

**Body size development of  
large mammals during the  
European Neogene:  
Trends and some environmental  
considerations.**

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# 1. Introduction

Body size (whether it means length, volume or mass) is one of the easiest characteristics to estimate in a living mammal. It is also a very valuable characteristic, because it is connected to a multitude of physiological and ecological characteristics. This makes body size a unique characteristic. On the other hand, this also complicates things. Because body size is connected to so many other parameters, it is also affected by many variables. Therefore one can rarely conclude something solid about body size alone. Usually body size gives a signal that is a mix of environmental adaptations, inherited characteristics and in situ adaptations. The latter ones are not always linked to environmental changes and therefore body size has to be interpreted through many different perspectives to make something out of it. For a review of problems to be considered when making body size analyses see Smith (1996). If one knows the strengths and weaknesses of body size analysis, then it can be used to a great extent for reconstruction of past environments.

There have been some studies that have used large datasets in order to find some patterns in body size development or have tried to apply findings of extant species to fossil species. There have been studies on population density and body size (e.g. Damuth 1981), population energy-use and body mass (Damuth 1987), on methods to analyze body size distribution at the community level (Legendre 1989) and on the development of mean body size through time (Alroy 1998), as well as on the preservation of fossil mammal assemblages (Damuth 1982).

Alroy's work (1998) resulted in finding the gap in body mass in the fossil record. It had been known before that there is an area in "body size space" that is occupied by very few species. This can be demonstrated using cenograms (Legendre 1989).

Alroy was the first to identify the time period when the gap started to develop. The development started in the Paleogene and the gap covers the body sizes that fall between 1 kg and 10 kg. There exists very few species of this size, and nobody has clearly demonstrated what is the reason for this gap.

The gap is connected to the idea of Cope's rule. It was discovered by Cope (1887) that the average size of mammals had become larger and larger throughout the Cenozoic. His explanation for this was that new groups of animals start their evolution as small and have a tendency to grow as lineages grow older. The smaller the animal, the more primitive it is. While it is true that within lineages the mean body size tends to grow, it is clearly not a characteristic that is only given to species.

In this study I will focus on the evolution of body size in Eurasian large mammals during the last 25 Ma. The first objective is to create a classification for body size so that one can use body size as a variable through time and space. After this I will try to focus on the ecological meaning of body size distribution and how one can use it in the reconstruction of past environments. One of the key issues in this study is to try to find out if there are some trends in the body size development during the Neogene. First I will focus on the biological significance of body size. Then I will try to summarize the stage where this all happens: the main phenomena concerning the animals and their evolution. After this I will describe the method used in analyzing body mass and the results gained. Finally I will try to interpret the result and try to see the connections to changing ecological and environmental settings.

## **2. Biological basis**

“Why is animal size so important” is the title of Schmidt-Nielsen’s (1984) book on body size. This is indeed an important question. Why do we need body size estimates for fossil mammals? What can body size alone tell about a mammal?

We know that body mass (or body size) is not strictly tied to a single environmental factor (e.g. temperature, precipitation). Instead it is a function of different environmental variables that are forced upon an individual. Therefore one cannot just make a correlation between body size and a single environmental variable.

On the other hand, body mass is one of the most important factors governing the metabolic rate and some other physiological variables. There are a number of excellent books written about the importance of mammal body size (e.g. Peters 1983, Calder 1984, Schmidt-Nielsen 1984). There is also a paper focusing on using the variables derived from body mass estimates in fossil data (McNab 1990).

These physiological variables can tell us a lot about the ecology of an animal. They can also be used the other way around, to try to explain the variance in body size through time with environmental changes. For this purpose these variables must be connected to ecological changes. But first the physiological basis. Here I will just summarise these relations, because there is wealth of literature on this subject.

### **2.1. Metabolism**

The relation between metabolic rate and body size was first discovered by Kleiber (1932, 1961). He showed that in most animals the basal metabolic rate (see e.g. Peters 1983) scales about as  $\frac{3}{4}$  power of body mass. The actual scaling power usually falls between 0.67 and 0.75 for different animals (McNab 1990) and it is also dependent on some other variables besides body size (like activity level, climate and temperature). The approximation of 0.75 is a good mean and easy to use in calculations.

The metabolic rate influences many other biological variables (of which respiration and ingestion are ecologically the most significant), so it is very useful to be able to calculate the basal metabolic rate of species.

Most of the other physiological variables work in simple power laws, which are derived from the metabolic rate. For example, the next variable to be discussed, the respiration rate, is simply  $M^{-0.26}$ . That is about  $M^{-1/4}$  which is  $1 / M^{1/4}$ .  $M^{4/4} \times M^{-1/4} = M^{3/4}$ . This means that when you multiply total body mass by body mass raised to -0.25 power (the respiration rate) you get the metabolic rate. You can get most of the physiological rate-variables by simple power equations derived from the metabolic rate and the 1/4 rule.

There are many papers that discuss the reason why physiological variables scale as 1/4 and why metabolic rate scales as  $3/4$  power of body mass. For the latest theories look at West *et al.* (1997, 1999a, 1999b) and Banavar *et al.* (2002).

## **2.2. Respiration**

The respiration rate is one of the key characters of an individual. This is because respiration is a one way system that is always negative. In this sense it is a fair approximation for the energy cost of an individual from the ecosystem's viewpoint. It does not have many uses as such in paleontology, but is sometimes used in combination with other variables. Respiration scales as  $-0.26$  to body mass (Stahl 1967).

## **2.3. Ingestion**

Ingestion rate means the ratio with which the different animals convert food to energy. Ingestion rate is dependent on metabolic rate. The metabolic rate can also be understood as the energy demand of an individual. In other words, the metabolic rate demands a certain amount of ingestion so that the animal survives.

The dietary preferences have almost no effect on the basal ingestion rate. Basal food intake is about 0.70 power of body mass for herbivores and 0.73 for carnivores (Farlow 1976, Nagy 1987), so as intake in absolute amount increases, proportionally it decreases. The realistic value is somewhere between 2.6 (Farlow 1976) and 4 (Nagy 1987) times the basal rate. So about half, or little more, of the ingested food is converted to energy. For calculations about food requirements one should still use the basal rate, as it is the best estimate.

## **2.4. Locomotion**

Locomotion is also dependent on body size. It has been shown in many studies (see Peters 1983, Schmidt-Nielsen 1984, McNab 1990 and the references therein) that the locomotionary costs increase with increasing body size and velocity. The locomotionary cost scales as 0.69 power of body mass, so the relative cost of moving a certain amount of mass is less for larger animals. The maximum speed of an animal increases with body size by 0.17 fold.

## **2.5. Water balance and temperature**

The larger you are, the relatively less water you need. The total intake of water and water that evaporates from the animal as perspiration etc. scale as 0.86 power of body mass.

The external heat (outside temperature) fluctuates, so mammals must have ways to maintain their temperature at the same level. Insulators used are feathers, thick skin and fur, which can be used to lessen heat loss. There is a minimum temperature when these are not enough to maintain the heat level. Then the only way to maintain a constant internal temperature is to produce more heat. Below this point the heat production and heat loss vary with body size. So heat loss and heat tolerance are body size dependent. There are reasons for this: larger animals have smaller relative skin areas. This is because the area grows as a square function ( $L^2$ ) and the volume as a cubic function ( $L^3$ ) when size increases. So the skin area changes in relation by  $L^2 / L^3$ . Furthermore, larger animals have more fur and a thicker skin and can store more fat in their bodies. This has the opposite effect when we consider the maximum temperatures that animals can

tolerate. Larger animals have more difficulty getting rid of their external heat when they are over-heated.

## **2.6. Time**

When we deal with animals, we usually use two different notions of time. One is actual time, with the day and night, the seasonal variation etc. The other is physiological time. Physiological time is best represented by the metabolic rate. As the metabolic rate is the same in all creatures, all creatures can enjoy about the same physiological time in their normal lifetime.

Yet, the hearts of small creatures beat faster, their respiration is faster and their metabolic turnover is quicker. So in real time they live a shorter span. In larger creatures time goes more slowly. This is explained by the equation  $M^{1/4} \times M^{-1/4} = M$ , where  $M^{1/4}$  is the metabolic rate increase and  $M^{-1/4}$  is the metabolic time increase. So they negate each other, and the physiological time remains the same whatever the size of the organism is. Real lifetime increases with body size.

## **2.7 Growth & reproduction**

Growth rate is a function of body mass. Time to sexual maturity is a function of body mass, as is the time of growth to adult size (e.g. Blueweiss *et al.* 1978, Peters 1983). Litter size is also dependent on body mass, although it is known to be bimodal. It seems to be relatively smaller with growing size. It seems that parental energy investment is lesser with larger animals and the development time longer (Blueweiss *et al.* 1978).

## **2.8. Population density**

Population density is not strictly connected to body size. This is because larger animals need more energy, and therefore the environment can sustain a lesser amount of larger animals than small ones. For herbivorous mammals the local population density is a negative exponent by which the metabolic rate increases (Damuth 1981). Within one trophic group the population energy use is body size independent. This means that the

population uses the same amount of energy, but the amount of individuals in the population is influenced by body size, so there is a negative relationship.

## **2.9. Home range size**

McNab's (1963) study showed that home range size varies as a function of body mass. This relationship is not far from that of size and metabolic rate. It has been shown (e.g. Harestad & Bunnell 1979, Swihart *et al.* 1988) that home range size is influenced also by the trophic level and different energy demands. It is also influenced by the behavior of individual species. There are studies on predicting home range using fractal geometry (Haskell *et al.* 2002) that show that there is a relationship between size and home range size, but it is not constant, as was thought before. Home range increases when habitats are more fragmented and energy sources more scattered.

### **3. Paleobiology & paleontological context**

The studied time period is from the start of the Neogene (25 Ma (mega-annum, millions of years) ago) to the mid-Pleistocene (about 1,8 Ma ago), the Villafranchian. The whole Neogene is covered as is part of the Quaternary. The basis for the analysis was the faunal data and faunal time-units, so that is why a part of the Quaternary was included also. This is if we use 2,5 Ma as the beginning of the Quaternary (as is the tradition among north-European Quaternary scientists). In central Europe and in the Mediterranean area it is usually placed at 1,8 Ma, because of differences in terrestrial and marine stratigraphy. 1,8 Ma is the limit according to marine stratigraphy.

The Miocene period covers most of the Neogene, from 25 Ma to 5,32 Ma ago. Here I'll explain something about the environmental conditions and the development of mammalian communities.

#### **3.1. Stratigraphy**

Usually the Miocene period is divided into three parts (tables 1, 2 and 3): early, middle and late Miocene. In addition there are various zones and age-categories for measuring time. There are local timescales, regional timescales, mammal zonation, pollen zonation, foraminifera and nannoplankton biozonations etc. For this study I will use only Mammals Neogene (MN) zones and Mammal megazones following Steininger (1999). If I will use other zonation, I will also refer to absolute time in Ma.

Based on oxygen isotopes (Shackleton & Kennett 1975, Miller *et al.* 1991) we can say that the early Miocene was very warm. The warmest climate of the Neogene was in the late early Miocene (c. 16 Ma ago). After this the temperatures started to decline. Around 15 Ma started the period that is known as the mid-Miocene cooling. It lasted from 14.8 Ma to 14.1 Ma (Flower & Kennett 1994), and was a turning point in the climatic development of the Neogene. So based on oxygen isotopes the Neogene can be divided into two distinct periods: the early Neogene warm period (25 – 15 Ma) and the late Neogene cool period (15- 2,5 Ma). After 2,5 Ma the world entered the Quaternary period, which is the time of extensive glaciations in the northern continents.

Table 1. Lower Neogene timescale (Steininger 1999)

TIME (Ma)	CHRONOS	POLARITY	PLANKTON - BIOZONATIONS				EUROPEAN LAND MAMMAL		EPOCH		AGES			
			FORAMINIFERA Baiggen et al. (1996)	BIOL (1989)	NANNOP/LANKTON Martini (1971)	BURKY (1973, 1975)	MEGA - ZONES	MN - ZONES	OLIG.	CHATT.	KALM.	MED	EAST PARA	EAST PARA
15	CSADn	[Normal]	M 7	Gt. parthoracuta Lin Z	N 10	CN 4	ASTARACIAN	MN 6	MIDDLE	LANGHIAN	SERR	BADENIAN	TARKHANIAN	
			M 6	O. sutur - Gt. parthor. IZ	N 9									
16	CSBR	[Normal]	M 5	b	Pr. glomerosa - O. suturalis ISZ	N 8	CN 3	ORLEANIAN (5.5 Ma.)	MN 5 (2.0 Ma.)	MIDDLE	LANGHIAN	SERR	BADENIAN	TARKHANIAN
				a	Pr. sicana - O. suturalis Z									
			M 4	a	Pr. sicana - Pr. parvica ISZ	N 7								
				b	Gt. insularis - RSZ Gt. dactylina - Gt. bispina IZ									
17	CSCh	[Normal]	M 3	Globigeninella insularis - Catapsydrax disirnilis Conc. RZ	N 6	CN 2	ORLEANIAN (5.5 Ma.)	MN 3 (2.5 Ma.)	MIDDLE	LANGHIAN	SERR	BADENIAN	TARKHANIAN	
				Conc. RZ										
18	CSDn	[Normal]	M 2	Catapsydrax disirnilis IZ	N 5	CN 1	ORLEANIAN (5.5 Ma.)	MN 2 (2.0 Ma.)	MIDDLE	LANGHIAN	SERR	BADENIAN	TARKHANIAN	
														Conc. RZ
19	CSEn	[Normal]	M 2	Catapsydrax disirnilis IZ	N 5	CN 1	ORLEANIAN (5.5 Ma.)	MN 2 (2.0 Ma.)	MIDDLE	LANGHIAN	SERR	BADENIAN	TARKHANIAN	
														Conc. RZ
20	CSEn	[Normal]	M 2	Catapsydrax disirnilis IZ	N 5	CN 1	ORLEANIAN (5.5 Ma.)	MN 2 (2.0 Ma.)	MIDDLE	LANGHIAN	SERR	BADENIAN	TARKHANIAN	
														Conc. RZ
21	CSEn	[Normal]	M 2	Catapsydrax disirnilis IZ	N 5	CN 1	ORLEANIAN (5.5 Ma.)	MN 2 (2.0 Ma.)	MIDDLE	LANGHIAN	SERR	BADENIAN	TARKHANIAN	
														Conc. RZ
22	CSEn	[Normal]	M 2	Catapsydrax disirnilis IZ	N 5	CN 1	ORLEANIAN (5.5 Ma.)	MN 2 (2.0 Ma.)	MIDDLE	LANGHIAN	SERR	BADENIAN	TARKHANIAN	
														Conc. RZ
23	CSEn	[Normal]	M 2	Catapsydrax disirnilis IZ	N 5	CN 1	ORLEANIAN (5.5 Ma.)	MN 2 (2.0 Ma.)	MIDDLE	LANGHIAN	SERR	BADENIAN	TARKHANIAN	
														Conc. RZ
24	CSEn	[Normal]	M 2	Catapsydrax disirnilis IZ	N 5	CN 1	ORLEANIAN (5.5 Ma.)	MN 2 (2.0 Ma.)	MIDDLE	LANGHIAN	SERR	BADENIAN	TARKHANIAN	
														Conc. RZ

Table 2. Upper Neogene timescale (Steininger 1999)

TIME (Ma)	CHRONONS	POLARITY	PLANKTON - BIOZONATIONS				EUROPEAN LAND MAMMAL		EPOCH		AGES		
			FORAMINIFERA Berger et al. (1986)	NANNIOPANKTON Martini (1971)	BUKRY (1973, 1975)	MEGA - ZONES	MN - ZONES	PLIOCENE	MED.	CENT. PARA.	EAST. PARA.	MESSINIAN	PONTIAN
5	C3n	Normal	PL 1 a	Gd. extensus? Gd. n. ISZ Gd. turrida - Gd. nepenthes ISZ	N19	NN 13	CN 10	RUSCINIAN	MN 14	EARLY	ZANCLIAN	CENT. PARA.	EAST. PARA.
6	C3a	Normal	M 14	Gd. turrida - Gd. nepenthes ISZ	N18	NN 11	CN 8	TUROLIAN (3.8 Ma.)	MN 13 (1.7 Ma.)	LATE	TORTONIAN	PANNONIAN	MAEOTIAN
7	C3a	Normal	M 13	Gd. turrida - Gd. nepenthes ISZ	N17	NN 9a-b	CN 7a-b	TUROLIAN (3.8 Ma.)	MN 12 (1.4 Ma.)	LATE	TORTONIAN	PANNONIAN	MAEOTIAN
8	C4r	Normal	M 13	Gd. turrida - Gd. nepenthes ISZ	N16	NN 10	CN 8	TUROLIAN (3.8 Ma.)	MN 11 (0.7 Ma.)	LATE	TORTONIAN	PANNONIAN	MAEOTIAN
9	C4a	Normal	M 13	Gd. turrida - Gd. nepenthes ISZ	N16	NN 10	CN 8	TUROLIAN (3.8 Ma.)	MN 10 (1.0 Ma.)	LATE	TORTONIAN	PANNONIAN	MAEOTIAN
10	C5n	Normal	M 12	Gd. turrida - Gd. nepenthes ISZ	N15	NN 9a	CN 7a	VALLESIAN (2.4 Ma.)	MN 9 (1.4 Ma.)	LATE	TORTONIAN	PANNONIAN	MAEOTIAN
11	C5r	Normal	M 12	Gd. turrida - Gd. nepenthes ISZ	N14	NN 7	CN 5b	VALLESIAN (2.4 Ma.)	MN 8 (2.4 Ma.)	MIDDLE	SERRAVALLIAN	PANNONIAN	MAEOTIAN
12	C5a	Normal	M 9	Gd. turrida - Gd. nepenthes ISZ	N12	NN 6	CN 5	VALLESIAN (2.4 Ma.)	MN 7+8 (2.4 Ma.)	MIDDLE	SERRAVALLIAN	PANNONIAN	MAEOTIAN
13	C5a	Normal	M 7	Gd. turrida - Gd. nepenthes ISZ	N10	NN 5	CN 4	VALLESIAN (2.4 Ma.)	MN 6 (1.5 Ma.)	MIDDLE	SERRAVALLIAN	PANNONIAN	MAEOTIAN
14	C5a	Normal	M 5	Gd. turrida - Gd. nepenthes ISZ	N9	NN 4	CN 3	VALLESIAN (2.4 Ma.)	MN 5	MIDDLE	SERRAVALLIAN	PANNONIAN	MAEOTIAN
15	C5b	Normal	M 5	Gd. turrida - Gd. nepenthes ISZ	N8	NN 4	CN 3	VALLESIAN (2.4 Ma.)	MN 5	MIDDLE	SERRAVALLIAN	PANNONIAN	MAEOTIAN

Table 3. upper Miocene-Pliocene timescale (Steininger 1999)

PLIOCENE TIME SCALE													
TIME (Ma)	CHRONOS	POLARITY	EPOCH	AGE	PLANKTONIC FORAMINIFERA		PARATETHYS-STAGES		EUROPEAN FAUNAL ZONES	EUROPEAN CHRONOSTRAT STAGES			
					Berggren (1973, 1977, this work)		CENTRAL-	EASTERN-					
					ATLANTIC	INDO-PACIFIC							
PLEISTOCENE													
2	C1r 2r	n	PLIOCENE	GELASIAN	LATE	PL6	<i>Gt. miocenica</i> – <i>Gl. fistulosus</i> IZ	<i>Gt. pseudomiocenica</i> – <i>Gl. fistulosus</i> IZ	STAGES NOT CORRELATED	1.95	1.95	1.95	
	C2n	n				PL5	<i>D. altispira</i> – <i>Gt. miocenica</i> IZ	<i>D. altispira</i> – <i>Gt. pseudomiocenica</i> IZ		2.6	MN - 17		
	C2r	n				PL4	<i>Sph. seminulina</i> – <i>D. altispira</i> IZ			3.4	MN - 16		
3	C2An	1n 2n 3n		PIACENZIAN	MIDDLE	PL3	<i>Gt. margaritae</i> – <i>Sph. seminulina</i> IZ			3.4			
	C2Ar	1n				PL2	<i>G. nepenthes</i> – <i>Gt. margaritae</i> IZ				MN - 15	NOT NAMED	
	C3n	1n 2n 3n 4n				ZANCLIAN	EARLY	PL1		b	<i>Gt. cibaoensis</i> – <i>G. nepenthes</i> ISZ	4.2	RUSCINIAN
	C3r	1n	a	<i>Gt. tumida</i> – <i>Gt. cibaoensis</i> ISZ	4.8				KIMMERIAN	MN - 14			
	C3An1n	1n		<i>Gt. tumida</i> – <i>G. nepenthes</i> IZ	5.3				DACIAN	5.3			
	C3r	1n	MIOCENE	MESS.	LATE	M14	<i>Gt. languaensis</i> – <i>Gt. tumida</i> IZ	5.6	PONTIAN	5.6	TUROLIAN	MN - 13	TUROLIAN

### 3.2. Mammals

Here I will explain only the major trends in mammalian community evolution during the Neogene. The general trends through the Neogene are the evolution of more open-habitat-adapted species, the slow extinction of closed-habitat-adapted species, and overall cooling of climate (Janis 1993).

In another sense, it is a story of six families: Felidae, Hyanidae, Equidae, Rhinocerotidae, Giraffidae and Bovidae. These mammalian families adapted to the changing Eurasian climate, and therefore radiated and diversified (Bernor *et al.* 1979, Bernor 1983, Bernor *et al.* 1984).

The spread of grasses and more open habitats is reflected in mammalian evolution. The development of more hypsodont species through the Miocene is one aspect of this and the other is the development of species with higher locomotionary capacity. Also the

general trend of larger body size through the whole Cenozoic is partly due to increased need for processing large amounts of low-quality food. (Behrensmayer *et al.* 1992)

The Eurasian mammal community was for the earlier part of the Miocene not very diverse. There is no large evolutionary change from Oligocene faunas. Species diversity as such was quite low. These earliest Miocene faunas are interpreted as impoverished Oligocene faunas (Bernor 1983). It is suggested that the reason for this was the geographical isolation of Europe from other continents.

The late early Miocene saw the emergence of large ruminant species. Most small ruminants had disappeared (Savage & Russell 1983). During the early Miocene also the pigs and rhinos diversified. In bovids this is a more general increase, happening in Spain during the Ramblian (Aegean) period (Moya-Sola & Agusti 1990). During the following Aragonian (Orleanian & Astaracian) time the diversity of bovids drops a little. In the Vallesian period the diversity is much lower, but in the Turolian it grows again. In cervids the diversity goes the other way. In Aragonian times they are less diverse, and their diversity peak is only after the Vallesian. (Moya-Sola & Agusti 1990). The diversity of suids is like that of bovids. They diversify radically in the early Aragonian times.

This (the early Miocene) is also a time of immigration - new species came from Asia and some from Africa (Moya-Sola & Agusti 1990). The first emigration wave from Africa comes already in the earliest Orleanian, MN3. This is known as the Proboscidean event, as first interpretations of the event suggested that only proboscideans immigrated (Bernor 1983). The next immigration wave comes already in the start of the Astaracian (MN6), when dispersal barriers (both geographical and ecological) were relaxed. There was an immigration to western Europe by various mammal genera from Africa and Asia (Behrensmayer *et al.* 1992). Artiodactyla as a whole diversified as did carnivores (Bernor *et al.* 1979). The early Miocene climate was warm and moist, in central Europe there were extensive taxodium swamps (Kvacek 1998, Bernor *et al.* 1988) with some tropical elements. This is also the case in western and southern Europe, where the climate was humid, from tropical to sub-tropical – warm temperate (Esu 1999).

In the middle Miocene started the cooling of climate. According to mollusc evidence (Esu 1999) there was a clear change in the climatic conditions of western and southern Europe. This change is probably the cause of the larger habitat variation seen in the mammal localities from the middle Miocene age onwards (Behrensmayer *et al.* 1992). But from the late middle Miocene onwards the climate began warming again, and this trend continued through the Vallesian into the Turolian (Esu 1999).

In the start of the late Miocene occurred the second turnover, which is known as the Vallesian crisis. The Vallesian begins with the immigration of the *Hippotherium*, one of the fossil equids, from the Americas to Eurasia. The Hipparion horses immigrated from North America to Eurasia quite rapidly, and the appearance is usually referred to as the Hipparion event, or the Hipparion datum (Bernor 1983, Agusti *et al.* 1999). Agusti *et al.* (1997) dated the Hipparion entry in Europe as 11.1 Ma (the beginning of MN9).

In the Spanish basins, where the Vallesian period is best represented, the start of the period is marked by a complete change in the composition of the faunas. From the end of the Aragonian (11 Ma) to the Vallesian the large mammal diversity increased, mainly because of the entrance of new taxa to southern Europe (Bernor 1983, Morales *et al.* 1999). Among them are the first “real” bears, *Indarctos*, the large carnivorous cat, *Machairodus*, and the Hipparions. In the middle Vallesian time the mammal diversity was the highest in the whole Neogene. After this began the short but important period known as the Mid-Vallesian Crisis (MVC), that is situated between MN9 and MN10.

During the MVC most of the Miocene warm and wet-tropical adapted species and genera disappeared. (Agusti & Moya-Sola 1990). Among the large mammals this affected most carnivores, suids and perissodactyls. The crisis corresponds to the overall reshaping of Neogene mammal faunas (Agusti *et al.* 1999), caused probably by a change in the environment from subtropical warm evergreen to temperate deciduous woodlands. After the MVC the disappearance of middle Miocene taxa continued at a lower pace.

The MVC can be also seen in Central Europe. The crisis affected most of the amphicyonids, whereas many other carnivores were not affected at all. On the whole

more than 50% of the carnivora taxa were replaced during this period. (Franzen & Storch 1999). The suids and the cervids were also hard hit in the crisis. In Central Europe the turnover was seen as the result of changing climate (Franzen & Storch 1999). The ever-green trees disappeared and were replaced by deciduous forests (Kovar-Eder *et al.* 1996). The climate was warm-temperate without a dry season in the Pannonian period, and it shifted towards more arid climate (with a dry season) from thereon (Bernor *et al.* 1988).

After the largest turnover of the Neogene comes the Turolian mammal megazone. It has been known from the 19th century (the “Pontian” faunas) from the representative sites of Pikermi, Maragheh and Samos. It is a long interval and the last mammal interval of the Miocene. During this time the faunas present more and more woodland-open taxa characters (Bernor 1983). This is the climax of the faunal development towards more open and cool habitats that started in the Astaracian. It is also an important period in the sense that the Paratethys disappeared and the geographical barrier was demolished. The early and middle Turolian is marked by the mixing of eastern and western faunas caused by accelerated immigration (Bernor 1984). The Alps remained as a geographical barrier. The open-habitat adapted families (Felidae, Hyanidae, Equidae, Giraffidae and Bovidae) enjoyed very high diversity particularly in central-eastern Europe. (Bernor 1983). The Turolian ends in MN13. In the end of MN13 is the Messian salinity crisis (see below). The transgression of open-habitat species continued to western Europe. In western and southern Europe the climate turned more arid during the latest Miocene (Esu 1999).

During the Pliocene the European faunas went through a series of turnovers (Behrensmayer *et al.* 1992, Janis 1993). The climate was first humid-temperate in the lower Pliocene. In Mid-Pliocene there were two distinct cold phases, at 4.5 Ma and 3.5 Ma ago (Suc *et al.* 1995), that marked the beginning of real cooling. The last warm breath was experienced 3.1-3.0 Ma ago, when there was a short warm period during the Brunssumian (Zagwijn 1960, Suc & Zagwijn 1983). After this started the late Pliocene (if we use 1,8 Ma as a limit for the Pleistocene). The Pliocene was the time when the cyclicality in the climate began to influence the environment radically, or at least we are able to see the effect of cyclicality here because of better time-resolution.

## **4. Methods**

The data used in this study was downloaded from the NOW (Neogene Old World) – database 19.08.2002. The public version of the database can be downloaded from the internet (<http://www.helsinki.fi/science/now>). The Dataset used in this study is available from the author.

The downloaded data cover the whole of Neogene, from MN1 (mammals neogene) to MN17 (see Mein [1989] for a review of MN zonation). The timescale and correlations used in this study are all from Steininger (1999) if not stated otherwise. The NOW database uses Steininger *et al.* (1996) for the basis of correlation, but the differences are minimal.

For the analysis data were processed in the following way: all singletons (species that have only a single occurrence, and localities with only one occurrence) were omitted from the study. Only localities that have an age-definition that falls inside one MN zone in Steininger *et al.* (1996) were taken on account. All other localities were omitted. After this all singletons within the MN zones were omitted also. All small mammals were omitted from the study. For the order-based analysis only orders Artiodactyla, Carnivora, Perissodactyla and Proboscidea were used, as other large mammal orders have insufficient data for such a precise analysis.

This means that for the analysis the data consists of about 5500 occurrences of the total of 12000 recorded in NOW database.

When the data was browsed for body mass values, I noticed that only about 60 % of the species had a body mass estimate. In order to include as many species as possible, I thought I should try some other way of estimating body mass and size.

For this purpose I decided to use body size classes introduced by the ETE consortium (Damuth *et al.* 1993). As a basis I used the class division in the ETE database. The idea was to first modify this division of body size classes on the basis of extant species data

and then apply this to the fossil record. In order to avoid the problem of splitting the data too far this classification was made quite crude. Another reason for using class estimates was to avoid the problem of under-representation, that rises from the inadequate level of body mass estimates in the NOW database. If I used a more general classification, the results would cover more species, because it would be easier to assign species to categories. And after this I still would have the estimated body mass data, which I could use to compare the results and the congruence of different methods.

There are also formulas for estimating body mass from body length (Jerison 1973). Even though the body size classification might be too crude for estimating body mass, the ecological signal should be the same.

I made a regression between body size and body mass in extant species using measurements of 50 extant species (figure 1). The result was that the  $r^2$  value is 0,947. This means that there is a very tight correlation between body size and body mass.

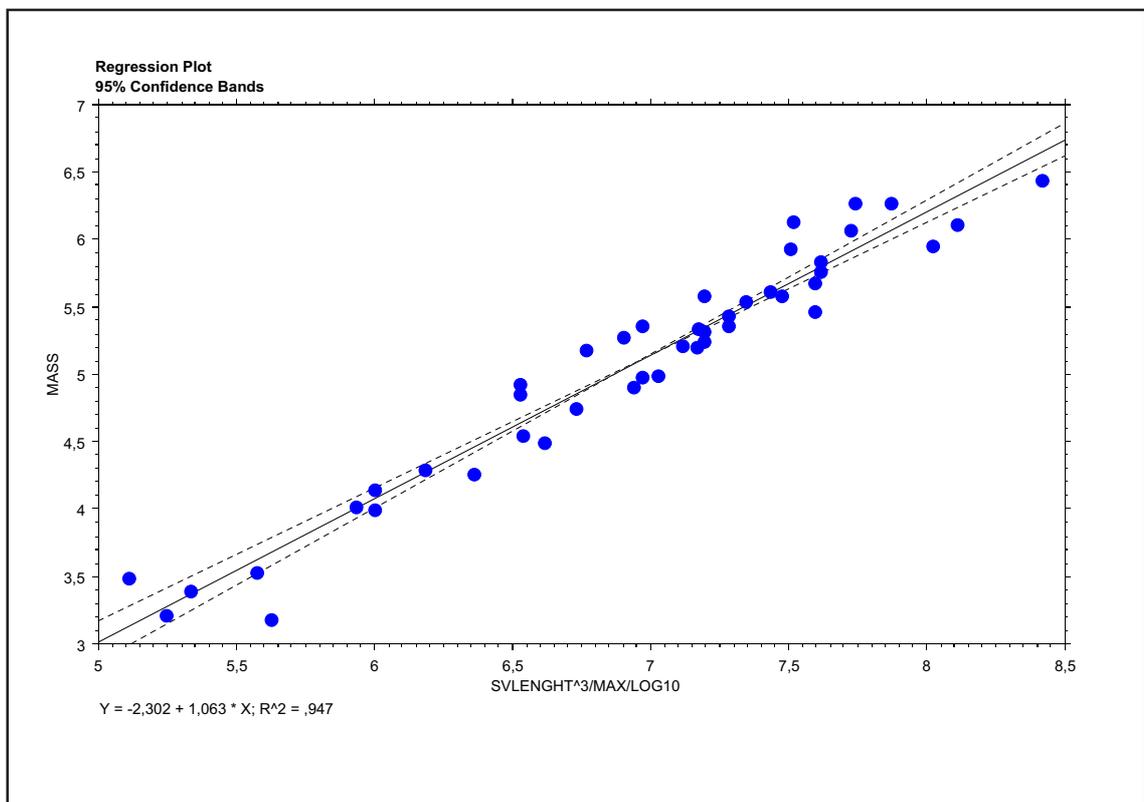


Figure 1. Linear regression between body mass and snout-vent length in extant large mammals. Data from Fortelius (unpublished).

Using this calculation I could estimate the length of individual species based on their body mass estimate in NOW.

The modified version of the class division of the ETE database (Damuth *et al.* 1993) is:

Class 1 = very small (<0,1 m)

Class 2 = small (0,1-1 m)

Class 3 = medium (1-2 m)

Class 4 = large (2-5 m)

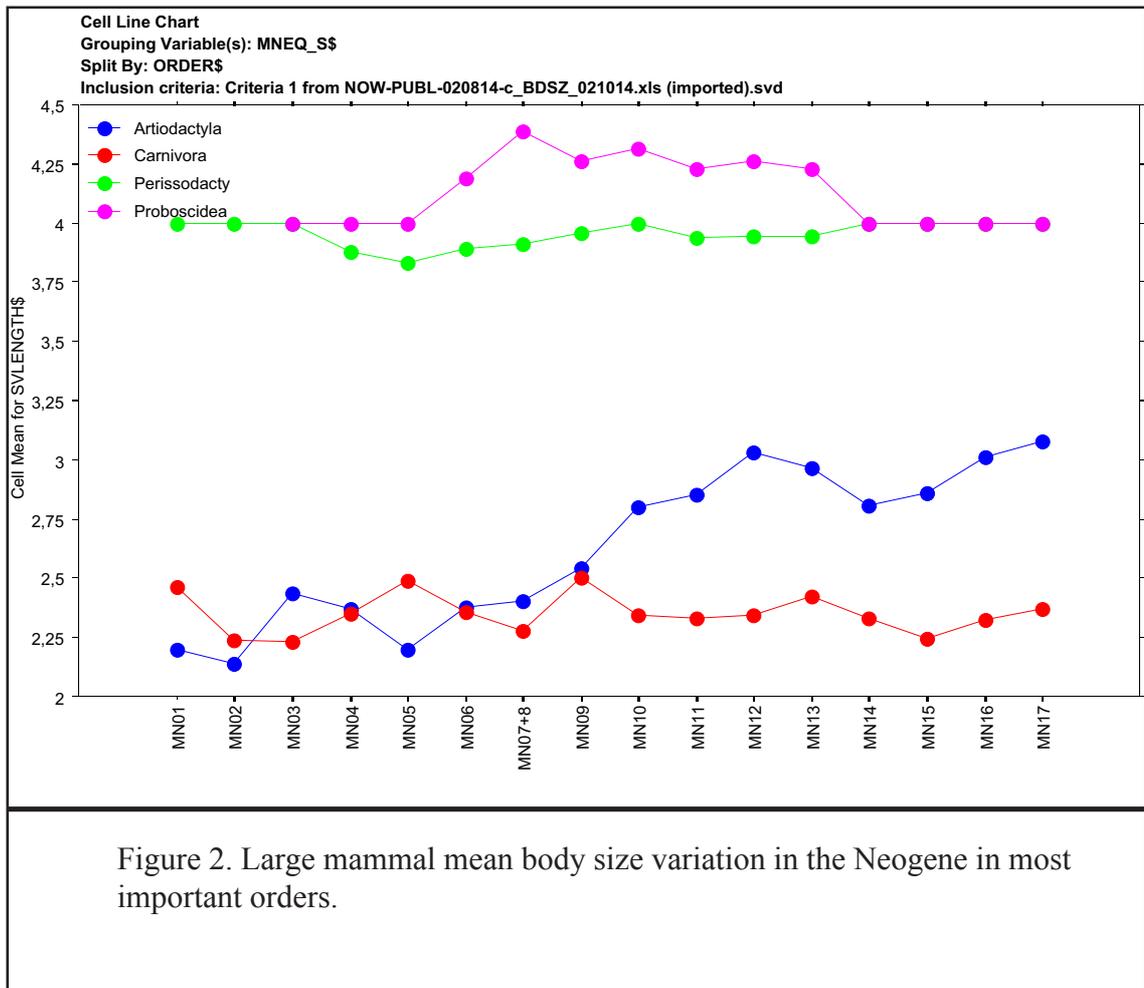
Class 5 = very large (5+ m)

The basis for classes was also checked from the extant species data (Nowak 1991, McDonald 1984). The species that have a body mass estimate in NOW were given a snout-vent length based on the regression of body mass vs. snout-vent length (figure 1). For these species also the approximate snout-vent length measure (in cm) was estimated from the regression equation for comparison with the classified data.

The remaining species that didn't have a body mass or body size estimate were given a body size class based on extant relatives and/or based on literature. The whole body size classification data was also sent to the NOW board members (Peter Andrews, Suvi Viranta, Gertrud Rössner, Alan Gentry, Ursula Göhlich, Mikael Fortelius, see also: <http://www.helsinki.fi/science/now>) for checking and corrections.

To analyse the above mentioned body size data, I processed the data statistically. First I made a simple graph where the mammals are divided into orders (Figure 2). I also made graphs for each body size class (figure 3).

Then I made a common-rare classification (Jernvall & Fortelius 2002) for the species. First I calculated the total amount of localities for each time unit. Then I calculated GLOCs (Genus Locality Occurrence) for each species for time units. The idea of SPLOC (SPecies Locality Occurance) was developed by Fortelius & Hokkanen (2001), here it is used in the same way as in Jernvall & Fortelius (2002).



Then I divided the GLOC value by the total amount of localities (for time units). I used 20% as the cutoff point for the common value. If a species occurs in more than 20% of the localities, it is common, if in less than 20%, it is rare. I also tried a 25% cutoff. It gives a clearer signal, but the line representing commons is cut at MN 9, because there are no common animals in MN9 with this cutoff. (figures 4a & 4b).

Next I further divided the common-rare data based on orders (Artiodactyla, Perissodactyla, Carnivora, Proboscidea) concerned in this study (figure 5). I also divided the common-rare data for the body size classes (figure 6). Here I used 25% as the cutoff between common and rare.

I also divided the data as east-west (Fortelius *et al.* 1996) (figure 7). The boundary between east and west is 20° E. The data was divided also using diet as a variable (herbivore, carnivore, omnivore)(figure 8), but there seems to be no real relation between diet and body size so this was not analysed further.

Finally I made maps. I made a map for all the MN-units and also for the European land-mammal ages (“megazones” of Steininger [1999]). The geographical span is Europe and Middle-East, as the locality coverage is sufficient. For Asia the coverage is not so good when one uses MN-units. It is sufficient for mega-zones, but then one runs into the pitfall of time correlation (the Asian mammal megazones are different from those used in Europe). So the geographical coverage was limited to Europe and Middle-East. All localities without coordinate values were omitted from this part of the study. Localities with clearly insular faunas were omitted, because body size distribution of insular faunas is different from other localities.

First all files used were calibrated manually by entering the lowest (2) and the highest (5) value outside the area of interest (coordinate points -45 W, 45 N and 180 E, 45 N). All maps were made using MapInfo 6 Desktop GIS.

The localities were first plotted in a recent base map for the same reasons as mentioned in Fortelius *et al.* (2002). Then I interpolated all the values using the following settings: cell size 10 km, cell radius 1000 km, border limit 1000 km. After this the program drew a color map based on the interpolation, using colors to indicate differences (figures 9 and 10).

Based on similarities detected between hypsodonty and body size, I made correlations between body size and hypsodonty (figure 11). I also made a correlation using only hypsodonty and body size values of artiodactyls (figure 12).

After this I standardised the scale used in hypsodonty and body size and made a comparison figure (figure 13) using all the data.

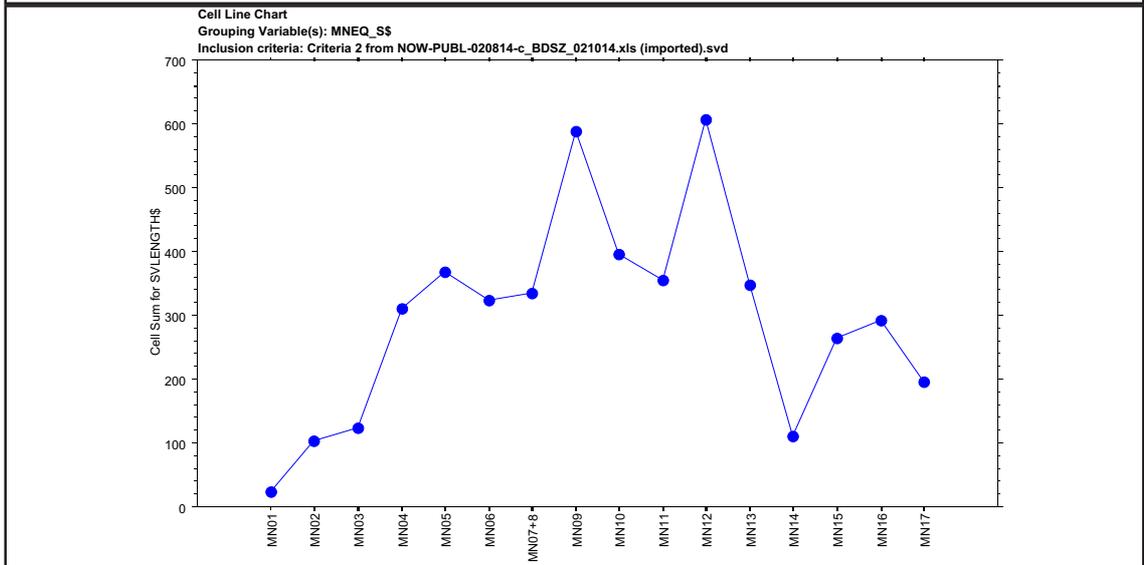
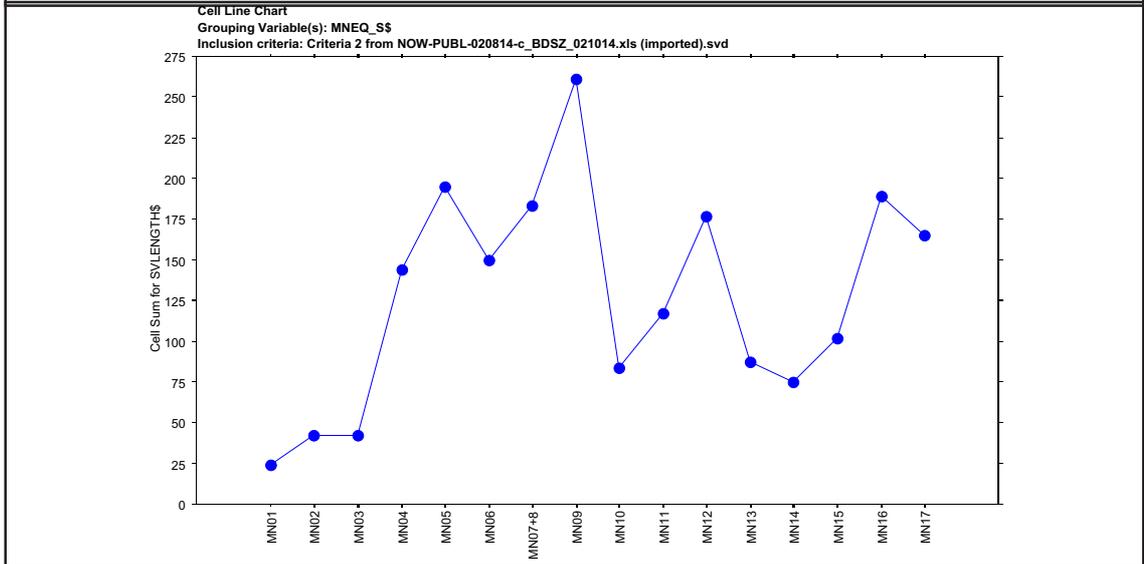
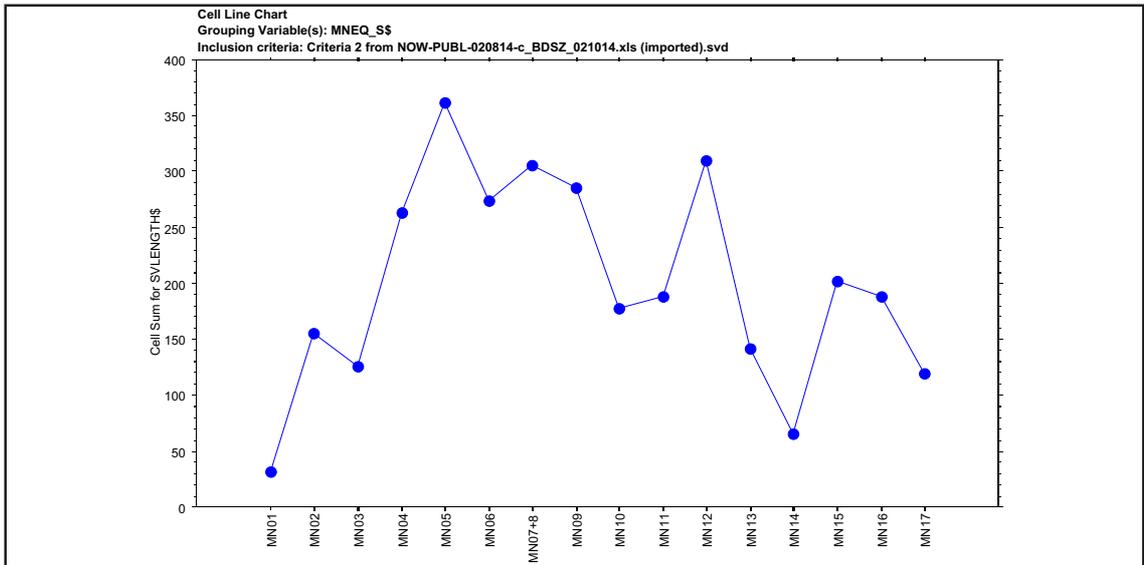
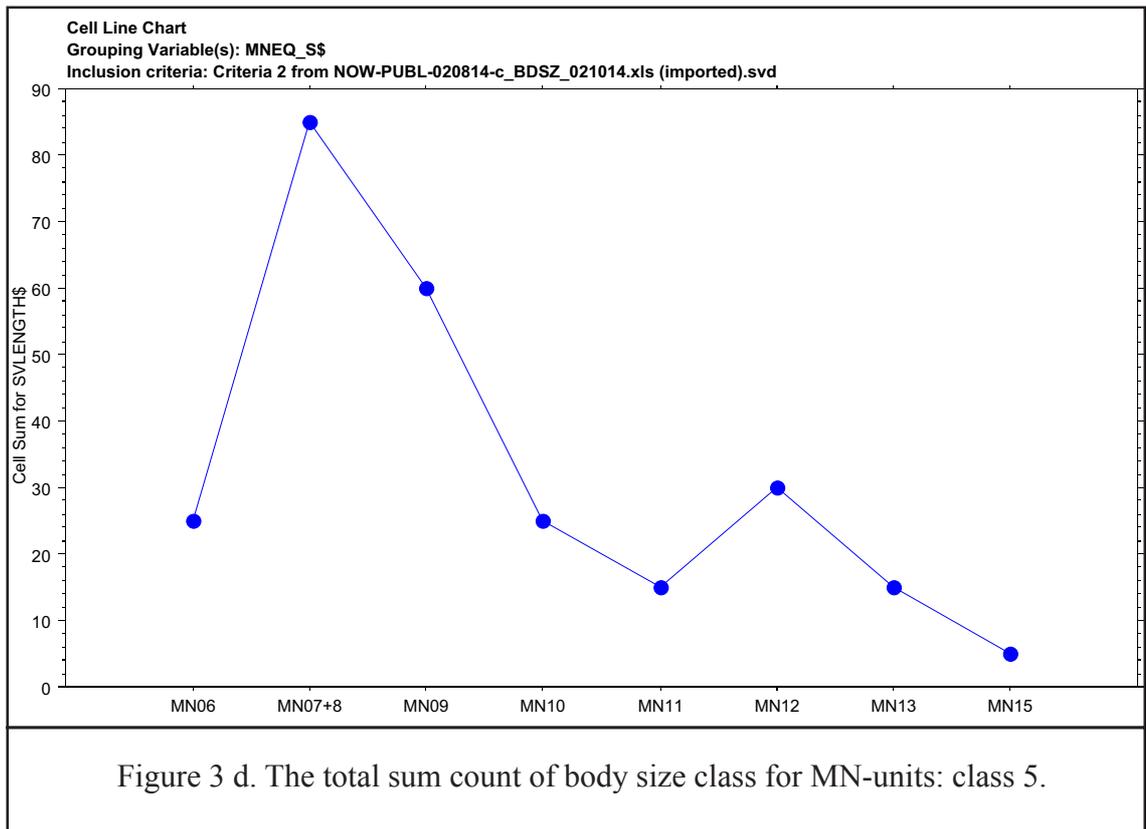


Figure 3 a,b,c. The total sum count of body size class for MN-units: class 2 (upper), class 3 (middle) and class 4 (lower)



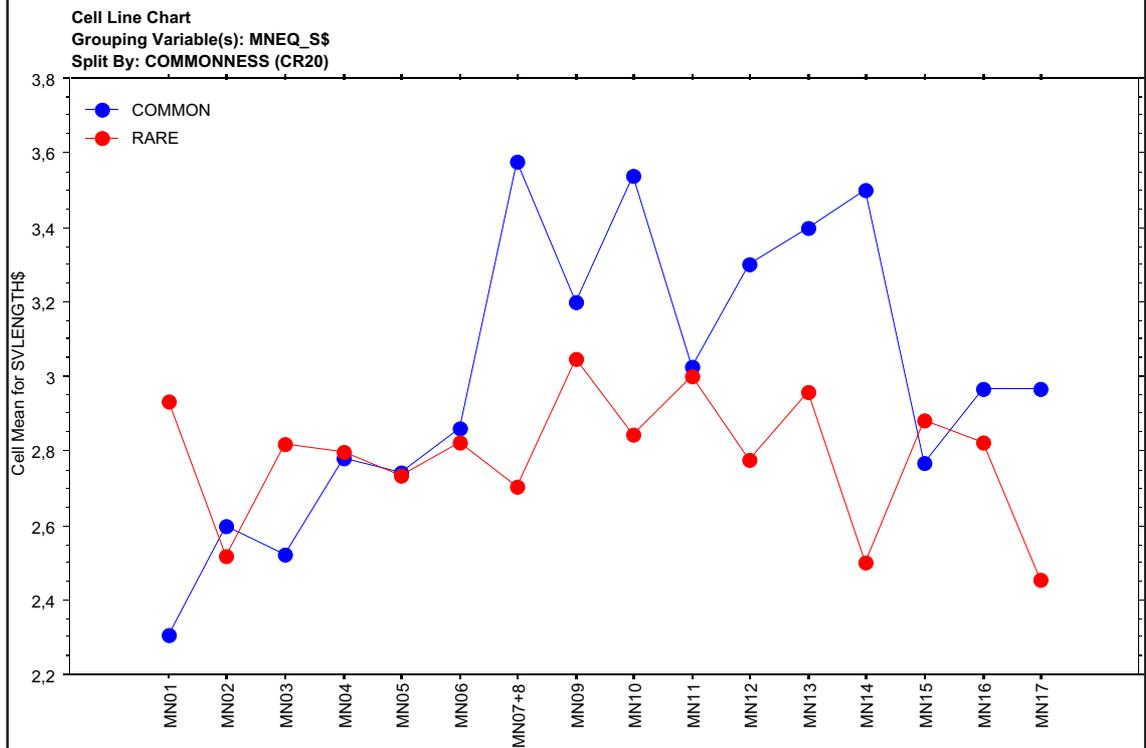
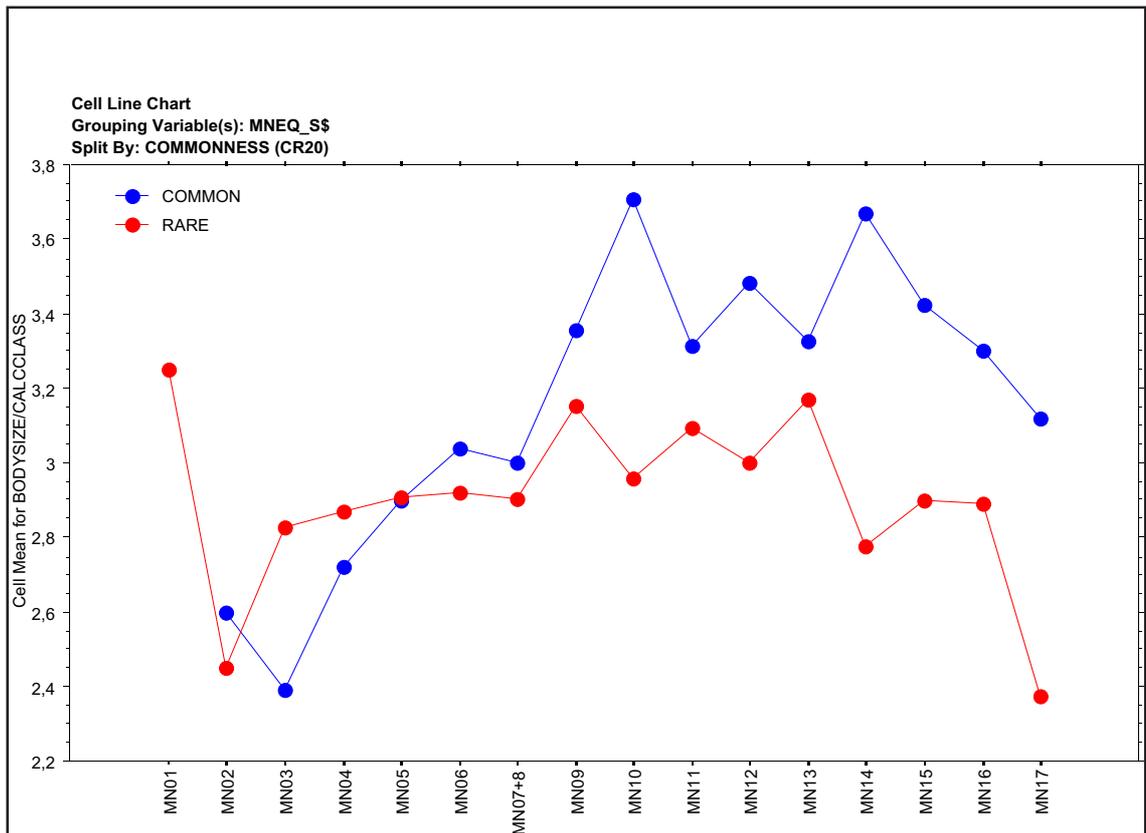


Figure 4 a. Common and rare distributions (SPLOCs) by body size classes (lower) and by regression estimated body size (upper). Cutoff between common and rare is 20%.

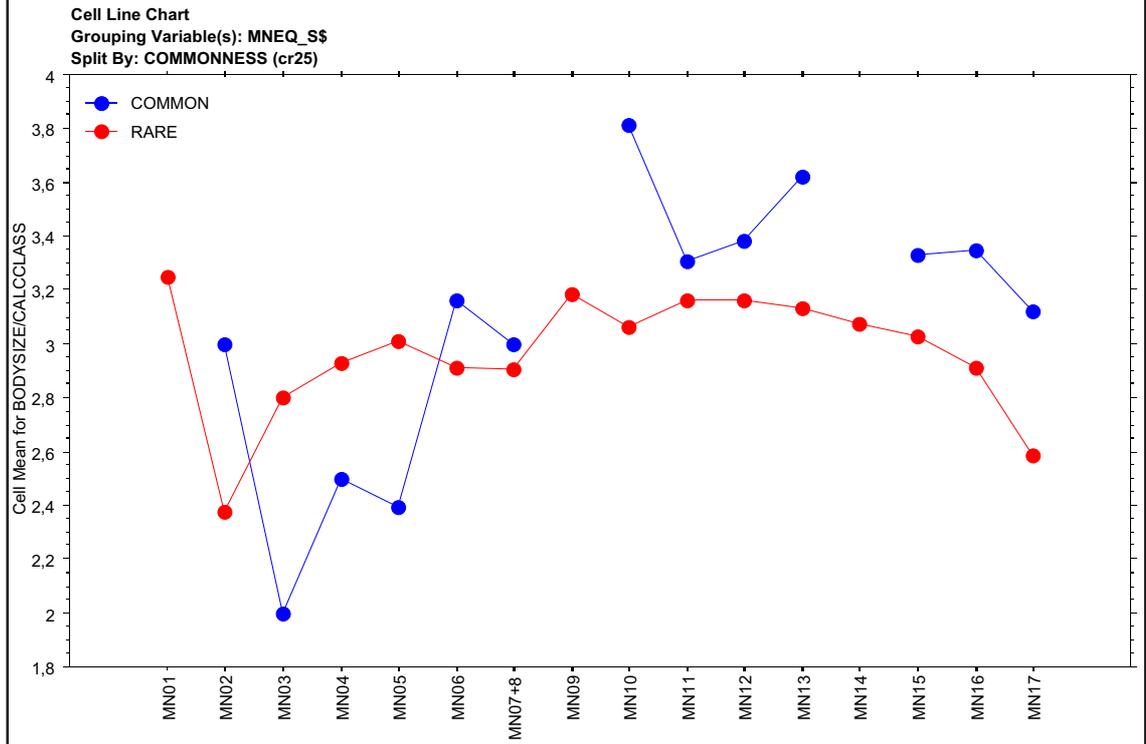
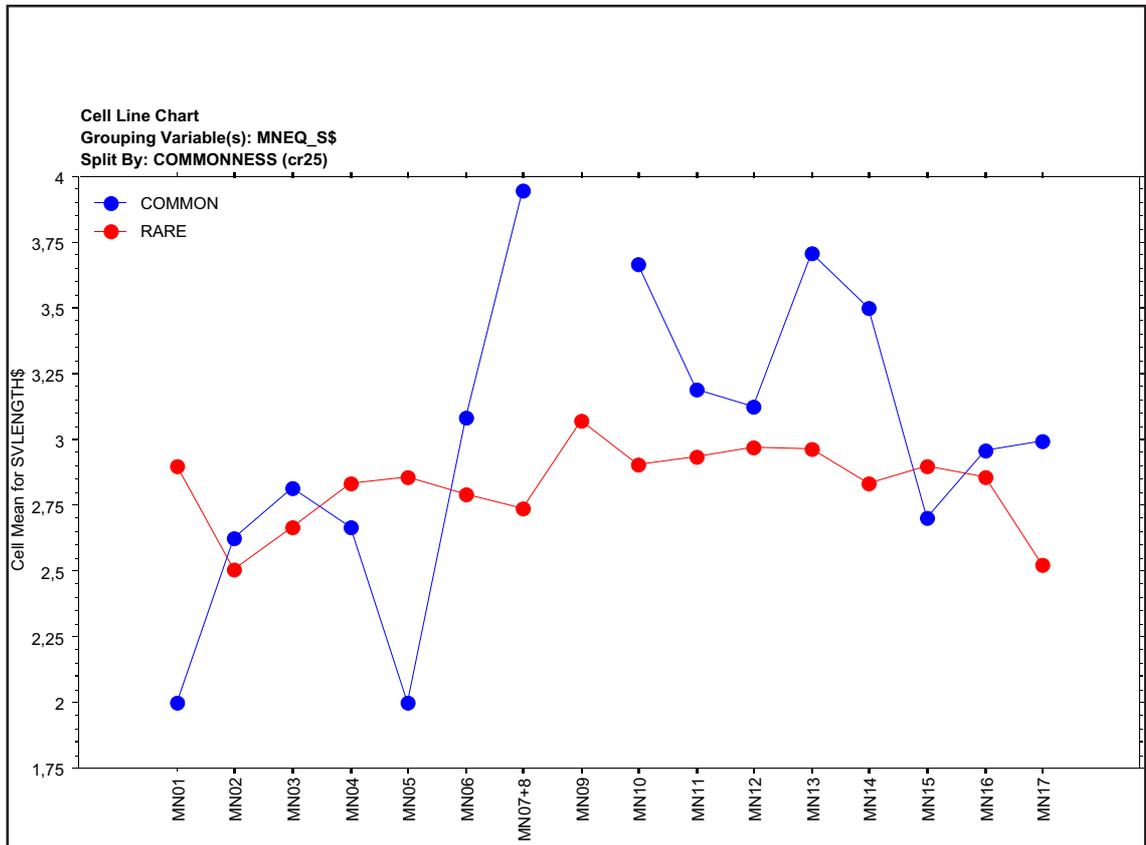


Figure 4 b. Common and rare distributions (SPLOCs) by body size classes (upper) and by regression estimated body size (lower). Cutoff between common and rare is 25%.

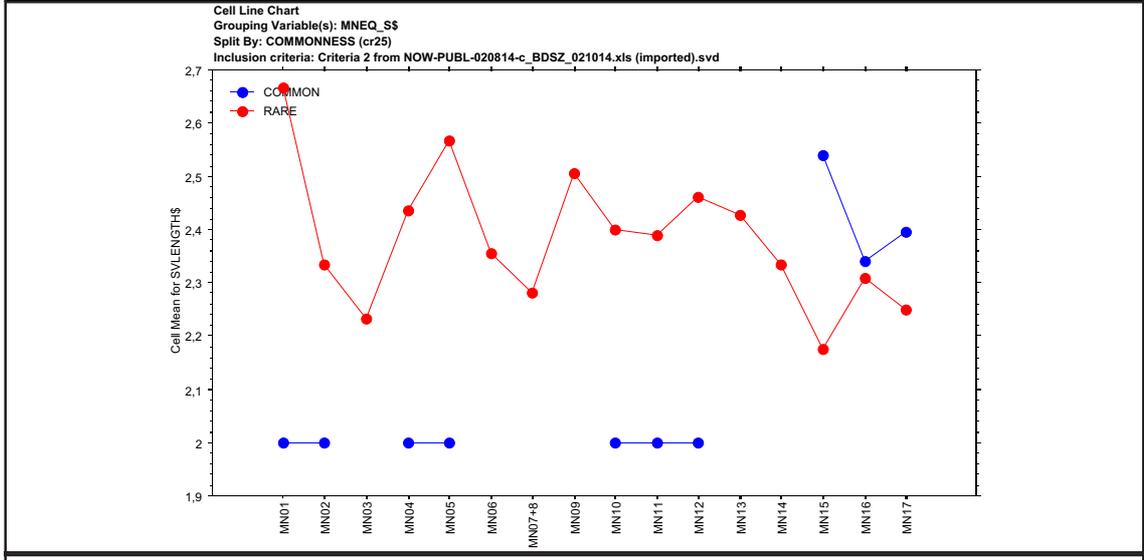
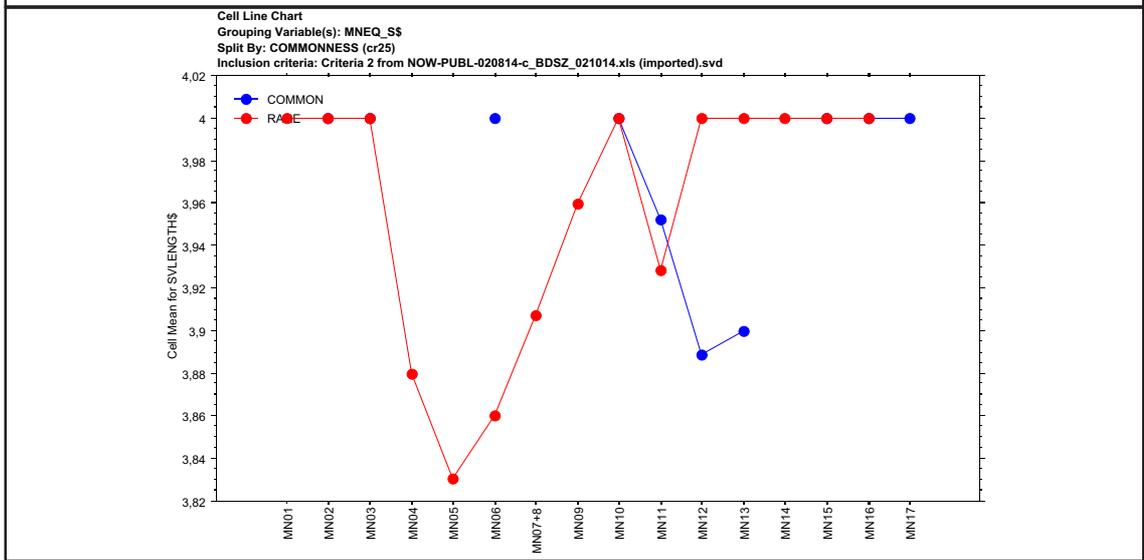
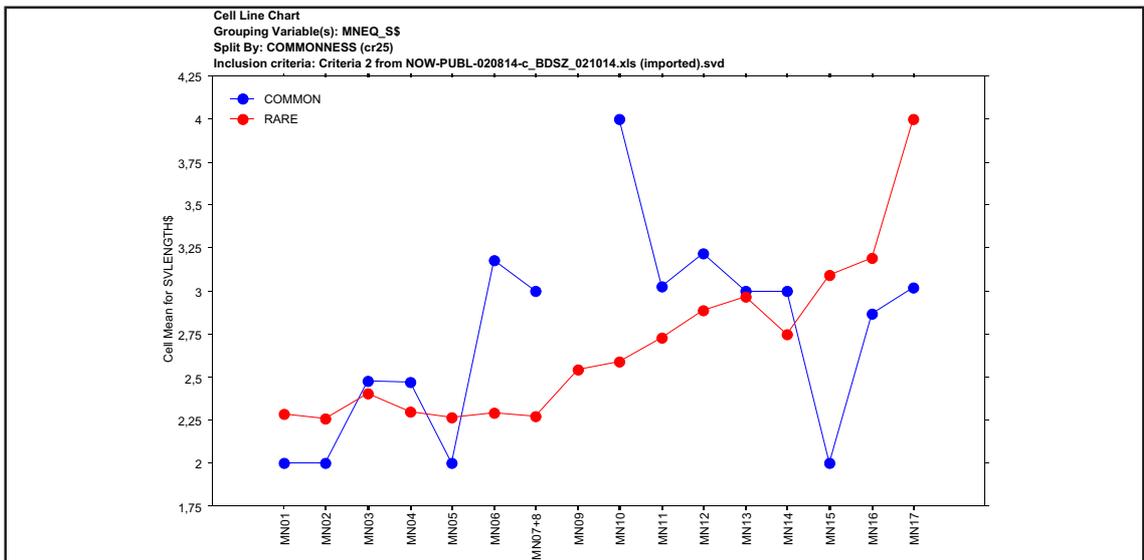


Figure 5. Common-rare distributions (SPLOCs) for orders Artiodactyla (upper), Perissodactyla (middle) and Carnivora (lower).

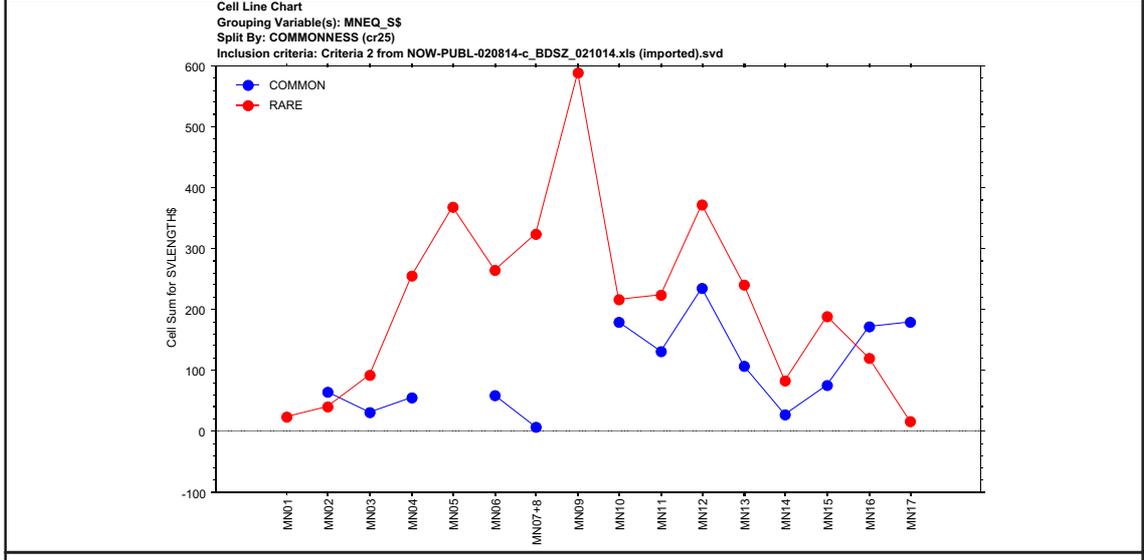
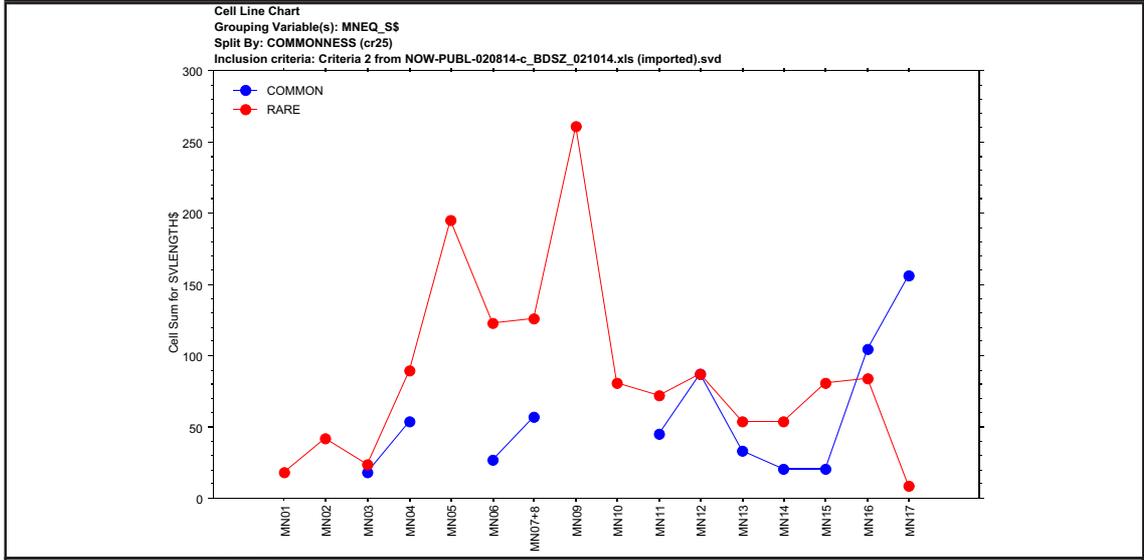
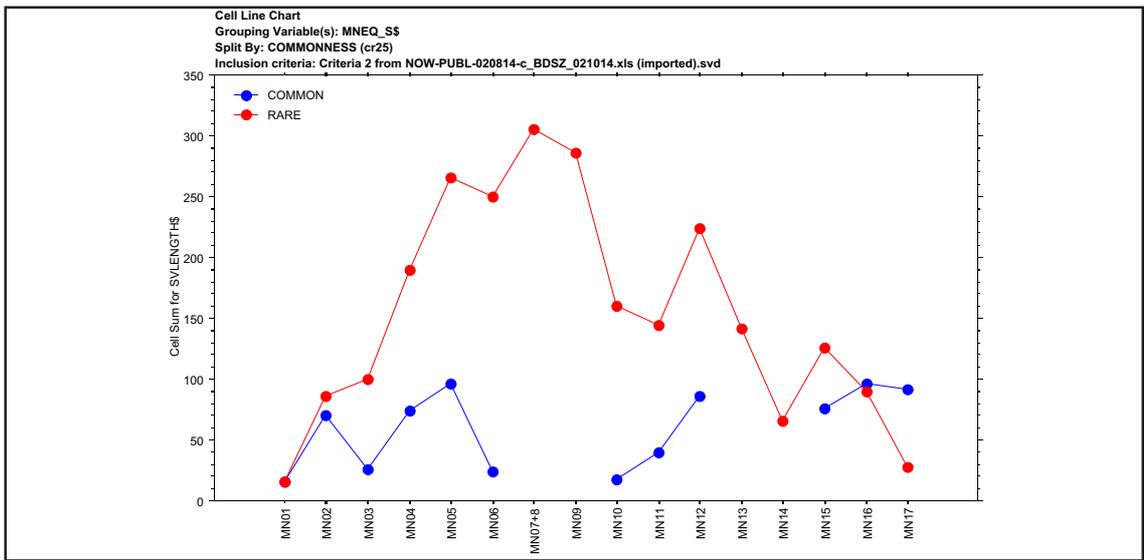


Figure 6. Common-rare distribution (total sum count) for different body size classes: 2 (upper), 3 (middle) and 4 (lower).

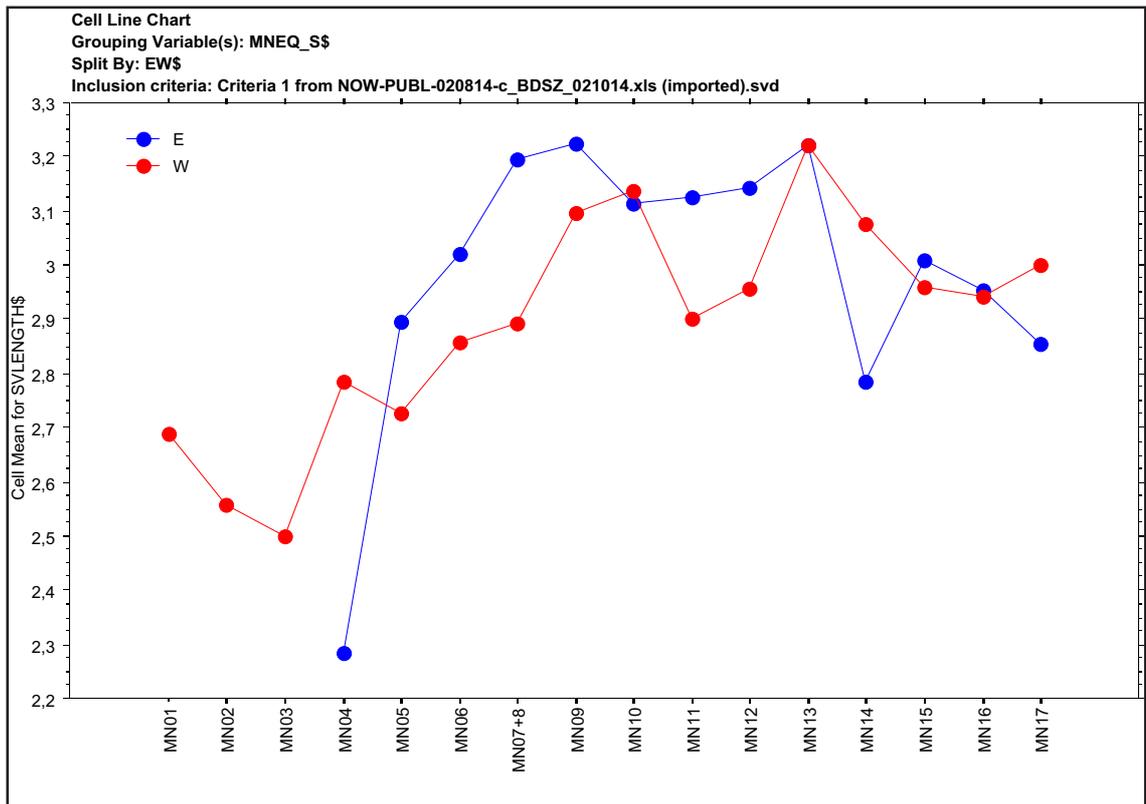


Figure 7. East-West distribution of body size through time.  
 E= East W= West

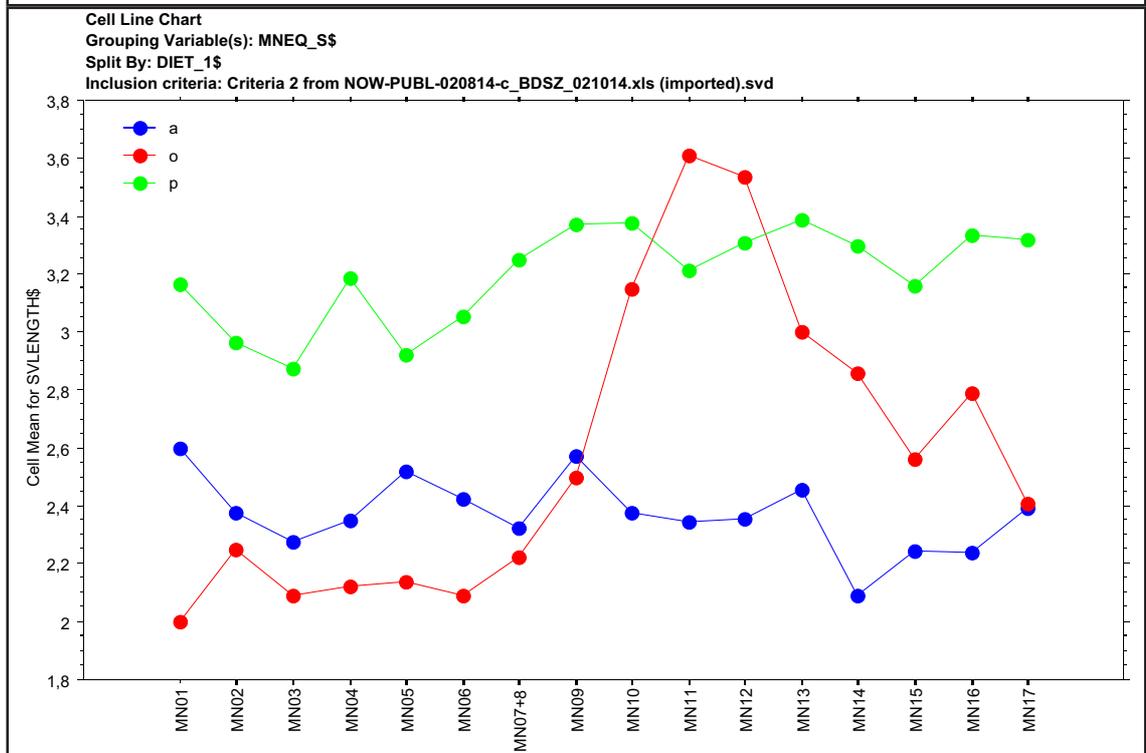


Figure 8. Species mean body size by body size classes by their diet.  
 a= carnivore p= herbivore o= omnivore

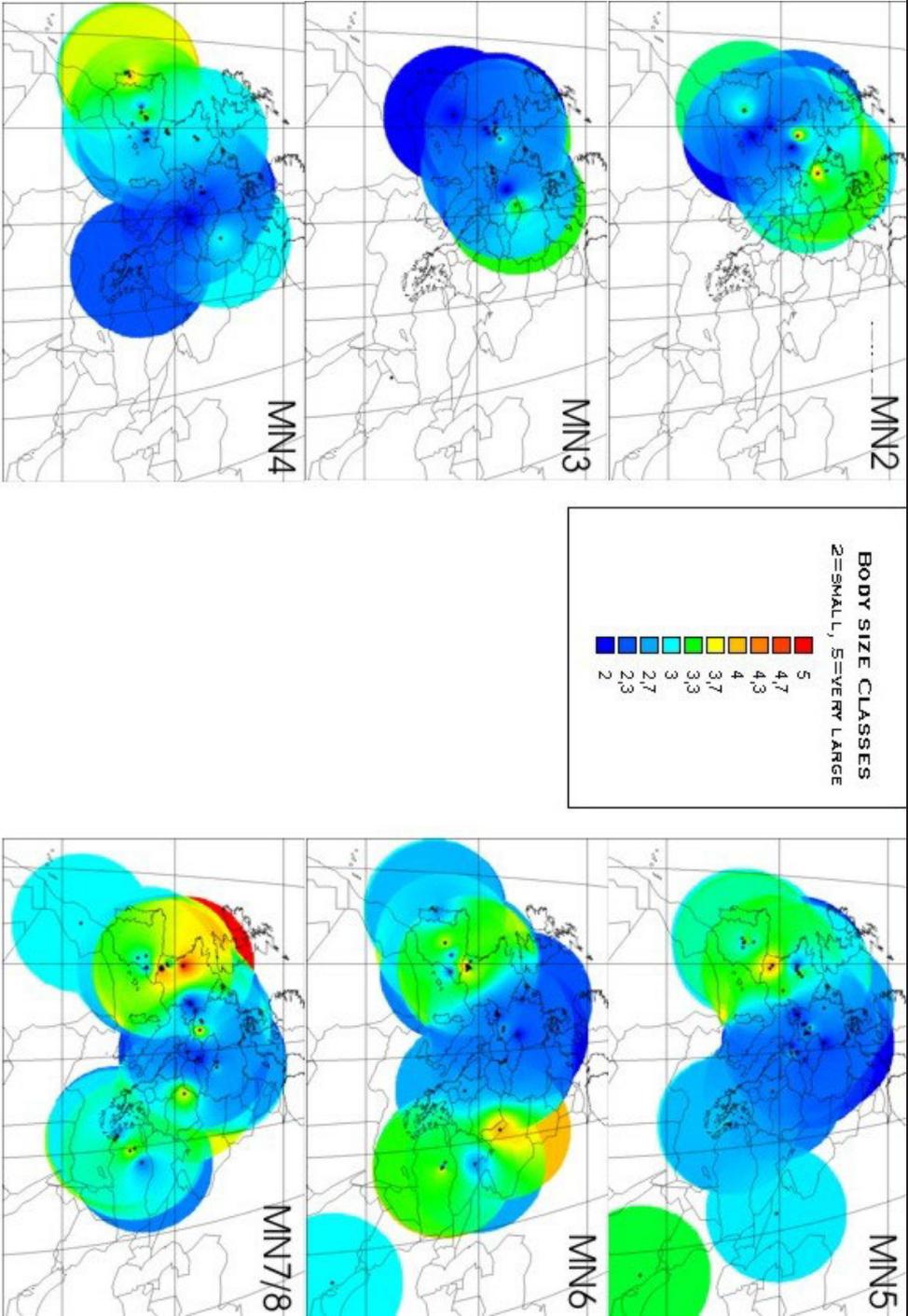


Figure 9. Mean body size maps for different timeslices for Europe

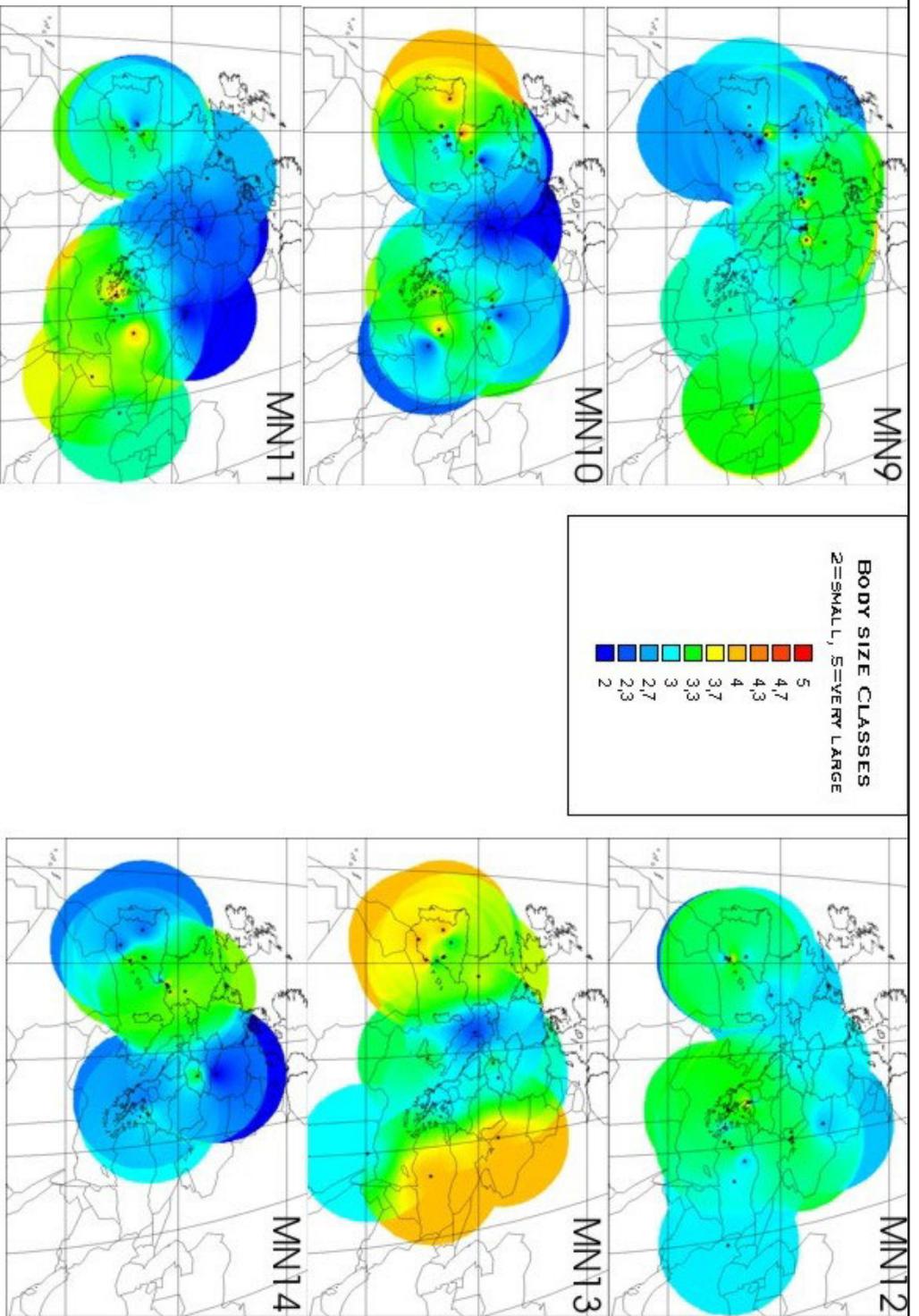


Figure 9. Mean body size maps for different timeslices for Europe (continued)

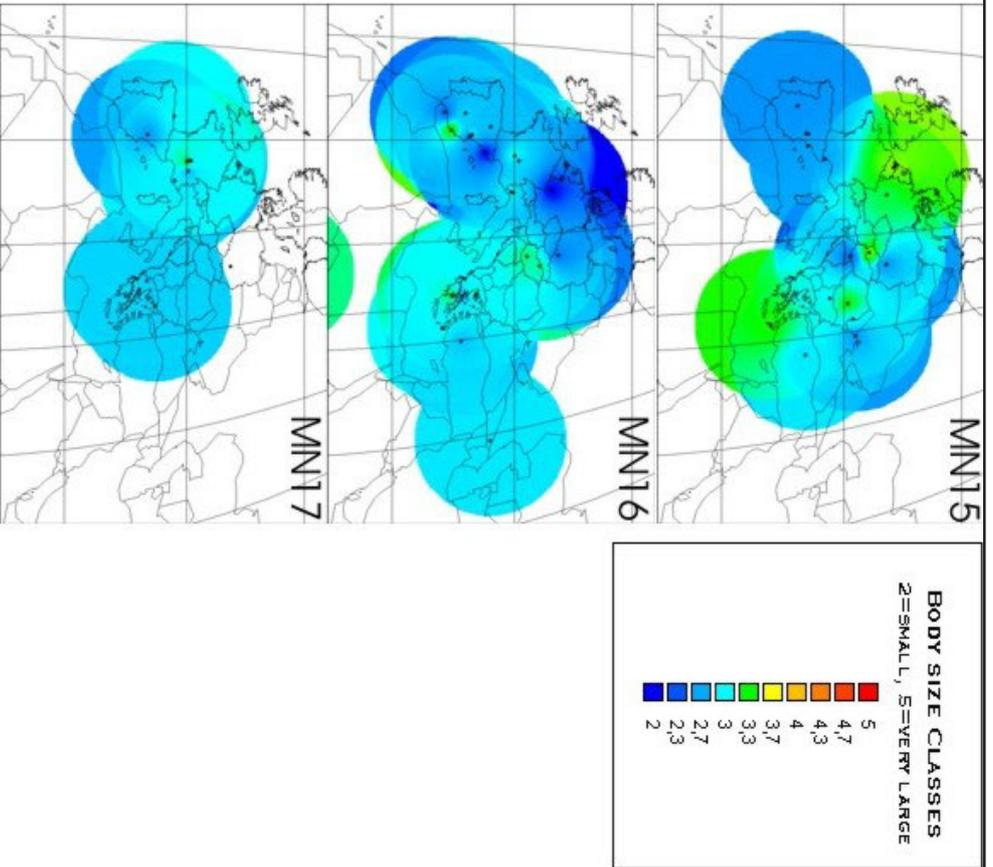


Figure 9. Mean body size maps for different timeslices for Europe (continued)

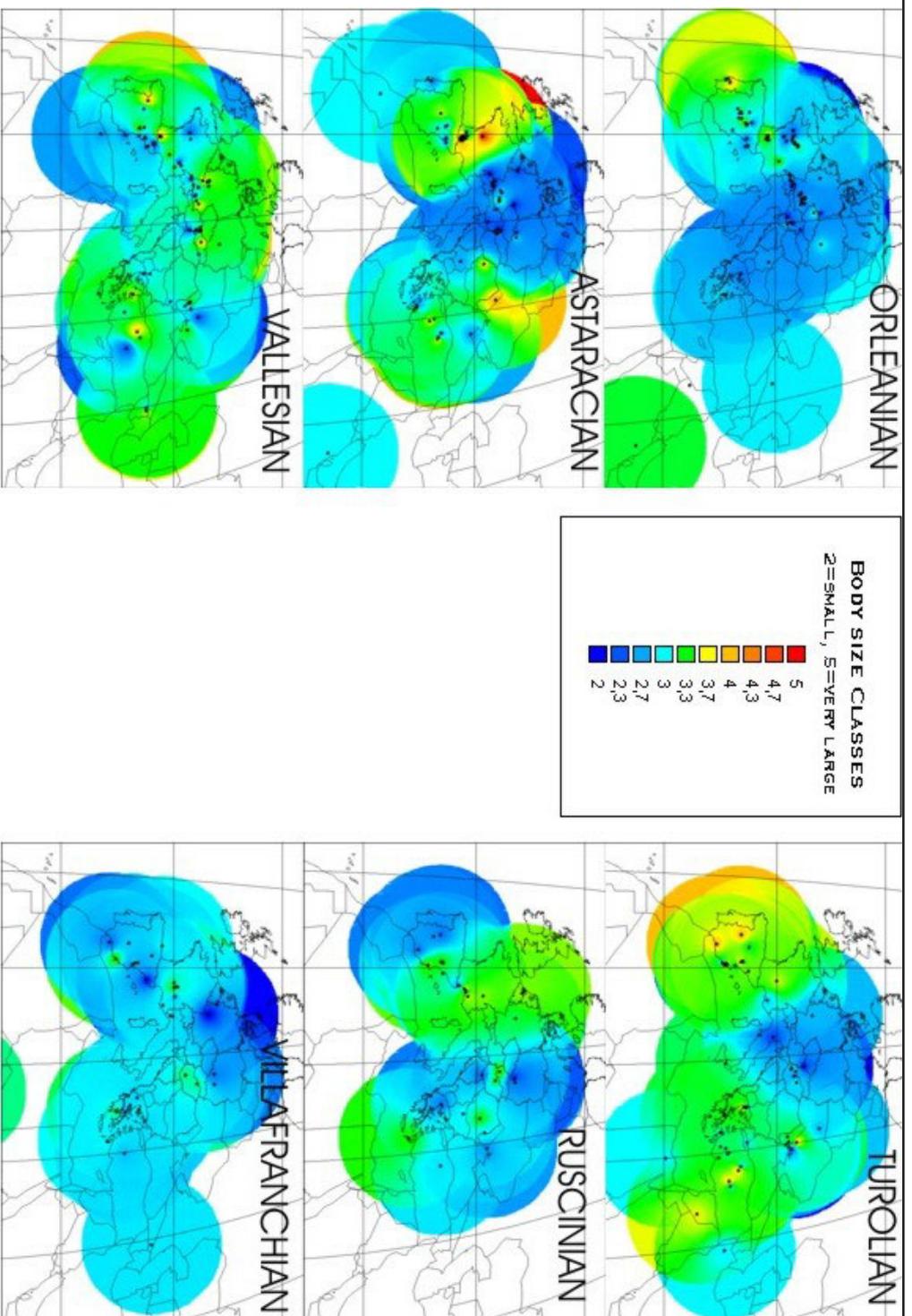


Figure 10. Mean body size maps for different timestslices for Europe (Megazones)

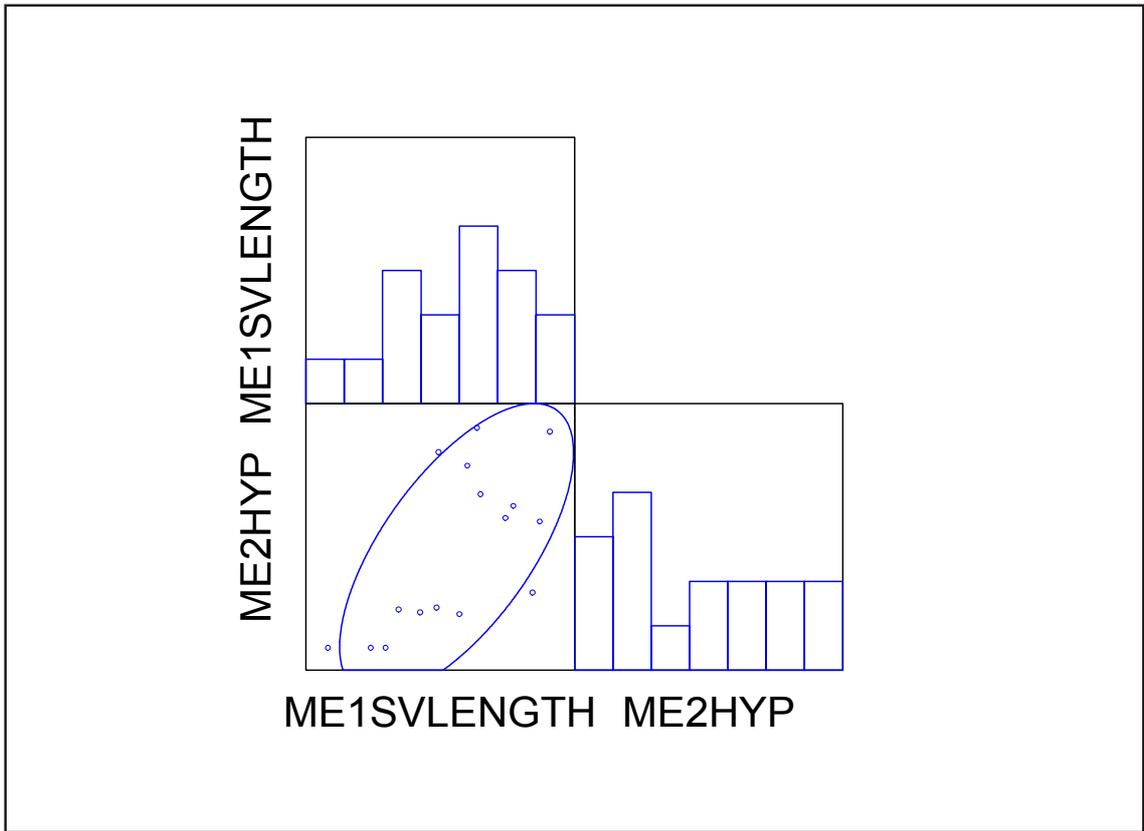


Figure 11. Correlation between ordinated hypsodonty and mean body size for time units. All mammal species considered in this study are included.

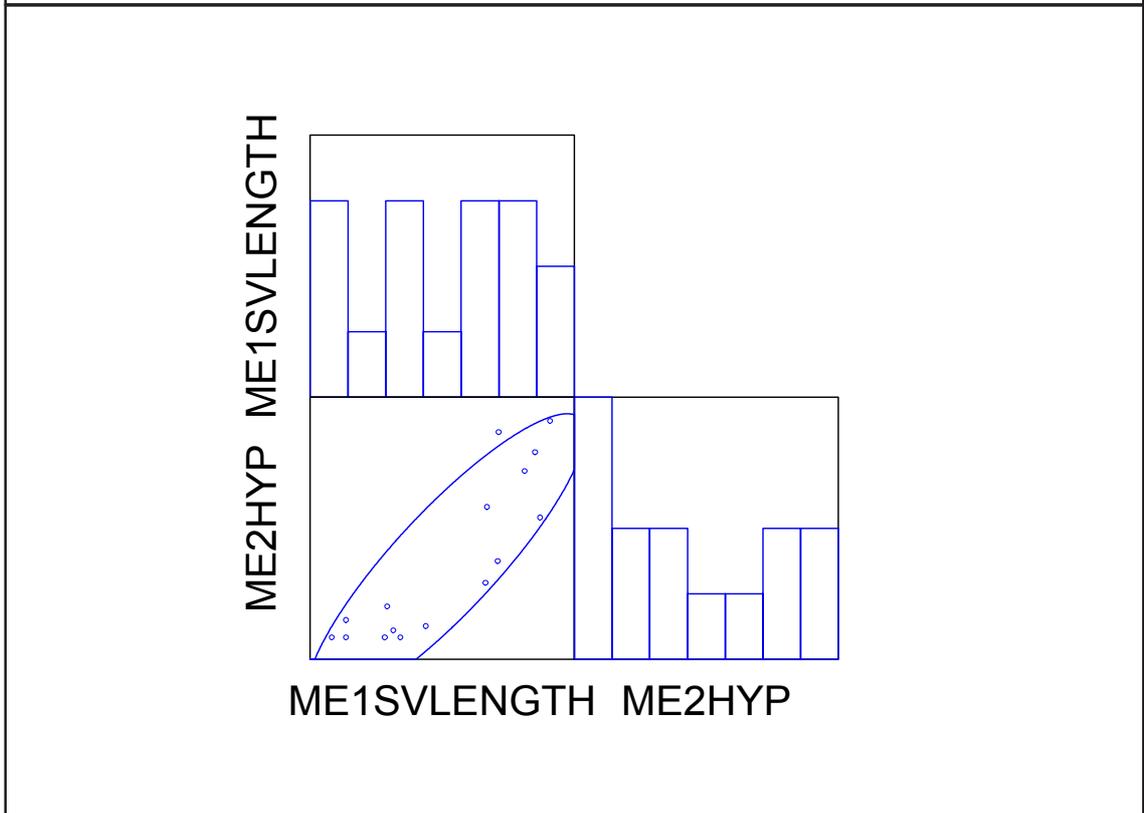


Figure 12. Correlation between hypsodonty and body size for Artiodactyla for time units

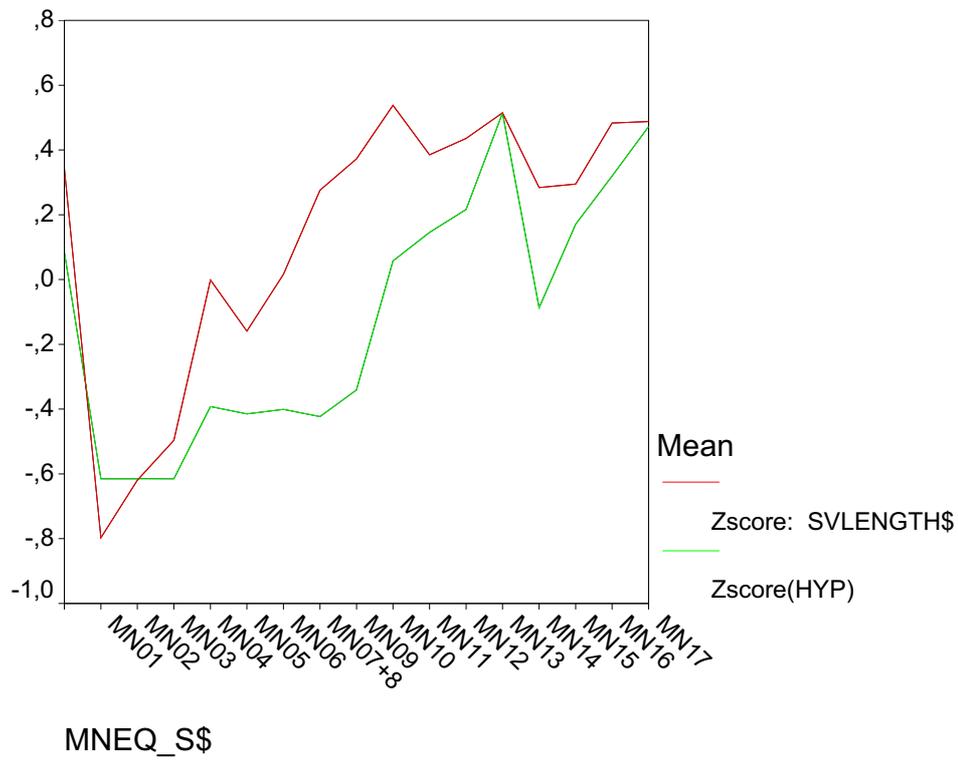


Figure 13. Hypsodonty and body size in the same (standardized) scale.

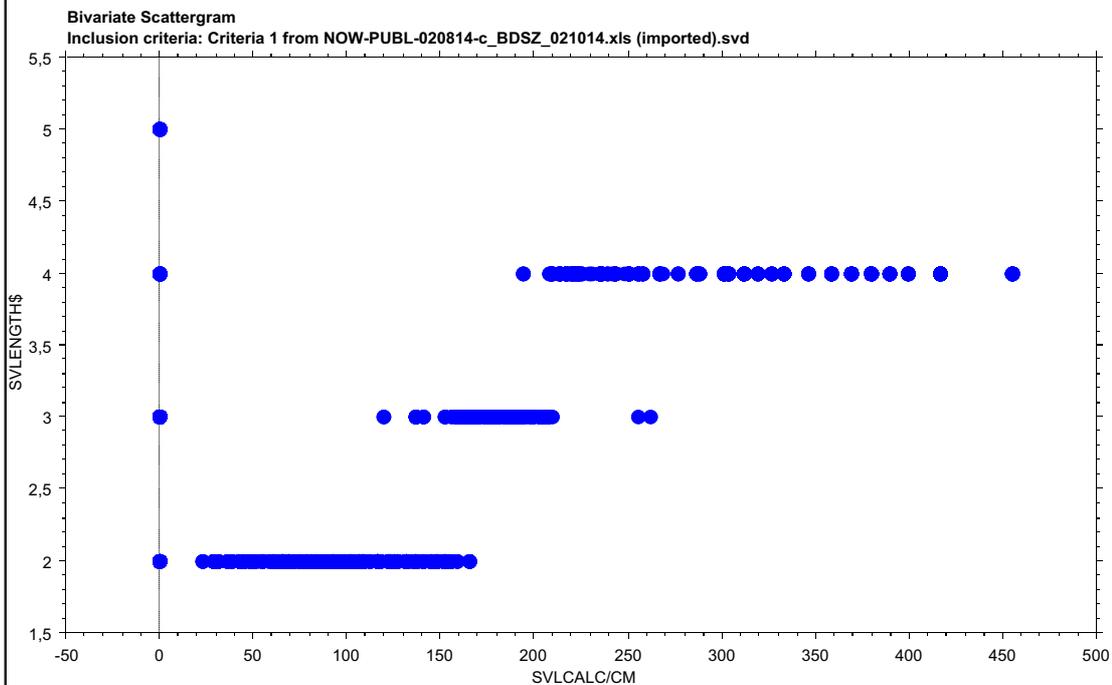
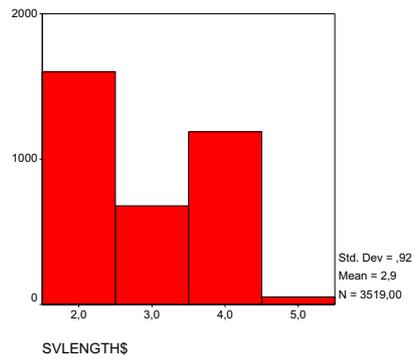


Figure 14. Distribution of body size values (estimated from the regression equation) in classes.

Graph



Graph

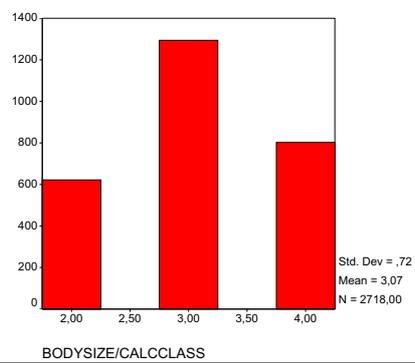


figure 15. Total sum count of species in different classes. The upper graph is for class estimates and the lower for estimates based on the regression equation.

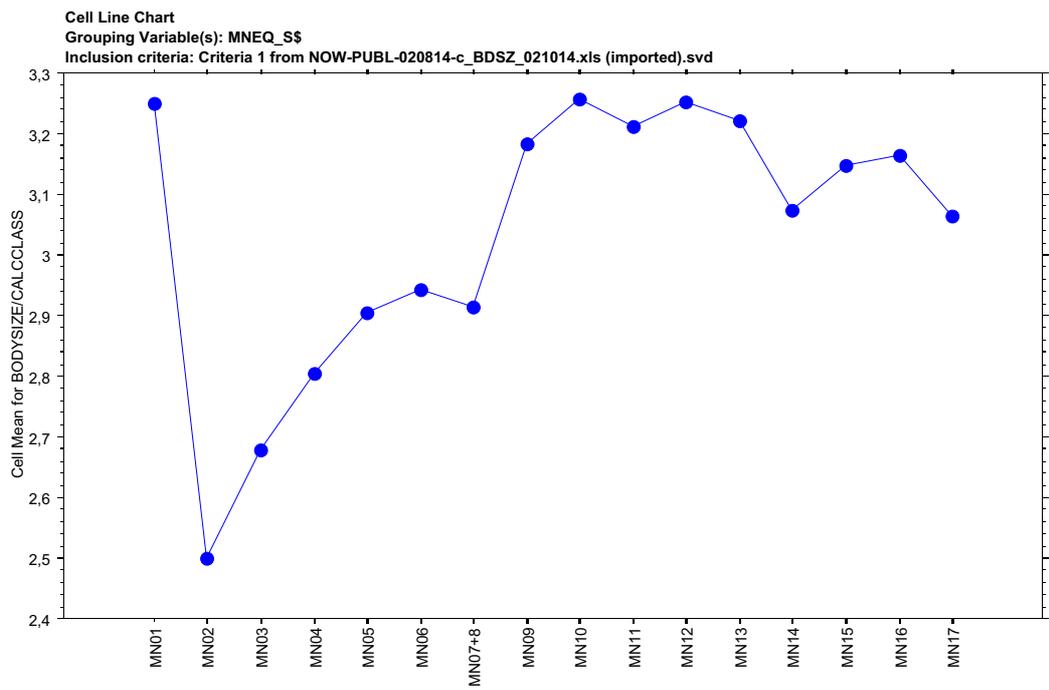
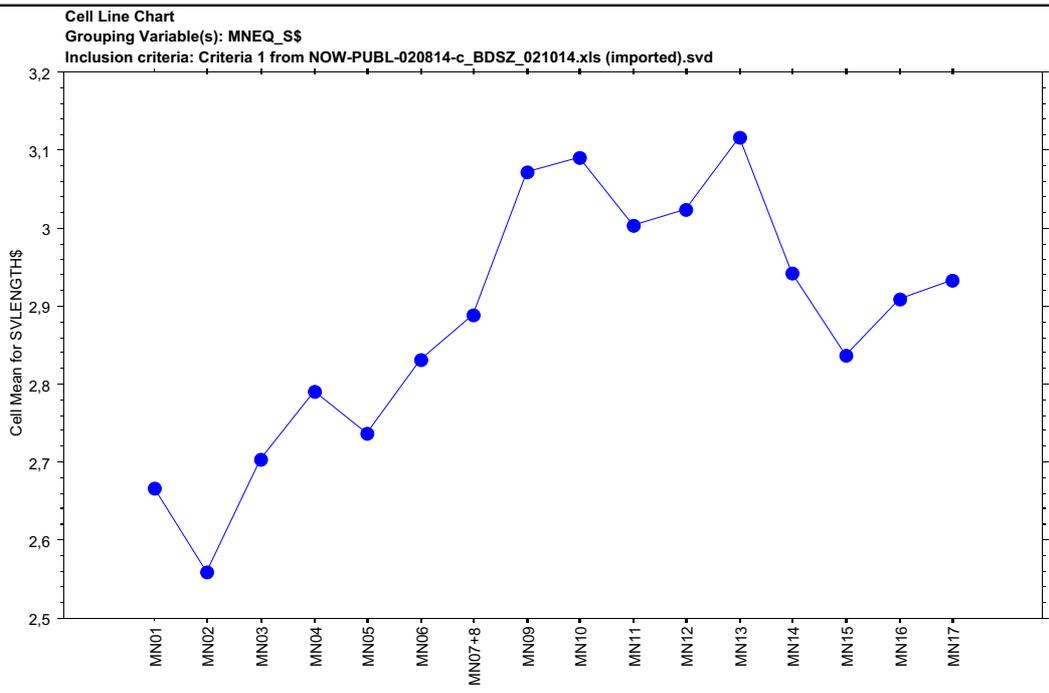


Figure 16. Body size development through time using class distribution (upper) and using class estimates from the regression equation (lower).

## 5. Results

The first notion from the data is that class 2 seems to include some species that are actually bigger and would belong to class 3. At the moment (and in this study) the cutoff between classes two and three is 100 cm. Based on Figure 14, it might also be worth trying a cutoff at 150 cm. This is a problem which plagues all studies that try to classify something that in reality forms a continuum without clear boundaries.

One should notice that even though the calculated values might look solid, they are made from bone-measurements, and carry some errors within them. For a review of problems of body mass estimates made from bones see Damuth & McFadden (1990).

When one compares the species distribution in classes from a different perspective (figure 15), things seem a little better. The problem of the class 2 and 3 cutoff is clearly seen here also, as the calculated values of 100 -150 cm pack in class 3 and in our estimates they are in class 2. The actual signal (figure 16) is still quite similar between these methods.

Using estimated values has three main strengths:

a) In values that were estimated using regression equation class 5 is totally missing because it is very problematic to try to estimate the weight of very large animals precisely (See Roth 1990, Fortelius & Kappelman 1993)

b) The number of species is larger in the estimated body class data , where  $N= 3519$ , as in the data made by using the regression equation  $N=2718$ .

c) Using values is basically a conservative procedure, because the mean of all body mass estimates is 2,9. In the calculated values the mean is 3,09. It is worth pointing out that this is the case even though estimated values have species that rank in class 5, whereas in the calculated values there is no class 5.

From these observations one can conclude that it is safe to use the class-estimates. There are probably some mistakes and the scale is quite crude, but this does not affect the analysis severely. In fact, from the above-mentioned facts it might even be suggested that small noise-variation is somewhat reduced using crude classes and conservative estimates.

For this study, the body size classification is the above mentioned. For future analyses it might be fruitful to try the 150 cm cutoff.

When we start to look at the overall trend of body size development, we see a clear rise in the mean body size through time (figure 16). This was first discovered by Cope in the 19th century, and here we see that it is true also for Europe.

When we look at the data at order -level, we see the mammals clumping into two groups (figure 2) . The ones having more small-sized species and thus having a lower mean body size are Artiodactyla and Carnivora, and the ones with a larger mean body size are Perissodactyla and Proboscidea. It is worth mentioning that based on this graph alone, it seems that not a lot happened to the orders Proboscidea and Perissodactyla, whereas especially Artiodactylas seem to have had most variation in the mean body size through time. The other feature in this graph is the “tight” coupling of the mean body size development between orders Artiodactyla and Carnivora before MN9. After MN9 the coupling disappears, and the mean body size of Artiodactylas seems to rise permanently.

When we look at the common-rare figures (figures 4a and 4b), it seems that the species which are common have a different signal than species which are rare. If we look at only rare species in figures 4b, they have about the same mean body size through the whole Neogene. The common species show most of the variation, and the “common curve” looks much like the mean body size development curve (figure 16).

Common and rare are not evolutionary characters. Species become common if they are succesful and can survive by adapting to environmental changes, or have so general requirements that they can exist even if the environment changes. The rare species are those who are too specialised or for some reason cannot adapt to a changed

environment. They survive in small numbers or die out. It is worth remembering that the common species are not the same for each time interval, so between time unit one species might change its “status” from rare to common and vice versa.

When we look at the east-west figure (figure 7), we see the odd low-value of East in MN4. This is because the “east” in MN4 consists only of one locality, Antonios (Greece). It is a fissure filling with an odd faunal composition. When Alroy *et al.* (2001) used an algorithm to assign localities to MN units based on their faunal composition alone, Antonios (called Aliveri in Alroy *et al.* 2001) ended up in MN7+8. Therefore it cannot be regarded as a real value. In MN5 the eastern faunas have a larger mean body size than the western ones, so we could conclude that the eastern faunas are larger right from the beginning of reliable observations. The eastern faunas seem to be larger for the main duration of the Neogene. Only in MN10 east and west have the same mean body size. In MN12 something happens, and the pattern switches completely. The western faunas have a larger mean body size during MN12-MN14. After this the mean body size seems to be about the same in east and west.

Looking at the sum of body size values for classes (figures 3a,b,c,d), we see that all classes rise in the beginning of the Neogene (MN2-5), after which there is a more or less constant period until the late Neogene (MN12-15) when all classes get lower values.

If we look at the common-rare figures (figure 6), we see clear patterns within each body size class. In the class 2 (figure 6) there is a gap of common species between MN7+8-9 and in MN13-14. The same applies to classes 3 and 4, where the gaps are in MN5 and in MN9-MN10. The common species are, as expected, always fewer than the rare ones.

The body size map consisting of the time from MN2 (middle Early Miocene) to MN17 (Mid-Pleistocene) (figure 9) shows the geographic variation in mean body size in detail. For large scale variations we should look at the map of mammal mega-zones (without Aegenian)(Figure 10). To have a better base for discussion I will concentrate on MN maps (figure 9).

MN2 shows some degree of geographical difference. In present-day Germany there is an area where the mean body size is larger than in more southern localities. There is also one French locality and one Spanish locality showing trend towards larger mean body size. The French locality Selles-sur-Cher has only two species, one tapir and one rhino, so it is not a very reliable reference point. The Spanish localities Loranca and Valquemado are situated close, and they have a good species mix (one rhino, three suids and one bovid). It is too daring to say anything about Spain based on one locality. The German localities have few species per locality, but they all give the same kind of signal, which shows a larger mean body size in German, and maybe in northern France during this time.

In MN 3 there is only data from western European localities. Of the localities showing medium to large mean body size, the French locality Les Beilleau has only one occurrence (a rhino) and should be discarded. The other French locality showing the same signal is Neuville-aux. It has three rhinos, one Anthracoderiidae and one *Palaeomeryx*. The only other place showing some difference is the Czech locality Tucharice, having a couple of large herbivores and one mid-sized Amphicyon. So there is only little basis for saying that mean body size shows anything but small size at this time.

MN4 has a more diverse overall picture. There is an area of larger mean body size in the Iberian peninsula, and it diffuses to southern France, whereas in central Europe there is no change from previous times. The Portuguese localities Quinta Grand, Quinta da Farinheira, Quinta da Noiva and Quinta das Pedreiras have a species composition of Proboscideans and rhinos (*Hispanotheriums*). It is interesting that the other Portuguese locality Lisboa V has a species composition of mid-sized pigs and one large carnivora, *Amphicyon giganteus*. Also the central Spain localities showing larger mean body size have the same species composition. These are the so-called *Hispanotherium* faunas.

MN5 has pretty much the same overall pattern as MN4. The Proboscidean-Rhinocerotiidae dominated faunas have reached southern France, where they can be found in localities Crastes and Reaup. The French locality Pontlevoy has a very rich fauna with one primate. The mean body size is of mid-to-large size. The other French

locality Faluns of Touraine & Anjou is a peculiar one with five rhinos and one primate. Nevertheless, the whole France gives quite a reliable data signal towards larger than mid-sized faunas. Also the Spanish localities show the same signal as before, the composition of faunas being rhinos, proboscideans, suids, primates and also mid-sized carnivorans. Central and eastern Europe don't yet show any change.

In MN6 the overall picture changes to bipolar. There are areas with a large mean body size in western Europe and in easternmost Europe and no change in central Europe. The Spanish localities have a species mix of small carnivorans, mid-sized pigs (*Listriodon*) and a few large rhinos. The French localities have large rhinos and proboscideans, without small-to-mid-sized species. An exception to this is Sansan, which has a rich fauna, verifying the real existence of a larger-than-average mean body size area in western Europe. In eastern Europe larger mean body size is not so evident. The Ukrainian locality Krivoj Rog has three species, one mid-sized cervid, one large rhino and one very large proboscidean. To contrast this, the Russian locality Sevastopol that has a good species coverage has mainly mid-sized species. All the Turkish localities have a good species mix and there seems to be a real basis for saying that in MN6 the mean body size distribution was bipolar in Europe. In the west and in the east the trend was mid-to-large body size, and in central Europe there were still mostly small body size species.

In MN7+8 there is no real change from MN6. The patterns remain and the species compositions are not much changed in the areas mentioned.

In MN9 large-scale changes happen in the mean body size distribution. There are large rhinos and proboscideans in most of the German localities. In the Molasse basin area (south Germany) and in Austria there are some localities with small sized faunas. The change from MN7+8 is considerable. In the west (France and Spain) the faunas change to small to mid-sized bovid, suid and mid-sized carnivora dominated. In the east there is not so much change, the faunas continue to be quite diverse.

Overall MN10 looks quite different from MN9. The Turkish localities have at this time large-sized faunas consisting of rhinos and large bovids. The only locality with equids is

in the western coast of Turkey, at Gülpınar. The locality Karain is an exception, but it has only two small carnivorous cats, so it is not so reliable. The Ukrainian localities have faunas dominated by large bovids, rhinos and mid-sized carnivores. There are only two localities with equids, Poksheshty and Grossulovo. The Greek localities have a species composition of equids, rhinos, large bovids and proboscideans. The only central European locality is Kohfidisch (Austria), which has only two carnivorous species and nothing more. With this data, nothing reliable can be said about mean body size in central Europe in MN10.

In Spain, there seems to be a very strong trend toward large mean body size. Unfortunately, the locality Can Trullas, having the largest mean body size value in Spain, has a poor fauna of only two rhinos. There is also the French locality Orignac, which shows a large mean body size. It also has poor fauna with three species, all large proboscideans. All the other Spanish and French localities have richer faunas, and they give an indication of mid-to-large sized faunas. Probably MN10 doesn't differ so much from the previous MN9 than it seemed at first glance.

MN11 continues to look like MN9 and MN10. There is an area of mid-to-large mean body size in Greece-Turkey, even though the locality Karacahasan has only two rhinos. The other localities showing a large mean body size are Samos Old Mines (Greece) and Taghar. Samos Old Mines has three equid species and one bovid, Taghar has a rich fauna.

The Spanish localities have small-to-mid-body size dominated faunas with a good mix of bovids, cervids, rhinos, suids and hyaenids. Central Europe is dominated by small carnivores and mid-sized felids with a mixture of small-to-medium sized bovids and cervids. There are also some rhinos and proboscideans.

The pattern seems to homogenize in MN12. The Spanish localities and the localities in Greece and Turkey are dominated by faunas with medium body sizes with almost the same species composition as before. The difference is that there are only a few localities in central Europe, and those are very scattered. An interesting observation is the

easternmost Turkish localities and the Iranian locality of Upper Maragheh. They consist of faunas with medium body sizes that differ from western Turkish and Greece localities.

In MN13 the overall pattern changes again. At first glance it seems that there is an overall increase in mean body size. Actually when one looks at the localities, the ones having the largest mean body size are always the ones having uncertainties with species composition (poor faunas etc.) . Nevertheless, the fact remains that in Spain the mean body size is larger than before, as is the case in the easternmost localities. The anomalous-looking Italian locality of Brisighella is reliable as are the Hungarian localities Baltavar and Hatvan and the Greek locality Dytiko, all having small-to-mid-sized species. So in MN13 we can say that in western and in easternmost Europe there are faunas dominated by large body size forms. In a wedge-like area going from Hungary and northern Italy to Greece there are faunas with small body sizes.

In MN14 the picture changes again. France and northern Spain are still an area of larger mean body sizes with a good range of different taxa. In western Spain there is an interesting area of smaller mean body sizes that differ not so much in overall composition from the north-eastern Spanish faunas. In eastern Europe there is no clear picture. The Greek localities have small-sized faunas, the Hungarian locality Gödöll has a mid-sized fauna, and the Polish locality Podlesice consists only of carnivores. Nothing sure can be said about eastern Europe. Overall, the species with small body sizes start to come back and the mean body size is smaller.

From MN15 onwards there are little if any patterns in geographical scale. The only thing that can be said is that the small body size faunas come back, and mean body size is considerably smaller than in MN13 or even in MN14.

The hypsodonty maps for MN-units (produced from the same data as the body size maps) are in Appendix I. For discussion about hypsodonty maps look at Fortelius *et al.* (2002). Although the maps produced here are for MN units, the discussion there is valid for these maps also. It is also worth remembering that carnivores do not have hypsodonty values, so they do not influence the hypsodonty maps at all.

Figure 11 shows the correlation between hypsodonty and body size for time units. The Pearson correlation value is 0.663, the Spearman rank correlation gives a value of 0.696. There are similarities between the hypsodonty development and body size development.

For Artiodactyla (figure 12), the correlation between hypsodonty and body size gives a value of 0.873 (Pearson). The Spearman rank correlation value is 0.861.

## **6. Paleogeography**

The story of the European Neogene geographical evolution is one of continental collision, ocean basin closure and foredeep basin-system building. In other words, it's the birth of the Mediterranean and the Paratethys, and the following continentalisation of Europe, that led to the disappearance of the Paratethys.

The African and European continental plates started to collide in the Late Cretaceous - Early Tertiary. The early evolution of this ocean basin closure and continental collision is still difficult to track, but from the Oligocene time onwards the plate tectonic geometry is understood well enough (Robertson & Grasso 1995). Good biostratigraphic evidence is available from Eocene time onwards, but there are still a lot of gaps (Rögl 1998). Of course, the farther we go back in time, the more uncertainties we must accept.

The whole paleogeographic evolution of Europe is out of the scope of this study. Here I will concentrate on the most important geographical changes that affected the mammalian communities. These are:

- 1) The forming of the Gomphotherium landbridge
- 2) Development of central Paratethys and Lower Rhine Embayment during the Miocene
- 3) The Messinian salinity crisis

### **6.1. The forming of the Gomphotherium landbridge**

In the Early Oligocene the Turgaj Strait (connecting the Tethys Ocean to the Arctic Ocean through western Siberia) was closed and became dry (Rögl 1998). This resulted in faunal exchange between Europe and Asia. In the Mediterranean area, tectonics closed off the sea connection in the area of Greece-Turkey, giving birth to the Paratethys (Robertson & Grasso 1995). Marine connections between the Paratethys and the western Mediterranean remained, but the Paratethys area became a realm of its own. The

Mediterranean - Indian Ocean connection remained during this time interval. The Early Oligocene Mediterranean basin configuration remained almost the same for a long time (Rögl 1998).

In the Early Miocene the tectonic development was also two-phase. In the northernmost section of the eastern Mediterranean area (Turkey- Greece) the subduction was advanced, as in the southern part (S. Greece, Cyprus) the collision and subduction was still very active. (Robertson & Grasso 1995). The beginning of subduction in the southern parts is the beginning of the Miocene (Meulenkamp *et al.* 1988).

In the Early Miocene there were probably marine connections between the eastern Mediterranean and the Paratethys through Turkey and Iran, but the exact connections and how long they lasted are still under debate (Rögl 1998). There was still a connection between the Indian Ocean and the Mediterranean in the late Early Miocene (Rögl 1998), but it was closed by the compression tectonics in the Levantine – middle East regions. (Robertson & Grasso 1995). This ‘Gomphotherium Bridge’ allowed faunal exchange between Africa and Eurasia. In the early Middle Miocene the seaway opened again, but was short-lived. In the late Middle Miocene it was closed again. This final closure of the connection resulted in the reorganisation of the circulation patterns of the oceans. Some have suggested that this was the trigger for the expansion of the East Antarctic Ice Sheet (Rögl 1998).

In the Iberian peninsula, as the mountain build-up in the edges and within the peninsula continued, the topography became very distinct. Many basins were formed, separated by mountain ranges of different orientations. Also the basins subsided because of the tectonics and became isolated from the Mediterranean and/or Atlantic.

In the Early Miocene the shattering of the Peninsula continued. In the Atlantic margin, some basins became again connected to the Atlantic (Meulenkamp *et al.* 2000b).

The tectonical setting persisted in the peninsula as almost the same until the Late Miocene. Small basins were created and in larger basins the sedimentation continued as continental extension of the Iberian range caused parts of the interior basin areas to

become non-deposit areas. In other larger interior basin areas the sedimentation changed from external to internal (lacustrine and fluvial). (Meulenkamp *et al.* 2000b)

## **6.2. Development of central Paratethys and Lower Rhine Embayment during the Miocene**

The Molasse Basin, the Vienna Basin, the Pannonian basin and the Carpathian basin are parts of the central Paratethys realm. Because the Paratethys areas are differentiated by their biostratigraphical development and endemism, the geographical lines are just approximations. Usually the border between the central and eastern Paratethys is between the Pannonian-Carpathian realm and the Black Sea. The Eastern Paratethys is a huge area compared to the central and western Paratethys. It covers all of Black Sea, Caspian Sea and Middle Asia, but is biostratigraphically its own, more or less heterogenous area.

In the Middle Oligocene there was a global sea-level fall, which resulted in continentalisation of the basin (Sissingh 1997). Following this regression, again thick alluvial-fan deposits started to accumulate in the front of the Alps. Because they were situated at the thrust-front, they were steep rivers. Down-stream they formed alluvial floodplains with meandering rivers.(Meulenkamp *et al.* 2000a) Probably typical swamp-lake environments of the time, known from the fossil findings, were situated in the marginal floodplain areas, away from the rising mountains. These environments remained more or less the same until Early Miocene times.

The tectonical processes in the Vosges - Black Forest area, Jura and Massif Central led to an uplift of the whole Molasse Basin in the Late Miocene.(Sissingh 1997, 2001). Because of the fall of sea-level at the same time, continentalisation was quite fast. Later development in the basin is erosional.

As the Molasse Basin area, the Carpathian - Pannonian region started to evolve during the Early Oligocene. The beginning was characterized by basins with stagnant water circulation and lessened salinities. In the later Early Oligocene the marine corridor from

southern central Paratethys (southern Bulgaria) was closed. Salinities remained low and probably water temperatures cooled because of the continuing isolation. (Rögl 1998).

During the late Early Miocene, the Central Paratethys region was connected to both Eastern and Western Paratethys (Meulenkamp *et al.* 2000b). As mentioned above, the Western Paratethys (Alpine Foredeep - Molasse Basin) was connected to the Rhine and the Rhone Grabens. So actually the Paratethys was almost a part of the world's oceans during this brief time.

During the Early Miocene, the Carpathian - Pannonian area was also tectonically active. Because of the tectonism, the Carpathian Foredeep became a lagoonal shallow-water deposition center. In the intra-Carpathians tectonism resulted in the disintegration of the former basins to smaller ones. (Meulenkamp *et al.* 2000b).

The Middle Miocene was regressive in the Molasse Basin and the European rift systems. It was also regressive in the Carpathian - Pannonian area. Still, marine connections remained to the Mediterranean. Regressions affected mostly the shallow parts of the basins. Circulation was strongly reduced for the Carpathian Foredeep and the intra-Carpathian basins. (Rögl 1998). In the shallow basin margins evaporitic deposition dominated. In the late Middle Miocene the connection to the Mediterranean was severed.

The European Rift System means the graben and depression features of western and central Europe. It comprises the Rhône - Besse rift system in the Northwest Mediterranean margin, its junction to the Rhine graben, the Rhine graben, and in the northernmost end of the Rhine graben the so called 'triple junction' (Rhine graben - Hessian Depression - Lower Rhine Embayment) (Sissingh 1998). It has largely affected the geographical evolution of western Europe.

In the Oligocene - Miocene transition the connection between the Paratethys and the North Sea was again severed (Rögl 1998). In the Early Miocene, the Rhine graben was probably a lagoon with stagnant water. Some brackish water sediments are found from this age. (Meulenkamp *et al.* 2000b).

In the Lower Rhine Embayment the continental deposition prevailed. There was an extensive swampy coastal lowland area, which was widened when the sea regressed in the late Early Miocene. The extensive Morcken Coal Seam was deposited at that time. In the early Middle Miocene the eustatic sealevel rise flooded the Lower Rhine Embayment. (Meulenkamp *et al.* 2000c)

In the latest Middle Miocene the Central Paratethys area started to continentalize, the seaways shrank and the basins became more isolated. In the end, the watermasses were isolated in the Pannonian region and formed the huge Lake Pannon.

Lake Pannon was a very long-lived body of water that filled the Pannonian basin from the late Middle Miocene to Pliocene times. Most of the time it was a brackish-water body, so to call it a lake is not exactly right. (Magyar *et al.* 1999). In the Middle Late Miocene Lake Pannon reached its largest extent. After this the lake shrank during the Late Miocene time almost by half. From the latest Miocene onwards Lake Pannon was slowly filled by sediments until it was transformed into a small freshwater, the Paludina Lake. The last stage of a huge inland sea ended in the Pliocene, when Lake Paludina eventually transformed into a series of small freshwater lakes.

### **6.3. The Messinian salinity crisis**

The Mediterranean is an inland sea, and its water budget is highly negative. This means that the loss of water by evaporation is more than double the gain of inflow from rivers and precipitation. The only source of water to balance the budget is the inflow from the Atlantic via Gibraltar and, in lesser amounts, from the Black Sea. The Atlantic waters enter the Mediterranean as a surface flow in the Gibraltar and the outflow to Atlantic is formed by very saline water at the bottom of the sea.

Even the cause of the Messinian salinity crisis is still under discussion. Today it is generally accepted that the main reason for the drying was tectonic activity in the Betic range, which resulted in the raising of the sills in the corridors connecting the Mediterranean to the Atlantic. This way, the outflow of saline water was disrupted and the salinity of Mediterranean water started to rise. Surface water still flowed to the

Mediterranean and was evaporated leaving only salt, which started to precipitate into the bottom of the sea, forming huge deposits of salt, which are thousands of meters thick. (Hsü *et al.* 1973, Clauzon *et al.* 1996, Krijnsman *et al.* 2000). If the Mediterranean would be desiccated completely, the salt in the Mediterranean seawater at one moment would form only deposits which would be in the range of couple of tens of meters. (Suc, pers. comm.)

Salt deposits are found everywhere in the Mediterranean realm. There are two kinds of salt deposits (evaporites): Abyssal, which are found in the central parts of the basins, and marginal, which are found in the margins of basins. There are also deep-cut canyons of Messinian age found in the Mediterranean margins (e.g. Rhône canyon, Nile canyon), which are filled by Pliocene sediments. But there is also evidence of open-marine conditions throughout the period of the crisis (Clauzon *et al.* 1996). These controversial evidences about erosion, deposition and marine conditions result in a large number of different opinions and models. The latest model is that of Clauzon *et al.* (1996), in which the desiccation of Mediterranean is a two-phase phenomena.

The exact nature of the Messinian salinity crisis is an interesting and important topic. Unfortunately it is out of the scope of this study. For this study it must suffice to say that there was a desiccation of the Mediterranean and that the sill at Gibraltar was overflowed 5.32 Ma ago refilling the Mediterranean again.

## **7. Discussion**

Jernvall & Fortelius (2002) argued that common animals “drive” the evolution of hypsodonty in the Neogene, whereas the rare species just stay constant and produce “noise”. “Drive” is actually not a good word to use, because animals that are common at one time have first adapted to the environment and by adapting have been able to become common. From the above mentioned results, this seems to hold also with mammal body size.

When we consider the possible causes for the rise in mean body size of common species in MN5-6 (figure 4a & 4b), one phenomenon is easily seen as a cause: the Mid-Miocene cooling (Flower & Kennett 1994) dated as 14.8 to 14.1 Ma ago. MN6 is at the same time, the base of the MN6 being 15 Ma following Steininger (1999). If we look at the MN maps, there is a rise in body mass seen in the Iberian peninsula and in easternmost Europe. The rise in MN6 can be seen partly as immigration through the late Gomphotherium land bridge from Africa, even though first Gomphotheriidae in Europe are from MN3 (MN4 in this study, because some localities were omitted from the analysis). It might also be connected to the mid-Miocene cooling. The central European small sized faunas might be seen in the context of stagnant lagoons in the Rhine Embayment and small lakes of the Molasse Basin (Sissingh 1998), with lakeside forests and swamps dominated by *Taxodium* (Gebka *et al.* 1999, Kovar-Eder *et al.* 1996, Bernor *et al.* 1988), although the same kind of climate was witnessed also in southern Europe (Esu 1999). On the other hand, changes in the ocean circulation (Flower & Kennett 1994) affect first the localities in the Iberian peninsula and in eastern and southeastern Europe, as the Mediterranean affects the climate there more than in central Europe, where the effect of the Paratethys might have dampened or buffered the effect of cooling. An interesting note is that in the overall analysis the body size of eastern faunas rises above the western faunas (figure 7) during this period. The rise in body size was more pronounced in east than in west.

If we look at the Astaracian (figure 10) as a whole, we see that indeed in the east the rise was more uniform than in the west. This might have been caused by immigrants first

arriving in the east, the mid-Miocene cooling or the continentalization (Rögl 1998, and above-mentioned references) of the Paratethys, which resulted in more open habitats.

The next clear change in body size happens in MN9. This coincides with the mid-Vallesian crisis (MVC) (Agusti *et al.* 1999), between MN9 and MN10. We see the Vallesian crisis (in the sense of Morales *et al.* (1999)) affecting mostly the small species, classes 2 and 3 (figure 6). All animals become rare during MN9, but relatively the largest drop is in class 2 (figure 3). The Vallesian is also seen in the east-west comparison (figure 7). In MN9 and MN10 the size difference between the east and the west is very low. Overall this might be seen as turmoil in the mammal community, a period when a large stock of immigrants came and everything mixed.

Focusing on the geographical perspective of the Vallesian a little more, we see that in MN9 only the westernmost France and Iberia are still dominated by small faunas. But then again, in MN10 the pattern is almost the same. The Austrian locality that dominates the whole central Europe alone is Kohfidisch, with only two carnivorean species. Therefore it should be considered a somewhat unreliable signal, and not accounted for. The MVC is situated exactly between these units (Morales *et al.* 1999). During the Vallesian the continentalization of the Paratethys continued further, so this could be seen as moving towards more open habitats (Bernor 1983).

This is interesting if we fit it together with the picture we are getting from MN11 and MN12. They all seem to hold the same pattern, which shows that in east and south of the Alps there are mid-to-large sized faunas, but in the central Europe the faunas seem to be small-sized. This is probably a reflection of the transgression of “Pontian” (open habitat) faunas to these areas.

MN13 is the period when the Messinian salinity crisis (Hsü *et al.* 1973) happens. In the mammalian data rarely something can be related to the Messinian salinity crisis. Body size seems to react to the salinity crisis. In MN13 the mean body size is larger all over Europe, and when we look at the individual classes, we see that the common species of body size class 2 disappear (figure 6). There is a lowering of the total sum in other classes

as well, but the only class that becomes totally rare is the smallest cohort. Also, the overall body size peak in commons (figure 4a & 4b) as well as in the total (figure 16) is in MN13. Body size change represents here dryness or water-stress, as can be the case (Peters 1983). The interpretation is that the habitats became more open and woodland-type (Bernor 1983), if we use body size as a function of openness. An interesting notice is that in MN13 there is also the continuing presence of small body size faunas in Hungary and in localities Brisighella (Italy) and Dystiko (Greece).

After the Messinian crisis the environments in Europe changed. The warmth of the Miocene was gone forever, and during the Pliocene the coldness of the Quaternary became closer and closer. MN14 is the start of the Pliocene. In figure 7 we see that for the first time since early Miocene the faunas in the east are smaller in size than the faunas in west. When we look at figure 9, we notice that it can be seen also in more detail. The east is a domain of the small and in the west the faunas are mid-sized, except in westernmost Spain.

This implies that after the Messinian the Miocene conditions never returned, and different environmental dynamics started to rule Europe. MN14 sees the return of small body size species from the east, like the small (class 2) primates which are found in MN13 only from Dystiko, Hatvan and Baltavar, but in MN14 also from France and in MN15 from France, Germany, Hungary, Romania and Slovakia. There are no small suids and only one mid-sized suid species (*Potamochoerus provincialis*) with one occurrence (from locality Hatvan) in MN13, and in MN14 there are two mid-sized suid species (*Potamochoerus provincialis* and *Sus arvensis*) with 10 occurrences all over Europe.

There was also disappearance or decrease in numbers of some large sized species. For instance, there are 13 occurrences of Proboscideans in MN13, of which 3 are very large (class 5). In MN14 there are only 7 Proboscidean occurrences and in MN15 8 occurrences, of which none is a very large (class 5) species. There are 8 Proboscidean species in MN13 and only 2 species in MN15.

In Perissodactyla, there are 54 occurrences in MN13, 16 in MN14 and 20 in MN15. The species composition does not change much. This is also the case for large carnivores (class 4). They decrease from 4 species and 9 occurrences in MN13 to 3 species and 3 occurrences in MN15.

This change in mean body size might be seen in the context of returning humidity to the Mediterranean (Griffin 2002).

MN15 represents also the Pliocene fluctuations between warm and cold environments. There are documented Pliocene cold intervals at 4.5 and 3.5 Ma ago (Suc *et al.* 1995) and a Pliocene warm interval at 3.1 to 3.0 Ma ago (Zagwijn 1960, Suc *et al.* 1995). This is represented also by the fact that the common species show a lower mean body size than the rare ones (figure 4a & 4b) in MN15.

So for some reason - probably because of rapid short duration climatic fluctuations - the pattern in Europe starts to homogenize.

In MN16 and MN17 we see just small to medium body sizes all over Europe. This is probably because the warm and cold interval faunas are mixed in the maps, and our resolution is not high enough to pick up the differences. This is backed up by the fact that the maps give the most homogenous picture of the whole Neogene during this period (Figure 9). Also the common-rare differentiation (Figure 4a & 4b) doesn't give any clear difference during this time, and neither does the east-west separation (Figure 7). So the Villafranchian (MN16-17) seems to be out of the reach of interpretation with data of this resolution. The development of warm-cold stages begins already in the Late Pliocene (Suc & Zagwijn 1983), and that might be the reason why already MN15 is hard to interpret.

When we start to compare the hypsodonty signal (Fortelius & Eronen 2001, Fortelius *et al.* 2002) and the body size signal based on the maps (Figures 9, 10 and 11 and appendix I) we see that there are similarities. This is first seen in MN 5-7+8. The MN5 Spanish high hypsodonty is the *Hispanotherium*-fauna (Fortelius *et al.* 2002). After that in MN6 the hypsodonty is low again in western Europe, but somewhat towards brachydont-dominated faunas in eastern Europe, while in body size it has started to rise in MN5 and continues also in MN6.

In MN9 hypsodonty rise is seen in the east but not yet in the west, but in body size it is already seen in most of Europe. In MN10 hypsodont equids become common and the hypsodonty signal jumps quickly to very hypsodont. But actually the same signal is also seen in the body size (if we exclude the Austrian locality). The pattern seems similar. This is the MVC, and it has been shown earlier (Morales *et al.* 1999) that it was a time of mixing of the faunas. It was very similar all over Europe, and was caused by the disappearance of small sized brachydont animals in the east (Fortelius *et al.* 1996). In reality, this means that the forms living in humid closed forests disappeared, and more open-habitat forms started to dominate, as was predicted by Bernor (1983) and Bernor *et al.* (1984) long ago.

Another time when the body size signal and the hypsodonty signal give a similar pattern is in MN13, which is the Messinian. The only difference is hypsodonty signal from the Italian locality Gravitelli in Sicily, which controls the whole mid-Mediterranean. In both maps central Europe gives low values, and east and west Europe with the whole Mediterranean (except Gravitelli) is a domain of large hypsodont species. As discussed above, here also the case is rather the disappearance of small brachydont species than mid-sizes faunas getting larger.

After the Messinian the hypsodonty signal shows the return of brachydont faunas. The body size signal shows the trend of return of small body size species. This agrees very well with the idea of returning humidity to the Mediterranean (Griffin 2002).

The interesting thing is that faunas tend to become larger before they start to develop from brachydont towards more hypsodont (figure 13). The lag between these is really long, something between 4-5 MN units. Body size starts to rise at MN5 and continues to rise until MN10. Hypsodonty starts to rise at MN9 and continues to rise until MN13. Between MN13 and MN14 both values drop considerably, body size less than hypsodonty. Hypsodonty rises again from MN14 onwards, but body size starts to rise only in MN15. It seems like there was a some kind of environmental pattern or mechanism in the Neogene that changes after the Messinian event.

## **8. Conclusions**

From the results we can say that the body size classes are a good, if somewhat crude, method for observing changes in the environmental development of European Neogene. Body size exhibits the same common-rare difference as hypsodonty (Jernvall & Fortelius 2002).

The interesting mechanism of body size - hypsodonty signal congruence is not clear. It seems that something happened during the early Middle Miocene that started the body size development (or change of faunas) towards large-species dominated communities that lasted almost uninterrupted until the Messinian times. The hypsodonty signal started to develop approximately 4 Ma later (the timespan between the end of MN5 and the beginning of MN9)

Body size seems to react to different environmental variables, and it shows in many occasions the same signal as hypsodonty. It has been demonstrated that hypsodonty is connected to generalized water stress (Fortelius *et al.* 2002) and dryness. Damuth & Fortelius (2001) have also demonstrated that hypsodonty is connected to rainfall. The generalized humidity rather than only rainfall is closer to reality according to Fortelius (pers. comm.). Therefore it could be assumed that one of the main variables affecting body size is humidity changes, or the effects of those changes on the environment. When it is more humid, habitats are more closed, and when it is more arid, habitats are more open.

This explains a good part of the signal. The differences between hypsodonty and body size signals might be the result of body size reacting also to temperature. Hypsodonty is for the most part only affected by aridity, so the reason for the difference might be that body size reacts also to temperature.

So, based on the results, it seems that the changes in body size through the Neogene consist of reactions to two variables: aridity and temperature. These reactions are mainly seen in the common species, so it is safe to assume that the common animals “are driven

by” the evolution of body size, as well as that of hypsodonty (Jernvall & Fortelius 2002).

Even though we know that the total body size is rising through the whole Neogene, it is not seen geographically. There are differences between places (Figures 9 & 10), and a clear trend that the overall body size is rising can be seen only in some instances (like between MN12 and MN13).

The overall trend of larger body sizes through the Neogene might be seen as reacting to cooler and cooler temperatures, and the lack of geographic unity as reacting also to aridity and to small scale local variability. We must not forget also the effect of sampling that might affect the geographical patterns we see.

The peaks in body size are during the Messinian crisis (MN13). The difference between the eastern faunas and the western faunas is constant and remarkable. Only in the times of stress, like the mid-Vallesian crisis, the difference of body sizes between the east and west, as well as between common and rare, is lessened and the overall picture is one of mixing.

This study leaves many question unanswered, like why there is a lag between body size rise and hypsodonty development, even though they are very closely correlated. Another question is the mechanism and the actual cause for the body size development start in the early Middle Miocene. The cause might be mid-Miocene cooling, but not necessarily.

What happened during the Messinian that caused the mechanism to switch? Before Messinian the body size rise was seen first and hypsodonty after that, and the eastern faunas had a larger mean body size than the western faunas. After the Messinian rise in the hypsodonty is seen first and only after that a rise in mean body size. The western faunas seem to have a larger mean body size than the eastern.

Because of this it might be fruitful to try to fix body size classes more precily (cutoff at 150 cm) and resolve the relationship between body size and temperature.

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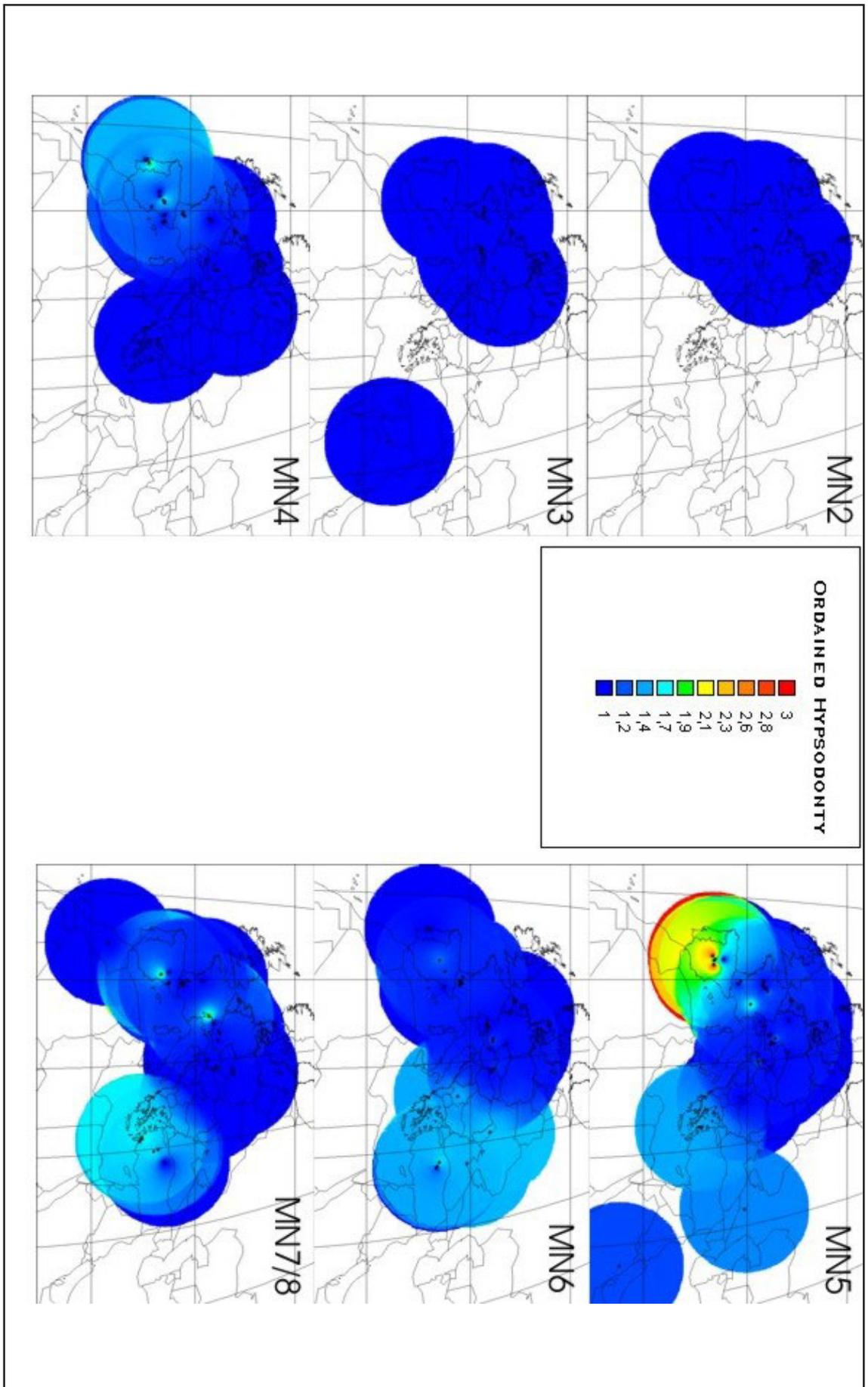
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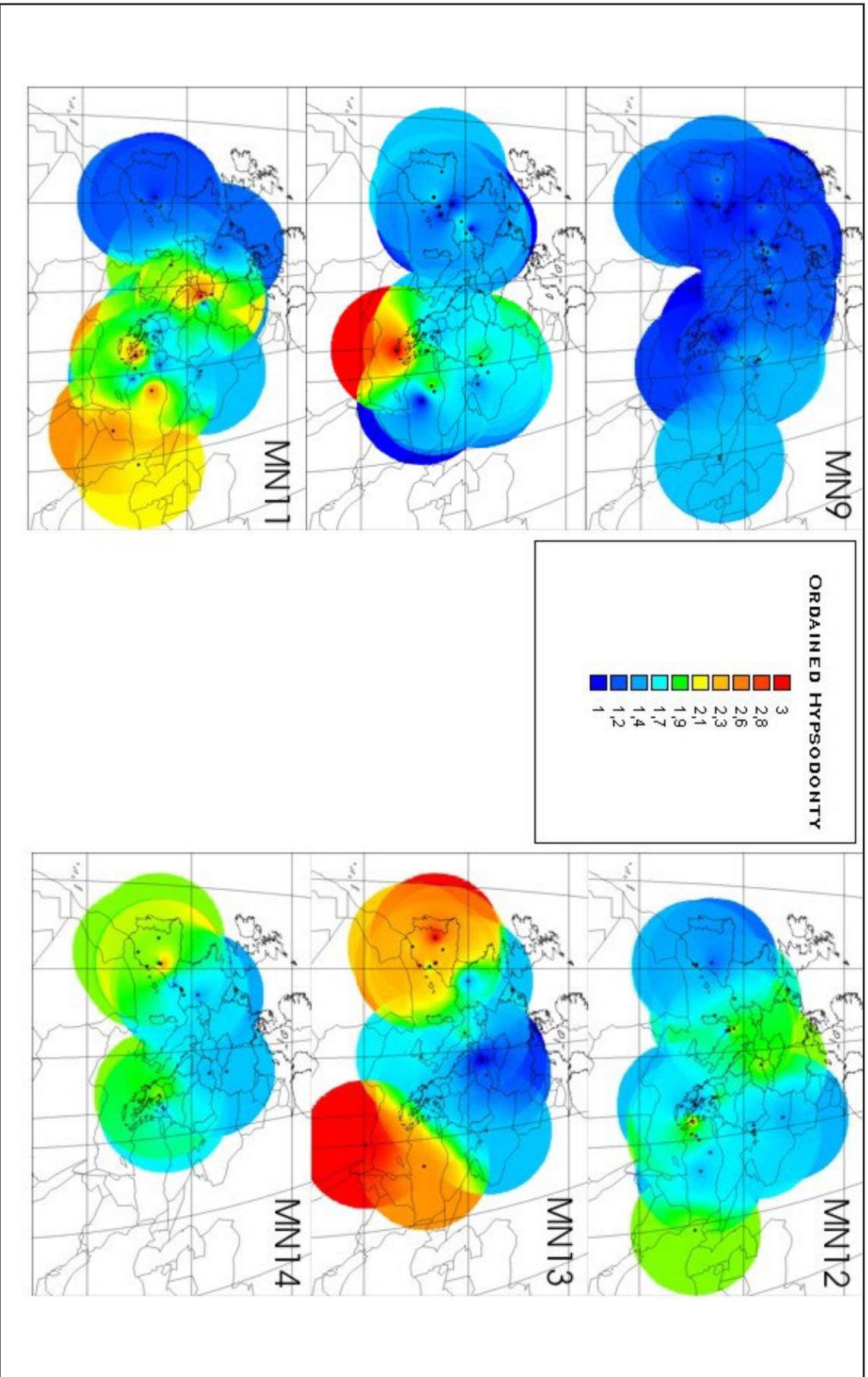
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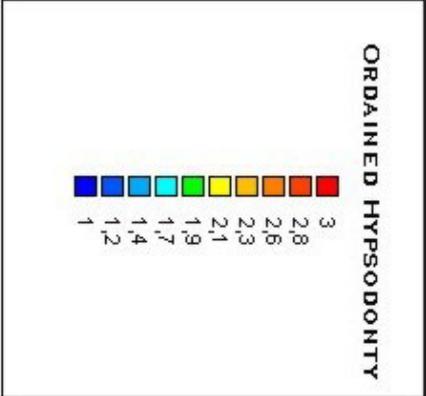
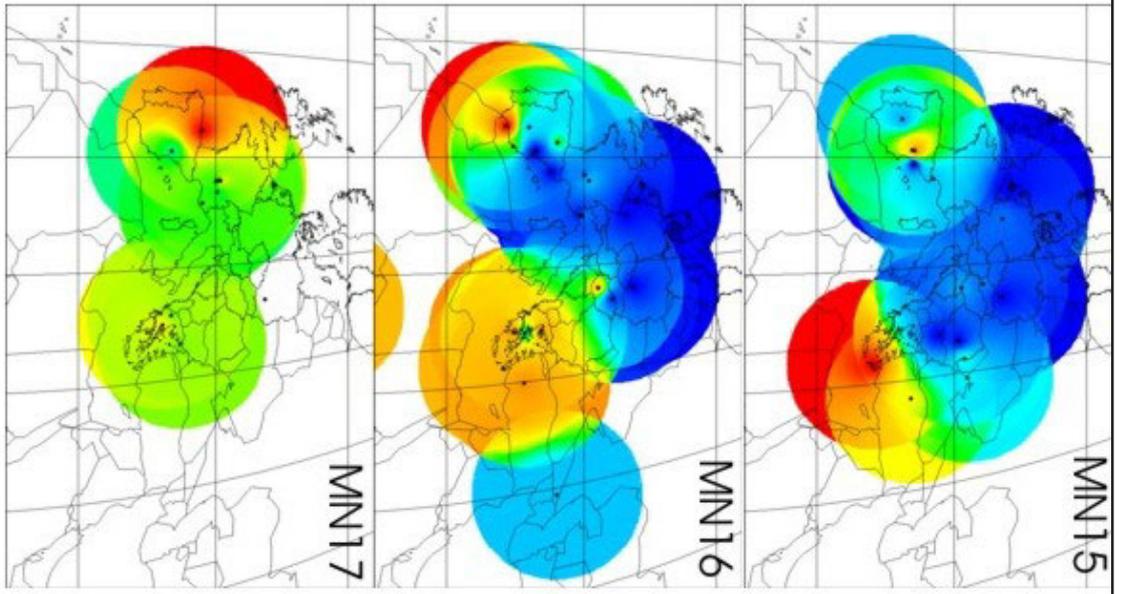
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# Appendix I: The hypsodonty maps







## Appendix II: Locality list

<u>AGE</u>	<u>NAME</u>	<u>COUNTRY</u>
<u>MN02</u>	<u>Barbotan-Les-Thermes</u>	<u>France</u>
<u>MN02</u>	<u>Budenheim</u>	<u>Germany</u>
<u>MN02</u>	<u>Cetina de Aragon</u>	<u>Spain</u>
<u>MN02</u>	<u>Chemin des Falaises</u>	<u>Switzerland</u>
<u>MN02</u>	<u>Haslach</u>	<u>Germany</u>
<u>MN02</u>	<u>Haut du Calvaire</u>	<u>Switzerland</u>
<u>MN02</u>	<u>Hessler</u>	<u>Germany</u>
<u>MN02</u>	<u>La Borde</u>	<u>Switzerland</u>
<u>MN02</u>	<u>La Chaux 7</u>	<u>Switzerland</u>
<u>MN02</u>	<u>Langy</u>	<u>France</u>
<u>MN02</u>	<u>Laugnac</u>	<u>France</u>
<u>MN02</u>	<u>Le Tunnel</u>	<u>Switzerland</u>
<u>MN02</u>	<u>Loranca</u>	<u>Spain</u>
<u>MN02</u>	<u>Montaigu-le-Blin</u>	<u>France</u>
<u>MN02</u>	<u>Saint-Gérard-le-Puy</u>	<u>France</u>
<u>MN02</u>	<u>Selles-sur-Cher</u>	<u>France</u>
<u>MN02</u>	<u>Ulm-Uniklinik</u>	<u>Germany</u>
<u>MN02</u>	<u>Ulm-Westtangente</u>	<u>Germany</u>
<u>MN02</u>	<u>Valquemado</u>	<u>Spain</u>
<u>MN03</u>	<u>Agreda</u>	<u>Spain</u>
<u>MN03</u>	<u>Bierkeller</u>	<u>Switzerland</u>
<u>MN03</u>	<u>Brüttelen</u>	<u>Switzerland</u>
<u>MN03</u>	<u>Chilleurs-aux-Bois</u>	<u>France</u>
<u>MN03</u>	<u>Chitenay</u>	<u>France</u>
<u>MN03</u>	<u>Dénezé-sous-le-Lude</u>	<u>France</u>

<b><u>MN03</u></b>	<b><u>Esvres - Continental Sands</u></b>	<b><u>France</u></b>
<b><u>MN03</u></b>	<b><u>Goldinger Tobel 8</u></b>	<b><u>Switzerland</u></b>
<b><u>MN03</u></b>	<b><u>Grès de la Molière</u></b>	<b><u>Switzerland</u></b>
<b><u>MN03</u></b>	<b><u>Les Brosses</u></b>	<b><u>France</u></b>
<b><u>MN03</u></b>	<b><u>Neuville-aux-Bois</u></b>	<b><u>France</u></b>
<b><u>MN03</u></b>	<b><u>Pontigne</u></b>	<b><u>France</u></b>
<b><u>MN03</u></b>	<b><u>Semsettin 1</u></b>	<b><u>Turkey</u></b>
<b><u>MN03</u></b>	<b><u>Trub-Sältenach</u></b>	<b><u>Switzerland</u></b>
<b><u>MN03</u></b>	<b><u>Tuchorice</u></b>	<b><u>Czhech Repub</u></b>
<b><u>MN03</u></b>	<b><u>Wintershof-West</u></b>	<b><u>Germany</u></b>
<b><u>MN04</u></b>	<b><u>Aérotrain</u></b>	<b><u>France</u></b>
<b><u>MN04</u></b>	<b><u>Antonios (ANT)</u></b>	<b><u>Greece</u></b>
<b><u>MN04</u></b>	<b><u>Armantes 1</u></b>	<b><u>Spain</u></b>
<b><u>MN04</u></b>	<b><u>Artenay</u></b>	<b><u>France</u></b>
<b><u>MN04</u></b>	<b><u>Artesilla</u></b>	<b><u>Spain</u></b>
<b><u>MN04</u></b>	<b><u>Belchatow C</u></b>	<b><u>Poland</u></b>
<b><u>MN04</u></b>	<b><u>Bezian</u></b>	<b><u>France</u></b>
<b><u>MN04</u></b>	<b><u>Buñol</u></b>	<b><u>Spain</u></b>
<b><u>MN04</u></b>	<b><u>Can Canals</u></b>	<b><u>Spain</u></b>
<b><u>MN04</u></b>	<b><u>Can Julia</u></b>	<b><u>Spain</u></b>
<b><u>MN04</u></b>	<b><u>Córcoles</u></b>	<b><u>Spain</u></b>
<b><u>MN04</u></b>	<b><u>Els Casots</u></b>	<b><u>Spain</u></b>
<b><u>MN04</u></b>	<b><u>Erkertshofen 2</u></b>	<b><u>Germany</u></b>
<b><u>MN04</u></b>	<b><u>La Romieu</u></b>	<b><u>France</u></b>
<b><u>MN04</u></b>	<b><u>Langenau 1</u></b>	<b><u>Germany</u></b>
<b><u>MN04</u></b>	<b><u>Lisboa V</u></b>	<b><u>Portugal</u></b>
<b><u>MN04</u></b>	<b><u>Montreal-du-Gers</u></b>	<b><u>France</u></b>

<b><u>MN04</u></b>	<b><u>Moratines</u></b>	<b><u>Spain</u></b>
<b><u>MN04</u></b>	<b><u>Munébrega 1</u></b>	<b><u>Spain</u></b>
<b><u>MN04</u></b>	<b><u>Oberdorf 3 (O3)</u></b>	<b><u>Austria</u></b>
<b><u>MN04</u></b>	<b><u>Oberdorf 4 (O4)</u></b>	<b><u>Austria</u></b>
<b><u>MN04</u></b>	<b><u>Pellecahus</u></b>	<b><u>France</u></b>
<b><u>MN04</u></b>	<b><u>Petersbuch 2</u></b>	<b><u>Germany</u></b>
<b><u>MN04</u></b>	<b><u>Quinta da Farinheira</u></b>	<b><u>Portugal</u></b>
<b><u>MN04</u></b>	<b><u>Sant Mamet</u></b>	<b><u>Spain</u></b>
<b><u>MN04</u></b>	<b><u>Tavers</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Avaray</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Baigneaux-en Beauce</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Beaugency-Tavers</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Belometchetskaja</u></b>	<b><u>Georgia</u></b>
<b><u>MN05</u></b>	<b><u>Chatzloch</u></b>	<b><u>Switzerland</u></b>
<b><u>MN05</u></b>	<b><u>Chios</u></b>	<b><u>Greece</u></b>
<b><u>MN05</u></b>	<b><u>Crastes</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Eibiswald</u></b>	<b><u>Austria</u></b>
<b><u>MN05</u></b>	<b><u>Esvres - Marine Faluns</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Faluns of Touraine &amp; Anjou</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Gallenbach 2b</u></b>	<b><u>Germany</u></b>
<b><u>MN05</u></b>	<b><u>Georgensgmünd</u></b>	<b><u>Germany</u></b>
<b><u>MN05</u></b>	<b><u>Gisseltshausen</u></b>	<b><u>Germany</u></b>
<b><u>MN05</u></b>	<b><u>Göriach</u></b>	<b><u>Austria</u></b>
<b><u>MN05</u></b>	<b><u>Häder</u></b>	<b><u>Germany</u></b>
<b><u>MN05</u></b>	<b><u>Käpfnach</u></b>	<b><u>Switzerland</u></b>
<b><u>MN05</u></b>	<b><u>La Retama</u></b>	<b><u>Spain</u></b>
<b><u>MN05</u></b>	<b><u>Mala Miliva</u></b>	<b><u>Serbia</u></b>

<b><u>MN05</u></b>	<b><u>Montejo de la Vega</u></b>	<b><u>Spain</u></b>
<b><u>MN05</u></b>	<b><u>Münzenberg (Leoben)</u></b>	<b><u>Austria</u></b>
<b><u>MN05</u></b>	<b><u>Obergänserndorf 2 (OG2)</u></b>	<b><u>Austria</u></b>
<b><u>MN05</u></b>	<b><u>Pontlevoy</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Poudenas</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Puente de Toledo</u></b>	<b><u>Spain</u></b>
<b><u>MN05</u></b>	<b><u>Réaup</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Reisensburg</u></b>	<b><u>Germany</u></b>
<b><u>MN05</u></b>	<b><u>Rothenstein 1</u></b>	<b><u>Germany</u></b>
<b><u>MN05</u></b>	<b><u>Sandelzhausen</u></b>	<b><u>Germany</u></b>
<b><u>MN05</u></b>	<b><u>Savigné-sur-Lathan</u></b>	<b><u>France</u></b>
<b><u>MN05</u></b>	<b><u>Seegraben (Leoben)</u></b>	<b><u>Austria</u></b>
<b><u>MN05</u></b>	<b><u>Stallhofen</u></b>	<b><u>Austria</u></b>
<b><u>MN05</u></b>	<b><u>Teiritzberg 1 (T1)</u></b>	<b><u>Austria</u></b>
<b><u>MN05</u></b>	<b><u>Thymiana</u></b>	<b><u>Greece</u></b>
<b><u>MN05</u></b>	<b><u>Torrijos</u></b>	<b><u>Spain</u></b>
<b><u>MN05</u></b>	<b><u>Viehhausen</u></b>	<b><u>Germany</u></b>
<b><u>MN05</u></b>	<b><u>Voggersberg</u></b>	<b><u>Germany</u></b>
<b><u>MN05</u></b>	<b><u>Ziemetshausen 1b</u></b>	<b><u>Germany</u></b>
<b><u>MN06</u></b>	<b><u>Arroyo del Val</u></b>	<b><u>Spain</u></b>
<b><u>MN06</u></b>	<b><u>Çandır</u></b>	<b><u>Turkey</u></b>
<b><u>MN06</u></b>	<b><u>Castelnau-d'Arbieu</u></b>	<b><u>France</u></b>
<b><u>MN06</u></b>	<b><u>Elgg</u></b>	<b><u>Switzerland</u></b>
<b><u>MN06</u></b>	<b><u>Hambach 6C</u></b>	<b><u>Germany</u></b>
<b><u>MN06</u></b>	<b><u>Haulies</u></b>	<b><u>France</u></b>
<b><u>MN06</u></b>	<b><u>Inönü I (AS_24A)</u></b>	<b><u>Turkey</u></b>
<b><u>MN06</u></b>	<b><u>Klein Hadersdorf</u></b>	<b><u>Austria</u></b>

<b><u>MN06</u></b>	<b><u>Krivoj Rog</u></b>	<b><u>Ukraine</u></b>
<b><u>MN06</u></b>	<b><u>Laymont</u></b>	<b><u>France</u></b>
<b><u>MN06</u></b>	<b><u>Lussan</u></b>	<b><u>France</u></b>
<b><u>MN06</u></b>	<b><u>Marciac</u></b>	<b><u>France</u></b>
<b><u>MN06</u></b>	<b><u>Miélan</u></b>	<b><u>France</u></b>
<b><u>MN06</u></b>	<b><u>Montesquiou-sur-L'Osse</u></b>	<b><u>France</u></b>
<b><u>MN06</u></b>	<b><u>Neudorf-Sandberg</u></b>	<b><u>Slovakia</u></b>
<b><u>MN06</u></b>	<b><u>Neudorf-Spalte</u></b>	<b><u>Slovakia</u></b>
<b><u>MN06</u></b>	<b><u>Paracuellos 5</u></b>	<b><u>Spain</u></b>
<b><u>MN06</u></b>	<b><u>Pero Filho</u></b>	<b><u>Portugal</u></b>
<b><u>MN06</u></b>	<b><u>Póvoa de Satarém</u></b>	<b><u>Portugal</u></b>
<b><u>MN06</u></b>	<b><u>Prebreza</u></b>	<b><u>Serbia</u></b>
<b><u>MN06</u></b>	<b><u>Riedern</u></b>	<b><u>Germany</u></b>
<b><u>MN06</u></b>	<b><u>Rümikon</u></b>	<b><u>Switzerland</u></b>
<b><u>MN06</u></b>	<b><u>Sansan</u></b>	<b><u>France</u></b>
<b><u>MN06</u></b>	<b><u>Sevastopol (Sebastopol)</u></b>	<b><u>Ukraine</u></b>
<b><u>MN06</u></b>	<b><u>Steinberg</u></b>	<b><u>Germany</u></b>
<b><u>MN06</u></b>	<b><u>Stätzling</u></b>	<b><u>Germany</u></b>
<b><u>MN06</u></b>	<b><u>Thannhausen</u></b>	<b><u>Germany</u></b>
<b><u>MN06</u></b>	<b><u>Trimmelkam</u></b>	<b><u>Austria</u></b>
<b><u>MN06</u></b>	<b><u>Tüney</u></b>	<b><u>Turkey</u></b>
<b><u>MN06</u></b>	<b><u>Wiesholz</u></b>	<b><u>Switzerland</u></b>
<b><u>MN07+8</u></b>	<b><u>Alan (N.D. de Lorette)</u></b>	<b><u>France</u></b>
<b><u>MN07+8</u></b>	<b><u>Alan (Pompat)</u></b>	<b><u>France</u></b>
<b><u>MN07+8</u></b>	<b><u>Anwil</u></b>	<b><u>Switzerland</u></b>
<b><u>MN07+8</u></b>	<b><u>Atzgersdorf (WIEN)</u></b>	<b><u>Austria</u></b>
<b><u>MN07+8</u></b>	<b><u>Bachas</u></b>	<b><u>France</u></b>

<u>MN07+8 Beni Mellal</u>	<u>Marocco</u>
<u>MN07+8 Can Almirall</u>	<u>Spain</u>
<u>MN07+8 Cassagnabère</u>	<u>France</u>
<u>MN07+8 Castelgaillard</u>	<u>France</u>
<u>MN07+8 Castell de Barberà</u>	<u>Spain</u>
<u>MN07+8 Çatakbagyaka</u>	<u>Turkey</u>
<u>MN07+8 Cerro del Otero</u>	<u>Spain</u>
<u>MN07+8 Coueilles (Rte de Riolas)</u>	<u>France</u>
<u>MN07+8 Crêt-du-Loclc</u>	<u>Switzerland</u>
<u>MN07+8 Escanecrabe</u>	<u>France</u>
<u>MN07+8 Escobosa</u>	<u>Spain</u>
<u>MN07+8 Hachan</u>	<u>France</u>
<u>MN07+8 Hostalets de Pierola Inferior</u>	<u>Spain</u>
<u>MN07+8 La Grive St. Alban</u>	<u>France</u>
<u>MN07+8 Laichingen</u>	<u>Germany</u>
<u>MN07+8 Lower Sinap</u>	<u>Turkey</u>
<u>MN07+8 Markt Indersdorf</u>	<u>Germany</u>
<u>MN07+8 Minisu de Sus</u>	<u>Romania</u>
<u>MN07+8 Opole 2</u>	<u>Poland</u>
<u>MN07+8 Péguilhan</u>	<u>France</u>
<u>MN07+8 Poudenas-Cayron</u>	<u>France</u>
<u>MN07+8 Przeworno 2</u>	<u>Poland</u>
<u>MN07+8 Saint-Gaudens (Valentine)</u>	<u>France</u>
<u>MN07+8 Sant Quirze</u>	<u>Spain</u>
<u>MN07+8 Sariçay</u>	<u>Turkey</u>
<u>MN07+8 Sofça</u>	<u>Turkey</u>
<u>MN07+8 Sopron</u>	<u>Hungary</u>

<u>MN07+8 St. Gaudens</u>	<u>France</u>
<u>MN07+8 St. Stephan im Lavanttal</u>	<u>Austria</u>
<u>MN07+8 Steinheim</u>	<u>Germany</u>
<u>MN07+8 Toril 3</u>	<u>Spain</u>
<u>MN07+8 Yaylacilar</u>	<u>Turkey</u>
<u>MN07+8 Yeni Eskihisar 1</u>	<u>Turkey</u>
<u>MN09 Atavaska</u>	<u>Moldova</u>
<u>MN09 Ballestar</u>	<u>Spain</u>
<u>MN09 Belchatow A</u>	<u>Poland</u>
<u>MN09 Bermersheim</u>	<u>Germany</u>
<u>MN09 Bonnefont</u>	<u>France</u>
<u>MN09 Bou Hanifia</u>	<u>Algeria</u>
<u>MN09 Can Ponsic</u>	<u>Spain</u>
<u>MN09 Charmoille</u>	<u>Switzerland</u>
<u>MN09 Dinotheriensande</u>	<u>Germany</u>
<u>MN09 Doué-la-Fontaine</u>	<u>France</u>
<u>MN09 El Firal</u>	<u>Spain</u>
<u>MN09 Eldari I</u>	<u>Georgia</u>
<u>MN09 Eppelsheim</u>	<u>Germany</u>
<u>MN09 Esme Akçaköy</u>	<u>Turkey</u>
<u>MN09 Esselborn</u>	<u>Germany</u>
<u>MN09 Esvres - Upper Faluns</u>	<u>France</u>
<u>MN09 Gaiselberg</u>	<u>Austria</u>
<u>MN09 Gau-Weinheim</u>	<u>Germany</u>
<u>MN09 Gorna Susica</u>	<u>Bulgaria</u>
<u>MN09 Götzendorf</u>	<u>Austria</u>
<u>MN09 Hammerschmiede</u>	<u>Germany</u>

<u>MN09</u>	<u>Himberg</u>	<u>Austria</u>
<u>MN09</u>	<u>Hinterauerbach</u>	<u>Germany</u>
<u>MN09</u>	<u>Hostalets de Pierola Superior</u>	<u>Spain</u>
<u>MN09</u>	<u>Höwenegg</u>	<u>Germany</u>
<u>MN09</u>	<u>Kalfa</u>	<u>Moldova</u>
<u>MN09</u>	<u>Los Valles de Fuentidueña</u>	<u>Spain</u>
<u>MN09</u>	<u>Mariathal</u>	<u>Austria</u>
<u>MN09</u>	<u>Markt Rettenbach</u>	<u>Germany</u>
<u>MN09</u>	<u>Melchingen</u>	<u>Germany</u>
<u>MN09</u>	<u>Mistelbach</u>	<u>Austria</u>
<u>MN09</u>	<u>Nebelbergweg</u>	<u>Switzerland</u>
<u>MN09</u>	<u>Nombrevilla</u>	<u>Spain</u>
<u>MN09</u>	<u>Oberföhring</u>	<u>Germany</u>
<u>MN09</u>	<u>Pedregueras</u>	<u>Spain</u>
<u>MN09</u>	<u>Priay II</u>	<u>France</u>
<u>MN09</u>	<u>Rudabánya</u>	<u>Hungary</u>
<u>MN09</u>	<u>Salmendingen</u>	<u>Germany</u>
<u>MN09</u>	<u>Santiga</u>	<u>Spain</u>
<u>MN09</u>	<u>Seu d'Urgel</u>	<u>Spain</u>
<u>MN09</u>	<u>Trie-sur-Baïse</u>	<u>France</u>
<u>MN09</u>	<u>Udabno I</u>	<u>Georgia</u>
<u>MN09</u>	<u>Varnitsa</u>	<u>Moldova</u>
<u>MN09</u>	<u>Wartenberg</u>	<u>Germany</u>
<u>MN09</u>	<u>Westhofen</u>	<u>Germany</u>
<u>MN09</u>	<u>Wissberg</u>	<u>Germany</u>
<u>MN09</u>	<u>Vösendorf (WIEN)</u>	<u>Austria</u>
<u>MN10</u>	<u>Basbereket</u>	<u>Turkey</u>

<b><u>MN10</u></b>	<b><u>Berislav</u></b>	<b><u>Ukraine</u></b>
<b><u>MN10</u></b>	<b><u>Can Llobateres I</u></b>	<b><u>Spain</u></b>
<b><u>MN10</u></b>	<b><u>Can Trullàs</u></b>	<b><u>Spain</u></b>
<b><u>MN10</u></b>	<b><u>Çorak Yerler</u></b>	<b><u>Turkey</u></b>
<b><u>MN10</u></b>	<b><u>Croix-Rousse</u></b>	<b><u>France</u></b>
<b><u>MN10</u></b>	<b><u>Grossulovo</u></b>	<b><u>Ukraine</u></b>
<b><u>MN10</u></b>	<b><u>Gülpinar</u></b>	<b><u>Turkey</u></b>
<b><u>MN10</u></b>	<b><u>Karain</u></b>	<b><u>Turkey</u></b>
<b><u>MN10</u></b>	<b><u>Kastellios</u></b>	<b><u>Greece</u></b>
<b><u>MN10</u></b>	<b><u>Kohfidisch</u></b>	<b><u>Austria</u></b>
<b><u>MN10</u></b>	<b><u>La Roma 2</u></b>	<b><u>Spain</u></b>
<b><u>MN10</u></b>	<b><u>La Tarumba 1</u></b>	<b><u>Spain</u></b>
<b><u>MN10</u></b>	<b><u>Masía del Barbo</u></b>	<b><u>Spain</u></b>
<b><u>MN10</u></b>	<b><u>Montredon</u></b>	<b><u>France</u></b>
<b><u>MN10</u></b>	<b><u>Novoukrainka</u></b>	<b><u>Ukraine</u></b>
<b><u>MN10</u></b>	<b><u>Orignac</u></b>	<b><u>France</u></b>
<b><u>MN10</u></b>	<b><u>Pentalophos 1 (PNT)</u></b>	<b><u>Greece</u></b>
<b><u>MN10</u></b>	<b><u>Ravin de la Pluie (RPL)</u></b>	<b><u>Greece</u></b>
<b><u>MN10</u></b>	<b><u>Ravin des Zouaves 1</u></b>	<b><u>Greece</u></b>
<b><u>MN10</u></b>	<b><u>Sherullah 9</u></b>	<b><u>Afghanistan</u></b>
<b><u>MN10</u></b>	<b><u>Soblay</u></b>	<b><u>France</u></b>
<b><u>MN10</u></b>	<b><u>Subsol de Sabadell</u></b>	<b><u>Spain</u></b>
<b><u>MN10</u></b>	<b><u>Terrassa</u></b>	<b><u>Spain</u></b>
<b><u>MN10</u></b>	<b><u>Villadecavalls</u></b>	<b><u>Spain</u></b>
<b><u>MN10</u></b>	<b><u>Xirochori 1 (XIR)</u></b>	<b><u>Greece</u></b>
<b><u>MN11</u></b>	<b><u>Baccinello V0</u></b>	<b><u>Italy</u></b>
<b><u>MN11</u></b>	<b><u>Crevillente-2</u></b>	<b><u>Spain</u></b>

<u>MN11</u>	<u>Csakvar</u>	<u>Hungary</u>
<u>MN11</u>	<u>Dorn Dürkheim</u>	<u>Germany</u>
<u>MN11</u>	<u>Garkin</u>	<u>Turkey</u>
<u>MN11</u>	<u>Karacahasan</u>	<u>Turkey</u>
<u>MN11</u>	<u>Kayadibi</u>	<u>Turkey</u>
<u>MN11</u>	<u>Kemiklitepe D</u>	<u>Turkey</u>
<u>MN11</u>	<u>Küçükçekmece</u>	<u>Turkey</u>
<u>MN11</u>	<u>Lower Maragheh</u>	<u>Iran</u>
<u>MN11</u>	<u>Novo-Elizavetovka 2</u>	<u>Ukraine</u>
<u>MN11</u>	<u>Piera</u>	<u>Spain</u>
<u>MN11</u>	<u>Prochoma</u>	<u>Greece</u>
<u>MN11</u>	<u>Puente Minero</u>	<u>Spain</u>
<u>MN11</u>	<u>Ravin des Zouaves 5</u>	<u>Greece</u>
<u>MN11</u>	<u>Samos Old Mill Beds</u>	<u>Greece</u>
<u>MN11</u>	<u>Sümeg</u>	<u>Hungary</u>
<u>MN11</u>	<u>Taghar</u>	<u>Afghanistan</u>
<u>MN11</u>	<u>Vathylakkos 2 (VTK)</u>	<u>Greece</u>
<u>MN11</u>	<u>Vivero de Pinos</u>	<u>Spain</u>
<u>MN12</u>	<u>Belka</u>	<u>Ukraine</u>
<u>MN12</u>	<u>Casa del Acero</u>	<u>Spain</u>
<u>MN12</u>	<u>Cerro de la Garita</u>	<u>Spain</u>
<u>MN12</u>	<u>Chobruchi (Tchobroutchi)</u>	<u>Moldova</u>
<u>MN12</u>	<u>Chomateres</u>	<u>Greece</u>
<u>MN12</u>	<u>Çobanpınar (AS_42)</u>	<u>Turkey</u>
<u>MN12</u>	<u>Concud</u>	<u>Spain</u>
<u>MN12</u>	<u>Crevillente 15</u>	<u>Spain</u>

<b><u>MN12</u></b>	<b><u>Ebic</u></b>	<b><u>Turkey</u></b>
<b><u>MN12</u></b>	<b><u>Györszentmárton</u></b>	<b><u>Hungary</u></b>
<b><u>MN12</u></b>	<b><u>Kemiklitepe A-B</u></b>	<b><u>Turkey</u></b>
<b><u>MN12</u></b>	<b><u>Kinik</u></b>	<b><u>Turkey</u></b>
<b><u>MN12</u></b>	<b><u>Los Aljezares</u></b>	<b><u>Spain</u></b>
<b><u>MN12</u></b>	<b><u>Los Mansuetos</u></b>	<b><u>Spain</u></b>
<b><u>MN12</u></b>	<b><u>Mahmutgazi</u></b>	<b><u>Turkey</u></b>
<b><u>MN12</u></b>	<b><u>Middle Maragheh</u></b>	<b><u>Iran</u></b>
<b><u>MN12</u></b>	<b><u>Molayan</u></b>	<b><u>Afghanistan</u></b>
<b><u>MN12</u></b>	<b><u>Mt. Luberon</u></b>	<b><u>France</u></b>
<b><u>MN12</u></b>	<b><u>Novaja Emetovka</u></b>	<b><u>Ukraine</u></b>
<b><u>MN12</u></b>	<b><u>Pikermi-MNHN (PIK)</u></b>	<b><u>Greece</u></b>
<b><u>MN12</u></b>	<b><u>Pyrgos Vassilissis</u></b>	<b><u>Greece</u></b>
<b><u>MN12</u></b>	<b><u>Samos Main Bone Beds</u></b>	<b><u>Greece</u></b>
<b><u>MN12</u></b>	<b><u>Samos White Sands</u></b>	<b><u>Greece</u></b>
<b><u>MN12</u></b>	<b><u>Thessaloniki</u></b>	<b><u>Greece</u></b>
<b><u>MN12</u></b>	<b><u>Tudorovo</u></b>	<b><u>Moldova</u></b>
<b><u>MN12</u></b>	<b><u>Upper Maragheh</u></b>	<b><u>Iran</u></b>
<b><u>MN12</u></b>	<b><u>Vathylakkos</u></b>	<b><u>Greece</u></b>
<b><u>MN13</u></b>	<b><u>Ananjev</u></b>	<b><u>Ukraine</u></b>
<b><u>MN13</u></b>	<b><u>Arenas del Rey</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>Arquillo</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>Arquillo 4</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>Baltavar</u></b>	<b><u>Hungary</u></b>
<b><u>MN13</u></b>	<b><u>Brisighella</u></b>	<b><u>Italy</u></b>
<b><u>MN13</u></b>	<b><u>Bunker de Valdecebro</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>Dytiko 1 (DTK)</u></b>	<b><u>Greece</u></b>

<b><u>MN13</u></b>	<b><u>Dytiko 2 (DIT)</u></b>	<b><u>Greece</u></b>
<b><u>MN13</u></b>	<b><u>Dytiko 3 (DKO)</u></b>	<b><u>Greece</u></b>
<b><u>MN13</u></b>	<b><u>El Arquillo 1</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>Gravitelli</u></b>	<b><u>Italy</u></b>
<b><u>MN13</u></b>	<b><u>Hatvan</u></b>	<b><u>Hungary</u></b>
<b><u>MN13</u></b>	<b><u>Kalmakpaj</u></b>	<b><u>Kazakhstan</u></b>
<b><u>MN13</u></b>	<b><u>La Alberca</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>La Gloria 5</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>Librilla</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>Milagros</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>Pavlodar</u></b>	<b><u>Kazakhstan</u></b>
<b><u>MN13</u></b>	<b><u>Puy Courny</u></b>	<b><u>France</u></b>
<b><u>MN13</u></b>	<b><u>Rambla de Valdecebro 6</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>Taskinpasa</u></b>	<b><u>Turkey</u></b>
<b><u>MN13</u></b>	<b><u>Wadi Natrun</u></b>	<b><u>Egypt</u></b>
<b><u>MN13</u></b>	<b><u>Venta del Moro</u></b>	<b><u>Spain</u></b>
<b><u>MN13</u></b>	<b><u>Villastar</u></b>	<b><u>Spain</u></b>
<b><u>MN14</u></b>	<b><u>Alcoy</u></b>	<b><u>Spain</u></b>
<b><u>MN14</u></b>	<b><u>Celleneuve</u></b>	<b><u>France</u></b>
<b><u>MN14</u></b>	<b><u>Gorafe 4</u></b>	<b><u>Spain</u></b>
<b><u>MN14</u></b>	<b><u>Gödöllö</u></b>	<b><u>Hungary</u></b>
<b><u>MN14</u></b>	<b><u>Kessani (KES)</u></b>	<b><u>Greece</u></b>
<b><u>MN14</u></b>	<b><u>La Gloria</u></b>	<b><u>Spain</u></b>
<b><u>MN14</u></b>	<b><u>La Gloria 4</u></b>	<b><u>Spain</u></b>
<b><u>MN14</u></b>	<b><u>Megalo Emvolon (MEV)</u></b>	<b><u>Greece</u></b>
<b><u>MN14</u></b>	<b><u>Montpellier</u></b>	<b><u>France</u></b>
<b><u>MN14</u></b>	<b><u>Orrios</u></b>	<b><u>Spain</u></b>

<b><u>MN14</u></b>	<b><u>Peralejos</u></b>	<b><u>Spain</u></b>
<b><u>MN14</u></b>	<b><u>Peralejos E</u></b>	<b><u>Spain</u></b>
<b><u>MN14</u></b>	<b><u>Podlesice</u></b>	<b><u>Poland</u></b>
<b><u>MN14</u></b>	<b><u>Saint Laurent des Arbres</u></b>	<b><u>France</u></b>
<b><u>MN14</u></b>	<b><u>Trévoux</u></b>	<b><u>France</u></b>
<b><u>MN14</u></b>	<b><u>Vendargues</u></b>	<b><u>France</u></b>
<b><u>MN14</u></b>	<b><u>Villalba Alta Rio 1</u></b>	<b><u>Spain</u></b>
<b><u>MN14</u></b>	<b><u>Villeneuve de la Raho</u></b>	<b><u>France</u></b>
<b><u>MN15</u></b>	<b><u>Anvers 1</u></b>	<b><u>Belgium</u></b>
<b><u>MN15</u></b>	<b><u>Apolakkia</u></b>	<b><u>Greece</u></b>
<b><u>MN15</u></b>	<b><u>Çalta</u></b>	<b><u>Turkey</u></b>
<b><u>MN15</u></b>	<b><u>Csarnota 2</u></b>	<b><u>Hungary</u></b>
<b><u>MN15</u></b>	<b><u>Ivanovce</u></b>	<b><u>Slovakia</u></b>
<b><u>MN15</u></b>	<b><u>La Calera</u></b>	<b><u>Spain</u></b>
<b><u>MN15</u></b>	<b><u>Malushteni</u></b>	<b><u>Romania</u></b>
<b><u>MN15</u></b>	<b><u>Muselievo</u></b>	<b><u>Bulgaria</u></b>
<b><u>MN15</u></b>	<b><u>Odessa Catacombs</u></b>	<b><u>Ukraine</u></b>
<b><u>MN15</u></b>	<b><u>Orrios 7</u></b>	<b><u>Spain</u></b>
<b><u>MN15</u></b>	<b><u>Perpignan</u></b>	<b><u>France</u></b>
<b><u>MN15</u></b>	<b><u>Sugas-Bai</u></b>	<b><u>Romania</u></b>
<b><u>MN15</u></b>	<b><u>Weze 1</u></b>	<b><u>Poland</u></b>
<b><u>MN15</u></b>	<b><u>Villalba Alta 1</u></b>	<b><u>Spain</u></b>
<b><u>MN15</u></b>	<b><u>Wölfersheim</u></b>	<b><u>Germany</u></b>
<b><u>MN16</u></b>	<b><u>Cova Bonica</u></b>	<b><u>Spain</u></b>
<b><u>MN16</u></b>	<b><u>Damatria</u></b>	<b><u>Greece</u></b>
<b><u>MN16</u></b>	<b><u>El Rincón</u></b>	<b><u>Spain</u></b>
<b><u>MN16</u></b>	<b><u>Etouaires</u></b>	<b><u>France</u></b>

<u>MN16</u>	<u>Gerakarou 1 (GER)</u>	<u>Greece</u>
<u>MN16</u>	<u>Gundersheim 1</u>	<u>Germany</u>
<u>MN16</u>	<u>Gülyazi</u>	<u>Turkey</u>
<u>MN16</u>	<u>Hajnácka</u>	<u>Slovakia</u>
<u>MN16</u>	<u>Hambach 11</u>	<u>Germany</u>
<u>MN16</u>	<u>Huélago</u>	<u>Spain</u>
<u>MN16</u>	<u>Kisláng</u>	<u>Hungary</u>
<u>MN16</u>	<u>Kvabebi</u>	<u>Georgia</u>
<u>MN16</u>	<u>La Higuieruelas</u>	<u>Spain</u>
<u>MN16</u>	<u>Pyrgos</u>	<u>Greece</u>
<u>MN16</u>	<u>Rebielice Królewskie 1</u>	<u>Poland</u>
<u>MN16</u>	<u>Tourkovounia 3-5</u>	<u>Greece</u>
<u>MN16</u>	<u>Triversa (Fornace RDB)</u>	<u>Italy</u>
<u>MN16</u>	<u>Udunga</u>	<u>Russia</u>
<u>MN16</u>	<u>Vassiloudi (VSL)</u>	<u>Greece</u>
<u>MN16</u>	<u>Vialette</u>	<u>France</u>
<u>MN16</u>	<u>Villafranca d'Asti (Arondelli)</u>	<u>Italy</u>
<u>MN16</u>	<u>Villaroya</u>	<u>Spain</u>
<u>MN17</u>	<u>Casablanca</u>	<u>Spain</u>
<u>MN17</u>	<u>Chilhac</u>	<u>France</u>
<u>MN17</u>	<u>Coupet</u>	<u>France</u>
<u>MN17</u>	<u>Dafnero (DFN)</u>	<u>Greece</u>
<u>MN17</u>	<u>Kadzielnia</u>	<u>Poland</u>
<u>MN17</u>	<u>La Puebla de Valverde</u>	<u>Spain</u>
<u>MN17</u>	<u>Pardines</u>	<u>France</u>
<u>MN17</u>	<u>Roccaneyra</u>	<u>France</u>
<u>MN17</u>	<u>Saint Vallier</u>	<u>France</u>

<u>MN17</u>	<u>Senèze</u>	<u>France</u>
<u>MN17</u>	<u>Sesklon (SES)</u>	<u>Greece</u>
<u>MN17</u>	<u>Volax (VOL)</u>	<u>Greece</u>