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**FOSSIL VERTEBRATES OF SKELIA PODIL'SKA 2
(DNISTER AREA, UKRAINE): A DISTINCTIVE
INTERGLACIAL FAUNA OF THE EARLY CHIBANIAN**

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Fossil vertebrates of Skelia Podil'ska 2 (Dniester area, Ukraine): a distinctive interglacial fauna of the Early Chibanian. Popova, L., Veklych, Yu., Yanenko V., Rekovets, L., Mironchuk, T., Stepanchuk, V. — A new microvertebrate assemblage from Skelia Podil'ska 2 (Ternopil Oblast, the Dniester area, Ukraine) sheds light on faunal evolution during the Martonosha interglacial (Early Chibanian, Pleistocene). The fauna was discovered beneath a small rock shelter developed in the Shyrokyne alluvial sandstones. The section comprises alluvial and subaerial deposits of the Zbruch valley, and records several palaeoincisions of different ages. The oldest, Martonosha palaeoincision, formed a cliff face hosting a small rock shelter in which the fossils were recovered. Taphonomic analysis of the findings and their palaeogeomorphological context indicates that the bones accumulated due to owl activity. The fossil assemblage includes amphibians and rodents and is taxonomically and ecologically attributable to the Kolkotovian association of the Tiraspol fauna (MIS 17). The fauna is characterised by the absence of steppe and semi-desert species, and by a pronounced dominance of the subgenus *Terricola* voles, particularly *Microtus (Terricola) arvalidens*. Amphibian remains constitute an unusually high proportion of the assemblage. Ecologically, the assemblage reflects warm and highly humid climatic conditions typical of the Martonosha interglacial. At the same time, the scarcity of strictly forest-associated vertebrates suggests that closed forests were locally poorly developed. This discrepancy is attributed to shallow limestone and sandstone bedrock, which limited forest development despite favourable climatic conditions.

Key words: Dniester area, amphibians, small mammals, *Terricola*, Early Chibanian.

Introduction

The study of Pleistocene microvertebrates provides important insights into how various environmental factors contribute to shaping faunal communities. The Kolkotovian association of the Tiraspol faunal complex is of a special interest in this respect. The Kolkotovian fauna (Rekovets, 1994; Rekovets & Nadachowski, 1995; Krokmal' et al., 2021) existed in the interglacial Martonosha environment, characterised by the expansion of forests, the richness of arboreal vegetation, and peak humidity (Gerasimenko, 2010). The Kolkotovian stage of the Ukrainian Pleistocene corresponds to the Cromer II interglacial of Western Europe, MIS 17, i. e., 0.78–0.65 MY (Gerasimenko, 2010; Krokmal' et al., 2021). The correlation between the international scale and Ukrainian regional stratigraphic units is described in Gradstein et al. (2020).

A characteristic trait of the Kolkotovian fauna is dominance of rodents preferring meadow and shrub habitats. Taxonomically, the dominant group consisted of voles of subgenera *Terricola* Fatio 1876 and *Microtus* Shrank 1798 (Rekovets, 1994; Rekovets & Nadachowski, 1995). Although such faunal composition is believed to have been most characteristic of the late Martonosha time, similar assemblages might have occurred among the Tiraspolian faunas until 0.45 MY (Rekovets & Nadachowski, 1995; Krokmal' et al., 2021; Krokmal' et al., 2023). Some Tiraspolian small mammal associations included two species of *Terricola*: *Microtus (T.) arvalidens* (Kretzoi, 1958) and *Microtus (T.) majori* Thomas, 1906, a unique situation that has never been repeated within the area of Ukraine since then (Rekovets & Nadachowski, 1995). Later, cooling and aridification led to a decrease in the occurrence and diversity of *Terricola*. In the Late Pleistocene, *Terricola* vanished from the Ukrainian area and had not reappeared until the Holocene (Popova, 2015).

The Kolkotovian fauna (the type locality is Kolkotova Balka III) was correlated by Rekovets (1994) with a time interval of West Runton and Voigtstedt in the Wes-

tern European faunas, and on this basis, with MIS 17 (Krokhmal' et al., 2021). Both West- and East-European faunas of this time are characterised by their rich and diverse composition indicating interglacial forest conditions; however, in contrast to the Ukrainian Kolkotovian, there was no such marked increase in the share of *Terricola* remains (Rekovets, 1994; Maul & Parfitt, 2010). Importantly, all currently known Ukrainian Martonosha vertebrate taphocoenoses (Krokhmal' et al., 2021) were restricted to the Black Sea area, south of the reconstructed forest zone, and largely retained steppe features. The discovery of a new taphocoenosis, Skelia Podil'ska 2 (Early Chibanian, the Dnister area, Ternopil' Oblast, Ukraine), for the first time allows shedding light on the palaeoecological features of typical Martonosha communities.

Geological and geomorphological settings

The Quaternary and Pre-Quaternary deposits in the vicinity of Skelia Podil'ska have been repeatedly studied, as they provide a remarkably complete record of Neogene-Quaternary sedimentation.

This area lies to the south of the most ancient terraces of the Dnister River and belongs to the valley of its left tributary, the Zbruch River. Palaeosols and loesses of the Shyrokyne-Martonosha-Sula stages (Late Calabrian-Early Chibanian) are widely distributed in the adjacent area, while younger loess and soil deposits, starting with the Lubny soil, may be exclusively seen in the palaeoincisions. The exception is the Zavadvivka soil, which is widely distributed there (Fig. 1). This indicates a post-Sulian regional decrease in loess accumulation rates, which, in turn, reflects large-scale lateral changes of the Quaternary sub-aerial sedimentation (Veklych, 2018).

Krokhmal' et al. (2009) revealed small mammal fauna in the alluvial deposits of the Zbruch River. Later, this fauna (**Skelia Podil'ska 1**) was attributed to the earliest (Luzanivkian; Shyrokyne-Pryazovsk) phase of the Tiraspol complex and MIS 20-21 (Krokhmal' et al., 2021). Respectively, our section should be designated as **Skelia Podil'ska 2**.

The new locality, Skelia-Podil'ska 2, was revealed in 2017, in the course of archaeological prospecting conducted by the Lower Palaeolithic expedition of the Institute of Archaeology of NASU, in the frame of "The earliest Palaeolithic sites of Ukraine in the context of the initial peopling of Europe", the project of the National Research Fund of Ukraine (Stepanchuk et al., 2017; Popova et al., 2024; Stepanchuk & Veklych, 2025).

The section of Skelia Podil'ska 2 is a wall of the quarry developed on the right slope of the Zbruch valley. Pleistocene loams (15 m) ranging in age from the Holocene to the Late Chibanian, overlie the Upper Calabrian gravel and medium-to-coarse-grained sand and loose sandstone. The latter correspond to the sandstones containing the small mammal fauna of Skelia Podil'ska 1 (Krokhmal' et al., 2009). These deposits are underlain by Badenian lithothamnion sandstones, clays, and sands (Fig. 1).

A series of palaeoincisions is observed in the Pleistocene loam sequence (Fig. 1). The most ancient Martonosha palaeoincision cuts the Shyrokyne hydromorphic soil and alluvial sands and sandstones of the same age. The Martonosha slope soil (red-

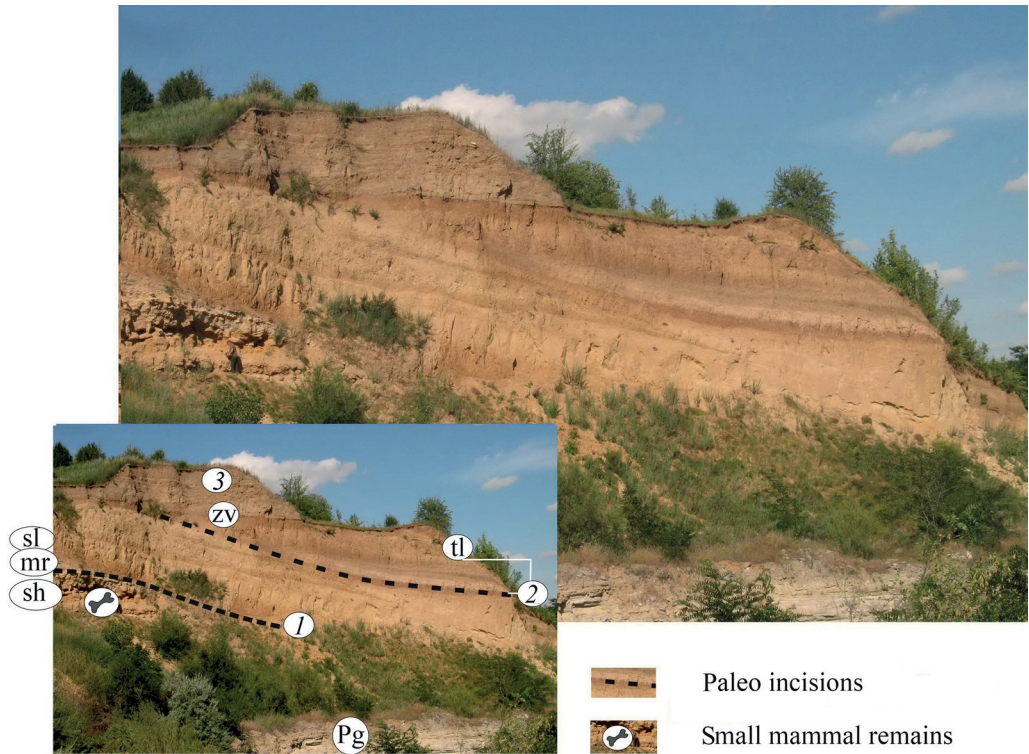


Fig. 1. The outcrop of Skelia Podil'ska 2: 1 — Martonosha palaeoincision; 2 — Lubny palaeoincision and several Lubny palaeosols with loess interlayers; 3 — technogenic deposits of the quarry; sh — sandstones and sands of the Shyrokyne alluvium; mr — reddish-brown loams of Martonosha soil; sl — the Sula loess; tl — Tyligul loess; zv — Zavadiivka soil; Pg — Paleogene

dish-brown loams and brown dense loams up to 1.4 m in thickness) forms the lower layer of the filling of this palaeoincision and dips steeply to the thalweg.

The age of the Skelia Podil'ska 2 microvertebrate fauna corresponds to the time of this Martonosha incision. Fossil microvertebrates were found in the filling of a minute rock shelter (with the maximal length of the cavity c. 0.3 m) in the loose Shyrokyne alluvial sandstone beneath a denser sandstone layer of the same age. Similar niches are frequently used by owls for nesting.

The rich-in-fossils filling of the niche (c. 2 kg) was collected into a plastic container and screen-washed with a 1 mm mesh metal sieve.

Results and Discussion

The Skelia Podil'ska 2 microvertebrate fauna displays the characteristic features of the Kolkotovian faunas: ecologically, by the absence of steppe species and dominance of wetland forms, taxonomically, by dominance of *Terricola*, and biostratigraphically, by the evolutionary level of voles (Table 1).

Signs of digestion on vertebrate remains (Fig. 2, 6) indicate their accumulation by avian or mammalian predators; while the size of the cavity with bones and its

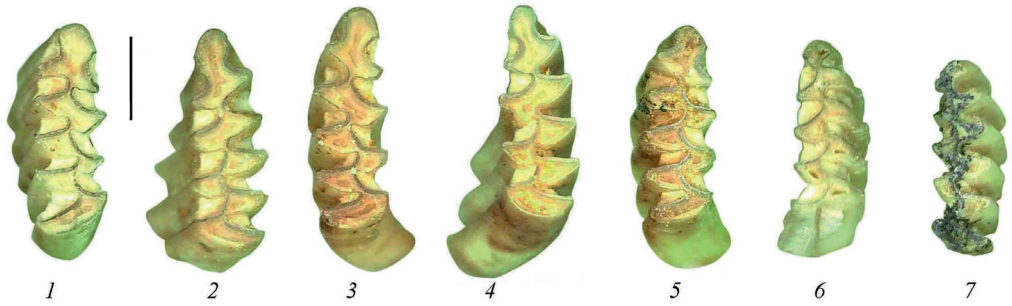


Fig. 2. Vole molars (m1) from Skelia Podil'ska 2: 1–4 — *M. (Terricola) arvalidens*; 5–7 — *M. (Microtus) nivaloides*; 6 — moderately digested m1; 7 — juvenile m1. Scale bar 1 mm

Table 1. Vertebrate remains from the Skelia Podil'ska 2 locality

Taxon	Number of identified remains			Minimum number of individuals
	total	digestion remains graded from moderate to strong	juveniles	
<i>Anura indet</i>	45	44		8
<i>Bombina</i> sp.	1	1		1
<i>Hyla</i> sp.	2	1		2
<i>Rana</i> cf. <i>temporaria</i>	4	4		3
<i>Rana</i> sp.	19	19		9
<i>Pelobates</i> cf. <i>fuscus</i>	5	5		2
<i>Bufo</i> sp.	16	12		4
<i>Rana</i> cf. <i>arvalis</i>	10	8		4
<i>Pelophylax</i> cf. <i>ridibundus</i>	9	8		5
<i>Clethrionomys</i> sp.	2	0	2	2
<i>Microtus (Terricola) arvalidens</i>	12	1	0	7
<i>Microtus (Microtus) nivaloides</i> Major, 1902	4	2	1	3
<i>Microtus</i> s. l. sp.	29	5	4	4

position in the Martonosha relief (in the cliff, at least 4 m above the thalweg of the valley) suggest owls as the most likely taphonomical agent. A complete absence of in situ molars and virtually 100% of broken postcrania — unusual for bone accumulation produced by predators — may be attributed to the increasing trampling effect due to the heterogenous texture and granulometric composition of the floor of the niche (loose sands with protruding denser sandstone, and more compact sandstone ceiling debris — Fig. 1). Such composition should have increased mechanic grinding of remains by trampling (Andrews, 1990). Relatively low total share of significantly digested molars in the taphocoenoses may be due to the dominance of *Terricola*, with its thick enamel on trailing ages of molar prisms. In contrast, the small sample of Skelia Podil'ska 2 *M. (M.) nivaloides* consists of 50% moderate to heavily digested molars (Table 1). Predatory digestion is known to affect prey molars differentially, with voles showing higher degrees of digestion than murids (Demirel et al., 2011). Here we observe a similar disparity for *Microtus* and *Terricola*.

The total absence of open-habitat species in the Skelia Podil'ska 2 is unique among Pleistocene vertebrate faunas in Ukraine. Steppe, tundra or semi-desert species are present in varying numbers in all other known localities; in most cases, they are dominant (Rekovets, 1994).

On the other hand, Skelia Podil'ska 2 cannot be regarded as a typical forest assemblage. A decisive argument for the zonal tree vegetation would be the presence of climbing tree-dwellers such as tree squirrels or glirids, which are absent in Skelia Podil'ska 2. The bank vole *Clethrionomys Tilesius*, 1850, another rodent indicator of the forest vegetation, is encountered in the fauna. The linkage of *Clethrionomys* with the forest environment is not as definite as in the case of tree-dwelling rodents since the bank vole may occur in pellet assemblages from the steppe zone (Kondratenko et al., 2006). However, paleoecological studies demonstrate that its occurrence has increased with climate warming and forest expansion (Rekovets, 1994). Still, the minor presence of *Clethrionomys* is a mere presence rather than the dominance, which should be expected based on the other palaeoenvironmental proxies (Gerasimenko, 2010). Amphibians of Skelia Podil'ska 2 do not belong to strictly forest-associated species either; they are species of near-water habitats of the forest-steppe or forest zone.

The absence or scarcity of forest species might have been partly explained by predator selectivity; however, in the case of Skelia Podil'ska 2, such an explanation is unlikely. In particular, significant selectivity biases may be introduced by such predators as the fox and the buzzard. The former is incapable of capturing tree-dwelling rodents. The latter specialises in the prey from open habitats. Consequently, arboreal species and *Clethrionomys*, a species that prefers dense vegetation, are typically underrepresented in buzzard pellet assemblages (Andrews, 1990). Given the palaeogeomorphological settings at Skelia Podil'ska 2 point toward an owl as the primary taphonomic agent, with owls being capable of capturing tree-dwelling species and the bank vole (Andrews, 1990, Append. Fig. 3; comparison of owl pellets and data of trapping; and, for the Ukrainian area, Kondratenko et al., 2006), the scarcity of forest fauna in Skelia Podil'ska 2 requires another, palaeoecological explanation.

Ecological preferences of dominant small mammals of Skelia Podil'ska 2, *M. (M.) nivaloides* and *M. (Terricola) arvalidens* are rather vague, which is quite common for extinct species. Maul & Parfitt (2010) consider *M. nivaloides* to be associated with open grasslands, while according to Pazonyi et al. (2018), this species was confined to forested areas. Possibly, *M. nivaloides* was merely less environmentally specialised compared to its likely descendants, such as *M. arvalis* and *M. agrestis*. In any case, *M. nivaloides* belongs to relatively mesophilic rodents rather than to a cold-tolerant or xerophilous ones.

Recent *Terricola* prefer meadow, shrub and forest habitats. Yet they rarely occur in closed forest stands as wetlands are more preferable for them (Shenbrot & Abramov, 1995). Ecological preferences of the extinct *M. arvalidens* are more diffuse. Although an increased proportion of *Terricola* usually corresponds to warm and wet stages of the Ukrainian Pleistocene, the species might have occurred in the steppe faunas (Semybalka 2, the second Protopotopovian association of the Tiraspolian complex, MIS 19) and sometimes, even dominated in them (Tykhonivka 1 and Lysa Gora, Tykhonovian and Nagirnian association of the Tiraspolian complex, MIS 16

and 12) (Rekovets & Nadachowski, 1995, Rekovets et al., 2014; Krokmal' et al., 2021). Moreover, the mentioned localities belong to the dry Azov steppe, with two of them, Tykhonivka 1 and Lysa Gora, assigned to the cold and dry stages of the Pleistocene. Probably, *M. arvalidens* occupied intrazonal wet-valley habitats within those zonal dry-steppe assemblages. Since all mentioned taphocoenoses of the Azov area are alluvial, the high proportion of near-water and wetland species (including *M. arvalidens*) among them is due to the local topography. In contrast, in the case of the owl pellet assemblage of Skelia Podil'ska 2, the dominance of *M. arvalidens* is a signal of climate humidification rather than a local phenomenon. Most Pleistocene European owl pellet assemblages are vole-dominated, but which species prevails is largely determined by climate (Andrews, 1990). The increased total proportion of amphibians in Skelia Podil'ska 2, which significantly exceeds the levels typically observed in different owl pellet assemblages (Andrews, 1990; Roulin & Dubey, 2013), shares the same climatic explanation.

Therefore, the microvertebrate fauna from Skelia Podil'ska 2 reflects a warm, and above all, highly humid climate. At the same time, this fauna does not provide a basis for reconstructing a zonal forest landscape, which should necessarily be expected under such conditions and is reconstructed on the basis of other palaeogeographical proxies (Matviishyna et al., 2010). The absence or scarcity of typical forest-associated vertebrates in the taphocoenosis may account for the local vegetation state. The near-surface position of limestone and sandstone deposits in the Zbruch valley during the Martonosha time (Fig. 1) is likely to have hindered the development of the forest cover even under favourable climatic conditions.

The increase in *M. (Terricola) arvalidens* seems to be a regional peculiarity of the Ukrainian Early Chibanian interglacials, particularly the Martonosha. This increase is in line with some other features of these faunas, which are still not fully understood. Thus, tree-dwelling rodents, which were common in the Pleistocene of Moldova and Poland, are extremely scarce in the Pleistocene fossil record of Ukraine (Rekovets, 1994) until the Holocene (Popova, 2015). Instead, *Miomymus* remains were recorded (Rekovets, 1994). Among European dormice, this is the only genus that avoids arboreal habitats. The structure of the Kolkotovian microvertebrate association definitely needs further study.

Conclusions

The newly discovered microvertebrate fauna from Skelia Podil'ska 2 (the Dnister area, Ternopil' Oblast) corresponds to the Martonosha interglacial of the Early Chibanian and is attributed to the Kolkotovian association of the Tiraspol faunal complex (MIS 17).

Typical characters of the Kolkotovian (the decline of steppe species, dominance of *Terricola*) are prominently manifested in Skelia Podil'ska 2.

Taphonomically, Skelia Podil'ska 2 is an owl pellet assemblage. The disparity in the share of moderate to heavily digested molars has been registered between *Microtus* and *Terricola*. This may be the consequence of differences in the enamel microstructure in voles of these subgenera.

The dominance of *M. (Terricola) arvalidens* and a high total proportion of amphibian remains in Skelia Podil'ska 2 indicate a significant humidification of the climate; in contrast, the absence or scarcity of strictly forest-associated vertebrates may be attributed to specific geological settings of the area (a near-surface position of limestone and sandstone deposits, which prevented a complete forestation despite the climatic conditions of the Martonosha time).

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