

# Associations of Ruminants in Miocene Ecosystems of Eastern Alpine Region

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**Abstract**—The dynamics of biodiversity of ruminants and changes in their adaptations in the Late Miocene of Austria are analyzed in connection with changes in environment and climate. At the end of the Middle Miocene through the beginning of the Late Miocene, the major reorganization of ruminant associations was recorded at the Vallesian–Turolian transition (about 8.7 Ma).

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## INTRODUCTION

Ruminants are good indicators of landscapes and climate. Shifts in their associations with time, change of dietary and locomotor adaptations and migration features provide valuable information for the reconstruction of the history of Late Cenozoic land ecosystems.

Fascinating new data on changes in associations of ruminants in the Late Miocene at the Vallesian–Turolian boundary were obtained in the course of the Austrian project “Changes in Eastern Alpine Miocene Ecosystems Reflected by Vertebrates.” The project is an addition to the international project EEDEN (“Environments and Ecosystem Dynamics of the Eurasian Neogene”).

The goals of the Austrian project include the reconstruction of land ecosystems and correlation of changes in Miocene land communities and climate in the Middle and Late Miocene within one of the intervals, which is under study by the EEDEN, HRI 2 (high resolution time interval 2), spanning the Late Middle through the early Late Miocene (12–8.5 Ma). This time interval evidences the early stages in the development of the hipparion fauna. Ruminants, which were dominant in Late Miocene faunas, are among the basic groups in the focus of the study.

Austria is rich in Middle and Upper Miocene mammal localities. The chronology of local Miocene faunas is based on studies of Thenius (1948a, 1948b, 1950, 1952, 1954, 1956a, 1956b, 1974), Zapfe (1948), Bernor et al. (1990, 1993), Mein (1999), Franzen and G. Storch (1999), and other researchers. The region presents clear data on the coevolution of phytophagous mammals and plant communities due to the co-occurrence of flora localities in some faunal horizons (Bernor et al., 1990, Kovar-Eder et al., 1994).

The present article analyzes changes in diversity and adaptations of ruminants during the Late Miocene of

Austria in connection with changes in environment and climate. Additionally, biogeographical links with a number of neighboring regions, in particular, with Eastern Europe and the Balkans, and the basic dispersion events are discussed.

The bulk of the ruminant fossils examined come from the Kohfidisch locality in southern Austria. In addition, the revision also includes materials from other Miocene localities housed in the Vienna Museum of Natural History.

Currently, there is no commonly accepted opinion concerning the age of the main stratigraphic boundaries and biochronological levels of the Late Miocene. The stratigraphic scheme used in this work resulted from multidisciplinary studies of Austrian investigators. The detailed stratigraphic scale of the Central Paratethys, based on the study of marine and continental deposits, is successfully applied in interregional correlations and in reconstruction of the history of ecosystems.

The biochronology of the Late Miocene of Austria (Vienna and Pannonian basins) became considerably more detailed during the last decade due to rodent studies (Daxner-Höck, 1996, 2001, 2003, 2004). These results are of key importance for correlations of the Austrian faunas with the mammal zones of the Neogene (MN units) and the paleomagnetic scale (Geomagnetic Polarity Time Scale) (Brujin et al., 1992; Cande and Kent, 1995; Rögl and Daxner-Höck, 1996; Daxner-Höck, 1996, 2001, 2003, 2004) (Fig. 1).

The boundary of the Middle and Upper Miocene is drawn at the level of 11.6 Ma (Daxner-Höck, 2004). In the Central Paratethys, it corresponds to the boundary of the Sarmatian *sensu stricto* and the Pannonian. The lower boundary of the Vallesian is drawn inside the Subchron C5r.2r and dated 11.2 Ma, while the upper boundary coincides with the boundary of zones MN10

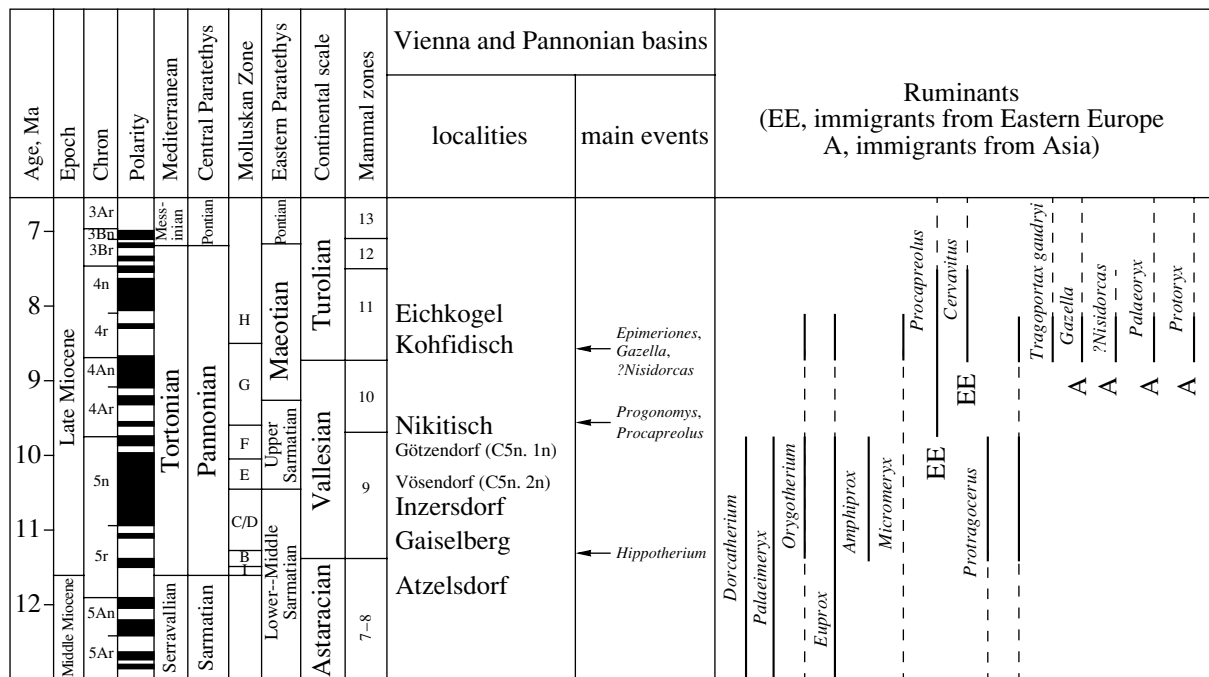


Fig. 1. Distribution of ruminants in the Middle and Late Miocene of Austria.

and MN11 and is estimated as 8.7 Ma (the base of the Chron C4r.2r) (Daxner-Höck, 2004). The boundary between zones MN9 and MN10 is considered to be equal to 9.7 Ma (the base of the Chron C4Ar.3r) (Steininger, 1999). The upper boundary of Zone MN11 is drawn at the level of 7.5 Ma (the base of the Chron C4n.1n) (Krijgsman et al., 1996; Agusti et al., 2001; Daxner-Höck, 2004), rather than at 8.1 Ma (Steininger, 1999).

Considerable progress has been made in refining the Neogene paleogeography of the Central Paratethys (Rögl, 1998, 1999a, 1999b; Harzhauser et al., 2003) and the history of plant communities of this region (Kovar-Eder, 1987; Kovar-Eder et al., 1994).

## EASTERN ALPINE LAND ECOSYSTEMS IN THE LATE MIOCENE

### *Paleofaunal Data*

The beginning of the Late Miocene was the time when the mammalian Hipparion Fauna was established in Palearctic. It existed there for more than 7 m.y., up to the middle of the Pliocene.

The main dominant of the fauna, a hipparion of the genus *Hippotherium*, migrated from North America at about 11.5 Ma ago, near the boundary of the Middle and Late Miocene (i.e., that of the Sarmatian sensu stricto and Pannonian) along the Bering Land Bridge, which emerged after a regular drop in the level of the World Ocean.

Among phytophagous mammals of the hipparion fauna, the most numerous were various ruminants.

Together with hipparion and other phytophages, these primary consumers actively developed various habitats.

The formation of the hipparion fauna was closely connected to changes in vegetation. The history of this fauna is linked with gradual transformation of forest landscapes community into the savanna communities. The rates of transformation depended on global factors and local geographical conditions.

The hipparion fauna achieved its acme in the Maeotian, with the commonly implied wide development of grassy plains (Gabunia and Chochieva, 1982; Thenius, 1982; Gabunia, 1985). However, an opinion recently emerged that the extensive Late Miocene Pikermian biome, which was spread from Spain to China, was represented by sclerophyllous evergreen forests with differentiated biotopes, including riparian and perilacustrine ecotones, and by coastal plains rather than by savannas or grassy plains (Solounias and Dawson-Sanders, 1988; Solounias et al., 1999). The ancestors of many inhabitants of the modern African savanna most likely originated within this biome (Solounias et al., 1999).

The early stages of the development of the hipparion fauna are traced in a number of places, including Austria. Special local conditions at the beginning of the Late Miocene, and new possibilities for faunal exchanges, promoted the emergence of faunas with co-occurring forest-dwelling hipparions, represented by one or two conservative species (Bernor et al., 1988, 1990, 1993), and very diverse artiodactyls, particularly, ruminants. Elements of the hipparion fauna populated the East Alpine Region, alongside with Middle Miocene forms that survived in wet situations.

List of Late Miocene ruminants of Austria (Thenius, 1948, 1954, 1960; Zapfe, 1948, 1997, etc.)

MN Zone	9					9/10	10		11	
	Gaisel- berg	Vienna 3	Vösen- dorf	Inzers- dorf	Götzen- dorf	Somme- rein H	Niki- tisch	Himberg	Kohfi- disch	Eichko- gel
Palaeomerycidae										
<i>Orygotherium heinzi</i>									+	
<i>Orygotherium</i> sp.					+					
<i>Palaeomeryx</i> sp.	+									
Giraffidae										
Giraffidae gen.									+	
Tragulidae										
<i>Dorcatherium naui</i>	+									
Cervidae										
<i>Micromeryx</i> sp.									+	
<i>Euprox dicranocerus</i>		+	+						+	
<i>Euprox</i> sp.									+	
<i>Amphiprox anocerus</i>			+						+	
<i>Cervavitus</i> sp.									+	
<i>Procapreolus loczyi</i>							+	+	+	
<i>Procapreolus</i> sp.									+	+
Bovidae										
<i>Gazella aff. pilgrimi</i>									+	
? <i>Nisidorcas</i> sp.									+	
<i>Protragocerus chantrei</i>						+				
<i>Miotragocerus pannoniae</i>	+		+	+					+	
<i>Tragoportax gaudryi</i>									+	
<i>Palaeoryx</i> sp.									+	
<i>Protoryx</i> sp.									+	

The earliest hipparion of the region, *Hippotherium primigenium* (= "*Hipparion*" *primigenium*), is known from Hovorany and Gaiselberg, the Vienna Basin (Bernor et al., 1988; Rögl and Daxner-Höck, 1996). It is supposed that this hipparion appeared in this territory at the beginning of the Pannonian not earlier than 11.5 Ma, at the boundary of zones B and C (Bernor et al., 1988, 1990; Rögl, 1998) or in the Zone C (Rögl and Daxner-Höck, 1996), soon after its migration to Eurasia.

A rather rapid dispersal of hipparions and the formation of the hipparion fauna were promoted by geographical conditions that existed at the boundary of the Middle and Late Miocene and during the early Late Miocene.

#### *Paleogeographic Features*

At the end of the Middle Miocene and the beginning of the Late Miocene, the East Alpine Region witnessed a gradual increase of the area and diversification of land

ecosystems. This environmental diversification was closely connected to changes to the Central Paratethys area (Rögl, 1999a, 1999b; Daxner-Höck, 2003; Harzhauser et al., 2003).

Miocene land ecosystems of the East Alpine Region were influenced by the Paratethys during their entire history. The land fauna was strongly influenced by geographic changes at the end of the Middle Miocene and the beginning of the Late Miocene with the change of marine ecosystems into terrestrial ones in the Pannonian and Vienna basins. At the end of the Middle Miocene (the end of the Sarmatian *sensu stricto*), a giant brackish-water basin of the Paratethys, which spread in the Early Sarmatian from the Alps to the Aral Sea, considerably decreased in area (Rögl, 1999a, 1999b; Nevesskaya et al., 2003).

At the boundary of the Middle and Late Miocene, its western part, the Pannonian Basin, turned into a lake. This lake reached its maximum size in the Early Pannonian (Zone E, Early Vallesian, MN9) and shrank considerably in the Late Pannonian.

At about 9.9 Ma (Zone F, the end of the Early Vallesian, end of MN9), Pannonian Lake abandoned the Vienna Basin, leaving in its place a flat plain with a river system and small lakes (Daxner-Höck, 2003; Harzhauser et al., 2003) and diverse terrestrial biotopes, which were intensely developed by autochthons and newcomers.

### *Climate*

The climate was generally warm–temperate and humid, without a notable dry season (Thenius, 1982; Kovar-Eder, 1987; Bernor et al., 1988, 1990). The temperature of the coldest month ranged from  $-3^{\circ}\text{C}$  to  $+18^{\circ}\text{C}$ , while that of the warmest month exceeded  $22^{\circ}\text{C}$  (Kovar-Eder, 1987). According to Gregor (1982), the average annual temperature north of the Alps was  $12\text{--}15^{\circ}\text{C}$ , the average January temperature was more than  $0^{\circ}\text{C}$ , while the July temperature was  $-25^{\circ}\text{C}$ , with annual precipitation of 1000–1200 mm.

The study of mammal communities of the East Alpine Region suggests that the climatic changes proceeded from humid climate in the Vallesian towards drier conditions with more expressed seasonality at the beginning of the Turolian, after 8.7 Ma (Daxner-Höck, 2003).

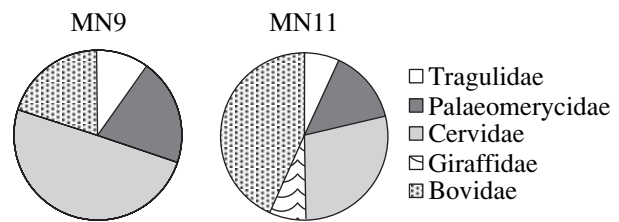
### *Paleobotanical Data*

Starting from the second half of the Middle Miocene, the evergreen subtropical elements of the Paratethys Region experienced a decrease in diversity and an increased role of mesophilous arboreal species and grasses, and the formation of forest–meadow landscapes (Gabunia and Chochieva, 1982; Gabunia, 1985). Ginkgo, an element of warm deciduous forest communities, appeared in the Paratethys area at the end of the Middle Miocene after *Platanus leucophylla* and *Acer quercifolium* (Kovar-Eder et al., 1994).

In the East Alpine Region, grassy associations belonged to the forest biome and hydrophilous communities (Bernor et al., 1988). Along with the differentiation of vegetation and an increase in diversity of plant formations on plains, mountain floras started to develop in central Europe from the Middle Miocene (Dorofeev, 1966; Kovar-Eder, 1987).

In the Pannonian, the area of the Central Paratethys was inhabited by warm–temperate mixed mesophytic forests, with deciduous species prevailing over evergreen and coniferous forms (Kovar-Eder, 1987; Bernor et al., 1988). Some areas are also known to host aquatic communities, reed and riparian vegetation, and swampy forests (Kovar-Eder, 1987).

Paleofloristic data suggest the existence of a microclimatic zonality connected with diverse environmental conditions. Such a zonality is recognized for the Zone E (Kovar-Eder, 1987).



**Fig. 2.** Proportions of ruminant families in the Vallesian and Turolian.

### DYNAMICS OF DIVERSITY OF RUMINANTS IN THE EAST ALPINE REGION DURING THE LATE MIOCENE

The analysis of changes in ruminants diversity based on the NOW database (Neogene Old World) revealed the differences between the faunas of central Europe and other regions of Europe (Rössner and Koufos, 2004). According to this analysis, the species diversity of ruminants here was highest in the Middle Miocene and insignificant at the beginning of the Turolian, whereas in western and southeastern Europe, it sharply increased in the Turolian.

New data received through the study of materials from the Kohfidisch locality (lower part of MN11) in Austria (Vislobokova and Daxner-Höck, 2004) improved this scheme (Fig. 2). A considerable decrease in the ruminant diversity in the East Alpine Region was established at the boundary of the Early and Late Vallesian, rather than at the Vallesian–Turolian transition. The latter boundary, on the contrary, has evidence of significant growth in their diversity.

The increase in ruminant diversity in the Early Turolian of Austria corresponds to the general trend in the change of ecosystems of central Eurasia at the boundary of the Vallesian and Turolian.

In Austria, the upper Middle Miocene and the lower Upper Miocene yielded 22 ruminant species belonging to 18 genera and 5 families. The history of ruminants of this interval can be divided into three stages:

**1. Early Vallesian** (MN 9, 11.6–9.7 Ma, Early Pannonian, zones B–E, and F) (Rögl and Daxner-Höck, 1996; Daxner-Höck, 2004).

**Localities:** Gaiselberg, Atzelsdorf, Vösendorf, Inzersdorf, Götzendorf, and Sommerein (Zapfe, 1948; Thenius, 1954, 1956a, 1960).

**List of taxa:** Palaeomerycidae: *Palaeomeryx* sp. and *Orygotherium* sp.; Tragulidae: *Dorcatherium navi*; Cervidae: *Euprox furcatus*, *E. dicranocerus*, *Heteroprox larteti*, *Dicrocerus elegans*, and *Amphiprox anocerus*; Bovidae: *Protragocerus chantrei* and *Miotragocerus pannoniae*.

**Description.** Ruminants are dominated by the muntiacine–paleomericid assemblage. Cervids prevail. Cavicorns are represented by two or three species.

**Remarks.** It is possible that the bovine genus *Tragoportax* (= *Tragocerus*) first appeared in Austria within the same interval. *Tragocerus* sp. was recorded in the Tiefnitzgraben locality (Thenius, 1952).

**2. Late Vallesian** (MN10, 9.7–8.7 Ma, beginning of the Late Pannonian, Zone G) (Rögl and Daxner-Höck, 1996; Daxner-Höck, 2004).

The Late Vallesian ruminant association of Austria is much poorer than the Early Vallesian association.

**Localities:** Nikitisch and, probably, Himberg (Thenius, 1948a, 1956b).

**List of forms:** Cervidae: *Procapreolus loczyi* and, probably, *Cervavitus*.

**Description.** The appearance of the roe genus *Procapreolus* and, probably, the pliocervine genus *Cervavitus*.

**Remarks.** The first occurrence of *Procapreolus* in Austria in the Nikitisch locality is probably dated 9.7 Ma based on the correlation with the boundary of zones F and G (Thenius, 1956b).

*Cervavitus variabilis* is determined in the Himberg Fauna (Thenius, 1948a). Although the exact stratigraphic position of this Pannonian fauna is not known, the presence of *Cervavitus* in the Late Vallesian of Austria is quite plausible. Further eastward, for example, in Moldova (Pokshesty), *Cervavitus* already existed.

**3. Early Turolian** (MN11, 8.7–7.5 Ma).

**Localities:** Kohfidisch, Mönnhof, and Eichkogel (Bachmayer and Zapfe, 1969; Zapfe, 1997; Franzen and Storch, 1999; Vislobokova, 2004; Vislobokova and Daxner-Höck, 2004)

**List of taxa:** Palaeomerycidae: *Orygotherium heinzi*; Giraffidae: Giraffidae gen. indet.; Cervidae: *Micromeryx* sp., *Euprox* sp., *Cervavitus* sp., *Procapreolus* sp., and *P. loczyi*; Bovidae: *Gazella* cf. *pilgrimi*, *?Nisidorcas* sp., *Miotragocerus pannoniae*, *Tragoportax gaudryi*, *Palaeoryx* sp., and *Protoryx* sp.

**Description.** The ruminant association was essentially renewed. About 40% of ruminant species appeared for the first time, including about 70% of cavicorns, a number of archaic species disappeared. The total number of events, first and last occurrences, (i.e., the absolute turnover) is eight. The relative turnover amounts to 33%.

The diversity of palaeomerycids decreased (Fig. 3). The diversity of deer strongly decreased due to the impoverishment of muntiacines. Deer comprise less than one-third of ruminants (about 30%). In comparison with the Early Vallesian, the number of cavicorns nearly doubled and became about 40% of all ruminants. Rodents also show a very high level (25%) of FODs (first occurrence datum) (Daxner-Höck, 2003).

Early roe (*Procapreolus*), the primitive true deer pliocervines (*Cervavitus*), and bovines (*Tragoportax*) became numerous. The caprine genera *Protoryx* and *Palaeoryx* appeared.

## DEVELOPMENT OF ADAPTATIONS IN RUMINANTS AND RECONSTRUCTION OF PALEOENVIRONMENTS

Changes in the tooth crown height (hypsodonty), diet, and dimensions of Neogene Miocene ruminants, along with data on diversity dynamics, have been used successfully for paleoenvironmental reconstructions (Solounias and Dawson-Saunders, 1988; Bonis et al., 1992a, 1992b; Solounias et al., 1999; Fortelius et al., 2003). Changes in these parameters in Late Miocene ruminants of central Europe show both the main tendencies and certain climatic and landscape changes.

According to paleobotanical data and the history of hipparions, the ecosystems of Central Europe in the Late Miocene changed very little (Bernor et al., 1990). The low diversity of Late Miocene hipparions in the region, which is notably lower than in the southwest and southeast of Europe, in opinion of Bernor et al. (1990), indicates rather stable environments. The fact that forest mammal associations dominated is also evidence of stable conditions in the region (Thenius, 1959). The absence of sharp climatic changes at the boundary of the Middle and Late Miocene and at the beginning of the Late Miocene in central Europe obviously contributed to the role of this region as an area of evolution of some mainstream ruminant lineages, in particular, cervids of the *Dicrocerus*–*Cervavitus* lineage and the genus *Procapreolus*.

In the Vienna Basin area, elements of savanna-like faunas appeared later than in the southwest or southeast of Europe (Thenius, 1982). This region basically continued to host deciduous forests, likely, in conditions of less expressed climatic seasonality than in the west and east of the continent (Bernor et al., 1990). However, warm mesophytic forests of this region apparently also continued to be replaced by more thermophilic forests with more diverse biotopes.

Transformations of rodent and ruminant associations show that, in the Vallesian and the Early Turolian, the East Alpine Region experienced certain changes (Daxner-Höck, 2003; Vislobokova, 2004; Vislobokova and Daxner-Höck, 2004). The differentiation of landscapes, the increase in diversity of biotopes contributed to the diversification of morphofunctional adaptations and ecological differentiation of taxa.

Early Vallesian ruminant associations of central Europe prove the existence here of more humid conditions than in the west and east. In particular, hypsodont taxa were absent from these associations.

The data on Early Vallesian ruminants agree with the data on other groups and indicate that Austria was forested and had a rather warm climate. The arboreal association of Petauristidae–Sciuridae–Gliridae–Eomyidae and the presence of the primate *Anapithecus* confirms this inference (Daxner-Höck, 2003).

In the Early Vallesian, different types of forest habitats and wet stations were occupied by tragulids (*Dorcatherium*), diverse muntiacines (*Micromeryx*, *Euprox*,

*Amphiprox*, *Heteroprox*, and *Dicrocerus*), palaeomerycids (*Palaeomeryx* and *Orygotherium*), and brachyodont forms of bovids (*Miotragocerus* and *Protragocerus*). They basically fed on foliage, fruits, and tree branches.

Early Vallesian ruminants were dominated by very small (at most 4 kg), small (from 4 to 14 kg), and medium-sized animals (weighing less than 100 kg, i.e., no larger than a fallow deer). The last group includes *Palaeomeryx*, *Miotragocerus*, and *Protragocerus*.

Modern communities existing in closed conditions typically show a rather high proportion of very small forms, with a body weight ranging from 6 to 14.9 kg (46.2%) (Bonis et al., 1992b).

The decrease observed in ruminant diversity in the Late Vallesian was probably caused by incompleteness of the fossil record, but it may reflect certain real events in the development of faunas of the region. This time shows an increasing role of medium-sized cervids (the early roe *Procapreolus* and pliocervines).

The occurrence in the terminal Vallesian and basal Turolian of less thermophilic species and species adapted to biotopes of sparse forests and ancestors of boreal taxa was connected with a decrease in humidity and increasing seasonality of the climate.

The Late Vallesian record shows a significant transformation of rodent associations, with rodent species demonstrating 38% of LODs (last occurrence datum) and 12% of FODs (Daxner-Höck, 2003).

The onset of the Turolian was characterized by an increase in biotopic diversity, the reduction of abundance and diversity of small pecorans and abundance of medium-sized cervids, and the appearance of new medium-sized bovids and large ruminants. The major role in this renewal was played by evolutionary advanced autochthons and migrants. Central Europe continued to be a refugium for many forest ruminants characteristic of the Vallesian (Franzen and Storch, 1999; Vislobokova, 2004).

The composition of ruminant association from Kohfidisch points to the existence of forest habitats and a tendency to formation of thinner forests (Vislobokova, 2004). In addition to inhabitants of thickly wooded areas (palaeomerycid genus *Orygotherium*; the cervids *Micromeryx*, *Euprox*, and *Procapreolus*; and the bovid genus *Miotragocerus*), the association of Kohfidisch contains a number of bovids adapted to less thickly wooded habitats, such as *Tragoportax gaudryi*, *?Nisidorcas* sp., *Palaeoryx* sp., *Protoryx* sp., and *Gazella* aff. *pilgrimi*.

In contrast to the Vallesian, the Early Turolian showed the appearance of ruminants with a mixed diet that also included grasses.

The majority of ruminants were browsers (giraffids, cervids, and bovids, except for *Palaeoryx* and *Protoryx*). Some Early Turolian autochthonous relicts (*Orygotherium heinzi* and *Micromeryx* sp. nov.) were repre-

sented by species distinguished from their predecessors by the complex structure of cheek teeth showing well-pronounced adaptations to leaf browsing. Representatives of the genus *Tragoportax* were browsers or had mixed dietary adaptations, resembling extant deer from South Asia (Solounias et al., 1999). *Palaeoryx* and *Protoryx* with tooth crowns of medium height, belonged to the group of mixed-feeders with intermediate dietary adaptations, according to the statistical analysis of ruminant chewing characters (Solounias and Dawson-Saunders, 1988). Like many inhabitants of savannas and other open landscapes, they were not adapted to grazing.

The prevalence of species with brachyodont cheek dentitions and a small number of forms with subhypodont teeth and intermediate feeding adaptations confirm that the Early Turolian fauna of the East Alpine Region lived in a rather humid climate. Most likely, though, it was less humid than in the Vallesian.

The leveled frequency of species (without one or two dominants) in Early Turolian faunas indirectly indicates a rather warm and stable climate (Bonis et al., 1992a).

The rather high proportion of small-sized taxa retained in the Early Turolian is typical for closed habitats. However, an increase in the diversity of bovids and a notable increase in the number of medium-sized and large ruminants in conditions of a moderately warm climate indicate the emergence of more open biotopes among mostly forest landscapes. In modern communities of open landscapes, large and small forms prevail, while medium-sized taxa are almost completely absent (Bonis et al., 1992a).

The presence of drier and relatively more open biotopes at the beginning of the Turolian is indicated by the abundance of the cricetine genus *Kowalskia* or the murid genera *Progonomys* and *Parapodemus*, and the presence of the porcupine genus *Hystrix* (Daxner-Höck, 2003).

#### BIOGEOGRAPHICAL CONNECTIONS AND THE BASIC DISPERSIVE EVENTS

Landscape and climatic restructuring in the region, which developed on the background of global changes in the environment and climate in the Vallesian and at the Vallesian–Turolian transition, promoted the speciation of land mammals and led to dispersal of some species from southern and eastern areas to the Central European Province.

The essentially forest biomes of this region also included some more open habitats, which hosted evolutionary advanced autochthons and newcomers mainly from the east and southeast.

The dominant east–west direction of migrations was determined by both biogeographic conditions (expansion of terrestrial biomes, dispersal waves of aridiza-

tion) and an earlier occurrence of some elements of the hipparion fauna in Eastern Europe and the Near East.

The fauna of ruminants of central Europe differs from faunas of other regions of Europe in the diversity dynamics and the level of hypsodonty (Rössner and Koufos, 2004).

The distribution of hypsodonty values in the Late Miocene on the map of Eurasia in many respects resembles a modern distribution based on precipitation rather than temperature (Fortelius et al., 2003). The modern precipitation pattern was essentially formed in the Late Miocene after the main phase of uplift of the Himalayas and the Tibetan Plateau at about 10 Ma. This event strongly influenced the intra-Vallesian crisis (see Fortelius et al., 2003), which, as in other regions (Agusti et al., 2001), was expressed in a notable reduction of Middle Miocene and Early Vallesian ruminant taxa.

The East Alpine Region, with a rather low index of hypsodonty, is bordered in the south and east by the areas with higher indices and, hence, a drier climate. The decline of humidity in the East Alpine Region in the terminal Vallesian and at the Vallesian–Turolian transition promoted the penetration into this region of animals that previously lived to the south and east of it.

In the western and eastern Mediterranean, the initial differentiation of hipparions was associated with more expressed changes in plant communities than in Central Europe (Bernor et al., 1990). Savanna-like landscapes and ungulates characteristic of semi-open and open spaces appeared there earlier. In the areas with even smaller level of precipitation, in particular, in Central Asia, elements of the hipparion fauna established adaptations to open landscapes more rapidly than in Europe. Moreover, the reorganization of the Middle Miocene assemblages that produced the hipparion fauna most likely took place earlier than in the Paratethys belt (Gabunia, 1985).

Judging from the scheme proposed by Nevevskaya et al. (2003), in the region of the Eastern Paratethys, the Early Vallesian corresponds to a part of the Middle Sarmatian *sensu lato* (Bessarabian) and the beginning of the Late Sarmatian (Khersonian), while the Late Vallesian is correlated with the end of the Late Sarmatian (Mitridatian time) and the beginning of the Maeotian.

As early as the end of the Late Sarmatian *sensu lato* (Berislav, Sevastopol) and at the beginning of the Maeotian (Grebeniki), open areas overgrown by grassy vegetation expanded over most of the continental margin of the Eastern Paratethys (Gabunia and Chochieva, 1982). At the beginning of this stage, though, some regions (Moldova) retained a combination of forested and forestless landscapes, while some areas (Georgia) were still dominated by forest communities (Gabunia and Chochieva, 1982).

The East European Province showed a high rate of evolutionary development and a significant ecological differentiation (Lungu, 1990). The first elements of the hipparion fauna appeared there at approximately the

same time as in central Europe. The immigration of hipparion corresponds to the Middle Sarmatian *sensu lato* (Novomoskovsk beds of the Bessarabian) (Lungu, 1990), which is correlated with the basal Pannonian.

The earliest Middle Sarmatian hipparion faunas are known from Kalfa, Buzhor 1 (Moldova), and Gritzev (Ukraine). They are similar in composition to the Early Vallesian fauna of Central Europe. Kalfa and Buzhor 1 most likely correspond to the Subchron C5r.2n. E.A. Vangengeim (personal communication) proposed that these faunas were older and could have belonged to Subchron 5An.1n. Normally magnetized deposits of these localities were earlier correlated with Epoch 11 (= Subchron 5An.1n) (Pevzner and Vangengeim, 1984, 2000; Pevzner et al., 1987; Vangengeim and Pevzner, 1993). Kalfa and Buzhor 1 yielded *Lagomeryx flerovi*, *Euprox aff. furcatus*, and *Miotragocerus pannoniae* (Pevzner et al., 1987). In Gritzev, *Hippotherium primigenium* coexisted with *Anchitherium*, dicrocerines, lagomerycines, and *Miotragocerus (Dystychoceras sp.)* (Korotkevich, 1988). Reverse magnetized deposits of this site are correlated with Epoch 10 (Korotkevich, 1988), i.e., Chron C5r.

A decrease in humidity and a change in the temperature regime in the region at the boundary of the Middle and Late Sarmatian, apparently, about 10 Ma resulted in the disappearance of many Middle Miocene taxa and appearance of new elements characteristic of warmer temperate forests and semi-open landscapes. Middle Sarmatian faunas from Varnitsa (Moldova) and Sevastopol (Ukraine), which correspond to the second half of the Early Vallesian, show an increase in the number of cavicorns and the appearance of *Palaeotragus (Achtaria)*. The currently accepted boundary between the Middle and Late Sarmatian, which is dated as 11.2 Ma, makes these events considerably older.

The faunas from Berislav (Ukraine) and Poksheshty (Moldova), which are correlated with the Late Vallesian, according to Vangengeim and Pevzner (1993), correspond to Epoch 9 or Chron C5n. At that time, the region was inhabited by *Cervavitus*, *Procapreolus*, *Graecoryx*, and *Gazella* along with diverse hipparions, including *Hipparion verae*, which is typical of rather dry habitats (Korotkevich, 1988). The proportion of savanna–steppe species of ungulates grows from 10–20% at the beginning of the Early Vallesian (Gritzev and Kalfa) to about 50% at the end of the Early Vallesian (in the fauna of Sevastopol) and in the Late Vallesian (Berislav) (Korotkevich, 1988, text-fig. 40).

At the beginning of the Turolian (MN11), the southwestern and southeastern areas of Europe show a wide spread of animals adapted to open landscapes, including large ungulates and carnivores. The Early Turolian fauna of Grebeniki in Ukraine, however, still retains numerous inhabitants of forest biotopes, the proportion of savanna–steppe species amounts to not less than 50% (Korotkevich, 1988). The first appearance of *Tragocerus frolovi*, *Protragelaphus skouzeri*, and

*Palaeoryx majori* is recorded (Korotkevich, 1988). These taxa probably migrated from the eastern Mediterranean (northern part of the Greek–Iranian Province), a migration route of many ungulates.

In Macedonia (Greece), faunas of the Late Vallesian (Ravin de la Pluie) and Turolian (Ravin de Zouaves, Vathylakkos, and Proochoma) existed in conditions of more open landscapes than the Middle and Late Turolian faunas (Pikermi, Dytiko) (Bonis et al., 1992a). In the former, one or two species of ungulate typically prevail, whereas of the Middle and Late Turolian faunas show a more balanced species composition (Bonis et al., 1992a). Early Turolian faunas included a very high proportion of artiodactyls (65.6% in Ravin de Zouaves 5); cavicorns composed more than 58%, while tragulids and cervids were absent (Bonis et al., 1992a). The more diverse Pikermian megafauna of the Mediterranean inhabited the biome of evergreen and broad-leaved deciduous forests (Solounias and Dawson-Saunders, 1988).

The savanna–steppe landscapes of the southern Greek–Iranian Province were a center of speciation for many cavicorns (Dmitrieva, 1977; Lungu, 1990). *Gazella* and *Protoryx* are also believed to have emerged in this region (Köhler, 1987).

*Gazella* from Sinap (Loc. 22), Turkey, is dated 10.08 Ma (Koufos, 2003). In Greece, the first gazelles most likely appeared in MN10 (Nikiti 1 and Pentolophos 1) along with *Protoryx* and, probably, *Palaeoryx* (Bonis and Koufos, 1999; Koufos, 2003). At approximately the same time, gazelles penetrated into the East European Province, where they coexisted with *Procapreolus* and *Cervavitus*. There are no records of *Protoryx* in Eastern Europe, and the first occurrence of *Palaeoryx* is dated MN11 (Grebeniki, Novaya Emetovka 1) (Korotkevich, 1988; Krakhmal'naya, 1996).

The bovids *Gazella* aff. *pilgrimi*, *?Nisidorcas*, *Tragoportax gaudryi*, *Protoryx*, and *Palaeoryx* apparently migrated to central Europe from the Greek–Iranian Province at the Vallesian–Turolian transition.

Outside of this province, *Nisidorcas* is only known from Piram Island (India). This genus penetrated into the eastern Mediterranean at the beginning of the Turolian (Koufos, 2003). The distribution of *Gazella pilgrimi* is restricted to Zone MN11.

The cosmopolitan *Tragoportax gaudryi* existed in faunas of the Late Vallesian and Turolian from Spain to Iran, with its earliest remains found in Turkey. The age of *T. gaudryi* in Sinap (Loc. 108) is about 10.135 Ma (Koufos, 2003). The first occurrence of this species in Europe is recognized in later faunas (younger than 9 Ma), such as Nikiti 1 (Greece) and Piera (Spain), which correspond to either the end of MN10 (Bonis and Koufos, 1999) or MN11 (Gentry et al., 1999; Gentry, 2003). This species occurred in the Early Turolian in association with *Nisidorcas*, *Protoryx*, and *Palaeoryx* in the Greek–Iranian Province only (Kayadibi, Turkey) (Köhler, 1987).

A close geographical position of Kohfidisch to the northern boundary of the province explains the migration of this association to central Europe during the succeeding period of global cooling and drop in the World Ocean level.

## CONCLUSIONS

The absence of sharp climatic changes at the boundary of the Middle and Late Miocene and at the beginning of the Late Miocene in central Europe apparently included this region in the area of evolutionary development of a number of the major lineages of ruminants, particularly, cervids of the phyletic line *Dicrocerus–Cervavitus* and the genus *Procapreolus*. In addition, central Europe remained a refugium for some Middle Miocene endemic taxa.

At the beginning of the Late Miocene, environmental changes in Vienna and Pannonian basins created new conditions for the development of mammalian communities and faunistic exchanges.

The development of the hipparion fauna in this region was accompanied by essential changes in ruminant associations. These changes were associated with migrations, and proceeded against a background of relatively slow evolutionary transformation of hipparions and autochthonous ruminants. The main events in the history of ruminants of the region were synchronous with changes in rodent associations established by G. Daxner-Höck (2003) and corresponded to global events.

Judging from the data on ruminants, the most drastic landscape and climatic reorganizations within the interval of 12–8.5 Ma are recognized at the Vallesian–Turolian transition, between zones MN10 and MN11, at about 8.7 Ma. This is evidenced by the considerable transformation of ruminant communities, their increased biodiversity due to the renewal of generic and species composition and diversification of dietary strategies. The intra-Vallesian crisis at the MN9–MN10 boundary at about 10 Ma is expressed in the region discussed by the first appearance of two cervid genera (*Procapreolus* and, probably, *Cervavitus*) characteristic of the Late Miocene and Pliocene.

About 8.7 Ma, several cavicorn taxa from the Greek–Iranian Province (*Gazella* aff. *pilgrimi*, *?Nisidorcas*, *Tragoportax gaudryi*, *Protoryx*, and *Palaeoryx*) dispersed to the East Alpine Region. These taxa coexisted there with a number of Middle Miocene autochthons (*Orygotherium*, *Dorcatherium naui*, *Micromeryx*, *Euprox*, *Amphiprox anocerus*, and *Miotragocerus pannoniae*).

The increase in diversity of the Early Turolian ruminants in the East Alpine Region corresponds to a general trend in the transformation of ecosystems of central Eurasia during the Vallesian–Turolian transition. Substantial changes in communities of phytophagous mammal and the appearance of less thermophilic species, species adapted to light forests, and of the ancestors of boreal species, were caused by decreasing humidity and increasing climatic seasonality.

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