D. surachanica*. We did not find these two faunal groups co-occurring in any section. A preliminary conclusion was made about the Hyrcanian age of the noted fauna.

Analysis of the species composition of the Hyrcanian malacofauna from the deposits of the northern part of the paleo-Caspian Sea shows that it is represented by 22 species, the main part of which, as in the Late Khazarian fauna, are Caspian endemic genera

Didacna, *Monodacna*, *Hypanis*, and *Adacna*. Of the types of leading *Didacna* common in the Late Khazarian fauna, only two were noted in the Hyrcanian—*Didacna pallasi* and *Didacna subcatillus*. The first of them is rare; the second, on the contrary, forms the basis of the Hyrcanian fauna, while it is rare in the Late Khazarian fauna. Characteristic species for the Hyrcanian fauna are *Didacna subcatillus* and *Didacna cristata*. In contrast to the Late Khazarian, Didacnae are dominated by trigonoid and catilloid forms, which indicates a lower salinity of the basin. Numerous slightly brackish water species confirm this. Shell finds of *Corbicula fluminalis* indicate its thermal conductivity. The basin was desalinated and was larger in size than the Late Khazarian basin. Palinospectra indicate a slight cooling and humidification of the climate (Yanina et al., 2014).

The abundance of catilloid and trigonoid didacnus in the Hyrcanian fauna, as well as the first appearance of the species *Didacna parallela*, *Didacna protracta* Eichwald, 1841, *Didacna zhukovi*, and *Didacna ebersini* Fedorov, 1953, which became widespread at the next stage of development of the Caspian Sea, in the Khvalynian basin, and overall created its "Khvalynian-like" appearance, led to the fact that L.A. Nevesskaya in her monographic work (Nevesskaja, 2007) described the Hyrcanian fauna as Khvalynian. In our opinion, the attribution of the described malacofauna to the Khvalynian malacofauna is incorrect, since this is contradicted by the stratigraphic position of the deposits that include it: sediments with the "real" Khvalynian malacofauna are separated from the Hyrcanian deposits by a thick thickness of different facies, mainly subaerial Atelian formations bearing a number of fossil soils, indicating a long regression of the Caspian between these transgressive basins. Between the Late Khazarian and Hyrcanian transgressive stages, a decrease in sea level, reflected in the structure of sedimentary strata in the Northern Caspian, is reconstructed (Yanina et al., 2014; Bezrodnykh et al., 2015). At present, there is no data by which to judge the scale of the regressive phase.

Age estimates for these paleogeographic events are derived from dating data. According to uranium–ionium dating, the age of the Late Khazarian transgressive stage is 127000–122000 years (Shkatova, 2010). Using the optically stimulated luminescence (OSL) method, the age of continental sediments corresponding to the Late Khazarian and Hyrcanian stages of the Caspian Sea was determined within the entire stage of MIS 5 (Yanina et al., 2017; Kurbanov et al., 2022).

Manych. The Manych Depression played an important role in the history of the Ponto–Caspian Sea basin as an area of periodically opened strait between the basins. The Zunda Tolga and Salskoye uplifts, located in its eastern and western regions, respectively, in the Pleistocene served as "thresholds" for the penetration of water from both the Caspian Sea and the Black Sea. The structure of the sedimentary strata in the depression provides a unique opportunity to analyze the relationship between the Caspian and Black Sea sediments and to reconstruct the relationship between the basins and the periods of operation of the strait. We studied the core of four wells in the central part of the Manych Depression. Well 1 was drilled 7 km southwest of Proletarsk; well 2, 5 km north-northwest of the village of Manych (Kurbanov et al., 2018); well 3, on Levyi Island 3 km west of Highway P-216; and well 4, on the northern shore of Levyi Island 4 km east of Highway P-216 (Semikolennykh, 2022).

In the lower part of the core from wells 1 and 2, located in the western half of the central part of the depression, there are deposits that include shells of marine Karangatian mollusks (Table 2). All types are euryhaline or moderately stenohaline, but stenohaline are absent. The malacofauna community characterizes marine conditions with a basin salinity of about 18‰. The Karangatian deposits are overlain by a layer with shells of both Caspian (predominant) and Black Sea mollusks (Table 2). Marine species are representatives of the most euryhaline Karangatian fauna. Caspian mollusks belong to the characteristic species of the Hyrcanian transgression of the Caspian Sea. The community corresponds to a reservoir with a mixture of Black Sea and Caspian waters with a salinity of 10–12‰. In the core of well 4, located in the eastern half of the central part of the depression, sediments with a mixture of marine and Caspian mollusks were also identified. *Cerastoderma glaucum* Bruguiere, 1789 is the most euryhaline Karangatian species; *Didacna cristata* and *Didacna hyrcana* are characteristic species of the Hyrcanian fauna of the Caspian Sea. Salinity conditions are 8–10‰.

Above the layer with mixed fauna in the core of wells 1 and 2, there are sediments with shells of Caspian mollusks (Table 2). Didacnae represent the Hyrcanian fauna of the Caspian Sea. The composition of the malacofauna is characterized by a brackish water (Caspian) reservoir with a salinity of 8–10‰. The layer with Hyrcanian malacofauna opened in well 4.

Judging by the structure of the sedimentary strata and the composition of the mollusk shells contained in it, we can assume the development of the following paleogeographic events in the central part of the Manych Depression. (1) Ingression gulf of the Karangatian transgression of the Black Sea. The fact that this was a bay and not a strait is evidenced by the absence of any species of Karangatian fauna in the Caspian Sea and their gradual disappearance towards the eastern edge of the central depression area. (2) Karangatian Bay, which retreated to the western half of the central part of the depression, with the discharge of waters from the Hyrcanian transgression of the Caspian Sea into it. Using the OSL dating method, the age of this event was determined to be approximately 119000 ± 7000 years ago

Table 2. Composition of the Karangatian and Hyrcanian malacofauna in the Manych locations

Species	Location							
	Karangatian fauna		Karangatian-Hyrkanian fauna			Hyrcanian fauna		
	well 1	well 2	well 1	well 2	well 3	well 1	well 2	well 4
Cerastoderma glaucum (Bruguière, 1789)	M	M	R	R	E			
Mytilaster lineatus (Gmelin, 1791)	M	R	R					
Ostrea edulis (Linnaeus, 1758)	M	M	E					
Chamelea gallina (Linnaeus, 1758)	M	R						
Parvicardium exiguum (Gmelin, 1791)	R	E						
Loripes orbiculatus (Poli, 1795)	E							
Paphia senescens (Cocconi, 1873)	E	E						
Donax sp.	E							
Bittium reticulatum (da Costa, 1778)	R	R						
Didacna pallasi Pravoslavlev, 1939					E		E	
Didacna subcatillus Andrusov, 1910							E	R
Didacna cristata Bogachev, 1932			M	M	M	M	M	R
Didacna hyrcana Popov, 1983					E	E	E	R
Didacna elongatoplana Popov, 1983								R
Didacna cristata–ebersini (Fedorov, 1953)							E	
Monodacna caspia (Eichwald, 1829)			M	E	R	M	M	
Dreissena caspia Eichwald, 1855			E		R			R
Dreissena polymorpha Pallas, 1771			M			M	M	

(Kurbanov et al., 2018). (3) Liberation of the central part of the depression from the Karangatian waters and filling it with the waters of the Hyrcanian transgression. The time of this event was determined by the OSL dating method at 107000 ± 7000 years ago (Kurbanov et al., 2018).

Pont. According to the unanimous opinion of researchers of the Black Sea region, at the beginning of the Late Pleistocene, in MIS 5, a large interglacial transgression, the Karangatian one, developed here (Arkhangelskii and Strakhov, 1938; Fedorov, 1965, 1978; Nevesskaya, 1965; Sorokin, 2011; Yanina, 2012; Krijgsman et al., 2019). It was characterized by the highest level in the Neopleistocene (6–7 m above the modern one) and the highest salinity (up to 30‰). The development of transgression has been established in stages: two transgressive stages have been identified by P.V. Fedorov (1963, 1978) and T.A. Yanina (2012); three phases of transgression were established by L.A. Nevesskaya (1965), V.V. Yanko et al. (1990), A.E. Dodonov et al. (2000), A.L. Chepalyga (*Dinamika...*, 2002), and A.A. Svitochem (2009).

In the northeastern part of the region, we studied natural outcrops exposing Karangatian deposits with fauna on the Kerch and Taman peninsulas, as well as drilling materials on the adjacent shelf.

The Kerch Peninsula is a reference area for the study of the Black Sea Pleistocene faunas. The most complete section of Karangatian sediments is Eltigen, proposed by P.V. Fedorov (1963) as a stratotype for Karangatian deposits and Karangatian fauna. The section is long (about 4 km), and we studied the deposition in various parts. In the southern part of the section in the marine strata, there are three cycles of accumulation of lagoonal and coastal–marine sediments (Semikolennykh, 2022; Semikolennykh et al., 2023), which reflect minor fluctuations in the level of the Karangatian Sea. A feature of the faunal composition of sediments is the distribution of the most euryhaline marine (Mediterranean) species, *Cerastoderma glaucum* and *Abra segmentum* (Recluz, 1843) at the initial stage of sedimentation (with noticeable dominance of the first), the appearance of a euryhaline species *Mytilaster lineatus* (Gmelin, 1791) at the next stage, and then a gradual increase in the number of shells and species diversity: along with *Cerastoderma glaucum, Abra segmentum,* and *Mytilaster lineatus,* the complex includes *Parvicardium exiguum* (Gmelin, 1791) and *Paphia senescens* (Cocconi, 1873). Higher up through the section, moderately euryhaline mollusks are observed in the faunal composition of *Ostrea edulis* (Linnaeus, 1758) and *Chamelea gallina* (Linnaeus, 1758); the latter predominates, and euryhaline species fade into the background (Table 3).

Analysis of the ecological preferences of mollusk species in the outcrop shows a significant content of

Table 3. Composition of the Karangatian malacofauna in the Pontian locations

Location	Eltigen			Tuzla		Maly Kut	Sea of Azov	Kerch Strait		NE shelf	
Species	Complexes										
	1*	2	3	2	3	2	2	2	3	2	3
Cerastoderma glaucum (Bruguière, 1789)	M	M	R	R	R	M	R	R	M	R	R
Parvicardium exiguum (Gmelin, 1791)	R	R				R	R		R		
Papillicardium papillosum (Poli, 1791)										R	
Acantocardia tuberculata (Linnaeus, 1758)		R						E		R	
Acantocardia paucicostata (GB Sowerby II, 1834)				R				R			
Abra segmentum (Recluz, 1843)	M	M	R	R		R					
Abra alba (W. Wood, 1802)								E	R		
Mytilaster lineatus (Gmelin, 1791)	R	R	R			R	R		E	R	
Paphia senescens (Cocconi, 1873)		R	R	R	R	M	R	R			R
Paphia sp.										R	
Ostrea edulis (Linnaeus, 1758)	R	M	R	R		M		R		R	R
Chamelea gallina (Linnaeus, 1758)	R	M	M	R	R	M	R				R
Flexopecten glaber (Linnaeus, 1758)	R	M		R		R	R	R		R	R
Spisula subtruncata (da Costa, 1778)		M	R	M	M	R		R		R	
Mytilus galloprovincialis (Lamarck, 1819)		M	R	M	R		R	R		R	R
Mactra corallina (Linnaeus, 1758)		R				R					R
Solen vagina (Linnaeus, 1758)		R		R		R					
Donax venustus (Poli, 1795)		R	R	R				E			
Cerithium vulgatum (Bruguière, 1792)		R		R		R	R	E			
Bittium reticulatum (da Costa, 1778)		R		R		R			E	R	
Loripes orbiculatus (Poli, 1795)						R	R				
Gastrana fragilis (Linnaeus, 1758)						R					
Irus irus (Linnaeus, 1758)						R					
Gibbula magus (Linnaeus, 1758)						R	R	E		R	
Lucinella divaricata (Linnaeus, 1758)						R					
Varicorbula gibba (Olivi, 1792)							R	R			
Corbula mediterranea (O. G. Costa, 1830)							R		E		
Rissoa splentida (Eichwald, 1830)							R				
Rissoa membranacea (J. Adams, 1800)							R				
Nassa reticulata (Linnaeus, 1758)							R		E	R	R
Retusa truncatula (Bruguière, 1792)							R				
Didacna sp.									R		
Didacna nalivkini Vassoevich, 1930									R		
Didacna cristata Bogachev, 1932									R		R
Didacna subcatillus Andrusov, 1910											R
Dreissena polymorpha Pallas, 1771											R
Lithoglyphus naticoides C. Pfeiffer, 1828											R

1, 2, 3*, Karangatian malacofaunal complexes.

euryhaline species with dominance of *Cerastoderma glaucum*, with the exception of the uppermost unit of coastal–marine sands, where the species diversity of mollusks increases and moderately euryhaline and stenohaline species, characteristic of basins with water salinity above 14‰, are found. This distribution of malacofaunal communities along the section indicates a gradual increase in the salinity of the basin, despite the fact that sedimentation conditions changed from lagoonal (mud layer) to coastal–marine (sandy layer). The greatest species diversity of malacofauna, with a predominance of moderately euryhaline and stenohaline species, was noted in the uppermost part of the Karangatian sediments of this (southern) part of the section.

The structure of the central part of the section is different. Here, in the Karangatian strata, two units of sediments differing in sedimentation conditions are distinguished. In the lower part of the outcrop (initial stages of sedimentation), the species composition of the malacofauna is dominated by moderately euryhaline species with dominance of *Ostrea edulis*. Higher in the thickness of marine sediments, stenohaline species appear; *Ostrea edulis*, *Flexopecten glaber* (Linnaeus, 1758), *Chlamelea gallina*, and *Abra segmentum*. Further in its composition appear *Cerastoderma glaucum*, *Paphia senescens*, *Spisula subtruncata* (da Costa, 1778), and *Mytilus galloprovincialis* (Lamarck, 1819); rare shells of *Acanthocardia tuberculata* (Linnaeus, 1758), the most salt-loving species (lives at a salinity of 28‰) as part of the Karangatian faunal complex, are found. In the upper part of the marine strata, in beach sediments, the composition of the faunal community is represented by euryhaline and moderately euryhaline species (Table 3). There are no stenohaline species in it, which indicates a decrease in the salinity of the basin as its level decreases.

A comparative analysis of the faunal composition of the southern and central parts of the Eltigen section indicates less favorable living conditions for mollusks during the accumulation of sediments in the southern part of the section. This is caused by repeated changes from the coastal–marine environment to the lagoonal one. The latter was characterized by desalination of water by streams flowing into the lagoon, as well as siltation due to oxygen deficiency. But in both the southern and central parts of the section, the diversity of malacofauna increases from bottom to top, as transgression develops and salinity increases.

L.A. Nevesskaya (1965), who identified three phases of the Karangatian transgression based on the results of malacofaunal analysis of the sediments of this section, called them (1) Tobechik, with a rather poor fauna of marine mollusks that are found in the Black Sea at the present time; (2) Karangatian, in which salinity and temperature reached their maximum, and a quarter of the fauna were Mediterranean halophilic species, absent in the modern Black Sea; and (3) Tarkhankutian with a depleted fauna, reflecting a gradual decrease in salinity with a decrease in sea level. Many researchers have adopted these divisions.

On the Taman Peninsula, we studied the Karangatian fauna in the Tuzla and Malyi Kut sections. The Tuzla section is located on the shore of the Kerch Strait at the base of the Tuzla Spit. The structure of the Karangatian strata in it, as well as the composition of the mollusks contained in it, are heterogeneous (Kurbanov et al., 2020; Semikolennykh, 2022). At its base lie coastal marine sediments with shells of euryhaline and moderately euryhaline species of mollusks *Ostrea edulis*, *Mytilus galloprovincialis*, and *Solen vagina* (Linnaeus, 1758). Above, there is an increase in biodiversity along with a decrease in the relative occurrence of *Mytilus galloprovincialis*. Euryhaline *Cerastoderma glaucum* and *Abra segmentum* become widespread, indicating shallowing of the basin. Higher up through the section, transgressions characteristic of the maximum phase appear with *Flexopecten glaber* and *Donax venustus* (Poli, 1795). The layer with them is again replaced by the appearance of *Cerastoderma glaucum* and *Chlamelea gallina* as part of the malacofaunal community, indicating a phase of shallowing and desalination of the basin. There are significantly fewer shells in the overlying layer; detritus predominates in the malacofaunal material. Obviously, this layer indicates a gradual retreat of the sea: continental sediments lie above.

Paleoecological analysis of the malacofauna of the Tuzla section reflects the dynamics in the conditions of its existence: from a calm shallow warm-water basin with a salinity of 12–14‰ to an increase in its level and an increase in salinity to 17‰ and higher, and again to a decrease in both the level and salinity. All species found in the sediments of the section, with the exception of *Paphia senescens*, live in shallow-water areas of the modern Black Sea basin; therefore, salinity in the area of Cape Tuzla did not reach 28–30‰, characteristic of the Karangatian basin, which may be a consequence of the influence of local desalination factors. Dating of the sediments of the section using the OSL method (Kurbanov et al., 2020; Semikolennykh, 2022) showed that the thickness of the marine sediments of the section accumulated in the time interval from 132900 ± 5800 to 129000 ± 6600 years ago, which corresponds to the phase II of the Karangatian transgression (MIS 5e), identified in the Eltigen section, and the Mikulino interglacial era.

In the Malyi Kut section, located on the western shore of Taman Bay, the Karangatian marine sediments include mainly Mediterranean species, both euryhaline and stenohaline (Table 3). On the northern coast of the Sea of Azov, sections of a vast loess plain are exposed. Karangatian marine sediments occur below sea level. The malacofauna of them consists of marine (mostly euryhaline and moderately euryhaline) species (Table 3); sometimes an admixture of

Caspian mollusks is observed at the top of the Karangatian deposits (Semenenko and Sidenko, 1979; Popov, 1983). G.I. Popov (1983) refers the latter to the Hyrcanian formations.

The Karangatian sedimentary sequence, uncovered by wells in the Kerch Strait (*Geologiia shel'fa...*, 1981), includes two malacofaunal complexes. The lower of them is represented by Mediterranean species, both euryhaline and stenohaline; the upper one has a euryhaline composition; rare shells of Caspian didacna are found (Table 3). The composition of the complexes makes it possible to attribute the first of them to the maximum second (in terms of level and salinity) stage of the Karangatian transgression, and the second to the third stage of transgression development. The presence of Caspian Hyrcanian didacnes indicates the influence of Caspian waters and Caspian fauna on the formation of the biodiversity of the basin.

We performed a malacofaunal analysis of cores from three wells drilled on the shelf in the northeastern region of the Black Sea at a depth of about 22 m, 12 km southeast of Cape Zheleznyi Rog. The wells penetrated a sedimentary layer with a maximum thickness of 50 m. Karangatian sediments occur in the range from 27 to 13 m (Bezrodnykh et al., 2019; Sorokin et al., 2022). The lower 8 m are represented by relatively deep-sea clays with thin layers of sand, saturated with shell detritus, containing inclusions of shells and their fragments: *Mytilaster lineatus*, *Cerastoderma glaucum*, *Papillicardium papillosum* (Poli, 1791), *Mytilus galloprovincialis*, *Flexopecten glaber*, *Paphia* sp., and *Acantocardia tuberculata.* We interpret it as the maximum phase of the transgression.

Above (6 m) lies a predominantly sandy sequence consisting of two strata. The lower one is composed of silt and fine-grained sand with inclusions of shells, the accumulations of which form lens-shaped layers. They contain *Ostrea edulis*, *Chamelea gallina*, *Acantocardia tuberculate*, *Nassa reticulata* (Linnaeus, 1758), *Mytilus galloprovincialis*, *Flexopecten glaber*, *Gibbula magus* (Linnaeus, 1758), *Bittium reticulatum* (da Costa, 1778), and *Spisula subtruncata*. The upper strata has a more clayey composition and represents an interlayering of sandy and clayey sediments. The roof of the strata contains numerous shells of mollusks: *Flexopecten glaber*, *Ostrea edulis*, *Mytilus galloprovincialis*, *Paphia senescens*, *Cerastoderma glaucum*, *Chlamelea gallina*, *Nassa reticulata*, *Mactra corallina* (Linnaeus, 1758), *Dreissena polymorpha*, *Didacna cristata*, *Didacna subcatillus*, and *Lithoglyphus naticoides.* These are sediments from the final phase of transgression with lower sea levels. Of particular interest is the presence in them, along with marine species of Mediterranean origin, of shells of brackish-water mollusks, which include typical representatives of the Hyrcanian transgressive basin of the Caspian Sea *Didacna cristata* and *Didacna subcatillus.* Above lies a layer of regressive sediments.

An analysis of the species composition of the Karangatian malacofauna from sediments of the northeastern part of the Pontian basin shows that it is represented by 37 species, the main part of which are Mediterranean marine species, both euryhaline and stenohaline. They owe their appearance and distribution in the Black Sea basin to the waters of the Tyrrhenian transgression of the Mediterranean Sea, which followed the interglacial rise in the level of the World Ocean; they entered the Pontian basin after crossing the threshold of the Bosphorus. The Karangatian fauna consist of three complexes, corresponding to three stages of development of the transgression of the same name. The first or earliest of these includes the most euryhaline Mediterranean species (*Cerastoderma glaucum*, *Abra segmentum*), adapted to living in a desalinated aquatic environment. As seawater entered and the salinity of the Karangatian basin increased, the diversity of malacofauna increased due to the appearance of moderately euryhaline, and then moderately stenohaline and stenohaline species.

The greatest diversity with the presence of the most halophilic elements, currently absent in the Black Sea (*Acantocardia tuberculata*), distinguishes the second complex, corresponding to the stage with the highest level. The waters of the Tyrrhenian transgression completely filled the basins of the Black Sea and the Sea of Azov, going beyond their limits and forming an ingression gulf in the Manych Depression. This is the largest influx of Mediterranean waters into the Pontian basin in the Quaternary period, leading to the highest salinity of the basin (up to 28‰).

The third complex is distinguished by the absence of halophilic species and a wide distribution of euryhaline and moderately euryhaline fauna. It corresponds to the third stage of the Karangatian transgression, with a sea level close (or slightly lower) to the modern one. An important feature of this complex is the presence in it, along with the Mediterranean fauna, of Caspian brackish water species characteristic of the Hyrcanian transgression of the Caspian Sea (*Didacna cristata*, *Didacna subcatillus*, *Didacna nalivkini*), and *Dreissena polymorpha* and *Lithoglyphus naticoides.* The presence of these species and their distribution in the Hyrcanian sediments of the Manych indicate the functioning of the strait between the basins. The flow was one-way from the Caspian Sea to the Pontian basin, since no representatives of marine malacofauna were found in the Hyrcanian sediments of the Caspian Sea. Age estimates of Karangatian deposits determine the time interval for the development of transgression by the epoch corresponding to MIS 5 (Kurbanov et al., 2019, 2020; Semikolennykh et al., 2023).

DISCUSSION

Comparing the biodiversity of malacofauna in the Caspian and Pontian basins under the climatic conditions of the MIS 5 era, we can conclude that it is inextricably linked with the history of their development. Thus, in the isolated Caspian Sea, the composition of the malacofauna was determined by a number of factors. The first factor is the degree of inheritance from the malacofauna of the previous basin, which, in turn, depended on the depth and duration of the regressive stage between them, during which a restructuring of the composition of the mollusk fauna took place. Currently, there is no paleogeographic data on the depth of the pre-Late Khazarian (Chernoyarsk) regression, but judging by the high degree of inheritance of the Late Khazarian fauna from the Early Khazarian fauna, it can be assumed that it was not significant. There is also no data on the depth of regression between the Late Khazarian and Hyrcanian basins. Judging by the structure of the sedimentary strata, it was also not significant.

In the case of the Late Khazarian transgression, the increased salinity of the basin influenced a significant reduction in the composition of the Late Khazarian fauna of trigonoid didacnes, which formed the basis of the Early Khazarian fauna, and the flourishing of crassoid forms. The same crassoid species that were inherited by the Late Khazarian fauna acquired massive shells (thick valves) and larger sizes. The desalination of the Hyrcanian Northern Caspian Sea, apparently caused by the flow of water from a periglacial lake into it (Panin et al., 2020), led to a significant change in the species composition of the malacofauna, with a wide distribution of trigonoid didacnes preferring desalination (*Didacna cristata*). The wide distribution in the Hyrcanian fauna of the catilloid species *Didacna subcatillus,* a group burrowing into the ground that tolerates a lack of oxygen and high turbidity of the aquatic environment, confirms the abundant runoff from the land. Thus, a random factor in the form of a breakthrough of a periglacial lake and the flow of its waters into the Caspian Sea sharply changed the biodiversity of the Hyrcanian basin compared to the Late Khazarian basin, even despite a slight regressive phase between the basins.

The massiveness of the shells of Late Khazarian mollusks also indicates the warm water of the basin and its favorable nutrient environment for them. The warm water content of the Late Khazarian basin is confirmed by the presence of the freshwater species *Corbicula fluminalis,* an indicator of warm environmental conditions, in the fauna. This species, in smaller numbers, is also noted in the Hyrcanian fauna, which also indicates the warm water of the reservoir. However, compared to the Late Khazarian basin, conditions were colder. This is indicated by the materials of palynological analysis (Yanina et al., 2014; Sorokin et al., 2018) and the relative thinness of the shells. We believe that it was not climatic conditions that played an important role in reducing the water temperature of the Northern Caspian Sea, but the runoff of cold periglacial waters from northern Europe. Thus, the temperature factor is also important in the formation of the biodiversity of the Caspian malacofauna.

We have already noted the presence of freshwater corbicula even in the saline Late Khazarian waters, which is a consequence of the influence of the Volga waters in the estuarine zone. River flow and the introduction of freshwater species with them is also one of the factors in the formation of the biodiversity of the Caspian malacofauna.

Since the Caspian Sea was an isolated sea–lake, there was no introduction of elements of marine malacofauna into it. The formation of the composition of the malacofauna was predominantly evolutionary in nature: isolation is an important factor for evolution. In each basin with different environmental conditions, a new composition of mollusks was formed, characteristic only of that basin. Hence, the role of malacofauna in the biostratigraphic division of Quaternary deposits of the Caspian Sea is great.

In the Pontian basin, the situation is different. The Black Sea, both in our day (modern interglacials) and in the interglacial epochs of the Quaternary period, had a connection with the Mediterranean Sea. The higher the level of the World Ocean rose, the higher the level of the Mediterranean Sea rose, the waters of which, having overcome the Dardanelles–Bosporus rapids system, filled the Black Sea basin with seawater, which in glacial periods often had a level below the Bosphorus threshold (Yanina, 2012). The Karangatianian transgression was caused by the transgression of the Tyrrhenian Sea into the Mediterranean. The first penetration of sea waters into the Pontian basin dates back to 135000–127000 years ago (Semikolennykh, 2022). At this stage, the estuary malacofaunal complexes inherited from the Uzunlarian basin in the northeastern region of the sea were replaced by liman–marine ones, and then by marine ones, with a predominance of euryhaline Mediterranean species that managed to adapt to the desalinated conditions of the Pontian basin. Sea waters did not penetrate into the Manych Depression during this initial phase of the transgression.

The development of the second phase of transgression corresponds to the interglacial maximum (MIS 5e) and the highest level of the World Ocean and the Mediterranean Sea. The level of the Karangatian Sea at this stage exceeded the modern one by 6–7 m. The most heat-loving mollusks living in water salinities above 28‰ settled in the basin. Some estuarine areas were desalinated by the waters of inflowing rivers: we reconstructed such conditions in the area of the paleo-Tobechik lake and off the eastern coast of the Kerch Strait, in the area of the Tuzla section. During this transgressive stage, sea waters penetrated deeper into the Manych Depression for more than 300 km. In the area of the modern Manych–Gudilo Lake, there was a reservoir with a salinity of about 18‰. The diversity of its malacofauna was determined primarily by the ability of marine Karangatian species to exist in these salinity conditions. These were euryhaline and moderately euryhaline species. To the eastern part of the bay, the biodiversity of malacofauna declined, and dominance passed to euryhaline species (the leading positions were occupied by *Cerastoderma glaucum*).

The third stage of the Karangatian transgression was distinguished by a lower level, close to the modern one. The diversity of malacofauna was determined by the salinity of the basin: according to the results of studies in the Sea of Marmara (Çağatay et al., 2009), the volume of incoming Mediterranean waters decreased significantly, while the influence of river runoff increased. As a result, stenohaline elements disappeared from the malacofauna. After the level of the Karangatian Sea dropped, the ingression gulf in the Manych Depression gradually shrank and its waters were drawn into the Black Sea basin. The simultaneous increase in the level of the Caspian Sea and the development of the Hyrcanian transgression in it led to the Caspian waters overcoming the Manych threshold and filling the depression with them. The influence of the Caspian waters can be traced in the faunal composition of three wells: in the eastern region of the central part of the Manych Depression, the influence of the Caspian waters predominated, the malacofauna was dominated by Hyrcanian species, and the most euryhaline marine mollusks were found only sporadically (*Cerastoderma glaucum*). To the west, this species also predominated, but the number of mollusks was significantly higher. The diversity of the malacofauna was determined by mixing of sea (Karangatian) and Caspian (Hyrkanian) waters, and the cohabitation of Mediterranean and Caspian species.

As part of the malacofauna of the third stage in the northeastern region of the Black Sea shelf, along with Karangatian species, Caspian species characteristic of the Hyrcanian transgression were common. Their appearance is due to the retreat of the Karangatian waters from the Manych Depression and the opening of the Hyrcanian Strait. The diversity of malacofauna in the strait was determined by the salinity of its waters, which was formed from the Caspian Hyrcanian waters, desalinated by watercourses flowing into the strait. The only freshwater species in the strait was *Dreissena polymorpha*, but there were quite a few of them in the Hyrcanian basin; they adapted well to living in brackish waters.

Thus, the species diversity of malacofauna in the Pontian basin during the interglacial era was determined by the composition of the malacofauna that migrated there with seawater from the Mediterranean Sea. At the final stages of the development of the Karangatian transgression, its faunal composition was influenced by Caspian invasive species that penetrated into the Pontian basin with the waters of the Hyrcanian transgression through the Manych Strait. There was no evolutionary component in the development of the Black Sea malacofauna.

CONCLUSIONS

The biodiversity of malacofauna in the Caspian–Manych–Pont system under the climatic conditions of the MIS 5 era is inextricably linked with the history of the development of the basins.

Two transgressive basins have been reconstructed in the Caspian Sea: Late Khazarian and Hyrcanian. The Late Khazarian malacofauna of the northern part of the paleo-Caspian Sea is represented by 26 species, the main part of which are Caspian endemics belonging to the family Cardiidae. The index species is *Didacna surachanica*. The Hyrcanian malacofauna includes 22 species, the main part of which, as in the Late Khazarian fauna, are Caspian endemics. The characteristic types are *Didacna subcatillus* and *Didacna cristata*.

In the Pontian basin, the Karangatian transgression developed in three stages. The malacofaunal composition in the northeastern part of the Pontian basin is represented by 37 species, the main part of which are marine Mediterranean euryhaline and stenohaline species. Each stage is characterized by its own complex of malacofauna with varying degrees of development of euryhaline or stenohaline elements. The first (early) complex includes the most euryhaline Mediterranean species, adapted to living in a desalinated aquatic environment. The second complex is distinguished by the greatest diversity and the presence of the most halophilic elements, currently absent in the Black Sea. The third complex is distinguished by the absence of halophilic species and a wide distribution of euryhaline and moderately euryhaline fauna. Its important feature is the presence of Caspian species characteristic of the Hyrcanian transgression of the Caspian Sea.

In the Manych Depression, events closely related to the development of the Caspian and Pontian basins were reconstructed: the ingression gulf of the Karangatian transgression of the Pontian basin in the second stage of its development; reduction in the length of the bay with the simultaneous advance of waters of the Hyrcanian transgression and their discharge into the bay; and complete liberation of the depression from Karangatian waters and filling it with waters of the Hyrcanian transgression with their discharge into the Karangatian basin in its third stage of development.

In the isolated Caspian Sea, the composition of the malacofauna was determined by the main factors: the degree of inheritance from the malacofauna of the previous basin (which, in turn, depended on the depth and duration of the regressive stage between them, during which a restructuring of all natural systems took place), the salinity and temperature of the aquatic environment, and the introduction of river runoff of freshwater fauna. The influence of "random" catastrophic factors is significant: the breakthrough of a periglacial lake and the flow of its waters into the Caspian Sea, which desalinated the Northern Caspian Sea and lowered its temperature, sharply changed the biodiversity of the Hyrcanian basin compared to the Late Khazarian basin, even despite the insignificant regressive phase between them.

In the Pontian basin, which had a connection with the World Ocean, species diversity was determined by the composition of the malacofauna that migrated to it with sea waters from the Mediterranean Sea. At the maximum level of transgression, the diversity of malacofauna was the greatest. At the final stages of the development of the Karangatian transgression, its faunal composition was influenced by Caspian invasive species that penetrated into the Pontian basin with the waters of the Hyrcanian transgression through the Manych Strait.

In the Caspian Sea, the formation of the malacofauna composition was predominantly evolutionary in nature. There was no evolutionary component in the development of the Black Sea malacofauna; its formation was of a migratory nature.

FUNDING

This study was supported by the Russian Science Foundation, project no. 22-27-00164 (2022–2023) "Evolution of the natural environment of the Ponto-Caspian Sea under the conditions of the last interglacial epoch."

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human or animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

REFERENCES

Abramova, T.A., Results of paleobotanical study of Quaternary deposits on the western coast of the Caspian Sea, *Kompleksn. Issled. Kasp. Morya*, 1972, no. 3, pp. 134–146.

Arkhangel'skii, A.D. and Strakhov, N.M., *Geologicheskoe stroenie i istoriya razvitiya Chernogo morya* (Geological Structure and History of the Black Sea Development), Moscow-Leningrad: Akad. Nauk SSSR, 1938.

Bezrodnykh, Yu.P., Deliya, S.V., Romanyuk, B.F., Sorokin, V.M., and Yanina, T.A., New data on the upper quaternary stratigraphy of the North Caspian Sea, *Dokl. Earth Sci.*, 2015, no. 462 (1), pp. 479–483.

Bezrodnykh, Yu.P., Romanyuk, B.F., Sorokin, V.M., and Yanina, T.A., Stratigraphy of Upper Quaternary deposits of the Taman shelf area, in *Geologiya morei i okeanov. Materialy XXIII Mezhdunarodnoi nauchnoi konferentsii (Shkoly) po morskoi geologii* (Geology of Seas and Oceans, Proc. XXIII Int. Sci. Conf. (School) on Marine Geology), 2019, vol. 1, pp. 29–33.

Bolikhovskaya, N.S., Spatial-temporal patterns of vegetation and climate development in Northern Eurasia in the Neopleistocene, *Arkheol., Etnogr., Antropol. Evrazii*, 2007, no. 4 (32), pp. 2–28.

Bolikhovskaya, N.S. and Molod'kov, A.N., Correlation of the loess-soil formation and marine deposits of Northern Eurasia, in *Problemy paleogeografii i stratigrafii pleistotsena* (Problems of Paleogeography and Stratigraphy of the Pleistocene), Moscow: Mosk. Gos. Univ., 2000, pp. 149–178.

Brauer, A., Allen, R.M., Mingram, J., Dulski, P., Wulf, S., and Huntley, B., Evidence for last interglacial chronology and environmental change from southern Europe, *PNAS*, 2007, no. 104 (2), pp. 450–455.

Çağatay, M.N., Eriş, K., Ryan, W.B.F., Sancar, Ü., Polonia, A., Akçer, S., Biltekin, D., Gasperini, L., Görür, N., Lericolais, G., and Bard, E.K., Late Pleistocene–Holocene evolution of the northern shelf of the Sea of Marmara, *Mar. Geol.*, 2009, no. 265, pp. 81–100.

Dinamika landshaftnykh komponentov i vnutrennikh morskikh basseinov Severnoi Evrazii za poslednie 130000 let (Dynamics of Landscape Components and Inland Sea Basins of Northern Eurasia over the Last 130000 Years), Moscow: GEOS, 2002.

Dodonov, A.E., Tchepalyga, A.L., Mihailescu, C.D., Zhou, L.P., Markova, A.K., Trubikhin, V.M., Simakova, A.N., and Konikov, E.G., Last interglacial records from Central Asia to the northern Black Sea shoreline: Stratigraphy and correlation, *Neth. J. Geosci.*, 2000, vol. 79, nos. 2–3, pp. 303–311.

Fedorov, P.V., *Stratigrafiya chetvertichnykh otlozhenii i istoriya razvitiya Kaspiiskogo morya* (Stratigraphy of Quaternary Deposits and History of the Caspian Sea Development), Moscow: Akad. Nauk SSSR, 1957.

Fedorov, P.V., Stratigraphy of Quaternary deposits of the Crimean-Caucasian coast and some issues of the geological history of the Black Sea, *Tr. Geol. Inst. Akad. Nauk SSSR*, 1963, vol. 88.

Fedorov, P.V., *Pleistotsen Ponto-Kaspiya* (Pleistocene of the Ponto-Caspian), Moscow: Nauka, 1978.

Geologiya shel'fa Ukrainy. Kerchenskii proliv (Geology of the Ukrainian Shelf. Kerch Strait), Kyiv: Naukova Dumka, 1981.

Geomorfologiya zapadnoi chasti Prikaspiiskoi nizmennosti (Geomorphology of the Western Part of the Caspian Lowland), Moscow: Mosk. Gos. Univ., 1958.

Head, M.J., Formal subdivision of the Quaternary System/Period: Present status and future directions, *Quat. Int.*, 2019, no. 500, pp. 32–51.

Helmens, K.F., The last interglacial-glacial cycle (MIS 5-2) re-examined based on long proxy records from central and northern Europe, *Quat. Sci. Rev.*, 2014, no. 86, pp. 115–143.

Il'inskii, S.M., Caspian deposits of the eastern part of the North Caucasus lowland, *Geol. SSSR*, 1947, vol. 9, part 1.

Krijgsman, W., Tesakov, A., Yanina, T., Lazarev, S., Danukalova, G., Van Baak, C.G.C, Agusti, J., Alcicek, M.C., Aliyeva, E., Bista, D., Bruch, A., Buyukmeric, Y., Bukhsianidze, M., Flecker, R., Frolov, P., Hoyle, T.M., Jorissen, E.L., Kirscher, U., Koriche, S.A., Kroonenberg, S.B., Lordkipanidze, D., Oms, O., Rausch, L., Singarayer, J., Stoica, M., van de Velde, S., Titov, V.V., and Wesselingh, F.P., Quaternary time scales for the Pontocaspian domain: Interbasinal connectivity and faunal evolution, *Earth-Sci. Rev.*, 2019, no. 188, pp. 1–40.

Kukla, G., McManus, J.F., Rousseau, D.D., and Chuine, I., How long was the last interglacial, *Quat. Sci. Rev.*, 1997, no. 16, pp. 605–612.

Kukla, G., Bender, M., de Beaulieu, J.-L., Bond, G., Broecker, W.S., Cleveringa, P., Gavin, J.E., Herbert, T.D., Imbrie, J., Jouzel, J., Keigwin, L.D., Knudsen, K., McManus, J.F., Merkt, J., Muhs, D.R., Müller, H., Poore, R.Z., Porter, S.C., Seret, G., Shackleton, N.J., Turner, C., Tzedakis, P.C., and Winograd, I.J., Last interglacial climates, *Quat. Res.*, 2002, no. 58, pp. 2–13.

Kurbanov, R.N., Yanina, T.A., Murray, A.S., and Borisova, O.K., Hyrkanian epoch in the Late Pleistocene history of the Manych Depression, *Vestn. Mosk. Univ., Ser. 5: Geogr.*, 2018, no. 3, pp. 77–88.

Kurbanov, R.N., Yanina, T.A., Murray, A.S., Semikolennykh, D.V., Svistunov, M.I., and Shtyrkov, E.I., The age of the Karangatian (Late Pleistocene) transgression of the Black Sea, *Vestn. Mosk. Univ., Ser. 5: Geogr.*, 2019, no. 6, pp. 29–39.

Kurbanov, R.N., Semikolennykh, D.V., Yanina, T.A., Tyunin, N.A., and Murray, A.S., New data on the age of the Karangatian transgression of the Black Sea, *Vestn. Mosk. Univ., Ser. 5: Geogr.*, 2020, no. 6, pp. 139–145.

Kurbanov, R.N., Buylaert, J.P., Stevens, T., Taratunina, N.A., Belyaev, V.R., Makeev, A.O., Lebedeva, M.P., Rusakov, A.V., Solodovnikov, D.S., Rogov, V.V., Strletskaya, I.V., Murray, A.S., and Yanina, T.A., A detailed luminescence chronology of the Lower Volga loess-palaeosol sequence at Leninsk, *Quat. Geochronol.*, 2022, vol. 73, p. 101376.

Leont'ev, O.K., Maev, E.G., and Rychagov, G.I., *Geomorfologiya beregov i dna Kaspiiskogo morya* (Geomorphology of the Coasts and Bottom of the Caspian Sea), Moscow: Mosk. Gos. Univ., 1977.

Litt, T. and Gibbard, P., Definition of a global stratotype section and point (GSSP) for the base of the Upper (Late) Pleistocene subseries (Quaternary System/Period), *Episodes*, 2008, vol. 31, no. 2, pp. 260–263.

Moskvitin A.I., The Pleistocene of the Lower Volga region, *Tr. Geol. Inst. Akad. Nauk SSSR*, 1962, vol. 64.

Nevesskaya, L.A., *Pozdnechetvertichnye dvustvorchatye mollyuski Chernogo morya, ikh sistematika i ekologiya* (Late Quaternary Bivalve Mollusks of the Black Sea, Their Systematics and Ecology), Moscow: Akad. Nauk SSSR, 1965.

Nevesskaja, L.A., History of the genus Didacna (Bivalvia: Cardiidae), *Paleontol. J.*, 2007, vol. 41, no. 9, pp. 861–949.

Panin, A., Astakhov, V., Komatsu, G., Lang, J., and Winsemann, J., Middle and late Quaternary glacial lake-outburst floods, drainage diversions and reorganization of fluvial systems in northwestern Eurasia, *Earth-Sci. Rev.*, 2020, vol. 201, p. 103069.

Popov, G.I., The Hyrcanian transgression in the Northern Caspian region, *Byull. Kom. Izuch. Chetvertichn. Perioda*, 1967, vol. 33, pp. 77–86.

Popov, G.I., *Pleistotsen Chernomorsko-Kaspiiskikh prolivov* (The Pleistocene of the Black Sea-Caspian Straits), Moscow: Nauka, 1983.

Sedaikin, V.M., *Reference Sections of Quaternary Deposits in the North-Western Caspian Region*, VINITI, 1998, no.1594-V-88, 1988.

Semenenko, V.N. and Sidenko, O.G., Reflection of deep structures in marine Quaternary deposits in the central part of the Azov Sea, in *Pozdnechetvertichnaya istoriya i sedimentogenez okrainnykh i vnutrennikh morei* (Late Quaternary History and Sedimentogenesis of Marginal and Inland Seas), Moscow: Nauka, 1979, pp. 87–99.

Semikolennykh, D.V., Paleogeography of the Ponto-Caspian straits in the Late Pleistocene, *Extended Abstract of Cand. Sci. (Geogr.) Dissertation*, Moscow: Inst. Geogr. Russ. Acad. Sci., 2022.

Semikolennykh, D.V., Kurbanov, R.N., and Yanina, T.A., Chronology of the Karangatian transgression of the Black Sea based on luminescence dating data, *Izv. Ross. Akad. Nauk, Ser. Geogr.*, 2023, vol. 87, no. 1, pp. 88–101.

Shackleton, N.J., The last interglacial in the marine and terrestrial records, *Proc. R. Soc.*, 1969, no. 174, pp. 135–154.

Shkatova, V.K., On the age of sediments of the Khazarian complex in the Lower Volga region, in *Khronologiya pleistotsena i klimaticheskaya stratigrafiya* (Pleistocene Chronology and Climatic Stratigraphy), Leningrad: Geogr. O-vo SSSR, 1973, pp. 203–223.

Shkatova, V.K., Paleogeography of the Late Pleistocene Caspian Basins: Geochronometry, paleomagnetism, paleotemperature, paleosalinity and oxygen isotopes, *Quat, Int.*, 2010, no. 225, pp. 221–229.

Sorokin, V.M., Correlation of Upper Quaternary deposits and paleogeography of the Black and Caspian Seas, *Stratigr., Geol. Correl.*, 2011, vol. 19, no. 5, pp. 96–112.

Sorokin, V.M., Yanina, T.A., Bezrodnykh, Yu.P., and Romanyuk, B.F., Identification and age of submarine Girkanian sediment beds (Upper Pleistocene) in the Caspian Sea, *Quat, Int.*, 2018, no. 465(A), pp. 152–157.

Sorokin, V.M., Yanina, T.A., and Romanyuk, B.F., Finds of karangat deposits in the east of the Black Sea, *Moscow Univ. Geol. Bull.*, 2022, vol. 77, no. 6, pp. 729–735.

Svitoch, A.A., Stratotypes of the karangat of the Taman and Kerch peninsulas (Comparative analysis), *Dokl. Akad. Nauk*, 2009, no. 424, pp. 669–671.

Svitoch, A.A. and Yanina, T.A., *Chetvertichnye otlozheniya poberezhii Kaspiiskogo morya* (Quaternary Deposits of the Caspian Sea Coasts), Moscow: Ross. Akad. S-Kh. Nauk, 1997.

Svitoch, A.A., Selivanov, A.O., and Yanina, T.A., *Paleogeograficheskie sobytiya pleistotsena Ponto-Kaspiya i Sredizemnomor'ya (materialy po rekonstruktsii i korrelyatsii)* (Paleogeographical Events of the Pleistocene of the Ponto-Caspian and Mediterranean (Materials on Reconstruction and Correlation)), Moscow: Ross. Akad. S-Kh. Nauk, 1998.

Vasil'ev, Yu.M., *Antropogen Yuzhnogo Zavolzh'ya* (Anthropogene of the Southern Trans-Volga Region), Moscow: Akad. Nauk SSSR, 1961.

Vasil'ev, Yu.M. and Fedorov, P.V., On the stratigraphic position of the Upper Khazarian deposits of the Lower Volga region in the unified scale of the Caspian region, *Izv. Akad. Nauk SSSR, Ser. Geol.*, 1965, no. 12, pp. 1843–1851.

Yakhimovich, V.L., Nemkova, V.K., Dorofeev, P.I., Popova-L'vova, M.G., Suleimanova, F.I., Khabibullina, G.A., Alimbekova, L.I., and Latypova, E.K., *Pleistotsen nizhnego techeniya r. Ural* (Pleistocene of the Lower Ural River), Ufa: Bashkir. Filial Akad. Nauk SSSR, 1986.

Yanina, T.A., *Neopleitstotsen Ponto-Kaspiya: biostratigrafiya, paleogeografiya, korrelyatsiya* (Neopleistocene of the Ponto-Caspian: Biostratigraphy, Paleogeography, Correlation), Moscow: Mosk. Gos. Univ., 2012.

Yanina, T.A., Sorokin, V.M., Bezrodnykh, Yu.P., and Romanyuk, B.F., The Girkan stage in the Pleistocene history of the Caspian Sea, *Vestn. Mosk. Univ., Ser. 5: Geogr.*, 2014, no. 3, pp. 3–9.

Yanina, T.A., Svitoch, A.A., Kurbanov, R.N., Murray, A.S., Tkach, N.T., and Sychev, N.V., Experience in the optically stimulated luminescence dating of Pleistocene deposits of the Lower Volga River area, *Vestn. Mosk. Univ., Ser. 5: Geogr.*, 2017, no. 1, pp. 21–29.

Yanina, T., Sorokin, V., Bezrodnykh, Yu., and Romanyuk, B., Late Pleistocene climatic events reflected in the Caspian Sea geological history (Based on drilling data), *Quat. Int.*, 2018, no. 465 (A), pp. 130–141.

Yanko, V.V., Frolov, V.T., and Motnenko, I.V., Foraminifers and lithology of the stratotypic horizon (Anthropogene of the Kerch Peninsula), *Byull. Mosk. O-va. Ispyt. Prir., Otd. Geol.*, 1990, vol. 65, no. 3, pp. 85–97.

Publisher's Note. Pleiades Publishing remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.