Vestnik zoologii, **48**(2): 129–136, 2014
DOI: 10.2478/vzoo-2014-0013

UDC 567.5(477.64)

BONY FISHES FROM THE LATE MIOCENE AND PLIOCENE STRATA OF POPOVO LOCALITY (UKRAINE): TAXONOMIC CHANGES AND THEIR PALAEOECOLOGICAL EXPLANATION

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Bony Fishes from the Late Miocene and Pliocene Strata of Popovo Locality (Ukraine): Taxonomic Changes and Their Palaeoecological Explanation. Kovalchuk, O. M. — The present paper deals with results of studying of the fossil fish remnants from the Late Miocene and Pliocene strata of Popovo locality (Southern Ukraine). Our aim was to show local taxonomic changes in freshwater fish communities through-out the specified range of geological time. Twenty seven species of the 20 genera, 6 families (Cyprinidae, Cobitidae, Siluridae, Salmonidae, Esocidae, Percidae) and 5 orders (Cypriniformes, Siluriformes, Salmoniformes, Esociformes, Perciformes) were identified from the 4 heterochronous bonyferous layers. Basing on taxonomic richness, diversity, complexity and similarity of communities, it can be assumed, that changes in their qualitative and quantitative composition were caused by hydrological regime transformation, palaeogeographical alterations and also local taphonomic features.

Key words: bony fishes, Teleostei, Late Miocene, Pliocene, Popovo, Southern Ukraine, taxonomic diversity, taphonomy, palaeoecology.

Костистые рыбы из отложений позднего миоцена и плиоцена местонахождения Попово (Украина): таксономические изменения и их палеоэкологическое объяснение. Ковальчук А. Н. — Статья посвящена результатам изучения ископаемых остатков рыб из отложений позднего миоцена и плиоцена местонахождения Попово на юге Украины. Целью работы было показать локальные таксономические изменения в пресноводных сообществах костистых рыб на протяжении указанного отрезка геологического времени. Из четырех разновозрастных костеносных толщ определены остатки 27 видов, относящихся к 20 родам, 6 семействам (Cyprinidae, Cobitidae, Siluridae, Salmonidae, Esocidae, Percidae) 5 отрядов (Cypriniformes, Siluriformes, Salmoniformes, Esociformes, Perciformes). На основании показателей таксономического богатства, разнообразия, сложности и сходства сообществ можно предположить, что изменения их качественного и количественного состава были вызваны трансформацией гидрологического режима, палеогеографическими перестройками и локальными тафономическими особенностями.

Ключевые слова: костистые рыбы, Teleostei, поздний миоцен, плиоцен, Попово, юг Украины, таксономическое разнообразие, тафономия, палеоэкология.

Introduction

Popovo locality of the fossil fauna was discovered in 2007 by expedition of the National Museum of the Natural History, National Academy of Sciences of Ukraine (NMNH NASU, Kyiv). It is situated near Vasilevka, Zaporizhia region (Southern Ukraine). Fossil site is located in a ravine, on the slope of an ancient beam on the southern outskirts of the village Verkhniaya Krynitsa (fig. 1). Broad description of the geological section, characteristics of small mammal remains from the bonyferous strata of Popovo and justification of their age were shown in the work of Rekovets and Pashkov (2009). The section includes four heterochronous strata with numerous remains of bony fishes, reptiles and mammals, as well as the individual bones of amphibians: Popovo 3 (Late Miocene, MN 11), Popovo 2, Popovo 1 and Popovo 0 (Late Pliocene, MN 16). This section can be viewed as two rhythms of sedimentation — river and lake-lagoon deposits.

The present paper is based on the study of 1757 fish remnants, 1718 of which (97.78 %) are determinable to species or at least to genus level. Interpretation of the fossil ichthyologic material and also palaeoecological explanation of taxonomic changes on the Popovo locality are presented in this article.

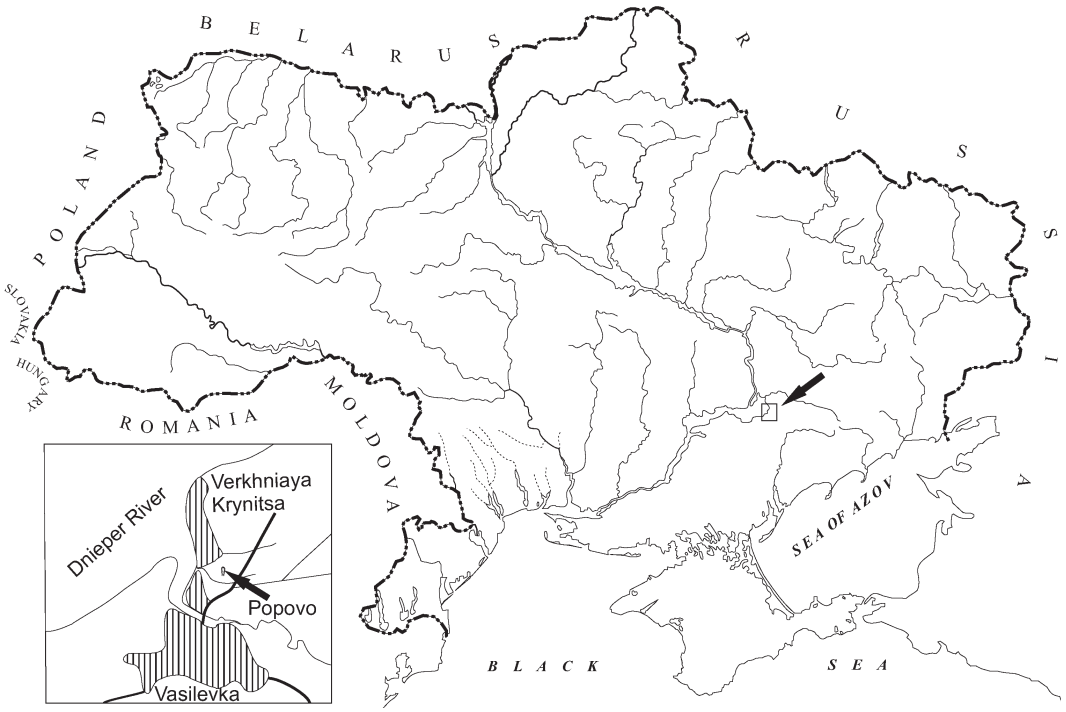

Fig. 1. Location map of the Miocene and Pliocene multilayered Popovo locality.

Рис. 1. Локализация многослойного местонахождения миоцена и плиоцена Попово.

Material and methods

Investigated material was collected during the 2007–2013 and recently housed in the department of vertebrate paleozoology (NMNH NASU, collection N 29/1472–3381). Fish remnants are represented by disarticulated bones (e. g., isolated pharyngeal teeth and bones of carp fishes, visceral bones, teeth, fin rays, vertebrae and scales of some other groups of teleost fishes). Majority of them (n = 1642) are derived from the most ancient, Late Sarmatian bonyferous layer Popovo 3 (Late Miocene, MN 11). Other bones (n = 55; 33; 27) are from younger (Pliocene) strata of Popovo 2, Popovo 1 and Popovo 0, respectively. Current correlation of the Eastern Paratethys stages with European Mammal Neogene Zones was essentially taken from Nesin and Nadachowski (2001), with changes.

Systematic determination of the fossil remnants is provided by the author using diagnostic features under the methodology of Sytchevskaya (1989) and Rutte (1962) for carp fish bones, Lepiksaar (1994) and Miranda and Escala (2005) for skeletal elements of other groups. Recent fish bones from the department of vertebrate paleozoology NMNH NASU were used for comparison. Ichthyologic systematics follows Nelson (2006) and Movchan (2011).

Taxonomic richness is determined basing on the sum of the different-rank taxa (species, genus, family and order levels), that are components of communities inhabiting a given territory through-out the specified range of geological time (Topachevsky et al., 2000). Paliy-Kovnatsky index is used for the calculation of relative dominance of a species in a community: more than 10 % — dominant; from 1 to 10 % — eusubdominant; from 0.1 to 1 % — subdominant; less than — 0.1 % — secondary member of community (Shitikov et al., 2003). Indicators of diversity of the faunal assemblages (species diversity, H and taxonomic diversity, H_{tax}), proposed by Emelyanov et al. (1999), were calculated using the Shannon index (Shannon, Weaver, 1949) and provide an opportunity to quantify the taxonomic structure of the biotic communities (Magguran, 1992; Topachevsky et al., 2000). Statistical analysis was carried out in MS Excel 2007 and PAST. We used Sorensen index (S) and Jakkar coefficient (K_J) for quantification the degree of similarity between taxonomic lists of heterochronous bonyferous strata (Odum, 1975).

Discussion

General data about qualitative and quantitative composition of bony fish fauna from heterochronous strata of the Popovo locality are shown in the table 1. Faunal list includes 27 species belonging to 20 genera, 6 families (Cyprinidae, Cobitidae, Siluridae, Salmonidae, Esocidae, Percidae) and 5 orders (Cypriniformes, Siluriformes, Salmoniformes, Esociformes, Perciformes). Basing on the distribution of diagnostic bones by families, carp fishes are predominate in the composition of fosilliferous strata (except Popovo 2): their share in the fauna of Popovo 3, Popovo 1 Popovo and 0 are 48.5 %, 51.7 % and 81.8 %, respectively. The same situation is marked for the distribution of remains as belonging to specific and generic rank taxa. The family Cyprinidae is represented by numerous species and genera, while only 2 species are determined by Esocidae (*Esox lucius*, *Esox* sp.) and Percidae (*Perca* sp., *Sander* cf. *zaissanicus*), one species of Cobitidae (*Cobitis* sp.), Siluridae (*Silurus* sp.) and Salmonidae (? *Salmo* sp.). Bony fish community composition of the Popovo locality is fairly typical for the Late Miocene and Pliocene, exhibiting a significant degree of similarity with ichthyologic complexes of the same age on the south of Ukraine (Kovalchuk, 2012; Kovalchuk, 2013 a, b). Most of the identified genera are morphological analogues of modern forms.

Table 1. Qualitative and quantitative composition of the Late Miocene and Pliocene freshwater fish communities from Popovo locality

Таблица 1. Качественный и количественный состав пресноводных сообществ рыб позднего миоцена и плиоцена из местонахождения Попово

Taxon	Amount of the fish bones			
	Popovo 3	Popovo 2	Popovo 1	Popovo 0
Leuciscus sp.	2	–	1	–
Squalius sp.	43	–	–	–
Idus idus (Linnaeus, 1758)	2	–	–	–
Rutilus frisii (Nordmann, 1840)	100	4	–	–
Rutilus cf. *frisii* (Nordmann, 1840)	33	–	–	–
Rutilus sp.	–	2	1	1
Scardinius erythrophthalmus (Linnaeus, 1758)	350	2	–	2
Scardinius sp.	34	–	2	–
Chondrostoma sp.	3	–	2	–
Alburnus sp.	3	–	–	–
Blicca sp.	5	–	–	–
Abramis cf. *brama* (Linnaeus, 1758)	–	–	1	1
Abramis sp.	4	–	–	1
Pelecus sp.	2	–	–	–
Barbus sp.	42	1	–	1
Carassius carassius (Linnaeus, 1758)	–	2	–	2
Carassius sp.	19	–	2	–
Palaeocarassius sp.	25	–	–	–
Tinca tinca (Linnaeus, 1758)	–	4	3	–
Tinca sp.	121	–	2	1
Cobitis sp.	–	–	2	–
Silurus sp.	757	19	8	–
? *Salmo* sp.	–	–	1	–
Esox lucius Linnaeus, 1758	–	–	4	1
Esox sp.	33	19	–	1
Sander cf. *zaissanicus* (Lebedev, 1959)	42	–	–	–
Perca sp.	5	–	–	–
Total	1625	53	29	11

Table 2. Taxonomic richness of the Popovo locality

Таблица 2. Таксономическое богатство местонахождения Попово

Locality	Richness				Amount of taxa
	spe	gen	fam	ord	
Popovo 3	20	18	4	4	46
Popovo 2	8	7	3	3	21
Popovo 1	12	11	5	4	32
Popovo 0	9	7	2	2	20

Species diversity and taxonomic structure of cenoses are closely related to the structure of ecological communities (Topachevsky et al., 2000). It may be concluded from table 2 that taxonomic richness of ichthyofauna significantly changes in chronologic order. The maximum richness is marked for the Late Miocene Popovo 3 community (46 taxa), minimum — for the most geologically younger (Late Pliocene) strata Popovo 0. Bony fish faunas from the Popovo 2 and Popovo 0 are comparable in taxonomic richness (21 and 20 taxa, respectively). It may be explained by taphonomical features, and also palaeogeographic changes during sedimentation. Fluctuations of the bony fish diversity at the species, genus and family levels are shown in the fig. 2.

Freshwater ecosystems are experiencing declines in biodiversity far greater than those in terrestrial systems because of multiple and interacting factors (Davis et al., 2013). These include flow modification, destruction and degradation of habitats and invasion by exotic species (Dudgeon et al., 2006). Flow is a major determinant of physical habitat in streams, which in turn is a major determinant of biotic composition (Bunn, Arthington, 2002). The movement of water across the landscape influences the ecology of rivers across a broad range of spatial and temporal scales (Sparks, 1995; Poff et al., 1997). Many fish species display a preference for particular types of habitat such as pools, riffles, or backwater areas (Angermeier, 1987; Pusey et al., 1993). The richness of the fauna often increases as habitat complexity increases, with depth, velocity, and cover being the most important variables governing this relationship (Schlosser, 1982; Pusey et al., 1995). Fish assemblage structure (i. e., taxonomic composition and relative abundance pattern) is also strongly related to habitat structure (Meffe, Sheldon, 1988).

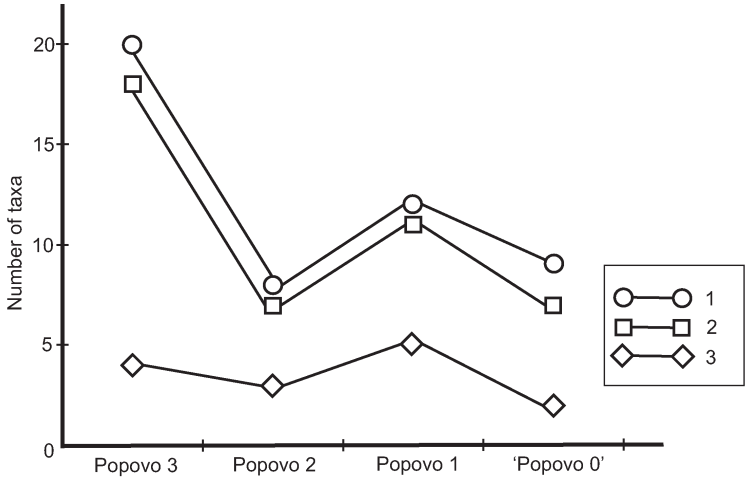

Fig. 2. Dynamics of taxonomic changes in bony fish communities from Popovo during the Late Miocene and Pliocene: 1 — species level; 2 — genus level; 3 — family level

Рис. 2. Динамика таксономических изменений в сообществах костистых рыб из местонахождения Попово на протяжении позднего миоцена и плиоцена: 1 — уровень вида; 2 — уровень рода; 3 — уровень семейства.

Table 3. Taxonomic diversity of the bony fish communities from the Popovo locality

Таблица 3. Таксономическое разнообразие сообществ костистых рыб из местонахождения Попово

Locality	Diversity (H)				H_{tax}
	spe	gen	fam	ord	
Popovo 3	2.5830*	2.4148	1.2818	1.2818	1.6649
	4.3219**	4.1219	1.0219	1.0219	
Popovo 2	2.2671	2.1632	1.5765	1.5765	1.8608
	3.0000	2.7500	1.0613	1.0613	
Popovo 1	3.2457	3.0783	1.8475	1.5476	1.8537
	3.5850	3.4183	1.5850	1.2075	
Popovo 0	3.0958	2.7322	0.6840	0.6840	1.7129
	3.1699	2.7255	0.7642	0.7642	

* Amount of remnants is taken into account in calculations.
** Amount of remnants is not taken into account in calculations.

Analysis of ichthyocomplexes diversity was made taking into account the number of remnants, as well as at the qualitative level, without regard to indices of abundance of individual taxa. In the first case poor results were gave for the Popovo 3 and partly — for Popovo 2 and Popovo 1. This is due to the fact that they are composed of species represented by numerous remains and are dominant forms: Popovo 3 — *Silurus* sp. (757 bones, 46.6 %), *Scardinius erythrophthalmus* (350 bones, 21.5 %); Popovo 2 — *Silurus* sp. (19 bones, 35.8 %), *Esox* sp. (19 bones, 35.8 %); Popovo 1 — *Silurus* sp. (8 bones, 27.6 %). The quantitative composition of the Popovo 1 fauna is aligned and allows emphasizing the dominant species. It is safe to say, that the data in the qualitative composition of Popovo reflects the real situation in detail (table 3). In particular, the maximum values of H_{spe} and H_{gen} were given for the Popovo 3 fauna (4.3219 and 4.1219, respectively), minimum — for the Popovo 2 (3.000; 2.7500) and Popovo 0 (3.1699 and 2.7255). Maximum values of H_{fam} and H_{ord} were marked for the Popovo 1 community (1.5850; 1.2075), minimum — for the Popovo 0 (0.7642; 0.7642). It can be explained by local variations in the palaeogeographic situation (maybe, considerable change of the hydrological regime).

Analysis of the degree of similarity (S) of studied communities shows that Popovo 2 / Popovo 0 (0.5882) are taxonomically the most similar, less than similar — Popovo 1 / Popovo 0 (0.3810), and Popovo 3 / Popovo 1 (0.3750). The minimum Sorensen index value is for Popovo 2 / Popovo 1 (0.3000). Jakkar coefficient value (Kj) is correlated with mentioned data (table 4). It demonstrates the reliability of the calculated similarity index values.

Table 4. Degree of similarity of the bony fish communities from the Popovo locality

Таблица 4. Степень сходства сообществ костистых рыб из местонахождения Попово

Locality		Index of similarity (S)			
		Popovo 3	Popovo 2	Popovo 1	Popovo 0
Jakkar coefficient (K_j)	Popovo 3	×	0.3571	0.3750	0.3448
	Popovo 2	0.2174	×	0.3000	0.5882
	Popovo 1	0.2308	0.1765	×	0.3810
	Popovo 0	0.2083	0.4167	0.2353	×

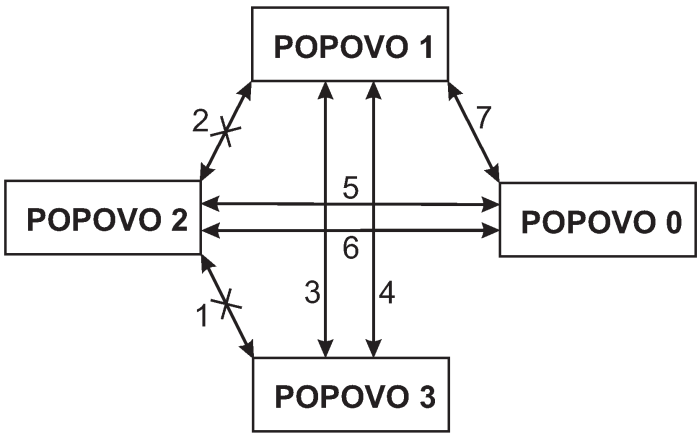

Fig. 3. Connection between heterochronous bony fish communities from the Popovo locality: 1, 2 — minimal connection; 3, 5 — similar level of the taxonomic richness; 4, 6, 7 — substantial similarity of faunistic lists.

Рис. 3. Связь между разновозрастными сообществами костистых рыб из местонахождения Попово: 1, 2 — минимальная связь; 3, 5 — сходный уровень таксономического богатства; 4, 6, 7 — значительное сходство фаунистических списков.

Conclusions

According to the above-mentioned data, it can try to restore the palaeogeographic situation on the Popovo locality, as well as to identify factors that have the greatest influence on the structure and functioning of freshwater bony fish communities from the Late Miocene to the Late Pliocene.

A quite large river with moderate stream and well-warmed water flowed in this area in the Late Sarmatian, 9–10.5 Mya. Favourable environment, abundant resources and a considerable ecotopic variety helped to increase the qualitative and quantitative composition of the various groups of aquatic organisms, including bony fishes (Popovo 3). The latter were represented by various environmental groups and trophic forms (table 1).

Later, at the end of the Sarmatian — Early Maeotian (8–9 Mya), the river probably changed its course. It has led to the isolation of the former river bed area, which has become an oxbow lake. This hypothesis suggests a significant break in sedimentation, as well as a significant difference in species composition of the fish community Popovo 2 from an older Popovo 3 (fig. 3). Marked limitation of biotic resources due to local changes in the hydrological regime has led to the impoverishment of the ichthyocomplex taxonomic diversity (disappearance of typical reophiles, reduction the number of trophic specialized forms — malacophagous, piscivorous, etc.).

A communication gap with nearby flowed river was partially restored in the Late Pliocene. These changes were accompanied by an increase in the species abundance and the approach of qualitative composition of the bony fish Popovo 1 community to the typical river ones (e. g., Popovo 3). Taking into account that Popovo 1 and Popovo 0 complexes have a slight difference in the time being, and substantial similarity of their faunal lists, it can be assumed that they represent successive stages in the development of one cenosis. The gradual extinction of ichthyocomplex, followed by a decline in species diversity, could be a response to climate change, and the effect of scarce resources for the existence of a developed community of aquatic organisms.

We extend our gratitude to Prof. Dr. L. I. Rekovets for his constant support in our research. We also thank Prof. Dr. I. G. Emelyanov (NMNH NAS of Ukraine) and Dr. I. I. Dzeverin (Schmalhausen Institute of Zoology, NAS of Ukraine) for their valuable comments and advices.

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Received 16 October 2013
Accepted 4 February 2014