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Late Miocene and Pliocene small mammal faunas (Insectivora, Lagomorpha, Rodentia) of Southeastern Europe

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Abstract: A biochronologic range of 25 genera of insectivores, 12 genera of lagomorphs, and 68 genera of rodents from almost 40 fossil assemblages of Late Miocene and Pliocene age in Southeastern Europe is reviewed. The position of faunal complexes, subcomplexes, and reference localities within the stratigraphic scale of Central and Eastern Paratethys and their correlation with the MN unit system is presented and discussed. The relatively high provinciality among small mammal faunas as well as insufficient evidence of radioisotopic and palaeomagnetic datings makes this correlation difficult in some points.

Key words: micromammals, Neogene, biostratigraphy, Ukraine.

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I. INTRODUCTION

During the last two decades the knowledge of Neogene small mammal faunas of Southeastern Europe has made remarkable advances. The description of several new fossil sites and assemblages provide an opportunity to establish the biostratigraphic framework for Southeastern Europe and to correlate chronologic, systematic, and biogeographic aspects of European Neogene.

The mammal biozonation of the European continental Neogene (Mammal Neogene Zones) introduced by MEIN (1975) was revised during the last decade several times (DE BRUIJN et al. 1992; MEIN 1990,1999; STEININGER et al. 1990; FEJFAR et al. 1997a, b; STEININGER 1999).

In the former Soviet Union local subdivisions and zonations were established by V. I. GROMOV (1948). Consequently, the Russian and Ukrainian authors defined several Neogene faunal units as "faunistic complexes". They have always been straightforward biostratigraphic units comparable with MN-Zonation. However, in many cases subdivisions of faunal complexes do not correspond precisely with the Mammal Neogene Zones and their usefulness has sometimes been questioned (e.g. PEVZNER et al. 1996).

The palaeogeographical reconstructions of Southeastern Europe during Miocene and Pliocene are connected with the complicated history of the Paratethys (RÖGL 1998, 1999). The northern part of Eastern Paratethys is characterized by the presence of marine sequences which interfinger with terrestrial deposits containing mammal faunas. In marine sequences of Sarmatian s.l., Maeotian, and Pontian stages there occur, relatively frequently, quasi-marine facies and infrafacies of continental sediments developed as prodeltaic alluvial derivations (JONES & SIMMONS 1996). These infrafacies often contain small mammal assemblages which can be compared with Central Paratethys fossil land mammal assemblages. Their taxonomic composition, faunal succession and biostratigraphy was studied during the last two decades by many authors (e.g. LUNGU 1978, 1981; KOROTKEVICH 1988; PRISYAZHNYUK & SHEVCHENKO 1987; TOPACHEVSKY et al. 1988, 1990, 1992, 1997, 1998; MOS'KINA & MATSUY 1992; PEVZNER & VANGENGEIM 1993; VANGENGEIM & PEVZNER 1993; NESIN & TOPACHEVSKY 1999 and others). Notwithstanding the efforts undertaken, the comprehensive biostratigraphic mammal zonation for Eastern Paratethys has still not been established.

The regional subdivision of Eastern Paratethys Stages for the Late Miocene and Pliocene presented in this paper was based on the Stratigraphical Code of Ukraine (TESLENKO 1997), accepted by the National Stratigraphic Committee of the Ukraine, while land mammal zonation follows the version presented by MEIN (1999). The biochronologic range of small mammals was based on studies of fossil assemblages from 32 sites and almost 40 assemblages (Fig. 1).

For the Neogene, starting from middle Sarmatian (=Bessarabian), the following complexes and subcomplexes were distinguished on the basis of large mammal faunas: Grytsevian (KOROTKEVICH 1988); Kalfian (LUNGU 1978); Berislavian complex with two subcomplexes Berislavian and Grebenikian (KOROTKEVICH 1988); Belkian complex with two subcomplexes Novoelizavetovkian and Belkian (KOROTKEVICH 1988); Cherevichnian (KOROTKEVICH 1988); Tavrian (KOROTKEVICH 1988); Moldavian (ALEXEEVA 1961), and Khaprovian (GROMOV 1948).

On the basis of small mammal faunas, the following complexes and subcomplexes were distinguished: Mikhailovkian (TOPACHEVSKY et al. 1997); Frunzovkian (TOPACHEVSKY et al. 1997); Fontanian (TOPACHEVSKY et al. 1997); Vinogradovkian (TOPACHEVSKY et al. 1997), and Kuchurganian (SHEVCHENKO 1965).

Descriptions of complexes in this paper are based exclusively on small mammal assemblages (TOPACHEVSKY et al. 1997, 1998). Some complexes were defined on the basis of both large and small mammal faunas under different names. To avoid misunderstandings concerning names of faunal complexes and to maintain the rules of priority, the names published earlier are used as far as possible. However, the reference localities are distinguished on the basis of faunal diversity of small mammals.

The authors are aware of the fact that the proposed biostratigraphic zonations are not sufficiently precise and will need further detailed studies as new data appear.

A c k n o w l e d g e m e n t s. The authors wish to thank Professor Vadim A. TOPACHEVSKY for his advice and help during the development of this project and all of those colleagues from the National Natural History Museum in Kiev who offered suggestions and remarks. They are also very grateful to Dr Yuriy SEMENOV for providing them with the map of Southeastern European mammal localities.

II. LATE MIOCENE AND PLIOCENE SMALL MAMMAL COMPLEXES

Characteristics of the Late Miocene and Pliocene small mammal complexes were established mainly on the basis of detailed taxonomic analyses of widely distributed taxa of the Palaearctic rodents (Cricetidae, Muridae, Spalacidae, Dipodidae, Arvicolinae) and lagomorphs (Palaeolagidae and Leporidae). Also helpful were preliminary determinations of insectivores (Erinaceidae, Talpidae, Dimylidae, Soricidae), lagomorphs (Ochotonidae) and some other rodents (Sciuridae, Gliri-

Fig. 1. Distribution of Late Miocene and Pliocene mammals sites. 1 – Grytsev; 2 – Kalfa; 3 – Buzhor; 4 – Mikhailovka 1,2; 5 – Frunzovka 2; 6 – Shirokino; 7 – Liventzovka; 8 – Obukhovka 1,2; 9 – Kotlovina 1,2,3; 10 – Andreevka; 11 – Novoukrainka 1; 12 – Orekhovka; 13 – 16th St. of Bolshoy Fontan; 14 – Odessian Catacombs; 15 – Orlovka; 16 – Vinogradovka 1,2,3; 17 – Frunzovka 1; 18 – Krasnopol; 19 – Velikomikhailovka; 20 – Voinichevo; 21 – Novopetrovka; 22 – Yurkovka; 23 – Trudomirovka; 24 – Grebeniki; 25 – Novoukrainka 2; 26 – Salcha and Kagul Rivers; 27 – Lucheshty; 28 – Novoelizavetovka 2,3; 29 – Protopopovka 2,3; 30 – Cherevichnoe 2,3; 31 – Zhevakhova Gora 11, 15; 32 – Kryzhanovka 2.

Table I

Correlation chart and distribution of the Late Miocene and Pliocene small mammal genera (after TOPACHEVSKY et al. 1997, 1998; changed). Absolute dating (Ma) after CHUMAKOV et al. (1992a,b, modified) and STEININGER et al.(1996)

Epoch	Eastern Paratethys Stages	European Land Mammal Mega-Zones	Mammal Neogene Zones	Faunal complexes and subcomplexes		Order / Families / Genera / Investigated localities	1
Pliocene	1.7 Kuyalnikian =Akchagylian	Villanyian	17	Khaprovian	late	Kotlovina 3 – upper level Kotlovina 2 – middle level	2
			16		middle	Cherevichnoe 2 (middle level) Kryzhanovka 2 Zhevakhova Gora 11 (middle level) Zhevakhova Gora 15 (lower level)	3
					early	Liventsovka Obukhovka 2 Shirokino	4
	3.4 Kimmerian	Ruscinian	15	Moldavian	late	Odessian catacombs Vinogradovka 3	5
					middle	Kotlovina 1 (lower level), gravels of Salcha and Kagul Rivers, Lucheshty, Vinogradovka 2	6
					early	Obukhovka 1 Grebeniki 2	7
			14	Kuchurganian		Krasnopol, Velikomikhailovka, Novopetrovka, Frunzovka 1, Voinichevo, Trudomirovka, Yurkovka	8
Late Miocene	5.4 Pontian	Turolian	13	Vinogradovkian		Vinogradovka 1, Orlovka	9
				Fontanian		16 th Station of Bolshoy Fontan = Odessa (lectostratotype of Pontian)	10
	7.1 Maeotian			Cherevichnian		Orekhovka Andreevka Novoukrainka 1	11
			12	Belkian	Belkian	Protopopovka 3 Novoelizavetovka 3	12
	9.88				Novoelizavetovkian	Novoukrainka 2 Cherevichnoe 3 (lower level)	13
	Sarmatian s.l. Khersonian 11.0		11	Berislavian	Grebenikian	Novoelizavetovka 2	14
					Frunzovkian (= Berislavian)	Frunzovka 2 Mikhailovka 2 (Southern Bug River)	15
	Bessarabian	Vallesian	10	Mikhailovkian		Mikhailovka 1 (Southern Bug River)	16
				Kalfian		Kalfa Buzhor	17
			9	Grytsevian		Grytsev	18

– predominant taxa

Table I ctd

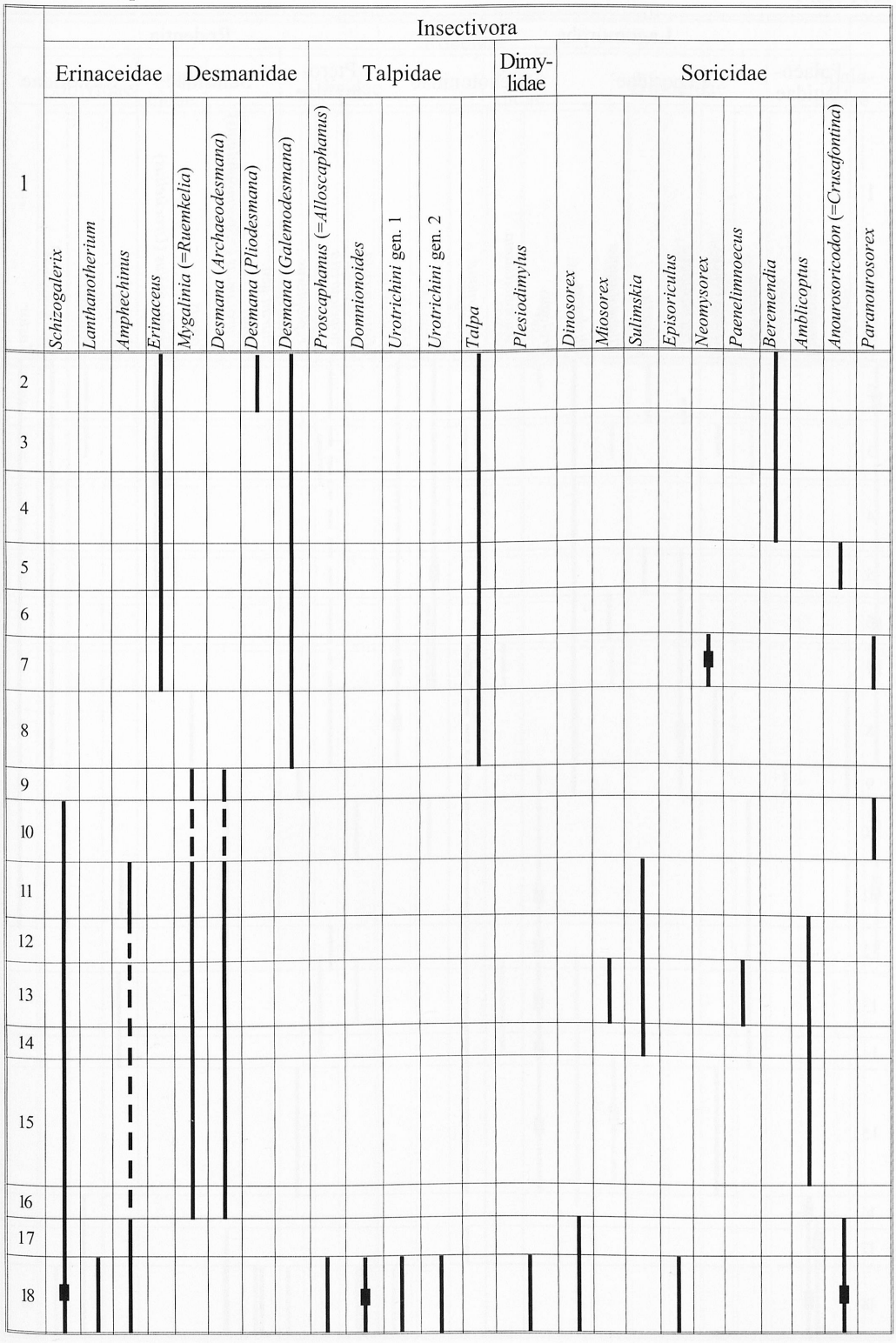

Table I ctd

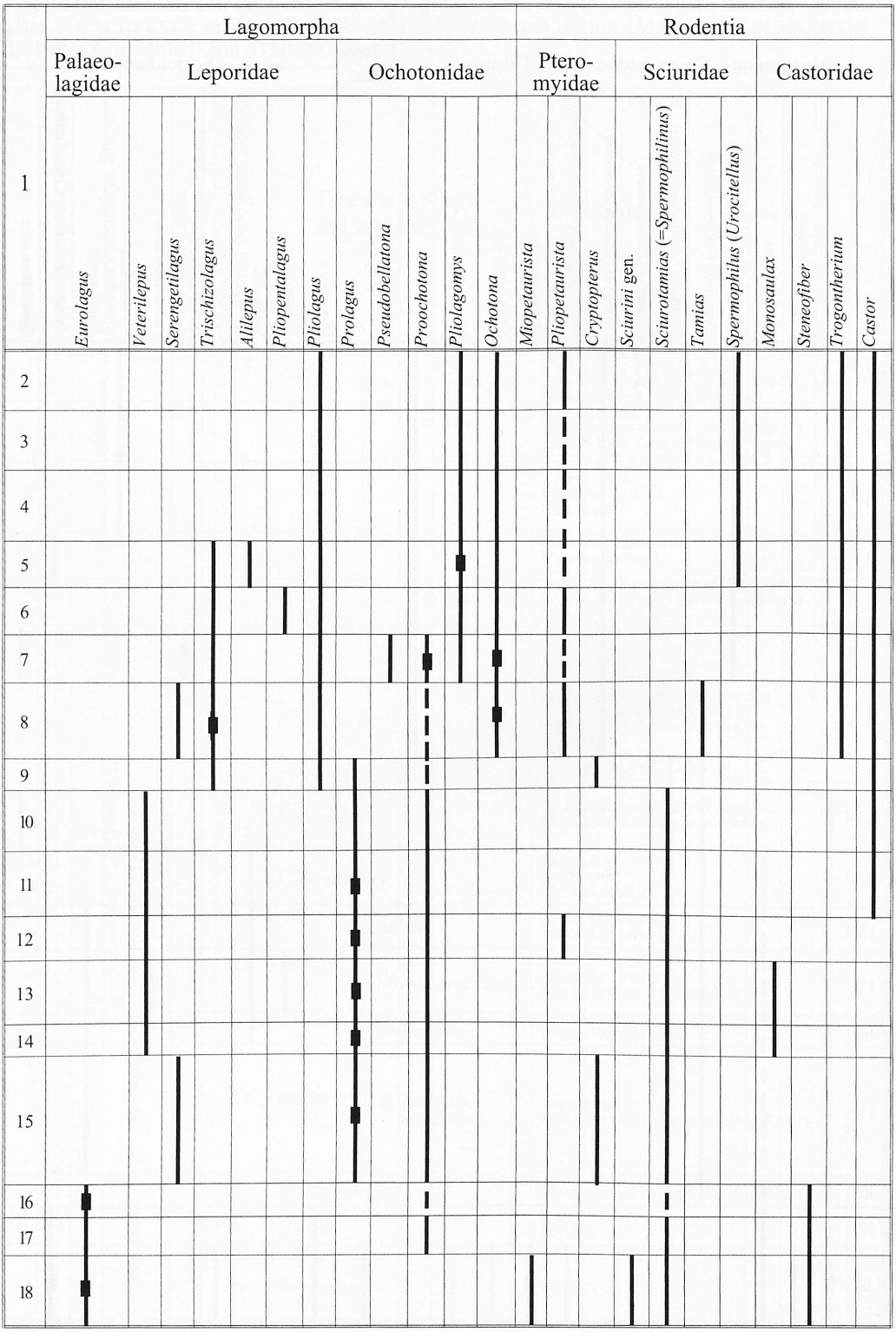
Lagomorpha
Rodentia
Palaeo-lagidae
Leporidae
Ochotonidae
Ptero-myidae
Sciuridae
Castoridae
1
Eurolagus
Veterilepus
Serengetilagus
Trischizolagus
Alilepus
Pliopentalagus
Pliolagus
Prolagus
Pseudobellatona
Proochotona
Pliolagomys
Ochotona
Miopetaurista
Pliopetaurista
Cryptopterus
Sciurini gen.
Sciurotamias (=Spermophilinus)
Tamias
Spermophilus (Urocitellus)
Monosaulax
Steneofiber
Trogontherium
Castor
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Table I ctd

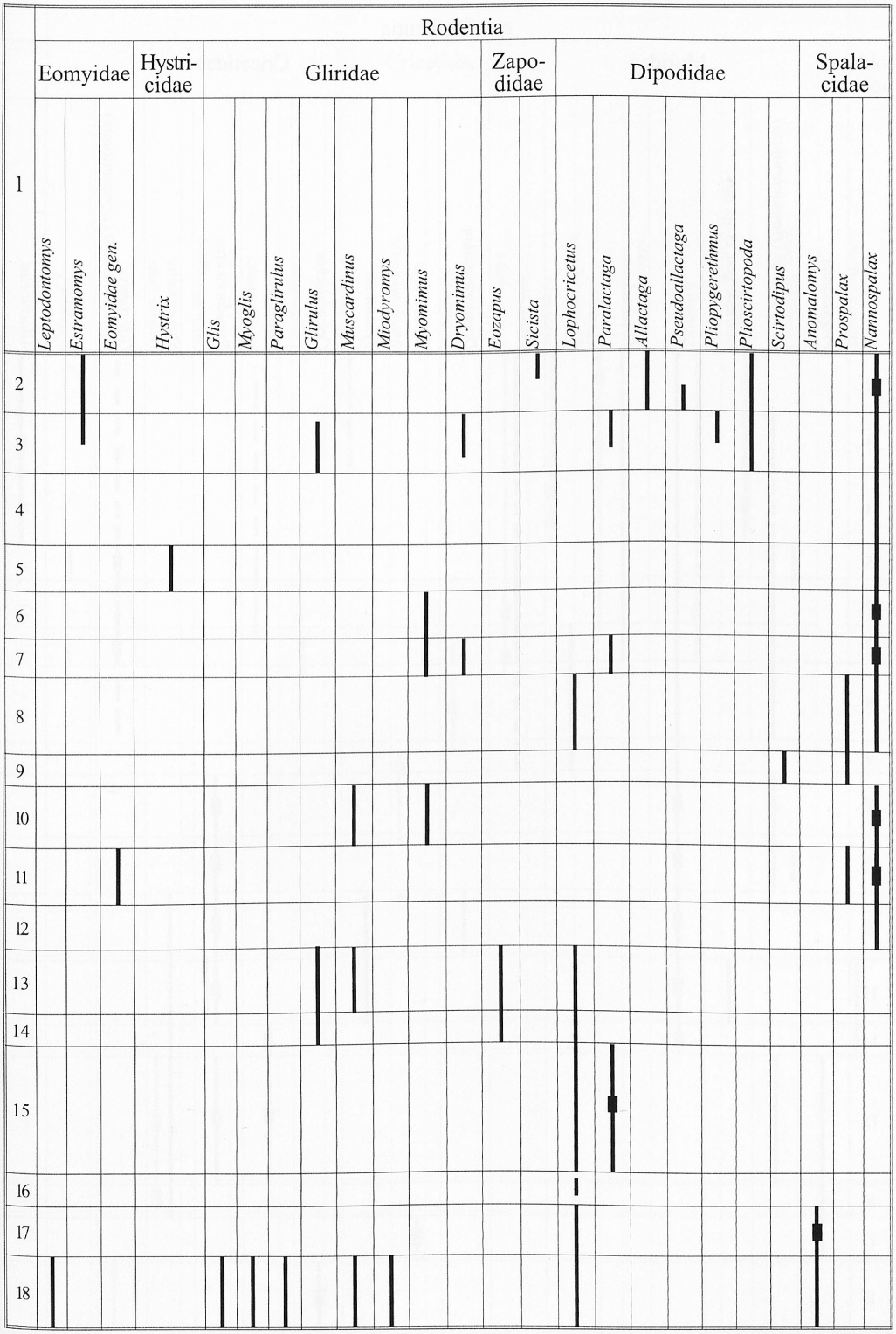
Rodentia
Eomyidae
Hystricidae
Gliridae
Zapodidae
Dipodidae
Spalacidae
1
Leptodontomys
Estramomys
Eomyidae gen.
Hystrix
Glis
Myoglis
Paraglirulus
Glirulus
Muscardinus
Miodyromys
Myomimus
Dryomimus
Eozapus
Sicista
Lophocricetus
Paralactaga
Allactaga
Pseudoallactaga
Pliopygerethmus
Plioscirtopoda
Scirtodipus
Anomalomys
Prospalax
Nannospalax
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Table I ctd

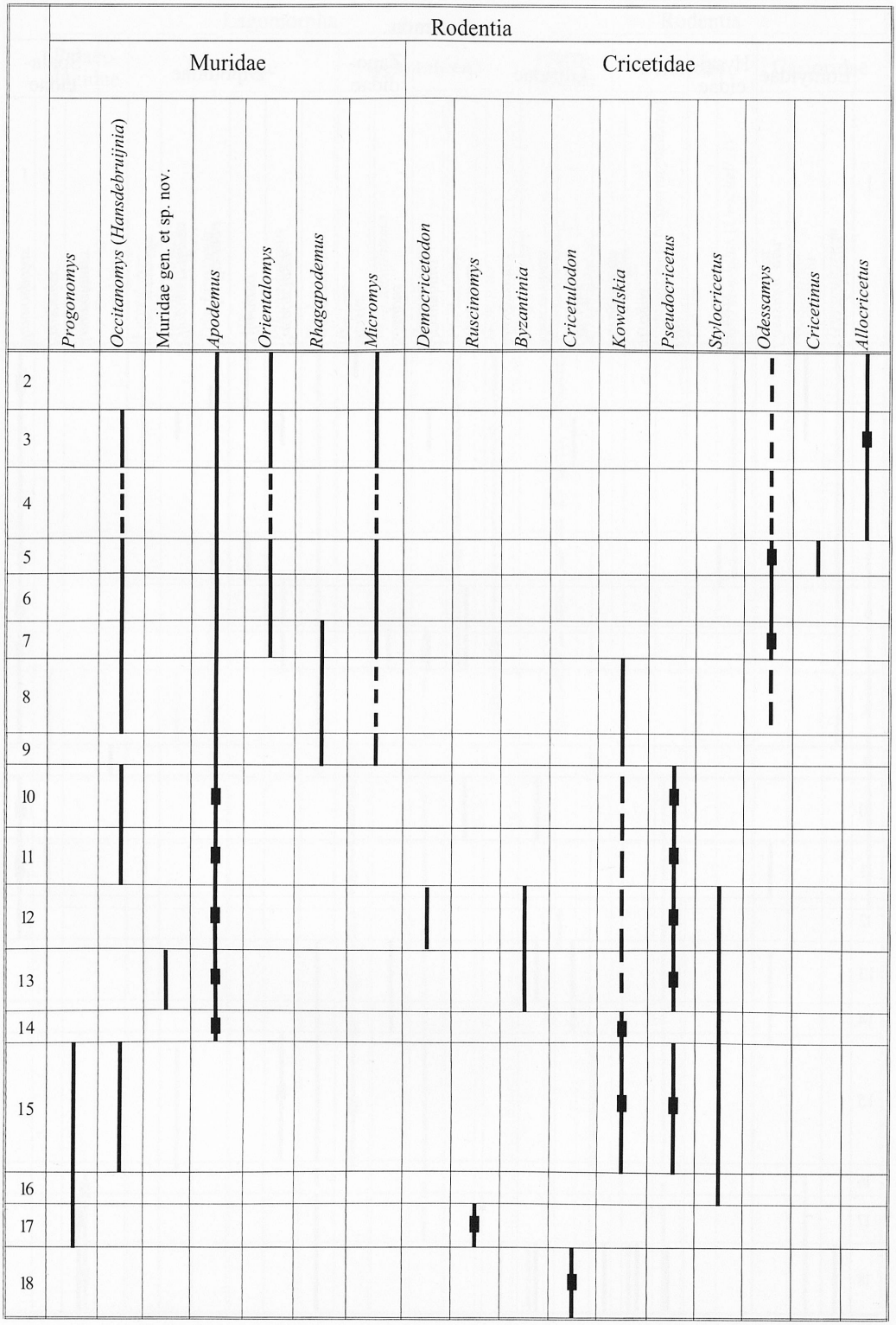
Rodentia
Muridae
Cricetidae
Progonomys
Occitanomys (Hansdebruijnia)
Muridae gen. et sp. nov.
Apodemus
Orientalomys
Rhagapodemus
Micromys
Democricetodon
Ruscinomys
Byzantinia
Cricetulodon
Kowalskia
Pseudocricetus
Stylocricetus
Odessamys
Cricetinus
Allocricetus
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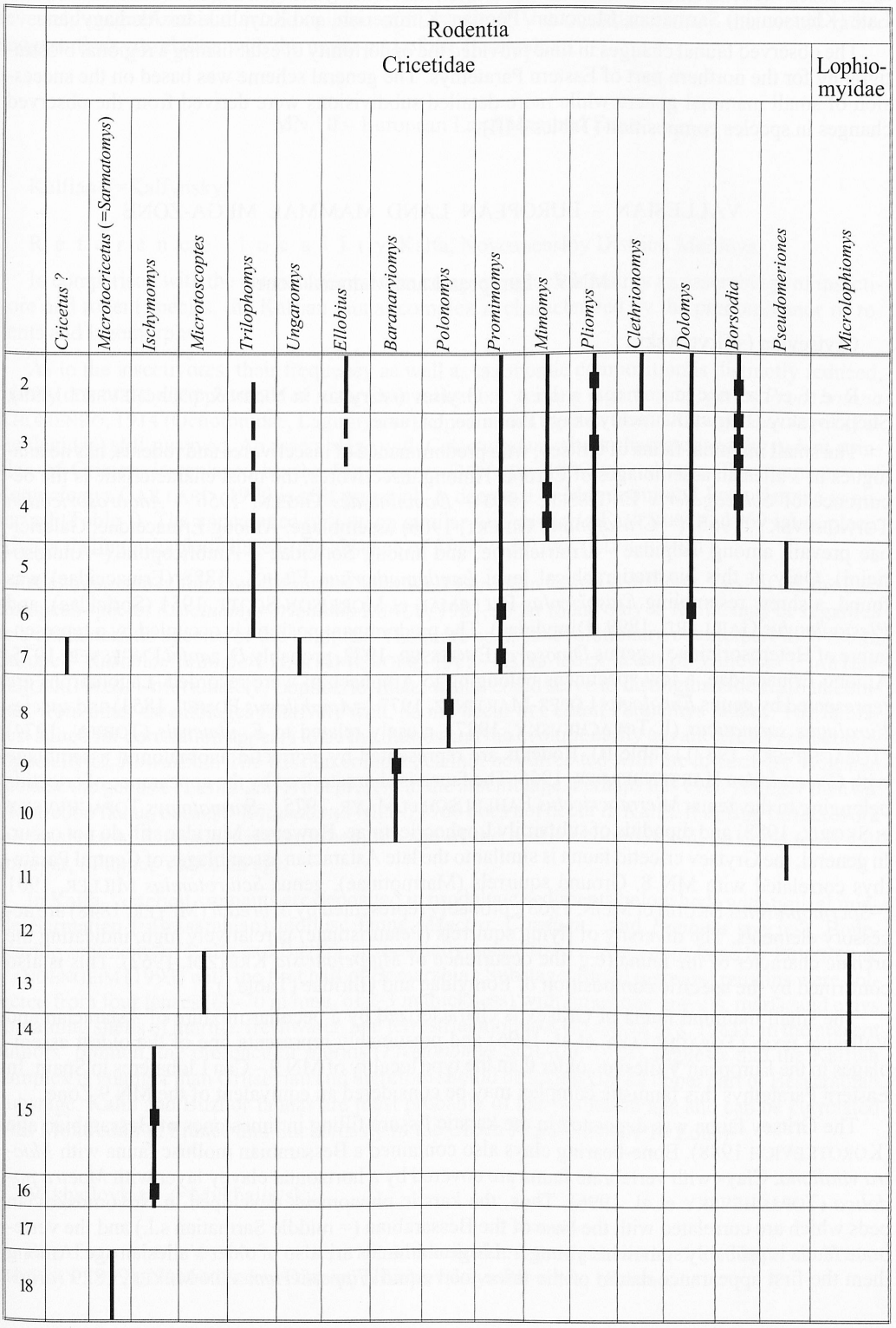
Table I ctd


Rodentia
Cricetidae
Lophiomyidae
Cricetus ?
Microtocricetus (=Sarmatomys)
Ischymomys
Microtoscoptes
Trilophomys
Ungaromys
Ellobius
Baranarviomys
Polonomys
Prominomys
Mimomys
Pliomys
Clethrionomys
Dolomys
Borsodia
Pseudomeriones
Microlophiomys
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dae, Eomyidae). Analyses of faunistic data gave the possibility of distinguishing complexes (in some cases subcomplexes) for the following Eastern Paratethys stages: Middle (Bessarabian) and Late (Khersonian) Sarmatian, Maeotian, Pontian, Kimmerian, and Kuyalnikian=Akchagylian.

The observed faunal changes in time provided the opportunity of establishing a regional biostratigraphy for the northern part of Eastern Paratethys. The general scheme was based on the succession of small mammal genera while more detailed subdivisions were derived from the observed changes in species composition (Tables I-III).

VALLESIAN – EUROPEAN LAND MAMMAL MEGA-ZONE

MN 9 – European Land Mammal Zone

Grytsevian (=Grytsivsky)

R e f e r e n c e l o c a l i t y: Grytsev (=Grytsiv in NESIN & TOPACHEVSKY 1999), Shepetovskiy District, Khmelnytskaya Province, Ukraine.

The small mammal fauna of Gritsev, with predominance of insectivores and rodents, has no analogues in Vallesian assemblages of Europe. Among insectivores, the most characteristic is the occurrence of *Schizogalerix* ENGESSER, 1980 – *Domninoides* GREEN, 1956 – *Anourosoricodon* TOPACHEVSKY, 1965 (= *Crusafontina* GIBERT, 1966) assemblage. Among Erinaceidae, Galericinae prevail, among Talpidae – Urotrichinae, and among Soricidae – Amblicoptini (=Anurosoricini). Only at this biostratigraphical level *Lanthanotherium* FILHOL, 1888 (Erinaceidae) was found, a shrew resembling *Episoriculus* ELLERMAN et MORRISON-SCOTT, 1951 (Soricidae), and *Plesiodimylus* GAILLARD, 1899 (Dimylidae). The predominant position is occupied by a representative of Heterosoricinae – genus *Dinosorex* ENGESSER, 1972, probably *D. zapfei* ENGESSER, 1975. Among Erinaceidae, a few specimens belonging to Amphechini were recorded. Lagomorphs are represented by genus *Eurolagus* LÓPEZ-MARTINEZ, 1977 (=*Amphilagus* POMEL, 1853) and species *Eurolagus sarmaticus* (I. TOPACHEVSKY, 1987), closely related to *E. ulmensis* (TOBIEN, 1974) (TOPACHEVSKY 1987) (Table II). Rodents are represented by a cricetid-anomalomid assemblage with *Cricetulodon* HARTENBERGER, 1966. The fauna is characterized by the appearance of cricetids belonging to the genus *Microtocricetus* FAHLBUSCH et MAYR, 1975 (=*Sarmatomys* TOPACHEVSKY et SKORIK, 1988) and dipodids of subfamily Lophocricetinae. However, Muridae still do not occur. In general, the Grytsev cricetid fauna is similar to the late Astaracian assemblages of Central Paratethys correlated with MN 8. Ground squirrels (Marmotinae), genus *Sciurotamias* MILLER, 1901 (=*Spermophilinus* BRUIJN et MEIN, 1968), probably represented by *S. bredai* (MEYER, 1848) are accessory elements. The diversity of flying squirrels (Petauristinae) is relatively high, indicating the archaic character of the fauna (e.g. the occurrence of *Miopetaurista* KRETZOI, 1962). This is also confirmed by the specific composition of Eomyidae and Gliridae (Table I).

The small mammal fauna of Gritsev is characterized by a peculiar mixture of Astaracian and Vallesian taxa (TOPACHEVSKY et al. 1996) and presumably represents one of the oldest assemblages in the European Vallesian, older than the type locality of MN 9 – Can Llobateres in Spain. In Eastern Paratethys this faunistic complex may be considered an equivalent of the MN 9 Zone.

The Gritsev fauna was deposited in the karstic fissure filling in limestones of Bessarabian age (KOROTKEVICH 1988). Bone-bearing clays also contained a Bessarabian mollusc fauna with *Mactra vitaliana*. Clays with vertebrate fauna are covered by a horizontal clayey layer with *Mactra podolica* (TOPACHEVSKY et al. 1996). Thus, the karstic phenomena developed in Novomoskovian beds which are correlated with the base of the Bessarabian (= middle Sarmatian s.l.) and the vertebrate fauna is probably somewhat younger. Large mammals are also of older Vallesian age. Among them the first appearance datum of the three-toed equid *Hippotherium* VON MEYER, 1829 (origi-

nally described as *Hipparion*), represented by two forms of different size (KOROTKEVICH 1988; KRAKHMALNAYA 1996), is especially important. However, the bone-bearing clays of Gritsev are reversely magnetized and, in the opinion of PEVZNER & VANGENGEIM (1993), this would rather suggest their correlation with the upper part of the Bessarabian.

MN 10 – European Land Mammal Zone

Kalfian (=Kalfynsky)

Reference locality: Kalfa, Novoanenskiy District, Moldova.

In comparison with the previous Gritsevian complex, which is mainly an assemblage of insectivore and rodent species, the Kalfian faunal complex is characterized by the predominance of rodents and lagomorphs.

As to the insectivores, their frequency as well as taxonomic composition is distinctly reduced, mainly due to the disappearance of Astaracian relict taxa. Among lagomorphs, genus *Proochotona* KHOMENKO, 1914 (Ochotonidae, Lagomyinae) appeared for the first time, although *Eurolagus* (Palaeolagidae) still survived. An assemblage with *Cricetulodon*, which characterized the rodent complex of Gritsev, is replaced by the *Ruscinomys* DEPÉRET, 1890 assemblage. The frequency of *Anomalomys* GAILLARD, 1900 is still essential. A decrease in Marmotini and Petauristinae is observed (Table I). The appearance of a taxon similar to *Kowalskia* FAHLBUSCH, 1969 takes place. Also, a distinguishable feature is the absence of *Microtocricetus* (LUNGU 1981).

A comparison of this faunal complex with West European faunas is difficult. First of all, the East European species *Ruscinomys orientalis* LUNGU, 1981, so far found only in Kalfa, may be regarded as a characteristic species of the complex. The more so as its evolutionary counterpart in Western Europe – *Ruscinomys thaleri* HARTENBERGER, 1965 – is an index taxon of Vallesian (HARTENBERGER 1965). Unfortunately, Lophocricetinae, which could serve to distinguish the Kalfian complex from other assemblages relatively well, do not occur in Central Paratethys faunas. The family best suited for correlation appears to be the murids and the evolutionarily advanced early cricetids – especially cf. *Kowalskia*. The Kalfian complex cannot be correlated with the lowermost Vallesian because the genus *Cricetulodon* is not present in the assemblage. Perhaps it is even younger than the Montredon fauna, because *Rotundomys* MEIN, 1966 does not occur in Kalfa. If during further work the presence of *Kowalskia* is confirmed, the age of the Kalfian complex will be considered still younger, of upper Vallesian age.

In Kalfa, vertebrate remains are deposited in prodeltaic sediments below beds with typical middle Sarmatian (=Bessarabian) mollusc fauna (*Mactra, Cardium*, and *Paphnia* species). Bone-bearing sediments of Kalfa and Buzhor are normally magnetized and are correlated by PEVZNER & VANGENGEIM (1993) with the first half of Bessarabian Substage. Small mammal remains were collected from four lenses (60-70 m long, of 2-3 m thickness) with limestone gravels, marls, and clays containing shells of marine, freshwater, and terrestrial molluscs (LUNGU 1978, 1981). In the present authors' opinion, the presence of murids (*Progonomys* SCHAUB, 1938) suggests that the Kalfian complex is younger than Gritsevian and therefore should be located in the upper part of Bessarabian Substage. Kalfa and Buzhor faunas are most probably of late Vallesian age and can be correlated with Montredon in France and Suchomasty in the Czech Republic (MN 10 Zone)

Mikhailovkian (=Mykhailivsky)

Reference locality: Mikhailovka 1 (=Mykhailivka 1 in NESIN & TOPACHEVSKY 1999), Novoodesskiy District, Nikolaevskaya Province, Ukraine.

Table II

Correlation chart and distribution of the Late Miocene and Pliocene species of lagomorphs belonging to Palaeolagidae, Leporidae and Ochotonidae (after TOPACHEVSKY et al. 1997, 1998; changed)

Epoch	Eastern Paratethys Stages	European Land Mammal Mega-Zones	Mammal Neogene Zones	Faunal complexes and subcomplexes		Order / Families / Genera / Investigated localities	1
Pliocene	1.7 Kuyalnikian =Akchagylian	Villanyian	17	Khaprovian	late	Kotlovina 3 – upper level Kotlovina 2 – middle level	2
			16		middle	Cherevichnoe 2 (middle level) Kryzhanovka 2 Zhevakhova Gora 11 (middle level) Zhevakhova Gora 15 (lower level)	3
					early	Liventsovka Obukhovka 2 Shirokino	4
	3.4 Kimmerian	Ruscinian	15	Moldavian	late	Odessian catacombs Vinogradovka 3	5
					middle	Kotlovina 1 (lower level), gravels of Salcha and Kagul Rivers, Lucheshty, Vinogradovka 2	6
					early	Obukhovka 1 Grebeniki 2	7
			14	Kuchurganian		Krasnopol, Velikomikhailovka, Novopetrovka, Frunzovka 1, Voinichevo, Trudomirovka, Yurkovka	8
Late Miocene	5.4 Pontian	Turolian	13	Vinogradovkian		Vinogradovka 1, Orlovka	9
				Fontanian		16 th Station of Bolshoy Fontan = Odessa (lectostratotype of Pontian)	10
	7.1 Maeotian			Cherevichnian		Orekhovka Andreevka Novoukrainka 1	11
			12	Belkian	Belkian	Protopopovka 3 Novoelizavetovka 3	12
	9.88				Novoelizavetovkian	Novoukrainka 2 Cherevichnoe 3 (lower level)	13
	Sarmatian s.l. Khersonian 11.0		11	Berislavian	Grebenikian	Novoelizavetovka 2	14
					Frunzovkian (= Berislavian)	Frunzovka 2 Mikhailovka 2 (Southern Bug River)	15
	Bessarabian	Vallesian	10	Mikhailovkian		Mikhailovka 1 (Southern Bug River)	16
				Kalfian		Kalfa Buzhor	17
			9	Grytsevian		Grytsev	18

Table II ctd

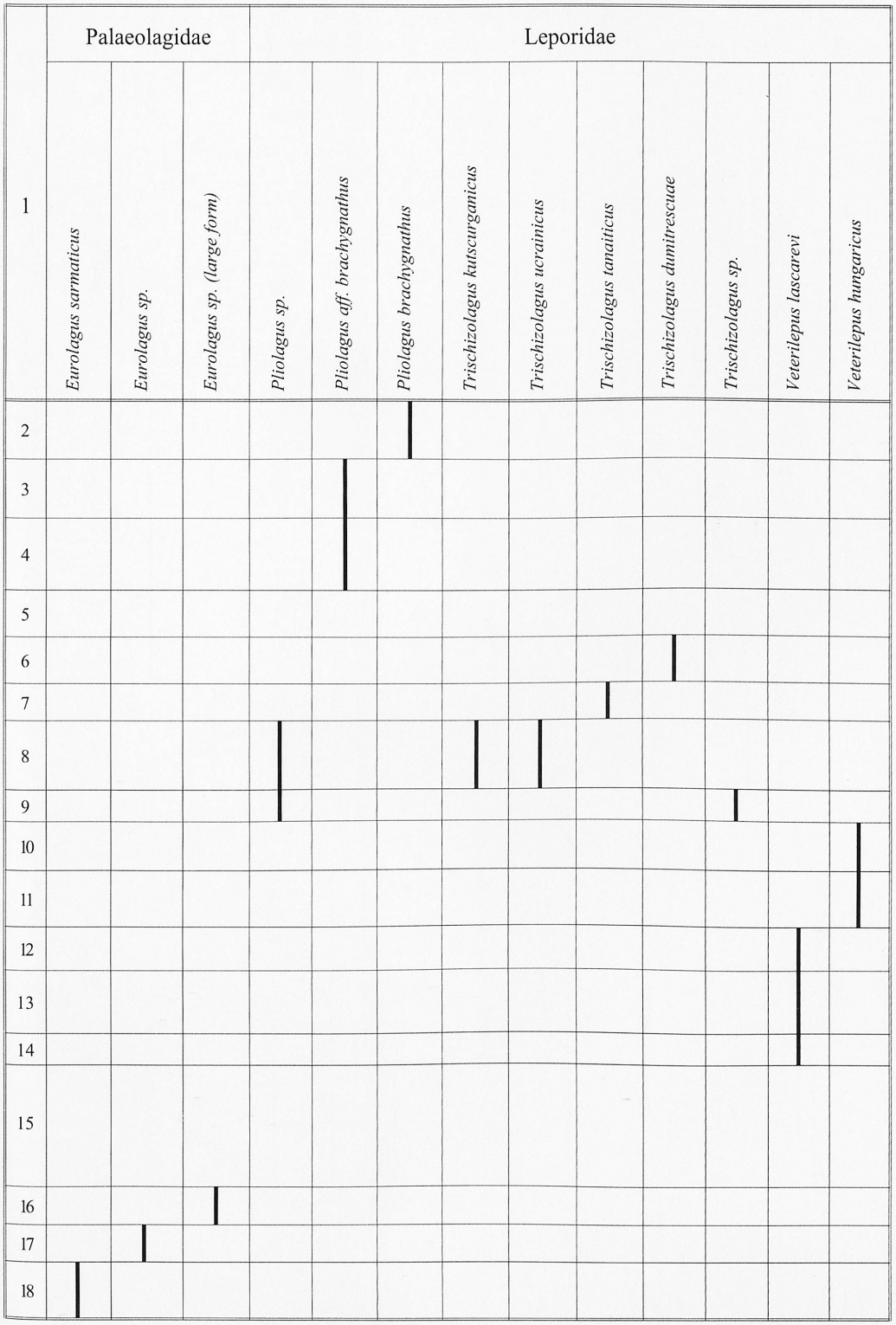
1
Palaeolagidae
Leporidae
Eurolagus sarmaticus
Eurolagus sp.
Eurolagus sp. (large form)
Pliolagus sp.
Pliolagus aff. brachygnathus
Pliolagus brachygnathus
Trischizolagus kutscurganicus
Trischizolagus ucrainicus
Trischizolagus tanaiticus
Trischizolagus dumitrescuae
Trischizolagus sp.
Veterilepus lascarevi
Veterilepus hungaricus
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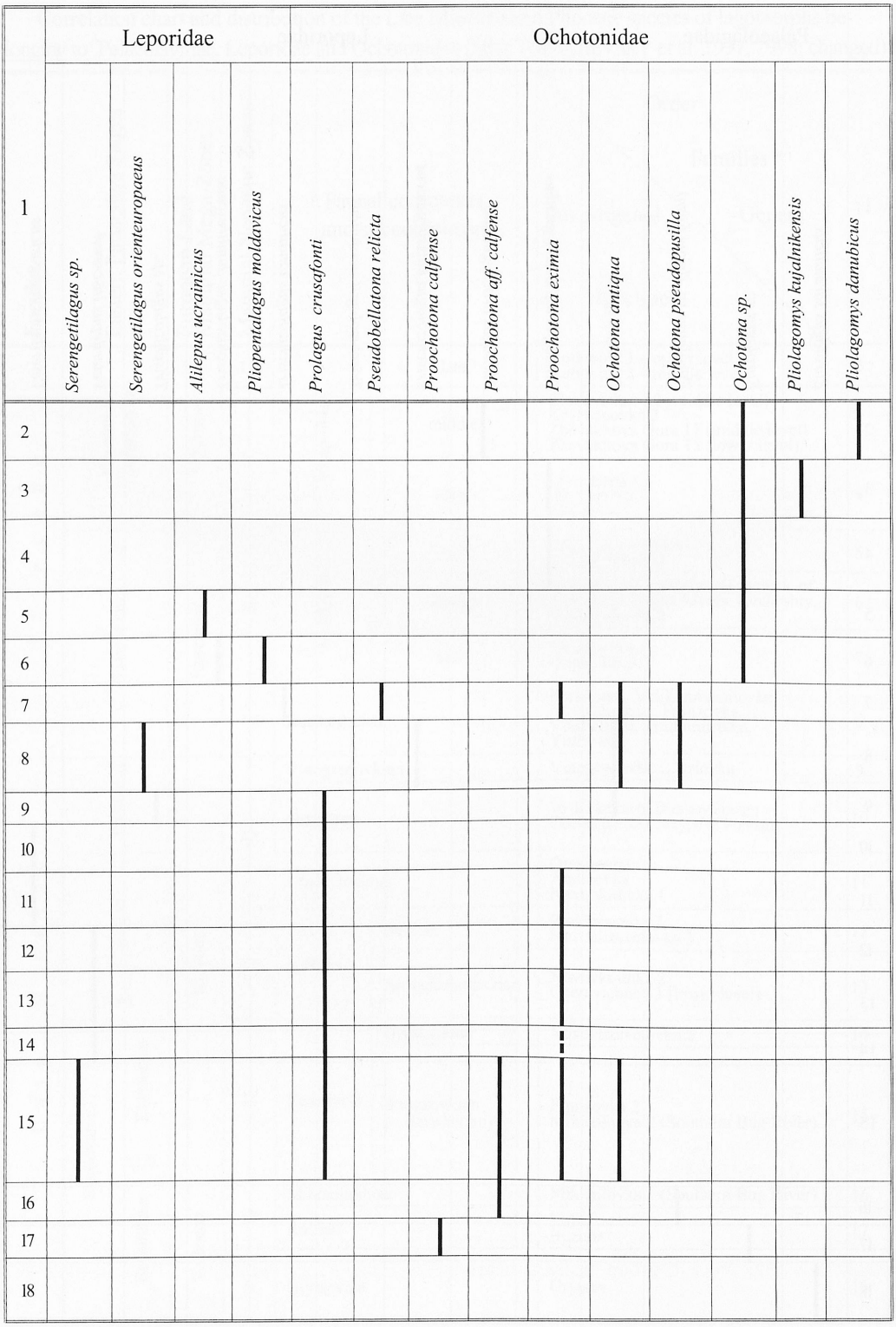
Table II ctd


Leporidae
Ochotonidae
1
Serengetilagus sp.
Serengetilagus orienteuropaeus
Alilepus ucrainicus
Pliopentalagus moldavicus
Prolagus crusafonti
Pseudobellatona relicta
Proochotona calfense
Proochotona aff. calfense
Proochotona eximia
Ochotona antiqua
Ochotona pseudopusilla
Ochotona sp.
Pliolagomys kujalnikensis
Pliolagomys danubicus
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18

Mikhailovka 1 fauna is characterized by the predominance of Desmaninae, especially *Mygalinia* Schreuder, 1940 (=*Ruemkelia* RZEBIK-KOWALSKA et PAWŁOWSKI, 1994) and *Desmana* GÜLDENSTAEDT, 1877. Lagomorphs are still represented by primitive taxa: *Eurolagus* (large form) and *Proochotona*. There appear microtoid cricetids of the genus *Ischymomys* ZAZHIGIN, 1977 (Ischymomyini) which, together with the first true Cricetini of genus *Stylocricetus* TOPACHEVSKY et SKORIK, 1992, predominate among rodents. *Progonomys* is a representative of Muridae (NESIN 2000).

It is probable that small mammals of Mikhailovkian faunistic complex can be correlated with the large mammal complex distinguished by KOROTKEVICH (1988). However, that author failed to define the geological background properly. The section in Mikhailovka consists of several layers with terrestrial and freshwater mollusc fauna which can be correlated with Dniepropetrovsk beds of uppermost Bessarabian and ostracods which probably indicate upper Sarmatian (=Khersonian) age (TOPACHEVSKY et al. 1992). The presence of *Eurolagus* in Mikhailovka 1 rather suggests late Bessarabian age (NESIN 2000). This complex represents the terminal phase of development of Vallesian faunas and has no analogues in Western Europe. Most probably, the Mikhailovkian complex belongs to the upper part of MN 10 Zone.

TUROLIAN – EUROPEAN LAND MAMMAL MEGA-ZONE

MN 11 – European Land Mammal Zone

Berislavian (=Beryslavsky)

R e f e r e n c e l o c a l i t y: Berislav, Khersonian Province, Ukraine.

Subcomplex: Frunzovkian (=Berislavian)

R e f e r e n c e l o c a l i t y: Berislav (for large mammals) and Frunzovka 2, Frunzovskiy District, Odesskaya Province, Ukraine (for small mammals).

Subcomplex: Grebenikian (=Grebenykivsky)

R e f e r e n c e l o c a l i t y: Grebeniki, Velikomikhailovskiy District, Odesskaya Province, Ukraine (for large mammals) and Novoelizavetovka 2 (=Novoelyzavetivka 2 in NESIN & TOPACHEVSKY 1999), Shiryaevskiy Distict, Odesskaya Province, Ukraine (for small mammals).

The Berislavian complex was distinguished by KOROTKEVICH (1988) on the basis of large mammal fauna and can be divided into two subcomplexes: Frunzovkian (=Berislavian), defined also by small mammals (TOPACHEVSKY et al. 1997), and Grebenikian, distinguished on the basis of large mammals (KOROTKEVICH 1988). TOPACHEVSKY et al. (1997) distinguished Novoelizavetovka 2 fauna as a reference locality of Grebenikian for small mammals.

A taxonomic composition of Frunzovka 2 (Frunzovkian) fauna is characterized, in comparison with other assemblages, by a distinct increase in species indicative of aridity of the climate. Unfortunately, insectivores are scarce and faunal analyses are based entirely on rodent and lagomorph assemblages. Among lagomorphs, *Prolagus* POMEL, 1853 preserved its predominant position in comparison with *Proochotona* and *Ochotona* LINK, 1795, other leporids being under study. The rodent assemblage is characterized by an almost complete change of its faunal composition. Probably at this time there took place a great migration event of Asian forms into the northern part of Eastern Paratethys. The first appearance of fivedigital dipodids (Allactaginae) (which in classic Asian localities Pavlodar, Ertemte, Wa-Yao-Po occur at the Miocene/Pliocene boundary), is observed. Already as a predominant group, there appears genus *Paralactaga* YOUNG, 1927 (Allactaginae),

accompanied by Ischymomyini (Table I). Among murids, *Occitanomys hispanicus* MICHAUX, 1971 is present for the first time (Table III).

The Frunzovka 2 assemblage in this paper is treated as fauna of late Sarmatian (=Khersonian) age, which probably has no analogues among other Eastern and Central Paratethys localities. This subcomplex most probably represents an early Turolian fauna. In almost all previous schemes Frunzovka 2 was treated as an assemblage of Pontian age belonging to the lower part of MN 14 Zone (TOPACHEVSKY et al. 1997, 1998) although NESIN (1996b) and FEJFAR et al. (1997b) already discussed the possible assignation of its fauna to upper Sarmatian (MN 11 Zone).

Insectivore and rodent assemblages of Mikhailovka 2 (Frunzovkian) do not differ distinctly from Mikhailovka 1 (Mikhailovkian). Insectivores *Mygalinia* and *Desmana* (subgenus *Arhaeodesmana* TOPACHEVSKY et PASHKOV, 1983) are still predominant. Among lagomorphs Palaeolagidae definitely disappear while *Proochotona* is still present, with very low frequency. Also, *Ischymomys*, *Stylocricetus,* and *Progonomys cathalai* SCHAUB, 1938 maintain their high frequency in the complex.

Fossil-bearing strata of Mikhailovka 2 are located in Khersonian limestones, just above the zone of contact of middle and upper Sarmatian s.l. Remains of small mammals in Mikhailovka 2 were found directly below the damaged limestones containing shells of marine molluscs (TOPACHEVSKY et al. 1997). The same stratigraphic position was occupied by a large mammal assemblage in Berislav (KOROTKEVICH 1988). It is clear that both faunas can be correlated with MN 11 Zone.

The second Grebenikian subcomplex, represented by fauna of Novoelizavetovka 2, is characterized by a distinct change in faunal composition. Insectivores are represented above all by Soricidae: *Amblycoptus* KORMOS, 1926 (Amblycoptini) and cf. *Sulimskia* REUMER, 1984 (Blarinini), which appear for the first time. The soricid fauna replaced desmans (Desmaninae) which played a predominant role in the previous Mikhailovka 2 assemblage. Lagomorphs change their faunal composition completely. The first true leporids are represented by *Veterilepus* RADULESCU et SAMSON, 1967 while among ochotonids genus *Prolagus* (Prolaginae) is predominant. Among rodents, instead of Ischymomyini, the predominant position is occupied by true Cricetini represented by *Kowalskia* and murids of the genus *Apodemus* KAUP, 1829. *Lophocricetus* SCHLOSSER, 1924 (TOPACHEVSKY et al. 1984), and first Zapodidae of the genus *Eozapus* PREBLE, 1899 are relatively common.

Fossil small mammals of Novoelizavetovka 2 were found in gravels above sandy sediments with *Mactra* molluscs of upper Sarmatian (=Khersonian) age (TOPACHEVSKY et al. 2000a). The profile of Novoelizavetovka yielded two additional fossil mammal assemblages: the first one, with large mammals of middle Turolian age, named Novoelizavetovka 1 (KOROTKEVICH 1988), deposited above Novoelizavetovka 2, and the second – a small mammal assemblage Novoelizavetovka 3, in the upper part of the section, belonging to MN 12 Zone. The Grebenikian subcomplex may be considered a typical Turolian assemblage. Such faunas developed throughout the Maeotian.

Both Frunzovkian and Grebenikian subcomplexes should probably be correlated with MN 11 Zone, showing relatively different faunal compositions. Frunzovka 2 and Mikhailovka 2 seem to have no analogues in Europe and probably define the beginning of MN 11 Zone. Most probably, the Novoelizavetovka 2 site represents the uppermost phase of MN 11 Zone and can be correlated with Dorn-Dürkheim in Central Europe.

MN 12 – European Land Mammal Zone

Belkian (=Bilkynsky)

R e f e r e n c e l o c a l i t y: Belka, Rozdelnyanskiy District, Odesskaya Province, Ukraine

Table III

Correlation chart and distribution of the Late Miocene and Pliocene species of rodents belonging to Zapodidae, Dipodidae, Spalacidae, Muridae, Cricetidae and Lophiomyidae (after TOPACHEVSKY et al. 1997, 1998; changed)

Epoch	Eastern Paratethys Stages	European Land Mammal Mega-Zones	Mammal Neogene Zones	Faunal complexes and subcomplexes		Order / Families / Genera / Investigated localities	1
Pliocene	1.7 Kuyalnikian =Akchagylian	Villanyian	17	Khaprovian	late	Kotlovina 3 – upper level Kotlovina 2 – middle level	2
			16		middle	Cherevichnoe 2 (middle level) Kryzhanovka 2 Zhevakhova Gora 11 (middle level) Zhevakhova Gora 15 (lower level)	3
					early	Liventsovka Obukhovka 2 Shirokino	4
	3.4 Kimmerian	Ruscinian	15	Moldavian	late	Odessian catacombs Vinogradovka 3	5
					middle	Kotlovina 1 (lower level), gravels of Salcha and Kagul Rivers, Lucheshty, Vinogradovka 2	6
					early	Obukhovka 1 Grebeniki 2	7
			14	Kuchurganian		Krasnopol, Velikomikhailovka, Novopetrovka, Frunzovka 1, Voinichevo, Trudomirovka, Yurkovka	8
Late Miocene	5.4 Pontian	Turolian	13	Vinogradovkian		Vinogradovka 1, Orlovka	9
				Fontanian		16 th Station of Bolshoy Fontan = Odessa (lectostratotype of Pontian)	10
	7.1 Maeotian 9.88			Cherevichnian		Orekhovka Andreevka Novoukrainka 1	11
			12	Belkian	Belkian	Protopopovka 3 Novoelizavetovka 3	12
					Novoelizavetovkian	Novoukrainka 2 Cherevichnoe 3 (lower level)	13
	Sarmatian s.l. Khersonian 11.0		11	Berislavian	Grebenikian	Novoelizavetovka 2	14
					Frunzovkian (= Berislavian)	Frunzovka 2 Mikhailovka 2 (Southern Bug River)	15
	Bessarabian	Vallesian	10	Mikhailovkian		Mikhailovka 1 (Southern Bug River)	16
				Kalfian		Kalfa Buzhor	17
			9	Grytsevian		Grytsev	18

Table III ctd

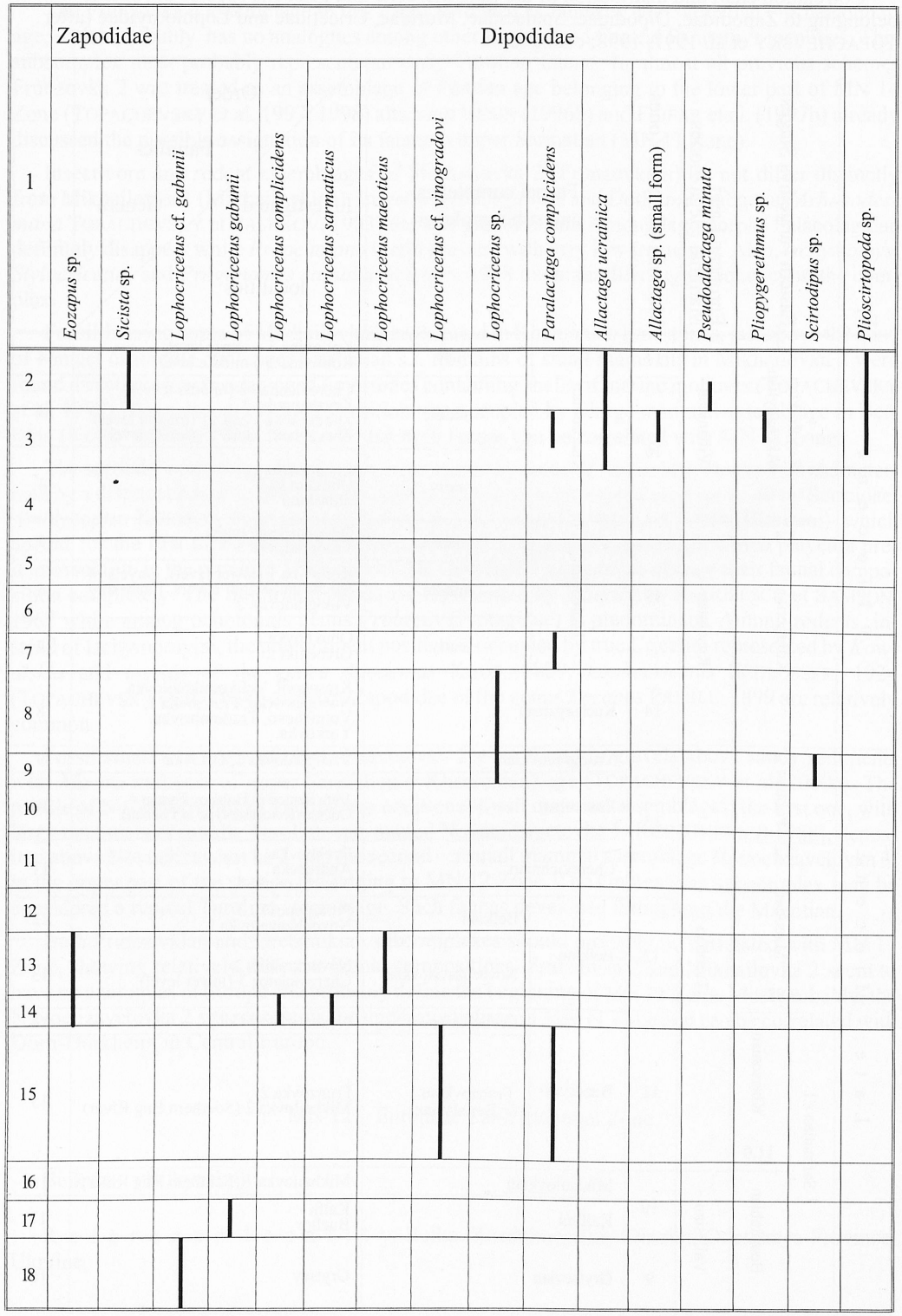
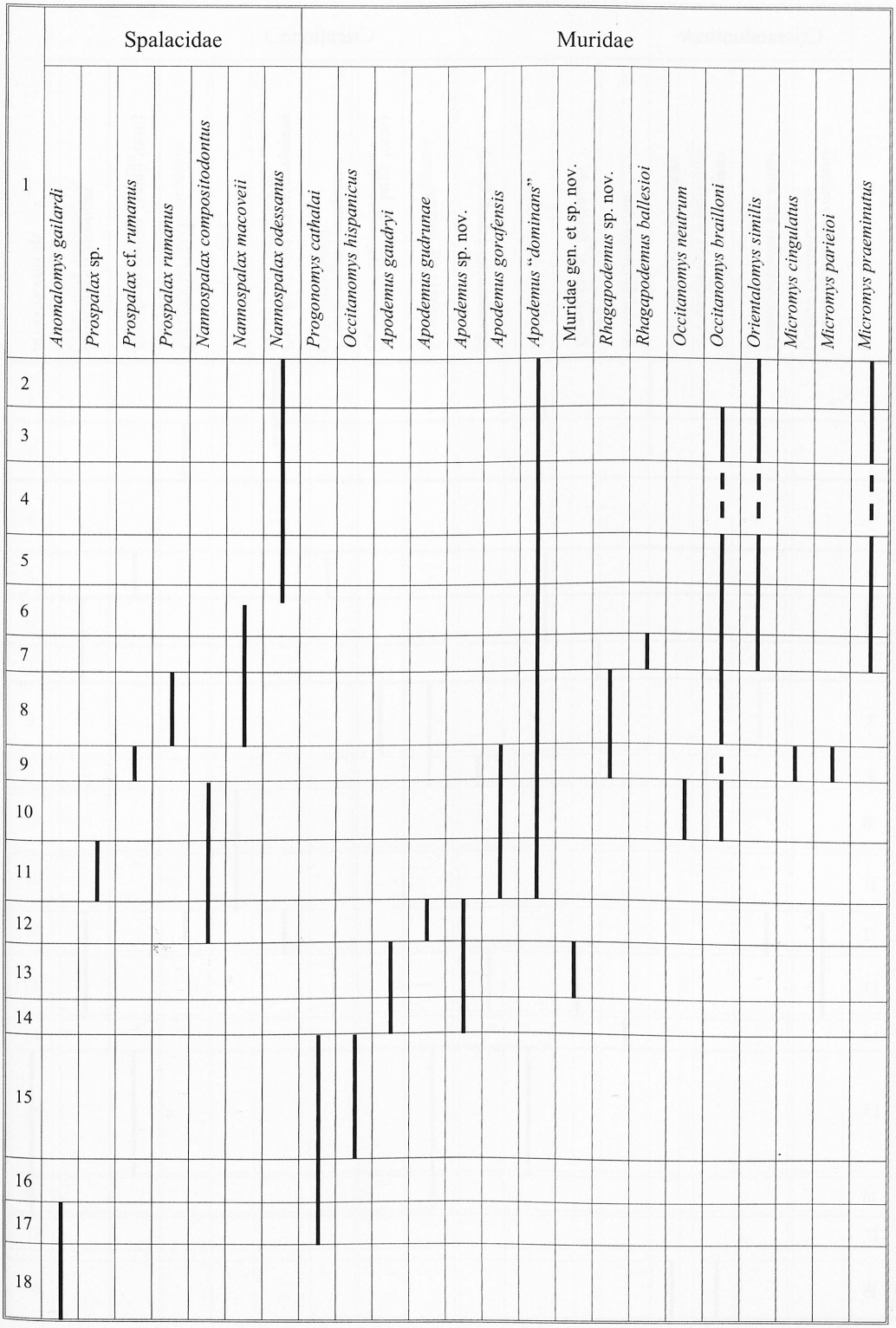


Table III ctd



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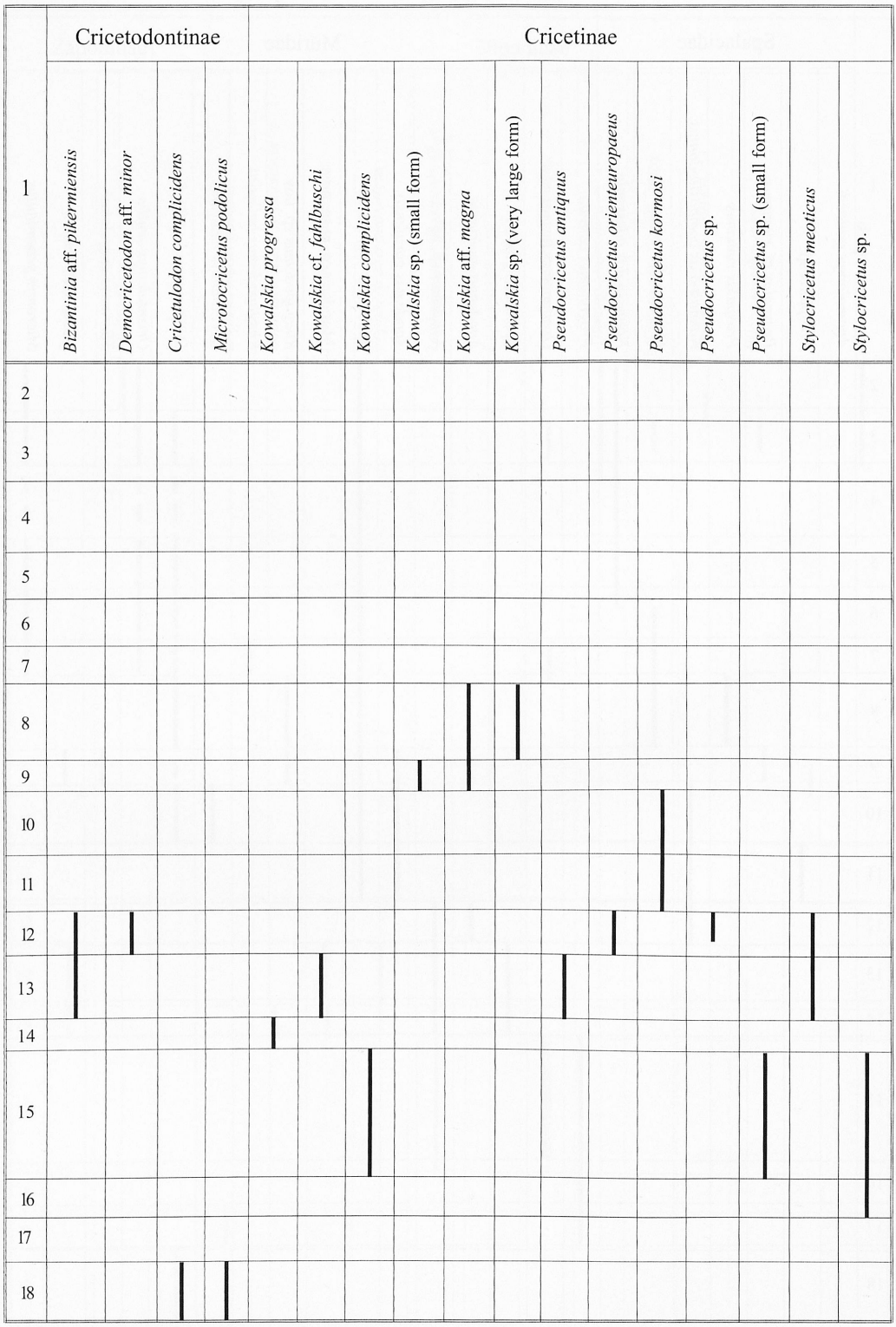

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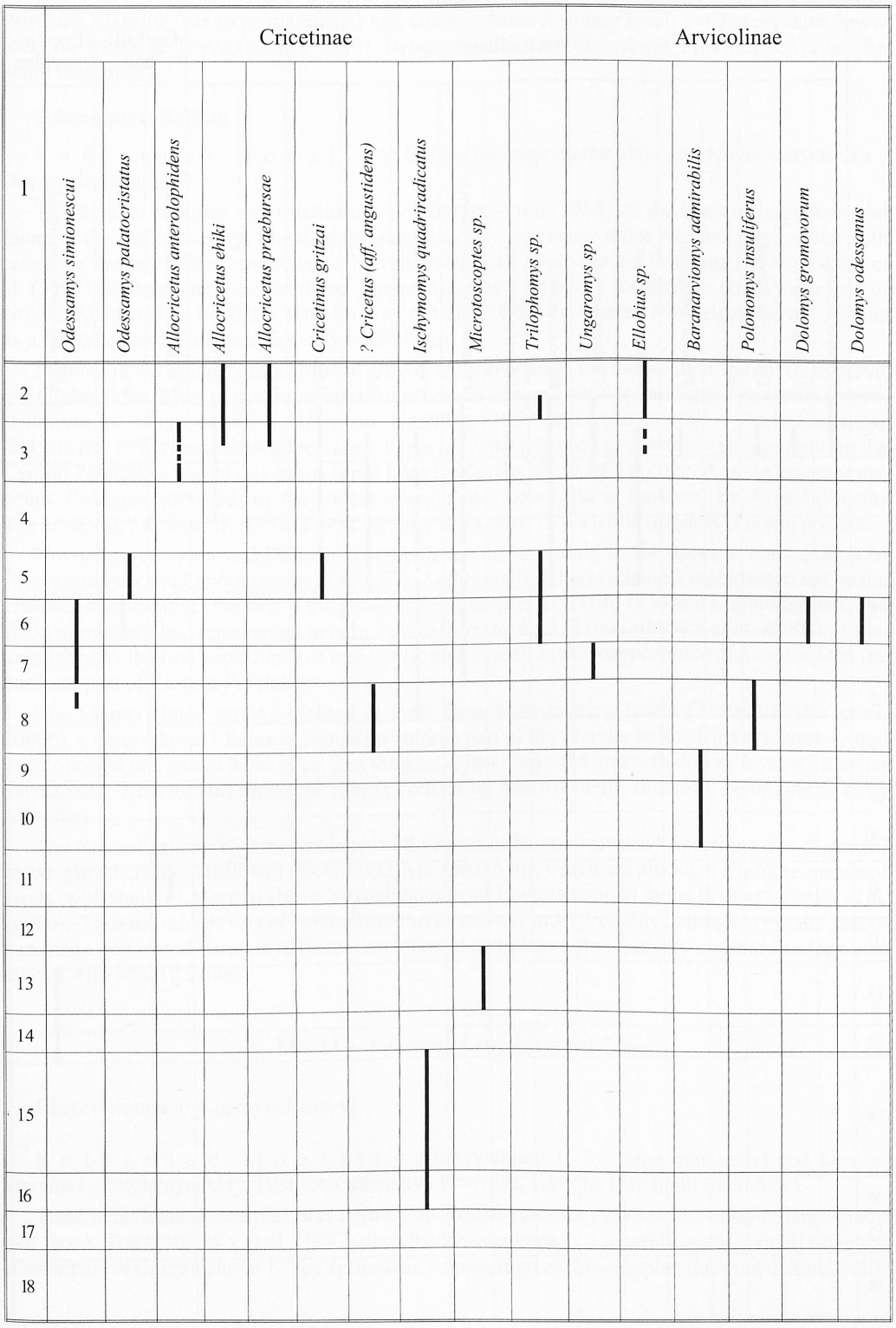

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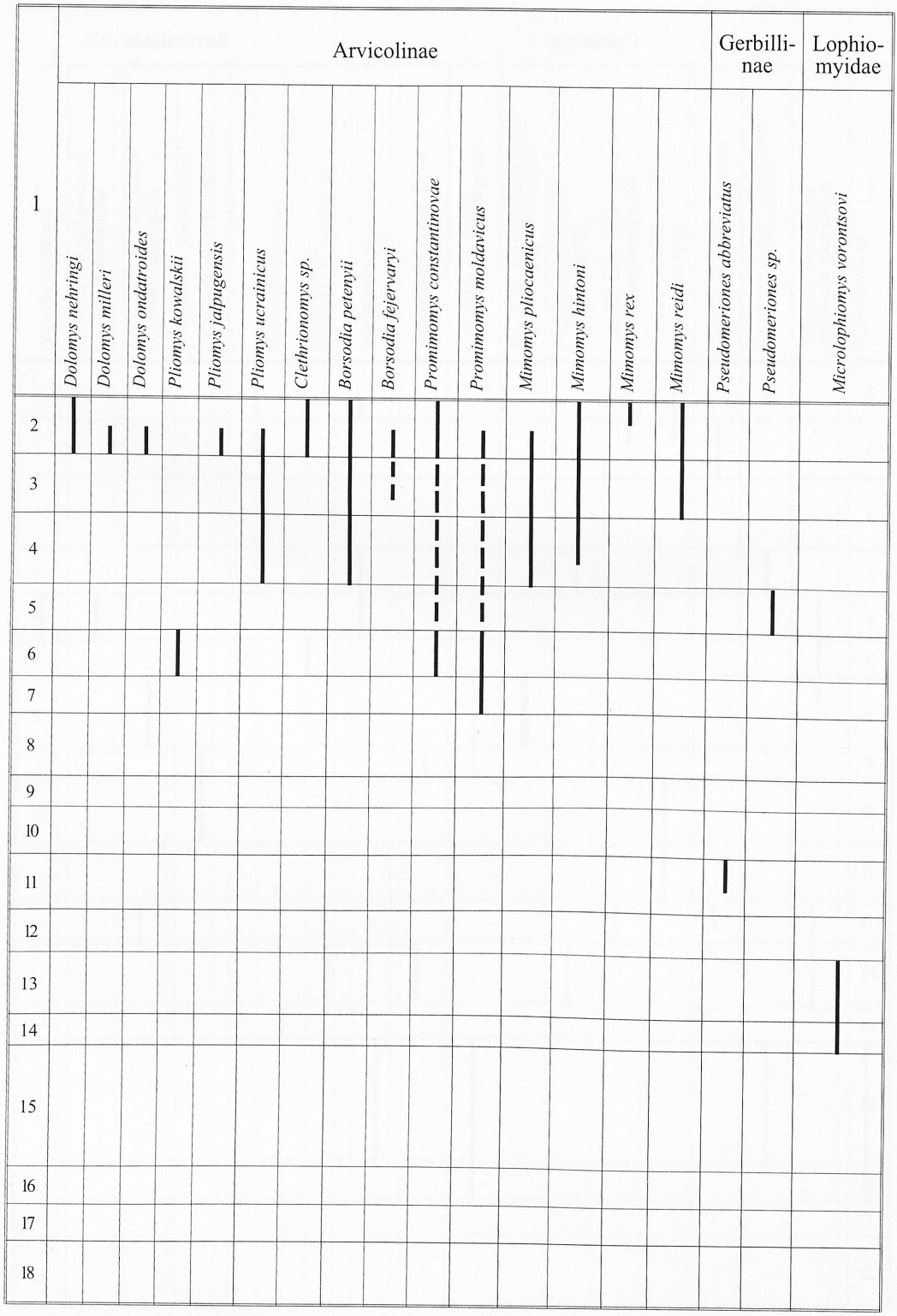

Subcomplex: Novoelizavetovkian

R e f e r e n c e l o c a l i t y: Novoelizavetovka 1, Shiraevskiy District, Odesskaya Province, Ukraine (for large mammals) and Cherevichnoe 3 (lower level) (=Cherevychne, lower level, in NESIN & TOPACHEVSKY 1999), Belaevskiy District, Odesskaya Province, Ukraine (for small mammals).

Subcomplex: Belkian

R e f e r e n c e l o c a l i t y: Belka (for large mammals), and Novoelizavetovka 3 (for small mammals).

The Belkian complex was established by KOROTKEVICH (1988) on the basis of large mammal fauna of the Belka locality. She distinguished two subcomplexes: older Novoelizavetovkian with reference locality of large mammals – Novelizavetovka 1, and younger Belkian. TOPACHEVSKY et al. (1997) distinguished Cherevichnoe 3 assemblage as a reference locality for small mammals of Novoelizavetovkian. Recently TOPACHEVSKY et al. (2000a) designated Novoelizavetovka 3 fauna as a reference small mammal locality for Belkian.

In general, the faunal composition of Novoelizavetovkian is not markedly different form previous Grebenikian. Most of insectivorous taxa in Cherevichnoe 3 survived and some new ones (representatives of Oligosoricini – *Miosorex* KRETZOI, 1959 and Allosoricini – *Paenelimnoecus* BAUDELOT, 1972) made their appearance. Especially, the presence of *Miosorex* is important. In the Central Paratethys region this genus is not found in faunas above MN 8 Zone. Among lagomorphs, genus *Prolagus* survived. In the rodent assemblage *Kowalskia* is replaced by *Pseudocricetus* TOPACHEVSKY & SKORIK, 1992 (TOPACHEVSKY & SKORIK 1992) while *Apodemus* is still present.

Novoelizavetovkian and Belkian subcomplexes differ mainly in the specific composition of *Pseudocricetus* and *Lophocricetus* (Table III). Additionally, Cherevichnoe 3 is characterized by the presence of microtoid cricetids of the genus *Microtoscoptes* SCHAUB, 1934 and Lophiomyidae. The Belkian subcomplex, represented here by Novoelizavetovka 3 (TOPACHEVSKY et al. 2000a), is distinguished by the first appearance of true Spalacidae as well as the reappearance of *Kowalskia* in the northern part of Eastern Paratethys.

The Cherevichnoe section yielded at least three bone-bearing levels (TOPACHEVSKY et al. 2000b). Cherevichnoe 3 fauna occupies the middle part of the section, below Cherevichnoe 1, and was collected in a gravel layer of ca. 2 m thickness, just above the greenish-clayey layer with upper Sarmatian (=Khersonian) limestone matrix containing *Mactra* shells, therefore belonging to early Maeotian.

The Novoelizavetovka 3 assemblage (middle part of Novoelizavetovka section) was deposited in two gravel layers of different thickness (1.5 m and 0.5 m), which are placed in a long sequence of sands (with shells of *Mactra*) above Novoelizavetovka 1 large mammal fauna (TOPACHEVSKY et al. 2000a). Thus the middle part of Novoelizavetovka section most probably belongs to middle Maeotian Stage. In Central Paratethys Basins such faunal complexes are relatively common and are correlated with MN 12 Zone.

MN 13 – European Land Mammal Zone

Cherevichnian (=Cherevychansky)

R e f e r e n c e l o c a l i t y: Cherevichnoe 1 (for large mammals) and Novoukrainka 1, Rozdelnyanskiy District, Odesskaya Province, Ukraine (for small mammals).

The Cherevichnian complex was defined by KOROTKEVICH (1988) on the basis of large mammal fauna. TOPACHEVSKY et al. (1997) described Novoukrainka 1 assemblage as a small mammal counterpart of Cherevichnoe 1. The systematic composition of this complex does not distinctly dif-

fer from the previous one. The observed differences occur mainly at species level (Tables II-III). Among insectivores the taxonomic diversity of Soricidae is considerably reduced in comparison with the Belkian (Table I). Blarinini do not change their frequency; there appear Soriculini. Among lagomorphs the assemblage of *Prolagus-Veterilepus* survives with predomination of the former taxon. However, *Veterilepus* is represented by different species (Table II). The principal taxonomic changes take place in murids. They are represented by large and small species of *Apodemus* and subgenus *Hansdebruijnia* STORCH et DAHLMAN, 1995 of the genus *Occitanomys* MICHAUX, 1969. Spalacidae distinctly increase their frequency and are represented by genus *Nannospalax* PALMER, 1903 and *Prospalax* MÉHELY, 1908 which appears for the first time in Eastern Paratethys. Also, the first appearance of gerbillids of the genus *Pseudomeriones* SCHAUB, 1934 occurs (TOPACHEVSKY et al. 1993).

Novoukrainka 1, Andreevka and Orekhovka assemblages represent the terminal phase of development of the Maeotian small mammal faunas. The Cherevichnian faunal complex is situated in the uppermost part of Maeotian, just below sand beds dated for lower Pontian Stage (TOPACHEVSKY et al. 1990). The Cherevichnian complex is probably an equivalent of the lower part of MN 13 Zone.

Fontanian

Reference locality: 16th Station of Bolshoy Fontan (lectostratotype of Pontian), Odessa, Ukraine.

This is the oldest small mammal complex of the Pontian age. Unfortunately, large mammals have so far not been found here. The taxonomic composition and the predominance of main systematic groups do not differ grately from the previous complex. However, in comparison with Cherevichnian, Fontanian is characterized by an increase in Spalacidae, though represented by *Nannospalax* only. In general, the whole assemblage can be considered a Cricetidae-Spalacidae-Muridae association. The diversity of murids is increased (Table III). The biochronologic assessment of Fontanian is based on the first appearance datum of microtoid cricetids represented by non-diagnostic teeth, most probably belonging to *Baranarviomys* NESIN, 1996 (NESIN 1996a). *Baranarviomys* seems to be an index taxon for Pontian age for Eastern Paratethys. The presence of similar taxa in Central Paratethys Basins is characteristic of late Turolian faunas.

The reference site – 16th Station of Bolshoy Fontan – is located at the level of prodeltaic gravels which cover a clayey layer with Pontian nanoplankton and malacofauna, just below the series of clays and marls distinguished as a lectostratotype of Pontian (TOPACHEVSKY et al. 1988). This series shows reversed magnetisation (TRUBIKHIN 1984). It seems that Fontanian complex may be considered an equivalent of MN 13 Zone, although, TOPACHEVSKY et al. (1998) referred it to the lower part of MN 14 Zone.

Vinogradovkian

Reference locality: Vinogradovka 1, western bank of Yalpug Lake, Bolgradskiy District, Odesskaya Province, Ukraine.

The species composition indicates an increase in humidity of the climate. Lagomorphs become more frequent This tendency is also preserved in the next Kuchurganian complex. As in previous assemblages, *Prolagus* is a predominant form, while Leporidae change their species composition entirely. Genus *Trischizolagus* RADULESCU et SAMSON, 1967 appears for the first time. Among rodents, microtoid cricetids (genus *Baranarviomys*) are predominant. Spalacidae are still frequent, but when compared with previous assemblages only *Prospalax* is present. Primitive cricetids are represented by genus *Kowalskia*. Among murids, *Micromys* DEHNE, 1841 and *Rhagapodemus* KRETZOI, 1956 appear for the first time.

Faunal assemblages are deposited in prodeltaic sediments which occur in series of sands with *Cardium* of Pontian age (PRISYAZHNYUK & SHEVCHENKO 1987; TOPACHEVSKY et al. 1997). The Vinogradovkian faunal complex refers to the upper part of the lower Pontian and has no direct analogues in Central Paratethys Basins, however, it could be correlated with the upper part of MN 13 and/or lower part of MN 14 Zones. TOPACHEVSKY et al. (1998) dated Vinogradovka 1 fauna as belonging to MN 14 Zone.

RUSCINIAN – EUROPEAN LAND MAMMAL MEGA-ZONE

MN 14 – European Land Mammal Zone

Kuchurganian

R e f e r e n c e l o c a l i t y: Krasnopol, Frunzovskiy District, Odesskaya Province, Ukraine

Insectivores are represented by scarce remains of genus *Desmana* (subgenus *Galemodesmana* TOPACHEVSKY et PASHKOV, 1983) which in following Moldavian and Khaprovian complexes becomes a constant element of fossil assemblages. The Kuchurganian complex represents a further stage of development of Ruscinian lagomorph faunas. Among ochotonids the genus *Ochotona* predominates over *Prolagus,* while among leporids *Trischizolagus* predominates over *Serengetilagus* DIETRICH, 1941. In rodents, evolutionary advanced *Polonomys* KRETZOI, 1965 replaces the primitive *Baranarviomys*. *Kowalskia* still predominates among cricetids. Also, there appears, for the first time in this assemblage, cf. *Cricetus* LESKE, 1779 which is morphologically closely related to *Cricetus angustidens* DEPERET, 1880 and/or *Cricetus barrierei* MEIN et MICHAUX, 1970. Spalacids are once more represented by *Nannospalax* but *Prospalax* (*P. rumanus* SIMIONESCU, 1930) survives, though with low frequency. Distinct changes occur in the murid fauna: there appear *Micromys*, *Occitanomys* MICHAUX, 1969. The appearance of cf. *Apodemus* (a taxon probably related to *A. dominans* KRETZOI, 1959) is observed.

This faunal complex probably refers to lower Kimmerian, which in the Northern Prichernomorie region is represented by continental sediments. The fauna was found in sands and gravels of Kuchurganian age (TOPACHEVSKY et al. 1997). Assemblage composition seems to be correlated with the uppermost phase of early Ruscinian faunas dated at MN 14 Zone.

MN 15 – European Land Mammal Zone

Moldavian

R e f e r e n c e l o c a l i t y: Kotlovina 1 (lower layer), western bank of Yalpug Lake, Reniyskiy District, Odesskaya Province, Ukraine (for both large and small mammals).

The most characteristic feature of insectivore assemblage is a distinct increase in Soricidae frequency. Predominant forms belong to the tribe Soriculini (*Neomysorex* RZEBIK-KOWALSKA, 1981). Other soricids represented by *Paranourosorex* RZEBIK-KOWALSKA, 1975 (Amblycoptini) occur with lower frequency. In Moldavian complex faunas there appear for the first time representatives of the tribe Beremendini (*Beremendia* KORMOS, 1930) which survive till Villanyian. An early and middle part of Moldavian complex is characterized by the predominance of lagomorphs. However, in comparison with the previous Kuchurganian complex, the number of Ochotonidae is markedly higher (*Ochotona* – several species, *Proochotona*, *Pliolagomys* ERBAJEVA, 1983) (Table II). The genus *Trischizolagus* (Leporidae) is represented by other species and, moreover, in the middle

Moldavian there additionally appears genus *Pliopentalagus* GUREEV et KONKOVA, 1964. Only in late Moldavian is the occurrence of *Alilepus* DICE, 1931 recorded. Among rodents the predominant position is taken by *Promimomys* KRETZOI, 1955 (Arvicolinae) and *Odessamys* TOPACHEVSKY et SKORIK, 1992 (Cricetinae). The diversity of arvicolines increases with time and in successive subcomplexes they are represented by: *Promimomys*, *Dolomys* NEHRING, 1898 – *Promimomys* – *Pliomys* MÉHELY, 1914, and *Promimomys* – *Pliomys*, respectively. Similar changes in species composition concerns the genera *Odessamys* and *Nannospalax* (Table III). Muridae maintain their species diversity as well (*Occitanomys*, *Orientalomys* DE BRUIJN et VAN DER MEULEN, 1975, *Apodemus, Rhagapodemus* and *Micromys*).

It is important to note that representatives of camelids (genus *Paracamelus*, SCHLOSSER, 1903) reappear in the region, having become predominant large mammals during the terminal phase of Moldavian.

In general, the faunal composition of the complex confirms an increase in aridity of the climate in Southeastern Europe. This complex was established by ALEXEEVA (1961) in Kotlovina 1 and is traditionally correlated with fluviatile deposits of lower Pliocene – Kimmerian Stage (TOPACHEVSKY & NESIN 1989). However, correlation with marine sediments of Kimmerian Stage are so far not fixed. This complex may be correlated with faunas of Séte, Csarnota 2, Ivanovce, and Węże, belonging to MN 15 Zone.

MN 16 and MN 17 – European Land Mammal Zones

Khaprovian

R e f e r e n c e l o c a l i t y: Zhevakhova Gora (layers 11 and 15), village Kotovka, Odessa, Ukraine (for small mammals) and Khapry (for large mammals).

Khaprovian is characterized by distinct changes in faunal composition in almost every systematic group. First of all a decrease in lagomorph frequency is observed. Various groups of rodents play a major role in this complex. Khaprovian is mainly distinguished by a significant development of Arvicolinae (*Borsodia* JÁNOSSY et VAN DER MEULEN, 1975; *Mimomys* F. MAJOR, 1902; *Ellobius* FISCHER VON WALDHEIM, 1814) as well as Cricetinae (*Allocricetus* SCHAUB, 1930), Dipodidae (*Allactaga* F. CUVIER, 1836), and Marmotinae (*Spermophilus* CUVIER, 1825: subgenus *Urocitellus* OBOLENSKY et BRANDT, 1827). Some other arvicolines (*Dolomys* NEHRING, 1898, *Pliomys* MÉHELY, 1914 and *Promimomys*) change their species composition (Table III). Representatives of murids are diversified and belong to *Apodemus* (small and large species), *Occitanomys, Orientalomys*, and *Micromys*. Among rodents *Borsodia petenyii* (MÉHELY, 1914) seems to be the index species in all associations, being the predominant taxon in most of them. Only in Shirokino and Liventsovka (lower level) assemblages do the species of *Mimomys* prevail (TOPACHEVSKY et al. 1987). At the terminal phase of development of the faunistic complex another species of *Borsodia* – *B. fejervaryi* (KORMOS, 1934) predominats.

This complex occurs in sediments of Kuyalnikian=Akchagylian stage and can be correlated with Villanyian faunas. Khaprovian was established on the basis of large mammal fauna by V. I. GROMOV (1948). TOPACHEVSKY et al. (1979) distinguished a lectostratotype of Khaprovian complex with small mammals in Zhevakhova Gora (layers 11 and 15). Khaprovian is a terminal phase of development of the Pliocene faunas. Assemblages of this complex can probably be correlated with faunas of Rębielice Królewskie (MN 16), Hajnáčka (MN 16), Arondelli (MN 16), Villány 3 (MN 17), and Kadzielnia (MN 17).

III. CONCLUSIONS

Methods for correlating fossil mammal faunas in Southeastern Europe are greatly influenced by the application of "mammal complex" units. The efforts to correlate them with the MN units system was in some cases not successful enough. This is especially well visible with Late Miocene assemblages treated as late Vallesian and Turolian faunas. Most of the distinguished faunal complexes and subcomplexes of Sarmation (Bessarabian and Khersonian), Maeotian, and Pontian age have no analogues with Central and West European assemblages owing to relatively high provinciality observed among small mammal faunas. Also, still insufficient evidence of radioisotopic datings and palaeomagnetic studies impedes this correlation. The proposed age and duration of most of the distinguished complexes should be verified in the future.

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