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Southeastern Europe as the Arena of Vertebrate Evolution in the Late Miocene

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Abstract—The paper considers the main features of the late Miocene faunas of terrestrial vertebrates and marine mammals of Southeastern Europe and their general dynamics in connection with landscape and climatic changes. We note that the geographical area corresponding to the modern northwestern and northern Black Sea region with adjacent territories was a territory of intense diversification during the late Miocene. The revealed biogeographic significance of the region is associated with the fact that a border between the forest biome and open and/or semi-open landscapes occurred on this territory in the late Miocene. Accelerated diversification in this transitional (ecotone) zone is supposed to be associated with the fragmentation of species' geographical ranges under pronounced spatial differentiation of plant associations and a wide representation of mosaic habitats caused by significant climatic fluctuations. We further discuss the general evolutionary potential of peripheral communities, as exemplified by the *Hipparion* vertebrate faunas of southeastern Europe.

Keywords: vertebrates, late Miocene, diversification, endemics, Eastern Europe

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INTRODUCTION

The late Miocene stage of biotic evolution is one of the most important ones in the Cenozoic history of the organic world. This was an age characterized by global ecosystem change in the low and temperate latitudes of Eurasia where the global trend towards cooler and more arid climate (Zachos et al., 2001) led to the widespread expansion of open and semi-open savanna-like landscapes that in certain time periods covered an area from the Iberian Peninsula in the west to Eastern China in the east. The vertebrate associations that inhabited these landscapes, with members of the so called *Hipparion* terrestrial mammal faunas as their core, also enjoyed a wide distribution in the late Miocene; it was from these associations that the younger Pliocene communities developed, which, in turn, were the predecessors of both the Pleistocene and some of the modern faunal associations of Africa and, in part, of the inner parts of Asia (Kaya et al., 2018).

The general course of the formation of the late Miocene savanna faunal associations of mammals has been well documented; its source regions were, on one hand, the Eastern Mediterranean (Greco-Iranian), and on the other, the Central Asian (Tungur) faunal assemblages (Mirzaie Ataabadi et al., 2013). The combination of lineages that for a long time evolved separately in these two hotspots of aridity led to the formation of the relatively integrated Eurasian savanna-like faunas which in modified form persisted in Eurasia up to the end of the early Pleistocene. However, the taxonomic composition of the *Hipparion* faunas was neither homogeneous in space nor constant in time, but rather reflected the variability of local landscapes and climatic environments.

The Eastern Paratethys rim is one of the classical regions of the distribution of the *Hipparion* fauna of the late Miocene. At least four stages in the transformation of faunal communities have been recognized here (Korotkevich, 1988; Lungu, 1990). In this context, the transformation of the biota in the peripheral regions of the savanna biome (such as the Northern Black Sea Coastland) has been treated exclusively in terms of the change in the ratio between the autochthonous taxa associated with the more closed forest habitats and the migrant taxa from the Afro-Asiatic savanna hotspots, which inhabited open xerophytic landscapes (Korotkevich, 1988; Lungu, 1990). At the end of the Miocene (latest Turolian, Pontian/Messinian) the *Hipparion* communities of Europe were impacted by the dispersal of North American migrants, associated with a cooling episode and yet

Fig. 1. The geographical position of the main localities of Late Miocene terrestrial vertebrates discussed in this article. (1) Bujor, Kalfa; (2) Gritsev; (3) Mikhaylovka-1; (4) Shkodova Gora; (5) Morskaya 2; (6) Gaverdovsky, Fortepyanka 2; (7) Solnechnodolsk; (8) Beshpagir.

greater expansion of open landscapes (Korotkevich, 1988). The increase in the number of immigrant taxa marks the periods of greater aridity, but the question of their local evolution is rarely raised.

The recent study of ostrich (Aves: Struthionidae) paleobiodiversity unexpectedly showed the unique role of the Northwestern Black Sea Coastland in the evolutionary history of this group, a characteristic member of the *Hipparion* faunas and further belonging to the core of the savanna associations (Mikhailov and Zelenkov, 2020). In the Northern Black Sea Coastland and Eastern Europe in general, ostriches are typical allochthonous immigrants which first dispersed here at the same time as the hipparions at the beginning of the late Miocene (Vallesian) and persisted at least until the early Pleistocene. The existence of several ostrich taxa in this region throughout the Miocene–Pleistocene was usually treated as the result of waves of dispersal from Anatolian and Central-Asian faunas (Kurochkin and Lungu, 1970; Mikhailov and Kurochkin, 1988; but see Burchak-Abramovich, 1953). However, it has been shown that during one of these events (in the Maeotian), ostrich dispersal was associated with autochthonous evolution which resulted in the formation of the phylogenetic lineage that has persisted in the savanna faunas to the present (Mikhailov and Zelenkov, 2020). First appearing in the fossil record in the Maeotian of the Northwestern Black Sea Coastland, ostriches of the modern type then dispersed throughout the vast spaces of Asia and Africa, gradually displacing or replacing the older lineages of the genus *Struthio* (Mikhailov and Zelenkov, 2020).

To what extent the pattern of ostrich evolution reflects the biogeographic significance of Northern and Western Black Sea Coastlands is a question that has not previously been addressed. However, this biogeographical pattern may well be more general in character: for instance, it has been shown that the formation of the common Eastern European Pikermian fauna of large mammals (Maeotian) was to a large extent due to the expansion of the autochthonous Balkanic taxa (Kostopoulos, 2009). In this article we attempt to analyze original and published data on vertebrates in order to show that the modern-day Western and Northern Black Sea Coastland, as well as Southwestern Europe in general, may have been an evolutionary hotspot in the late Miocene. The biogeographic significance of this region may be associated with the instability of landscape, climatic, and paleogeographic environments of the ecotone area.

In this article we discuss the region of the northern and northwestern rim of the Eastern Paratethys, which in general terms corresponds to the modern Northern Balkans, as well as the modern region of the Northern and Western Black Sea Coastland (Fig. 1). As the Eastern Paratethys regressed, this region also came to include the Northern Caucasus. The region as a whole corresponds to the northern part of the Eastern European paleoprovince (Lungu, 1990; Tobien, 1967), or the northern part of the Greco-Iranian paleoprovince (Fortelius et al., 1996) previously recognized from mammal faunas. Chronologically, the faunal sequences of the region are closely related to the stages in the development of the brackish basins of the Eastern Paratethys: Sarmatian (Khersonian and Bessarabian), Maeotian and Pontian (Fig. 2). The dates for these marine regional stages, as well as their correlation with Neogene zones and mammal ages which form the European biochronological scale, remain a debated issue. We follow the latest revisions of the MN zone boundaries (Hilgen et al., 2012) and the paleohydrological events of the Eastern Paratethys (Palcu, 2018; Palcu et al., 2019). Mammal assemblages of the Neogene of Eastern Europe and their correlation with the regional stages of the Eastern Paratethys have been

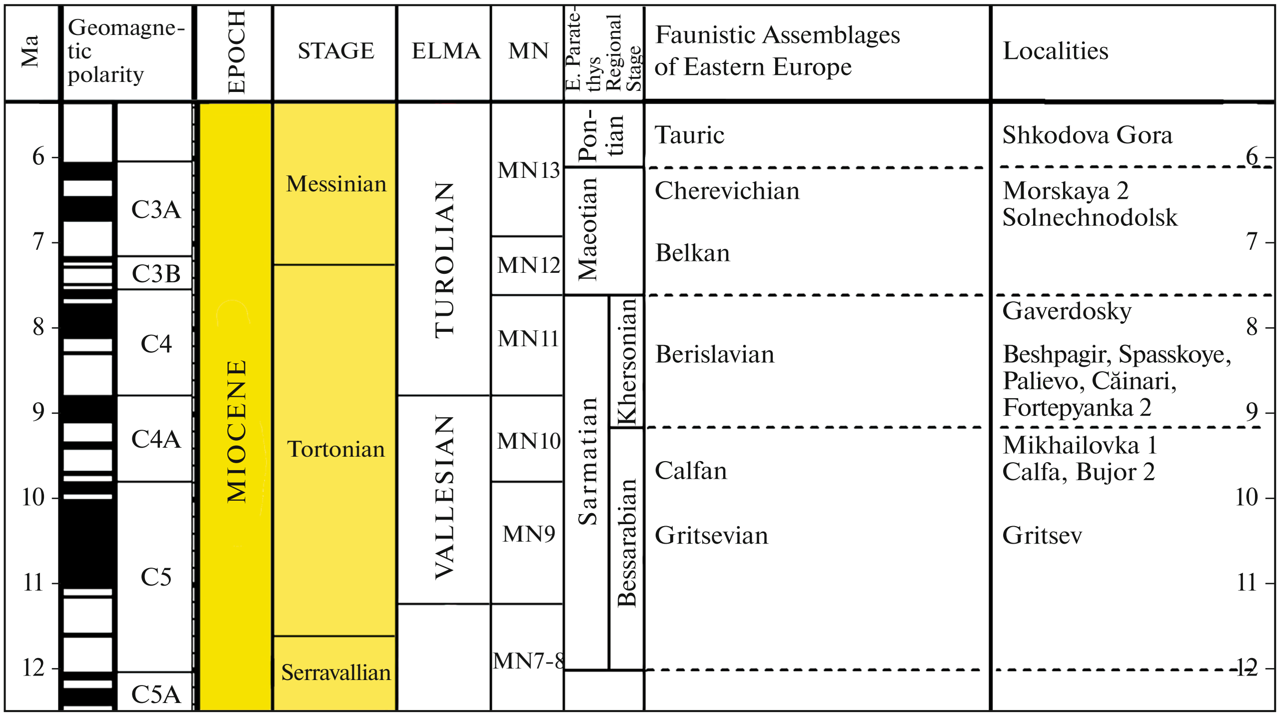

Fig. 2. Stratigraphic position of the main localities of late Miocene vertebrates discussed in this article.

synthesized after E.L. Korotkevich (1988) and V.A. Nesin (2013).

FORMATION OF LATE MIOCENE (*HIPPARION*) FAUNAS OF TERRESTRIAL VERTEBRATES OF EURASIA

The most important biochronological event marking the beginning of the formation of late Miocene communities of Eurasian terrestrial vertebrates is the dispersal of American equines *Hipparion* s.l., with their oldest European representatives often being treated within the genus *Hippotherium* (Woodburne et al., 1996). The appearance of *Hipparion* as part of terrestrial vertebrate assemblages marks the beginning of the Vallesian age of the late Miocene according to the biochronology of terrestrial mammals of Europe or the Bahean age in China (Qui et al., 2013). The exact time of *Hipparion* dispersal to Eurasia has long remained a matter of debate and until recently was conventionally set at 10.8 Ma (Hilgen et al., 2012), which is significantly later than the Serravallian-Tortonian boundary (i.e. above the boundary between the middle and the late Miocene; 11.63 Ma). The oldest European *Hipparion* records recognized were the finds from several localities of Pannonian zone C of the Vienna Basin of Central Europe (Woodburne et al., 1996). However, recent research has convincingly shown that the base of zone C in the Vienna Basin is dated 11.6 Ma, i.e., it obviously coincides chronologically with the boundary between the middle and the late Miocene (e.g., Lirer et al., 2009; Ter Borgh et al., 2013). The oldest localities with *Hipparion* fossils from zone C of the Pannonian Basin (Gaiselberg and Atzelsdorf), however, are dated as 11.4–11.0 Ma, which roughly corresponds to the age of the oldest *Hipparion* in the more western regions in the Iberian Peninsula (Bernor et al., 2017). Therefore the appearance and dispersal of *Hipparion* at the beginning of the late Miocene can be seen as a relatively synchronous event in Central and Western Europe.

Since *Hipparion* is unequivocally recognized as an American migrant (Bernor et al., 2017, 2021), it seems important to trace its possible dispersal throughout Eurasia, but such information is scarce. E.A. Vangengeim et al. (2006) dated the first appearance of *Hipparion* in Eastern Europe (in the middle Sarmatian of the Eastern Paratethys of Moldova) to 11.8 Ma, which formally is equivalent to the upper Serravallian, i.e. the end of the middle Miocene. This would mean an earlier appearance of *Hipparion* in Eastern Europe compared to the Central Paratethys, which would generally be in line with the earlier appearance of semi-open savanna-like habitats in this area (Fortelius et al., 1996). However, the upper age estimate of the Moldovan localities with *Hipparion* fossils (such as Calfa, Bujor 1, etc.) was greatly dependent on the lower boundary of the upper Sarmatian in the Eastern Paratethys, which in the cited paper (Vangengeim et al., 2006) was dated as 9.6 Ma. The lower boundary of the upper Sarmatian was subsequently estimated as 8.6 Ma, and later as 9.1 Ma (Palcu, 2018). Therefore, the age of the Moldovan *Hipparion* from the Bessarabian may correspond to the time interval of the late Bessarabian, for instance, at 10.8 Ma (Vasiliev et al., 2011) or younger (Sinitsa and Delinschi, 2016). In that case, the oldest Asian (and, possibly, Eurasian) *Hipparion* would be the ones from the Dongxiang in the Linxia Basin in China, dated to 11.5 Ma (Fang et al., 2016; Zhang et al., 2019). Commonly, however, the age of appearance of *Hipparion* in China is estimated at 11.1–10.0 Ma (Wang et al., 2013).

Although the appearance of *Hipparion* in terrestrial vertebrate faunas is undoubtedly a marker of important biotic processes that defined the evolution of terrestrial biota throughout the following several million years, the formation of late Miocene faunas was far from simultaneous throughout Eurasia. It has been shown (Fortelius et al., 1996), that forest paleoenvironments persisted in Central Europe for a long time (at least until the end of the Messinian), so that it can be treated as a distinct paleobiogeographic province. At the beginning of the late Miocene, forest environments persisted in other Eurasian regions as well, such as the Iberian Peninsula or the modern-day Northwestern Black Sea Coastland (Moldova). However, although already in the earliest Tortonian *Hipparion* had colonized these forest environments as well, their appearance at first did not cause any significant transformations in community structure. For instance, early Vallesian faunas of the Iberian Peninsula and the oldest middle Sarmatian *Hipparion* faunas of Moldova (the Calfan faunal assemblage) still preserve an entirely middle Miocene appearance (Agustí et al., 2001; Lungu, 1984). The situation may have been different at the southern boundary of the Paleo-Palearctic paleogeographic province in southern China in the context of the actively rising Tibetan Plateau. During the earliest late Miocene, *Hipparion* and *Anchiterium* (middle Miocene) faunas coexisted during the time period of 11.6–11.1 Ma in the Linxia Basin but were compartmentalized into different topographic areas due to complex terrain (Zhang et al., 2019).

The subsynchronous appearance of *Hipparion* in the vast spaces of the temperate and southern latitudes of Eurasia (approximately 11.5–11.1 Ma) is likely associated with paleogeographic change around the middle–late Miocene boundary. The wide dispersal of *Hipparion* as, originally, inhabitants of semi-open forest-steppe habitats in the temperate and partly southern regions of Eurasia (except the Oriental province), as well as Africa, has been possible due to the formation of a vast arid belt in this region already at the end of the middle Miocene (Flower and Kenneth, 1994), which must have promoted the expansion of open or semi-open habitats. The global trend towards aridization in Eurasia has been a characteristic feature of late Miocene paleoenvironments in particular (Fortelius et al., 2006), so that the dispersal of *Hipparion* into Eurasia at the late Miocene boundary and its subsequent late Miocene radiation and the obvious evolutionary success of this group can be considered one of the markers of this particular interval of the Cenozoic.

An important biochronological boundary at the end of the late Miocene that partly completes the formation of the general aspect of *Hipparion* faunas of large mammals is the immigration of the *Paracamelus* camels (Camelidae) and the *Eucyon* canids from North America into Eurasia across the Beringian land bridge. Members of these genera quickly spread throughout Eurasia, occupying savanna-like landscapes: their fossils are known from the Messinian (MN 13) of Spain and Italy (Caballero et al., 2021; Colombero et al., 2017; Sotnikova and Rook, 2010). Independent evolution of Camelidae in Eurasia started by the Messinian, and only in Pliocene did the descendants of the Miocene Eurasian camels, similarly to the ancestors of the modern ostriches (see above), reach Africa (Titov and Logvinenko, 2006). Camel fossils are known in the Northern Black Sea Coastland and in Crimea from several localities of the Tauric faunal assemblage which are associated with lower Pontian deposits: Odessa, Sinyavskaya, Novocherkassk, and the Mamay mines (Mamayskie kamenolomni). The migration routes of these animals from Asia to Southern Europe likely passed along the northern coast of the Pontian Sea (Titov and Logvinenko, 2006). *Eucyon* fossils in the region under consideration are known only from the beginning of the early Pliocene (Sotnikova and Rook, 2010), but it should be noted that late Turolian large mammal faunas from Eastern Europe remain incompletely studied (Korotkevich, 1988; Kovalchuk et al., 2017).

UNIQUENESS AND EVOLUTIONARY POTENTIAL OF TERRESTRIAL FAUNAS OF SOUTHWESTERN EUROPE

Vallesian. A vivid example of evolutionary significance of the discussed region is provided by the hipparions themselves. *Hippotherium*, which in Vallesian inhabited regions of the Eastern and Central Paratethys, is believed to be a descendant of the genus *Cormohipparion*, derived from the middle Miocene of North America and preserved in practically unmodified form in the Vallesian of the arid belt of the southern Palearctic (in particular, in Anatolia and Northern India; Bernor et al., 2021). In the more forested environments of Europe, the autochthonous differentiation of hipparions occurred at the end of the middle Sarmatian of Moldova and southern Ukraine, which is believed to be linked with landscape change and gradual expansion of the more open biotopes in this region (Lungu, 1984). Differentiated hipparions are known already from the middle Sarmatian faunas of Bujor 2, Gritsev and Sebastopol (Vangengeim et al., 2006). In addition to hipparions, autochthonous evolution at the end of the middle, and especially the late Sarmatian in the discussed region was recorded for several other mammal groups (including hornless rhinoceroses

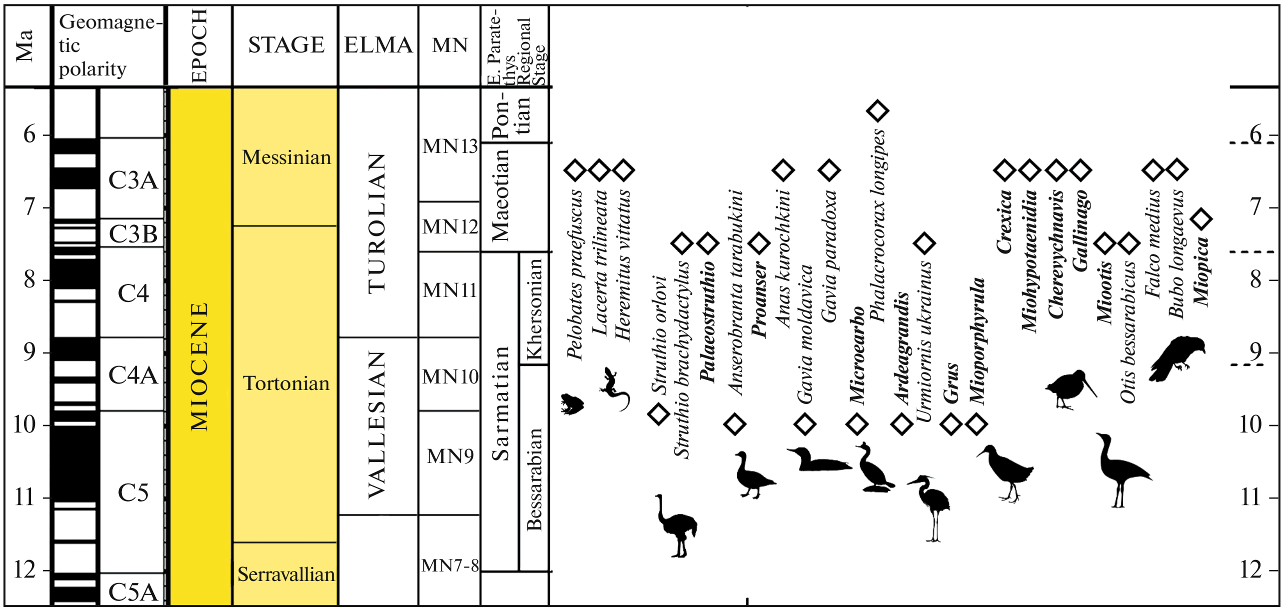

Fig. 3. Taxa of amphibians, reptiles and birds, for which the earliest appearance in the paleontological record is associated with the late Miocene of Eastern Europe (including endemics).

Aceratherium and *Chilotherium*; Korotkevich, 1988; Lungu, 1984, 1990). In the more western parts of Europe, differentiation of hipparions did not occur, since conservative humid forest habitats were preserved there (Lungu, 1984).

Autochthonous evolution in several phylogenetic lineages and the transformation of landscapes and ecological conditions produced faunal assemblages without analogues elsewhere. The Vallesian small mammal assemblage of the Gritsev locality (zone MN 9) in western Ukraine is of special interest. It is characterized by a predominance of archaic middle Miocene taxa, where insectivores dominate but the typical late Miocene rodent taxa appear as well (dormice of the genera *Glis* and *Muscardinus*, the first *Lophocricetus* among the Dipodidae, and *Cricetulodon* among the Cricetodontidae; Nesin, 2013). Notably, the absence of other typical late Miocene taxa, Muridae and Ochotonidae, which potentially indicates the relatively old age of this fauna (sometimes considered to be the oldest in the Vallesian of Europe; Nesin, 2013), stands in stark contrast with the advanced evolutionary stage of the differentiated hipparions of Gritsev (Vangengeim et al., 2006), i.e. the archaic aspect of this fauna may be due to its forested character and the conservative "Vallesian" fauna of forest habitats. Yet another small mammal fauna without analogues in the Vallesian of the Northwestern Black Sea Coastland comes from the early Sarmatian (MN 10) Mikhailovka 1 locality (Nesin, 2013). Cluster analysis of large mammal communities clearly indicates the uniqueness of the biozone MN 10 faunas of Ukraine and Moldova (Casanovas-Vilar et al., 2005). The provincialism of Moldovan Vallesian faunas is manifested in the presence of several endemic taxa (Figs. 3, 4), of which at least some may in fact have their origin in the discussed region.

Vallesian bird communities remain poorly studied both in Eastern Europe and globally, but several genera of water birds (e.g., crane, *Grus*; cormorant, *Microcarbo*) are recorded for the first time in the fossil record in the early Vallesian of Moldova (localities of Chișinău and Golbocica), of which two are extinct regional endemics: the heron *Ardeagrandis* and the rallid *Mioporphyrula* (Zelenkov and Kurochkin, 2015). Also, several bird species are known in the Vallesian of Moldova and Ukraine that have so far not been found outside of this region, including the oldest ostrich in the region, *Struthio orlovi* (Zelenkov and Kurochkin, 2015). On the other hand, anatid assemblages both in Central (Hungary) and Eastern Europe in the Vallesian were composed of middle Miocene taxa that were very widely distributed throughout Eurasia (from France to China; Zelenkov, 2017, 2020; Zelenkov et al., 2018).

Vallesian herpetofaunas of Eastern Europe are very poorly known compared with those of Western and Central Europe. The herpetofaunal assemblage of the early Sarmatian of Moldova already includes open landscape elements, but most of the assemblage is composed of middle Miocene forest biotope relicts (Zerova, 1987). The herpetofauna of Gritsev (Ukraine) has been better studied; along with several archaic elements, such as the urodele *Palaeoproteus* and the boa *Bransateryx*, it includes the anguid lizard *Pseudopus pannonicus* (Roček, 2019), which becomes

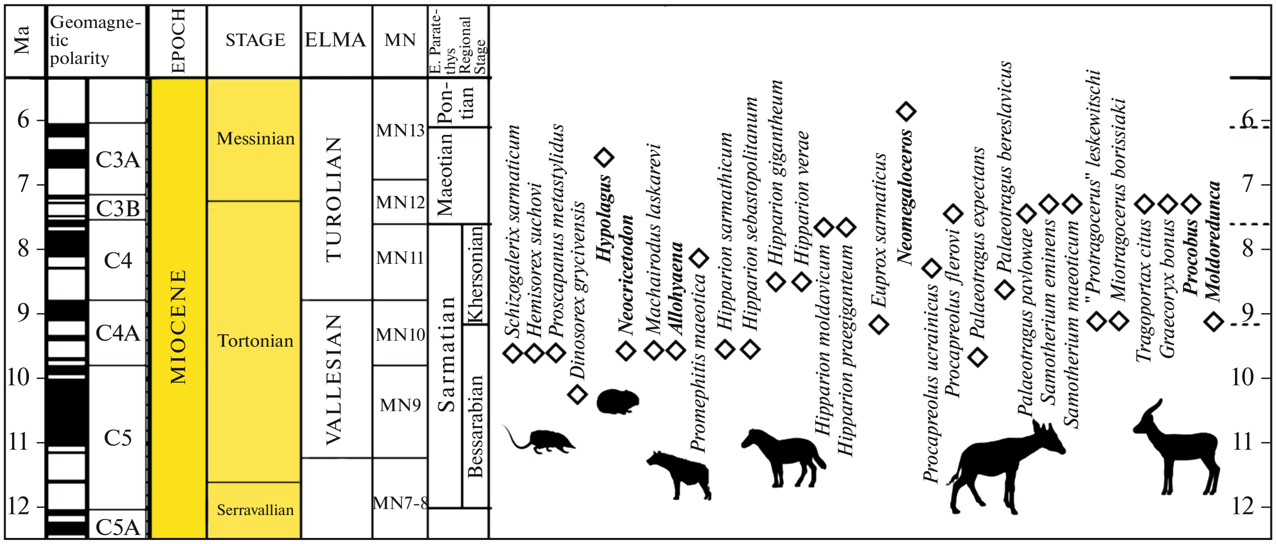

Fig. 4. Selected mammalian taxa for which the earliest appearance in the fossil record is associated with the late Miocene of Eastern Europe (including endemics).

a common species in Europe only at the end of the Miocene.

Late Sarmatian localities of the Berislav mammal assemblage (Beshpagir, Spasskoye) from the Caucasian Foreland (Stavropol territory) have a generally similar aspect. The index species in these communities, along with *Hipparion giganteum* and *H. verae*, were such taxa as *Deinotherium* cf. *giganteum*, *Tetralophodon longirostris*, *Choerolophodon* aff. *pentelici*, *Tragocerus* cf. *frolovi*, *Procapreolus* sp., and *Cervavitus* sp. (Shvyreva and Titov, 2020; Volokitin et al., 2021). The ruminant association of *Euprox* and *Protragocerus* which is typical for Gritsev, was also found in Northern Caucasus, for instance in the late Sarmatian locality of Fortepyanka 2 (Vislobokova and Tarasenko, 2019) which can be assigned to the early Turolian. The composition of early Turolian mammal faunas in the Northern Caucasus is unique. Localities of Gaverdosky and Volchya Balka are correlated with the end of the late Sarmatian. The mammal fauna here is distinctly mesophylic and mostly associated with closed landscape habitats. The unique feature of these faunas is the diversity of semiaquatic urodeles and anurans and the presence of Vallesian elements in the small mammal fauna, for instance, the dormouse *Paraglirulus* (Tesakov et al., 2017).

Turolian. The second half of the late Miocene is characterized by the widest distribution of taxonomically quite similar savanna-like faunas in the temperate and subtropical zones of the Palearctic (e.g., Fortelius et al., 1996; Kaya et al., 2018; Mirzaie Ataabadi et al., 2013). The Turolian (Europe) and the coeval Baodean (China) communities completely lack middle Miocene relicts and hipparions undergo intensive morphological evolution (Bernor et al., 2021). In Eastern Europe, in particular, *Hipparion giganteum* is replaced by *H. moldavicum* (Krakhmalnaya, 1996).

Generally, the Turolian faunas of the south of Eastern Europe show great similarities with the faunas of the Balkans and Turkey, which include, for instance, the abundance of lophodont mastodonts and deinotheres, as well as the presence of the lagomorph *Prolagus*. In addition to species and genera having vast transpalearctic ranges, the presence of lophodont jerboas *Sibirosminthus*, microtoid cricetids and the camels *Paracamelus* indicates increased Asian influence on the communities of the northern coasts of the Maeotian and Pontian basins of the Eastern Paratethys (Titov and Tesakov, 2013; Titov et al., 2017). At the Vallesian-Turolian boundary or in the early Turolian, several typical taxa from the Greco-Iranian paleofaunal province (*Gazella* aff. *pigrimi*, ?*Nisidorcas*, *Tragoportax gaudryi*, *Protoryx*, and *Palaeoryx*) even reach the forested Central Europe (Vislobokova, 2006).

In recent years, fairly representative data have been obtained on the evolution of Turolian terrestrial vertebrate communities (zones MN 11–12) in the Azov Sea Coastland and the Caucasus Foreland (Podvintsev et al., 2016; Tesakov et al., 2017; Titov et al., 2006). These data supplement the known information about the Belkan and Cherevichian faunal assemblages described using material from the Western Black Sea Coastland. However, whereas the similarities between mammal faunas of this age in the vast territory of Eurasia have long been established, the paleobiogeographic patterns for other groups are only beginning to become clear.

For instance, bird fossils clearly show differences between Turolian and Vallesian bird faunas (Zelenkov, 2016). Notably, a series of savanna bird taxa appear in the Turolian faunas of Eurasia (including Eastern Europe), such as the marabou storks, hornbills, and buttonquails (Boev and Kovachev, 2007; Mlíkovský, 2002; Zelenkov et al., 2016). This occurs despite reduced interchange between Africa and Eurasia in the Turolian compared with the Vallesian (Bibi, 2011), so that dispersal of savanna elements into the communities of the Northern Black Sea Coastland most likely is associated with the expansion of taxa inhabiting the Anatolian and Central Asian arid hotspots. The savanna elements in the avian fauna, such as the lark buttonquails *Ortyxelos*, currently inhabiting the Sahel in Africa, were widely distributed in Eurasia at that time and even reached Central Europe (Zelenkov et al., 2016). The wide distribution of similar ostrich taxa (based on eggshell morphology) during this time period is illustrative in this regard: from the Iberian Peninsula in the west to Eastern China (Mikhailov and Zelenkov, 2020).

Turolian amphibian and reptile faunas are heterogeneous and are characterized by high ecological and taxonomic diversity. Compared to Vallesian faunas, they generally indicate greater aridity, although some regions were favorable for hydrophylic taxa. The appearance of the pond turtles of the genus *Emys* at the beginning of the Turolian (MN 11) in the Northern Black Sea Coastland resulted in their active diversification (four separate taxa), successful dispersal throughout Eastern Europe and, later, in Central and Western Europe in the Plio-Pleistocene. Amphisbaenids of the genus *Blanus* appear in the Maeotian of the Northern Black Sea Coastland, which differ from the Miocene and all extant Eastern European amphisbaenids of the *Blanus strauchi* complex. By the end of the Turolian, the herpetological assemblages of the Northern Black Sea Coastland develop distinctly arid and unique features. The high diversity of Lacertidae lizards in the late Miocene (MN 13) of the Caucasus Foreland (Solnechnogorsk locality) makes this region one of the most important for the evolution of some lineages of this reptile group. For instance, it contains the oldest records of the lizards *Lacerta trilineata* and the bridled mabuya *Heremites vittatus* (Čerňanský and Syromyatnikova, 2019, 2021), which today are the typical inhabitants of open landscapes of Southeastern Europe and the Middle East. The presence of archaic elements, however, such as *Anguis* cf. *rarus* and *Ophisaurus* cf. *spinari* makes the composition of this fauna unique (Čerňanský et al., 2020). The appearance of the first *Pelobates praefuscus* here may have given rise to the radiation of the modern European spadefoot toads *P. fuscus* (Syromyatnikova, 2019).

Despite broad similarity between Turolian faunas of terrestrial vertebrates in the vast territories of Southern Eurasia, new data has been accumulating that shows all the more clearly the biogeographic significance of the region under consideration. The most illustrative example is arguably the already mentioned formation of the modern ostrich lineage on the western periphery of the Eastern Paratethys: the structure of the pore system in the eggshell of late Miocene ostriches of the Black Sea Coastland reflects increased adaptive specialization to nesting in especially arid conditions (Mikhailov and Zelenkov, 2020). The formation of this morphotype is likely associated with one of the aridization episodes in the region and may date to the beginning of the Turolian (biozone MN 11). It is during that time (ca. 8.6 Ma), according to recent research (Palcu et al., 2019) that an episode of severe late Khersonian aridification began in the Eastern Paratethys, which led to a significant regression of the Khersonian Basin that peaked during 7.65 Ma. The instability of paleoclimatic environments in this region during the Turolian has been shown for Bulgaria: relatively arid phases were recorded for biozone MN 11 (7.8–8.2 Ma), and another (more pronounced) one, for biozone MN 12 (7.4– 6.8 Ma; Böhme et al., 2018). In southern Ukraine, the first time period is represented by the small mammal fauna of Frunzovka 2, where the jerboa *Allactaga* (*Paralactaga*) and microtoid cricetid *Schymomys* are recorded for the first time in this region. Tellingly, this assemblage is without analogues in Europe (Nesin, 2013). At the same time in Greece several typical members of the so called Pikermian late Turolian fauna of large mammals are recorded for the first time; the fauna formed by the merger of Balkan and Anatolian faunas and existed during the time interval of 7.3–7.2 Ma (Kostopoulos, 2009). Importantly, the formation of the Pikermian biota proceeds by expansion of Balkan species southward, rather than vice versa (Kostopoulos, 2009). This indicates higher competitiveness of mammal taxa that evolved on the northwestern periphery of the Eastern Paratethys and is in agreement with the pattern observed in the evolution of ostriches (the ostrich that formed in the discussed region later dispersed throughout Eurasia and Africa). The expansion of the Pikermian biota in the Balkans coincides with a sharp increase in the proportion of arid-adapted C^4 grasses and the appearance of dust transported from the Sahara (Böhme et al., 2017).

At least some other members of Turolian faunas evolved more intensively as a response to climate instability and increasing aridity on the western margins of the Eastern Paratethys. For instance, Böhme et al. (2018) register pronounced morphological evolution in hyenas of Bulgaria during the arid intervals of the Turolian. It has been suggested that some of the important stages in the evolution of Hominini may have taken place in Southeastern Europe (Böhme et al., 2017; Fuss et al., 2017). The oldest representative of the clade Hominini may turn out to be *Graecopithecus freybergi*, known from the 7.2 Ma old deposits of Greece and Bulgaria and showing similarity with the earlier Vallesian Greek (but, importantly, not Anatolian) Homininae (Spassov et al., 2012).

Several specialized Turolian mammal taxa of uncertain affinities have been described from the region under consideration. It is quite likely that these may also be a result of autochthonous evolution in the context of climatic variability at the end of the late Miocene. For instance, the fossil hare *Alilepus lascarewi* from the Turolian (MN 12) of Ukraine differs from all Miocene and Pliocene Old World representatives of the genus (Čermák et al., 2015). Discussing the unusual morphology of the species, the authors suggest that it may represent an Asian migrant, although no similar taxa are known from Asia, whereas the earliest undoubted records of the genus *Alilepus* in Europe occur in the lowermost zone MN 11 in Moldova (Căinari locality) and in Ukraine (Palievo locality). The earliest *Alilepus* has also been found in the Northern Caucasus (Gaverdovsky). A similar evolutionary history has been assumed for *Vasseuromys tectus* from the Turolian (MN 11–12) of Ukraine, the most specialized species of that genus, prior to its extinction (Sinitsa and Nesin, 2018). Dormice of the genus *Vasseuromys* are a characteristic element of the Miocene small mammal faunas of Central and Eastern Europe and Asia Minor. The hare of the genus *Hypolagus*, which later became widely distributed in Eurasia during the Pliocene–early Pleistocene, first appeared in the fossil record during the late Turolian of the Azov Sea Coastland (lowermost MN 13) (Averianov, 1996; Čermák, 2009). A diversification and evolution hotspot for deer of the genus *Cervavitus* is also associated with the late Miocene of the south of Eastern Europe (Petronio et al., 2007). One of the oldest representatives of the megalocerids, the endemic genus and species *Neomegaloceros gracilis*, known only from the late Miocene (supposedly MN 13) of southern Ukraine, is also of autochthonous East European origin (Korotkevich, 1988; Vislobokova, 2011).

Research on birds also confirms the biogeographic significance of the region discussed during the Turolian. Several bird taxa have been described from the Western and Northern Black Sea Coastland that so far have not been found elsewhere, including several genus-level taxa (the goose *Proanser*, the rallids *Crexica* and *Miohypotaenidia*, the bustard *Miootis*, the fossil wader genus *Cherevychnavis* and the oldest snipe in the fossil record *Gallinago azovica*, the corvid *Miopica*), as well as several endemic species both of water and land birds, including the flightless ergilornithid *Urmiornis ukrainus* (Bochenski et al., 2019; Zelenkov and Kurochkin, 2015; Zelenkov and Panteleyev, 2015). Notably, the late Turolian rallid fauna of the Northern Black Sea Coastland differed sharply, on the genus level, from that of Central Europe (Hungary; Zelenkov et al., 2017). The fauna of land birds was also not homogeneous: whereas advanced ergilornithids *Urmiornis* occurred in the Maeotian of Ukraine, the more archaic *Amphipelargus* occurred at the same time in continental Greece (Zelenkov et al., 2016). High taxonomic diversity has also been recorded for the region's ostriches, although the geographic and chronological distribution of particular taxa currently remains unclear (Mikhailov and Zelenkov, 2020). Small phasianids from the Turolian of the Azov Sea Coastland were initially assigned to *Plioperdix hungaricus* known from the coeval deposits of Central Europe (Zelenkov and Panteleyev, 2015), but new material and a taxonomic revision (Zelenkov and Gorobets, 2020) indicate genus-level differentiation of the Azov Sea Coastland taxon.

MARINE MAMMALS

During the late Miocene, marine mammal communities of the Eastern Paratethys were associated with shallow-water parts of the basin (Fig. 5). Several localities are associated with bryozoan bioherms inside lagoons: localities of Maykop, Polevoe, and Melek-Chesme (Tarasenko, 2020; Tarasenko and Pakhnevich, 2020; Tarasenko et al., 2020). Other localities are associated with the shelf zone and are characterized by greatly waterworn fossil material: Khomutovo, Zheltokamenka, and Zolotaya Balka (Koretsky et Rahmat, 2013). The biogeographic significance of the region is due to the diversity of environments in the shallow-water areas, from bays and lagoons to fully freshwater isolated subbasins (Palcu et al., 2019).

The Eastern Paratethys during the late Miocene was the area of intensive diversification of cetotheriid whales, especially at the boundary between the Bessarabian and the Khersonian (the second half of the Vallesian), which is confirmed by records of members of different cetotheriine genera in the Caucasus, Crimea, and adjacent territories (Gol'din and Startsev, 2014; Mchedlidze, 1964; Podvintsev et al., 2016; Tarasenko, 2014; Tarasenko and Lopatin, 2012; Tarasenko et al., 2020). Apparently, the development of the shallow-water Scythian shelf in the northern part of the Eastern Paratethys during the late Miocene, associated with the formation of numerous biogenic reefs, provided the diversity of local environments and possible isolation for particular groups of cetotheriid whales (Popov et al., 2004). Cetotheriines became widely distributed in the Eastern Paratethys, while the herpetocetines were more typical for the Western Paratethys. The systematic affinities of the cetotheriids of the Eastern Paratethys, previously assigned to the herpetocetines (Tarasenko and Lopatin, 2012), is now under revision (Tarasenko et al., 2018). The endemism of this region is likely associated with the tendency that became apparent already in the early Oligocene to form an isthmus around the Thracian Basin and the separation of the Eastern Mediterranean in the southwest (Popov et al., 2004). Only rare records of Cetotheriidae representatives are known from the Mediterranean (upper Miocene of Italy), which emphasizes the obvious rarity of the family in that basin and may indicate local competition from the ecologically similar grey whales, which, in turn, may explain the geographic isolation and the disparate

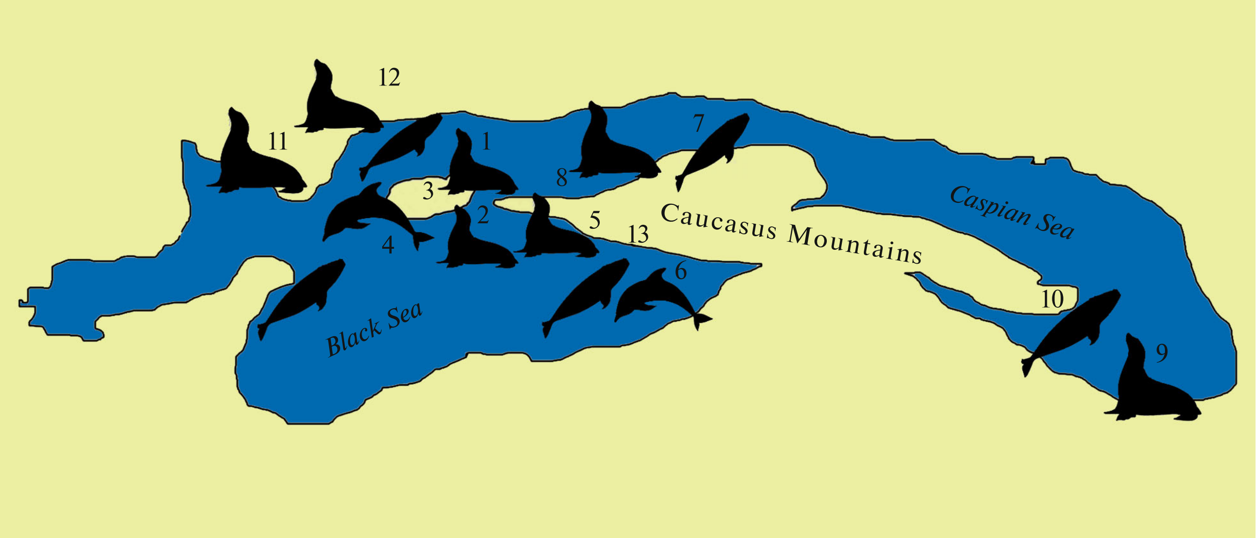

Fig. 5. The main localities of marine mammals in the Miocene of the Eastern Paratethys: (1) Yurkino; (2) Primorskoe; (3) Uzunlar; (4) Tarkhankut; (5) Fortepyanka 2; (6) Polevoe; (7) Besputka; (8) Pekly; (9) Eldar; (10) Pervomaisky quarry; (11) Zheltokamenka; (12) Gritsev; (13) Maykop-2.

geography of finds of the seemingly endemic cetotheriids in the Central Paratethys (Collareta et al., 2021). No records of late Miocene grey whales are known so far from the Eastern Paratethys.

It is believed that the semi-marine closed Sarmatian Basin only periodically came into connection with the Mediterranean; the Euxinian-Caspian Basin was connected with the Dacian Basin which was connected by a narrow Transcarpathian Strait with the Pannonian Basin of the Western Paratethys. In the northwest, the Western Black Sea depression was separated from the Carpathian Basin by a zone of shelves and land areas (Popov et al., 2004). The isolation of the Sarmatian Basin from the Mediterranean and the Western Paratethys, as well as its dilution with freshwater, contributed to the diversification of the cetotheriid whales in the Eastern Paratethys.

Members of Phocidae had a wide range in the late Miocene throughout the Paratethys (Koretsky, 2001). It is believed that the seals of the Paratethys were adapted to oxygen-rich circulating water of the shallow-water zone along the littoral; they were well adapted to temperatures of the fluvial systems (Koretsky, 2001). Adaptations of the late Miocene seals allowed them to become widely distributed in the shallow-water bays and reef islands in the eastern part of the Eastern Paratethys.

DISCUSSION

The review given in this article shows that as the climate became increasingly more arid and open landscapes expanded during the late Miocene, the region of the modern-day Northern and Western Black Sea Coastland was not only the destination for the dispersal of migrants from the older Eurasian arid hotspots (such as Anatolia or Central Asia), but for some vertebrates was also the place of autochthonous evolution and diversification. The biogeographical significance of this region can be explained, to a large extent, by its location on the boundary between the main biomes during the Miocene. For instance, at the end of the middle Miocene and at the beginning of the late Miocene (early–middle Sarmatian of the Eastern Paratethys), regions of the modern-day Northwestern Black Sea Coastland (Moldova and southwestern Ukraine) were mostly still covered by forests that included a considerable number of subtropical elements, whereas in eastern Ukraine, open herbaceous associations with grasses, forbs and chenopods were already widespread (Syabryaj et al., 2007; Velichko et al., 2005). The role of open biotopes increases in the Khersonian (upper Sarmatian of the Eastern Paratethys), when the first *Stipa* proto-steppe grasslands and semi-arid semi-desert associations appear in southern and eastern Ukraine (Syabryaj et al., 2007). In the area bordering the Eastern Paratethys from the north, the zone of mostly open landscapes at the end of the Miocene stretched east from the mouth of the Dnieper and included the Northern Azov Sea Coastland, the lower Don River Valley, areas in the Transcaspian and the south of Ural River. The eastern and southeastern boundaries of this zone were located in Central Asia (Semenenko and Teslenko, 1994). During the episode of increased aridity at the end of the Khersonian—beginning of the Maeotian, some xerophytic steppe floral elements are recorded well to the southwest of this zone, in the Lower Danube Lowland (southern Romania), although broadleaved forest associations remained the dominant vegetation type in that region up to the very end of the Miocene, and open landscapes only became widespread in the plains south of the Carpathians during the Pontian (Casas-Gallego et al., 2021). In the Central Balkans (Western Bulgaria), mixed mesophytic forests that grew in a warm and fairly humid climate were dominant even at the very end of the Miocene (Pontian; Ivanov et al., 2021). In the Carpathians of western Ukraine, forest biomes (boreal coniferous and broadleaved forests) also persisted up to the very end of the Miocene (Syabryaj et al., 2007).

Therefore, throughout the late Miocene the boundary between the forest biome and the open steppe-like or savanna-like landscapes passed through the region under consideration. The location of this boundary changed with time depending on the climate, and paleobotanical data indicates that the expansion of open landscapes westward was accompanied by a spatial differentiation of plant associations (Casas-Gallego et al., 2021; Syabryaj et al., 2007). This differentiation resulted in the appearance of mosaic semi-open habitats which have been reconstructed by multiple previous researchers (Korotkevich, 1988; Lungu, 1990; Nesin, 2013). Because of the mosaicity of ecosystems, the region of the Northern and Western Black Sea Coastland can be considered the transitional (ecotone) zone between the forested Central European and the savannic Greco-Iranian biogeographical provinces. Localities in the Carpathian (Gritsev) and the Caucasus Foreland (Gaverdovsky, Volchya Balka) demonstrate the great role played by mesophytic closed habitats.

The transformations of landscape and climatic environments caused by climate change may have played the main role in creating the conditions for the transformation of the faunas in the region under consideration. Unlike the preceding time period, late Miocene was characterized by pronounced climatic fluctuations that became manifest in the local landscape and climatic environments of Southwestern Europe and defined the dynamics of local plant associations (Ivanov et al., 2011; Palcu et al., 2019). The role of climatic fluctuations and the associated vegetation change for the transformation of faunas has been convincingly demonstrated in the case of the ungulates of the Cape Province in South Africa (Faith and Behrensmeyer, 2013). That research showed that faunal transformation is associated with species extinction and migration according to the geographic distribution of plant associations.

Diversification and morphological evolution of particular representatives of the terrestrial vertebrate fauna in the region discussed can be linked, to a large extent, to the vicariation of populations of ancestral taxa due to biotope fragmentation. Population fragmentation is believed to be the main factor of speciation that explains oscillatory dynamics of mammal faunas in the late Caenozoic (Vrba, 2005). In the Northern and Northwestern Black Sea Coastlands, fragmentation of tetrapod populations (except flying birds) may have additionally been caused by fluctuations of the Eastern Paratethys coastline which experienced a series of considerable transgressions and regressions of the late Miocene, creating the conditions for the appearance of large islands (Palcu et al., 2019; Popov et al., 2010). This geographic instability of sea basins also created the conditions for the diversification of marine mammals and water birds (first fossil records of several genera of extinct and extant genera comes from this region).

The biogeographical significance of the region under consideration hinges not only on diversification as such, but on the evolutionary and ecological success of taxa that formed in the ecotone zone. A vivid illustration is provided by the case of ostriches discussed above and several representatives of the Pikermian fauna of large mammals. As D. Kostopoulos (2009) showed, large mammal taxa that formed in continental Greece in the early Maeotian later (during faunal merger at the end of the Maeotian) expanded their ranges at least to the Anatolian province, even though an older hotspot of open xerophytic landscapes already existed there. The formation of a common Greco-Iranian Pikermian biota proceeded, therefore, by the enrichment of the old faunas of arid landscapes with migrants that formed on the periphery of the grassland biome. The important role of the peripheral regions in the formation of faunal communities of the climax ecosystems is corroborated by research on the formation of modern faunas: a similar effect has recently been shown in the case of the rich (about 1000 modern species) neotropical radiation of suboscines (Tyranni; Harvey et al., 2020). This group is most diverse in the tropical areas of South America having a warm climate and stable landscapes and climatic conditions, but although these regions accumulate taxa, their intensive diversification is associated with the marginal regions having a colder and drier climate, as well as instable landscapes and climatic conditions (Harvey et al., 2020).

The evolutionary success of representatives of peripheral communities can in general terms be explained as follows. Marginal faunas, due to the heterogeneity of landscapes and climatic conditions, undoubtedly contain less specialized species compared to the core areas of faunal associations. This sets up a different kind of ecological interactions, lowers competition between specialists and can promote diversification. Furthermore, impoverished composition of marginal faunas facilitates recruitment of taxa from geographically adjacent though ecologically different habitats. These factors themselves cause more rapid evolution and promote speciation. In the case of the open arid landscapes, their peripheral areas, such as the Northwestern Black Sea Coastland undoubtedly were secondary centers of morphological differentiation and evolution. Initially, these regions were colonized by ancient inhabitants of open landscapes that formed back in the Oligocene–middle Miocene. At least for some taxa their further morphological evolution occurred already in the late Miocene in the context of increasing climate aridity and habitat fragmentation at the periphery of the biome range. Taxa that evolved in these conditions can therefore be seen as "euadaptive" (Rasnitsyn, 1986), i.e., a result of longer evolution and therefore better adapted compared with "inadaptive" taxa that formed from unspecialized ancestral morphotypes by fast adaptation to changing conditions.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

REFERENCES

Agustí, J., Cabrera, L., Gracés, M., Krijgsman, W., Oms, O., and Parés, J.M., A calibrated mammal scale for the Neogene of Western Europe. State of the art, *Earth-Sci. Rev.,* 2001, vol. 52, pp. 247–260.

Averianov, A., The Neogene rabbit *Hypolagus igromovi* Gureev, 1964 (Lagomorpha, Leporidae) from southern European Russia, *Acta Zool. Cracov.,* 1996, vol. 39, pp. 61–66.

Bernor, R.L., Göhlich, U.B., Harzhauser, M., and Semprebon, G.M., The Pannonian C hipparions from the Vienna Basin, *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 2017, vol. 476, pp. 28–41.

Bernor, R.L., Kaya, F., Kaakinen, A., Saarinen, J., Fortelius, M., Old world hipparion evolution, biogeography, climatology and ecology, *Earth-Sci. Rev.,* 2021, vol. 221: 103784.
https://doi.org/10.1016/j.earscirev.2021.103784

Bibi, F., Mio-Pliocene faunal exchanges and African biogeography: the record of fossil bovids, *PLoS One,* 2011, vol. 6, e16688.
https://doi.org/10.1371/journal.pone.0016688

Bochenski, Z., Wertz, K., Tomek, T., and Gorobets, L., A new species of the late Miocene charadriiform bird (Aves: Charadriiformes), with a summary of all Paleogene and Miocene Charadrii remains, *Zootaxa,* 2019, vol. 4624, pp. 41–58.

Boev, Z.N. and Kovachev, D., *Euroceros bulgaricus* gen. nov., sp. nov. from Hadzhidimovo (SW Bulgaria) (Late Miocene)—the first European record of Hornbills (Aves: Coraciiformes), *Geobios,* 2007, vol. 40, pp. 39–49.

Böhme, M., Spassov, N., Ebner, M., Geraads, D., Hristova, L., Kirscher, U., Kötter, S., Linnemann, U., Prieto, J., Roussiakis, S., Theodorou, G., Uhlig, G., and Winklhofer, M., Messinian age and savannah environment of the possible hominin *Graecopithecus* from Europe, *PLoS One,* 2017, vol. 12: e0177347.
https://doi.org/10.1371/journal.pone.0177347

Böhme, M., Van Baak, C.G.C., Prieto, J., Winklhofer, M., and Spassov N., Late Miocene stratigraphy, palaeoclimate and evolution of the Sandanski Basin (Bulgaria) and the chronology of the Pikermian faunal changes, *Glob. Planet. Change.,* 2018, vol. 170, pp. 1–19.

Burchak-Abramovich, N.I., *Iskopaemye strausy Kavkaza i yuga Ukrainy* (Fossil Ostriches of Caucasus and Southern Ukraine), Baku: Akad. Nauk Azer. SSR, 1953.

Caballero, Ó., Montoya, P., Crespo, V.D., Morales, J., and Abella, J., The autopodial skeleton of *Paracamelus aguirrei* (Morales 1984) (Tylopoda, Mammalia) from the late Miocene site of Venta del Moro (Valencia, Spain), *J. Iber. Geol.,* 2021, vol. 47, pp. 483–500.

Casanovas-Vilar, I., Moyà-Solà, S., Agustí, J., and Köhler, M., The geography of a faunal turnover: Tracking the Vallesian Crisis, in *Migrations of Organisms. Climate. Geography. Ecology*, Elewa, A.M.T., Ed., Berlin, Heidelberg: Springer, 2005, pp. 247–300.

Casas-Gallego, M., Marza, A., and Tudor, E., Palaeovegetation and palaeoclimate evolution during the Late Miocene to Early Pliocene of SE Romania, *Geol. J.,* 2021, vol. 56, pp. 821–838.

Čermák, S., Angelone Ch., and Sinitsa, M.V., New late Miocene *Alilepus* (Lagomorpha, Mammalia) from Eastern Europe—a new light on the evolution of the earliest Old World Leporinae, *Bull. Geosci.,* 2015, vol. 90, pp. 431–451.

Čermák, S., The Plio-Pleistocene record of *Hypolagus* (Lagomorpha, Leporidae) from the Czech and Slovak Republics with comments on systematics and classification of the genus, *Bull. Geosci.,* 2009, vol. 84, pp. 497–524.

Čerňanský, A. and Syromyatnikova, E.V., The first Miocene fossils of *Lacerta* cf. *trilineata* (Squamata, Lacertidae) with a comparative study of the main cranial osteological differences in green lizards and their relatives, *PLoS One*, 2019a, vol. 14, e0216191.
https://doi.org/10.1371/journal.pone.0216191

Čerňanský, A. and Syromyatnikova, E.V., The first pre-Quaternary fossil record of the clade Mabuyidae with a comment on the enclosure of the Meckelian canal in skinks, *Pap. Palaeontol.,* 2021, vol. 7, pp. 195–215.

Čerňanský, A. and Syromyatnikova, E.V., The first record of amphisbaenian and anguimorph lizards (Reptilia, Squamata) from the upper Miocene Solnechnodolsk locality in Russia, *Histor. Biol.,* 2020, vol. 32, pp. 869–879.

Collareta, A., Marx, F.G., Casati, S., Di Cencio, A., Merella, M., and Giovanni, B., A cetotheriid whale from the upper Miocene of the Mediterranean, *Neues Jahrb. Geol. Palaeontol., Abh*., 2021, vol. 301, pp. 9–16.

Colombero, S., Bonelli, E., Pavia, M., Repetto, G., and Carnevale, G., *Paracamelus* (Mammalia, Camelidae) remains from the late Messinian of Italy: Insights into the last camels of Western Europe, *Histor. Biol.,* 2017, vol. 29, pp. 509–518.

Faith, J.T. and Behrensmeyer, A.K., Climate change and faunal turnover: testing the mechanics of the turnover-pulse hypothesis with South African fossil data, *Paleobiology.,* 2013, vol. 39, pp. 609–627.

Fang, X., Wang, J., Zhang, W., and Zan, J., Tectonosedimentary evolution model of an intracontinental flexural (foreland) basin for paleoclimatic research, *Glob. Planet. Change,* 2016, vol. 145, pp. 78–97.

Flower, B.P. and Kennett, J.P., The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling, *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 1994, vol. 108, pp. 537–555.

Fortelius, M., Werdelin, L., Andrews, P., Bernor, R., Gentry, A., Humphrey, L., Mittmann, H., and Viranta, S., Provinciality, diversity, turnover, and paleoecology in land mammal faunas of the Later Miocene of Western Eurasia, in *The evolution of Western Eurasian Neogene Mammal Faunas*, Bernor, R.L., Fahlbusch, V. and Mittmann, H.-W., Eds., N.Y.: Columbia Univ. Press, 1996, pp. 414–448.

Fortelius, M., Eronen, J., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I., and Zhang Z., Late Miocene and Pliocene large land mammals and climatic changes in Eurasia, *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 2006, vol. 238, pp. 219–227.

Fuss, J., Spassov, N., Begun, D.R., and Böhme, M., Potential hominin affinities of *Graecopithecus* from the late Miocene of Europe, *PLoS One,* 2017, vol. 12, e0177127. https://doi.org/10.1371/journal.pone.0177127

Gol'din, P.E. and Startsev, D.B., *Brandtocetus*, a new genus of Baleen Whales (Cetacea, Cetotheriidae) from the Late Miocene of Crimea, Ukraine, *J. Vertebr. Paleontol.,* 2014, vol. 34, pp. 419–433.

Harvey, M.G., Bravo, G.A., Claramunt, S., Cuervo, A.M., Derryberry, G., Battilana, J., Seeholzer, G.F., McKay, J., O'Meara, B., Faircloth, B., Edwards, S., Pérez-emán, J., Moyle, R., Sheldon, F., Aleixo, A., Smith, B., Chesser, R., Silveira, L.F., Cracraft, J., Brumfield, R.T., and Derryberry, E., The evolution of a tropical biodiversity hotspot, *Science,* 2020, vol. 370, pp. 1343–1348.

Hilgen, F.J., Lourens, L.J., and van Dam, J.A., The Neogene Period, in *The Geologic Time Scale 2012*, Gradstein, F.M., Ogg, J.G., Schmitz, M., and Ogg, G., Eds., Oxford: Elsevier, 2012, pp. 924–956.

Ivanov, D., Utescher, T., Mosbrugger, V., Syabryaj, S., Djordjevic-Milutinovic, D., and Molchanoff, S., Miocene vegetation and climate dynamics in Eastern and Central Paratethys (Southeastern Europe), *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 2011, vol. 304, pp. 262–275.

Ivanov, D., Utescher, T., Djorgova, N., Bozukov, V., Ahraf, A.R.,The late Miocene Beli Breg Basin (Bulgaria): palaeoecology and climate reconstructions based on pollen data, *Palaeobiodiv. Palaeoenvir.,* 2021, vol. 101, pp. 79–102.

Kaya, F., Bibi, F., Žliobaitė, I., Eronen, J., Hui, T., and Fortelius, M., The rise and fall of the Old World savannah fauna and the origins of the African savannah biome, *Nat. Ecol. Evol.,* 2018, vol. 2, pp. 241–246.

Koretsky, I.A. and Rahmat, S.J., First record of fossil Cystophorinae (Carnivora, Phocidae): Middle Miocene seals from the northern Paratethys, *Riv. Ital. Paleontol. Stratigr.,* 2013, vol. 119, pp. 325–350.

Koretsky, I.A., Morphology and systematics of Miocene Phocinae (Mammalia: Carnivora) from Paratethys and the North Atlantic Region, *Geol. Hung. Ser. Paleontol.,* 2001, vol. 54, pp. 1–109.

Korotkevich, E.L., *Istoriya formirovaniya gipparionovoi fauny Vostochnoi Evropy* (The History of the Formation of the *Hipparion* Fauna of Eastern Europe). Kiev: Naukova dumka, 1988.

Kostopoulos, D.S., The Pikermian Event: temporal and spatial resolution of the Turolian large mammal fauna in SE Europe, *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 2009, vol. 274, pp. 82–95.

Kovalchuk, O.M., Gorobets, L.V., Syromyatnikova, E.V., Danilov, I. G., Titov, V.V., Krakhmalnaya, T.V., Rekovets, L.I., and Zelenkov, N.V., Vertebrates from the Pontian of the Shkodova Gora locality (Northwestern Black Sea Region, Upper Miocene), *Paleontol. J.,* 2017, vol. 51, no. 4, pp. 414–429.

Krakhmalnaya, T.V., *Gipparionovaya fauna drevnego meotisa Severnogo Prichernomor'ya* (Hipparion Fauna of the Ancient Meotis of the Northern Black Sea Region). Kiev: Nauk. dumka, 1996.

Kurochkin, E.N. and Lungu, A.N., A new ostrich from the middle Sarmatian of Moldavia, *Paleontol. Zh.,* 1970, no. 1, pp. 118–126.

Lirer, F., Harzhauser, M., Pelosi, N., Piller, W., Schmid, H.P., and Sprovieri, M., Astronomically forced teleconnection between Paratethyan and Mediterranean sediments during the Middle and Late Miocene, *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 2009, vol. 275, pp. 1–13.

Lithological-Paleogeographic Maps of Parathethis: 10 Maps Late Eocene to Pliocene, Popov, S.V., Rögl, F., Rozanov, A.Y., Shcherba, I.G., and Steininger, F.F., Eds., Cour. Forschungs. Senckenb., E.Schwei.zerbrat'sche Verlagsbuchhandlung, Stuttgart, 2004, vol. 250.

Lungu, A.N., *Gipparionovaya fauna srednego sarmata Moldavii (kopytnye mlekopitayushchie)* (The *Hipparion* Fauna of the Middle Sarmatian of Moldavia (Ungulates)). Chișinău: Shtiintsa, 1984.

Lungu, A.N., Early stages of the development of the *Hipparion* fauna of the continental Paratethys, *Doctoral (Geol.-Mineral.) Dissertation*, Tiraspol', 1990.

Mchedlidze, G.A., *Iskopaemye kitoobraznye Kavkaza* (Fossil Cetaceans of the Caucasus), Tbilisi: Metsniereba, 1964.

Mikhailov, K.E. and Kurochkin, E.N., Eggshells of fossil Struthioniformes from the Palearctic and its place in the system of ideas about the evolution of Ratitae, in *Iskopaemye reptilii i ptitsy Mongolii* (Fossil Reptiles and Birds of Mongolia), Kurochkin, E.N., Ed., Moscow: Nauka, 1988, pp. 43–64.

Mikhailov, K.E. and Zelenkov, N., The late Cenozoic history of the ostriches (Aves: Struthionidae), as revealed by fossil eggshell and bone remains, *Earth-Sci. Rev.,* 2020, vol. 208, 103270. https://doi.org/10.1016/j.earscirev.2020.103270

Mirzaie Ataabadi, M., Liu, L., Eronen, J., Bernor, R., and Fortelius, M., Continental-scale patterns in Neogene mammal community evolution and biogeography: a Europe-Asia Perspective, in *Fossil mammals of Asia. Neogene Biostratigraphy and Chronology*, Wang, X., Flynn, L.J., and Fortelius, M., Eds., N.Y.: Columbia Univ. Press, 2013, pp. 629–655.

Mlíkovský, J., *Cenozoic Birds of the World. Part 1: Europe*, Praha: Ninox Press, 2002.

Nesin, V.A., *Neogenovye Murinae (Rodentia, Muridae) Ukrainy* (Neogene Murinae (Rodentia, Muridae) of Ukraine). Sumy: Univ. Kniga, 2013.

Palcu, D.V., The Dire Straits of Paratethys. Dating, matching and modeling connectivity between the Miocene seas of Eurasia, *Utrecht Stud. Earth Sci.,* 2018, vol. 155, pp. 1–200.

Palcu, D.V., Vasiliev, I., Stoica, M., and Krijgsman, W., The end of the Great Khersonian Drying of Eurasia: Magnetostratigraphic dating of the Maeotian transgression in the Eastern Paratethys, *Basin Res.,* 2019, vol. 31, pp. 33–58.

Petronio, C., Krakhmalnaya, T., Bellucci, L., Di Stefano, G., Remarks on some Eurasian pliocervines: characteristics, evolution, and relationships with the tribe Cervini, *Geobios.,* 2007, vol. 40, pp. 113–130.

Podvintsev, V.G., Kurshakov, S.V., Malyshkina, T.P., Orlov, N.A., Syromyatnikova, E.V., Tarasenko, K.K., Tesakov, A.S., and Titov, V.V., A new heterogeneous locality of marine and terrestrial vertebrates of the Late Miocene Gladkovskoye (Krasnodar Krai), in *Mater. LXII Yubil. sess. Paleontol. Obsch. Ross. Akad. Nauk* (Proc. 62 Sess. Paleont. Soc. Russ. Acad. Sci.), St. Petersburg, 2016, pp. 267–268.

Popov, S.V., Antipov, M.P., Zastrozhnov, A.S., Kurina, E.E., and Pinchuk, T.N., Sea level fluctuations on the northern shelf of the Eastern Paratethys in the Oligocene-Neogene, *Stratigr. Geol. Correl.,* 2010, vol. 18, no. 2, pp. 99–124.

Qiu Zhan-Xiang, Qiu Zhu-Ding, Deng, T., Li, Ch-K., Zhang, Zh.-Q., Wang, B.-Y., and Wang X., Neogene land mammal stages/ages of China: Toward the goal to establish an Asian land mammal stage/age, in *Fossil Mammals of Asia. Neogene Biostratigraphy and Chronology*, Wang, X., Flynn, L.J., and Fortelius, M., Eds., N.Y.: Columbia Univ. Press, 2013, pp. 29–90.

Rasnitsyn, A.P., Inadaptation and euadaptation, *Paleontol. Zh.,* 1986, no. 1, pp. 4–7.

Roček, Z. A contribution to the herpetofauna from the late Miocene of Gritsev (Ukraine), *C. R. Palevol.,* 2019, vol. 18, pp. 817–847.

Rögl, F., Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene), *Ann. Naturhist. Mus. Wien.,* 1998, vol. 99, pp. 279–310.

Semenenko, V.N. and Teslenko, Yu.V., Geological events in the Eastern Paratethys at the Miocene-Pliocene boundary, *Geol. Zh.,* 1994, no. 1, pp. 58–68.

Shvyreva, A.K. and Titov, V.V., Late Sarmatian fauna from the deposits of the Beshpagirsky quarry (Stavropol Territory), in *Mater. LXVI Sess. Paleontol. Obshch. Ross. Akad. Nauk “Biogeografiya i evolyutsionnye protsessy”* (Proc. 66 Sess. Paleont. Soc. Russ. Acad. Sci. “Biogeography and Evolutionary Processes”), St. Petersburg: Vseross. Nauchno-Issled. Geol. Inst., 2020, pp. 281–282.

Sinitsa, M.V. and Delinschi, A., The earliest member of *Neocricetodon* (Rodentia: Cricetidae): a redescription of *A. moldavicus* from Eastern Europe, and its bearing on the evolution of the genus, *J. Paleontol.,* 2016, vol. 90, pp. 771–784.

Sinitsa, M.V. and Nesin, V.A., Systematics and phylogeny of *Vasseuromys* (Mammalia, Rodentia, Gliridae) with a description of a new species from the late Miocene of Eastern Europe, *Palaeontology.,* 2018, vol. 61, pp. 679–701.

Sotnikova, M. and Rook, L., Dispersal of the Canini (Mammalia, Canidae: Caninae) across Eurasia during the Late Miocene to Early Pleistocene, *Quart. Int.,* 2010, vol. 212, pp. 86–97.

Spassov, N., Geraads, D., Hristova, L., Markov, G.N., Merceron, G., Tzankov, T., Stoyanov, K., Böhme, M., Dimitrova, A., A hominid tooth from Bulgaria: the last pre-human hominid of continental Europe, *J. Hum. Evol.,* 2012, vol. 62, pp. 138–145.

Syabryaj, S., Utescher, T., Molchanoff, S., and Bruch, A.A., Vegetation and palaeoclimate in the Miocene of Ukraine, *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 2007, vol. 253, pp. 153–168.

Syromyatnikova, E.V., Redescription of *Pelobates praefuscus* Khosatzky, 1985 and new records of *Pelobates* from the late Miocene—Pleistocene of Eastern Europe, *Histor. Biol.,* 2019, vol. 31, pp. 888–897.

Tarasenko, K.K. and Lopatin, A.V., New baleen whale genera (Cetacea, Mammalia) from the Miocene of the Northern Caucasus and Ciscaucasia: 1. *Kurdalagonus* gen. nov. from the Middle—Late Sarmatian of Adygea), *Paleontol. J.,* 2012, vol. 46, no. 5, pp. 531–542.

Tarasenko, K.K. and Pakhnevich, A.V., Formation of stromatolite biogerms on the bones of fossil cetaceans, in *Mater. LXVI sess. Paleontol. Obshch. Ross. Akad. Nauk “Biogeografiya i Evolyutsionnye Protsessy”* (Proc. 66 Sess. Paleont. Soc. Russ. Acad. Sci. “Biogeography and Evolutionary Processes”), St. Petersburg: Vseross. Nauchno-Issled. Geol. Inst., 2020, pp. 159–160.

Tarasenko, K.K., Kovalenko, E.S., and Podurets, K.M., New data on the morphology of the bone labyrinth of the stony bone of the Miocene baleen whale from Chechnya — Vampalus sayasanicus, *in Mater. LXIV sess. Paleontol. Obshch. Ross. Akad. Nauk* (Proc. 64 Sess. Paleont. Soc. Russ. Acad. Sci.), St. Petersburg: Vseross. Nauchno-Issled. Geol. Inst., 2018, pp. 234–235.

Tarasenko, K.K., Lopatin, A.V., and Startsev, D.B., First record of Late Miocene baleen whales *Zygiocetus* (Cetotheriidae, Mysticeti) in Crimea (Melek-Chesme locality, Kerch Peninsula), *Dokl. Biol. Sci.,* 2020, vol. 491, no. 1, pp. 176–179.

Tarasenko, K.K., New data on sedimentology and taphonomy of the Late Miocene locality Polevoe 1 (Northwest Caucasus, Republic of Adygea), in *XXI Int. Conf. Young Geol. Herlany*, Kraków: MINERALPRESS, 2020, pp. 79–82.

Tarasenko, K.K., New genera of Baleen Whales (Cetacea, Mammalia) from the Miocene of the Northern Caucasus and Ciscaucasia: 3. *Zygiocetus* gen. nov. (Middle Sarmatian, Adygea), *Paleontol. J.,* 2014, vol. 48, no. 5, pp. 534–550.

Ter Borgh, M., Vasiliev, I., Stoica, M., Knežević, S., Matenco, L., Krijgsman, W., Rundić, L., and Cloetingh, S., The isolation of the Pannonian basin (Central Paratethys): New constraints from magnetostratigraphy and biostratigraphy, *Glob. Planet. Change,* 2013, vol. 103, pp. 99–118.

Tesakov, A.S., Titov, V.V., Simakova, A.N., Frolov, P., Syromyatnikova, E.V., Kurshakov, S.V., Volkova, N., Trikhunkov, Ya.I., Sotnikova, M., Kruskop, S., Zelenkov, N., Tesakova, E., and Palatov, D.M., Late Miocene (Early Turolian) vertebrate faunas and associated biotic record of the Northern Caucasus: Geology, palaeoenvironment, biochronology, *Fos. Impr.,* 2017, vol. 73, pp. 383–444.

Titov, V.V. and Logvinenko, V.V., Early *Paracamelus* (Mammalia, Tylopoda) in the Eastern Europe, *Acta Zool. Cracov.,* 2006, vol. 49, pp. 163–178.

Titov, V.V. and Tesakov, A.S., Late Miocene (Turolian) vertebrate faunas of the southern European Russia, in *Fossil Mammals of Asia. Neogene Biostratigraphy and Chronology*, Wang, X., Flynn, L.J., and Fortelius, M., Eds., N.Y.: Columbia Univ. Press, 2013, pp. 536–543.

Titov, V.V., Tesakov, A.S., Sotnikova, M.V., Syromyatnikova, E.V., Kurshakov S.V., Frolov P.D., and Simakova A.N., Late Miocene terrestrial communities of vertebrates and mollusks of the Caucasus Foreland, in *Mater. Vseross. Nauch. Prakt. Konf. "Geologiya i bioraznoobraziye Tetisa i Vostochnogo Paratetisa"* (Proc. Russ. Res. Conf. "Geology and Biodiversity of the Tethys and Eastern Paratethys"), Popov, S.V., Ed., Goryachy Klyuch, 2017, pp. 89–93.

Titov, V.V., Tesakov, A.S., Danilov, I.G., Danukalova, G.A., Mashchenko, E.N., Panteleev, A.V., Sotnikova, M.V., and Sychevskaya, E.K., The first representative vertebrate fauna of the Late Miocene in the south of European Russia, *Dokl. Biol. Sci.,* 2006, vol. 411, no. 5, pp. 715– 717.

Tobien, H., Subdivision of Pontian mammal faunas, *Giorn. Geol.,* 1967, vol. 35, pp. 1–5.

Vangengeim, E.A., Lungu, A.N., and Tesakov, A.S., Age of the Vallesian lower boundary (continental Miocene of Europe), *Stratigr. Geol. Correl.,* 2006, vol. 14, no. 6, pp. 81–91.

Vasiliev, I., Iosifidi, A.G., Khramov, A.N., Krijgsman, W., Kuiper, K., Langereis, C.G., Popov, V.V., Stoica, M., Tomsha, V.A., and Yudin, S.V., Magnetostratigraphy and radioisotope dating of upper Miocene–lower Pliocene sedimentary successions of the Black Sea Basin (Taman Peninsula, Russia), *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 2011, vol. 310, pp. 163–175.

Velichko, A.A., Akhlestina, E.F., Borisova, O.K., Gribchenko, Yu.N., Zhidovinov, N.Ya., Zelikson, E.M., Iosifova, Yu.I., Klimanov, V.A., Morosova, T.D., Nechaev, V.P., Pisareva, V.V., Svetlitskaya, T.V., Spasskaya, I.I., Udartsev, V.P., Faustova, M.A., and Shik, S.M., East European Plain, in *Cenozoic Climatic and Environmental Changes in Russia, Spec. Pap.—Geol. Soc. Amer.*, 2005, vol. 382, pp. 31–66.

Vislobokova, I.A., Associations of ruminants in Miocene ecosystems of Eastern Alpine region, *Paleontol. J.,* 2006, vol. 40, no. 4, pp. 438–447.

Vislobokova, I.A., Historical development and geographical distribution of giant deer (Cervidae, Megacerini), *Paleontol. J.,* 2011, vol. 45, no. 6, pp. 674–687.

Vislobokova, I.A. and Tarasenko, K.K., Finds of ruminants and new data on the stratigraphy of the late Miocene locality of Fortep'yanka 2 (Northwest Caucasus, Adygea Republic), *Paleontol. J.,* 2019, vol. 53, no. 6, pp. 660–665.

Volokitin, V.V., Shvyreva, A.K., and Titov, V.V., Bunodont mastodons (Gomphotheriidae) from the Late Sarmatian of Stavropol territory, in *Mater. LXVII sess. Paleontol. Obsch. Ross. Akad. Nauk "Teoreticheskie i prikladnye aspekty paleontologii"* (Proc. LXVII Sess. Paleont. Soc. "Theoretical and Applied Aspects of Paleontology"), St. Petersburg: Vseross. Nauchno-Issled. Geol. Inst., 2021, pp. 102–103.

Vrba, E.S., Mass turnover and heterochrony events in response to physical change, *Paleobiology.,* 2005, vol. 31, Suppl. 2, pp. 157–174.

Wang, X., Flynn, L.J., and Fortelius, M., Eds., *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*, N.Y.: Columbia Univ. Press, 2013.

Woodburne, M.O., Bernor, R.L., and Swisher, C.C., An appraisal of the stratigraphic and phylogenetic bases for the "Hipparion" datum in the Old World, in *The Evolution of Western Eurasian Neogene Mammal Faunas*, Woodburne, M.O., Bernor, R.L., and Swisher, C.C., Eds., N.Y.: Columbia Univ. Press, 1996, pp. 124–136.

Zachos, J., Pagani, M., and Sloan, L., Thomas, E., and Billups, K., Trends, rhythms, and aberrations in global climate 65 Ma to present, *Science,* 2001, vol. 292, pp. 686–693.

Zelenkov, N.V., Evolution of bird communities in the Neogene of Central Asia, with a review of the Neogene fossil record of Asian birds, *Paleontol. J.,* 2016, vol. 50, no. 12, pp. 1421–1433.

Zelenkov, N.V., The revised avian fauna of Rudabánya (Hungary, Late Miocene), in *Paleontologia y Evolución de las Aves*, Acosta Hospitaleche, C., Agnolin, F., Haidr, N. Noriega, J.I., and Tambussi, C.P., Eds., *Contribuciones del Museo Argentino de Ciencias Naturales, Buenos-Aires: Mus. Argent. Cienc. Natur.*, 2017, pp. 253–266.

Zelenkov, N.V., Cenozoic Evolution of Eurasian Anatids (Aves: Anatidae s. l.), *Biol. Bull. Rev.*, 2020, vol. 10, no. 5, pp. 417–426.

Zelenkov, N., Boev, Z., and Lazaridis, G., A large ergilornithine (Aves, Gruiformes) from the Late Miocene of the Balkan Peninsula, *Paläontol. Z.,* 2016, vol. 90, pp. 145–151.

Zelenkov, N.V. and Gorobets, L.V., Revision of *Plioperdix* (Aves: Phasianidae) from the Plio-Pleistocene of Ukraine, *Paleontol. J.,* 2020, vol. 54, no. 5, pp. 531–541.

Zelenkov, N.V. and Kurochkin, E.N., *Class Aves, Iskopaemye pozvonochnye Rossii i sopredel'nyh stran. Iskopaemye reptilii i ptitsy. Chast' 2* (Fossil vertebrates of Russia and neighbouring countries. Fossil reptiles and birds. Pt. 2), Kurochkin, E.N., Lopatin, A.V., and Zelenkov, N.V., Eds., Moscow: GEOS, 2015, pp. 86–290.

Zelenkov, N.V. and Panteleyev, A.V., Three bird taxa (Aves: Anatidae, Phasianidae, Scolopacidae) from the Late Miocene of the Sea of Azov (Southwestern Russia), *Paläontol. Z.,* 2015, vol. 89, pp. 515–527.

Zelenkov, N.V., Panteleyev, A.V., and De Pietri, V.L., Late Miocene rails (Aves: Rallidae) from southwestern Russia, *Palaeobiodiv. Palaeoenvir.,* 2017, vol. 97, pp. 791–805.

Zelenkov, N.V., Stidham, T.A., and Martynovich, N.V., Vokova, N.V., Li, Q., and Qiu, Zh., The middle Miocene duck *Chenoanas* (Aves, Anatidae): new species, phylogeny and geographical range, *Pap. Palaeontol.,* 2018, vol. 4, pp. 309–326.

Zelenkov, N.V., Volkova, N.V., and Gorobets, L.V., Late Miocene buttonquails (Charadriiformes, Turnicidae) from the temperate zone of Eurasia, *J. Ornithol.,* 2016, vol. 157, pp. 85–92.

Zerova, G.A., Localities of Late Miocene-Early Pleistocene lizards and snakes of Ukraine, *Tr. Inst. Zool. Akad. Nauk Ukrain. SSR,* 1987, no. 12, pp. 12–18.

Zhang, W., Appel, E., Wang, J., Fang, X., Zan, J., Yang, Y., Miao, Y., and Yan, X., New paleomagnetic constraints for Platybelodon and Hipparion faunas in the Linxia Basin and their ecological environmental implications, *Glob. Planet. Change,* 2019, vol. 176, pp. 71–83.

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