

## **Mammalian events in the Quaternary of Romania and correlations with the climatic chronology of Western Europe**

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**Abstract.** The succession of micromammalian faunas of the Quaternary of Romania is presented, and the main evolutionary and dispersal events within the phyletic lineages of arvicolids noted. The climate induced extinction phases of certain lineages and the renewal phases of the local mammalian communities by the influx of numerous immigrants, most often originating in Eastern Europe and more seldom in the oriental Mediterranean basin, are shown. Complementary data concerning large mammals are also considered, to more precisely establish the chronological and climatic framework in which the bioevents referred to occurred. The paper is accompanied by a biostratigraphic sketch of the Quaternary of Romania, mainly based on the information supplied by rodents, where the established correlations on a continental scale are outlined.

**Key words:** Quaternary, Pleistocene, Romania, Mammalia, Rodents, Arvicolids, climate, bioevent, evolution.

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### I. INTRODUCTION

The climate of the Quaternary, characterized by the rhythmic alternation of glacial and interglacial conditions, brought about fundamental environmental changes, thus influencing the whole of biological evolution.

In the case of mammals, the repeated changes in the climate and landscape led to large displacements of steppe and arctic species, as well as of thermophilous and temperate ones, resulting in the disappearance of the geographical biozonation at the end of the Pliocene, important changes in the composition of regional communities following the extinction of several taxa, and the speeding up of evolutionary processes within different lineages in their continual effort to set up an equilibrium with the fluctuating environment. In this paper, we shall follow the course of these biological events in the Quaternary faunas of Romania, especially those affecting the rodents.

Before presenting the data we must note that most of the documentation concerning the lower half of the Quaternary comes from Betfia, which on the limited area of about 1.5 square kilometers includes a succession of faunas covering the whole Eburonian-Cromerian interval. This privileged circumstance has given us, on the one hand, the certainty that the recorded biological phenomena have a real chronostratigraphical value and are not the result of local environmental fluctuations, and, on the other hand, it has enabled us to follow the evolutionary changes which took place within certain lineages of a high stratigraphic importance over a time span of about one million years.

In this context it is noteworthy, that owing to Romania's position at the crossroads of east European, boreal and Mediterranean influences, knowledge of the faunas of this area is indispensable for obtaining a broad insight into the dynamics of mammal faunas in the Quaternary.

## II. EVOLUTIONARY AND DISPERSAL EVENTS AMONG ARVICOLIDS DURING THE PLEISTOCENE

### Lower Pleistocene

It is commonly agreed that the beginning of the Quaternary in the continental deposits of the Holarctic region is marked by the appearance of the genus *Microtus*.

The oldest fauna in Romania where this event is seen comes from Betfia-XIII (Fig. 1, Table I). Here, *Microtus*, represented by its earliest form, *Microtus pliocaenicus deucalion*, is associated with another arhizodont arvicolid originating from eastern Europe, *Lagurus arankae*, and also with several Villanyian survivors such as *Prospalax priscus*, *Epimeriones dacicus*, *Villanyia exilis*, *Mimomys tornensis*, *Ungaromys*, etc. (TERZEA 1973c, 1978, 1984). The expansion of these two arvicolids (*Microtus pliocaenicus* as far as France and *Lagurus arankae* up to Central Europe) was certainly favoured by the climatic deterioration at the beginning of the Eburonian, a deterioration which also led to the extinction, or the extreme rarefying, of certain thermophilous forms that inhabited our regions during the Late Pliocene, such as *Manis*, *Paradolichopithecus arvernensis*, *Pliotragus ardeus*, *Gazellospira torticornis*, and *Mitilanotherium inexpectatum* (BOLOMEY 1965a, 1965b, 1983; RADULESCO & SAMSON 1991). The important change in the composition of the local fauna shows the amplitude of the climatic deterioration at the beginning of the Quaternary.

It is noteworthy that the fauna of Betfia-XIII, containing *Macaca sylvana* cf. *florentina* and where the Gliridae, Muridae and Castoridae (especially *Trogontherium*) are a significant component, is subsequent to the first Eburonian cooling, probably corresponding to a warming phase in the middle of this glacial complex (TERZEA 1984; TERZEA & JURCSÁK 1976). The beginning of the Pleistocene has been identified in the Vallachian Depression, namely in the faunas of Draganesti-Olt, Izvoru and Irimesti, which, even though lacking arhizodont arvicolids, contain other steppe immigrants, such as *Citellus primigenius*, *Allactaga* sp. and *Megalovis latifrons*, alongside species of *Mimomys* which are evolutionarily close to the species of Betfia-XIII (FERU et al., 1978, 1979; RADULESCO & SAMSON 1983, 1991).

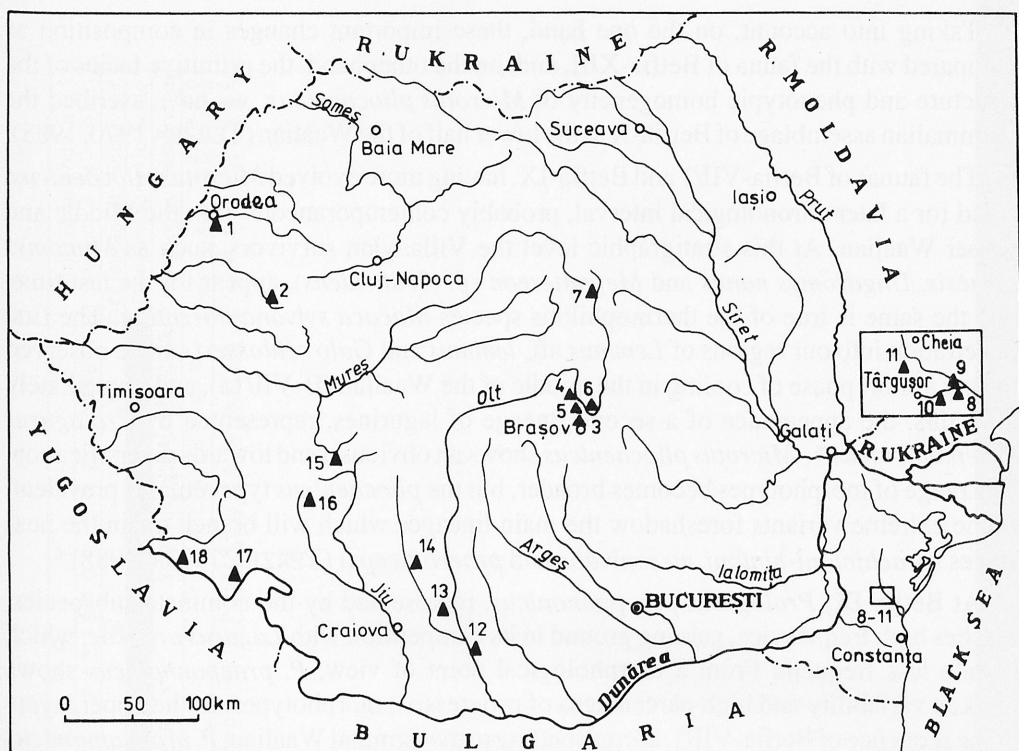


Fig. 1. Location of Quaternary sites of Romania given in Table 1: 1. Betfia V-XIII (code B), village Betfia, near Oradea; 2. Chiscau-1 (Ch-1), Pietroasa, county Bihor; 3. Brasov-Dealul Sprengiului (Gesprengberg) (Br.); 4. Rotbav-Dealul Tiganilor, levels 2-3 (RDT 2-3), Feldioara, county Brasov; 5. Feldioara-Cariera, level 2 (FC 2), county Brasov; 6. Ariusd-Drum (ArD), Vâlcele, county Covasna; 7. Sândomic 1-2 (SD 1-2), county Harghita; 8. Pestera Gura Dobrogei (GD), Târgusor, county Constanta; 9. Pestera Casian (Cas), Târgusor, county Constanta; 10. Pestera "La Adam", Târgusor, county Constanta; 11. Pestera Bursucilor (PB), Târgusor, county Constanta; 12. Draganesti Olt (DO), county Olt; 13. Izvoru (Iz), Ganeasa, county Olt; 14. Irimesti (Ir) and Tetoiu (T), county Vâlcea; 15. Pestera Ohaba-Ponor (OP), Pui, county Hunedoara; 16. Pestera Cioarei (PCI), at Borosteni, county Gorj; 17. Pestera lui Climente 1 (PC1), at Dubova, county Mehedinti; 18. Pestera Livadita (PL), near Pescari, county Caras-Severin.

All these Eburonian faunas of Romania lack *Mimomys ostramosensis*, a species common in contemporary mammalian assemblages of Central and Western Europe (Kolinany 3, FEJFAR & HORACEK 1983; Kadzielnia, KOWALSKI & NADACHOWSKI 1990; Montoussé 5, CHALINE 1986).

The second important biological event, the appearance of *Microtus p. pliocaenicus*, is recorded at Betfia-X, a site where the fauna shows a significant renewal. Here, most of the species of Villanyian origin are absent, with the exception of *Ungaromys nanus* and *Mimomys tornensis*, which even show a certain increase in frequency. The archaic genus *Prospalax* is replaced by *Spalax*, *Glis minor* by *Glis sackdillingensis*, and the first occurrence of *Cricetus cricetus nanus* in the region is recorded (TERZEA & JURCSÁK 1967, 1968). *Lagurus arankae*, the most frequent species in the mammalian assemblage, shows only primitive morphotypes.

Taking into account, on the one hand, these important changes in composition as compared with the fauna of Betfia-XIII, and, on the other hand, the primitive facies of the structure and phenotypic homogeneity of *Microtus pliocaenicus*, we have ascribed the mammalian assemblage of Betfia-X to the lower half of the Waalian (TERZEA 1970, 1988).

The faunas of Betfia-VII/1 and Betfia-IX, having more evolved *Microtus pliocaenicus*, stand for a later chronological interval, probably contemporaneous with the Middle and Upper Waalian. At this stratigraphic level the Villanyian survivors, such as *Mimomys tornesis*, *Ungaromys nanus* and *Megantereon* sp. (?*cultridens*), appear for the last time, and the same is true of the thermophilous species *Macaca sylvana florentina*. The first penetration into our regions of *Lemmus* aff. *lemmus* and *Gulo schlosseri* can be observed during a short phase of cooling in the middle of the Waalian (B-VII/1a), and immediately after this, the appearance of a second lineage of lagurines, represented by *Prolagurus praepannonicus*\*. *Microtus pliocaenicus* shows an obvious trend towards diversification. The range of morphotypes becomes broader, but the *pliocaenicus* type remains prevalent. Some extreme variants foreshadow the main lineages which will branch off in the next stages (*praehintoni-hintoni*, *mesonivalis* and *praeratticeps*) (TERZEA 1973a, 1988).

At Betfia-IX, *Prolagurus praepannonicus*, represented by the nominate subspecies, reaches high frequencies, gaining ground in its competition with *Lagurus arankae*, which is here less frequent. From a morphological point of view, *P. praepannonicus* shows marked variability and high percentages of progressive morphotypes. In the upper layers of the sequence of Betfia-VII/1, corresponding to the terminal Waalian, *P. praepannonicus* is already replaced by its successor, *P. pannonicus*.

The question arises if this last species differentiated in our regions or if we are dealing with a more evolved population, probably coming from the east. Taking into account both the occurrence, at about the same time, on Romania's territory of other newcomers (*Soergelia* cf. *elisabetae*, *Equus* cf. *suessenbornensis*, etc., at Tetoiu 3; RADULESCO & SAMSON 1991) and the presence of *P. pannonicus* in an earlier phase of the Waalian in Central Europe (Deutsch-Altenburg 2C1; RABEDER 1981), we are inclined to consider it as an immigrant. This interpretation is supported by the fact, that towards the end of the Waalian/?beginning of the Menapian, *Prolagurus pannonicus* already had a wide European distribution, reaching northeastern Spain, as is seen in the presence of its remains at Bagur-2 (province of Gerona), where it occurs in association with evolved *Microtus pliocaenicus* (LOPEZ et al., 1976). Its strong expansion to the west – more or less synchronic with the penetration into Spain of certain Ovibovines (*Soergelia minor*, *Praeovibos* sp., at Venta Micena; AGUSTI & MOYA-SOLA 1991) having affinities with the Asian forms of this group – seems to have been favoured by increased aridity during this

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\*Surely, the differentiation of *Prolagurus praepannonicus* from *Borsodia newtoni* (*B. hungarica*) took place much earlier than the appearance of this species at Betfia. The most primitive form of this taxon, *Prolagurus p. primaevus*, has been identified by TOPACHEVSKY (1973) in the upper layer of Kryzhanovka (the stratotype of the Odessan faunistic complex) and in the early Tamaian deposits of Jevakhova Gora and of Tiligul. It is possible that the remains on which *Prolagurus praepannonicus* was reported in Central Europe from the beginning of the Pleistocene (Kolinany 1 and Vcelare 3B/1; FEJFAR & HORACEK 1983) and in the Middle East towards 1.4 My (Ubeidiya; v. KOENIGSWALD et al., 1992), belong to the same primitive subspecies.)



epoch. Among the newcomers, mention should also be made of *Cricetus c. praeglacialis* and *Canis ?mosbachensis*.

In summary of the above, it can be said that the faunas of Betfia-VII/1 and Betfia-IX (with which the "Zone *Microtus pliocaenicus*" ends) show, on the one hand, the end of the process of extinction of the Villanyian species under the influence of the fluctuating climate, and, on the other hand, they announce the evolutionary changes that gain in amplitude in the following stages.

Thus, the fauna of Betfia-V, attributed by us to the Upper Menapian on the basis of the degree of evolution of arvicolids, is characterized by a marked renewal, due to the occurrence of a new wave of immigrants – especially large mammals (*Cynalopex praecorsac*, *Homotherium moravicum*, *Capreolus süssenbornensis*, *Praealces latifrons*, *Bison schoetensacki*, *Praemegaceros*, etc.) – and the acceleration of evolutionary processes in different lineages of rodents (KRETZOI 1941, 1965; TERZEA & JURCSÁK 1968).

Let us recall the most important of these evolutionary events.

1. Within the genus *Microtus* the first cladogenesis takes place, giving rise to *Microtus hintoni* (which combines the allophaiomyian, *praehintoni* and *hintoni* morphotypes) and to *M. burgondiae* (which groups a few nivalid and ratticepid morphotypes).

2. As a consequence of the trend towards polyisomery, the lineage *Lagurus arankae* - *L. lagurus* resulted in the development of *Lagurus transylvanicus*, which is a marker for the Upper Menapian and Bavelian.

3. As far as *Mimomys* is concerned, the first occurrence of *Mimomys savini* is reported, as well as the differentiation of a more evolved subspecies of *Mimomys pusillus* – *M. pusillus blanci*.

In all lineages of arvicolids the trend towards the increase in hypsodonty and the stressing of the structural complexity of the cheek-teeth becomes more manifest.

In the following stage, represented by the faunas of Chiscău-1 and Betfia-VII/3, and correlated with the Bavelian, the rate of evolution is increased, especially within the genus *Microtus* (TERZEA 1989, 1992). Successive speciations, in a quite short time interval, resulted in the differentiation of most of the Middle Pleistocene species. But it is almost impossible, at our present stage of knowledge, to point to the exact timing of these speciations and consequently to find a correlation with climatic evolution as established from palynological and isotopic data (cf. ZAGWIJN 1985).

As a hypothesis, we have suggested that a first speciation took place in the fauna of Chiscău-1, and therefore at the beginning of Bavelian, resulting in the separation of *Microtus nivalinus* from *M. ratticepoides*, starting from *M. burgondiae*.

It is a fact, that at Betfia-VII/3a, which might be placed in the Bavel interglacial, as shown by the presence of certain Mediterranean immigrants (*Apodemus mystacinus* and *Hystrix*) and the evolutionary level of the arvicolids, *Microtus (Terricola) arvalidens* and *M. (Chionomys) nivalinus* are already individualized; this allows us to suppose that a second speciation took place in the interval circumscribed by these two faunas, leading to the separation of the arvaloid and gregaloid forms, starting from *Microtus hintoni*. At Betfia-VII/3b, which dates from a colder phase (expansion of *Lemmus lemmus* and *Gulo*

*schlosseri* as far as Betfia), probably contemporary with the Linge glaciation, *Microtus* (*Stenocranius*) *gregaloides* and *M. (Microtus) nivaloides* have been reported. (We consider *Microtus nivaloides* FORSYTH MAJOR a synonym of *M. arvalinus* HINTON.) On the other hand, KOLFSCHOTEN (1990) mentions *Microtus arvalis* as present in the Netherlands (based on only one M<sub>1</sub>, it is true) since the end of Bavel interglacial, a fact showing that all these biological events occurred in quite a short time span.

As far as the Lagurines are concerned we note:

1. The important development of *Lagurus transylvanicus* during the first half of the Bavelian and the occurrence of certain progressive morphotypes (*praetransiens* and *transiens*) at ever higher percentages at Betfia-VII/3b and Betfia-VII/3c, the *transylvanicus* morphotype remaining prevalent.

2. The disappearance from our area of *Prolagurus pannonicus*, in a phase that might be placed towards the middle of the Bavel interglacial, probably because of competition from its contemporary, *Lagurus transylvanicus*. It was preserved in Eastern Europe and in southwestern Siberia till the Tiraspolian (Cromerian), giving rise, by gradual evolution, to *Prolagurus posterius*, the final form of this lineage, which left no successors (ZAZHIGIN 1980).

In the case of *Mimomys*, we find that *M. pusillus* becomes increasingly rare and dies out towards the end of the Lower Pleistocene, concomitantly with the ever more frequent occurrence of *Mimomys savini*.

### Middle Pleistocene

During the Cromerian Complex – a stage represented by the sites of Betfia-VII/4, Brasov, Rotbav-Dealul Tiganilor, Feldioara-Carieră, Gura Dobrogei-4, and Casian – a visible modernisation of the mammalian fauna took place through the replacement of most of the species characteristic of the Lower Pleistocene by taxa that survive today or that are the direct ancestors of the present-day ones.

The renewal of the fauna is evident from the beginning of this interval in the presence of *Microtus agrestis*, *Ursus deningeri* and *Mammuthus trogontherii* during a severe climatic fluctuation, correlated by us with the Glacial A of the Cromerian Complex. This phase of climatic deterioration was also marked by the last expansion of *Lemmus* over Romania's territory (B-VII/4a; TERZEA 1972b) (It is noteworthy that in the later stages of the Pleistocene, when the continental character of the climate becomes more marked, *Lemmus* no longer reached Romania in its migrations across temperate Europe.).

*Mimomys savini*, the marker of the Late Biharian, shows high frequencies at the beginning of this interval (B-VII/4a), but its importance diminishes in subsequent phases (B-VII/4b+c; GD-4; TERZEA 1992; RADULESCO & SAMSON 1986). Its latest appearance in our regions goes back to a phase of continental climate, which could be a chronological equivalent of the Glacial B of the Cromerian Complex of the Netherlands (B-VII/4c, GD-4) (In other regions of Eurasia this species persists as late as the Glacial C of the Cromerian, when the Biharian stage comes to an end [sensu FEJFAR & HEINRICH 1987]). In the same period we note the development of *Lagurus transiens* by phyletic evolution from *L. transylvanicus* (B-VII/4c; TERZEA 1992), and the spread into the southeast of Romania, together with a new lineage of lagurines represented by *Eolagurus gromovi*, of

a population of *Microtus* of east-European origin; designated *Microtus* ex gr. *hyperboreus-middendorffi*, it shows a degree of evolution higher than that of local populations (GD-4; RADULESCO & SAMSON 1986). This invasion by eastern and northern forms, in consequence of the widespread expansion of open land biotopes, also affected Central Europe, where a new wave of Ovibovines (*Praeovibos priscus* at Koneprusy; *Soergelia elisabetae* and *Ovibos moschatus* at Süßenborn), accompanied by *Rangifer arcticus*, is noticed.

The first appearance of *Arvicola cantiana*, identified in the faunas of Brasov (KORMOS 1933) and Rotbav-Dealul Tiganilor 2 (RADULESCO & SAMSON 1985), took place in a temperate phase (as shown by presence of *Hystrix*, *Glis glis*, *Mus musculus* and *Parapodemus coronensis*), contemporaneous with Cromerian IV. Towards the end of this phase – with which the Toringian begins – one also records the last occurrence of *Pliomys episcopalis*, a common element of the *Mimomys* faunas.

During the Elsterian, several east European (*Ellobius* cf. *palaeotalpinus*, *Microtus gregalis*, *Saiga*) and Aegean species (*Allactaga orghidani*, *Mesocricetus newtoni*, *Microtus guentheri*) spread across Romania's territory, pointing to an increase in continental influences on the climate (GD 1 and GD 2; SAMSON & RADULESCO 1972; PAUNESCO et al., 1982). And while some of these immigrants have become integrated into the local fauna and keep occurring in eastern Romania till the end of the Pleistocene (the genera *Lagurus* and *Eolagurus*), or even in the Recent (*Mesocricetus newtoni*), *Allactaga orghidani* and *Ellobius* seem to be limited to this chronological interval.

In the subsequent stages of the Middle Pleistocene, represented by the sites of Sândominic 1-2, Ariusd-Drum and "La Adam" (lower sequence of layers), evolutionary events are less numerous. Among the most significant mention should be made of:

1. The development of *Arvicola terrestris* and *Microtus (Terricola) subterraneus*, towards the end of the Holsteinian, and the last appearance, at the same time, of *Allocrietus bursae* and *Pliomys lenki* (Sândominic 1; RADULESCO & SAMSON 1985). According to CHALINE (in BARTOLOMEI et al., 1975) the latter species persisted in southwestern Europe till the early Weichselian (site of Lezetxiki, Spain).

2. The immigration, during an interstadial of the early Saalian, of the Asian genus *Rattus*, represented in our area by *Rattus dobrogicus*, and of *Allactaga major*, towards the end of this glacial complex (Cave "La Adam"; TERZEA 1972a, 1973b).

3. The occurrence of the species *Eolagurus luteus* and *Lagurus lagurus* at the beginning of the Saalian (Cave "La Adam", TERZEA 1970, 1972a).

Concerning this last event, we may add that the differentiation of the two modern species of lagurines took place a long time before their first occurrence in Romania. *Eolagurus luteus* must have evolved on the East European and Siberian steppes at the beginning of the Holsteinian. The most primitive chromomorph – *Eolagurus luteus volgensis* - is reported from the Gunki faunistic complex in the southern part of the Russian Plain, associated with *Arvicola cantiana* (Likhvin interglacial; MARKOVA 1990), and in chronologically equivalent faunas from western Siberia (ZAZHIGIN 1980). As for *Lagurus lagurus*, it occurred for the first time in western Siberia, in the faunas of Tatarka and Kalmanka, which include a primitive species of *Arvicola* (*A. kalmankensis*) and correspond to the Holsteinian (ZAZHIGIN 1980). During the second half(?) of this interglacial,



the species had already spread as far as the Aegean area (Chios Island, Latomi-1; STORCH 1975) and, towards the west, up to Hungary (Nagyharsányhegy 6; JÁNOSSY 1986). Being a better disperser than *Eolagurus luteus*, whose European range seems never to have exceeded the east of Romania, *Lagurus lagurus* spread, during the continental cold phase ending the Saalian, over all of temperate Europe, to southwestern England (Tornewton Cave; KOWALSKI 1967), and again in the early Weichselian as far as Belgium (CORDY 1988) and southwestern France (CHALINE 1972). These wide migrations, more or less synchronous with the expansion of *Allactaga major* in Central Europe and *Saiga tatarica* as far as the Dordogne (in the Late Saalian), were certainly climatically induced.

### Upper Pleistocene

During this subdivision of the Quaternary, very well represented in the numerous caves of Romania (e. g., Pestera Cioarei, Pestera Climente 1, Pestera "La Adam" – upper layers), evolutionary processes are of minor importance and the renewal of the local fauna by immigration is moderate. Among the newcomers we may note *Hystrix vinogradovi*, *Spalax microphthalmus*, *Sicista betulina*, *Citellus suslicus*, *Gulo gulo*, *Equus scyiticus*, *E. transylvanicus*, etc. (TERZEA 1972a, 1987; SAMSON 1975).

The most characteristic biological phenomenon of this interval is the alternation of two faunistic complexes with different climatic exigencies: one temperate, with some thermophilous species (*Hystrix vinogradovi*, *Rattus* sp., *Castor fiber*, *Microtus (T.) subterraneus*, *Apodemus sylvaticus*, *Panthera pardus*, *Capreolus capreolus*, *Sus scrofa*, etc.) and the other continental-cold, made up mostly of steppe species, with some cryophilous elements (*Allactaga major*, *Microtus gregalis*, *M. oeconomus*, *M. nivalis*, *Lagurus lagurus*, *Eolagurus luteus*, *Ochotona pusilla*, *Lepus timidus*, *Alopex lagopus*, *Rangifer tarandus*, *Saiga tatarica*, *Rupicapra rupicapra*, *Capra ibex*, *Coelodonta antiquitatis*, *Mammuthus primigenius*, etc.). Their displacements mark climatic fluctuations with an ever closer periodicity towards the end of the Weichselian.

This chapter should not end without taking note of the great faunistic change which occurred in the terminal Pleistocene following numerous extinctions among the large mammals, and the withdrawal from our area of all arctic forms and most of the steppe species (*Allactaga major*, *Marmota bobak*, *Citellus suslicus*, *Microtus gregalis*, Lagurines, *Ochotona pusilla*, etc.). These processes were completed by the end of Dryas II.

### III. FINAL REMARKS

The first important change in the composition of mammalian assemblages in our area occurs at the beginning of the Quaternary under the influence of the Eburonian cooling. The *Microtus pliocaenicus* dispersal event, characterizing the first part of the Lower Pleistocene, coincides, on the one hand, with the extinction of numerous thermophilous species which were present in Romania during the Late Pliocene, and, on the other hand, with the arrival of a number of immigrants, inhabitants of open landscapes [*Allactaga* sp., *Citellus primigenius*, *Allocricetus bursae*, *Lagurus arankae*, *Canis* cf. *falconeri*, *Equus stenonis* cf. *senezensis*, and *Megalovis latifrons*, in the first wave (sites: Draganesti-Olt, Izvoru, Irimesti, Betfia-XIII), and *Spalax* sp., *Cricetus cricetus*, *Prolagurus praepannoni-*

*cus*, *P. pannonicus*, *Lemmus*, and *Gulo schlosseri*, somewhat later (sites: Betfia-X, B-IX, B-VII/1)].

Judging by the composition of faunas, the climate of this interval of the Lower Pleistocene was characterized by an alternation of temperate phases of a slightly continental type, with others that were much cooler and probably much drier.

An equally impressive renewal of the local fauna takes place during the second half of the Lower Pleistocene, in the Menapian, when we see a new wave of immigrants, mainly large mammals, and an acceleration of evolutionary processes within different lineages of rodents (site of Betfia-V). It is in this interval that the cladogenesis of the genus *Microtus* begins and that the differentiation of *Lagurus transylvanicus* and the occurrence of *Mimomys savini* and *M. pusillus blanci* are reported. In the Bavelian, less sizable immigrations took place (*Apodemus mystacinus* and *Hystrix*, alternating with *Lemmus lemmus*), marking the climatic fluctuations (sites: Chiscău-1 and B-VII/3).

The paleontological data suggest that the climate was continental in the Menapian, warm and dry during the lower half of the Bavelian, and temperate with a suppressed continental character in the upper half. A short interval of cool and wet weather, marked by the reimmigration of *Lemmus*, was interposed between the two mild fluctuations, which covered the greatest part of the Bavelian.

During the Middle Pleistocene we note the extinction of all characteristic species of the *Mimomys* faunas and their replacement by more evolved forms, some of which have been preserved to the present. One of the most important evolutionary events of this interval is the replacement of *Mimomys savini* by its presumed descendant, *Arvicola cantiana*; this marks the beginning of the Toringian.

We shall not discuss on the bioevents which characterize the different stages of this interval since they have been mentioned earlier. Let us point out only some aspects concerning the climate and its impact on the biota.

1. Beginning with the second half of the Cromerian, the climate of our regions becomes more and more severe in the sense that during the cold stages a progressive decrease in temperature and humidity is recorded. This emphasis of continental influences and of cooling brought about a strong expansion of open biotopes and hence the invasion of successive waves of steppe immigrants, coming more often from eastern Europe and more seldom from the oriental basin of the Mediterranean. They are sometimes accompanied by arctic forms, but never by the genera *Lemmus* and *Dicrostonyx*. Among these immigrants one may note certain species of *Microtus* (*Microtus* gr. *hyperboreus-middendorffi*, in the ?Glacial B of the Cromerian, and *Microtus guentheri* during the Elsterian), which show a higher degree of evolution than that of the local populations belonging to this genus.

Therefore, one might assert that in contrast to the Lower Pleistocene, in which the local evolution of rodent lineages played an important role in the replacement of faunas, during the Middle Pleistocene migrations were more significant.

2. In close relation to the evolution of the climate we may note the emergence, during the Cromerian (?Glacial B of Cromerian Complex), of a marked biogeographic differentiation.

While in eastern Romania, in Dobrogea (GD-4), the open spaces of the dry steppe type prevail and the fauna is almost exclusively formed of steppe species, the lagurines being in majority, in the area of Betfia (B-VII/4c), forest and prairie tend to come into equilibrium with the steppe. Hence, the important development of *Microtus* gr. *arvalis-agrestis*, the decreased frequency of *Lagurus transiens* and the persistence of forest species in percentages that are not at all negligible.

This biogeographical differentiation is preserved to the end of the Pleistocene. And, judging from more complete data from the two last glaciations, the fauna of Dobrogea shows a clear cut distinction from the mammalian assemblages of the rest of Romania, not only in the high frequency of steppe forms (such as *Lagurus lagurus*, *Eolagurus luteus*, *Allactaga major*, and *Saiga*), but also in their great diversity. In its composition it shows greater affinities with the faunas of Crimea and of the south of the Russian Plain.

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## REFERENCES

- AGUSTI J., MOYA-SOLA S. 1991. Les faunes de Mammifères du Pléistocène inférieur et moyen de l'Espagne: Implications biostratigraphiques. *L'Antropologie*, **95**(4): 753-764.
- BARTOLOMEI G., CHALINE J., FEJFAR O., JANOSSY D., JEANNET M., KOENIGSWALD W. v., KOWALSKI K. 1975. *Pliomys lenki* (HELLER 1930) (Rodentia, Mammalia) en Europe. *Acta zool. cracov.*, **20**(10): 393-467.
- BOLOMEY A. 1965a. Contribution à la connaissance de la morphologie de *Pliotragus ardeus*. *Rev. Roum. Biol.-Zoologie*, **10**(5): 315-323.
- BOLOMEY A. 1965b. Die Fauna zweier villafrankischer Fundstellen in Rumänien. *Ber. Geol. Ges. DDR*, **10**(1): 77-88.
- BOLOMEY A. 1983. L'homme et son environnement au Pléistocène. In: DUMITRESCU V. et al. – Esquisse d'une préhistoire de la Roumanie. Ed. St. Enciclop., Bucuresti, pp. 12-28.
- CHALINE J. 1972. Les Rongeurs du Pléistocène moyen et supérieur de France. *Cahiers de Paléontologie*, Editions du CNRS, Paris.
- CHALINE J. 1986. Continental faunal units of the Plio-Pleistocene of France. *Mem. Soc. Geol. It.*, **31**: 175-183.
- CORDY J.-M. 1988. Apport de la paléozoologie à la paléocéologie et la chronostratigraphie en Europe du nord-occidental. *L'Homme de Néandertal, Liège*, **2**: 55-64.
- FEJFAR O., HEINRICH W.-D. 1987. Zur biostratigraphischen Gliederung des jüngeren Känozoikums in Europa an Hand von Muriden und Cricetiden (Rodentia, Mammalia). *Cas. Mineral. Geol., Praha*, **32**: 1-16.
- FEJFAR O., HEINRICH W.-D. 1990. Proposed biostratigraphical division of the European continental Neogene and Quaternary based on muroid rodents (Rodentia, Mammalia). *Int. Symp. Evol. Phyl. Biostr. Arvicolidis, Praha*, pp. 115-124.
- FEJFAR O., HORACEK I. 1983. Zur Entwicklung der Kleinsäugerfaunen im Villanyium und Alt-Biharium auf dem Gebiet der CSSR. *Schriftenr. Geol. Wiss., Berlin*, **19**(20): 111-207.
- FERU M., RADULESCO C., SAMSON P. 1978. Biostratigraphie (Micromammifères) des dépôts plio-pléistocènes de la zone de Slatina (dép. d'Olt). *Trav. Inst. Spéol. "E. Racovitza"*, **17**: 117-134.
- FERU M., RADULESCO C., SAMSON P. 1979. Biostratigraphie (Micromammifères) des dépôts plio-pléistocènes du domaine gétique de la Dépression Valaque. *Trav. Inst. Spéol. "E. Racovitza"*, **18**: 141-169.
- JÁNOSY D. 1986. Pleistocene Vertebrate Faunas of Hungary. *Akad. Kiadó, Budapest*.
- KOENIGSWALD W. v., FEJFAR O., TCHERNOV E. 1992. Revision einiger alt- und mittelpleistozäner Arvicoliden (Rodentia, Mammalia) aus dem östlichen Mittelmeergebiet (Ubeidiya, Jerusalem und Kalymnos-Xi). *N. Jb. Geol. Paläont. Abh.*, **184**(1): 1-23.

- KOLFSCHOTEN T. VAN 1990. Review of Pleistocene arvicolid faunas from the Netherlands. Int. Symp. Evol. Phyl. Biostr. Arvicolids, Praha, pp. 255-274.
- KORMOS T. 1933. Revision der präglazialen Wühlmäuse von Gesprengberg bei Brassó in Siebenbürgen. Paläont. Z., **15**: 1-21.
- KOWALSKI K. 1967. *Lagurus lagurus* (PALLAS 1773) and *Cricetus cricetus* (LINNAEUS 1758) (Rodentia, Mammalia) in the Pleistocene of England. Acta zool. cracov., **12**: 111-122.
- KOWALSKI K., NADACHOWSKI A. 1990. Review of fossil arvicolid faunas of Poland. Int. Symp. Evol. Phyl. Biostr. Arvicolids, Praha, pp. 297-304.
- KRETZOI M. 1941. Die unterpleistozäne Säugetierfauna von Befția bei Nagyvárad. Földt. Közl., **71**: 308-355.
- KRETZOI M. 1965. Die Nager und Lagomorphen von Voigtstedt in Thüringen und ihre chronologische Aussage. Paläont. Abh., Abt. A, II, **2-3**: 585-660.
- LOPEZ N., MICHAUX J., VILLALTA J. F. DE 1976. Rongeurs et Lagomorphes de Bagur-2 (Province de Gérone, Espagne). Nouveau remplissage de fissure du début du Pléistocène Moyen. Acta Géol. Hispanica, **9**(2): 46-54.
- MARKOVA A. K. 1990. Pleistocene microtheriofauna of European part of USSR. Int. Symp. Evol. Phyl. Biostr. Arvicolids, Praha, pp. 313-338.
- NIKIFOROVA K. V. et al. 1982. Chronostratigraphical Sketch of the Upper Pliocene-Anthropogene deposits of the European part of the USSR. In: SCHANZER V.E. Quaternary System. I. table 19, Moscow [in Russian].
- PAUNESCO A., RADULESCO C., SAMSON P. 1982. Découverte du Paléolithique inférieur en Roumanie. Trav. Inst. Spéol. "E. Racovitza", **21**: 53-62.
- RABEDER G. 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän un dem älteren Pleistozän von Niederösterreich. Beitr. Paläont. Österr., **8**: 1-373.
- RADULESCO C., SAMSON P. 1983. La lignée *Mimomys minor-coelodus* (Rodentia, Mammalia) dans le Bassin Dacique. Trav. Inst. Spéol. "E. Racovitza", **22**: 57-64.
- RADULESCO C., SAMSON P. 1985. Pliocene and Pleistocene Mammalian Biostratigraphy in southeastern Transylvania (Romania). Trav. Inst. Spéol. "E. Racovitza", **24**: 85-95.
- RADULESCO C., SAMSON P. 1986. Les Micromammifères du Pléistocène moyen de Gura Dobrogei-4 (dép. de Constanta, Roumanie). Trav. Inst. Spéol. "E. Racovitza", **25**: 67-93.
- RADULESCO C., SAMSON P. 1991. Traces d'activité humaine à la limite Pliocène/Pléistocène dans le Bassin Dacique (Roumanie). 114<sup>e</sup> Congr. nat. Soc. sav., Paris, Les premiers européens, pp. 203-207.
- SAMSON P. 1975. Les Equidés fossiles de Roumanie. Geol. Romana, **14**: 165-351.
- SAMSON P., RADULESCO C. 1972. Découverte de dépôts à faune mindélienne dans les grottes de la Dobrogea centrale. Trav. Inst. Spéol. "E. Racovitza", **11**: 317-326.
- STORCH G. 1975. Eine mittelpleistozäne Nager-Fauna von der Insel Chios, Ägäis (Mammalia: Rodentia). Senckenbergiana biol., **56**(4/6): 165-189.
- TERZEA E. 1970. Sur l'apparition et l'évolution de quelques genres d'Arvicolidés (Rodentia) pendant le Pléistocène. Livre du centenaire E. Racovitza, Ed. Acad. RSR., Bucarest, pp. 499-512.
- TERZEA E. 1972a. Remarques sur la morphologie dentaire et la répartition de *Microtus nivalis* MARTINS (Rodentia, Mammalia) dans le Pléistocène de Roumanie. Trav. Inst. Spéol. "E. Racovitza", **11**: 271-298.
- TERZEA E. 1972b. Sur la présence du genre *Lemmus* (Rodentia, Mammalia) dans le Pléistocène de la Roumanie. Folia quaternaria, **40**: 57-65.
- TERZEA E. 1973a. Sur un nouveau genre d'Arvicolidés (Rodentia, Mammalia) du Pléistocène de Roumanie. Livre du cinquantenaire de l'Inst. Spéol. "E. Racovitza", Ed. Acad. RSR, Bucarest, pp. 421-426.
- TERZEA E. 1973b. Les genres *Rattus* et *Lemmus* (Rodentia, Mammalia) dans le Pléistocène de Roumanie. Livre du cinquantenaire de l'Inst. Spéol. "E. Racovitza", Ed. Acad. RSR, Bucarest, pp. 427-436.
- TERZEA E. 1973c. A propos d'une faune villafranchienne finale de Befția (Bihor, Roumanie). Trav. Inst. Spéol. "E. Racovitza", **12**: 229-242.
- TERZEA E. 1978. *Epimeriones dacicus* n.sp. (Rodentia, Mammalia) du Villafranchien supérieur de Roumanie. Trav. Inst. Spéol. "E. Racovitza", **17**: 135-138.
- TERZEA E. 1984. Mammifères rares du Pléistocène inférieur de Befția-XIII (Bihor, Roumanie). Trav. Inst. Spéol. "E. Racovitza", **23**: 49-56.
- TERZEA E. 1987. La faune du Pléistocène supérieur de la grotte "Pestera Cioarei" de Borosteni (dép. de Gorj). Trav. Inst. Spéol. "E. Racovitza", **26**: 55-66.
- TERZEA E. 1988. La faune de Vertébrés du Pléistocène inférieur de Befția-IX (dép. de Bihor, Roumanie). Trav. Inst. Spéol. "E. Racovitza", **27**: 79-86.

- TERZEA E. 1989. Les Arvicolidés (Rodentia, Mammalia) du Pléistocène moyen de Chiscău-1 (dép. de Bihor, Roumanie). Trav. Inst. Spéol. "E. Racovitza", **28**: 57-72.
- TERZEA E. 1992. *Apodemus mystacinus* (DANFORD & ALSTON) (Rodentia, Mammalia) dans le Pléistocène inférieur final de Betfia-VII (Bihor, Roumanie). Trav. Inst. Spéol. "E. Racovitza", **31**: 83-94.
- TERZEA E., JURCSÁK T. 1967. Asupra unui nou punct fosilifer descoperit la Betfia. Lucr. Inst. Speol. "E. Racovitza", **4**: 193-209.
- TERZEA E., JURCSÁK T. 1968. Bemerkungen über die mittelpleistozänen Faunen von Betfia. Ber. deutsch. Ges. Geol. Wiss., A. Geol. Paläont., **13**: 381-391.
- TERZEA E., JURCSÁK T. 1976. Faune de Mammifères de Betfia-XIII et son âge géologique. Trav. Inst. Spéol. "E. Racovitza", **15**: 195-205.
- TOPACHEVSKY V. A. 1973. Rodents of the Tamanian faunistic complex of Crimea. "Naukova Dumka", Kiev [In Russian].
- ZAGWIJN W. H. 1985. An outline of the Quaternary stratigraphy of the Netherlands. Geol. Mijnbouw, **64**: 17-24
- ZAZHIGIN V. S. 1980. Late Pleistocene and Anthropogene rodents of the south of western Siberia. "Nauka", Moskow. [In Russian].