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REGIONAL FISH-BASED BIOSTRATIGRAPHY OF THE LATE NEOGENE AND PLEISTOCENE OF SOUTHEASTERN EUROPE

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Regional Fish-Based Biostratigraphy of the Late Neogene and Pleistocene of Southeastern Europe. Kovalchuk, O. M. — This paper presents analytical results of the study of numerous freshwater fish fossils from almost 40 localities in the territory of southeastern Europe. It has been established that freshwater fishes can be regarded as parastratigraphic group suitable for biostratigraphic studies. Ten ichthyofaunal assemblages have been distinguished and characterized in the paper. These assemblages represent successive developmental stages in freshwater fish communities within southeastern Europe during the late Miocene, Pliocene and Pleistocene. Indices of evolutionary transformations (extinction rate, origination rate, taxonomic rotation) for ichthyofaunal assemblages have been calculated, and their trend is discussed herein.

Key words: freshwater fishes, faunal assemblage, evolution, Cenozoic, Eastern Europe.

Introduction

The modern zoogeographical structure of freshwater ichthyofauna of the Northern hemisphere was formed in general terms during the late Cenozoic (Sytychevskaya, 1989). Restoration of the key stages and features of this process is impossible without a detailed study of numerous fossil remains of bony fishes, originating from alluvial deposits of heterochronous localities. The historical and faunal analysis of paleoichthyological material from the south of Eastern Europe allows us tracing the temporal change in the groups of freshwater fish, to determine the time of appearance of individual modern taxa and their groups in the paleontological record, to find out the centers of their origin and ways of distribution, as well as to indicate some regional features of the formation of their ranges in time.

An essential precondition for conducting paleogeographical reconstruction is the development of a stratigraphic scale. The accuracy and degree of completeness of paleogeographical conclusions depends on its minuteness and validity. The establishment of landscape-climatic zonation during a geochronological interval is usually carried out basing on biostratigraphic data. Changes in the composition of faunal assemblages in time usually occurred in response to transformational processes in landscape zones (Korotkevich, 1988). These processes proceeded unevenly, being dependent on the specificity of paleogeographical conditions of a certain territory.

Paleogeographical reconstruction for southeastern Europe during the late Cenozoic was associated with a complicated history of the Paratethys basin (Rögl, 1998, 1999; Popov et al., 2004, 2006; Hilgen et al., 2012). The idea of the existence of a correlation between periods of fish species formation and transgressions of the seas was proposed by Lindberg (1948). Transgressive and regressive events not only directly affect the intensity of this process, but also cause changes in environmental conditions, increasing or decreasing their diversity (Lebedev, 1960). The dynamics of sea basins is associated with the rise or fall of continental masses, which, in turn, are accompanied by orogenic processes. The cumulative effect of all these factors leads to a diverse change in the conditions of existence of different groups of organisms, in particular in freshwater reservoirs.

Instead of the 'orthodox' biostratigraphy, according to which the age of geological bodies was determined by the presence of certain characteristic species or groups of highest-rank taxa, recently a deeper understanding of the essence of stratigraphic units has come into being: the layers of sedimentary rocks and associated organic remains are regarded as traces of paleoecosystems, and the change of stratigraphic horizons — as the change of environmental conditions in time and space. An ecostratigraphic approach allows us finding out the features of their genesis and evolution (Chepalyga, 1980).

Different fossil taxa have unequal biostratigraphic significance, according to which orthostratigraphic or parastratigraphic groups are distinguished. Chkhikvadze (1989), considering the problems of methodology of biostratigraphic studies, identified the criteria or properties by which a certain group of organisms can be considered orthostratigraphic (i. e. ideal for biostratigraphy). Such criteria include wide geographical distribution, relatively short time of existence, number of remains, independence from facies, simplicity of definition, clearly visible morphological features, as well as good preservation (Chkhikvadze, 1989). Examples of groups that have all of the above-mentioned properties are foraminifera, nannoplankton, ostracods, mollusks, small and large mammals. Based on the study of their remains, biostratigraphic zonation of the Cenozoic deposits of southeastern Europe was successfully carried out, with allocation of faunal assemblages and their correlations with those in other parts of the world (Semenenko, 1987; Korotkevich 1988; Nesin, Nadachowski, 2001; Tesakov, 2004, etc.).

Instead, it is believed that fish, as most aquatic organisms, are characterized by relatively slow pace of evolutionary transformations. This belief was the basis for the inappropriateness or insignificant value of fossil remains of freshwater fishes for biostratigraphy. It is clear that the biostratigraphic resolution of fishes is incommensurate with such for foraminifera or some other orthostratigraphic groups. At the same time, as our data show, the allocation of faunal complexes of freshwater fish (and, accordingly, the phases of geoclimatic events in the studied region) is not inferior to the corresponding possibilities of biostratigraphic division for malacofauna or even for mammals. Considering the fact that the correlation of the continental deposits of southeastern Europe can often not be based on marine orthostratigraphic groups, the attraction of as many groups of organisms as possible to the solution of stratigraphic problems is of considerable scientific interest and is of particular relevance.

Freshwater fish fossils often occur (usually even more often than bones of mammals) in continental a deposit, which makes them a convenient object of biostratigraphic analysis. The significant number and diversity of paleoichthyological material is due to taphonomic features, as well as the presence of skeletal structures resistant to destruction (e. g., pharyngeal teeth, skull bones, vertebrae, etc.). These possibilities give us reliable grounds to consider freshwater fishes as parastratigraphic group.

Here we present the fish-based biostratigraphic scheme for the Late Neogene and Pleistocene deposits of southeastern Europe with reference to some other schemes based on mammal fossils.

Material and methods

The material for this study were osteological remains of bony fishes from alluvial and coastal marine deposits at 68 strata of almost 40 localities (fig. 1) dated back to late Miocene, Pliocene and Pleistocene age in the Northern and North-Western Black Sea region, Northern Sea of Azov, in lower courses of the Dniester River (Republic of Moldova) and the Don River (Russian Federation). These materials accumulated during the work of expeditions of the Department of Paleontology (National Museum of Natural History (NMNHU-P) NAS of Ukraine) in 1950–2017. Stratigraphic units are presented in accordance with the regional biostratigraphic schemes for the Neogene and Pleistocene associations of southeastern Europe (Topachevsky et al., 1997, 1998; Nesin, Nadachowski, 2001; Popov et al., 2006; Rekovets, Pashkov, 2009; Krokmal, Rekovets, 2010; Hilgen et al., 2012).

The total amount of processed fish remains is near 12 000 specimens (proportion of diagnostic elements is at least 75 %). Ichthyological material is represented by incomplete imprints of skeletons, isolated skull bones, pharyngeal teeth, gill arches, fin rays, isolated and articulated centra, otoliths, scaling plates, fragments of ribs, etc. The vast majority of these remains are deposited in the NMNHU-P collections (nos. 27, 29, 33, 35, 37, 38, 41, 42, 44, 45, 52, 53). We have also used osteological material from paleontological museums of Taras Shevchenko National University of Kyiv, I. I. Mechnikov Odesa National University and Transnistrian State University (Republic of Moldova).

Analysis of the fauna composed by groups of different origin and ecological needs usually begins with the identification of its elementary units (Shtegman, 1938; Bănărescu, 1968; Griffiths, 2006). Given the variability of facies, discontinuity of the vertical distribution and incompleteness of the fossil record, the allocation of fau-



Fig. 1. Localities with fossil remains of freshwater fishes dated back to late Miocene, Pliocene and Pleistocene age (indicated by black circles) at the territory of southeastern Europe.

nal assemblages is mostly used in biostratigraphic partition of the Late Cenozoic continental deposits instead of zonal principle. Such assemblages reflect evolutionary transformations in animal groups (Datsenko, 2008). Here we use the units of biostratigraphic division proposed by Korotkevich (1988): representative of fauna, faunal group, faunal assemblage, and fauna.

The representative of the fauna is the elementary faunal unit. Faunal group comprises all animal species from one locality. The faunal assemblage is a historically composed association of species with its spatial-temporal characteristics inherent to the corresponding zoogeographic unit, and with a certain level of evolutionary development of groups in general and in separate phyletic lines (Rekovets, 1994). Faunal assemblages of vertebrates are distinguished by the following parameters (Topachevsky, Nesin, 1989): the appearance of new taxa, the level of their evolutionary development, qualitative composition of dominant groups and their geographical variation. Simultaneous existence of assemblages in different regions characterizes both extinct and modern faunas (Rekovets, 1994). Faunal assemblages reflect the stages of paleogeographical events and are qualitative indicators of stratigraphic units (Korotkevich, 1988). An important characteristic of a faunal assemblage is the commonality of historical fate that provides similar requirements for environmental conditions (Nikolsky, 1956, 1980). It is difficult to establish the origin of species thus their distribution by assemblages is carried out basing on environmental interaction. Species belonging to the same faunal assemblage often have different origin. The general ecological features of individual species are not indicators of the commonality of their historical past. In Pugachev's (1999) interpretation, a faunal assemblage is a number of faunal elements that previously comprised other assemblages, as well as species which occurrence is associated with a certain physical and geographical zone. A fauna is a set of successive faunal assemblages that existed for a relatively long time and connected with the unity of composition, ethology and evolution of their representatives. As Nikolsky (1980) noted, most of the faunas are heterogeneous in their origin.

For the purpose of the allocation of regional ichthyofaunal assemblages, the indices of extinction, origination of taxa and fauna rotation proposed by Landini and Sorbini (2005 a, b) have been calculated. At the same time, each taxon was considered as existent in the time interval between its first (FO) and the last (LO) occurrences (registration on paleontological material). The extinction rate (ER) is the ratio of the number of last occurrences to the total number of species (N) represented in the corresponding time range multiplied by its duration T (in millions of years): $ER = LO / NT$. The origination rate (OR) has been calculated using the same principle, but taking into account the number of first appearances of the species: $OR = FO / NT$. The turnover rate (TR) is the sum of the first two indices: $TR = ER + OR$. In order to minimize the error in determination of FO and LO at the boundary of the chronostratigraphic levels (because of possible inaccurate determination of their relative geological age), an arbitrary distribution of these values was taken — to the higher level (in the case of FO) and the lower level (in the case of LO). Graphs were prepared using the MS Excel 2010 package.

Results of the study

The evolution of all living beings, according to the concept of Yablokov-Khinzoryan (1963), is characterized by a general rhythm. In relatively conservative biotopes (e. g., in freshwater environment), evolutionary processes occur more slowly than those in labile ones (marine or terrestrial), which are characterized by more contrasting conditions. Certain periodicity in the evolutionary process can be observed on the example of the change of taxonomic composition in groups of freshwater fishes. According to the results of our study, ten regional ichthyofaunal assemblages (IFAs) were allocated¹. The first five (table 1) combine a number of late Miocene communities of freshwater fishes, while the following three (table 2) include the orictocoenoses

¹ Mykhailivkian IFA is considered here the oldest faunal assemblage in the studied region. However, significantly older freshwater fish remains from the Grytsiv locality (Shepetivka District, Khmelnytskyi Region, Ukraine) have been found recently. They are represented by two dentaries and two distal fragments of pectoral-fin spines belonging to catfish (determined previously as *Heterobranchus* ? sp.), as well as palatine of pike (*Esox* sp.). Allocation of a separate ichthyofaunal assemblage based on such pure material is currently not feasible.

Table 1. Biostratigraphic scheme for the late Miocene of southeastern Europe

Stage		Age, Ma	MN-zonation	Faunal assemblage		Localities	1					
Western Mediterranean	Eastern Paratethys			Microtheriofauna (after Nesin & Nadachowski, 2001, changed)	Freshwater ichthyofauna (our data)							
Messinian	Pontian	5.33	13	-	Pontian	Kalynivka	2					
						Shkodova Gora	3					
				Vinogradovkian		Vynogradivka 1	4					
				Fontanian		Pontian lectostratotype	5					
Tortonian	Maeotian	7.10	12	Cherevichnian	Cherevychnian	Orikhivka	6					
						Andriivka	7					
						Novoukrainka 1	8					
						Egorivka 1	9					
				Egorivka 2		10						
				Protopopovka 3		11						
				Novoelizavetivka 3		12						
				Verkhnya Krynitsya 2		13						
	Sarmatian	Upper	8.20	11		Berislavian	Vasylivka 1	14				
							Tretya Krucha	15				
							Novoukrainka 2	16				
							Cherevychne 3	17				
							Novoelizavetivka 2	18				
		Middle					8.70	10	Mikhailovkian	Mykhailivkian	Kubanka 2	19
											Lysa Gora 2	20
											Otradovo	21
											Palievo	22
		9.88			Popovian	Frunzivka 2	23					
						Lobkove	24					
						Pokshesht	25					
						Popovo 3	26					
						Mykhailivka 2	27					
		11.0				Mykhailivka 1	28					

Table 1 (continuation)

1	Ac*	Cyprinidae											
	<i>Acipenser gueldenstaedtii</i>	<i>Leuciscus</i> sp.	<i>Squalius</i> cf. <i>S. cephalus</i>	<i>Idus</i> cf. <i>I. idus</i>	<i>Rutilus tungurukensis</i>	<i>Rutilus robustus</i>	<i>Rutilus</i> cf. <i>R. rutilus</i>	<i>Rutilus frisii</i>	<i>Rutilus</i> cf. <i>R. frisii</i>	<i>Rutilus</i> sp.	<i>Scardinius haueri</i>	<i>Scardinius ponticus</i>	<i>Scardinius erythrophthalmus</i>
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3													
4													
5													
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25													
26													
27													
28													

* Ac — Acipenseridae.

Table 1 (continuation)

1	Cyprinidae													
	<i>Scardinius</i> sp.	<i>Chondrostoma</i> sp.	<i>Alburnus</i> cf. <i>A. alburnus</i>	<i>Blicca</i> sp.	<i>Abramis bliccoides</i>	<i>Abramis</i> sp.	<i>Aspius</i> sp.	<i>Pelecus</i> sp.	<i>Gobio</i> sp.	<i>Luciobarbus</i> sp.	<i>Ctenopharyngodon</i> sp.	<i>Palaeocarassius</i> sp.	<i>Carassius</i> sp.	<i>Tinca</i> sp.
2	■	■				■								■
3					■						■			■
4				■				■						■
5	■	■				■			■	■				
6	■			■										
7														
8		■				■		■		■				
9									■	■				
10						■	■					■		
11		■				■				■			■	
12												■	■	
13		■				■	■		■	■				■
14													■	
15														
16														
17			■			■				■				
18							■							
19	■	■												■
20						■				■			■	
21		■								■				■
22		■				■								
23	■							■						
24			■			■								
25									■					
26	■	■		■		■	■			■		■		■
27		■												
28							■							

Table 1 (continuation)

1	Cl*	Siluridae				Sa**	Esocidae		Mo***
	<i>Heterobranchius austriacus</i>	<i>Silurus spinosus</i>	<i>Silurus soldatovi</i>	<i>Silurus glanis</i>	<i>Silurus</i> spp.	<i>Hucho</i> sp.	<i>Esox sibiricus</i>	<i>Esox</i> spp.	<i>Morone</i> cf. <i>M. nobilis</i>
2									
3									
4									
5									
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8									
9									
10									
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21									
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26									
27									
28									

* Cl — Clariidae; ** Sa — Salmonidae; *** Mo — Moronidae.

Table 1 (continuation)

1	Percidae						Sp*	Ce**	Sc***	Gobiidae		
	<i>Leobergia zaissanica</i>	<i>Sander svetovidovi</i>	<i>Sander lucioperca</i>	<i>Sander</i> sp.	<i>Perca lepidopoma</i>	<i>Perca</i> sp.	<i>Pagrus</i> sp.	<i>Lates</i> sp. Ukraine	<i>Genyonemus?</i> sp.	<i>Ponticola dorsorostralis</i>	<i>Neogobius bettinae</i>	<i>Neogobius rhachis</i>
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4												
5												
6												
7												
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27												
28												

* Sp — Sparidae; ** Ce — Centropomidae; *** Sc — Sciaenidae.

of Pliocene age, and the last two (table 3) characterize the successive developmental stages of the ichthyofauna of southeastern Europe during the Pleistocene. Allocated IFAs are characterized by varying duration and different rates of evolutionary transformations. We allow further clarification of their time limits and taxonomic composition (if some additional representative material will be found). The absolute values of geological age of the stratigraphic episodes for the Eastern Paratethys are given after Steininger et al. (1996), Popov et al. (2006), Hilgen et al. (2012). In some cases, the average values of absolute dates were calculated for the correlation of paleomagnetic data and MN-zones based on evolutionary changes in small mammal communities during the Neogene.

The names of ichthyofaunal assemblages are distinguished mainly after reference localities, from which the most representative osteological material was obtained. We used (whenever possible) the names of the assemblages proposed earlier for other groups of vertebrates (including mammals) basing on the “Occam’s Razor” principle. In tables 1–3, black cells reflect the fact that a particular taxon is present in a particular oritocoenosis. The entire stratigraphic range of each species (between the first and last appearance in the paleontological record of the studied region) is marked by gray color.

Table 2. Biostratigraphic scheme of the Pliocene deposits of southeastern Europe

Epoch	Stage		Age, Ma	MN-zonation	Faunal assemblage		Localities	1
	General	Regional			Microtheriofauna (after Nesin & Nadachowski, 2001, changed)	Freshwater ichthyofauna (our data)		
P L I O C E N E	Gelasian	Akchagylia	1.81	17	Khaprovian	Shirokinian	Kotlovina 3	2
							Kotlovina 2	3
	Cherevychne 2		4					
	Kryzhnivka 2		5					
	Obukhivka 2		6					
	Shirokine 2		7					
	Zanclean	Kimmerian	3.60	15	Moldavian	Obukhivkian	Priozerne	8
							Odesa Catacombs	9
							Kotlovina 1	10
							Vynogradivka 2	11
							Kamianske	12
							Novokyivka	13
							Obukhivka 1	14
Kuchurganian	Kuchurganian	4.20	14	Kuchurganian	Kuchurganian	Uyutne	15	
						Nikolske	16	
						Novopetrivka	17	
		5.33						

Table 2 (continuation)

1	Siluridae				Esocidae			Percidae				Sparidae	
	<i>Silurus soldatovi</i>	<i>Silurus glanis</i>	<i>Silurus cf. S. glanis</i>	<i>Silurus</i> spp.	<i>Esox sibiricus</i>	<i>Esox moldavicus</i>	<i>Esox</i> spp.	<i>Leobergia zaissanica</i>	<i>Sander lucioperca</i>	<i>Sander</i> sp.	<i>Perca fluviatilis</i>	<i>Perca</i> sp.	<i>Pagrus cinctus</i>
2		■				■			■				
3		■				■			■		■		
4		■	■	■		■							
5		■	■			■	■						
6		■		■		■	■						
7	■	■	■	■		■	■	■					■
8	■	■	■	■		■	■						■
9	■	■	■	■		■	■	■	■				■
10		■				■	■	■	■				
11		■				■	■						
12	■					■	■	■			■		
13	■					■	■				■		
14	■					■	■				■		
15	■					■	■				■		
16		■				■	■						
17	■	■	■	■	■	■	■	■	■		■	■	■

LATE MIOCENE FAUNAL ASSEMBLAGES

Mykhailivkian ichthyofaunal assemblage (11.0–9.88 Ma)

Reference locality: Mykhailivka 1.

Several genera of carp fishes (*Rutilus*, *Scardinius*, *Aspius*, *Luciobarbus*, *Palaeocarassius*, *Tinca*) appear for the first time in water bodies of southeastern Europe; at least some of them (e. g., *Scardinius haueri*) are represented by primitive forms. Only for this faunal assemblage the presence of temperate basses (*Morone* cf. *M. nobilis*) and croakers (*Genyonemus* ? sp.) is noted. Representatives of the family Gobiidae (*Ponticola dorsorostralis*, *Neogobius bettinae*, *N. rhachis*) were quite numerous at that time. Meanwhile, such characteristic groups of the Neogene freshwater ichthyofauna as catfishes, pikes, and perches are completely absent here. Thus, the Mykhailivkian assemblage is quite archaic and somewhat pure in its taxonomic composition.

Popovian ichthyofaunal assemblage (9.88–8.70 Ma)

Reference locality: Popovo 3.

The assemblage is characterized by a significant increase in the number of species belonging to the family Cyprinidae, which become the dominant group. In particular, new genera (*Leuciscus*, *Squalius*, *Chondrostoma*, *Abramis*, *Carassius*, *Alburnus*, *Blicca*) appeared. The species variety of roaches (*Rutilus*) is significant. *Scardinius haueri* is recorded for the last time; instead, it is replaced by *S. erythrophthalmus*. Dace (*Leuciscus*), rudd (*Scardinius*), barbel (*Luciobarbus*) and tench (*Tinca*) are in the composition of all orictocoenoses of the Popovian IFA. Catfishes are represented by two families — Clariidae (*Heterobranchus austriacus*) and Siluridae (*Silurus spinosus*). In addition, pike remains (belonging to *Esox sibiricus*) are registered for the first time in southeastern Europe. A characteristic feature of the Popovian IFA is the first appearance and distribution of percid fishes (*Perca*, *Leobergia*, and *Sander*). In general, the described assemblage brings together representatives of all major groups of the Neogene freshwater ichthyofauna.

Table 3. Biostratigraphic scheme of the Pleistocene deposits of southeastern Europe

Epoch	Stage	Age, Ma	Ichthyofaunal assemblage	Locality	First occurrence (FO)	Last occurrence (LO)
PLEISTOCENE	Upper	0.0117	Semibalkian	Savintsy	<i>Squalius cephalus</i> , <i>Salmo</i> sp., <i>Perca neopleistocenica</i>	<i>Salmo</i> sp., <i>Perca neopleistocenica</i> , <i>Pagrus cinctus</i>
				Dnieper Alluvium		
	Novgorod-Siverskyi					
	Medzhybizh 1, 2					
	Lysa Gora 1					
	Besimmenne					
	Tykhonivka 1					
	Protopopovka 1, 2					
	Semibalka 1					
	Bilshovyk 2					
	Cherevychno 1					
	Semibalka 3					
	Middle Neopleistocene	0.781	Nogaikian	Port-Katon	<i>Cyprinus carpio</i> , <i>Esox lucius</i> , <i>Esox nogaicus</i> , <i>Zingel nogaicus</i>	<i>Esox nogaicus</i> , <i>Zingel nogaicus</i>
				Limany		
				Taman		
				Kairy		
				Nogaik		
				Nova Etuliya		
				Zhevakhova gora 1		
Calabrian Eopleistocene	1.81		Tiligul			

Frunzivkian ichthyofaunal assemblage (8.70–8.20 Ma)

Reference locality: Frunzivka 2.

Carp fishes retain their dominant position both in the number of remains and in taxonomic diversity during the existence of this assemblage. Representatives of the genera *Idus* and *Pelecus* appear for the first time; *Rutilus* cf. *R. rutilus* is additionally registered, while *Alburnus* and *Blicca* are temporarily absent. The rising of catfishes is observed at that time: *Heterobranchus austriacus* is represented in all oritocoenoses (except Lysa Gora 2) and disappeared at the end of existence of this assemblage; primitive *Silurus spinosus* is replaced by another species of this genus — *S. soldatovi*. *Hucho* is registered for the first time in the paleontological record of Europe, which, in fact, limits the taxonomic diversity of salmonids in the studied region at that time. The remains of pike, although they are present in the collection from almost all localities of the Frunzivkian IFA, are so poorly diagnostic that it is practically impossible to establish the species affiliation at the present time. Possibly, they represent a typical late Miocene form of the studied region — *Esox sibiricus*. Frunzivkian IFC is characterized by the absence of percids, which is due to certain taphonomic features of investigated localities. In general, the described faunal assemblage looks impoverished (in comparison with the previous one) and characterizes the level of evolutionary development of the freshwater ichthyofauna at the final phase of the late Sarmatian.

Cherevychnian ichthyofaunal assemblage (8.20–7.10 Ma)

Reference locality: Cherevychna 3.

This faunal assemblage in general (table 1) is similar to the previous one, except for the presence of percid fishes (*Leobergia*, *Sander*, *Perca*). Pikeperches of the genus *Sander* are represented by two species — *S. svetovidovi* and a form morphologically identical to the extant *S. lucioperca*. Certain changes are observed in the taxonomic composition of carp fishes: *Rutilus robustus*, *Gobio* sp. are recorded for the first time; *Rutilus* cf. *R. rutilus*, *Rutilus* cf. *R. frisii*, *Aspius* sp., *Pelecus* sp. disappear at the final developmental stage of the assemblage, and *Alburnus* cf. *A. alburnus* appeared for the last time. Catfishes (Siluridae) are represented by *Silurus soldatovi*, while pikes — by *Esox sibiricus*. Since the described ichthyofaunal assemblage existed during the entire Maeotian, it is assumed that certain stagnation in the development of freshwater ecosystems in southeastern Europe took place at that time.

Pontian ichthyofaunal assemblage (7.10–5.33 Ma)²

Reference locality: Shkodova Gora.

Among allocated regional faunal assemblages, Pontian IFA is one of the most specific (table 1). Acipenserid fishes (morphological analogue of *Acipenser gueldenstaedtii*) appeared for the first time in water bodies of the studied region. Significant changes in species diversity of fishes belonging to the family Cyprinidae are due to general impoverishment of their taxonomic composition (*Leuciscus*, *Squalius* and *Carassius* are absent; *Idus* cf. *I. idus*, *Blicca* sp., *Gobio* sp. and *Luciobarbus* sp. are recorded for the last time in the region; there is a decrease in the number of species belonging to *Rutilus* and *Scardinius*). At the same time, there is a replenishment of the ichthyofaunal assemblage by taxa, which ranges covered the water bodies of Western Siberia, Eastern Kazakhstan, Altai and Mongolia at that time. In particular, *Rutilus tungurukensis*, *Abramis bliccoides*, *Ctenopharyngodon* sp. appear for the first time (and last time for the studied region). The appearance of *Silurus glanis* and its coexistence with *S. soldatovi* are noted. The remains of pikes (*Esox sibiricus*) and percids (*Leobergia zaissanica*, *Sander lucioperca*, *Perca lepidopoma*) are not numerous. The characteristic feature of this assemblage is the presence of sparids (*Pagrus* sp.) and latids (*Lates* sp. Ukraine).

² The name of the faunal assemblage is due to the age and epoch name. Alternatively, “Odesian IFC” (by geographical location of most of the investigated oritocoenoses) can be used.

PLIOCENE FAUNAL ASSEMBLAGES

Kuchurganian ichthyofaunal assemblage (5.33–4.20 Ma)

Reference locality: Novo-Petrivka.

There is a significant rise of sturgeons (*Acipenser gueldenstaedtii*, *Acipenser* cf. *A. sturio*, *Acipenser* sp.) represented by numerous remains. Carp fishes lose their dominant position and their diversity at that time is reduced: there are some species of the genera *Rutilus*, *Scardinius*, *Tinca*; *Luciobarbus* is replaced by *Barbus* (at the late stage of the assemblage's development). Catfishes (*Silurus soldatovi*, *S. glanis*, *Silurus* cf. *S. glanis*) become widely distributed. The presence of *Esox sibiricus* is recorded for the last time for the studied region. Percid fishes are absent in this assemblage, while *Pagrus cinctus* appears in southeastern Europe for the first time.

Obukhivkian ichthyofaunal assemblage (4.20–3.60 Ma)

Reference locality: Obukhivka 1.

The taxonomic variety of acipenserids is reduced compared to those of the previous assemblage. There is a partial restoration of the taxonomic composition of carp fishes (table 2). Some thermophilous species (e. g., *Scardinius ponticus*, *Silurus soldatovi*, *Leobergia zaissanica*) are recorded for the last time, being displaced by cold-tolerant extant forms (*Scardinius erythrophthalmus*, *Silurus glanis*, and *Sander lucioperca*). *Esox moldavicus* (presumably endemic) appears and becomes widely distributed at this time.

Shirokinian ichthyofaunal assemblage (3.60–1.81 Ma)

Reference locality: Shirokine 2.

Cyprinids are dominant group in freshwater fish communities (table 2). *Rutilus robustus* (a relic representative of the thermophilous Miocene fauna) disappears. Forms unpretentious to living conditions (*Carassius*, *Tinca*) become widespread. Catfishes are represented by *Silurus glanis*. Remains of *Esox moldavicus* are registered in all investigated orictocoenoses. *Perca fluviatilis* appears for the first time in water bodies of southeastern Europe.

PLEISTOCENE FAUNAL ASSEMBLAGES

Nogaïskian ichthyofaunal assemblage (1.81–0.70 Ma)

Reference locality: Nogaïsk.

The faunal assemblage is characterized by the absence of sturgeons and a rather impoverished taxonomic composition of carp fishes (Cyprinidae). At this time, fishes of the genus *Rutilus* (presumably represented by extant species) become well distributed, while remains belonging to dace and ide are not so numerous. Among carp fishes, the representatives of *Barbus*, *Carassius* and *Tinca* are dominant in number, and the common carp *Cyprinus carpio* reliably appears for the first time. Pikes are represented by at least two species — the endemic *Esox nogaicus* and *E. lucius*, which is still widespread in Eurasian freshwater bodies. The family Percidae is represented in the Nogaïskian IFA by three genera — *Sander*, *Perca* and *Zingel* (and this is the only registration of the latter genus in the fossil record of Eastern Europe). Besides, a handful number of remains belonging to sparid fishes (*Pagrus* sp.) were identified. Nogaïskian IFA is composed of depressive orictocoenoses. The reduction of taxonomic diversity is continued due to the final displacement of thermophilous species by cold-resistant extant forms.

Semibalkian ichthyofaunal assemblage (0.70–0.0117 Ma)

Reference locality: Semibalka 1.

The taxonomic composition of this faunal assemblage is somewhat mixed (maybe due to inclusion of fish remains from the Dnieper alluvium). There are not numerous sturgeons (Acipenseridae) and porgies (Sparidae). Dace, rudd, bream, barbel, crucian carp and tench become common among carp fishes. Fishes of the families Siluridae and Esocidae

are represented only by extant species. The same applies to percid fishes (except *Perca neopleistocenica*, which species status requires further confirmation). The Semibalkian faunal assemblage also includes salmonid fishes (*Salmo*).

Thus, in contrast to the opinion of Yakovlev (1961) and some other researchers, we can assert that the Neogene (and the entire Late Cenozoic) cannot be regarded as a single stage in the evolutionary development of freshwater ichthyofauna. At that time, there were significant changes of taxonomic composition in freshwater fish communities at the regional and global levels. However, it was possible to formulate such a conclusion only basing on accumulation and detailed study of a considerable amount of paleoichthyological material from numerous localities at the territory of southeastern Europe.

Discussion

Allocation of the regional ichthyofaunal assemblages would have been impossible without taking into consideration the facts of appearance (speciation) and disappearance (extinction) of individual taxa in the fossil record of the studied region, as well as without calculation the gross rotation of the freshwater fish fauna during certain periods of geological time.

The problem of evaluation of evolutionary transformations of the ichthyofauna of southeastern Europe during the late Cenozoic is methodologically complicated. This is due to the following reasons: 1) the incompleteness of the fossil record (usually only the most numerous forms are presented, which are the most typical for a certain fauna (in our case Cyprinidae), while other important components of ancient fish communities (in particular Salmonidae) are practically absent); 2) the diagnostics of fragmentary osteological material in case of separate groups of freshwater fishes is not sufficiently developed and there is a necessity of frequent use of the open nomenclature for the description of some taxa; 3) the absence or fragmentation of data on distribution and dynamics of the ranges of freshwater fish fauna in Europe and Asia during the late Cenozoic. Therefore, it should be borne in mind that the values of the indices for the origination (OR) and extinction of taxa (ER), as well as the rotation of the fauna (table 4) can be slightly underestimated, and the conclusions drawn on their basis are preliminary and require clarification.

We consider that the most expedient is to carry out the characteristic of the above-mentioned values at the level of individual ichthyofaunal assemblages. Moving to higher levels (for example, merging of consecutive IFAs into groups in chronological order, etc.) somewhat distorts the real situation, therefore we were forced to refuse the application of such approach.

The duration of allocated faunal assemblages (table 4) varies from 0.50 million years (Frunzivkian IFA) to 1.79 million years (Shirokinian IFA); an average value is 1.1 million years. It is slightly higher than the corresponding values calculated for faunal assemblages allocated basing on mammals of the same age (Korotkevich, 1988; Nesin, Nadachowski, 2001).

The number of orictocoenoses and taxa included in their composition also significantly differs depending on the ichthyofaunal assemblage, which we take into consideration (table 4). The oldest IFA for the studied region (Mykhailivkian) is characterized by a minimum number of both values (1 and 11, respectively). At the same time, the largest number of orictocoenoses (12) characterizes the Cherevychnian and Semibalkian faunal assemblages, and the latter is also characterized by the maximum number of taxa (30). Such distribution depends on the geological age and it is due to taphonomic reasons. At the same time, it is not yet possible to draw a correlation between a certain epoch and the above-mentioned values. Every isolated IFA has an average of about seven orictocoenoses and 23 freshwater fish taxa.

Table 4. Indicators of evolutionary changes in the late Cenozoic freshwater ichthyofaunal assemblages of southeastern Europe

Ichthyofaunal assemblage	Duration, millions of years	Number of		Indices			
		orictocoenoses	taxa	Extinction rate (ER)	Origination rate (OR)	Taxonomic rotation (TR)	
Semibalkian	0.769	12	30	0.130	0.130	0.260	0.3
Nogaiskian	1.029	11	25	0.078	0.155	0.233	0.2
Shirokinian	1.790	6	20	0.140	0.028	0.168	0.2
Obukhivkian	0.600	7	21	0.397	0.079	0.476	0.5
Kuchurganian	1.130	3	17	0.156	0.260	0.416	0.4
Pontian	1.770	4	25	0.203	0.203	0.406	0.4
Cherevychnian	1.100	12	28	0.292	0.065	0.357	0.4
Frunzivkian	0.500	6	22	0.091	0.364	0.455	0.5
Popovian	1.180	4	27	0.063	0.659	0.722	0.7
Mykhailivkian	1.120	1	11	0.379	0.833	1.212	1.2

The results of calculating the origination (OR) and extinction rates (ER), as well as taxonomic rotation (TR) in the region under study are also quite interesting. The range of their values significantly varies. The smallest one is for ER — the maximum value (0.397), calculated for the Obukhivkian IFA, is only 3 times higher than the minimum for the Popovian IFA (0.063). At the same time, the maximum and minimum values of TR and OR calculated for ichthyofaunal assemblages differ 7 and 30 times, respectively (table 4). It is clearly visible (fig. 2) that during the existence of the first three faunal assemblages in freshwater bodies of the studied region, there appeared much more new taxa than disappeared during the corresponding period of time. As for the following assemblages, the situation looks somewhat different: for example, ER and OR values for the Pontian and Semibalkian IFAs coincide (how many new species appeared, as many others or the same forms disappeared from the fossil record of southeastern Europe). For all other faunal assemblages of the late Miocene and Pliocene age (except Kuchurganian and Nogaiskian), the extinction of taxa dominated over their appearance.

The pace of evolutionary transformations in freshwater ichthyofauna of the investigated region is presented on fig. 3. For better visibility, the index values calculated for each faunal assemblage are presented on a logarithmic scale. In addition, trend lines were constructed for each of them. There is a sharp decline in OR and TR (their trend lines

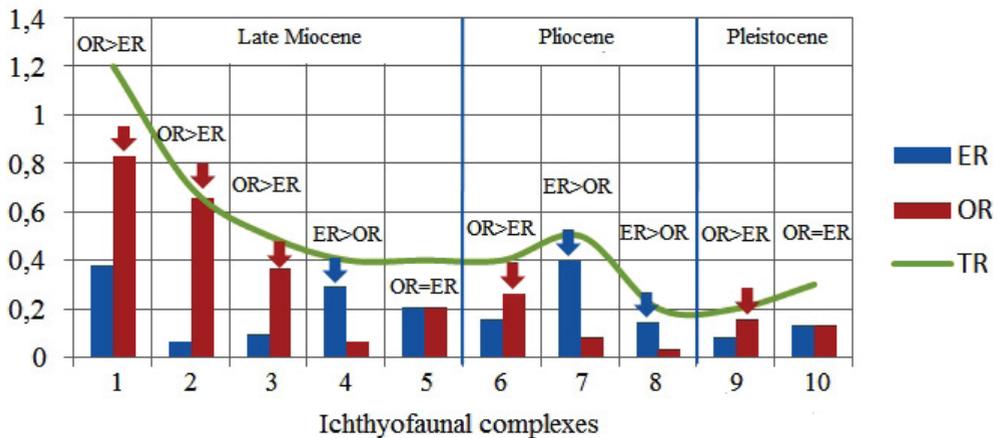


Fig. 2. Dynamics of evolutionary transformations in the ichthyofaunal assemblages of the studied region during the late Neogene and Pleistocene. IFAs: 1 — Mykhailivkian; 2 — Popovian; 3 — Frunzivkian; 4 — Cherevychnian; 5 — Pontian; 6 — Kuchurganian; 7 — Obukhivkian; 8 — Shirokinian; 9 — Nogaiskian; 10 — Semibalkian. The numbers on the ordinate axis indicate the range of index values.

are sub-parallel). This indicates a constant decrease over time of the number of appearance of new taxa in the composition of successive faunal assemblages and the associated slowdown in the pace of rotation of the ichthyofauna (fig. 3). At the same time, the trend line of ER also shows a downturn, but it is almost horizontal. This indicates the relative stability of the disappearance of taxa of the studied region in time, due to extinction or change of their habitats. In addition, the position of the trend lines for various indices indirectly confirms the correctness of allocation of the described here ichthyofaunal assemblages.

Intersection of OR and ER lines, according to fig. 3, occurred between the 4th (Cherevychnian) and the 5th (Pontian) IFAs. At that time (i. e. on the Maeotian-Pontian boundary) there were irreversible changes in the taxonomic composition of freshwater ichthyofaunal assemblages in southeastern Europe, caused by significant fluctuations in the sea level (in turn caused by the activation of orogenic processes) and global climate change. In the Pliocene, as a result of active tectonic alterations and a decrease in average annual temperatures, a rich freshwater ichthyofauna has experienced a significant depletion (due to extinction of thermophilous species).

An interesting pattern was noted: changes in the ichthyofaunal assemblages of the studied region become slower over time. Thus, the highest value of TR (1.2) is obtained for the oldest (Mykhailivkian) IFA. In order to achieve such a high value, the two next consecutive faunal assemblages (Popovian and Frunzivkian), then three (Cherevychnian, Pontian, Kuchurganian) and, eventually, four (table 4) should have changed. Accordingly, the time required for the implementation of these changes has also steadily increased in such order (in millions of years): 1.12, 1.68, 4.00, 4.19. Given the possibility of genetic ties between the components of different faunal assemblages (in a specific analogy with an increase of biological age during the change of human generations), this pattern can be explained by the transition to a higher level of organization of fish assemblages, formation of a more complex system of relationships between their representatives and an increase in ectopic differentiation in the face of more uniform geoclimatic conditions.

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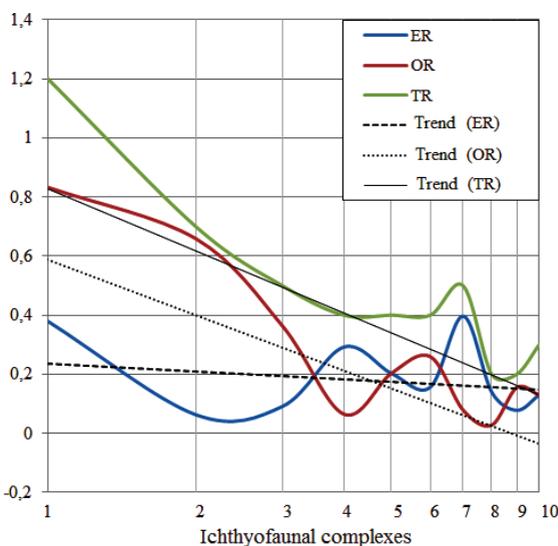


Fig. 3. Extinction rate (ER), origination rate (OR) and taxonomic rotation (TR) in the ichthyofaunal assemblages of southeastern Europe and their trends on a logarithmic scale. Ichthyofaunal assemblages: 1 — Mykhailivkian; 2 — Popovian; 3 — Frunzivkian; 4 — Cherevychnian; 5 — Pontian; 6 — Kuchurganian; 7 — Obukhivkian; 8 — Shirokinian; 9 — Nogaiskian; 10 — Semibalkian.

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