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P. V. Putshkov

**WERE THE MAMMOTHS  
KILLED BY THE WARMING ?  
(TESTING OF THE CLIMATIC VERSIONS  
OF WURM EXTINCTIONS)**

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**WERE THE MAMMOTHS KILLED BY THE WARMING ?  
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**PUTSHKOV P.V.**

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## **WERE THE MAMMOTHS KILLED BY THE WARMING ? (Testing of the climatic versions of Wurm extinctions)**

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**WERE THE MAMMOTHS KILLED BY THE WARMING ? (TESTING OF THE CLIMATIC VERSIONS OF WURM EXTINCTIONS).** Putshkov P. V. — The climatic explanations of Wurm megafaunal extinctions without replacement (MEWR) are inconsistent with the bulk of neo- and paleoecological evidence. The extinct giant herbivores (GH) were highly euryoecious forms, that lived under wide range of climates and landscapes. For example, woolly mammoths and rhinos certainly lived not only under extremely crioarid conditions of periglacial tundra-steppes, but also under far milder conditions. They subsisted on a wide range of vegetation types and could cope with the deep snow and the frozen snow crust better than any of living ungulates. No climatic extinctions doctrine could explain the absence of MEWR during numerous pre-Wurm deglaciation events. Such explanation is easy for the panbiotic doctrine that pays due attention to biotic interactions in Pleistocene and Holocene ecosystems. The 'Prehistoric pastures' were highly favorable to large herbivores owing to the biotic reasons and not due to the climatic ones. GH acted as peculiar 'mega-gardeners'. Their feeding, trampling, seed-planting, soil-fertilizing and other activities created highly productive and highly mosaic plant-communities. Due to GH zoogenic open woodlands, parklands and savannas occupied vast regions, climatically fit for closed forests, bushlands or, on the contrary — for completely treeless open grasslands. Woolly mammoths and rhinos exerted the strong effects not only on vegetation, but on the snow cover as well. The effects of GH were favorable for the majority of smaller (20-1000 kg) megafaunal species (SMS). The other decisive component of the 'Prehistoric Equilibrium' were the largest predators (LP). They regulated the density of GH, other herbivores and subdominant predators, including the hominids. Thus the LP maintained the ecosystems diversity. During the most of the Anthropogene the combined stabilizing action of GH and LP prevented the MEWR in spite of the numerous climate-induced stresses. Only the man has triggered the crisis, being liberated from the large carnivores control. Human hunters removed GH from the ecosystems partially (Paleotropis) or completely. This removal caused environmental changes and numerous secondary extinctions of SMS. The different secondary extinctions range in various parts of the world was the outcome of various additional reasons, that also were mostly of the biotic nature. So, contrary to the classic overkill concept, the panbiotic one states that only the GH weighing more than 1 ton were overhunted. The 'key-herbivores removal' idea is an obligatory but not unique element of the panbiotic concept. The interactions of the man and hominids with the LP also played an outstanding role in the run of the Pleistocene crisis. The same is true for the evolutionary changeable aptitude of animals to adapt to both direct and indirect anthropic, biotic and climatic effects.

**К е у в о р д с:** Pleistocene, mammoth, extinctions, climate, biotic interactions, panbiotic concept.

**ПОГУБИЛО ЛИ МАМОНТОВ ПОТЕПЛЕНИЕ ? (АНАЛИЗ КЛИМАТИЧЕСКИХ ВЕРСИЙ ВЮРМСКИХ ВЫМИРАНИЙ).** Пучков П. В. — Показана несостоятельность климатических версий вюрмских вымираний. Обоснована необходимость их замены панбиотической версией, всесторонне учитывающей важнейшие биотические взаимодействия в плейстоцене. В первую очередь это средообразующие эффекты гигантских фитофагов и крупнейших хищников, а также разрушительное воздействие людей на эти звенья. Очень важна и изменчивая во времени способность представителей мегафауны противостоять антрополическим, биотическим и климатическим воздействиям. Названные и другие вопросы применительно к мамонтовым экосистемам рассмотрены в работе подробно. Применительно к другим экосистемам они рассмотрены кратко.

**К л ю ч е в ы е с л о в а:** плейстоцен, мамонты, вымирания, климат, биотические взаимодействия, панбиотическая концепция,

As Darwin predicted in 1836 the problem of mass extinctions without replacement of terrestrial Pleistocene megafauna could not be solved until the question was not cleared up on what global factor(s) favored the worldwide thriving of diversified sets of large quadrupeds (Darwin, 1953). Was this factor of the

climatic or of the biotic nature? Were the climatic changes the prime cause of the mentioned extinctions?

These two questions are discussed below. Some uncommon abbreviations are used: 'kyr BP' — 'thousand of years before present'; 'climatists', 'anthropists' and 'biotists' — proponents of the climatic, anthropic (overkill) and panbiotic (including 'key herbivores removal') Pleistocene extinction models correspondingly. **Anthropogene** is considered as being consisted of **Eopleistocene** (3-2 million years BP), **Pleistocene** (2 million — 10 kyr BP) and **Holocene** (10 kyr BP — now). Alpine terminology of Pleistocene epochs is preferred to the regional ones.

## 1. THE PROBLEM OF PLEISTOCENE MASS EXTINCTIONS

### 1. 1. The range of mass Late Wurm and earlier Pleistocene extinctions

Modern biota is the result of extinctions as well as of the appearance and the expansion of new forms. Thus the striking irregularity of the geographic distribution of large (more than 50 kg) and, to a lesser extent, medium-sized (10-50 kg) continental mammals (table 1) is a result of a very different range of mass extinctions without replacement among large continental vertebrates during Late Wurm and early Holocene (40-4 kyr BP) (table 2).

In the mainland Palearctic part of Eurasia, the following megamammals perished: woolly mammoth (*Mammuthus primigenius*), straight-tusked (*Palaeoloxodon antiquus*) and namadic (*P. namadicus* = *P. tokunagae* = *P. naumanni*) elephants, woolly (*Coelodonta antiquitatis*), forest (*Dicerorhinus kirchbergensis*), steppe (*D. hemitoechus*) and eastern (*D. choukoutensis*) rhinos, European hippopotamus (*Hippopotamus amphibius*), Eurasian musk-ox (*Ovibos moschatus* = *O. pallantis*), 'primitive' bisons (*Bison priscus s.l.*), baikalian yak (*Bos grunniens baikalensis*), transbaikalian hartebeest (*Parabubalis capricornis*), spiral-horned antelope (*Spirocerus kiakhtensis*), western (*Megaceros giganteus*) and eastern (*M. ordosianus s.l.*) giant deer, northern caballine horses (*Equus caballus s.l.*, including ssp. *latipes*, *uralensis* and *lenensis*), European ass (*E. hydruntinus*), cave bears (*Ursus spelaeus*, *U. rossicus*), lion (*Felis leo spelaeus*) and hyena (*Crocota spelaea*) (Kurten, 1968; Vereshchagin & Baryshnikov, 1985; Putshkov, 1989b; Stuart, 1991; Schule, 1990, 1992; etc.). The list of the hosts of extinct American proboscideans, edentates, ungulates, giant rodents and carnivores, few dozens of Australian marsupials, certain imposing birds and reptiles (ibid.; Kurten & Anderson, 1980; Anderson, 1984; Martin, 1984, etc.) is too long to be dwelled upon here. The same is true for dozens of Old World proboscideans, carnivores, primates, ungulates and some other beings that were expired in Anthropogene before Late Wurm (ibid.).

**Table 1. The present distribution of continental large and medium-sized mammals of various sizes through different zoogeographical realms**

Region	Giants (over 1000 kg)	Very large (400-1000 kg)	Large (150-400 kg)	Moderately large (50-150 kg)	Medium- sized (10-50 kg)	Small (beneath 10 kg)
Afrotropical	5	3	22	30	53	661
Oriental	3	5	10	17	37	762
Palearctic	0	5	9	20	34	376
Nearctic	0	2	4	7	14	421
Neotropical	0	0	3	9	24	955
Australian	0	0	0	3	20	350

**Explanations:** Afrotropical realm is treated here without Madagascar but with Sahara and Southern Arabia; Oriental one — with South China up to Yangtze, Indonesia, Ceylon, Taiwan, Philippines; Palearctic — with Maghrib, Tibet, East China up to Yangtze river and Japan; Nearctic — with most of

Mexico; Neotropic — without Antilles; Australian — with Tasmania and New Guinea. Species that are common for two or more realms are counted for the each one. Species that were extinct during last 4 000 years (for example aurochs) are counted (except for residual North East Siberian bisons, musk-oxen and mammoths of Wrangel I.).

**Table 2. Extinctions range of the continental large and medium-sized mammals from 40 to 4 kyr BP (by Putshkov, 1991 with some precisions) in different zoogeographical realms**

Realm	Giants (over 1000 kg)	Very large (400-1000 kg)	Large (150-400 kg)	Moderately large (50-150 kg)	Medium-sized (10-50 kg)
Aftrotropical	6 to 1 (16.6%)	4 to 1 (25%)	25 to 3 (12%)	32 to 0 (0%)	69 to 2 (2.9%)
Oriental	5 to 2 (40%)	6 to 1 (16.7%)	10 to 1 (10%)	20 to 3 (15%)	56 to 1 (1.8%)
Palaearctic	8 to 8 (100%)	10 to 5 (50%)	14 to 5 (35.7%)	23 to 3 (7.7%)	41 to 1 (2.4%)
Nearctic	5 to 5 (100%)	10 to 8 (80%)	26 to 22 (84.6%)	20 to 13 (65%)	25 to 9 (36%)
Neotropic	9 to 9 (100%)	12 to 12 (100%)	17 to 14 (82%)	20 to 11 (55%)	35 to 5 (14.3%)
Australian	4 to 4 (100%)	5 to 5 (100%)	6 to 6 (100%)	16 to 13 (81.2%)	25 to 10 (40%)
Total	33 to 26 (78.8%)	46 to 31 (67.4%)	86 to 47 (54.7%)	113 to 41 (36.3%)	215 to 23 (10.1%)

**Explanations:** The first cipher in a window is total number of species of the corresponding size in the region about 40 kyr BP. The second one is a number of species that were extinct. The third (in brackets) is the percentage of extinct species. The total number of species is smaller than their sum from all windows due to the modern or former presence in several realms. Borders of these realms are treated as in Table 1.

## 1.2. Particularities of Pleistocene uncompensated extinctions

Since the crisis was world-wide, its main mechanisms can be conceived only on a world-wide scale. Regional particularities also should be considered to explain the geographic differences of the extinction range. The extinctions display a set of features (Martin, 1984; Putshkov, 1989a) that distinguish them from previous Cenozoic and earlier extinctions.

1) Extinction rates increase in direct proportion to the size of the land mammals (tab. 2). At the same time almost all small continental mammals of Wurm are represented now by the same or slightly changed species. Before Wurm mammals of different size died out in similar proportion (Savage & Russell, 1983, etc.).

2) Large mammals died out without an adequate ecological replacement (except for some rare cases) up to the complete disappearance of species of 1, 2 or 3 largest weight classes out of ecosystems (tables 1 & 2).

3) No connection or unclear connection of the extinctions with trophic, landscape and climatic predilections of megafauna. Grazers (mammoths, woolly and steppe rhinos, horses, asses, central Asian bovines — *Parabubalis* and *Spirocerus* in Eurasia, mammoths, camels, horses, gliptodons, dwarf pronghorns, giant beaver in America, etc.), browsers (forest rhino and elephant, last stegodons, North American mastodon, several deer and many land sloths, etc.), omnivores (cave and giant spectacled bears, extinct peccaries, pampatheres) and carnivores of different specialization sustained similar losses. These forms lived in woodlands and parklands, grasslands and swamps, deserts and mountains, situated in various climatic zones of both hemispheres.

4) No connection with the evolutionary level. North American mastodons expired together with mammoths and South American ones — in the absence of the latter. The disappeared American horses, camels, some llamas and peccaries, toxodons and *Macrauchenia* were not replaced by any 'advanced' ruminant competitors. On the contrary — American deer, bovines and pronghorns sustained considerable losses themselves (Kurten & Anderson, 1980; Anderson, 1984). Hosts of Australian marsupials died out without placental competitors and foes (except for man) (Martin, 1984). It is sufficient to remind that during the Neogene and (except some cases for the Old World) most of Anthropogene, proboscideans, ungulates and carnivores expired only with the replacement by other, more evolutionary advanced forms. Thus many Old World mastodons were ousted by elephants (Kurten, 1968; Gabunia, 1969; Savage & Russell, 1983).

5) Increased survival rates in the Old World. Here survived elephants, camels, horses, lion, chita, dhole that became extinct in the New World. The opposite cases (musk-ox, wood bison) are few. This particularity is the reverse to the dominant trend of earlier epochs of Anthropogene: mastodons (*Mammuth*, *Gomphotheriinae*) and saber-toothed cats (*Smilodon*, *Homotherium*) prospered in America tens and hundreds of years after the extinctions of their Old World relatives (Kurten & Anderson, 1980).

6) Moderate extinction rates in the Old World, in spite of the early beginning of the process. Wurm extinctions here were only the final stage of the uncompensated Quaternary impoverishment of the megafauna. The beginning of this process can be traced down in Palaeotropis to Eopleistocene (P. Putshkov, 1989a; 1993a). Extinctions, including their Wurm stage, were quite gradual, and, finally, moderately devastating.

7) High extinction rates and dramatically rapid course of the process in the New World and Australia. Here the devastating extinctions episodes of final Wurm (New World) or the mid-Wurm (Australia) were not preceded by previous impoverishment of their Quaternary megafauna; only extinctions with replacements took place (Quaternary..., 1984).

8) Increased survival rates in the tropics. In the Old World this regularity is better pronounced.

9) No marked connection with the taxonomic position — mammals and other vertebrates of various orders and families became extinct.

10) The absence of the extinctions of the sea animals (the sole exception is the sea cow of North Pacific continental littoral — Kurten & Anderson, 1980).

### 1.3. Present state of Pleistocene extinctions debate

The search for a cause of these extinctions has been issued from the reasoning of T. Molineux on the extinction of 'Irish elk' (*Megaceros*) in 1697 (Sutcliffe, 1986) and from the discussion about the frozen 'Siberian elephants' (mammoth) on the session of Russian Academy of Sciences in 1728 (Putshkov, 1989a). Curious enough is the fact, that now the diversity of opinions is even more stunning than it was at the days of the mentioned session. Some opinions complement each other, some are mutually exclusive [Quaternary..., 1984, etc.]. Certain authors speak even, that Pleistocene extinctions debate 'has long reached an impasse and, in its present form, seems to be irresolvable' (Guthrie, 1990b: 42).

However the situation is not so hopeless. There are two conditions, serving as a trustworthy touchstone for testing of the Pleistocene extinctions doctrines. First, any hypothesis has to explain all the mentioned (Sect. 1.2.) extinctions particularities. Second, it should be consistent with all the body of an accumulated evidence and not only with some selected facts, considered separately. It has been shown (e.g., Martin, 1967, 1984; Edwards, 1967; Putshkov 1988, 1991a, 1992c; Stuart, 1991, etc.) that panzootic, asteroid fall, 'species senescence' and 'multi-factors' models do not correspond to both these conditions. Consequently, they should be ruled out.

The long-traditional **classic anthropic** or the **prehistoric overkill** version states that all extinct Wurm large and medium-sized herbivores were directly overhunted with primitive weapon and (or) fire. Then the majority of large predators have disappeared due to the impoverishment of prey. This model, especially its modification, splendidly advocated by P. S. Martin (1967, 1984, 1990, etc.), explains well the Pleistocene extinctions particularities. For example the early beginning and moderate range of the Old World megafaunal extinctions appear to be the outcome of the long coevolution of hominids with their prey. Similarly the late beginning and high extinctions rates in the New World and Australia could be explained by the effects of the invasion of the skillful hunters to the lands of the «naive» game (ibid.; Edwards, 1967; MacDonald, 1984, etc.). However man seems to be present on these continents few thousand years or more before the extinctions (MacNeish, 1976; Guidon, 1987, etc.). Besides many other objections, climatists assert that man could not carry out such a slaughter, because of giant herbivores were too dangerous, while other animals were too prolific. Also they constantly reproach anthropists for the neglecting of the fact that the environmental fitness of Pleistocene ecosystems to large mammals was greater than that of the Holocene. The radical shifts in range distribution of many extant species happened at the onset of the Holocene. They were a part of the drastic community reorganization with the recombination of species associations. For the most part these shifts cannot be explained by human activity, being easily explicable by the climate-induced environmental changes (Vereshchagin, 1967; Guthrie, 1990a,b; Graham, 1985, etc.).

**Climatic models** that are used for various geographical regions are very different from each other. However most of them share the following points: 1) Pleistocene ecosystems and, particularly, plant communities, were very different from the Holocene ones, being more favorable for the megafauna; 2) the climatic turnover



and climate-induced environmental changes at the Pleistocene/Holocene boundary were more drastic and/or faster than ever before during the Pleistocene; 3) correspondingly, the climate of the Holocene is rather different from those of the Interglacials ones; 4) the extinct forms, giant herbivores in particular, were extremely stenoecic beings, overspecialized to Pleistocene conditions. Correspondingly, the smaller survived herbivores were (and, naturally, are) more euryoecic; 5) so the giants prospered throughout the Pleistocene but near the Holocene boundary were eliminated by climate directly or indirectly (through climatically determined changes of the environment, including the competition with extant herbivores); 6) the large size is a handicap in the competition of herbivores under stressed environmental conditions.

Climatists try to prove the last of the above-mentioned points by the following. In the case of a severe drought a 'mastodon' would be doomed to extinction by a 'rabbit or even by a smaller competitor.' The latter proliferates in numbers and deprives the giant of its, already scarce, food (Morris, 1895: 255; Hester, 1967: 188-9). According to Guilday (1967) the extant ungulates accomplished in such way the so-called **competitive constriction** of the Wurm giants in their biotopes, reduced and (or) transformed due to the changes of the climate.

In other words climatic models explain the 1st and 2nd of the Pleistocene Extinctions particularities (Sect. 1.2.) by the stenoecic properties of giant and large herbivores and by their lowered competitive ability. The 3rd and the 4th ones are often negating, though this is against the evidence (Putshkov, 1989a,b). The climatic explanations of 5th, 6th and 7th extinctions particularities are not valid or, at least, insufficient (ibid.; partially — Sect. 5.; 6.). Despite this, climatists felt more confident than their opponents. The former emphasize the differences between Pleistocene and Holocene ecosystems, and gave to these phenomena purely climatic explanations. They insist upon the coincidence of extinctions and radical shifts in range distribution of extant species with climatic changes as well as with climate-induced community reorganization.

The 'extreme' or 'irreconcilable' climatists discard any significant role of man in Pleistocene extinctions (Guilday, 1967, etc.; Hester, 1967; Kowalski, 1967; Sher, 1986, etc.; Velichko, 1973; Guthrie, 1990a, etc.; Graham & Lundelius, 1984, etc.). The 'moderate' ones recognize that hunters could inflict a '*coup de grace*' over already climatically stressed populations (Sect. 6.2.). The logic of the first position is evident: if the 'natural causes' alone were sufficient then it would be no reason to invoke the 'human factor.' It is another question, whether they were really sufficient. At any rate it is unlikely that the long-lasting «man or climate» controversy could be solved by the simple mechanistic compromise of the contending doctrines (Sect. 6.2.).

The chief cause of the 'impasse' situation of the Pleistocene extinctions debate appears to be the common approach that unites, strange as it may seem, the most irreconcilable doctrines (Putshkov, 1989a). All considered models have centered only on a destructive role of one or another adverse factor(s), considering animals only as passive victims. However in communities contradictions between organisms and their environment are solved not only at the cost of organisms but at the expense of the environment as well (Shennikov, 1964; Zherikhin, 1987, etc.). It is a commonplace that every species transforms the biotic and abiotic surroundings in its own way. The global climate itself is not only a condition of an existence of the biosphere, but an outcome of it to the same extent (Kadatsky, 1986; Schule, 1992b). The Pleistocene extinctions without replacement can never be understood without the full scale consideration of the biotic interactions in Pleistocene mainland ecosystems. These interactions include the various feed-back effects of living beings on their milieu, predation and competition relations, ability of species as well as ecosystems as units to adapt themselves to effects of climatic changes and human activity. Biotic factors interacted with climatic and anthropic ones, variously modifying, diminishing or increasing the each other's effects. This accounts for the stunning regional differences of the pattern and of the range of extinctions (Putshkov, 1989b, etc.). These ideas became the prerequisites of the **panbiotic** Pleistocene extinctions doctrine.

#### 1.4. The panbiotic concept

The absence (America, Australia) or moderate range (Old World) of the megafaunal extinctions without replacement before Wurm in spite of numerous pre-Wurm climatogenic stresses were the results of the joint ecosystem impact of top predators (Putshkov, 1989a, etc.) and top herbivores (ibid.; Owen-Smith, 1987, etc.; Schule, 1990, etc.; etc.). This impact minimized the consequences of the mentioned stresses for ecosystems and efficiently prevented the crash of the megafaunal communities. Contrary to climatic doctrine giant herbivores (weighing more than 1 ton) are considered not only as highly euryoecic and highly competitive creatures, but also as the major environment-making agents. Their feeding, locomotive, soil fertilizing and other activity maintained highly mosaic plant communities and exerted other environmental effects beneficial to the majority of not so large (50-1000 kg) phytophagans and large predators (Sect. 8.; 9.; 10.). The latter however also largely contributed to the maintenance of the ecosystem stability and megafaunal diversity. They prevented the overproliferation either of giants and that of other herbivores and subdominant predators (Sect. 9.). All this resulted in the 'Prehistoric Equilibrium' — the high resilience of the structure of Eopleistocene and Pleistocene ecosystems to the climate-induced stresses (Sect. 7.; 9.).

The Pleistocene crisis included (Putshkov, 1988; 1989a,b, 1991a,b, 1992a,b,c, 1993a,b, 1994, 1995a,b) the next main processes: 1) liberation of humankind from the control of the largest carnivores; 2) removal by man of giant herbivores; 3) drastic changes of plant-communities and other effects of this removal; 4) increase of populations of some herbivores, more fit for such changes; 5) extinctions of other herbivores, less fit for such changes; 6) extinctions of some or all largest predators due to the 2nd, 3rd and 5th processes and, partially, to the competition with man; 7) increase of populations of predators, formerly suppressed by the largest ones; 8) extinctions of some kinds of prey because of the new regime of predation in a changed environment; 9) extinctions of other beings, ecologically dependent on the victims of the mentioned processes; 10) installation of the new equilibrium.

The duration of the coevolution with hominids and other reasons caused considerable geographic differences in the pattern of the crisis and in the rate of extinctions.

Therefore in the Old World tropics the crisis started about 3 million years ago, when *Homo* or even some *Australopithecus* began to kill pachyderms, unwary to new biped predators, thrusting wooden spears in their bellies (Putshkov, 1989a, etc.; Schule, 1990, etc.). Quite early the crisis zone also engulfed the southern regions of the Palearctic. The crisis progressed slowly as the hunting skill and numbers of hunters increased. The course of the crisis was inhibited due to behavioral adaptations of giants and other animals to direct (chiefly hunting) and indirect (changes of various biotic interactions in ecosystems due to human hunting, burning and other activity) human effects on ecosystems. The course of the crisis was also inhibited by the large carnivores, powerful foes and competitors of hominids. Preventing the overproliferation of hominids and humans (mostly women and children), big cats, hyenas, bears and dholes slowed down or prevented the overexploitation of pachyderms, thus ensuring the maintenance of the 'prehistoric equilibrium' (Putshkov, 1989a,b, 1993a). The emancipation of humankind from the pressure of large carnivores was an arduous and long-lasting process (ibid.). Only gradually has man mastered the situation due to the improvement of weapons, the perfection of social organization, the mastering of fire and the increase in the efficiency of the symbiosis with the 'pre-dogs' (anthropophilous ecotypes of wolves and probably, to a lesser extent, those of jackals and extinct Eurasian coyotes). The

progressive course and completion of this process, together with other factors, resulted in the increase of the human population as compared to previous epochs. It led to the increase of the hunting pressure of man on the megafauna.

Smaller (1000—50 kg or less) ungulates resisted well to direct human predation due to sufficiently high reproductive rates. The slowly proliferating giants, which gradually learned to treat man as a foe, were protected by their size and strength. However these advantages became insufficient due to the increased skill of hunters. The latter invented new hunting methods more rapidly than the prey changed the behavior. Giants had the most value among all human prey and were easily found by hunters. Due to this they were sought and hunted with zeal even when they became very rare. The hunters remaining too numerous for the survival of giants, the number of the former was kept up by the more fecund prey and other food items. The populations of giants were retained to a deep and steady depression. The constantly depressive populations were doomed to destruction by local catastrophic events, epizootics, degeneration. The depression and subsequent extinctions of giants entailed the changes, pernicious for many other animals, as the cases of the extirpation of modern pachyderms prove (Sect. 8.6.). The other man-made effects (artificial burnings, suppression and/or exclusion of the largest predators, proliferation of the subdominant ones, 'underkill' of the fecund prey, etc.) also influenced the run and the results of the Pleistocene crisis (Putshkov, 1989a,b, 1992b, 1993a,b).

In the Paleotropis the rivalry of man with the largest predators was less acute than in Palearctic, because of the comparative abundance of food resources alternative to megafauna (plants, insects, small vertebrates). For the same reason primitive hunters pursued gigantic herbivores in the southern regions less zealously than in the northern ones. For this and certain subsidiary reasons in Paleotropis some pachyderms could survive. Those species that became more resistant to human predation ousted other pachyderms, who acquired the 'anti-man' behavior less efficiently (ibid.; Schule, 1990, 1992). In this way the extant elephants mastered all the variety of biotopes of their regions, previously divided between several species of proboscideans. Conditions of existence for other Paleotropical megafauna underwent only moderate changes due to the survival of some giants. But for some species even such changes were baneful (ibid.).

Correspondingly the seasonal shortage of food resources alternative to megafauna in northern regions has determined the more acute extent of rivalry of man with the largest predators as well as the more severe hunting pressure of man on the giants (Putshkov, 1989a,b, 1993b). Due to this the victory of humans over predators was more complete than in the South, whereas pachyderms of temperate and northern regions were completely lost, inflicting considerable secondary extinctions (cave bear, giant deer, etc.). Nevertheless the Wurm extinctions of Palearctic pachyderms were staggered and gradual, because they were highly resistant to human predation due to the long previous coevolution with *H. sapiens* ssp. and *H. erectus*. Thus there was no sudden transition from an environment saturated with pachyderms to that with no pachyderms at all. Ungulates had time to adapt. This is the main reason of the conservation of horses and camels in the Palaeartic and their extinctions in Americas (ibid.).

Thus the origin of man in the Old World and its long coevolution with the megafauna of the region are responsible both for the early beginning of the extinction process and that of the moderate range of the latter. The survival of part of the Palearctic pachyderms, and indirectly, that of some other megafaunal species is indeed 'climatically induced'. However the climate effect, crucial for their survival was exerted not over them, but over humans and their food items, alternative to megafauna (ibid.).

There was no man and, consequently, no crisis in Americas and Australia before Wurm. Due to this herbivores had low resistance to human predation; far

more animals than in the Wurm of the Old World continued to depend vitally on the impacts of gigantic herbivores and/or on these of the largest predators. For the same reason many herbivores were dependent on pyrophobic vegetation as natural fires were rare due to the high density of gigantic grazers (in the Old World the frequency of fires has been increased starting from the times of *H. erectus*). After reaching the New World and Australia the 'modern' man (i.e. *H.s.sapiens*) consisted an entirely new factor that led to a quick and drastic crisis. The sudden suppression and extinctions of giants caused equally sudden changes in primary production consuming, fire regime, predation and competition relationships. Not only hosts of large, but also many medium-sized mammals (as well as many birds and reptiles) could not adapt to such changes.

There are however data on the presence of man in America about 10-50 kyr (MacNeish, 1976; Guidon, 1987, etc.) and in Australia about 5-10 kyr before the crisis. These data seem to be persuasive, though they are questioned or negated by many authors (e.g., Martin, 1984; West, 1986, etc.). According to R. Gruhn the 'first Americans' did not hunt on large animals, being specialized on gathering food within the intertidal zone. The same is plausible concerning the 'first Australians'. It has been supposed (Putshkov, 1994) that these people being out of contact with skilled hunters of Eurasia needed quite a long time to acquire the skill of giant herbivores killing. The population growth of these unskillful hunters/gatherers was hampered also by formidable foes and competitors — carnivores in America and giant monitors and land crocodiles in Australia (ibid., 1989a,b). The emancipation of people from the predators' control went on in the same way as in the Old World though far more rapidly.

An adequate substantiation of all these statements with the elucidation of the models of extinctions of particular taxa needs too much place to be dwelled upon here. It has been exposed previously in many details (Putshkov, 1989a,b, 1991a, 1992a,b, 1993a,b, 1994).

### 1.5. The formation of the panbiotic concept

For the most part, ideas of the outlined doctrine have been proposed separately by proponents of other concepts. Darwin (1953) as early as in 1836 thought that the unknown reason(s) of the worldwide thriving of the Prehistoric terrestrial megafauna had nothing to do with climatic zonality. Nevertheless the decisive direct and indirect proofs of the stunning suitability of Pleistocene mainland ecosystems to large mammals were presented in works of the proponents of **climatic extinctions doctrines** (Vereshchagin, 1967, etc.; Guilday, 1967, 1984; Reed, 1970; Vereshchagin & Baryshnikov, 1980a, 1983; Guthrie, 1984; 1990a; Graham, 1985, etc.). The advocates of the version of the **prehistoric overkill** (Pidoplichko, 1951; Komiets, 1962; Martin 1967, 1984, 1990, etc.; Edwards, 1967; Tatarinov, 1969, etc.; Alekseeva E., 1980; Spaulding, 1983; McDonald, 1984; etc.) presented equally important evidence in favor of the connection of the Pleistocene extinctions with the evolution and expansion of man and its ancestors. D. Steadman & P. Martin (1984) have brilliantly explained the secondary extinctions of many birds due to the disappearance of large mammals. Attention to the role of the **prehistoric underkill** principle in Pleistocene extinctions has been drawn by G. Krantz (1970). Then it was established that large Pleistocene herbivores exerted the strong influence on plant communities on local (Turner, 1975; Stuart, 1976; Stuart & Hibbard, 1986 [other sources see in May, 1993]), regional (Janzen & Martin, 1982; Cole, 1985) and global (Janzen, 1984) scales.

At last, the reconsideration of the ecological effects of modern giant herbivores led to the deduction that only the giant herbivores in weight over 1 ton were overhunted. Their removal triggered the drastic environmental changes and secondary extinctions of other animals. This idea was first published by Owen-Smith (1987, 1989) and got the names '**Megaherbivores removal, key herbivores removal, keystone removal and domino effect**' model. Putshkov (1988, 1989a, etc.), Schule (1989, 1990, etc.) and Flannery (1989) proposed similar models quite independently from Owen-Smith, as well as from each other. There are some differences in the versions of the mentioned authors. So W. Schule supposes that interaction man/Megaherbivores had a considerable effect even over the global climate. P. Putshkov insists not only on the ideas that are common with the 'keystone' model, but also on the outstanding role of other biotic interactions. He considers the stabilizing and destabilizing effects of Megacarnivores, adaptation of 'giants dependent' herbivores and predators to the exclusion of giants from ecosystems, the 'underkill' idea, etc. Being wider than Owen-Smith's 'keystone model,' these versions probably deserve a separate title. The term '**panbiotic model**' seems preferable to the rather awkward expression '**anthropobiotic conception**,' which has been proposed previously (Putshkov, 1989a). The name 'panbiotic' seems suitable also because *Australopithecus* and *Homo spp.* were members of the

Pleistocene ecosystems too. Efforts are undertaken to conceive the generalities and peculiarities of men/giant herbivores/other ecosystem components interactions on a world-wide (Owen-Smith 1987, 1989; Putshkov, 1988, 1989a, b, 1992a, b, 1993a, b, 1994, 1995a; Schule, 1989, 1990, 1991, 1992a, b, 1995) and regional (ibid.; Flannery, 1989; Maslov & Antipina, 1991, 1995; May, 1993) scales.

## 1.6. Panbiotic concept and the Pleistocene extinctions debate

With the appearance of the 'key Herbivores removal' concept and its wider panbiotic modifications antropists take the upper hand in their discussion with climatists. Being as consistent with the Pleistocene extinctions particularities as the overkill model is, these models give a non-climatic explanation of the peculiarities of the Pleistocene ecosystems. They also explain from biotic positions those features of early Holocene community reorganization that were the most important to megafauna. It is worth mentioning that climatists, but for some rare exceptions (Guthrie, 1990b), prefer to take no notice of this explanation rather than try to refute it.

Such refutation is, however, possible if the impossibility of the overkill of giant herbivores by early man were decisively proven. It is possible also, if not only the first, but the other common points of climatic versions (Sect. 1.3.) were proven as well. So the substantiation or refutation of these points is as crucial both for climatists, and for anthropists. The issue of the contention depends now much more on the reason that killed the largest herbivores than on the particular reasons of extinctions and range contractions of smaller species. Only the former could be the prime cause of the crisis. It could well be the climate, if the large size were really a handicap in the competition of herbivores and if giant herbivores were indeed stenoecic creatures.

The best way for testing such opinion, as well as the **Wurm competitive constriction theory** (Sect. 1.3.), is to make sure how much the viability of the modern larger herbivores is lowered (or not lowered) in comparison to that of the smaller ones.

## 2. WHO IS 'STRONGER': A 'MASTODON' OR A 'RABBIT' ?

### 2.1. Some reasoning

The large animals really need more water and food; it is difficult for them to find shelters (Morris, 1895; Wallace, 1898; Guilday, 1967; Pianka, 1981, etc.). Their populations include far fewer specimens than those of small animals; the generation change is slow (ibid.); hence the assumption for the lowered viability and evolutionary potential of large beings is derived. However other important facts are disregarded in these ideas.

Large animals are better equipped for active struggle with environmental challenges than the small ones. They are more resistant to cold and hunger. They do not so often perish due to predators, diseases, fires and floods. Thus the need of shelters is not so crucial for them (Severtsov, 1951; Pianka, 1981; Kingdon, 1979, etc.), as it is to 'little beings.' They resist to adverse natural forces due to strength, mobility and endurance which are far superior than those of small mammals. These features are due in part to special morpho-physiological adaptations and in part they are mere outcomes of the large size: a step of an elephant is a different thing than that of a mouse.

Large herbivores do need more food than the small ones. But the former are more capable of gathering it due to their higher mobility and endurance. Also they are adapted to more efficient utilization of food resources. The size itself, that requires the large absolute quantity of food, does not allow them to be stenophagous. As a rule, large herbivores eat broader range of fodders than the small ones. The former are not so particular about the food quality. They extract more nutrients out of fodder due to the longer stay of the fodder-mass in intestines (Damuth, 1981; Demment & Van Soest, 1985; Wagner, 1987; Owen-Smith, 1987). They use fodders from various biotopes, diverse types and storeys of vegetation. Large herbivores are mainly gregarious. They exploit the common pasture instead of individual home ranges, as in the case of rodents. The grazing of a herd under natural conditions makes pasture more productive for every animal, contrary to the case of the individual grazing (Kingdon, 1979; McNaughton, 1984).

Relatively low population densities and low reproductive rates of largest herbivores impede the exhaustion of their food resources. Thus these features are useful for animals, which are communities

dominants (Severtsov, 1951). Contrary to a widely believed thought, these traits do not limit the genetic and evolutionary potentialities. This is testified by the history of amblipods, titanotheriums, rhinocerotoids and proboscideans. They evolved as fast as the small mammals and certainly faster than most of Cenozoic insects (Gabunia, 1969; Zherikhin, 1987; Carroll, 1987, etc.). Low population number of large mammals is balanced by the rapid 'flow of genes': high mobility of individuals favors the propagation of beneficial characters over the specific area (Pianka, 1981). Even more important is the fact that the veritable selection, based on non accidental elimination of less fit individuals, is more efficient among large animals. Among the small ones the non-selective elimination, this mighty decelerator of evolution, plays a leading role (Severtsov, 1951; Putshkov, 1991).

## 2.2. Modern ecosystems: the larger outcompetes the smaller

Due to the aforesaid peculiarities (and contrary to the views of climatists) it is the large herbivores that usually dominate over the smaller ones in ecosystems. The competitive possibilities of the latter are diminished because it takes them much more time and/or energy to escape predators or even being inactive during the daily drops of temperature (the case of many rodents and insects). This gives time to larger herbivores to eat up their, necessarily large, amount of food, thus restricting the food resources for small competitors. It hampers the overproliferation of the latter. The theoretical possibility of the victory of a 'rabbit' over a 'mastodon' (Sect. 1.3.) has never been realized in modern ecosystems: cases of the suppression of pachyderms by rodents or lagomorhes are unknown.

But real rabbits (*Oryctolagus cuniculus*) in England surely limit through trophic competition the population growth of an orthopteran insect *Chortippus brunneus* (Grayson & Hassall, 1985): it is the rabbit who is a 'mastodon' in this pair of competitors. In arid regions of the West USA the bighorn sheep (*Ovis canadensis*) is not harassed by numerous plant-eating insects and rodents. It is badly harassed here by the feral ass (*Equus asinus*), his unique larger adversary (Mills, 1982). Larger ungulates often chase away the smaller ones in pasture and mineral licks encounters as, e.g., horses do it with bighorns, pronghorns and black-tailed deer in USA (Berger, 1985). In cases of winter trophic deficiency and high density of both cervids, red deer invariably win over roes (Geptner & al., 1961; Varnakov, 1975). On salt-licking places red deer wait for the departure of mooses, roes — this of red deer. If such place is too frequented by mooses, red deer never go there (ibid.). Chamoises in the Caucasus readily use rich alpine pastures and forest glades when there are no red deer and capricornes (*Capra cylindricornis*) in the locality. In case they are present, chamoises retreat to the most inaccessible rocks (Weinberg, 1983).

In 1869 Ordos region Mongols were slaughtered or chased away by Dunghans. Their domestic animals ran wild in the depopulated land. Feral sheep were soon exterminated by wolves, though feral cattle and camels efficiently resisted to predation until the country was repopulated again (Przhewalsky, 1875).

The food and habitat selection of African ungulates is not determined by the competitive press of rodents. It is an outcome of their relations with each other and with their predators (Sinclair, 1985; Kingdon, 1979, 1982; McNaughton, 1984, etc.; Wagner, 1987, etc.). Moreover in the short-grass communities of Serengeti the population density of hares, rodents and orthopterans is restricted by ungulates that eat up to 90-94% of the phytomass annual production (Sinclair, 1975). Due to this the intrannual and interannual oscillations of population density of small mammals never take here the character of outbreaks. There are many other cases (e.g., Kingdon, 1979, 1982) of smaller herbivores being suppressed by the larger ones.

## 2.3. Modern ecosystems: the smaller outcompetes the larger

Could the mentioned outbreaks of numbers of small phytophagans be considered as facts speaking in favor of the Wurm competitive constriction hypothesis? It is doubtful because the proliferated small herbivores destroy their own trophic base and not only that of large herbivores. These or other ecological

mechanisms invariably stop an outbreak. Outbreaks are usually over well before the even local extinction of euryoecic and polyphagous large herbivores occurs. The latter survive by temporal departure from devastated area and/or by eating usually rejected food up to the committers of the disaster. For example dzeren or Mongolian gazelle (*G. gutturosa*) leaves pastures devastated by the overproliferated Brandt voles (*Microtus brandii*) (Geptner & al., 1961). Lemmings are eaten by reindeer, locusts — by elephants as well as by many of African ungulates. Wild boars in Asia move on with 'marching troops' of locust nymphs, devouring them; the usual feeding activities of wild boars being given up. They also dig out and eat voles and muskrats (*Ondatra*) both in cold and warm seasons. Rodents that have a chance to escape from their destroyed dwellings, often perish from cold or predators (ibid.; Shirayev, 1975). Only squirrels, being introduced to the Caucasus beech forests, became serious competitors of swine. Squirrels consume a lot of beech nuts still on trees (Geptner & al., 1961). Swine were forced to change their habitat and trophic behavior. Locusts, gipsy-moths, lemmings or other famous 'outbreakers' never become stable ecosystem dominants.

An interesting exception to this rule is that of rabbits in Australia. They not only successfully compete with cattle, sheep and kangaroos, but perform a long-lasting environmental effect baneful to some and beneficial to other kangaroos species (Cheal, 1986, etc.). But even more interesting is the explanation of this uncommon situation. Rabbits could take such a position due to tremendous ecological gap left with the Wurm extinctions of herds of Australian large herbivores, the former dominants of ecosystems (Flannery, 1989). Probably frequency and scope of outbreaks of at least some periodically mass proliferating species have been increased all over the World due to Wurm extinctions of so many large herbivores (Martin, 1967; Putshkov, 1989a,b).

Cases of trophic suppression of larger ungulates by smaller ones also could hardly be used in favor of Wurm constriction theory. They are usually connected not with climatic impacts but with the exclusion by man of large carnivores from the ecosystems. For instance in the second half of XIX century red and fallow deer oppressed in Biyeloviezha reserve mooses (elks). The same had happened in this century in Voronezhsky reserve. Deer ate up a lot of accessible browse and were more willingly going to the feeding-racks (Varnakov, 1975). In Biyeloviezha they also oppressed wisents (European bisons) by browsing in March and April green sprouts — the limited source of vitamins indispensable for pregnant cows of wisents (Nature ... Poland, 1961). Due to this many calves were dead-born or died soon after birth. The survivors became weak, sickly and often — sterile adults. Some authors interpreted these data as competitive superiority of deer (ibid.; Geptner & al., 1961; Kowalski, 1967, etc.), others — as signs of the racial senescence of wisent (Danilevsky, 1885) or even as remote consequences of the ecological stress that was endured by the species during Ice Age (Serebrovsky, 1937). All these interpretations discount the decisive reason of this case of smaller game superiority: deer became abnormally numerous in well protected hunting reserve of tsars only in absence of wolves. Similarly the Javan rhino loses the trophic competition with feral cattle and bantengs in Ujung-Kulong reservation not only because the unfavorable quasinatural habitat changes forced it to non-optimal diet. Rhinos' odds are also lost due to the extinction of tigers [What ... Rhinos ?, 1982]. In African parks with numerous carnivores the situation is opposite: elephants, hippos and buffaloes leave to smaller ungulates relatively small part of the annual accrue of herbaceous phytomass (Lock, 1972, etc.).

#### 2.4. Modern elephants: the largest — the fittest ?

In the context of the Wurm competitive constriction theory elephants should be the forms of the least competitive ability. In this connection the unintentional 'experimental testing' of this theory is very interesting. It was some African parks encircled with anthropocenoses that served as 'proving grounds' especially Tsavopark in Kenya. There were all conditions required by the theory. Numerous phytophagans of various sizes competed on the restricted territory for equally limited food and water resources. Drastic environmental changes had happened due to severe droughts of 1960-61 and 1970-71 years and because of the overbrowsing and overgrazing (elephants transformed bush/savanna mosaic to open grasslands and, partially, to semi-deserts). Only results were beyond expectations. Elephants turned out to be the strongest competitors due to their extreme eurytopicity and polyphagy. They feed at every vegetation storey from the underground (roots, bulbs, etc..) to the toppest parts of crowns (due to their ability to fell down trees). They resist to the drought both by digging 'wells' at the beds of dried lakes and rivers and by eating the water-soaked wood of baobabs that are crushed by tusks (Laws, 1970; Nasimovich, 1975; Bannikov & Flint, 1977; Wagner & Schneiderova, 1984). No animal could compete with these long living giants of low natural mortality rates. Exterminating trees, bushes and grass elephants caused population decline of various browsers and grazers up to their local extinctions or retreat from park

(ibid.). Then the population collapse of giants themselves began. The partial elephants cropping became necessary.

The losses of elephants during this collapse were terrible — about 30 000 individuals (Beard, 1989). But it would be an oversimplification to blame only natural cause — a drought and to see here a proof for climatic versions of Wurm extinctions. It is man who should be blamed for the present impossibility for superfluous elephants to migrate out of parks (ibid.; Spinage, 1963; Wager, 1963; Wagner, 1987, etc.). It is man, who is responsible not only for overkill of large game in historical times but also for the ‘underkill’ of elephants in Tsavo park before the catastrophe (Laws, 1971; Beard, 1989). Before man the number of pachyderms was regulated by predators who killed their calves. Be it as it may the ‘experiment’ shows that elephants have been succumbed by the environmental stresses **after** and not **before** other savanna herbivores. Two thirds of Tsavo elephants have been survived to the end of the drought (Owen-Smith, 1977). Clearly elephants could become extinct only due to such environmental changes that were intolerable to the majority of the other megafauna of African savanna biome.

The outstanding adaptive potentiality of elephants is more than evident. None of Palearctic ungulates is as polyphagous as are African and Asian elephants. None of the ungulates lived in such a variety of diverse habitats and climatic zones as lived the elephants before man-made contraction of their areas in recent and historical times (Pidoplichko, 1951; Deraniyagala, 1955; Nasimowich, 1975; Bannikov & Flint, 1977; Olivier, 1978; Kingdon, 1979, etc.).

Likewise hippos and rhinos, with the partial exception of the white rhino, are far more euryoecic and polyphagous (Kingdon, 1979; Penny, 1987; Owen-Smith, 1987, 1989) than it is usually believed. For instance opinion that greater one-horned rhinoceros (*Rh. unicornis*) is a habitat specialist, completely dependent from tall flood plain grasslands with *Sacharum spontaneum* as obligatory diet staple, is founded on the ecology of the remaining populations in Chitwan (Nepal) and Kaziranga (Assam) parks (Dinerstein, 1991a, etc.). It is mixt browser/grazer that lives, or lived in the recent past, also in dry and wet, dense and sparse forests, shrublands, savannas, grasslands on plains as well as in hills and on quite steep mountain slopes (Talbot, 1960). It has been driven out of most of its area by man, and not by the natural reasons (ibid.).

## **2.5. Conclusion: ‘mastodons’ would be stronger than ‘rabbits’ but for man ?**

As evidenced from the foregoing account, under natural conditions the inconveniences of a large size are overbalanced by its advantages. Large land mammals in general and elephants in particular are highly euryoecic forms. Their ecological and evolutionary success is based on two complementary strategies. The first one is the increased resistance of individuals to various adverse forces of nature (Sect. 2.1.—4.). The second one is the increased aptitude to change favorably their environment (Sect. 8.4.). However both strategies fail when humans comes to the scene...

## **2.6. Extinct giants: eury- or stenoecic forms ?**

Starting from the exposed data it would be expected that Wurm giants were euryoecic to the same extent as their living counterparts. However the climatists state the reverse, often in spite of the evidence, given in their proper works.



It is impossible to discuss here all climatic versions. The most attention is paid to the presently dominant 'tundra-steppe crash' scenario of extinctions of woolly mammoth and rhino, Eurasian musk-ox, northern caballine horses, and 'primitive' bisons (Sect. 3.). These herbivores are called below rather arbitrarily 'mammoth and their satellites', 'mammoth and their suite' or 'mammoth and their retinue'. These terms are also known in several broader senses with the inclusion of diverse other extinct and extant animals (e.g., Ukraintseva, 1993). Then climatic models of extinctions of some other forms are considered less extensively (Sect. 4.; 5.).

### 3. 'TUNDRA-STEPPE CRASH CONCEPTION' OF MAMMOTH EXTINCTION

#### 3.1. Preliminary observations to further account

Problems of interregional correlations, use of 'long-' and 'short Interglacials' time-scales, other terminological and conceptual disagreements cause the boring controversies concerning the timing of the Pleistocene events. Fortunately these debates are of minor importance for the extent of precision necessary for the decisive points of our considerations. Terms 'Pre-Wurm', 'Early and Middle Wurm', 'Late Wurm Pleniglacial' and 'Wurm Anaglacial' that are used below, almost correspond to terms 'Early Glacial', 'Early and Middle Pleniglacial', 'Late Pleniglacial' and 'Lateglacial' *sensu* Stuart (1991).

Fortunately the next and more important circumstances are well established:

- 1) Pre-Wurm (about 113-73 kyr BP) was on the average cooler than now but considerably warmer and moister than Early and Middle Wurm (about 73-24 kyr BP); the Late Wurm Pleniglacial (24-14 kyr BP) was everywhere the coldest epoch.
- 2) Several major waves of strong coolings (stadials) and warmings (interstadials) occurred during every of the four above-mentioned epochs; every stadial or interstadial was complicated with series of climatic oscillations of lesser duration and/or intensity.
- 3) These oscillations, although global, often were of variable intensity and/or duration in different parts of Holarctic region.
- 4) The environmental conditions were very variable throughout the extensive range of woolly mammoths (Sect. 3.14.); these conditions were even more changeable due to the mentioned climatic oscillations.
- 5) Constant parts of the Wurm mammoths range were Siberia, most of Kazakhstan and Europe northwards of Pyrenees, Alps and Dinarids except for glaciated regions but including southern France and England (Kurtén, 1968; Vereshchagin, 1971a, Vereshchagin & Baryshnikov, 1985; Vangenheim, 1977; Kozhamkulova & Kostenko, 1984; Stuart, 1974, 1976, 1991; Musil, 1985).
- 6) Borders of mammoths' range were displacing due mainly but not exclusively (Sect. 3.16.) to the aforementioned climatic changes.
- 7) Mammoths of Riss-Wurm, Pre-Wurm, Early and Middle Wurm are specifically (in part even subspecifically) the same as those of the Late Wurm (L. Alekseeva, 1980, 1990; Garutt, 1986, pers. comm.; Vangenheim, 1977; Stuart, 1976, 1991; Foronova & Zudin, 1986; Lister & Bahn, 1994, etc.); it permits to believe that ecological properties of the Late Wurm mammoths were similar to those of the earlier ones.

#### 3.2. 'Tundra-steppe crash' conception

The 'irreconcilable' climatists insist that woolly mammoths and rhinos lived exclusively in specific periglacial landscape — 'tundra-steppe', 'steppe-tundra' or 'mammoth steppe' (Kowalski, 1967; Reed, 1970; Velichko, 1973; Sher, 1971, 1982; Guthrie, 1976, 1990a, 1990b; Tomirdiaro, 1977, etc.). They argue that this formation occupied at the Late Wurm Pleniglacial all extratropical Eurasia. Conditions for the existence of tundra-steppe were ultracontinental climate, permafrost and potent cold winds from oceanic and continental ice-shields. These winds decreased ranges, density and activity of blood-sucking insects. Also they carried dust particles from periglacial polar deserts. This dust has been transformed then in layers of 'cold' (periglacial) loess. Covering vegetation, the dust acted abrasively on teeth. However it gave to phytophagans the necessary mineral nutrients. High-crowned (hypsodont) and complicated teeth of mammoths, rhinos, horses, bisons, musk-oxen, saigas, tundra-steppe hares (*Lepus tanaiticus*) were highly resistant to the wear by coarse, dust-covered grasses.

Tundra-steppe is thought to be an open completely or nearly treeless landscape, overgrown by mosaically distributed patches of herbaceous and low shrubby or demi-shrubby vegetation (Sect. 3.14.3.). Plants that grew side by side in tundra-steppes, grow now separately in tundras, lowland and alpine cold steppes or intrazonal meadows (ibid.; Velichko, 1973; Sher, 1971, 1982; Tomirdiaro, 1977, etc.). According to Yurtsev (1976) the high productivity of tundra-steppe for mammoths and their satellites was ensured mainly owing to the high proportion of patches of meadow grasses and herbs; such patches play a modest role in modern tundras.

Proponents of tundra-steppe crash scenario of mammoths and rhinos extinctions believe that these giants were stenoecic crioerophiles completely dependent on tundra-steppe extreme crioarid conditions. Giants are thought to be killed by the outcomes of the global warming. They could neither feed themselves in the established Holocene forests, swamps and tundras, nor withstand the mass direct

weather-caused losses (Vereshchagin, 1971, 1977b, 1988, etc.; Kowalski, 1967; Reed, 1970; Sher, 1971, 1982, 1986, etc.; Velichko, 1973, etc.; Guthrie, 1976, 1990a, 1990b; Vereshchagin & Kuzmina, 1977; Kvasov, 1977; Tomirdiario, 1977, 1994, etc.; Vangengeim, 1977; Vereshchagin & Baryshnikov, 1985; Ukraintseva, 1985; 1993; Musil, 1985; Alekseeva & Tikhomirov, 1989; Alekseeva, 1990; Surmely, 1993, etc.). Due to the warming the climate of Northern Eurasia and Alaska has been quickly switched to the humid oceanic type with deep winter snows that hampered the movement and feeding of animals. The frozen snow crust that appeared because of the frequent thaws rapidly alternated with frosts and/or wind-packed snows were even more pernicious obstacles for feeding of herbivores (ibid.). The shaggy coat of mammoths and their satellites, being adapted to the most intense but dry cold, has been soaking with water during thaws, especially under wet snow-falls or cold season rains. Then hairs were frozen together up to the skin in a sort of ice armor, when even the feeble frost occurred after the thaw. In summer animals perished in the mire of melting permafrost and were harassed by swarms of blood-sucking insects.

Climatists think that all this resulted in the elimination of mammoths and their satellites from the present-day tundra, taiga and mixed forest zones, where extant cervids have managed to prosper. The latter are believed to be more resistant to the mentioned weather and food quality challenges (ibid.). It is also believed that mammoth, rhino and musk-ox could not retreat to southern steppes as did equally snow-dreading saiga, hemionos and southern horses, for summers there became too hot (Kowalski, 1967, etc.). Why did not they survive in the belt of fertile north-western steppes and forest steppe on chernozem soils? Some authors accuse too mild climate with excesses of cold season thaws (see above) (Velichko, 1973). Extinctions, caused by the environmental turnover due to permafrost melting, are also considered to have simply preceded the installation of such steppes (Vereshchagin & Kuzmina, 1977). There is also opinion that vegetation of modern steppes, as well as that of other biomes, became too monotonous. It could ensure the normal well balanced feeding of mammoths and other extinct herbivores no more (Lister & Bahn, 1994), or could even inflict the poisoning of giants (Guthrie, 1984; Graham & Lundelius, 1984).

### 3.3 How to test the 'tundra-steppe crash' extinctions scenario ?

The strongest point of the outlined theory is the convincing evidence in favor of climatic causes of the emergence, existence and disintegration of tundra-steppe periglacial biome (see sources in Sect. 3.2.). The questions are as follows: 'Whether all the environmental changes could be explained merely by the climatic changes?' and 'Were mammoths and rhinos really so stenoeic as to be killed by those changes that could not kill the extant Holarctic ungulates?'

Any kind of the '**mammoths killed by the warming**' conception can not be proven without positive answers to these questions. The tundra-steppe crash explanation of the extinctions of mammoths and their satellites would be convincing if the animals really possessed features that were incompatible with Holocene conditions **over all their former area**. It should also be shown that they indeed lived **exclusively in tundra-steppes** and similar **ultra crioarid** environments and expanded or contracted their areas in **exact correspondence** with the expansion or contraction of these formations. It is not sufficient to prove that mammoths and their satellites indeed lived in ecosystems without modern analogies. These differences could be considered as climatically driven only if the **alternative possibility of creation of 'mammoth' biomes' by mammoths themselves were eliminated**. At last the survival of mammoths and their satellites during previous interglacial warmings **should be explained satisfactorily**.

### 3.4. Whether mammoths existed only in regions with extremely severe climates ?

According to some authors (Sher, 1971, etc.; Velichko, 1973; Guthrie, 1990a,b, etc.) there is no modern climate that would be suitable for woolly mammoths and rhinos. Even that of inner parts of East Siberia is thought to be insufficiently cold and dry.

Mammoths and their satellites indeed could live under such degree of climatic crioaridity that is unknown at present. At the Late Wurm winter frosts in Arctica (Sect. 3.14.1.1.) and some parts of East Siberia could attain  $-100^{\circ}\text{C}$  or even more, whereas the snow cover was nearly or completely absent (Tomirdiario, 1994, 1996,

etc.). Such were the effects of immense land and oceanic ice-shields. But in most cases these animals lived under much milder conditions.

For example mean annual temperature in England for about 14 kyr BP was  $-8^{\circ}\text{C}$ . That for about 13 kyr BP —  $+8^{\circ}\text{C}$  (Stuart, 1991). Here the level of precipitation for Wurm stadials is estimated as 260-370 mm and for Upton Warren interstadial (about 42 kyr BP) — 450-650 mm per year (Lockwood, 1979). Both values are higher than, e.g., the mean annual precipitation is (about 200 mm) in modern Central Yakutia (Karavayev & Skryabin, 1971). In some localities of this country (Verkhoyansk district, etc.) there are even 130 mm/year and  $-16,1^{\circ}\text{C}$  of mean annual temperature (mean January —  $-50^{\circ}\text{C}$ !) (Kostin & Pokrovskaya, 1961). Other conditions for cold-adapted megafauna are also favorable here. The meadow-like herbaceous cover is well-developed. Larches are widely spaced. It is often possible to travel by car among them in every direction for many kilometers (Karavayev & Skryabin, 1971). The snow cover here is thin and the soil is dry. There are even patches of steppes. Nevertheless these formations are considered as unfit for mammoths and their satellites due to their insufficient productivity (Verkhovskaya, 1989, etc.). This conclusion seems, however, not convincing enough. Domestic cattle and horses feed themselves here all year round (Karavayev & Skryabin, 1971; Filina & Filin, 1980).

Wurm climate of Middle Dnieper and Low Desna basins is sometimes estimated as colder and drier than that of modern Central Yakutia (Rekovets, 1985: 141). But complex paleopedological and paleobotanical data indicate less severe climate even for the coldest phase (Bugsky stage = Late Wurm Pleniglacial). Mean annual precipitations rate reached up to 200-250 mm/year; mean temperature of the warmest month —  $+6^{\circ}\text{C}$ ; that for the winter months —  $-19^{\circ}\text{C}$  (Sirenko & Turlo, 1986: 175). At the Middle Wurm Interstadial (Vitachevsky stage) these values were correspondingly 400-550 mm/year,  $+18^{\circ}\text{C}$  and  $-5^{\circ}\text{C}$  (ibid.: 174). At Riss-Wurm Optimum (Priluksky stage) it was 550-600 mm/year in the Northern and 450-600 mm/year in the Southern Ukraine with the mean summer temperature for  $2^{\circ}\text{C}$  and the mean winter one for  $5^{\circ}\text{C}$  higher than now (ibid.). What about the distribution of mammoths in East Europe during these epochs ? Contrary to the doctrine of the obligatory crioarid specialization of these giants, they were absent in southern part of East Europe (Crimea, Caucasus, most of present-day steppe zone) not during the warmest, but during the coldest Late Wurm Pleniglacial time (Vereshchagin & Baryshnikov, 1985, etc.). Throughout the less severe Early and Middle Wurm (ibid.; Korniets, 1962) and the warm Riss-Wurm (L. Alekseeva, 1980; 1990) they thrived in steppes and forest-steppes of the South of East Europe.

There are many other cases when both pachyderms were present under climatic conditions not more severe, but well milder than in modern Yakutia or Mongolia (Sect. 3.14. and 3.17.). It is, however, possible that it was not mean annual or seasonal temperature and/or humidity, but some special climate-induced environmental particularity(ies), which was (were) important. Let us consider the probable particularities one after another.

### 3.5. Could the mammoths do without the 'cold' loesses accumulation climate ?

Certainly **could**. Climatists themselves indicate that during the Pleistocene, including the time of the existence of the species *M. primigenius*, periods without considerable or any 'cold' loesses accumulation were at least twice as long as those of such an accumulation (Velichko, 1973; Ukraintseva, 1993, etc.). Mammoths' remains derived from the humus layers of Middle Wurm Interstadial age in Kostionki site (Don region) are 9 times less numerous than those from the younger Late Wurm loess layers (Vereshchagin & Baryshnikov, 1977). This phenomenon is treated as the result of mammoths better adaptation to crioarid 'tundra-steppe' than to previous mesic forest-steppe conditions (ibid.). It could be, however, the simple consequence of the increase of the skill of ~~Paleolithic hunters (Dutshkov, 1989b, 1993b).~~

### 3.6. Whether the permafrost presence was so indispensable to mammoths ?

According to some climatists it was. They issue out of the fact that mammoth range at Late Wurm Pleniglacial coincides with that of permafrost (Velichko, 1973; Tomirdiario, pers. comm.). But mammoths inhabited some regions without permafrost, as, e.g., Ussuri region (Ovodov, 1977a) even at that epoch. Woolly rhinos were spread far beyond these regions in Spain, south of Ukraine, North Iran and Middle Asia (Kurten, 1968; Vangenheim, 1977; Kozhamkulova, 1981, etc.). During Riss-Wurm Optimum both giants lived in warm forest-steppes of Southern Russia (Sect. 3.17.2.). There were no traces of permafrost there. Also their return to West Europe at Postoptimal stage of Riss-Wurm took place many thousand years before that of permafrost (Stuart, 1991).

Permafrost is the direct consequence of a crioarid continental climate. But its traces do not prove by themselves the former existence of tundra-steppes. Several types of tundras, boreal forests and steppes are situated in the present-day permafrost regions (Filina & Filin, 1980).

### 3.7. Were the melting of permafrost and glaciers so terrible ?

It was certainly so for the individuals, who fell into hidden thermocarst wells and in other traps, derived due to this melting (Vereshchagin, 1979; Kozhevnikov, 1983, etc.). But such deaths always were accidental. They should not be confound with the reasons of the extinction of species (ibid.; E. Alekseeva, 1980, etc.). The permafrost melting in Europe, Kazakhstan and West Siberia, although being rapid (geologically speaking), was neither instantaneous in the scale of individual life, nor simultaneous all over the area. For large herbivores the negative sides of this process, such as certain difficulties for walking and the accidental deaths in the mentioned traps, were counterbalanced by positive ones. The lakes, originated due to thermocarst processes, were replaced then by excellent 'alas' meadows; the latter existed for 15-20 years before their transformation to climax tundra or taiga communities (Vereshchagin & Baryshnikov, 1980a; Verkhovskaya, 1989). Besides this, melting of glaciers led to the saturation of soils with almost distilled water that neutralized soil reaction by leaching the soluble salts. As a result many acidofuge plants prospered (Kozhevnikov, 1977). They were far more precious for the large herbivores feeding than acidophile ones, prevailing in spruce forests and some types of tundra (Sect. 10). What is more — mammoths' feet were well adapted for boggy and melting soils (Sect. 3.11.).

### 3.8. Were the mammoths stung off by insects ?

Quite often good pastures are unfavorable for herbivores due to swarms of gadflies, gnats, breezes, botflies, and other pests (Przhewalsky, 1875; Geptner & al., 1961, etc.). It is possible that conditions for these parasites were unfavorable in the notorious wind-blown Arctida (Sect. 3.14.1.1.) with its 'quasi-Martian climate' (expression of S.V. Tomirdiario). Maybe the same was true for some parts of the Late Wurm Eastern Siberia (Vereshchagin, 1977b). But herbivores that subsisted or even prospered under more 'normal' climatic conditions (Sect 3.14. and 3.17.) certainly had no such an advantage. Not to speak on Interglacials, with their climatic zonality, similar to the modern one, warm summers of the stadials continental climate, favoring rapid growth of the mammoths pastures vegetation has certainly favored insects too, including the pests of herbivores. The presence of so famous parasites as *Tabanidae* is directly proven for Byelorussia even for the time of maximal Wurm Glaciation (Nazarov, 1984). At any rate it is highly improbable that insects or other parasites could be a principal extinction agent over the all former range of mammoths and woolly rhinos. On the contrary — their specific parasites should suffer. So a gasterophilid gadfly *Cobboldia rusanovi*, whose larvae were parasites in stomach of mammoths, became extinct (Grunin, 1973).

### 3.9. The mammoth clad in ice-armour ?

Idea that shaggy coat of mammoths was a 'dry cold' hyperspecialization that doomed them to extinction (Sect. 3.2.) under climate with thaws (Vereshchagin, 1977b; Vereshchagin & Baryshnikov, 1977) is not so extreme as the view of complete inability of mammoths to stand any contact with ice and snow (Neuville, 1921; Krause, 1978). Such views were born because the presence of sebaceous

glands in the skin of mammoths has been negated (*ibid.*) or doubted (Lister & Bahn, 1994) for a long time. Without sebum their hairs and skin could have no water-proof qualities. It should be wetted under rain or snowfall and even due to the contact with laying snow during sleep. Then appearance of the ice-armor due to frost was inevitable (Neuville, 1921; Krause, 1978).

It was impossible to detect the sebaceous glands in ice-conserved and partly defrozen mammoth corps due to the post-mortem destruction of the glands. Study of non-defrozen specimens by means of new methods revealed that these glands were numerous and well-functioning (Gorbachev & Zadalsky, 1989). This discovery means that mammoth wool and skin had normal water-proof properties. They were no more prone to be frozen to the state of ice-armor than those of any of living arctic, boreal and temperate zone mammals (Putshkov, 1991).

### 3.10. A story of mammoth, saiga and reindeer (beginning)

Climatists reject the idea of the euryecity of mammoths due to frequent occurrence of their bones in so-called 'disharmonious' faunal associations, that is to say with the rests of animals that seldom or never occur now together. Particular attention has been paid to the cooccurrence of saiga and reindeer in numerous 'mammoth sites' (Formozov, 1946, 1990; Sher, 1971; Velichko, 1973; Tomirdiario, 1977; Guthrie, 1990b, etc.).

Now these animals never occur together. The reindeer is the best equipped among ungulates for the life in a modern tundra environment. Also it coexists with other deer over most of taiga zone (Formozov, 1990; Geptner & al., 1961). Saiga does not live in woods. It can neither move on boggy ground nor feed under snow cover over 10-20 cm. It evades the regions with frequent thaws, being helpless in cases of wind-packed snow and of frozen snow crust that cut her thin-skinned legs (*ibid.*). Hence the climatic explanation of the presently non-overlapping areas of saiga and reindeer is clear. Saiga would perish in modern taiga and tundra due to a set of insurmountable impediments to its feeding and locomotion. Reindeer is 'not energetically efficient enough in locomotion, dietary exploitation, and other life history aspects to be competitive' in steppes (Guthrie, 1990b: 45).

The climatic explanation of the common occurrence of these two ungulates during Glacials is also cogent. Tundra-steppes were complex plaid of habitats. There were enough open arid flats of wind-blown smooth substrate, where saiga excelled. 'In addition, there were local habitats where reindeer could find sufficient year-round resources to prosper ...' (*ibid.*). At least in some parts of tundra-steppe zone rich mesic meadows constituted an important part of the vegetation cover and played an outstanding role in feeding of reindeer (*ibid.*) as well as of extinct herbivores (Yurtsev, 1976). Thus the withdrawal of reindeer, lemmings, arctic fox to the North and saiga, hemione, pika to the South with the installation of the Holocene zonality seems logic and natural consequence of the disintegration (Aleksееva, 1995) or 'winnowing out' (Guthrie, 1990b) of mammoth-steppe biome.

The same cannot be said of the deduction (*ibid.*; Sher, 1971; Velichko, 1973; Tomirdiario, 1977, etc.) that mammoths and rhinos had the same disgust to woodlands, swampy and snowy countries as saiga has. It would be sufficient to remind the striking dissimilarity between the thin stick-like legs of saiga and the pillar-like legs of pachyderms for distrust such a queer conclusion (Putshkov, 1991). However the ideas of extreme **chionophobia** (inability to cope with even moderately deep and/or long-lasting snow-cover) and **palustrophobia** (inability to cope with swampy or even moderately mild and humid soils) of mammoths and their satellites are so deep-rooted that climatists often take them for granted (Formozov, 1946, 1990; Sher, 1971, etc.; Velichko, 1973; Bgatov & al., 1989, etc.). This point is crucial for the 'tundra-steppe crash' concept of Wurm extinctions. It is the unavoidable reverse of a paradigm that '... saiga, horses, woolly rhino, and woolly mammoths' were '... extremely arid-adapted species' (Guthrie, 1990b: 43). Therefore, it should be proved or disproved only by careful point by point testing with diverse neo- and paleoecological evidence.

### 3.11. Were mammoths 'sick' with 'palustrophobia' ?

It is a delusive impression that elephant or rhino are more prone to be stuck in the mud than smaller ungulates are. The broad ends of pillar-like legs of pachyderms distribute an immense weight over large area. Hence they are well fit for diverse types of hard and mild (sandy, boggy, etc.) substrata. It is misleading to deny the possibilities of a proboscidean to march over boggy substrata issuing only out of the fact that pressure on the elephant foot is 510-660 and the pressure on the reindeer foot is only 140-180 grams per 1 square cm (Guthrie, 1990a, etc.). Mammoths, as well as living elephants, had the large subdigital cushion of

connective tissue (Stuart, 1991; Surmely, 1993). This elastic cushion expands considerably and spreads fingers apart, when animal leans upon the leg. The cushion contracts and hangs under fingers thus bringing them together, when elephant raises the leg. As a result, the animal, marching on the boggy or other unstable ground, makes pits there that are considerably wider than the diameter of the extracting leg near the foot and even near the body. Due to such adaptation elephants can march easily through the sands of the desert Namib (Clements & al., 1984) as well as through the bogs and quagmires impenetrable for other animals (Bauer, 1964; Bannikov & Flint, 1977). Mammoths similarly used such miraculous feet. The subdigital cushion was less developed in rhinos, but their feet were statically much wider than forearms and shanks. In complete accordance with these considerations both giants did inhabit swampy regions of arctic and boreal types (Sect. 3.14.).

### **3.12. Were mammoths 'sick' with incurable chionophobia ?**

Ungulates were divided on more (chionevphorous) and less (chionophobous) snow tolerant species (Formozov, 1946, 1990). Climatists are sure that mammoths belonged to the second group. This deduction is based upon the crioixerophilous adaptations of extant organisms that were in Wurm members of the tundra-steppe biome. But some of these organisms are really specialized to steppe (saiga, jerboa) and/or tundra (lemmings) conditions while the others, as wolf or stoat are ubiquitous (or nearly so), tolerant to much wider range of environments. To what group have belonged the mammoths in reality ?

#### **3.12.1. Snow cover problems for large and medium-sized herbivores**

The snow cover imposes a set of problems to ungulate species. It impedes feeding and locomotion. This leads to death from exhaustion, starvation, maladies and predators. In tundra soil is covered with snow for most of the year, in southern countries (up to Iran and Israel) it appears sporadically, resting, however, a painful trial to megafauna.

In tundras under the repeated action of potent arctic winds, snow often condenses and becomes firm (wind-packed snow). There are lands (*e.g.*, Okhotsk region) where it becomes in places so hard that could not be hacked with an ax but only cut with the saw (Formosov, 1990). Evidently even milder wind-packed snows (that could be dug with a spade) presents a severe hazard to herbivores grazing. In steppes wind-packed snows appear less frequently and for shorter periods. Usually here they are not so firm and not continuous (*ibid.*).

The soft 'crumbly' snow cover occurs mainly, though not exclusively, in forests. Every ungulate has the critical threshold of snow cover depth that makes its feeding and locomotive activity energetically inefficient (Formozov, 1990; Geptner & al., 1961; Guthrie, 1990a). Even more pernicious is the frozen snow crust that appears over sufficiently thick 'crumbly' snow due to thaw alternated with frost. This crust rubs sore places or even cuts the skin of the legs of a moving animal. Impediments to grazing are so serious that animals prefer to dig the thicker snow without crust than to dig the thin one with it. Especially baneful for hoofed animals are cases when thaws alternate with frosts and snow-falls. Such alternation creates 'multicrusted' snow cover (Vereshchagin, 1971a). If 'crumbly' snow under the crust is thicker than the height of the legs, animals immerse up to belly and 'hang' helplessly, having no support (Formozov, 1990; Geptner & al., 1961). Frozen snow crust occurs everywhere, but it is less frequent under crioarid conditions. It is thinner in wood and thicker in open places.

A 'sitting' ice-crust without underlain 'crumbly' snow appears if thaws, rains and frosts act over thin snow layer. It occurs mostly in steppes. Sometimes the thick snow rapidly melts to a 'mash' condition and transforms to the ice-crust of important thickness (up to 20 cm) with plant stems inside. Grazing on these plants becomes impossible. Animals easily slip and fall, often maiming themselves.

### 3.12.2. Snow cover adaptations of extant ungulates and extinct pachyderms

Extant ungulates possess features increasing or decreasing their possibilities to cope with the mentioned impediments (Formozov, 1946, 1990; Geptner & al, 1961; etc.). Some of these features aid or hamper them on other difficult substrata, notably the boggy ones.

These features are: a) size and strength; b) specific morphological adaptations; c) collective 'pathing' and 'breaching' of snow crust; d) switch to accessible winter forages; e) utilization of local differences in the snow-cover properties; f) seasonal migrations; g) capability to withstand press of predators.

The careful consideration of these features is necessary for the sound estimation of the snow resistance capacities of mammoths and rhinos.

### 3.12.3. Snow cover, size and strength of animals

All other things being equal, the larger and stronger are ungulates, the more successful they are both in locomotion over snow-clad country and procuring themselves with food. As an example musk-ox, a species, quite ill-adapted for undersnow feeding, satisfactorily digs out its fodder from under the snow-layer of 20-40 cm as compared to 10-20 cm of saiga. The critical threshold of the depth of 'crumbly' (neither wind-packed nor frozen crusted) snow for moose is 80-110 cm, for red deer — 50-70 cm, for roe — 30-50 cm. The snow-caused seasonal migrations of red deer (izyubrs) of Russian Far East and Caucasus were less frequent and of shorter distances than those of roes. Often red deer hibernated at localities, abandoned by roes that migrated to less snowy regions. Larger individuals and races of all three mentioned cervids are more resistant to snow than smaller ones (Formozov, 1946, 1990; Geptner & al, 1961). It is not by chance that only the largest of this trinity — moose is spread all over taiga. Contrary to previous indications (Formosov, 1946), it lives even in the most snowy Pechora and Lower Ob Basin (Formozov, 1990: 283).

Even some serious morphological disadvantages could be partly counterbalanced by size and/or strength. Thus one-hoofed extremity is considered as ill-adapted for the 'winter grazing' (Formozov, 1990). However Yakutian and Kazakh horses of year-round open air breeding cope with this task better than musk-ox and most of smaller artiodactyls (saiga, dzheiran, dzeren, chamois, ghoral, sheep and goats). Horses successfully dig the grass from under the snow layer of up to 0,5-0,6 m thickness (though less than 0,3 m is preferable) (Lazarev, 1980). Short legs are another grave fault. But snow cover depth tolerance of short-legged wild boar and long-legged roe are similar, as well as the northern borders of their ranges in Europe (Formozov, 1990; Geptner & al., 1961). In East Siberia wild boar does not penetrate to ample regions with thin snow-cover primarily due to the absence of acorns and some other important food items (Geptner & al., 1961).

If size and strength alone were taken into consideration, it would be expected that even woolly rhinos, to say nothing of mammoths, should be far less prone to be succumbed by winter snows than any of the living ungulates. Speaking about the dangers of the frozen snow crust to extinct pachyderms (Sect. 3.2.) some authors forget how dangerous to such crust would be effect of a living lorry weighing from 1 to 5 tons (Putshkov, 1991). Modern (to say — Holocene) frozen snow crusts of the forest zone often are solid enough for wolves but quite rarely — to deer and tigers (Sludsky, 1966). The simple passage of mammoth herd would trample down any 'crumbly' snow and would smash to pieces any frozen snow crust covering such snow. Wind-packed snow and 'sitting ice-crusts' could, however, resist to the weight of giants.

### 3.12.4. 'Snow-' and 'ice-combating' morphology: living ungulates

The importance of general size and strength of hoofed animals does not diminish the significance of more specific adaptations in their dramatic contest with the snow. For instance the most snow-tolerant species is a reindeer — large but not the largest among Holarctic ungulates.

Not mere general size is important but also the length of legs and the position of knee- and elbow-joints. If the snow layer is higher than knees, ungulates slow down their run. If snow reaches the level of the breast they could move only with

great difficulties (Formozov, 1990). Thus stilt-legged moose exceeds by its extent of the long-lasting 'crumble' snow-depth tolerance all three living races of bisons that have similar body mass. This tolerance is 80-110 cm for moose and 60-70 cm for bisons (Geptner & al., 1961; Filina & Filin, 1980; Guthrie, 1990a).

Every feature of feet enhancing their space of support is advantageous for 'the struggle with the snow'. Such features are: broad hooves, the capability to draw fingers apart considerably, the presence of well-developed and low positioned lateral fingers participating in the support function over mild substrata. The opposite features decrease the 'snow-combating' properties. So more wide-hoofed wild horses (*E. caballus silvaticus*, *E. c. gmelini*) in historical time were spread by far more westwards and northwards than narrow-hoofed hemionos and onagers (*E. hemionus*). The 'hard tiny hooves' of saiga play an outstanding role in the 'tundra-steppe crash' conception of mammoths extinctions (Sect. 3.2.; 3.10.). However this animal has in reality wider hooves and can draw its fingers apart to a greater extent than Mongolian dzeren (*Gazella gutturosa*) and, especially, Turano-Iranian dzheiran (*G. subgutturosa*). These gazelles, although being highly resistant to both cryptoarid (in winter) and thermoarid (in summer) conditions, are even less capable than saiga to resist winter snows and ice-crusts (Geptner & al., 1961). Among deer forms with well developed lateral fingers (reindeer, musk-deer, moose) are more snow-tolerant than those with moderately developed ones (roe, red deer), not to speak of the less snow-tolerant sika and fallow deer with the smallest lateral fingers (ibid.; Formozov, 1990).

The features discussed above concern mostly adaptations to cope with 'crumbly' snow cover. As for the firm wind-packed snow, frozen snow crust over 'crumbly' snow and 'sitting' ice-crust without underlain 'crumbly' snow, most ungulates have no special morphological adaptations to cope with these calamities. They resist to them only by behavioral mechanisms (Sect. 3.12.7.; 3.12.8.; 3.12.9.). There are two important exceptions.

The first is the Canadian forest bison or 'wood buffalo' (*Bison bison athapaska*). It has broad sickle-like hooves with interposing tips. Gaps in frozen snow-crust, maden with such hooves, are considerably wider than distal part of the legs. Due to this the animal pearses the crust and drags out the leg without wounding it (Fleurov, 1977). This bison is almost identical to the bison (*B. priscus occidentalis*) of East Siberian mammoth sites, that had the same hooves structure (ibid.). Their different specific and subspecific titles reflect the usage of the typologic species concept. As it was correctly stated by Guthrie (1990b: 46) '... it is mainly a matter of reference convenience that we use different specific designations' for extinct and living Eurasian and American bisons.

Another one is the reindeer with even wider hooves that enlarge additionally to the beginning of the cold season. Then they are used alternatively as walking skis and shovels (Formozov, 1990; Geptner & al., 1961; Vereshchagin & Baryshnikov, 1980a). The shovel function is accomplished mainly due to sharp margin and concave dorsal surface of two median hooves. They form together an efficient tool for shoveling not only soft but crusted or even wind-packed snow as well (except the hardest types of the latter). All four fingers and their hooves are engaged in the ski function. Due to wide hooves and well-spreadable fingers reindeer moves quickly over the rugged, irregular tussocky, moss and lichens bumped, boggy and soft snow covered surfaces. The frozen snow crusts often resist to its weight. If no — it extracts legs harmlessly for the same reason as the Canadian forest bison does. The unbelievable for an ungulate flexibility of its body and legs articulations strongly helps it to move through 'crumbly' snows both with and without the frozen snow-crust (ibid.). At last the wide-footed legs of reindeer support it better than those of other ungulates over the slippery ice covered terrain.

### 3.12.5. 'Snow-' and 'ice-combating' morphology: woolly mammoth and rhino

It is of prime importance that adaptations of feet that enable ungulates to move efficiently over snow are the same that permit them to cope with swampy and other mild substrata. It justifies the analogies between the abilities of elephants to march over swamps (Sect. 3.11.) and these of mammoths to march over snows. Mammoths could efficiently use their feet with miraculous subdigital cushions not only for quaggy and sandy soils but for soils covered with deep snow as well (Surmely, 1993).

Due to the structure of feet (Sect. 3.11.) the diameter of gaps that were made in the frozen snow crust by the legs of both giants should be invariably wider than their leg thickness. Their thick-skinned legs were additionally protected from cutting by hard and stiff hairs. These peculiarities combined with the effects of the weight and size of animals (Sect. 3.12.3.) permitted to pachyderms to pass through snow crusted spaces with complete impunity. In addition adult mammoths broke and scraped out the snow crust with their tusks (see below).

Certain disadvantages of giants were relatively low legs of woolly rhinoceroses and low position of mammoth knees and elbows. They should inevitably slow down



the pace of giants through deep snows. Giants counterbalanced these faults with their strength. The absolute height of woolly rhino legs and mammoth knees being large enough is worth mentioning too.

It has been stated that Holocene polar fox and reindeer became more long-legged to be able to cope with increased thickness of the snow cover (Kuzmina, 1971, Kuzmina, oral communication in 1991). It is evident, however, that even the longest leg of a reindeer (not to speak of that of a polar fox!) is absolutely shorter than leg of an ordinary mammoth. It is also important that the loss in speed for giants was not such an impediment as it would be for smaller ungulates that have to escape predators (Sect. 3.12.10.). Certainly it is true only in case, if we discount the idea of man hunting on giants, following the pure climatists' position.

Mammoths' pace was confident also on slippery substrata such as ice and 'sitting' ice-crusts in winter, moist stones and melted permafrost soils, quaggy on the surface and ice-clad in the depth in spring and summer. Thick (3,5-6,0 cm) mammoth soles were furnished with the system of numerous deep furrows that reliably prevented the slipping (Surmely, 1993).

Indeed the mammoth was a living cross-country vehicle (*ibid.*) that marched on any ground more surely than other herbivores!

So the winter locomotion was not too difficult for the giants. The question of their undersnow grazing is less clear.

Many specialists are sure that mammoths used their tusks for scraping and shoveling the snow, providing the snow was not too thick. Heavy and tremendous tusks of adult mammoths with ends directed mediodorsally one to another are believed to be excellently adapted for this aim (Garutt, 1977; Stuart, 1991; Surmely, 1993; Lister & Bahn, 1994, etc.). Mammoth reconstructions with tusk-ends spreaded laterodorsally are proven to be incorrect (Garutt & Dubinina, 1951, etc.). Young mammoths, whose tusks were still short and slightly curved, executed this work with the tips of the tusks. However even calves with tusks of 5-6 cm that could not reach the ground, had the used tusk tips. It has lead N.K. Vereshchagin (1977a; 1979) to the conclusion that calves and young mammoths used their tusks for barking trees, while adult ones broke tree branches with them. He, as well as H. Krause (1978), questioned the possibility of tusk utilization for the snow shoveling.

Probably tusks could well be used for all the mentioned purposes (as well as for the combats of males). The section of tusks was round. It seems that even enormous spiraled tusks of adult individuals with ends directed mediodorsally one to another were ill-adapted for the scraping and shoveling of thick snow cover. However the giants could easily use their tusks for breaking and scraping the crusts, that covered the snow. Once the 'crumbly' snow has been exposed, mammoths could easily pluck stems with their long woolly trunk even from under the snow of considerable thickness. The sufficiently deep 'multicrusted' snow may be repeatedly handled with tusks.

Mammoth tusks were used even for hard work of breaking out the pieces of ice from subterranean ice-veins in loess. This ice was important water resource of mammoths during long snowless winters of ultracontinental Eastern Siberia during pleniglacials (Tomirdiario, 1991). If so — why they should not be used for the elimination of the frozen snow crust by the mammoths that lived under other types of climates ?

Likewise there are indications that formidable (up to 1, 35 m) horns of woolly rhinos were used for the snow-raking purposes (Arembowsky, 1956; Kozhamkulova & Kostenko, 1984; N. Garutt, 1995, etc.). It is plausible as far as both African rhinos efficiently use their horns for digging roots of some herbs, grasses and bushes (Penny, 1987).

Probably legs of both pachyderms were used to some extent as additional tools to tusks or horns in the winter grazing.

### 3.12.6. 'Collective works' in winter

Wild boars and all northern cervids are known to trample down the snow thus making the network of paths, so important for their survival in winter (Formozov, 1990; Geptner & al., 1961). Animals in herds move and feed more efficiently than solitary ones. Weaker individuals (including young and pregnant females) use paths and accesses to food that were 'paved' by stronger ones. On march reindeer that have been advancing in front of the herd, drop behind when they become tired. The reposed individuals from the rear replace them (*ibid.*).

There are no reasons to think that highly social mammoths behaved otherwise. Woolly rhinos also lived in family groups or in small herds as the modern white rhinos live (Guerin, 1983). Rhinos and, particularly, mammoths being infinitely stronger than deer, trampled paths in snow and smashed frozen snow crusts on their pastures on an incomparably larger scale (Putshkov, 1989a, 1993b). Due to this not only their young, but many other mammals got the best chances to hibernate (*ibid.*).

### 3.12.7. Switch to winter forages

When grazing becomes difficult or impossible, whereas twigs and bark rest accessible, any ungulate (including such inveterate grazers as sheep, goats, chamois, ghorals), become exclusive or predominant browsers. They eat lichens too. For reindeer and muskdeer lichens normally is the main winter forage (Formozov, 1990; Geptner & al., 1961). Woolly mammoths and rhinos did eat woody plants (Sect. 3.15.1.4.). This being the case, there are no reasons to think that they could not switch to browsing. It is a different matter that mighty beasts with rather efficient adaptations for feeding on grass and bushes from under the snow (Sect. 3.12.5.) were probably not very often forced to feed on adult trees. However they should turn to the latter, being deprived of their habitual food by thick snow cover or by the 'sitting' ice crust during the critical episodes of the cold season. The exhausting of winter pastures by mammoths grazing could force giants to such switch as well.

### 3.12.8. Utilization of the local snow-cover differences

Due to the local differences of relief, soils, vegetation, action of winds, particularities of melting and other reasons, the snow-cover is never uniform. Ungulates largely use these differences. So reindeer in tundras try not to feed in the depressions with too deep 'crumbly' snow. They also evade tops of elevations, covered with too firm wind-packed snow or snowless with meager food due to constant winds. Reindeer use for feeding those parts of slopes, where snow is neither too firm nor too deep, while forage is satisfactory. The snowless and wind-packed snow parcels are used as comode roads to feeding-places (Formozov, 1990; Geptner & al., 1961).

In forests cervids begin to rake the snow near the tree trunk. Here the snow cover is the thinnest. It is easier to begin here the work. Then they progress to tree periphery, where there are more fodder. For displacements human footpaths and roads are willingly used.

In steppes and deserts snow cover, if present, is usually patchy. Spaces covered with 'sitting' ice-crust are alternating with those of deeper snow (crusted or not) in depressions and/or among bushes. Usually there are many snowless spaces (due to winds and high insolation). They are largely used by wild and domestic ungulates. Due to this nomads did not recur to the hay-stocking (Przewalsky, 1875; Formozov, 1990).

In mountains the dissimilarities of snow-cover are extreme. Even in snowy regions there are good winter stations (Formozov, 1990; Geptner & al., 1961). Not only the alpine ungulates in the proper sense, but every other species could usually find such stations either on slope of favorable exposition or in a certain valley. For example in generally very snowy Sayan mountains (East Siberia) there is a valley of river Gutar with thin snow cover. Snow is here blowing out by winds. Cattle and horses graze here without additional feeding all year round (Formozov, 1990). Such valleys could well be a winter station for mammoths and/or rhinos.

There are no reasons why mammoths that should have been as clever, as modern elephants, were not using local differences of snow cover to the same extent as living ungulates. On the contrary, due to strong direct and indirect (through the influence of giants on vegetation) pachyderms' impact on snow-cover (Sect. 10.5), these differences in mammoths' times should be even greater than during the prehistoric part of the Holocene.

### 3.12.9. Seasonal migrations

It is an efficient way that permits to ungulates to resist to seasonal calamities. Horizontal and vertical migrations are known for every ungulate species, living in regions with snow-cover (Formozov, 1990; Geptner & al., 1961). These migrations (as well as other aspects of winter behavior) are so plastic, so changeable due to local and regional particularities (ibid.), that they could not be considered as the 'blind instinct' actions or be compared with the desperate migrations of lemmings, caused by the overpopulation stress. Experienced adult ungulates certainly know why and where they go, and which roads should be chosen.

Thus till the beginning of XX century there were massive regular autumn migrations of roes in different parts of Russia (Formozov, 1990; Geptner & al., 1961). Animals used the same ways, the same fords on rivers. Hunters killed them by hundreds and thousands in suitable places. But the range and other peculiarities of migrations oscillated from year to year due to the weather conditions. More or fewer animals remained on their summer territories, using appropriate plots of the local stations to overwinter. Paths, trampled by wild boars and red deer (izyubrs) were used largely. Then migration behavior became less favorable than sedentary one due to the increased mortality from hunters and man-made changes of landscape. There are no more large scale migrations of roes (Formozov, 1990; Geptner & al., 1961). Their population density now is considerably below than that of previous migrations times. It is regulated not only by hunt but by the surface of the suitable winter stations and their food resources as well (ibid.).

Not only in mountains (Sect. 3.12.8.), but even on vast plains covered with thick snow, there are enough stations, favorable for the hibernation of ungulates. These are slopes of the southern exposition of the latitudinally situated river valleys. Due to better insolation, snow cover here is always thinner and not so long-lasting than on the plain; the food resources are richer. That is why all the roes, the majority of wild swine and red deer and considerable part of mooses of the Moscow region gather in winter on the first terrace over the flood-lands of Oka river in Serpukhov district (Zablotskaya, 1975).

Again there are no reasons why mammoths that surely were not less witty than elk (moose), reindeer or roe, should be sedentary in seasonally inhospitable countries. It is worth reminding that both extant elephants have largely recurred to migrations, when man did not hinder them. In autumn the Irtysh basin elks march confidently to less snowy regions with mean speed 30 km per day (Formozov, 1990). What could forbid mammoths to do the same ? What could forbid them to seek the above-mentioned slopes of latitudinal river valleys ? Gently sloped steppe or forest-steppe slopes of the valleys of Mongolian, Transbaikalian, Kazakhstan and Chinese mountains are (or were) used as safe winter stations by domestic ungulates and/or dzerens. Why woolly rhinos could not use them in the similar way ? Most specialists accept that such a voracious being as mammoth should be as or even more migrant, as are modern elephants. They think that mammoths fed in winter (Garutt, 1965; Kornietz, 1962; Vereshchagin, 1979; Vereshchagin & Baryshnikov, 1985, etc.) or all year round (Soffer, 1985, etc..) in or near the river valleys and terraces.

### 3.12.10. Scourge of winter predation

'Last but not least' is just this factor in the redoubtable set of winter misfortunes. Winter mortality from predators of virtually all ungulates by far exceeds that in other seasons (Formozov, 1990; Geptner & al., 1961; Ungulates..., 1975). Only the freshly fallen 'crumbly' snow gives advantage to high-legged prey. All the other types of snow cover give the odds to predators.

Wolves, lynxes, wolverines easily run over such moderately condensed or frozen crusted snows that impede drastically movements of cervids, bovids and swine. In sufficiently deep crusted snow even solitary wolf easily kill moose or stag that could withstand to a pack of wolves under other conditions.

Wolverine and lynx, with their broad snow-shoe shaped feet, do such exploits with reindeer and other cervids even in deep 'crumbly' snow. Hoofed animals are helpless also on ice. That is why wolves chase them on the ice of lakes and rivers (Formozov, 1990; Geptner & al., 1961). Often the chase is unnecessary: at snowy winters red deer and mooses come on ice in order of browsing over the hanging branches of riverside trees. In early spring the exhausted wintered ungulates are eagerly persecuted by hungry bears, freshly appeared from their dens (Geptner & al., 1961; Ecology..., 1981). In steppes, at the times of snow-storms and 'sitting' ice-crust, hosts of exhausted saigas, dzheirans, dzerens (formerly also hemionies, wild horses and camels) are fiercely decimated by wolves and dogs of herdsmen. Wolves, dogs and wolverines often kill far beyond the necessity, out of mere pleasure of killing (ibid.; Formozov, 1990). The biped hunter on skis also takes such odds over the prey that are unimaginable at snowless seasons.

There are two circumstances that decrease the losses from quadruped foes. The first one is the patchwork system of paths and plots trampled by herds in their winter stations (Sect. 3.12.6.). Ungulates have here far better possibilities for combat or evasion. Moose or stag, even more the herd of mooses or red deer, are no more helpless over the ground of trampled snow even if it is surrounded by the deep snow and frozen crusted spaces. Another one is again the size of a prey. Mooses are feebly molested by wolves even in winter, if weaker prey is present (Geptner & al., 1961). Roes of Crimea and some other territories were killed in masses during snowy winters even by foxes (ibid.; Formozov, 1990) — something impossible for mooses, red deer, wild boars. During snowy winters at the beginning of XX century all roes in Bryansk region were forced to restricted stations, including haystacks and roads. Here they were completely exterminated by wolves and stray dogs. Region was repopulated by roes, issued from west and south only in forties (Vatomin, 1975).

Starting from the exposed evidence woolly mammoths and rhinos were again in the best position for overwintering than any of survived ungulate. Adult mammoths, as well as their young in herds, were difficult prey even for the most formidable predators. The more so that saber toothed cats (*Megantereon*, *Homotherium*), specialized hunters on young and weakened pachyderms (Kurten, 1968; Kurten & Anderson, 1980), died out in the Old World well before Wurm (Stuart, 1991, etc.). Cave lions and pack of hyenas were certainly dangerous to solitary young pachyderms or even to exhausted solitary adults. If the exposed considerations (Sect. 3.12.3.—9.) are correct, pachyderms need not be either solitary or exhausted too often due to the natural reasons. At any rate even an exhausted mammoth was a more difficult prey even for a lion than a horse or a reindeer.

### 3.12.11. Scourge of catastrophic winters

The said does not mean that any thaws, snows or ice-crusts would be harmless to mammoths. Probably such winter as that of 1860 would be disastrous even for them. During this winter in the usually snowless parts of Ukrainian steppes the thickness of snow in front of obstacles reached the height of the roofs of huts. In regions with mean annual snow cover of 0,7-1,2 m (e.g., Pechora Basin, Northern Kamtchatka, some parts of West Caucasus, etc..) catastrophically high (2-3,5 m and more) snow arrives more frequently. Helpless boars, deer, sheep, capricornes are took in deep snow by bare-handed people (Formosov, 1990). Abnormally thick snow-falls occurred mostly at the end of the winter, when animals are already exhausted. Certainly mammoths and rhinos should be perishing in mass when such, as the mentioned, or even thinner snows were partially melted and then converted into thick 'sitting' ice-crust with all stems inside. But it is clear too that even under such conditions mammoths and rhinos would have more chances to reach food (e.g., reeds, bush thickets or the nearest birch grove) than deer, saigas or horses had. Likewise they would have much fewer chances to become themselves the food for wolves, lions and hyenas. Even red deer perished at West Caucasus during terrible snows not so frequent as roes! (ibid.). No catastrophe exterminates widespread species over all area. Species recovers due to arrival of individuals from distant regions and/or due to survivors that had chances to be at the moment of the disaster at favorable stations (Sect. 3.12.8.—9.). Occasional weather calamities could well oppress the local populations of mammoths and rhinos or even exterminate them completely. But the pivotal cause of their extinctions could be only the

permanent reason that prevented the recovery of the species **between** such calamities (Putshkov, 1989a, 1992b).

### 3.13. A story of mammoth, saiga and reindeer (suite)

Thus mammoths due to their enormous strength and size, tusks, used for scraping snow and ice (both for drinking and forage-exposing purposes) and spreading cushioned feet have been enabled to cope with snow better than any other large beast of arctic, subarctic or temperate environments (Putshkov, 1989b, 1991; Stuart, 1991; Surmely, 1993). Snow thickness ruinous for them should exceed the limits of snow depth tolerance of other large herbivores. However snow cover of 1 m or more is rare on plains (snow-drifts in front of obstacles are not considered). In the mountains and rugged countries there would be a mosaic of deep-snow, shallow-snow and snowless plots. Mammoths could profit the suitable plots, as the extant herbivores do (Formozov, 1990; Geptner & al., 1961). At last mammoths could seasonally leave country that became inhospitable.

Climatists pay due attention to moist/cold adaptations of the reindeer to explain its survival in the Holocene. They acknowledge also its dry/cold adaptations to explain its prosperity in The Pleistocene tundra-steppes (Sect. 3.10). However they often disregard the fact that this animal inhabits the forest zone as well. It is (or was recently) spread over nearly all Eurasian taiga zone up to Jaroslavl region, Kama river, North Kazakhstan, Altai mountains, North Mongolia and Ussuri region (Geptner & al., 1961; Kozhamkulova & Kostenko, 1984). So it is widely sympatric with mammals of boreal forest and, marginally (some parts of Transbaikalia and Ussuri region) with these of mixed forest.

This circumstance is noteworthy for there are many cases when rests of reindeer, mammoth and woolly rhino occur in Pleistocene sites with boreal and temperate woodland animals, but not with these of saiga (Sect. 3.14.2.; 3.14.4.). It means that ecologically plastic and highly snow-tolerant reindeer is more reliable index of snow-resisting qualities of both pachyderms than saiga, although the snow-combating adaptations of reindeer and pachyderms were rather different.

It remains to add that in immense inner parts of East Siberia as well as in Mongolia mammoths and their suite have died out too, though they were here unmolested by frequent thaws and other particularities of oceanic climate. There was no significant climatic switch in Transbaikalia and Mongolia during Wurm/Holocene transition (Endrikhinsky, 1982; Kalmykov, 1987). Climate here remains arid, winters are severe but snow is scanty and crumbly (Przhewalsky, 1875; Kostin & Pokrovskaya, 1961; Alisov & Poltoraus, 1974; Formosov, 1990). Snow, soil and trophic conditions seem favorable to mammoths and their satellites in central Yakutia too (Sect. 3.4.).

So the only visible reason why saiga, and not reindeer or bison, has been chosen as model for the estimation of mammoth 'snow-combating' properties, seems to be the ardent desire to consider the mammoth a snow-dreading creature. The exposed arguments could be, however, refuted if the rests of both pachyderms were **invariably** accompanied by these of saiga. Let us check this possibility (Sect. 3.14).

### 3.14. Woolly giants and their landscapes

Not only climates (Sect. 3.4.) but also vegetation types and faunas of mammoths ecosystems were very diverse.

#### 3.14.1. Mammoths' pastures at the Late Wurm Pleniglacial (24-14 kyr BP)

##### 3.14.1.1. Group I. Completely treeless landscapes

S.V. Tomirdiario (1994, 1995, etc.) fervently argues that the best habitats for mammoths were the tall grass meadows on fertile loess and volcanic ash soils of Arctida. Arctida was a land mass constituted by ice and loess permafrost formation over dried Arctic shelves and, further north, over the ice cover of deeply frozen Arctic Ocean. Loess and ashes particles were bringing there by winds from climatically driven arctic deserts and volcanoes. Fertile soils and meadows appeared here due to the melting of loess/ice formation (yedomas) during the cloudless demi-year long Arctic 'day' (ibid.). The main pastures of mammoths and other herbivores here are thought as the highly productive monospecific thickets of the tall hidrophytic grass *Arctophilla fulva*, that grew on immense spaces covered with melted water of 5-10 cm deep. The demi-year long Arctic 'night' with '... frosts below -100 degrees centigrade ...' the fauna passed '... in a kind of metabolic stupor' (Tomirdiario, 1995: 710). In other words S.V. Tomirdiario adds to notorious arid tundra-steppes of the mainland another 'mammoth-paradise'— the tall grass meadows of Arctida wetlands.

Many authors consider these ideas debatable. However the large size of the Late Wurm mammoths and horses from Arctic Ocean islands (that were then part of mainland) gives them certain plausibility.

Much smaller mammoths and horses lived in cold and dry, wormwood dominated, steppes that occupied vast territories to the South of Arctica (Tomirdiario, 1994). Some authors think that mammoths and their satellites were fed there mostly on crioarid steppe-like vegetation (Guthrie, 1990b, etc.). According to Yurtsev (1976, pers. comm.), and, even more, Kozhevnikov (1986, etc.) during stadials in Arctic and Subarctic regions were enough mesic and higrophytic plant communities (meadows, bush willow thickets, etc.), that served as the principal mammoths pastures. The latter argues that the productivity of the crioarid steppoid arctic and subarctic vegetation is very low. 'Enmynveem' mammoth of Chukotka that perished at the cold episode of the Kargin Interstadial, lived in mosaic surrounding of grass and brush (dwarf birches and willows) vegetation (Lozhkin, 1989).

Almost treeless were Late Wurm steppes on soils with and without permafrost at the East and Southern Ukraine (Sirenko et Turlo, 1986). It is true, however, that mammoths and rhinos were rare here at this epoch (Stanko, 1989, etc.) in contrast to the earlier ones.

### 3.14.1.2. Group II. Sparsely wooded landscapes

Correspondingly with the paleoclimatic data (Sect. 3.4.) even during the coldest episode (20-18 kyr BP) of the coldest epoch of the Late Wurm Pleniglacial (24-14 kyr BP) not only Northern Ukraine but also the central parts of the Russian Plain were covered with boreal forest-steppes. Stands of pines, birches, larches and willows were separated by spaces of dry steppe grass/wormwood/chenopodiaceen vegetation as well as by those of the mesic meadow ones (Grichuk — cit. by Soffer, 1985; Sirenko & Turlo, 1986, etc.). More to the South this cold forest-steppe was changed into cold steppe and then (from Low Dnieper to Low Volga Basins) — into xerotic steppes. Pine and birch stands were completed with spruces, junipers and even broad-leaved trees in the more moist Dniestr Basin and Subcarpathian regions. Open spaces were here occupied mostly by mesic grasses and forbs (ibid.). In Pleniglacial not only larch but also spruce, not so resistant to dry cold, was present in Byelorussia (Nazarov, 1984).

Epoch after the 'Glacial Maximum' (18-12 kyr BP) was an alternation of relatively warmer and colder (though not so cold as 20-18 kyr BP) episodes. At Russian Plain the role of woody vegetation has been increased, as well as the importance of spruce. At the North of Ukraine oak, elm, linden, probably even beech were present (Pidoplichko, 1976; Sirenko & Turlo, 1986, etc.). Nonetheless pine, larch, birch and willow were still dominant among trees. It is widely accepted that woody plants were confined to river valleys and adjacent terraces, whereas interfluves and plateaus were 'occupied with cold meadow-steppe' (Soffer, 1985: 180). According to other opinion more resistant trees (larch, pine) were present on interfluves too (Verkhovskaya, 1989).

Mammoths and their suite inhabited parkland landscapes with coppices of pines, birches, alders, willows, junipers and highly mosaic herbaceous storey of steppe, tundra and meadow plants in many regions of Western and Central Europe (Musil, 1985, etc.). In Italy and some parts of France they lived in the wooded steppes of cold-temperate type whereas in Cantabrian Spain — in those of the warm-temperate one (Freeman, 1973; Musil, 1985).

In Southern Siberia, due to its complicated relief, the mosaic of steppe, forest-steppe and forest-tundra landscapes was invariably present (Ovodov, 1977a; Kalmykov, 1987, etc.).

According to some reconstructions Late Wurm (Sartan) Central Yakutia was covered with vast meadow-steppes (on chernozem soils!), interspersed with patches of dry steppes, salines, river valleys meadows, bush thickets, pine, birch, willow and spruce stands. Northwards these landscapes, haunted by mammoths and many other large ungulates, were superseded by forest-tundras and tundras, though patches of meadow-steppes penetrated even to high Arctic (Karavayev & Scryabin, 1971). Probably such situation was true for warmer episodes and not for colder ones (Verkhovskaya, 1989, etc.), when even deserts existed in southern Yakutia

(Tomirdiario, 1994). However it changes nothing. Important is that landscapes with boreal trees were haunted by mammoths and other large herbivores (Karavayev & Scryabin, 1971; Verkhovskaya, 1989).

It is highly probable that other vast territories of Europe and Asia, that are proclaimed to be occupied by 'the treeless tundra-steppes', were in reality covered by larch parklands. The presence of larch is not always detectable by pollen specters (Filina & Filin, 1980; Verkhovskaya, 1988), whereas herbaceous cover in larch stands is often rich (Sect. 3.4.).

### 3.14.1.3. Group III. Well wooded landscapes

Mammoths, woolly rhinos, bison, horses and yaks of the Ussury region of Russia, Korea, and north-eastern China lived in a veritable taiga woodland. Here birches and various conifers (mostly spruce) prevailed but the admixture of various broad-leaved trees was invariably present (Ovodov, 1977a; Liu & Li, 1984; Olsen, 1987).

### 3.14.2. Fauna of Late Wurm Pleniglacial mammoth' ecosystems

The vegetation diversity of mammoth ecosystems was accompanied by the faunistic one. Entomofauna of North/East Siberian 'tundra-steppes' was indeed strongly dominated by steppe crioxerophytes, such as certain weevils of the genera *Stephanocleonus*, *Coniocleonus* and *Trichalophus*, carabid-beetle *Pterostichus subg. Derus*, byrrid-beetle *Chrysobryrulus rutilans*, and so on (Kiselev, 1981). Now these insects have local or strongly disjunctive distribution in cold steppes of Yakutia, Altai, Transbaikalia and dry steppe-like patches of Eastern tundras. However in Byelorussia these insects were represented by the few species and were of minor importance, when compared to insects of more mesic tundra and forest zone meadows associations (Nazarov, 1984). Here lived even *Xylophagus cinctus* — a typical taiga dipteran. Its larvae develop exclusively in wood of old conifer trees (ibid.). In England the aforesaid steppe ultracryoxerophiles were absent, though some mesic Siberian insects are found (Coop — cit. from Nazarov, 1984). There are also other differences of the Late Wurm entomofaunas at the eastern and western parts of mammoths-inhabited area that prove the progressive westwards reduction of the degree of continentality of the climate (Nazarov, 1984).

The same is true for theriofaunas. Siberia and most of East Europe were populated by a particular tundra-steppe hare (*Lepus tanaiticus*), highly adapted to feeding on coarse grasses (Vangenheim, 1977; Rekovets, 1985). Its close relative, the 'normal' extant white hare (*L. timidus*), lived in Crimea and Western Europe. It ate not so abrasive grasses and herbs that developed under less severe climate. It is the latter species and not *L. tanaiticus* that is represented now by isolated populations in Alps, Pyrenees and Ireland. Mammoths inhabited equally well zones, where rodents were represented only by steppe and tundra species, zones, where these species were accompanied by mesic forest and meadow mice and voles and those, where lemmings did not penetrate at all (Spain, most of Italy, Ussuri region of Russia, large part of China). Mammoths coexisted not only with tundra, steppe and taiga animals. In many regions of West and Southern Europe they lived also with those of temperate forest, wooded steppe and meadow environment, such as rabbit, wildcat, wild boar, aurochs, porcupine, etc. These animals testify the relatively mild climatic conditions (Kurten, 1968; Freeman, 1973; Stuart, 1974; Musil, 1985, etc.). Rests of saiga are not known from the sites of northern Ukraine (Kiev, Cherkassy and Chernigov regions) though it lived more southward and eastward (Korniets, 1962; Pidoplichko, 1976; Soffer, 1985; Bibikova & Belan, 1989). It means that in Northern Ukraine the snow, although being thinner than

now (Baryshnikov & Markova, 1990), was too thick for saiga and not too thick for mammoth, bison, horse and rhino.

The Late Wurm Spanish, Rumanian and, with rare exceptions, Ukrainian mammoths had cheek teeth of 'boreal' type (L. Alekseeva, 1990; V. Garutt, pers. comm.). This type indicates on noticeable presence of trees (Sect. 3.15.1.4.). In East Siberia it appeared only during Riss-Wurm and Preboreal warmings (Foronova & Zudin, 1986).

Mammoths, woolly rhinos, horses and yaks that inhabited taiga woodlands of the South of the Ussuri region were not accompanied by saiga, polar fox and musk-ox. They lived here amidst the complete set of extant dwellers of taiga and Far Eastern temperate forests: mooses, roes, red deer, muskdeer, sika deer (numerous!), ghorals, wild boars, common and ground squirrels, rat (probably *Rates norvegicus*), sable and yellow-throated marten (*Martes zibellina*, *M. flavigula*), eastern tiger cat (*Felis bengalensis*), tiger, dhole, raccoon dog, etc.) (Ovodov, 1977a). In the Late Wurm of Japan (it was linked then with mainland), mammoths, horses and hemiones lived in company with similar fauna, added with giant deer (*Sinomegaceros yabei*), forest rhino (*Dicerorhinus sp.*) and strait-tusked elephant (*Palaeoloxodon namadicus* = *P. tokunagai* = *P. naumanni*) (Kamei, 1981).

### 3.14.3. Whether all this could be called 'tundra-steppe' ?

Certainly **not**. According to such ardent proponent of 'tundra-steppe crash extinctions concept' as A. Sher (1982), tundra-steppes vegetation was: 1) crioxerotic; 2) complex (composed mainly of tundra, steppe and north boreal intrazonal plants); 3) treeless; 4) highly mosaic (patchy); 5) highly productive to large herbivores; 6) growing on permafrost soils. It is evident that only 4th and 5th of these conditions are applicable to every type of mammoth ecosystem.

The most wide spread group of mammoths ecosystems are parklands with stands of boreal trees and rich herbaceous cover (Sect. 3.14.1.2.). Climatists mostly also call them 'tundra-steppes' or 'mammoth-steppes' (e.g., Guthrie, 1990a, 1990b) in spite of the significant (or even prevalent) role of mesic (and/or humid) meadows and presence of boreal (or even temperate) trees. Such definitions are even more misleading in cases of parklands/meadows associations during the major warmings (Sect. 3.14.4.2; 3.17.2; 3.17.3), when both storeys included much more species, adapted to temperate climate. The best name for these associations appears to be 'criophitic savannas' (Verkhovskaya, 1988), adopted by some other authors (Putshkov, 1989a, etc.; Baryshnikov & Markova, 1990). However even such definition could not be used for well wooded mammoths inhabited areas (Sect. 3.14.1.3.).

In a word the 'tundra-steppe' or 'mammoth-steppe' in a sense of the **completely or nearly** treeless formations over permafrost grounds, where only crioxerophilous or largely euryoecic organisms could survive, was not the unique mammoths' environment even at the most crioarid epoch of the Pleistocene. Contrary to extreme assertions (Velichko, 1973; Tomirdiaro, 1977; Guthrie, 1990b, etc.) it did not occupy all extratropical Eurasia. This concept of the homogenous 'periglacial tundra-steppe hyperzonal' met with insurmountable difficulties. Considerable climatic gradients between Megaberingia on one side and Europe and Amour Basin on the other side, as well as differences inside these regions, have never vanished (Nazarov, 1984; Verkhovskaya, 1989, etc.).

### 3.14.4. Mammoth ecosystems at pre-Wurm, Early Wurm and Middle Wurm times

#### 3.14.4.1. Europe

Pre-Wurm (about 113-73 kyr BP) is included in Riss-Wurm by 'long Interglacials' time-scales (e.g., Kurten, 1968; Stuart, 1974; Vereshchagin, 1988; Putshkov, 1989a, b, 1991, 1993b, etc.; etc.) and



in Wurm by 'short interglacial' ones (e.g., Stuart, 1991, 1993, etc.). It was on the average cooler than now but considerably warmer and moister than Early and Middle Wurm. Even during its' cold stages there were probably no major glaciation (Stuart, 1991) and surely no 'extremely cold and dry tundra-steppes' in Europe. Temperate broadleaf forests consisted of oaks, hornbeams, hazel, lime, ash, elm reached Central Europe during interstadials. Boreal woodlands dominated by pine, spruce and birch were spread further North. Woolly mammoths and rhinos did not retreat to tundra-steppes that if they existed as zonal formations, were confined to some parts of East Siberia. The giants inhabited all Europe northwards of Pyrenees, Alps and Dinarids, including Crimea, southern France and England. During Middle and Early Wurm (about 73-24 kyr BP) in Europe both stadials and interstadials were much colder than those of Pre-Wurm. However climate has never become so severe as during the Late Wurm Pleniglacial (Musil, 1985; Velichko, 1973; Soffer, 1985; Stuart, 1991). Mammoths and woolly rhinoceroses occupied roughly the same area as in previous phase. Climatic conditions and faunal contexts in different countries and during different epochs varied from mild to severe. Nowhere climate became as crioarid as in the present-day Mongolia and inner parts of Eastern Siberia. Consequently, mammoths and their satellites lived in a wide variety of mosaic landscapes where more or less important woodland spaces were alternated with open terrains. Mammoth woodlands, parklands and forest-steppes were of boreal or temperate types. Their herbaceous component consisted of meadow, steppe and/or tundra plants (Stuart, 1974, 1991; Musil, 1985). The oak-groves and characteristic oak-insects (beetle *Acalles*) were present in Byelorussia at some Early Wurm Interstadial (Nazarov, 1984). In the Middle Wurm Interstadial (Bryansky or Vitachevsky stage) not only Northern Ukraine but also the central part of the Russian Plain was covered with temperate climate mixed woodlands and parklands (forest-steppes). Lime-trees, hornbeams and oaks grew there (in Ukraine were present also elms, maples, hazels, etc.), not to speak about trees more resistant to dry and/or cold conditions (Grichuk — cit. by Soffer, 1985; Sirenko & Turlo, 1986, etc.). Woods grew on interfluves at least during some interstadials (Nazarov, 1984; Sirenko & Turlo, 1986; Verkhovskaya, 1988). But even if they were grown only in river valleys, while interfluves and plateaus were covered with meadow-steppe vegetation (Soffer, 1985), it is clear that conditions in the Middle Wurm Ukraine were much milder than in modern Central Yakutia. There are no oaks, lindens, hornbeams, hazels and elms in modern Aldan or Middle Lena valley (Karavayev & Skryabin, 1971).

Correspondingly not only arctic and/or steppe mammals but also ones of woodlands and mesic meadows were well represented in the mammoths' sites (Kurten, 1968; Stuart, 1974, 1991; Musil, 1985). Some of these woodland or parkland dwellers (beaver, glutton, lynx, moose, roe, red deer, brown bear) may be imagined in zonal tundra-steppes with small patches of taiga. However the other, such as dormouse, giant and fallow deer, aurochs, wild boar, wild cat, porcupine, etc., are completely incompatible with crioarid conditions. It is clear that mammoths, woolly rhinos, reindeer, bison and horses, being accompanied by such fauna, grazed on meadow or steppe plots and not on 'tundra-steppes' *sensu* Sher (1982) (see Sect. 3.14.3.).

The presence of saiga has not been ascertained for the Pre-Wurm of Europe. In Early and Middle Wurm its common occurrence with mammoths is far less frequent than for the Late Wurm. Saiga was constantly present in Southern Ukraine and Czechoslovakia. It had penetrated at earlier episodes (Wurm 1 stadial and Wurm 1/2 interstadial) to Germany and Poland and later — even to France near Pyrenees (Wurm 2 stadial) (Musil, 1985). Such cases certainly prove the thinness of winter snow layer, but not the existence of overigorous tundra-steppe conditions. Thus in Czechoslovakia and southern Germany aurochs, giant deer, moose, roe, beaver, even wild boar and wild cat, coexisted with saiga and mammoths with retinue (*ibid.*: 9). In Odessa region of Ukraine woolly rhino coexisted not only with saiga and reindeer, but with porcupine and badger as well (Korniets, 1962); it indicates quite warm forest-steppe and not tundra-steppe conditions. It is worth noting that saiga lived up to XVIII century in East European steppes westwards to Moldavia (Pidoplichko, 1951; Baryshnikov & Krakhmalnaya, 1994).

In France mammoths and woolly rhinos coexisted even with rabbits, and (at stadial Wurm 1) also with straight-tusked elephants, forest rhino, hippopotamus and fallow deer. The cooccurrence of mammoths and/or woolly rhinos with wild boar and cat, forest rhino and porcupine with saiga being absent is registered also for Italy, Dalmatia and Hungary (Musil, 1985).

One can add that mammoths of Ukraine were of 'boreal' type (Sect. 3.15.1.4.). These of Crimea were so thick-enameled that half of specimens were originally determined by V. Gromov as *M. trogontherii* (Vereshchagin & Baryshnikov, 1980b).

### 3.14.4.2. Asia

Mammoths were constantly present over most of Siberia and Kazakhstan, inhabited Caucasus (Vereshchagin & Baryshnikov, 1984, 1985; Vangenheim, 1977; Kozhamkulova & Kostenko, 1984; Vasiliev, 1995) and, from 70 to 33 kyr BP, even

Syria and Israel (Tchernov, 1984). At some phases of Middle Wurm they deeply penetrated to East China up to Yangtze river about 30th latitude (Ovodov, 1977a). The greater part of Fore, Middle and Central Asia seems never being populated by woolly mammoths.

Early Wurm Glacial that is called in Siberia Zyryansky Glaciation, was not as arid as the Late Wurm one. Correspondingly the common occurrence of saiga with mammoth is far less usual than later. For instance saiga was absent in boggy tundra with scattered birches in river valleys that dominated the basin of Lower Irtysh during Zyryansky Glaciation. Mammoth inhabited this landscape in company with woolly rhino, bison, musk-ox, horse (that had wide hooves, adapted for the locomotion over swampy soil) and moose (Vangenheim, 1977: 33-34). It shows once more that saiga is a poor model for the estimation of the ecological plasticity of extinct large herbivores. Saiga was rare also during Zyryansky glacial time in East Siberia (*ibid.*: 43, 93, 94).

The climatic oscillations of Middle Wurm (53-24 kyr BP), being rather weak in West Europe (Stuart, 1991), were very accentuated in Siberia. This period is called here Karginy Interglacial because it was warmer than now in East Siberia during its two optimums. There were, naturally, no tundra-steppes during these episodes: the treeline shifted northwards 100-150 km more **than at present** (Karavayev & Skryabin, 1971; Lozhkin, 1976, etc.). Mammoths and their satellites lived mostly in criophytic savannas with boreal trees and luxuriant mesic meadows vegetation; these animals also exploited regions dominated by swampy larch parklands, shrub-tundras and forest-tundras (Ukrainitseva, 1985; Lozhkin, 1989). The documented presence of saiga during Kargin time in Siberia and Alaska (Kurten & Anderson, 1980; Baryshnikov & Krakhmalnaya, 1994; Sher, pers. comm.) probably corresponds not to optimums but to cold and dry episodes (Kozhevnikov, pers. comm.). Besides this extinct large herbivores probably made pasture conditions more favorable for saiga (Baryshnikov & Krakhmalnaya, 1994).

### **3.14.5. Whether mammoths penetrated in mountains ?**

Certainly yes. Many upland regions in West and Central Europe, East Siberia, Southern Crimea, Caucasus and Levant were occupied by mammoths for more or less lengthy periods. In Austria these animals certainly used alpine valleys (Fladener, 1995, pers. comm.). In Kazakhstan they inhabited the North Thian Shan and Kendyktas mountains (Kozhamkulova, 1981). Rare occurrence of mammoth bones in cave Paleolithic sites (Caucasus, etc.) is probably the result of the extra-cave utilization of heavy carcasses.

### **3.14.6. Conclusion on mammoth' ecosystems**

The outlined evidence proves that mammoths were less dependent from climatic gradients and types of landscape than the majority of living North Eurasian mammals. Such euryoecic species could not become extinct due to the replacement of tundra-steppe or criophytic savannas by modern North Eurasian ecosystems. This is as inconceivable as to produce the extinction of African elephants by the replacement of tropical savannas and grasslands by various types of bushlands and forests. In this case many ungulates would be lost. But not elephants that live (or lived in historical times) in all kinds of tropical and subtropical forests (including the swampy ones), constituted by Paleotropical, Mediterranean and Capean plant-communities, and in all African mountains. However analogies between woolly mammoths and modern elephants could be invalidated, if mammoths were stenophagous creatures. Is such supposition correct ?

### 3.15. Were the mammoths killed by their food ?

#### 3.15.1. What was the food of woolly mammoths and rhinos ?

##### 3.15.1.1. Food specialists or food generalists ?

This is the most crucial question. If these giants were food generalists, they could switch to a wide range of fodders. Consequently, the climatic versions of their extinction would lose much of their credit. If the giants were obligatory food specialists, these versions would gain the credibility.

All modern pachyderms, with partial exceptions of white rhinos, are trophic generalists. They consume different plants from various habitats, though are also able to rely on monotonous diet, if the environment does not propose them too much choice. Both extant elephants, in spite of the considerable difference of their teeth (more browsing type of African species), can subsist and proliferate on a diet from completely browsing to almost completely grazing type, though mixed diet is preferable (Laws, 1970; Poniran, 1974; Nasimovich, 1975; Bannikov & Flint, 1977; Olivier, 1978; Kingdon, 1979; Wagner & Schneiderowa, 1984; Wagner, 1987; Owen-Smith, 1987, 1989, etc.). Hence it would be natural to expect that woolly mammoths and rhinos, whose milieu was so changeable in time and space (Sect. 3.14.), were trophic generalists too.

But clear cut grazing adaptations of these giants as well as the prevalence of grass and sedges in the digestive tracts of their frozen corpses, found in permafrost 'traps', have led to conclusion that these animals were 'strict grazers', the 'arid grasses' eaters that never '...made significant use of woody plants, especially the birch, alder, spruce, larch and pine...'. (Guthrie, 1990b: 50, 51). According to this point of view the 'arid grasses' were the staple of mammoth diet, though small admixture of woody and/or herbaceous dicots was necessary for animals in order to prevent trophic deficiencies.

Which of these views is more consistent with the bulk of the evidence ?

##### 3.15.1.2. Could the mammoths rely on not so 'arid grasses' ?

The study of the content of the digestive tract of frozen carcasses of Wurm interstadials Siberian mammoths shows that they ate numerous plant species. Although grasses and sedges are often (not always!) predominant, they are not 'arid' at all. These and other plants (mosses, brackens, dicots) are of humid and mesic habitats (Yuribey ..., 1982; Ukraintseva, 1985, 1991, 1993, etc.). It seems likely that in Arctic and Subarctic regions during the cold stages the situation was similar. It is meso- and hygrophytic vegetation that has the high productivity here (Yurtsev, 1976, etc.; Kozhevnikov, 1986, etc.; Matveyeva & Chernov, 1992; Tomirdiario, 1994, 1996, etc.). Considering that such vegetation even at cold stages retained strong positions throughout Arctic and Subarctic landscapes, it is reasonable to believe that mesic and hygrophytic plants remained then the staple of diet of mammoths and their satellites (Yurtsev, 1976, etc.; Kozhevnikov, 1977, 1986, etc.).

##### 3.15.1.3. And what about the 'arid' ones ?

The azonal patches of northern crioarid steppe-like associations (steppoids) are often considered as the relicts of notorious Pleistocene tundra-steppes (e.g., Tomirdiario, 1977; Vartanyan & al., 1993, etc.). They indeed occupied vast areas during stadials (ibid.; Verkhovskaya, 1988, etc.). However due to severe abiotic conditions, they consist of low, scattered and slowly growing plants. Their productivity, at least in Chukotka, is so negligible that even hares could not feed on them (Kozhevnikov, 1977: 445). That is why some researchers (ibid.; 1986; Verkhovskaya, 1988, etc.) do not believe that 'crioarid arctic steppes' did play any significant role in the feeding of mammoths and other large herbivores. So they defy the very important point of mammoths extinction through 'tundra-steppe crash' conception.

Although this view has strong support in the afore-mentioned evidence (Sect. 3.15.1.2.), it is probably a bit overigorous. In lower latitudes (Southern Siberia, most of Europe) spaces of 'periglacial' xerophilous steppe-like vegetation were most probably more similar to veritable steppes than to steppoids due to longer growth season than in northern latitudes. Besides this, pasture activities of large herbivores had probably somewhat raise the productivity even of the steppoids of high latitudes (Sect. 10.4.).

Probably both stadial and interstadial woolly mammoths that lived in veritable steppes were indeed predominantly 'arid grass' eaters. However mammoths were rare in dry Transbaikalian and Mongolian steppes, as opposed to woolly rhinos; mammoths evidently preferred less arid regions (Vangenheim, 1977, etc.).

### 3.15.1.4. What about woody plants ?

Although being predominant grazers on grasses and sedges, mammoths do eat variable quantity of different mosses, brackens, forbs and woody species (Ukrainitseva, 1985, 1991, 1993; Vereshchagin & Baryshnikov, 1985; Verkhovskaya, 1989; Surmely, 1993; Lister & Bahn, 1994, etc.). Feeding on larch, birch, willow, chosenia, alder and currant is undeniably attested by their macrorests. This on pine, spruce and poplar is possible, though not proven, for only pollen grains have been found. The validity of old indications of rests of spruce and pine branches in mammoths digestive tract (Indigirka mammoth) is recognized by some (Korniets, 1962; Soffer, 1985) but rejected by other modern specialists. Part of the macrorests of birches, alder and willows belongs to arboreal, other to dwarf and bush forms, or the differentiation between the forms is impossible (Ukrainitseva, 1985, 1993, etc.).

It should be stressed that we do not know the winter food of mammoths, when browsing could play far more important role (Vereshchagin & Baryshnikov, 1985, etc.). Although R.D. Guthrie (1990b: 50) states confidently that mammoths 'did not rely on browse for the dry winter season' there are no proofs for such a generalization. The woolly mammoths carcasses from permafrost zone belong to animals, perished during warm season (Ukrainitseva, 1985, 1993, etc.). Likewise the dung of Colombian mammoths (*M. jeffersoni*) from Bechan cave with only 5% of woody plants (Mead & al., 1986) reflects mostly warm season feeding. What is more it concerns the southern region (Utah) with thin and not long lasted snow-cover. In other words there are no direct evidence on winter feeding of mammoths that lived in regions with significant tree stands, such as the Ussuri region (Sect. 3.14.1.3; 3.14.2). Fortunately this gap partially makes up with the reliable indirect evidence.

Firstly, the data on modern large herbivores show that there is no grazing specialization that prevents the possibility of the shift to browsing (Sect. 10.2.). It is the opposite thing (that is to become mixt browser/grazer in spite of the manifest morphological adaptations for browsing), that is more difficult, though not impossible, as show, e.g., red deer and African elephants. If the latter, in spite to their browsing morphology, prefer the mixed diet, why hungry mammoths in winter should behave otherwise in surroundings with arboreal cover ?

This suggestion is confirmed by the pattern of the variability of woolly mammoths dentition in time and space. It is rather significant that teeth of so-called 'boreal' mammoths had lower crowns, thicker enamel, wider lamellae and narrower cement interspaces than teeth of 'periglacial' mammoths (Foronova & Zudin, 1986). 'Boreal' mammoths are considered as mixed grazers/browsers (ibid.; Vereshchagin & Baryshnikov, 1985; Soffer, 1985, etc.) or browsers/grazers (Pidoplichko, 1976) that ate milder foods with greater participation of forbs and woody plants. The 'periglacial' ones were more specialized to grazing on coarse grasses and sedges. During stadials the former lived in West Europe as well as in Ukraine, the latter — in most of East Europe and Siberia (V. Garutt — pers. comm.; L. Alekseeva, 1990; etc.). During interstadials the 'boreal' type has been spread over all Europe or even partially to Asia. During Riss-Wurm and the very end of Wurm/Early Holocene even East Siberian mammoths have acquired 'boreal' mixed grazing/browsing teeth (Foronova & Zudin, 1986). These changes and differences are in tight connection with the role of woody component and softer herbaceous vegetation in ecosystems. Extremely important is the fact of the evolutionary reversibility of all above-mentioned 'periglacial' dental adaptations to more plesiomorphic 'boreal' state, with the return of milder climatic conditions (ibid.).

The same phenomenon has been observed with the structure of skulls of woolly rhinos that changed from 'strictly grazing' to 'grazing/browsing' type in regions and/or epochs with more or less well developed woody vegetation (N.E. Garutt,

pers. comm.). The rests of woody plants (*Salix*, *Betula*, *Alnus*, *Picea*, *Abies*, *Larix*, *Ephedra*) that are found between teeth of some skulls of these beasts (Korniets, 1962; Vereshchagin, 1979; Vereshchagin & Baryshnikov, 1980a; Verkhovskaya, 1989) also prove that they could switch to a mixed feeding regime. It means that white rhino is not so good model of ecological adaptability of woolly rhino.

Of course the data on the feeding of the two extinct pachyderms are still rather incomplete. It is certain that the list of their food items would be longer than it is known at present, being based on restricted number of individuals.

It is acceptable, however, that both giants recurred to predominant feeding on large trees relatively rare, mostly in too snowy or ice-crusting weather, when even their raking or shoveling adaptations became insufficient, and/or when they thinned out their winter grazing resources (Sect. 3.12.4; 3.12.7.).

### 3.15.2. Were the mammoths knocked down by alkaloids ?

According to some opinions (Guthrie, 1984, 1990a,b; Graham & Lundelius, 1984) it was nearly so. It is believed that mammoths, together with other monogastric herbivores were obliged to use extremely variable set of plants. In such a manner they prevented the intoxication with plant defensive substances. Such diet could not be found in monotonous plant communities of modern taiga and tundra, consisted of plants with well-developed chemical protection (ibid.). These erroneous views concern many animals (Sect. 5.5.).

### 3.15.3. Two trophic degeneration theories

V. V. Ukraintseva, an eminent specialist on mammoths feeding, insists (1985, 1991, 1993: 228-237) that physiology of mammoths and their satellites was ill-adapted to the North-Eurasian vegetation of warm epochs and well adapted to that of the cold ones. Cold stage grass, sedges, herbs and bushes of steppes, dry and mesic meadows, were rich in calcium, potassium, phosphorus, other microelements. Among them silicium was extremely important for the growth of winter fur (Ukraintseva, 1993: 232). Microelements have been preserved in plants in winter due to short autumn and early beginning of frosts. Hence herbivores had high quality 'hay' for the all long winter season. Now this phenomenon illustrates domestic horses, hibernating in steppes. When autumn is short and frosts early, grass is of high quality and horses are fat during all the winter. When autumn is long and warm, grass loses its nutritional value and overwintered horses are meager. It explains why cold stage populations of mammoths and their satellites were large and prospering (ibid.: 234-235).

Then she states that unfortunately for herbivores such conditions lasted only as long as the climate was severe enough for the accumulation of 'cold' loess. None of the 'cold' loess stages lasted more than 50 kyr (stadials of Gunz, Mindel and Riss — 25-30 kyr, cold episodes of Kargin Interglacial — 2-4,5 kyr, Late Wurm Pleniglacial — about 8 kyr). Their total duration is 500 kyr whereas warm phases without loess accumulation (Interglacials plus interstadials) lasted at least twice more (ibid.: 233; Velichko, 1973, etc.). Mammoths and their satellites were constrained to feed on grasses, sedges and mosses of swamps of tundra and taiga zones. This vegetation is poorer in nutrients and, notably, in microelements than that of dry and mesic steppes and meadows. Warm stages populations of gregarious herbivores were becoming small and isolated by spaces of swamps and forests. Because of an insufficient food, natality of animals was low, winter mortality — high. Populations died out one after another. During previous warmings the process was interrupted by the return of colds. It was not the case of the Holocene with too sudden climatic changes at its beginning (see, however, Sect. 6.3.).

However it seems improbable that species could exist under unfavorable conditions for thousand years of loess 'non-accumulation' periods resting still 'non-adapted' for them. It should inevitably either adapt or die out completely. Riss-Wurm Optimum was warmer than Holocene (Sect. 3.17.; 6.4.; 7.2.), as author states herself (Ukrainitseva, 1993: 213-214). Hence it seems logical that mammoths should degenerate and die out due to warm autumns and other mild climate effects at that period and not in the Holocene. The frozen carcasses of mammoths, horse and bison that perished due to falling to permafrost-melting traps during warm stages are fat (only this of calf 'Dima' is meager) (Yuribeysky ..., 1982: 18, etc.). This circumstance also does not support the idea of the unsuitability of the warm stage Siberian vegetation to mammoths and their satellites.

V. I. Bgatov, P. A. Lazarev & M. A. Speshilova (1989) called attention to a very important aspect of mineral feeding of Pleistocene ungulates. All extant herbivorous mammals usually get too much potassium but not enough sodium with the vegetation. In many regions the vegetation contains too little or too much of calcium, phosphorus, magnesium, iron, silicon, or other microelements. Animals (including elephants) are obliged to recur to periodical lithophagy (eating of rocks and soils rich in the minerals under deficiency) for the sake of normalization of their metabolism. Ungulates pass sometimes many dozens of kilometers from their usual pastures with the aim to eat such rocks or soils. In northern countries the periods of the most considerable lithophagy are spring and autumn (before and during the reproduction season). Animals of both sexes and of all ages (including small calves) have need of such feeding.

Mammoths and woolly rhinos were 'fervent lithophagans' (ibid.: 16-24). This is proven by the analyses of food-masses from the digestive tracts of frozen carcasses ('Shandrin' and 'Kirguillyakh' mammoths, 'Churapchan' woolly rhino) as well as these of the faeces of Columbian mammoths (*M. jeffersoni*). Undoubtedly they procured themselves with rocks or soils in the same way as do modern elephants: by means of tusks and/or legs. The obtuse mammoth tusks and broad-footed pachyderms' legs were inappropriate tools for crumbling of frozen soils. As a result, pachyderms prospered in tundras, tundra-steppes and forest-tundras only until sufficiently large patches of non-frozen soils have been existed. They immediately died out when these patches were caught with the spreading permafrost. Their retreat to steppes was impossible due to dense taiga forests with small quantity of grass and thick snow cover. Ungulates with hard hooves could crumble the frozen soils and balance with it their metabolism. Therefore horses, bisons, musk-oxen, cervids survived. Reindeer with the hardest hooves became the fittest (ibid.: 28-31).

Thus according to the second degeneration model mammoths and rhinos were killed by permafrost — the consequence of cooling. The model does not explain what has been occurred with mammoths and rhinos that did exist at the territories of modern steppe and forest-steppe zones as well as in other southern regions (Sect. 3.14; 3.17.). They need not to pass through taiga and deep snows (not to speak that mammoths, perishing in snows and forests is rather bogie than reality — ibid.; Sect. 3.12.). If permafrost was such a pernicious thing for mammoths, the best times for their extinctions would be the Late Riss or the Late Wurm Pleniglacials. Then not only loess's accumulation but also permafrost regions were the most wide spread (Velichko, 1973; Sirenko & Turlo, 1986; Tzuj & Sje, 1982, etc.). Equally their extinctions should be decelerated by Wurm Anaglacial and early Holocene warmings and this was not the case (Sect. 3.16.).

The most interesting thing reveals out of the contrasting of the most important positive evidence used in the two contending trophic degeneration doctrines. Early frost and short autumn conserve nutrients in vegetation for winter feeding of herbivores (Ukrainitseva, 1993: 233). It means that the necessity of lithophagy became reduced just at the stadials, when the possibilities for lithophagy were restricted, due to the expansion of permafrost. Milder climate 'spoils' the quality of

vegetation as source of mineral nutrients (Ukrainitseva, 1993), but drastically enhances the possibilities to lithophagy (Bgatov & al., 1989). It means that neither coolings nor warmings could condemn mammoths and their satellites to trophic degeneration.

Of course the reality always was more complicated. The necessity of lithophagy during 'cold loess' stages has been even more reduced due to loess particles that covered vegetation. These particles were carried by winds from desert spaces of dried shelves, periglacial and some other regions (Sect. 3.2.; 3.14.1.1.). Pachyderms could get some quantity of the precious 'mineral dust' by supervising the 'mineral procuring works' of reindeer or other hard-hoofed ungulates and chasing them away from the freshly beaten plots. In addition existed also possibility to seek mineral licking places in the unfrozen soils of river valleys.

During warm stages pachyderms could take certain part of their mineral feeding by gnawing dead bones, as do now cervids. Neither during cold nor during warm stages both feeding and lithophagic conditions were uniform over the immense range of mammoths and their satellites, as they are not uniform now. It is worthy of notice that in different regions animals are obliged to recur to lithophagy not at the same degree. There are even cases when herbivores '... get ... with the vegetable diet ... quantities of calcium, phosphorus, magnesium and other microelements ...' that are '... sufficient for normal physiological development' (Bgatov & al., 1989: 6). Content of microelements in vegetation of different habitats varies greatly and herbivores often cover the deficiency instinctively finding the best pastures (McNaughton, 1989). If Holocene steppe horses (both domestic free-keeping and wild) manage to overwinter well in years with short autumn and satisfactory in these with long one (Ukrainitseva, 1993: 233), why was it forbidden for mammoths and rhinos of steppe and forest-steppe to survive at the same conditions ?

There are absolutely no reasons why mammoths and rhinos could not choose the proper strategy according to their morpho-physiological and behavioral possibilities and to local peculiarities of the environments.

### 3.16. Timing and dynamics of the mammoths extinctions

If mammoths were indeed the stenoecic creatures, completely dependent on periglacial landscapes, their extinction (or, at least, decline) should everywhere be rigorously coincident with the degradation of these formations. In other words their area at the time of Late Wurm Pleniglacial should be larger than during Early and Middle Wurm. The extinctions should not begin till approximately 13,5 kyr BP — the onset of Boelling, the first considerable Anaglacial warming. If increase of warmth and humidity with corresponding changes of vegetation were pernicious to woolly giants, their size should increase with coolings and decrease with warmings.

The evidence is mostly inconsistent with both these predictions. It was neither always nor everywhere that changes of the environment to more cold and dry conditions were favorable to mammoths. Both Siberian (Garutt, 1965) and Beringean (Guthrie, 1990a) mammoths became larger during interstadials and smaller during stadials, when the dry tundra-steppes expanded. The mammoths of relatively mild boreal climate that lived in England during Boelling warming (about 13,5-12,5 kyr BP) were, on the average, larger than Late Glacial and Anaglacial mammoths of Russian Plain and Northern Siberia that lived under more severe climatic conditions (Coop & Lister, 1987; Mashchenko, 1991; Lister & Bahn, 1994). Also the onset of the staggered process of the extinction of Eurasian mammoths has well preceded the degradation, and, partially, even the maximal expansion of periglacial landscapes. It was not the Late, but the Middle Wurm when mammoths range was the maximal in East Europe, West and East Asia.

It is a matter of common knowledge that in North and West Palearctic the Middle Wurm cooling (about 38-35 kyr BP) was not so intense as stadials of notorious Late Wurm Pleniglacial (24-14 kyr BP). The data on former permafrost traces in fossil soils show that the same is true for China (Tzuj & Sje, 1982). Nonetheless mammoths during the former cooling advanced more to the south (up to Sichuan) than during the latter (*ibid.*). The beasts expired here about 23-20 kyr BP in the very midst of the Late Wurm cooling in absence of any hint of climatic amelioration (Liu & Li, 1984).

Mammoths penetrated to Palestine at Early Wurm cooling near 70 and died out here near 33 kyr BP (Tchernov, 1984). So they were absent here during the coldest part of Wurm. The same is true for Crimea and Caucasus. In both regions mammoths and woolly rhinos were present in Early and Middle Wurm sites but absent in the Late Wurm ones (Bibikova & Belan, 1989; Vereshchagin & Baryshnikov, 1985).

Likewise decline of some European and Siberian mammoths populations has **preceded** the onset of the Anaglacial. Numbers of mammoths and rhinos dwindled in many regions contrary to the lasting increase or, at least, retention of the climatic crioaridity. This is the case of so different regions as Wurtemberg (Kurten, 1968), Western Ukraine (Bogutsky & al., 1974; Ivanova, 1977; Chernysh, 1977; Tatarinov, 1969, 1993), Pechora basin (Bader, 1974) and Southern Siberia (Endrikhinsky, 1982, etc.). Rests of both giants younger than 19-20 kyr BP are unknown from Byelorussia (Kalinovsky, 1991). The same is true for steppe regions northwards of Asov and Black seas (Stanko, 1989) and for Upper Yenisey basin (Ermolova, 1977). In North Angara region the two pachyderms were frequent during relatively less severe Early Wurm (Zyryan Glacial) and alternatively warm/moderately cold Middle Wurm (Kargin Interglacial). Then both became rare during the most crioarid Late Wurm (Sartan Glacial — 22-14 kyr BP) (Vassilyevsky & al., 1988). The same has been shown on the multilayers Biryussa site in the Middle Yenisey area. Mammoths and rhinos have been disappeared here well before the climatic amelioration — the continuing presence of Asian wild ass (= hemione) and saiga 'evidence sharply continental and arid climate' (Kuzmina & Sinitsyna, 1995: 683).

Anaglacial time (13,5-10 kyr BP) is characterized by a rapid alternation of considerable warmings (Boelling and Allerød) and coolings (Middle and Younger Dryases) that preceded the early Holocene (Preboreal) warming. [Older Dryas is usually considered as the very end of Pleniglacial]. From climatic standpoint it would be logical, if the warm phases were pernicious time of decline and extinctions and the cold ones — these of temporary recoveries of mammoths populations. Again there is no such a clear interrelationship.

The Boelling warming (about 13,5-12,5 kyr BP) does not chased mammoths from England. However it was strong enough for the installation in this country of quite humid boreal climate. The latter is testified by the insects (dung-beetle *Aphodius prodromus* and fly *Phormia terraenovae*), found with skeletons of mammoths at Condover (Coop & Lister, 1987). These mammoths were even larger than their contemporaries from Russian Plain and most of Siberia with their drier and colder climate. On the other hand during Middle and Younger Dryas stadials mammoths are unknown from Southern France, England, Poland and Hungary, notwithstanding the domination there of cold and dry climate and 'periglacial' flora and fauna (saiga, reindeer, lemmings, pika, etc.) (Stuart, 1974, 1991; Straus, 1983; Musil, 1985). [They may have existed there at low density]. In other parts of Europe mammoths also were rare after 12,5 kyr BP (*ibid.*; Coop & Lister, 1987; Alekseeva & Tikhomirov, 1989; Surmely, 1993). [They may have exist there at low density]. How might it be that still existing depressive populations of European mammoths have not recovered in Dryas stadials despite the return of periglacial conditions? Why they were not restored due to the arrival of pachyderms from Siberia? The first question is usually neglected by the 'irreconcilable' climatists. As for the second one two kinds of answers have been proposed.

According to the first of them European populations as early as 13 kyr BP were 'trapped' and cut off from Asian ones by thick forest belt that stretched from Black to Baltic sea (Stuart, 1991, 1993; Lister & Bahn, 1994). Then these 'Russian' forests progressed westwards and 'Spanish' forests — northwards up to the complete destruction of mammoths and 'mammoths-steppe'. It hardly needs saying



that steppe and forest steppe regions persisted at the south and middle part of Ukraine (Sirenko & Turlo, 1986, etc.) during Anaglacial as well as the corresponding fauna (Bibikova & Belan, 1989; Musil, 1985; Stanko, 1989). Likewise it is clear that forests dwindled drastically during Dryas coolings. Due to these reasons the eastern way for repopulating of Europe by mammoths was opened, even if the proofs of the ability of mammoths to live in woodlands (Sect. 3.14.1.3.; 3.14.2.; 10.3.) were not considered.

According to another explanation few hundred years lasting Dryas coolings were too short for the arrival of Siberian mammoths to Europe (Reed, 1970). This assertion contradicts the amazingly rapid peopling of suitable habitats by mobile animals (Vangenheim, 1977).

Evidently population density of Siberian mammoths during Anaglacial was below the carrying capacity of the environment. In the case of such underpopulation there are no 'superfluous' individuals and thus — no stimuli to the expansion of the species area. If the underpopulation is constant, the species area gradually contracts. Whatever reason caused the underpopulation of Siberia by mammoths 14-9 kyr BP, it was not the disappearance of periglacial landscapes: contrary to former ideas tundra-steppe has been outlived here by mammoths. It demonstrates the frozen corps of mammoth that was found on Gydansky Peninsula near Yuribey river. The beast lived during Preboreal warming about 9,6 kyr BP in forest tundra over abundantly moist soils (Yuribeysky ..., 1982). This mammoth was very well fed (ibid.). It does not conform with the idea of the unsuitability of warm epochs Siberian vegetation for mammoths feeding (Sect. 3.15.3; 5.5.).

Only demise of Arctic mammoths (Sect. 3.14.1.1.) perfectly corresponds to consequences of the warming. They perished or migrated together with other animals due to the grandiose melting of oceanic ice-armor (Tomirdiario, 1996, etc.). Beasts, isolated on Arctic islands, died out probably due to hunger. Dwarfed mammoths of Wrangel' Island survived up to the Middle Holocene — till 3,7 kyr BP (Vartanyan & al., 1993).

Likewise the definitive disappearance of periglacial landscapes was considerably outlived by Siberian bisons and musk-oxen (Vereshchagin & Baryshnikov, 1985) and, possibly, by horses (Lazarev, 1980; Bgatov & al., 1988). It is generally taken that the last mainland Eurasian mammoths and musk-oxen were killed by the further warming. Due to the latter tundras and forest-tundras became too marsh-riden and the depth of the snow-cover has been increased (Vereshchagin & Baryshnikov, 1985). As for the bison it is the cooling ('Little Ice Age') after the warming of Holocene Optimum that is accused. Due to it tundras replaced taiga forest of the Extreme North-East of Siberia — the last refuge of Asian bisons (Fleurov, 1977).

Let it be so. But why the animals so obstinately adhered themselves to the inhospitable regions with capricious weather? What killed their populations that lived in inner parts of the East Siberia with constantly continental anticyclone climate? Dense forests? This is not the case of Yakutian parklands (Sect. 3.4.). Dry regions with thin snow cover that are well-fit for musk-oxen, are small and not numerous in modern tundras. However they occupy vast regions in Transbaikalia, some cool Mongolian highlands and extensive Baikalo-Patom upland. The latter has been populated by musk-oxen as well as by mammoths, rhinos, horses and bisons during Riss-Wurm optimum time (Verkhovskaya, 1988).

For woolly rhinos the disappearance of the tundra-steppe was even less menacing than for the other herbivores of the 'mammoth-complex'. It originated in dry steppes of Central Asia at Eopleistocene time and completely retained his positions there later, after its expansion to mammoth ecosystems. Moreover its density in Wurm was higher in dry Mongolian and Transbaikalian steppes, almost avoided by mammoths, than in periglacial formations in the proper sense of the word (Vangenheim, 1977). Woolly rhinos extinction is even less explicable from the climatistic point of view, because there was no radical transformation of Mongolian and Transbaikalian landscapes during Wurm/Holocene transition (Endrikhinsky, 1982; Kalmykov, 1987). There are vast spaces of steppes and forest-steppes with continental climatic conditions that nourished innumerable domestic and wild ungulates in historical times (or feed now) in Kazakhstan, North-West China, partially — North-East China, Mongolia and South Siberia (Przhewalsky, 1875). [Of course steppes or any other ecosystems with and without rhinoceroses should differ from each other but the reasons were the rhinos themselves (Putshkov, 1989a, b, 1993b)]. Numerous mountains with gentle slopes presents wonderful winter stations for domestic and wild ungulates even during abnormally snowy winters. In the frame of the pure climatic mechanisms of the 'winnowing out' of tundra-steppe communities the woolly rhinoceroses should not become extinct but only withdraw to drier parts of Eurasian steppes as did hemionides and saigas.

### 3.17. Mammoth suite and interglacials

How could mammoths and their satellites persist through Mindel-Riss and Riss-Wurm Interglacials, notably through their optimal phases, if they were obligatory stenoecic crioxerophyles ? Climatists proposed few explanations.

#### 3.17.1. Higher resistance of ancestral forms ?

Some scientists believe that pre-Wurm mammoths and their satellites were more plastic ecologically and/or had larger evolutionary potentialities (Kowalski, 1967; Vereshchagin, 1971: 224-225, 1979: 172; Vangenheim, 1977; Alekseeva, 1995).

It is true that mammoths, woolly rhinos, horses and bison during Mindel, Mindel-Riss, Riss and Riss-Wurm invariably lived in a wide variety of landscapes (ibid.; Stuart, 1974; Lister & Bahn, 1994, etc.). But the range of environments of their Wurm descendants was by no means narrower (Sect. 3.14.). Moreover the teeth of the final Wurm (Anaglacial) Siberian mammoths have changed with the adaptation to more browsing food-regime (Sect. 3.15.1.4.). The same phenomenon has been occurred during previous warmings correspondingly to the increase of woody component in vegetation (Foronova & Zudin, 1986). Thus herbivores of the late Wurm 'mammoth complex' had scarcely lose their ecological and evolutionary plasticity.

#### 3.17.2. The vestigial populations in small refugia ?

According to S.V. Tomirdiaro (1977) and S.V. Kvasov (1977) small populations of mammoths and their satellites persisted through both Interglacials in cold and dry Mongolian and Transbaikalian steppes. Animals are thought to survive there, much as present-day musk-oxen survive now, being hidden in restricted parcels of American tundras with thin snow cover.

In reality these steppes have never become the 'last hope' of mammoths. They were only quite inhospitable marginal regions of the invariably vast mammoths range (Vangenheim, 1977). For woolly rhinos, horses and bison they always remained an ordinary inner part of their areas (ibid.). Even at the Riss-Wurm Optimum (Ipswich II *sensu* Stuart, 1974, 1976) mammoths have been retreated only from West Europe, covered with oak-dominated broadleaf forests and occupied by strait-tusked elephants (Kurten, 1968; Stuart, 1974, 1991). Together with woolly rhinos, horses and bison mammoths prospered not only in criophytic savannas of northern (Vangenheim, 1977: 146) and southern (Verkhovskaya, 1988) parts of East Siberia (musk oxen were distributed here too) but in warm wooded steppes of East Europe as well (L. Alekseeva, 1980). Mammoths already returned to West Europe at the Postoptimal stage of Riss-Wurm. This had happened well before the considerable rarefaction of woods and retreat of strait-tusked elephants and dicerorhine rhinos beyond Alps and Pyrenees.

To illustrate, in England mammoths reappeared at the onset of the Postoptimal stage of Riss-Wurm (Ipswich III *sensu* Stuart, 1974, 1976). They coexisted here with strait-tusked elephants, steppe rhinos (*Dicerorhinus hemitoechus*) and, at the beginning, even with hippopotamus. Summers were still warm and winters still were not too severe. Landscape was mixed hornbeam dominated forest with important meadow areas in the river valleys. These meadows were created not by climate but chiefly by the feeding and other activities of megabrowsers and megagrazers (Turner, 1975; Stuart, 1976). At the final stage of Riss-Wurm (Ipswich IV *sensu* Stuart, 1974, 1976) temperate forests were ousted by boreal ones. The cold climate rodents have been appeared (*Dicrostonyx torquatus*, *Lemmus lemmus*, *Microtus oeconomus*, *Citellus undulatus*). Still mammoths coexisted not only with musk-oxen and woolly rhinos but also with steppe rhinos and, at the beginning, with strait-tusked elephants (ibid.). The occurrences of mammoths with strait-tusked elephants and dicerorhine rhinos are registered also for the late Riss-Wurm and pre-Wurm (possibly — Early Wurm) of Germany and France (Musil, 1985; Stuart, 1991; etc.). In Novosibirsk region pre-Wurm (or final Riss-Wurm?) mammoths and woolly

rhinos lived in the surroundings of forest-steppe with boreal trees (spruce, birch, larch, Siberian 'cedar') (Vasiliev, 1995).

As for bisons and horses they never retreated from zones occupied by straight-tusked elephants (Kurten, 1968) with the possible exception for horse in England (Stuart, 1976).

Even the above-mentioned retreat of the Riss-Wurm Optimum mammoths from the West Europe was probably not complete. The Riss-Wurm age of mammoth bones from Sweden (Kurten, 1968) has been reevaluated as the Middle-Wurm one (Vereshchagin & Baryshnikov, 1977). Due to the lack of data it is unknown, whether mammoths were present or absent in Scandinavia and Russian forest zone during Riss-Wurm Optimum time. Mammoths and horses have been reappeared in England at the very beginning of the Riss-Wurm Postoptimum. It was before the disappearance of hippo from Britain, when its land connection with the continent was still absent. Probably it means that mammoths and horses persisted in Scotland at the Optimum time (Stuart, 1976).

Mammoths largely coexisted with straight-tusked elephants in Europe and Asia during Mindel-Riss Interglacial (Mania, 1983, etc.).

### 3.17. 3. Climate-caused persistence of tundra-steppes during Interglacials ?

According to this point of view the zonal tundra-steppe or 'mammoth-steppe' has not disappeared during Interglacial but only contracted its range (Vangengeim, 1977; Sher, 1971, 1982, 1986; Guthrie, 1976, 1990a, 1990b; Kiselev, 1981).

This concept is a confusion of two different questions. The first is: 'Whether open meadow-like, steppe-like and/or parkland-like formations, well-fit for mammoths and their satellites, were spread far wider during the Interglacials than during the Holocene?' Climatists say 'Yes' in complete accord with the paleoenvironmental evidence. Mammoths and other herbivores that required rich herbaceous vegetation have not disappeared as well as some cold steppe and dry tundra insects (*ibid.*; Verkhovskaya, 1988). The second is: 'Whether these differences were caused by more continental climate of the Palaeartic or, at least, that of Megaberingia in the Interglacials than in the Holocene?' Climatists again say 'Yes', although the evidence permits only the negative answer.

According to A. Sher (1971; oral communication in 1995) the Interglacial tundra-steppes were kept by the cooling influence of Arctic Basin. The latter is believed to be covered with thick and continuous ice-armor throughout the all Pleistocene, including the Interglacials. Only at the beginning of Holocene this armor has been broken. It triggered the previously unseen humification that caused the disintegration of the tundra-steppe biome (*ibid.*).

If this conjecture were correct, the continuous Arctic panocenic 'Super-ice-shield' should make the climate of Interglacial colder and drier throughout all North Hemisphere. But all known evidence on Mindel-Riss and Riss-Wurm Optimums soils, vegetation and fauna unambiguously indicates that climatic conditions were everywhere warmer or/and moister than in Holocene (Sect. 6.4). Could it be otherwise in Megaberingia ?

A. Sher (1971: 110) argues that Interglacials in North-East Siberia were 'cold', because there are no 'interglacial faunas' while paleobotanical data show that forest zone has been shifted northwards during Kazantsevo (Riss-Wurm) Optimum 'only for 200-300 km'. However this 'only' is extremely important. Paleobotanists speak of the Riss-Wurm treeline shift as compared to the **modern** north border of forest zone (Karavayev & Skryabin, 1971) and not to that during the previous Riss Glaciation. The decrease of climatic severity is distinguishable by species composition of plant-communities as well. Larch reached the banks of Arctic Ocean even on Chukotka Peninsula (Lozhkin, 1976). Spruce penetrated almost as far as the mouth of Lena (Karavayev & Skryabin, 1971). The Yano-Kolymanian

region was covered with taiga of the type, growing now one thousand kilometers to the South. The annual temperatures in Central Yakutia were from 7 to 10 degrees higher than now (ibid.). Spruce penetrated more northwards and westwards than now also in Alaska (Hopkins, 1972).

How could the ice-cover of Riss-Wurm Optimum Arctic Basin be continuous, thicker and larger than at present, how could its cooling influence be stronger than now, if global sea level was about 5-10 m higher than today? (Hopkins, 1972; Chapel & Shackleton, 1986). The lowlands of Taymyr, Gydan and Yamal peninsulas were under sea level and their uplands (Rranga mountains, etc.) became the islands (Gus'kov, 1986). What is more a series of Arctic mollusks retreated well to the North of the Bering Straits. Simultaneously a set of boreal ones penetrated during Riss-Wurm Optimum (Pelukian transgression) more to the North than even at the Optimum of Holocene (Hopkins, 1972). So mussel (*Mytilus edulis*) reached Wrangel Island, *Mya japonica* — Cape Barrow (now it is a Japanese species), *Natica janthostona* and *Protothaca adamsi* penetrated up to Nom. It means unambiguously that Bering, and, partially, even Chukotka Seas were not bound with ice. The three last mollusks could not exist in seas with long-lasting ice presence (ibid.). The global water temperature has risen 5 degrees more than at present (Emiliani & Shackleton, 1974).

Inasmuch as Arctic and other Oceans were larger and warmer, their humidifying influence over land was unfaillingly stronger than in the Holocene. Even the climate of inner parts of Megaberingia that were occupied by criophytic savannas and boreal forests, though being certainly of continental type, was apparently milder than now (Karavayev & Skryabin, 1971; Verkhovskaya, 1988). As for the coastal areas, they were occupied by veritable tundras growing under humid oceanic conditions (Yurtsev, 1976), though their space was smaller than at present (Hopkins, 1972). This refutes the suppositions (Sher, 1986; Guthrie, 1990a) that interglacial climates were at least drier if not colder than climate of Holocene.

All these land and water indices of climate show in the most unambiguous manner that constantly intact ice-armor of Arctic Ocean, invariably immune from the action of the global warmings, is as unrealistic as an ice-armor of the frozen mammoth wool (Sect. 3.9.). The exposed evidence proves that 'mammoth pastures' (treeless, parkland and open woodland formations with rich herbaceous cover of steppe-like and meadow-like types) were spread wider during Interglacials than during Holocene not due to the climate, **but in spite of it**. Such situation is inexplicable when climatic forces alone were taken into consideration. If Holocene warming has turned out to be sufficient for elimination of tundra-steppes and other kinds of mammoth-pastures, the stronger interglacial warmings, should be so much the more sufficient. Only the potent non-climatic factors could change the issue (Sect. 8.; 9.; 10.).

## 4. SOME OTHER CLIMATIC EXTINCTIONS MODELS FOR PALEARCTIC

### 4.1. Mammoths and melting of great glaciers

N.B. Verkhovskaya (1988) rejects any connection of mammoths and their satellites with ultracontinental crioarid treeless tundra-steppes. She holds that they lived exclusively in criophytic savannas under mesic and moderately cold or cold-temperate climates. These savannas were fast growing tall-grass mesic or humid meadows of prodigious nutritive value with scattered and/or gathered in groves boreal trees. Such formations existed due to powerful streams that flowed from under the Ice Age Glaciers and, partially, due to patchwork melting of permafrost (thermocarst processes). The currents were saturated with loess particles. They alternately deposited, washed away and redeposited the loess layers. Having no

constant river-beds, these numerous streams shifted over the plains and carried out something similar to a tremendous-scale ploughing. They converted plains to a sort of enormous deltas.

Contrary to 'tundra-steppe crash' model, Verkhovskaya argues that during Glacials mammoths and their satellites left crioid North-East Siberia (that was converted to barren land with rather scanty tundra-steppe or steppoid vegetation). Animals shifted to South Siberia and Europe together with their criophytic savanna biome that was sustained by the melting of plain and mountain ice-shields. During Interglacials and interstadials criophytic savanna biome shifted to North-East Siberia. Here the ecosystem was maintained by the melting of alpine glaciers as well as by intense thermocarst processes. With the onset of the Holocene thermocarst processes have been dramatically attenuated (they create now only small islands of valuable 'alas' meadows). The vast glaciers and, consequently, the potent glacial streams disappeared completely. It was the end of criophytic savannas. Mammoths and their satellites vanished. They could live neither in completely treeless (steppes, tundras) nor in taiga surroundings. Even sparse growing larch taiga that occupies now more than half of Yakutia is incompatible with mammoths. This parkland resembles the former criophytic savannas by floristic composition but differs drastically by meager productivity of its herbaceous component (Verkhovskaya, 1988).

Verkhovskaya rightfully underlines that the disappearance of the mammoth biome can not be understood without the understanding the reasons of its appearance. But arguing that only the onset of the Ice Age gives way to fertile pastures, she neglects the evidence. Rich complexes of land megafauna were omnipresent throughout Neogene and Pleistocene. They thrived under all types of climates (Savage & Russel, 1983; Carroll, 1987). Biomes that included mammoth's ancestors (*M. meridionalis*, *M. trogontherii*) existed under vast range of climates from boreal to subtropical ones. Megafaunal sets of these biomes were even richer than those of mammoth biome. Furthermore the 'criophytic savannas' were preferable, but not unique type of mammoths landscapes. Mammoths lived also in some completely deforested and well forested landscapes (Sect. 3.14.).

Neither glacial streams nor thermocarst processes were the *sine qua non* condition for the existence of the 'mammoth-biome'. By way of example, warm-temperate forest-steppes of Riss-Wurm Optimum at the south of East European Plain were densely populated by mammoths, woolly rhinos, horses and bison (L. Alekseeva, 1980). The same is true for mixed, hornbeam dominated, open woodland/parklands of England during the Riss-Wurm Postoptimal phase (Stuart, 1976, etc.). Also boreal and temperate woodland and forest-steppe landscapes of Europe and Asia during Final Riss-Wurm and Pre-Wurm were swarming with 'mammoth-fauna' in spite of the absence of major glaciation events (Stuart, 1974, 1991; Vangenheim, 1977; Kozhamkulova & Kostenko, 1984; Musil, 1985; Vasiliev, 1995). Which Glaciers and which permafrost created them? If those of Riss, they have melted many thousand years before, if these of Early Wurm, they appeared many thousand years after... . Ice-sheets of plains as well as of mountains have everywhere melted intensely only during short deglaciation phases (anaglacials and early postglacials) and not throughout most of Mindel-Riss and Riss-Wurm duration. Otherwise the worldwide sea level rise at the Riss/Riss-Wurm boundary should be gradual and not even more fast than during Wurm/Holocene transition, as it was in reality (Emiliani & Shackleton, 1974; Seidenkrantz, 1993). If the Holocene warming put a rapid end to 'meadow-making currents', the more important warmings of Mindel-Riss and Riss-Wurm would do it even faster. If mammoths pastures persisted then we must seek another force that maintained them.

## 4.2. Were the mammoths killed by the cooling ?

It need not dwell on this concept that does not correspond to the bulk of paleoecological evidence. It is eagerly rejected by modern authors, except H. Krause (1978). The sound grain of his position is that mammoths did live not only under severe criarid conditions but under far milder ones as well (Sect. 3.4.; 3.14.). It would be not out of place to observe that formerly 'mammoth killed by the cooling' conceptions were as popular (e.g., Morris, 1895; Neuville, 1921) as are now 'mammoth killed by the warming' ones. It seemed so natural that elephants, rhinos and lions should be frozen with the cold of Great Glaciation. Many decennies of accumulation of the evidence were needed to abandon the old paradigm, ... and to replace it with its reverse! However the evidence shows that warmings were not more able to kill mammoths and their satellites than coolings.

## 4.3. Riss Glaciation and Elasmotherium

This peculiar elephant-sized rhino with a horn on a forehead lived in Eurasian steppes and semi-deserts. It has been extinct during Riss Glaciation — indications of later occurrences are dubious (Alekseeva, 1977; Kozhamkulova, 1981). Climatists explain its extinction either by direct or by indirect, through competition with other ungulates effects of coolings of some of Riss stadials (Gabunia, 1969; Alekseeva, 1977, 1990).

It is difficult to imagine that *Elasmotherium sibiricum*, the last representative of the genus, originated in the semiarid zone of the Inner Asia (ibid.), was ill-adapted to criarid conditions. Its high crowned teeth, garnished with extremely complicated enamel pattern. They were better adapted to a grazing on coarse, dust covered grasses of arid steppes than teeth of any other ungulate. Enormous *bulbi olfactorii* speak of extremely well developed smell that permitted to find nutritive bulbs, tubers and rhizomes of ephemeral plants as well as the places, where water could be found by digging. The main trend of the climate of Inner Asia during Neogene and Anthropogene was an increase of the continentality (Sinitsyn, 1980; Yassamanov, 1985). Before Riss it was just at stadial coolings that elasmotherium expended its area to Central Europe (or even to France, if the indications are correct) due to the spreading of open landscapes. It was at the warm stages, when this rhino retreated eastwards (Kurten, 1968; Alekseeva, 1977). The climatic version of the elasmotheriums extinction would be more plausible, if the beasts were expired during the warm and humid Mindel-Riss Interglacial, and not during Riss glacial, when expanded their preferable landscapes. It is probable (though not certain) that the Riss cooling, synchronous with the extinction of elasmotherium, was stronger than the previous ones. Even if it was so, the stadial cooling could be neither instantaneous, nor equally strong all over the immense elasmotherium range. This range in Mindel-Riss has been stretched from Mid Volga (Kazan') to Mid Hawing Ho (Ordos, Inner Mongolia) basin and from West Siberia to Azerbaidjan and Uzbekistan (Gromova, 1965; Alekseev, 1978; Kozhamkulova, 1981, etc.). Animals, at least over part of this range, should have time for the adaptation or to southward and westward migration with all the steppe biome, as did other ungulates. Consequently, purely climatic models could not explain the extinctions of giant forehead-horned rhinos.

## 4.4. Were straight-tusked elephants victims of the maximal glaciation ...

Basing on the supposed absence of these animals (*Palaeoloxodon antiquus*) in the Riss-Wurm deposits of Eastern Europe (Gromova, 1965), V.V. Shcheglova (1968) stated that elephants were frozen to death during the Riss Glaciation. However these elephants did occur in Riss-Wurm even on Russian Plain (Alekseeva L., 1980) to say nothing of the Western Europe.

## 4.5. ... or those of the maximal cooling ?

More tenacious is the version that these elephants, together with European hippos, forest and steppe rhinos, were killed by the coolings of the Middle or Late Wurm stadials (Gromova, 1965; Kowalski, 1967; Velichko, 1973; partially — Stuart, 1991, 1993). It was based over the absence or disputability of these pachyderms rests aging younger than 40 kyr BP (ibid.; Kurten, 1968; Musil, 1985). But there are many facts non-consistent with this point of view.

These pachyderms, together with hydruntine asses and giant deer, were the members of temperate forest and forest-steppe biomes. In company with the living species of these biomes, they expanded to various extents their areas northwards and westwards during major Pleistocene warmings. During major coolings they retreated to southern Europe (Alekseeva L. 1977, 1980, 1990; Alekseeva E., 1980;

Kurten, 1968; Vangenheim, 1977; Stuart, 1991, etc.). Strait-tusked elephants lived in subtropical, temperate and boreal forests, woodlands and parklands dominated by oak, hornbeam, pine, birch and/or other trees (Gromova, 1965; Kurten, 1968; Stuart, 1974, 1976, 1993; Mania, 1983; May, 1993, etc.). They lived even on almost treeless meadows, as in some regions of Spain during Mindel Glaciation (Freeman, 1973). It proves that these elephants (as well as forest and steppe rhinos) were adapted to wide range of landscapes and climates. By all probability they were as cold resistant as are roes, wild boars and red deer. Straight-tusked elephants and forest rhinos could march through snow cover of considerable thickness due to their large sizes and foot structure, that were correspondingly similar to those of mammoths and woolly rhino (Sect. 3.11; 3. 3.12.3.). Probably their distribution to the North and to the East was limited not by snow cover, but by trophic factors and by competition with mammoths and woolly rhinos, even better adapted to severe conditions. Throughout most of Pleistocene the regions, where mammoths (or their ancestors) and straight-tusked elephants were the sole proboscideans were united by more or less wide belt of their co-dominance (Kurten, 1968; Stuart, 1976, 1991; Alekseeva, 1977, 1980, 1990; Mania, 1983). The same is true for the partially overlapped ranges of woolly rhino from one and forest and steppe rhinos from the other side. Even behemoth coexisted with woolly rhino! Ten cases of common occurrences of their rests has led to conclusion that the former could not be considered as obligatory index of warm conditions, while the latter certainly could live under conditions far milder than the periglacial ones (Guerin, 1980 — cit. by Alekseeva, 1990).

The Late Wurm Pleniglacial cooling was not as rigorous in the Southern Europe, as more to the North. Most of Italy, coastal areas of Balkan peninsula and mediterranean coast of France were occupied by forest-steppes of temperate type (Musil, 1985). Here persisted animals (aurochs, giant deer, wild boar, wild cat, rabbit, porcupine, etc.) that advanced to Central and/or Eastern Europe only during warm phases (ibid.; Gromova, 1965; Kurten, 1968). Even less suitable for the climate-induced extirpation of moderate climate pachyderms was Iberian Peninsula. Even in North Spain, dominated by warm-temperate forest steppes, warm climate mammals prevailed over the boreal ones (Freeman, 1973; Musil, 1985, etc.). Considerable spaces of broadleaf forests persisted in the southern part of the Peninsula (Lister & Bahn, 1994).

Climatists insist that intense Late Wurm Pleniglacial cooling and cooling-caused insulation effects, have killed in Europe not only the giants, but all fallow deer too. The latter are believed to be reintroduced during Antic and Middle Ages from Fore Asia (Kowalski, 1967; Kurten, 1968; Velichko, 1973). Although the indication of the fallow deer presence in Spain during the maximal cooling (Freeman, 1973) needs confirmation, the mentioned introduction hypothesis still does not work. It does not explain the presence of fallow deer in early Holocene deposits of southern Germany (Musil, 1985) and Slavonia (Geptner & al., 1961). At last, if fallow deer persisted in Fore Asia (it became there even more frequent during cold stages — Velichko, 1973), why the straight-tusked elephants and both rhinos could not do the same ?

It has been shown with more details that temperate climate European pachyderms could not be exterminated either by direct, or by indirect effects of the Late Wurm Pleniglacial cooling (Putshkov, 1989b). There are certain indications that all the four giants persisted for thousands of years under abnormally low density because of constant human predation during late Paleolithic time in Southern Europe and Fore Asia (Crusafont-Pairo, 1960; Kurten, 1968; Freeman, 1973; Tchernov, 1984; Putshkov, 1989a,b, 1993b). The most interesting one is the occurrence of the rests of straight-tusked elephant on San-Sidero site (Apulia, vic. of Otranto). Absolute age is about 10,3 kyr BP — approximately the same, as for the last mainland mammoths (De Giuli, 1980; Alekseeva, 1990). If these data are

correct, it means that still existent continental populations of straight-tusked elephants did not answer by their recovery to the favorable climatic changes of Anaglacial warming! By all probability the residual populations of elephants and other 'southern' giants persisted during Late Wurm Pleniglacial on dried Mediterranean shelves. The dwarfed insular hippos and elephants (those from Tilos are of Holocene age!) indirectly confirm this conjecture.

#### 4.6. Comments to climatic models of extinctions of other Palearctic megafauna

Climatists explain the extinction of 3 species of giant deer, European ass, 2 antelopes of Central Asia (*Spirocerus* and *Parabubalis*), cave bears (*Ursus spelaeus*, *U. rossicus*), cave lion and hyena by the climate-induced environmental changes. The panbiotic explanation also ascribes the principal role to environmental changes. It argues, however, that changes, crucial for the extinction of the mentioned beings, were induced by the depression and, then, extermination of giant herbivores by humans. Hunt and/or competition with man, interactions with other species, effects of climatic changes and man-made burnings played subsidiary role in the extinctions of the mentioned forms (Putshkov, 1989a,b, 1993b).

It has been shown (*ibid.*) that climatic explanations do not agree with the bulk of the evidence. First of all they fail to explain the survival of the mentioned species during previous Ana- and Interglacials. There are no such difficulties for the panbiotic concept. Let us illustrate it by the sole example. Climatists ascribe the extinction of giant deer to the early Holocene expansion of forests and to other repercussions of the general warming. It is partially true, but why these deer prospered under even milder Riss-Wurm conditions that were even more favorable for closed forests? The Interglacial forestation was not dangerous to them thanks to straight-tusked elephants and/or other pachyderms. Giants disintegrated the woods and maintained zoogenic meadows and parklands — the feeding areas of these deer and other ungulates (Putshkov, 1989b, 1993b; Schule, 1990; May, 1993). The uncompensated Wurm extinctions in Palearctic were treated more specifically in preceding articles (Putshkov, 1989a,b, 1993b).

### 5. THE UPSET OF CLIMATIC EQUABILITY AND SOME OTHER MODELS

American climatists, with rare exceptions (*e.g.*, Guthrie), are as devoted to climate continentalization extinctions models, as are their European colleagues to the 'tundra-steppe crash' and other climate oceanization extinctions scenarios. Some of the models are thought to have not only North American, but global implication. These models insist that Nearctic, or even the Holarctic climate in Wurm was more oceanic than now and winters were milder (Axelrod, 1967; Graham, 1985; Kurten & Anderson, 1980, etc.). In early Holocene winters became longer and colder, summers — hotter, climate of immense spaces became arid. The mentioned phenomena resulted in the baneful changes of vegetation. Different models attach much importance to one or another effect of climatic continentalization.

#### 5.1. Axelrod's hypothesis of the global upset of the climatic equability

It has been supposed that Pleistocene and Tertiary giant mammals thrived beyond the tropical zone due to the equable climate (Axelrod, 1967). Although mean annual temperatures in high latitudes were significantly below than those in tropics, everywhere the differences between warm and cold season temperatures were not so important, as now. The precipitation rate and, consequently, humidity, were high. Both these circumstances caused the existence of far richer flora and fauna. Now we see these effects on Terra del Fuego with its rich evergreen flora, hummingbirds and parrots, or in some other equable climate regions. Due to humid cool summers and mild short winters southern and northern forms coexisted over extensive regions. Equable climate was necessary for giants — mammoths, rhinos, mastodons, giant sloths, etc. The decrease of equability caused the disintegration of mixed communities and mass megafaunal extinctions in Northern Eurasia and North America. Giants suffered due to winters that became colder and summers that became hotter. Their young born out of season could not resist to cold and,



especially, hunger. Equally disastrous were the summer droughts and the aridization of immense regions. African megafauna survived due to feeble decrease of climatic equability in the sub-Saharan savannas. Tapirs survived due to wet and equable climate of selva (*ibid.*).

The sound grain of this model is that progressive cooling and/or aridization of most of Holarctic region from the Oligocene to the Pleistocene have led to stunning impoverishment of its biota with thermo- and hygrophilous plants and animals (*ibid.*; Velichko, 1973; Sinitsyn, 1980, Yassamanov, 1985). Many of them live now in East China, South-East USA, Transcaucasia, and other refuges. However proofs of highly unequable and severe climate of the periglacial mammoth ecosystems are so convincing that Axelrod's model is rejected, as applied to extinctions of mammoths and their satellites, even by many climatists. They prefer the opposite model of the climatic mildening as the primer cause (Sect. 3.). Many other circumstances are also overseen in the climatic equability model. For example: a) high degree of seasonability in African savannas rich in megafauna; b) miserable megafauna in climatically equable and moist South American selva; c) absence of megafauna in the above-mentioned forests of Terra del Fuego; d) devastating final Wurm extinctions in South America in spite of the early Holocene increase there of the regions with equable humid climate (Martin, 1984). Nonetheless variations of this model are largely used to explain extinctions in North America.

## 5.2. Inappropriate gestation time models

B. Slaughter (1967) and R. Kiltie (1984) consider the prolongation of winters as key extinctions agent. Calves of mammals with long gestation time were born at the time when there was still no accessible green forage. They starved to death. As a result mammals with the duration of pregnancy beyond 6, or, at most, 9 months, have disappeared from all regions beyond tropical zone.

However, the modern Central Asian winters are more inclement and longer than anywhere in USA. Nonetheless this region is inhabited by Przewalsky horse and wild Bactrian camels bearing their posterity over 11-12 and 13 months correspondingly. Woolly rhinoceroses and mammoths, being undeniably well adapted to the most continental climate with long and frosty winters (Sect. 3), should have even far longer pregnancy. These animals during Late Wurm Pleniglacial prospered under far more severe climates with longer and colder winters than those of the Holocene (Sect. 3.14.1.). The long pregnancy could not prevent the acquisition of the necessary seasonability of reproduction (McDonald, 1984). Rhinos and elephants, as well as any other mammals, have individual and interpopulational variability of reproduction cycle features. To illustrate, the pregnancy span of African elephant cows varies from 17 to 24 months, that of black rhino — from 14,5 to 18,3 months (Penny, 1987). Such variability of the gestation time would give the material for the work of natural selection if the necessity to adjust reproduction cycles to climatic changes were appear. It is known that these cycles have drastically changed in case of domestic and feral cattle, asses and horses, which were transported to southern hemisphere. The indistinct seasonability or the lack of seasonability in the reproduction of modern pachyderms, as well as the great variability of their gestation spans, are rather consequences than the reasons of their distribution in tropical zone.

At last the Slaughter-Kiltie's and the other Holocene continentalization models ignore the facts that climatic equability, humidity, winter and summer temperatures and winter duration have never changed uniformly in eastern and western, northern and southern, inland and coastal areas of low and middle latitudes (Jelinek, 1967; Spaulding, 1983; McDonald, 1984). These coastal areas always were dominated by mild and equable climate due to the influence of unglaciated ocean (McDonald, 1984). Slaughter (1967) explains the vicuna survival in highlands of Peru by the fact that low latitudes protected it from the frosts and high altitudes — from the heats. Axelrod (1967) ascribes the persistence of tapirs in humid Neotropical forests to their moisture and feebly disturbed climatic equability. But if such were the reasons, why other diverse Neotropical Pleistocene megafauna (mastodons of three genera, horses of three genera, dozens of other ungulates, large and gigantic edentates, etc.) that lived both in mountains and plains, forested and unforested regions (Patterson & Pascual, 1968; Anderson, 1984; Martin, 1984, etc.), has been disappeared too ?

## 5.3. Ice-shield removal

According to this model the immense ice shield of Wisconsin (Wurm) Glaciation that covered all Canada except for the part of Yukon Basin, had the mitigating effects on the climate of Great Plains (Bryson & al., 1970 — cit. by Grant, 1991). It protected them from cold and dry arctic winds. As a result, tall

grasses and many large tall grass grazers could exist there. The early Holocene deglaciation removed the shield. Cold and dry winds from Arctic Ocean have withered pastures. Tall mesic grasses were replaced by the xerophytic short grasses of low productivity. Large herbivores died out (*ibid.*).

First, this model explains extinctions neither beyond the Great Plains nor in the quite vast regions of Holocene tall grass prairies. Second, it is improbable that cold winds, caused by the near-by glaciation ice-shield, were less pernicious than those from the distant Arctic Ocean. Third, and this is most important, why there were no devastating extinctions without replacement at more than dozen pre-Late Wurm deglaciation events ?

#### 5.4. The 'Panamerican Drought' ?

According to J. Guilday (1967, 1984) the primer causes of North American extinctions were the aridization of most of the territory of the USA and simultaneous increase of pluviosity in the forest regions. Savannas that occupied in Pleistocene the Middle West and Far West regions, have been converted to deserts and treeless prairies of the modern type. As this happened, deserts have occupied not only the arid South West, but the considerable parts of the modern prairies zone as well. Correspondingly, prairies occupied the western part of the modern forested East. At the remaining part of the forest zone, the previous open woodlands were replaced by continuous closed forest. Due to these polar processes most of megafauna has been driven to extinctions directly or through the competition with the extant herbivores. It is believed also that in South America pampas have been completely dried out except for tiny patches at the foot-hills of Andes where no large herbivore but guanaco could survive. Guanaco was saved due to the contact with its more viable highland populations. Guanaco and some forest deer repopulated the pampas biome, restored after the drought (Guilday, 1967: 133).

The model does not offer a plausible explanation of the case of the North America. Till the extinctions time arid regions occupied only about 15% of the continent (McDonald, 1984). Till Holocene Optimum (Altitheermal) they occupied up to 25%, but this occurred about 3-4 kyr after extinctions. Such arid adapted species as sloth *Nothrotheriops*, camels, small horses and pronghorns should thrive and not become extinct in the arid zone (*ibid.*; Martin, 1967; Edwards, 1967; Spaulding, 1983). Other megafauna could easily retreat to the mesic North, East and to mountain belts. The territories that were lost at the West and South by mesic and moderately arid prairies in favor of more arid prairies and deserts were compensated at the East and North at the expense of forests. Forests indeed became more closed and prairies — more treeless than in the Pleistocene. But these changes were determined by other reasons than climate (Sect. 7.2.; 8.; 9.). The Riss-Wurm (=Sangamon) Optimum warming was more intense and aridization spread over the larger territories than in the Early or even in the Middle Holocene (King & Saunders, 1986). However there were no extinctions then (Jelinek, 1967; Martin, 1984).

For the South America the aridization model is even less convincing. The highlands of Andes were densely populated not only by extant vicuna and guanaco, but also by mastodons (*Cuvieronius andium*), horses (*Equus andium*), giant sloths (*Megatherium*, *Myloodon*, etc.), notoungulate *Macrauchenia*, large llama (*Palaeolama*) and other extinct forms (MacNeish, 1976; Anderson, 1984). Animals here were protected from the effects of the drought and other climatic changes due to orographic variety of biotopes. But even more important is that it was no terrible 'superdrought' at all! (Patterson & Pascual, 1968). During Final Wurm/ Early Holocene several dry and moist episodes have been alternated but the general trend was the increase of moisture and the expansion of selva (Martin, 1984). There was neither disappearance nor significant contraction of pampas. Selva has always been divided from pampas by the wide belt of changeable humidity. It was covered with savanna-like and/or bushland-like (*serrado*, *chako*, etc.) vegetation. Likewise savannas-llanos at the North of continent were neither completely forested, nor converted to deserts (Gruhn & Bryan, 1984).

#### 5.5. Were the herbivores poisoned with their food ?

For anthropists and biotists (*e.g.*, Putshkov, 1989b) this question seems to be out of place. They issue out of the extensive indirect and, sometimes, direct evidence, proving that extinct large herbivores should be, or certainly were highly polyphagous beings, capable to subsist on the wide range of plants. However for some climatists the polyphagy of the majority of large herbivores is the result of the imperfection of their trophic physiology.

According to R.D.Guthrie (1984) Late Tertiary and Pleistocene climates were characterized by high inter- and intraannual variability. This favored the global distribution of highly mosaic (patchy) plant communities. The local floristic diversity in these communities was unbelievably high. There were no differentiated

zones of tundra, taiga, steppe and other familiar biomes of cold, moderate and warm climates, but complex plaid of complex vegetation patches. Plants, growing now in different zones, grew then on the same patch or side by side on the neighboring patches of this 'plaid system'. Such floristic diversity permitted the coexistence of numerous large herbivores and their predators. Also the growth season of plants was everywhere long due to climatic reasons. As a result the trophic quality of plants was high during long part of the year or even all year round. The major climatic change near Wurm/Holocene transition has everywhere caused the decrease of the plants growth season duration as well as the drastic drop of the local floristic diversity. The zonal structure of vegetation has been appeared. Plant communities of each zone became monotonous. Climate, growth season length and plant communities structure are believed to have retained their Plio-Pleistocene features only over most of Africa.

The outcome of these changes was catastrophic for the monogastric herbivores such as mammoths, rhinos, horses, tapirs, giant edentates, etc. They were doomed to use an extremely variable set of plants. By this means they obtained the necessary nutrients and prevented the intoxication with antiherbivory substances, notably alkaloids. Different alkaloids of different plants neutralized each other in the animal organism. Such diet was possible only in the highly mosaic Tertiary and Pleistocene plant communities. Under Holocene conditions monogastric herbivores have been poisoned or oppressed with antiherbivore substances of dominant plants of each zone. They could not counterbalance these toxic substances with toxic substances of other plants. Ruminants degrade plant toxins in their rumen (paunch) due to the activity of microflora. This process is more efficient in paunches of large ruminants — bison, aurochs, moose, red deer (wapiti), reindeer. That is why they survived, while small pronghorns (*Stockoceros*, *Tetrameryx*, *Capromeryx*) and some cervids (*Sangamona*, *Navahoceros*) shared the fate of the monogastric herbivores. The paunch system of camelids is also considered by Guthrie as an insufficient one. Hence — the extinctions of *Camelops*, *Hemiauchenia*, *Paleolama*. The shortening of the growth season of plants had terrible consequences for the mentioned monogastrics and camelids too. Proboscideans, peryssodactyls and camelids have long gestation periods (from 10 to 24 months) and feed their calves with milk poor in protein content (Guthrie, 1984). Their embryos and calves were insufficiently fed under conditions of short plants growing season. This was one more reason why even those monogastrics and camelids that failed to be poisoned, could not resist to the competition from bovids and cervids. These ruminants are better adapted to Holocene trophic conditions due to their paunch systems, short gestation periods (6–9 months) and milk, rich in protein.

R. Graham and E. Lundelius (1984) also believe that the prime cause of large herbivores extinctions was the switch of plant communities from Pleistocene patchy to Holocene zonal structure. Some herbivores lost under new conditions their competitive abilities, others — were simply poisoned with their forages. Small mammals escaped extinctions by the redistribution of their ranges according to the new zonality. The same did herbivorous insects, whose ranges shifted with those of their food plants.

One more 'trophic' extinction model issues out of the increase of the share of C-4 grasses in early Holocene herbaceous cover of USA territory (Wilson, 1974 — cit. by Kurten & Anderson, 1980). These grasses, fixing the carbon by the way of Hatch-Slack, are of the less nutritional value for the phytophagans than C-3 grasses, fixing carbon exclusively by the way of Calvin (Harborn, 1985). That is why the raise of their relative numbers in Holocene is considered by some paleontologists (Kurten & Anderson, 1980) as an important factor of Wurm extinctions.

Unfortunately the trophic extinctions versions could not be considered here in due details. It is probable and even certain that peculiarities of trophic,

detoxification and reproductive physiology played an important role when herbivores resisted to the Wurm/Holocene environmental changes. It is not proven, however, that the most crucial of these changes were of climatic and not of biotic nature. The largest of herbivores could be neither empoisoned nor degenerated due to the decreasing of the mosaicity of the vegetation cover, because this phenomenon was the consequence and not the reason of their extinctions (Sect. 8.; 9.; 10.). Even the length of the growth season of plants can increase due to large herbivores feeding! One mechanism of this phenomenon is the compensatory growth, the other — zoogenic changes of plant communities (ibid.). Some of other objections are the following.

First, the global warming could be resulted neither in the quasiglobal shortening of the growth season of plants, nor in the universal decrease in the local floristic diversity (Sect. 7.2.). Second, the interactions of different plants antiherbivory compounds in the organism of monogastric herbivores play only subsidiary role in the detoxification processes. The prime one play the potent detoxification systems of the herbivores themselves (Herbivores, 1982; Harborn, 1985). These systems are complex, plastic, apt to accommodation according to changes of food items. Animals efficiently adapt and readapt themselves to plant items of their surrounding on individual and population levels. Different individuals possess different extent of adaptability to this or that substance. Due to this, the natural selection can efficiently operate in populations. Probably animals are able to adapt to any toxic substance, if they can obtain the necessary trophic ingredient only from toxic plants (Harborn, 1985: 190).

The monogastricity of extinct proboscideans and peryssodactyls is not a valid argument in favor of their trophic poisoning. It is not proven that horses and other monogastrics become empoisoned on pastures more frequently than ruminants. The absence of the rumen bacterial detoxification barrier is compensated by the more efficient work of the detoxification systems of the macroorganism itself. The non-ruminant hyraxes feed on plants, protected with potent glycosides (*Nerum oleander*), saponins and alkaloids (different *Solanacea*). Even more important is the circumstance that wild and feral ungulates, being led by instinct and experience, discern poisonous plants and choose the optimal proportion of feeding components under very different plant surroundings (ibid.). They perform it far more efficient than domestic ungulates do. In modern times feral asses and horses, in spite of their monogastricity, successfully populated vast regions of both Americas and Australia, being obliged to feed mostly on other plants than those of their native lands.

Guthrie's model seems doubtful also because extinct sloths, glyptodons, peccaries were rather poly- than monogastric, judging from their extant relatives. According to this model (see above) large ruminants detoxify antiherbivory compounds better than the small ones. However such extinct ruminants as American ovibovines (*Symbos* [ ?= *Bootherium*!], *Euceratherium*) and Eurasian giant deer (*Megaceros*) were larger than the majority of the survived camelids, bovids, and cervids.

The trophic versions are inconsistent with phytogeographical data too. Plants, rich in alkaloids and other antiherbivory substances are less numerous in temperate than in tropical zone (Levin, 1976; Herbivores, 1982). In Old World tropics, however, the megafauna thrives. Also C-4 grasses are more abundant there than under temperate and high latitudes (Harborn, 1985). Thus in Serengety park, fabulously rich in big game, C-4 grasses consist 90% of the herbaceous cover (McNaughton, 1985).

## 5.6. The particular climatic models of the extinctions of North American mastodons

According to Dreimanis (1968) the North American mastodons became extinct at the East of USA because the Glacial spruce forests were superseded by the pine forests of early Holocene. This version is based on the study of the macrorests of plants, found in the mouth and stomachal areas of the mastodon

skeletons conserved in the marsh silt. Rests of spruce forests plants (larch, hemlock, etc.) prevailed in most of cases. Pine woods became dominant due to the warming. Mastodons could not adapt to new food. The retreat to boreal woods of Canada was cut off by the pine wood zone on moraines and sand dunes near Great Lakes. This zone appeared at the very beginning of the warming. Being 'trapped' the beasts retreated to spruce forests patches, remaining in damper places. The warming went on, and these patches vanished together with giants (ibid.).

King and Saunders (1984, 1986) rejected this interpretation. They established that in Missouri during the Middle Wurm Interstadial (about 34 kyr BP) mastodons were abundant in pine dominated parklands without any trace of spruce. Authors decided that giants were killed at the onset of the Holocene not by pine, but by the broadleaf woods that became dominant with further climatic amelioration. The way to septentrional conifer forests is believed to be blocked by huge periglacial 'superlakes' of the melted water. Then these 'seas' have gradually reduced to the state of the modern Great Lakes, and pine, spruce and fir dominated forests, this 'mastodons dream', have been installed in the region. It was, however, too late. The giants, deprived of pines, have been already 'pined out' on the inappropriate food.

Both mentioned models were discounted in 1992 by J.G. Ogden. He studied the stomachal contents of the mastodon carcass, found in 1991 in the peat/silt trap in Ohio. The eaten food consisted uniquely of swamp plants. Similar cases were previously known for New York and Virginia where mosses, reeds, willow and other swamp plants were eaten without the admixture of plants of conifer woodlands (Dreimanis, 1968). Ogden argues that mastodons became extinct due to the drying of the immense bogs at the onset of the Holocene.

All three exposed versions are equally biased. In each model only some selected facts are considered, while the others — neglected. The mentioned proofs of mastodon feeding on the diverse swamp, spruce, damp and dry pine wood vegetation are equally convincing. If all the evidence were considered then we should come to an inevitable conclusion that North American mastodons were polyphagous and euryoecic creatures. It means that none of the above-mentioned changes could remove them. The periglacial 'superlakes', invoked by King and Saunders model, were situated on plains. Consequently, their banks should be low or even swampy. Owing to this reeds, willows, and other riverine and swamp plants should be abundant. Eating this rather suitable food, mastodons could easily survive till the Holocene 'advent' of the equally desirable plants of conifer forests. The retreating waters, depending on local relief, soil and climatic conditions, gave way to marches, pine or spruce forests that were all good mastodons pastures. Hence mastodons of the North-Eastern USA had no environmental reasons for extinction.

During Wurm the elevated Western part of USA was populated by mastodons too (Kurten & Anderson, 1980). There were no continuous 'superlakes' and beasts could go free to Canada. Likewise mastodons of the wet South-East had no environmental reasons to die. Broad-leaved trees became dominant here in the Holocene. Nonetheless various pines (chiefly *Pinus palustris*) and vast spaces of forested swamps remained abounding from Virginia to Florida and Mississippi delta (Watts, 1986).

Further still, if mastodons could feed on so different plants as moss or reeds of swamps and pines or hemlocks of dry and wet woodlands, then it is improbable that there were no broadleaf trees in the rich North American flora, corresponding to the requirements of these giants. Such cases are unknown among extant cervids and bovids. Owing to a considerable mass of forage necessary to mastodons, they hardly were too fastidious in feed choice (Sect. 2.). Undetermined leafed trees were eaten by a mastodon, found in Virginia (Dreimanis, 1968). According to Guthrie (1984) mastodons browsed mostly on deciduous trees. Unfortunately we do not know what was the food of mastodons of Mexico and Florida. It is sure that there was no spruce in Florida even during the coldest phase of Late Wurm Pleniglacial (20-18 kyr BP). There were mixed pine and broadleaf forests (McDonald, 1984; Watts, 1986), that were the home of mastodons too. The spacious dried shelves of the Gulf of Mexico, densely populated with mastodons (Lundelius & al., 1986), were probably covered with subtropical vegetation. Mastodons of Mexico and of the Middle West of USA lived among mosaic vegetation of 'savanna' or 'criophytic savanna' types under quite continental climate, although they should be connected here mostly with woodland patches (Kurten & Anderson, 1980). So the mastodons, much like the mammoths lived under various environmental conditions.

Mastodons were present during the warm episode about 60 kyr BP in broadleaf woodlands at the west of Missouri (Saunders & Tassy, 1987). It does not agree with the idea of their extinction due to the 'advent' of such vegetation at the onset of Holocene (ibid.). The regional climate at that episode was warmer than now, as suggests the presence of alligators and elephant turtles. Tree-stands were dominated by oaks, maples, walnuts, plum-trees, etc. It is true that mastodons were then far less numerous than later during pine parkland (50-29 kyr BP) and spruce woodland (25-12 kyr BP) periods (ibid.). It is possible, however, that mastodon numbers were reduced not due to the abundance of broad-leaved trees, but because of other reasons. One of such reasons could be the presence of another huge browser — ground sloths *Eremotherium*. There were no these sloths here in the subsequent phases (ibid.). Perhaps North American mastodons had greater competitive ability under cooler and/or wetter climates, while eremotheriums — under warmer and somewhat drier ones. The second reason was probably large proportion of open areas and small one of wet stations. It could be attested by the presence of camels (*Camelops*) and giant bisons (*Bison latifrons*). Later there were no camels whereas giant bisons were replaced by the smaller race (*B. antiquus*) (ibid.). It is worth noting that mastodons were always less frequent in the less wooded and more arid western part of the USA (Kurten & Anderson, 1980). They

completely retreated from Illinois at Riss-Wurm Optimum, when herbaceous plant communities began to dominate here (King & Saunders, 1986).

Even if one discounts these considerations as 'speculative' ones, climatists model still does not work: if the last Anaglacial/early Holocene environmental changes were so fatal, then why the mastodons survived the previous ones? They did not become extinct then, but prospered in woods from Florida up to Alaska (ibid.; Kurten & Anderson, 1980).

### 5.7. The particular climatic models of extinctions of several other Nearctic animals

The giant beaver (*Castoroides ohioensis*) of 150–200 kg is believed to be outcompeted by the extant Canadian one (*Castor canadensis*) of 15–30 kg (Kurten & Anderson, 1980). This contradicts to the long co-existence of both species throughout the Pleistocene and to the differences in their dentition, indicating the different food regimes. The giant beaver ate soft herbaceous plants of aquatic, semi-aquatic and mesic meadow biotopes. In contradistinction to Canadian beaver it used only small quantities of woody plants (ibid.).

Climatists think that North American peccaries (*Mylochius*, *Platygonus*), as large as European wild boar, were ousted and/or exterminated by black bear (*Ursus americanus*). The competition became intense due to the drastic contraction of the patchy woodland or parkland. These favorite peccaries landscapes were supplanted by the closed forests of the Holocene (Guilday, 1967; Kurten & Anderson, 1980; Anderson, 1984). Even considering this view partially correct, one must remember that all these species coexisted for two or more millions of years. They survived several Interglacials that were climatically even more favorable for forests than the Holocene was. Evidently the environmental changes, baneful for peccaries and other Pleistocene megafauna, were not of the climatic nature (Putshkov, 1989b).

It is often presumed, started from Ge.G. Simpson, that horrific short-faced bear (*Arctodus simus*), whose mean body weight was about 600 kg, has been outcompeted by grizzly (*Ursus arctos*) (e.g., Kurten & Anderson, 1980; Anderson, 1984; with some reserves — Guthrie, 1990b). Though grizzly has indeed occupied most of his Nearctic range only in the Holocene, this supposition is incorrect. It does not correspond with the accentuated flesh-eating adaptations of short-faced bear, such as dentition of a predatory type as that in polar bear and long legs, well adapted for the active chase of a prey (Kurten & Anderson, 1980; Anderson, 1980). It is even less consistent with the few thousand years long coexistence of both species during Late Wurm Pleniglacial in the Alaska-Yukon area, cut off from the other North America by Glaciation ice-shield (ibid.). The omnivorous and 2–3 times smaller grizzly should be rather a prey than a competitor of the terrible monster. Lesser short-faced bear (*A. pristinus*) from Atlantic coast and South American representatives of *Arctodus* were not so imposing. However grizzly did not penetrate to their areas. Considerable part of Pleistocene range of *A. simus* has also remained unoccupied by grizzly (ibid.).

Under exposed circumstances only a playful possibility remains for the climate-induced competitive exclusion of short-faced bears by grizzly: new Holocene vegetation, being eaten by grizzly, made its meat poisonous for short-faced bears. Then populations of greater short-faced bears, sympatric with grizzly, died out due to victims poisoned meat, whereas the allopatric ones became extinct out of solidarity with their congeners!!

Formerly, climatists ascribed the extinction of North American tapirs and larger elephant turtles (*Geochelone crassicaudata*) to the maximal cold during Late Wurm Pleniglacial (Slaughter, 1967, etc.). But this turtle lived up to Anaglacial in Florida (here is found its carapace pierced with a spear of the age 12 kyr BP), while tapirs — also in other states (Lundelius & al., 1986; West, 1986).

The panbiotic explanations of these and other extinctions cases were proposed earlier (Putshkov, 1989b; 1991a; 1994).

### **5.8. The Late Wurm Pleniglacial Climate of USA and the considered models**

The Holocene climate continentalization extinctions models definitively lose their meaning considering the data on the USA climate during Late Wurm Pleniglacial (23-17 kyr BP). It was only at the very end of Wurm-Wisconsin (the Anaglacial time), when the climate was more equable than now with cooler summers and milder winters. At Late Wurm Pleniglacial climate of USA was everywhere apparently more arid than now with longer and more inclement winters (Galloway, 1983). Boreal conifer trees could grow more southwards than now (up to the modern deserts of the Far West) not due to the increased precipitation rates, but due to lower temperatures (ibid.; Cole, 1983).

## **6. SOME FINAL REMARKS ON CLIMATIC EXTINCTION MODELS**

### **6.1. Whether any range contraction was climatically driven ?**

Considerable range contractions (or, on the contrary — extensions) of numerous extant species had happened at the onset of the Holocene. Since climatic reasons are obvious in many cases, climatists insist that the final Wurm megafaunal extinctions are nothing else than climatically driven range contractions 'to ground zero' (Guthrie, 1990b: 47). The extinct species simply could nowhere find the suitable habitat. Even if the climatic conditions of the region are suitable for certain extinct taxa now, they could be intolerable there at the onset of the Holocene. That is why, according to climatists, American horses died out at the end of the Pleistocene, though mustangs and burros are prospering now in many regions (Hester, 1967; Graham & Lundelius, 1984, Guthrie, 1984). [For the panbiotic explanation see Putshkov, 1988, 1989b, 1991a, 1994].

Here, as well as in the case of the interglacial mammoths pastures, two different things are treated together. It is amply evident that the retreats of lemmings, polar fox and owl, wolverine and reindeer to present-day tundra and/or taiga zones were mostly or exclusively climate-driven. The same is true for the retreat to steppes of saiga, hemoine, pika and certain rodents. There were no these animals in West Europe at the time of Riss-Wurm or Mindel-Riss Optimums. But it is equally evident that the Holocene range contractions of lion, leopard, dhole, horses, Eurasian bisons are quite another matter. There was no significant interglacial range contraction of these animals (Kurten, 1968; Stuart, 1974, 1976, 1991, etc.).

Only the range contractions of this second group are in the line with the megafaunal extinctions without replacement. Climatic changes could not be their prime cause. If American and north Eurasian horses and lions did barely contract their ranges at Interglacials (ibid.; Kurten & Anderson, 1980) it should be other reason than warming that has oppressed them at the onset of the Holocene. There are, however, the intermediate cases. So the absence of the musk-ox in the zone of temperate forest is a natural phenomenon — there were no musk-oxen in Riss-Wurm Optimum Europe. But its complete extinctions in the Palearctic is not 'natural', for it was present in vast regions of Riss-Wurm East Siberia (Vangenheim, 1977; Verkhovskaya, 1988).

### **6.2. Whether 'combined' explanation resolves the problem ?**

Attempts to reconcile climatic approach with the anthropic one are as old as are both these doctrines. Their frustration is in complete concordance with Goete's

aphorism: there is a problem and not a verity that lays between two extreme opinions. The intermediate ideas offer no advantages over the extreme ones only because they may seem more 'reasonable'. Only better correspondence with facts could give to whatever idea such an advantage.

So according to D.D. Kvasov (1977) small residual populations of mammoths and their satellites, hidden in crioarid refuges from the effects of the warming, were overhunted by man. S.V. Tomirdiario (1977: 70-71, 1991 — pers. comm.) specifies that these refuges were confined to cold and dry Mongolian and Transbaikalian steppes, and that the animals were overhunted due to the 'appearance of the equestrian nomadic tribes' (!). Both authors believe that if it would be no man, mammoths and rhinos could 'sit out' the Holocene warming in the mentioned refuges as they did during previous warmings.

According to 'combined overkill and environmental change hypothesis' of A. Stuart (1993: 105) 'human predation [is] only resulted in extinctions when geographical ranges were already severely contracted and populations greatly reduced by climatic/environmental changes'. He insists (1991: 476, 513) that European mammoths and woolly rhinos have been 'trapped' by forests that were spreading from the East and, partially, from the South. Over all Northern Eurasia ranges of the both pachyderms within 15-10 kyr BP 'were sharply reduced by ... warming and the large-scale invasion of open habitats by forest.' Under such conditions, hunting press '... inflicted irreparable damage on small populations ...' (ibid.: 549).

The similar model is advocated by A. Lister and P. Bahn (1994: 120-121, 136-137). Number of mammoths has been drastically reduced by the climatic and vegetation changes. The small residual populations retreated to the last plots of parklands and meadows of modern forest and tundra zone and to the last water sources of the drying steppes. Here they perished with or without the contribution of the prehistoric hunters.

The 'combined' models would be plausible, if mammoths and woolly rhinos Interglacial ranges were indeed confined to pitifully small refuges. But this was the case neither for Mindel-Riss, nor for Riss-Wurm (Sect. 3.17.2.). Moreover, mammoths, woolly rhinos, horses and bisons during Riss-Wurm in the southern part of East Europe were as usual as during Glacials (L. Alekseeva, 1980). The same is true for the Northern (from Taymyr to Chukotka) (Vangenheim, 1977) and Southern (e.g., Baikalo-Patom upland and Novosibirsk region) (Verkhovskaya, 1988; Vasiliev, 1995) parts of Siberia. Similarly the decline of pachyderms populations in most regions of Europe and Asia **did not coincide but precede** the warming and/or forestation (Sect. 3.16.). These facts are neglected by Kvasov and Tomirdiario.

They are partially recognized by three other authors, thus making their positions self-contradictory. So Stuart (1991: 490) rightly accepts the capability of mammoths to live in forested areas and writes that mammoth and woolly rhinoceros in Western Europe have disappeared before the forestation (ibid.: 513). If so, it is incomprehensible, why he ascribes (ibid: 476, 513, 549; 1993: 105) the leading role to climate, and not to man ?

The combined model seems more plausible for the European populations of strait-tusked elephants, steppe and forest rhinos and hippopotamuses (Putshkov, 1989b, 1993a, b; Stuart, 1991, 1993). Their areas indeed dwindled considerably before and during the Late Wurm Pleniglacial. However it was not the case of Asian strait-tusked elephants (*Palaeoloxodon namadicus* = *P. tokunagai* = *P. naumanni*), widely distributed in Japan, Southern China and Oriental region (Kamei, 1981; Baryshnikov & Markova, 1990, etc.). As this pachyderm died out without considerable climate-induced range contraction, it seems rather doubtful that for the extinctions of their European and, notably, Fore Asian counterparts climate and not humans played the major role (Putshkov, 1989a,b, 1993a,b).



These and other facts better agree to the concept that man was the principal agent of the decline of pachyderms populations, whereas climatic changes only accelerated or decelerated the process (ibid.; E. Alekseeva, 1980; Schule, 1990, 1991, 1992a, etc.). Proboscideans could not perish due to forestation, for they kept woods open (Sect. 8.4.2.; 9.; 10.3.). This work was, however, impossible for residual pachyderms populations, thinned out by man. Such abnormally small populations of giants, as well as populations of other open places animals in the surroundings with small or no pachyderms populations, indeed failed to prevent the unfavorable environmental changes (Putshkov, 1988, 1989a, b, 1992a, b, 1993b, etc.).

### 6.3. Wurm/Holocene and previous transitions: different speeds of climatic changes ?

Sometimes the demise of Pleistocene giants is being explained by the unusually high celerity of climatic changes at Wurm/Holocene boundary (Vereshchagin & Baryshnikov, 1985; Saunders & Tassy, 1987, etc.). It is believed that fast switch of short-time (from one hundred to one thousand years) global warmings and coolings at the end of Wurm was unique event in Pleistocene history. This opinion was based mostly on the insufficient evidence concerning previous climatic shifts. The study of sufficient quantity of samples of fossil soils shows that such oscillations were highly characteristic for all anaglacial phases (Sirenko & Turlo, 1986). It has been shown by the studies of the rests of benthic foraminifera and stable isotopes in their shells that warming and sea level rise at the Riss/ Riss-Wurm boundary were even faster than during Wurm/Holocene transition (Emiliani & Shackleton, 1974; Seidenkrantz, 1993). At the very end of Riss considerable warming (Flakket Interstadial) and cooling (Kattegat Stadial) each of about 1000 years took place. Then the definitive early Riss-Wurm warming came at last. The switches of climate were rather fast and all the anaglacial cycle is very similar to Allerød/Younger Dryas/Preboreal sequence of Wurm/Holocene transition (Seidenkrantz, 1993).

### 6.4. Is the Holocene climate really different from these of any Interglacials ?

Climatists strongly insist that none of the climates of Pleistocene was similar to the Holocene one (Slaughter, 1967; Guthrie, 1990b, etc.). They proclaim that the global Holocene climate is a unique phenomenon that has never been known before, though they disagree on the nature of these differences. Some authors (Slaughter, 1967; Axelrod, 1967; Kurten & Anderson, 1980; Graham & Lundelius, 1984, etc.) state that it was less continental, without too strong seasonal differences. Others, first of all the partisans of mammoths extinctions due to tundra-steppe crash conception, prefer the crioaridity model. Both views are biased, for it is proven convincingly that at different epochs of the Pleistocene the global and regional climates were alternately more severe and more mild than now (Sect. 3.14.; 3.17.; 5.8.).

Thus at Interglacials lemmings, picas, polar foxes, saigas, reindeer, musk-oxen, woolly rhinos and (for Riss-Wurm Optimums) mammoths, as well as the crioarid plants, retreated out of most of the Europe. In England the mean July Riss-Wurm Optimum temperatures were 2-3° higher than now and 1-2°C higher than during the 'Climatic Optimum' of the Holocene. Many warm-loving creatures that are absent now were present. For example in England lived pond turtle (*Emys orbicularis*), southern mollusks (*Corbicula fluminalis*, *Belgrandia marginata*), some insects (e.g., dung beetle *Aphodius opacicollis*) and plants (e.g., *Pyracantha coccinea*, *Acer monspessulatum*) that are restricted now to Mediterranean region (Stuart, 1976; 1991). Boxtree, holly and yew were spread in Middle Europe more widely than they are now as a result of the more oceanic and humid climate with milder winters (May, 1993). In Czechoslovakia mean annual temperatures were 2-3°C and precipitation level about 50% higher than now (Lozek — cyt. by Sirenko & Turlo, 1986).

In Riss-Wurm Optimum East Europe broadleaf forest vegetation was spread 5-6° northwards and 1-2° southwards of the recent limits (Gerasimov & Velichko, 1986). Tundra, as a zonal formation,

appears to be completely absent from Europe. The broad-leaved lime-tree (*Tilia platyphylla*) was spread over most of Europe. This, together with the omnipresence of 'Brasenia complex' of thermophilous fresh-water plants (*Brasenia*, *Trapa*, *Aldrovanda*, *Salvinia*), directly proves that climate was mild and moist (Sirenko & Turlo, 1986). This is underlined also by the presence of walnut (*Juglans regia*) in West Ukraine (ibid.). The elaterid beetle from the genus *Corymbitodes* lived in Byelorussia. The genus is distributed now in Far East and Kirghisian forests (Nazarov, 1984).

During some of Pleistocene epochs (glacials, especially - stadials) zones of crioarid climates were spread wider than in the Holocene; climate on the average was much colder than now. Such epochs have been alternated with those (interglacial optimums), when such zones were smaller and the global climate was warmer than now. This being the case, how one could trust the statement that the Earth has never passed the macroclimatic situation, similar to the modern one? Such situations should inevitably take place at episodes that postdated the peaks of optimums.

## 7. THE PUZZLE OF THE PREHISTORIC EQUILIBRIUM

The outlined evidence proves that climatic versions of Pleistocene extinctions without replacement have many feeble points. However one point rests unshakable: ecological capacity of the Pleistocene continental communities for megafauna has vastly exceeded that of the Holocene ones. What was the prime cause of these differences? This is the most crucial point of Pleistocene extinctions debate.

### 7.1. The 'paradox of tundra-steppe' or the 'paradox of prehistoric pastures' ?

The ecological structure of rich megafaunal set of 'mammoth ecosystems' strikingly resembled that of such sets of African savannas (Vereshchagin & Baryshnikov, 1983). Such megafauna is inconsistent with low productivity and certain other particularities of plant communities, dominating in modern tundras, boreal forests and, partially, even in steppes. This phenomenon has been called the 'paleoecological puzzle' or the 'paradox of tundra-steppe' (Vereshchagin, 1988). However this paradox is only a particular case of a more general problem that deserves to be called the 'paradox of prehistoric pastures' (Putshkov, 1989a, 1992a). The mainland ecosystems, highly favorable for large mammals, had the global distribution during most of Cenozoic era (Savage & Russell, 1983; Carroll, 1987; Anderson, 1984, etc.).

During the Pleistocene the plant communities of not only the 'mammoth-' (Yurtsev, 1976; Sher, 1982; Musil, 1985; Vereshchagin, 1988, etc.; Verkhovskaya, 1988; Guthrie, 1990a,b, etc.), but also of the other dominant mainland ecosystems (Guilday, 1967, 1984; Kurten & Anderson, 1980; Mania, 1983; Guthrie, 1984; Graham & Lundelius, 1984; Schule, 1992a, etc.; May, 1993; etc.) were more favorable for large mammals than the Holocene ones. The dominant Pleistocene plant communities were more productive and more mosaic (= more patchy) than the Holocene ones. The role of plant associations precious for the feeding of large herbivores was higher. Savannas, parklands and open woodlands occupied far greater spaces, while completely treeless grasslands and, especially, the closed forests — much smaller areas than in the Holocene (ibid.). The main Pleistocene plant communities were often similar not to modern zonal formations, but to the places of their contact (ecotones) or to non-climax communities of diverse stages of the plant succession. Due to this there were an increased local biotic diversity, including the unusually (in comparison with most Holocene ecosystems) high density and diversity of large mammals (Guilday, 1967, 1984; Kurten & Anderson, 1980; Mania, 1983; Guthrie, 1984; Graham & Lundelius, 1984; Schule, 1992a, etc.).

## 7.2. Does the climate explains the 'paradox' ?

Many attempts were made to find the solution of the prehistoric pastures riddle among the global climatic particularities of the Pleistocene. Some ideas are well founded, e.g., those of expansion of cold steppe and steppoid plant communities and contraction of areas of temperate woods in stadials. But the global distribution of ecosystems with rich megafaunal sets, and their preservation in spite of the reiterated global climatic oscillations does not permit to consider the reasons that acted only regionally and/or temporarily, as the principal causes.

At every epoch of the Pleistocene on every continent the climatic gradients were as diversified, as they are now, although their borders were largely shifting (Sinitsyn, 1980; Yassamanov, 1985; Lister & Bahn, 1994, etc.). In spite of this, plant communities with the described features (Sect. 7.1.) dominated over all climatic zones of all continents. Everywhere these features were retaining in spite of the numerous Pre-Late Wurm climatic oscillations. In other words the climate-induced changes of floristic and faunistic composition were not accompanied by major changes of the communities structure (except the regions, covered with ice or converted into deserts). The density and variety of large mammals remained invariably high (Quaternary Extinctions, 1984).

Climatists explain the dominance of continuous closed forests in West and Central Europe during the Early Holocene by wet and warm climate. However the climates of the Riss-Wurm and Mindel-Riss were even wetter, warmer and more equable (Sect. 3.17; 6.4.). For that reason they were even more favorable to such forests and less fit for the megafauna of open and semi-open spaces. In spite of it plant communities here remained highly mosaic and productive for the megafauna. Landscape was this of open woodlands with considerable patches of herbaceous and bushy vegetation (Reed, 1970; Turner, 1975; Stuart, 1976; Mania, 1983; Stuart & Hibbard, 1986; May, 1993, etc.). Therefore, large herbivores were represented not only of predominantly browsing species, such as strait-tusked elephants, forest rhinos, red, fallow and roe deer. The basically grazing forms (horses, bison, including large and large horned 'steppe' forms, aurochs) and other large beings, inconsistent with climax closed forests (giant deers, cave bears) were as common (ibid.; Kurten, 1968, 1976). Hence it is not surprising that large predators of this 'Palaeoloxodon biome' (cave lions and hyenas, leopards, wolves and dholes) were the same, as these of the mammoth one.

In other words the Europe of glacial and interglacial times was equally rich in megafauna (although its species composition and each species density were not identical), in spite of sharp climatic differences (Putshkov, 1989a,b). The same is true for other regions (ibid.; Quaternary Extinctions, 1984).

Nevertheless climatists persist in the belief that climates of even the warmest and of the coldest episodes of the Pleistocene were more similar to each other than to the intermediate Holocene climate. 'Greater climatic diversity produces greater biotic diversity, but we don't know whether this climatic diversity was intraannual, interannual, or interdecade, and we don't understand the nature of variability' (Guthrie, 1990b: 52). It is stated that in the Neogene and the Pleistocene climate has globally favored to great local diversity (mosaicity) of plant communities and to the long duration of the growth season of plants (Sect. 5.5.)

But how the **global warming** (not cooling!) could be resulted in the **quasiglobal shortening of the growth season of plants** ? It could well be so in regions subjected to severe aridization, but not in mesic and humid regions of tropical, subtropical and temperate zones. Can it really be true that even in Florida, Mexico and Brazil the plants began to vegetate insufficiently long for extinct megafauna ? How could the growth season remain be sufficiently long for equids and proboscideans in many zones of the Old World, if it become too short in every climatic zone of the New World ? Reasoning from this theory, we should admit that the growth season of the vegetation of Ukrainian open ground communities was sufficiently long for pachyderms under subtropical conditions of the Neogene as well as under subarctic ones of the Quaternary stadials. It should be recognized then that this season became short in the Holocene. Is it possible that the temperate Holocene climate, intermediate between the two non-crucial extremes, was the crucial one ? And again it should be explained, why temperate climates of Interglacials did not resulted in the pernicious shortening of the growth season.

Then it is improbable that **global or regional climate** could determine the **local 'fine and medium grain' patchiness** of the vegetation. Be this climate of whatever great 'intraannual, interannual and interdecade diversity' it could not act over the neighboring patches of the flat country ecosystem in different ways. The 'paradox of prehistoric pastures' can never be understood by taking into consideration only climatic influences on vegetation cover. Far more selective agent(s) should be invoked.

It is useless to seek them among non-climatic abiotic agents. Fires, storms, floods, thermoclast processes destroy locally the climax plant communities. Due to them appear good, though temporary, pastures for large herbivores. But the frequency of such phenomena is too much dependent on the general type of the climate (Shennikov, 1966; Walter, 1982, etc.) that was in Interglacials similar to the present models. Likewise there are no data that relief and tectonic activity in the Pleistocene were too different from those of the Holocene. Only biotic interactions were sharply different due to high density of various large herbivores and carnivores. The modern counterparts of such ecosystems are the ecosystems of the Old World tropics, primarily these of the East and Southern Africa.

## 8. THE BIOTIC UNRAVEL OF THE PUZZLE

### 8.1. Large herbivores and the increased productivity of pastures

The increased productivity of the African big game pastures is an outcome of the grazing that accelerates the nutrients and energy recycling. Large herbivores eat 17-94% of the primary plant production and quickly return the removed and processed substances to ecosystem with urine, excrements and intestinal gases (methane, etc..) (Sinclair, 1975; Riklefs, 1979; Schule, 1990; Putshkov, 1992a). The cropped plants regrow intensively due to the **compensatory growth** (McNaughton, 1979). Often several, or many stems are growing instead of the eaten one. The next grazing on the regrowing 'grazing lawn' is energetically more efficient than the feeding on the intact herbage. In the former case the animal takes more food per mouthful. The food is of better quality: it is young tissue, highly nutritive and weakly protected with antiherbivory substances that regrows after previous grazing or browsing (McNaughton, 1984). Grass, damaged by grazers, rests green longer than undamaged one during dry season. The former grows faster than the latter in case of a rain (*ibid.*). By this means herbivores could make the growth season longer. As time goes on the compensatory growth capability exhausts due to repeated feedings. But under natural conditions there are no degradation of pastures. It is prevented by seasonal migration of phytophagans as well as by the removal of excessive individuals by predators, diseases, periodical and non-periodical disasters (Abaturov, 1975; McNaughton, 1985). The 'wear' of pastures is prevented also by the different extent of the damage, inflicted by different herbivores to different plants (Wagner, 1987, etc.). At last ungulates largely contribute to the restoration of the pasture vegetation by propagation and 'planting' of seeds of many of their food-plants (Janzen, 1984).

### 8.2. Zoogenic mosaicity of vegetation

The patchiness of the pasture vegetation, caused by other factors, is always reinforced by the activities of large herbivores. The irregularity of herbivores feeding, trampling and fertilizing activity invariably creates patches differing from each other by the nannorelief, the structure and moisture of soil, content of nutrients in it, species composition of the soil fauna and microflora (McNaughton, 1985). Hence — the famous pasture mosaics, or alternation of patches with different vegetation. The vegetation succession on the temporary territories of the males of ostriches as well as of those of many antelope species also contributes to this mosaicity. The location of centers of these plots shifts from one year to another (McNaughton, 1983; Wagner, 1987, etc.). The more different herbivores species are present, the more patchy is the vegetation. And different patches are to a different degree suitable to different herbivores. Animals prefer not to seek their preferable plants over all territory. They go from one patch, where preferable plants are concentrated, to another, crossing without feeding the patches that are less attractive to them, though more suitable to other herbivores (McNaughton, 1983, 1985).

### 8.3. Feeding successions of herbivores

Usually some phytophagans ('dependents') graze or browse after the others ('predecessors'). The feeding without predecessors is disadvantageous for the dependents. The latter grow thin and lose their resistance to enemies, diseases and competitors. The population density of dependents is growing (up to the certain critical threshold) in direct proportion to that of the forerunners (Gwynne & Bell, 1968, etc.). Zebras (*Equus quagga*) and gnus (*Connochaetes taurinus*) prepare in Serengeti the pasture for Thompson's gazelle. The latter easily crop the short grass lawn that rests after the grazing of the mentioned large ungulates. Due to them gazelles get an access to low dicots that are important for gazelles subsistence during dry season (*ibid.*). For the Grant's gazelles those patches are preferable, where dicots begin to prevail over grasses due to intensive gnu grazing (Kingdon, 1982). Kobs (*Kobus spp.*) depend on the hippopotamus or buffalo (*Syncerus caffer*) grazing, whereas oribi (*Ourebia ourebi*) efficiently grazes after the grazing of kobs, kongoni (*Alcelaphus buselaphus*) and other ungulates (*ibid.*). At the edge of Kalahari dik-dik (*Madoqua kirki*) needs two predecessors: zebras, cropping the grass and greater kudu (*Tragelaphus strepsiceros*), browsing the shrubs to the level, satisfactory for the dik-dik feeding. Because of this the latter is frequent only in districts where both his forerunners are abundant (*ibid.*). At Umfolozi park (South African Republic) after the increase of the density of white rhinos (*Ceratotherium simum*), gnus and zebras became more numerous too. They graze efficiently over

the short grass lawns, created by the giant grazing over the moderately tall herbage (Owen-Smith, 1987).

At the same time the white rhino himself grazes inefficiently over the herbage taller than 1 m high (Kingdon, 1979). However at Garamba park (Zaire) it grazes over the 'elephant grass' of 2 m height or more, when the thickets are previously cropped and trampled by elephants, hippos and buffaloes (White Rhino ..., 1977). At the vicinity of Rukwa lake (Tanzania) the mentioned 'trinity' converts two meters tall riverine grasses to short grass lawns that remain green throughout the dry season. Zebras, elands (*Taurotragus oryx*), reedbucks (*Redunca redunca*) and topis (*Damaliscus lunatus*) feed on these lawns (Vesey-FitzGerald, 1960). Behemoths here march over the valley during wet season, making a patchwork of paths-ditches in soft, overhumid soil. These ditches are covered with green grass during dry season. This grass feeds antelope puku (*Kobus vardonii*), thus allowing it to survive at droughts (ibid.). At Ruvenzori or Queen Elizabeth park (Uganda), the grasses, producing rhizomes indispensable for the warthog (*Phacochoerus aethiopicus*) during dry season, are maintained not by fire, as in most other regions (Kingdon, 1979), but by the hippopotamus grazing. Without behemoth grazing, these grasses (mainly *Alternantera pungens*) would be ousted by other plants (Lock, 1972).

#### 8.4. Ecosystems impact of the modern pachyderms

With rare exceptions the predecessors in herbivores feeding successions are larger than the dependent species. It is logical that elephants are the veritable ecosystems edificators. They transform the milieu much more drastically than other herbivores (from mites to rhinos); this is the result of the force, voracity and euryoecity of elephants as well as of their low losses from predators, maladies, seasonal disasters (Kingdon, 1979; 1982; Owen-Smith, 1987, 1989, etc.). Among species, dependent on elephants, there are many representatives of the megafauna (ibid.). This circumstance is extremely important to the problem of Wurm extinctions. It is impossible to conceive their mechanisms, ignoring the ecosystems organizing role of elephants and other pachyderms.

##### 8.4.1. Pachyderms and system of paths

Thickets of thorny bushlands ('nyika', etc.), bamboo, skin-cutting 'elephant grass' would be impenetrable for most of large mammals if there were no elephants paths (Kingdon, 1979; Nasimovich, 1975; Wagner, 1987, etc.). Likewise paths of black rhinos are usually commode for other animals. These giants with evident pleasure carve their way in the bushlands (Penny, 1987). But branches of some trees (*Commiphora*, etc.) do not break. They are straightening after the passage of the beast (Kingdon, 1979). In localities, where these trees are too numerous, number of paths decreases: it became difficult for rhinos to make paths. Rhinos prefer to use elephant paths as highways, adding to them the network of their proper walking and feeding paths that are alternately either crossing the elephant roads, or going in parallel with them. Hosts of ruminants, zebras, carnivores, baboons and porcupines use the paths system of giants, being incapable neither make, nor even maintain it for a long time in the bushlands (Schenkel & Schenkel-Hulliger, 1969). Begemoths (Wagner, 1987) and elephants (Bannikov & Flint, 1977) are the principal path-makers in the Nile basin papyrus thickets and/or reedbeds.

##### 8.4.2. Pachyderms and tree stands density

Under condition of man non-interference most of African parklands and savannas would be converted into closed forests or bushlands, bur for elephants (Schenkel & Schenkel-Hulliger, 1969; Laws, 1970; Wilson & Ayerst, 1976). In their absence the increased frequency of fires often lead in the long run only to the replacement of the pyrophobic trees and/or shrubs by the pyrophytic ones (Hirst,

1975). Eating grass, domestic and wild ungulates in many cases reduce the effect of fires on woody plants up to zero (Owen-Smith, 1989; Schule, 1990, 1992a). Dense trees up to 2 m height or more oust grass completely if there are no fires during two or three successive years, while the overgrazing is going on, (Laws, 1970, etc.). Browsing ruminants are incapable to prevent this process. They rarely destroy bushes and trees that are resistant to browsing (Kingdon, 1979, 1982; Wagner, 1987). Thickets inevitably close, forcing all the large mammals out to their edges, in case of elephants and black rhinos being absent.

Black rhinos crop high shrubs, including thorny and fire resistant ones, up to the condition of 'brush', suitable for the repeated browsing by rhinos and smaller browsers. The 'brush' is one meter high in the center and only 10 cm high at the periphery (Schenkel & Schenkel-Hulliger, 1969; Kingdon, 1979). Some shrubs and young trees are uprooted with the horn (Penny, 1987). Herbage persists among 'brushes' and covers the places of the uprooted woody plants. Grazers use this herbage. Sometimes black rhinos, if they are numerous, could even alone prevent the ousting of grass plaids and stripes by the bushland, or stop the encroaching of the bushland over savanna. Nevertheless rhinos are usually incapable to rarefy significantly the climax tree-stands in the absence of elephants (Owen-Smith, 1987).

Adaptations, considerably diminishing the damage from ungulates (size of a tree, density of a tree-stand and of tree branches, thorns, highly aggressive and painfully biting symbiotic ants), protect woody plants against elephants no more than against bull-dozers (Wager, 1963; Kingdon, 1979, 1982; Wagner, 1987). Giants pull shrubs and saplings out or break them. Trees with trunk thickness up to 35 cm (rarely even up to 70 cm) and up to 12 m high are uprooted. Even larger trees are debarked. Pieces of the water-soaked wood are picked out of the baobab trunks (Laws, 1970; Nasimovich, 1975, etc.). These operations are executed with the help of tusks, trunk, forehead, legs and participation of the back and hind quarter muscles (*ibid.*). Only rarely a bush or a tree is eaten up completely. In some tree species elephants eat the bark of a fallen tree, in others — fruits, roots or young branches with leaves (often only small part of them) (*ibid.*). Males break or fell down trees, mostly not for the sake of feeding. Animals do it in the state of wrath due to sexual excitement or other reasons (Kingdon, 1979). Many other trees are crushed by animals (mostly by youngsters) simply out of pleasure due to the excess of forces (Wager, 1963). Still others are destroyed by both sexes to clear the paths: elephants are highly intolerable to anything that encumbers their roads. Still other trees are felled by lonely individuals to attract other elephants: tree-breaking sounds is an important element of proboscidean sound signals (Kingdon, 1979). Due to all this, elephants inevitably create in thickets a system of glades, connected by roads. Other large animals rush into the depth of a bushland or of a woodland using this system. Precious fruit trees, contrary to the others, are quite rarely damaged due to the afore-said reasons — only fruits are shaken down to the earth (Lundberg, 1987).

Due to the activity of elephants other trees-destructive forces become more efficient. Hurricanes fall down more trees in the rarefied tree stands than in the closed ones. Thousands of even partially debarked trees are doomed due to the loss of resistance to diseases, wood-boring insects and, especially, fires (Spinage, 1963; Boechner & Dawkins, 1971). Fire runs fast over the grass, appearing at the place of trees that were destroyed by elephants. In regions, climatically fit for closed tree-stands it is an elephant, who paves the way for a fire, rather than the reverse (Laws, 1970; Kingdon, 1979, etc.).

In the past elephants have temporarily left the localities, where woody fodders were running short (Spinage, 1963). Grazers, especially behemoths and white rhinos, accelerate the reforestation. These two giants convert the herbage to a state of a short grass lawn that rests green due to compensatory growth (Sect. 8.1.) for most of the dry season (Owen-Smith, 1987). Fire cannot spread over such lawn (*ibid.*; Kingdon, 1979). Then bushes and trees restore to the condition, suitable for the elephants feeding again. At some regions elephants themselves can fasten the reforestation, switching to the grazing on the tall grasses (Nasimovich, 1975). Elephants not only destroy trees but 'plant' them too. They propagate seeds of many tree species on far distances and trample them occasionally to the soil that becomes soft and moist due to rain (*ibid.*).

#### 8.4.3. Pachyderms and forage for other large herbivores

The question is partially considered above (Sect. 8.1.; 8.2; 8.3.). Elephants are the first and the most important chain of many feeding successions simply because they create and maintain parklands and savannas over considerable part of their territories (Sect. 8.4.2.). Grazers (white rhinos, behemoths, buffaloes, gnus, zebras,

topis, congonis, oryxes, etc.) feed on grass, sprouting over the place of trees and shrubs, destroyed by elephants and, to a lesser extent, by black rhinos (Nasimovich, 1975; Kingdon, 1979, 1982; Wagner, 1987; Penny, 1987, etc.). Obligatory and facultative browsers (black rhinos, eland, greater kudu, gerenuk (*Littocranius walleri*), sable (*Hippotragus niger*) and roane (*H. equinus*) antelopes, etc., use nutritive and abundant woody undergrowth. Their trophic base is amply increased due to the patchwork of elephants paths and glades: the feeding places area becomes much greater and food — more accessible. Also they eat many fallen branches, broken and not eaten by giants, as well as the intact crowns of fallen trees (ibid.; Wagner & Schneiderova, 1984). Without elephants these resources would be used only by insects, giraffes and monkeys.

Elephants raise the general productivity of savannas to greater extent than other mammals. They enrich soil with the enormous quantity of dung and cover it with the layer of the uneaten and trampled grass. This layer impedes the evaporation of the humidity and the losses of microelements (Nasimovich, 1975). Many grasses and herbs, precious for the feeding of ungulates, are ousting from the plant communities by other plants, more resistant to ungulate grazing. But the former plants reappear and thrive there, where soil has been ploughed by legs and tusks of elephants that were seeking bulbs and tubers (Wilson & Ayerst, 1976). Only under abnormally high population densities elephants are no more the benefactors of ungulates, but turned to be their redoubtable competitors (Sect. 2.4.).

#### 8.4.4. Pachyderms and droughts

Certain bushlands and savannas mammals (both rhinos, zebras, buffalo, gnus, puku, sable and roane antelopes, lion, hunting dog) should drink more frequently than others (warthog, giraffe, eland, bushbuck, reedbuck, topi, congoni, impala, spotted hyena, leopard, etc.). The third ones (oryx, lesser kudu, many gazelles, dik-diks, many rodents) could do without drinking at all (Vesey-FitzGerald, 1960; Water ..., 1968; Kingdon, 1982). Animals of the first and, sometimes, of the second group too, would have died out over immense areas of the periodically waterless regions much more often than they die in reality, but for the 'wells', dug by elephants in beds of dried up rivers (Vesey-FitzGerald, 1960; Kingdon, 1979; Wagner & Schneiderova, 1984). The depth of such 'wells', attains up to 1,5 m (Nasimovich, 1975), or even to 2,4 m (Haynes, 1987). Due to them giraffes, lions, zebras and black rhinos penetrate even to some parts of the Namib desert (Giraffes ..., 1981). Only during extremely long and severe droughts elephants do not leave the vicinity of the waterholes, chasing other animals and their proper young (Haynes, 1987).

'Wells' dug by Asian elephants, are similarly used by leopards, deer, and buffaloes in periodically arid parts of Ceylon and India (Krishnan, 1970; McKay, 1973).

'Wells' of 0,5 m depth, dug by black rhinos, are not so important, though smaller animals use them too (Penny, 1987). Hippopotamuses of the Rukwa valley (Tanzania) can live more than one month after the drying of a lake or a river. They lay in a quagmire of their wallows, created due to the active pressure of animals (Kingdon, 1979). Water, soaking in these wallows, as well as in hippos' footprints, though being of a very bad quality, is drinkable for behemoths themselves, as well as for antelope puku. This water often saves both of them from death during the dry season (Vesey-FitzGerald, 1960).

Pachyderms mightily help to other animals to cope with drought also by keeping the plants in a condition of active compensatory growth (Sect. 8.1.).

#### 8.4.5. Pachyderms and the diversity of the megafauna

Different ungulates are not at the same degree adapted to a different extent of tree-stand density as well as to other characteristics of the vegetation (Hirst, 1975; Kingdon, 1979, 1982). Due to this, vegetation changes influence the competitive ability of many ungulates. Most of them prefer the ecotones between densely wooded (forests or bush thickets) and open (grasslands or savannas) habitats. Certain species dwell such ecotones for they need mixed grazing/browsing diet. Others are grazers that use tree stands as shelter from predators and heat (ibid.). Some forms, as, e.g., oribi, need short grass patches for grazing and tall grass patches as hiding places (Kingdon, 1982).

'Elephant-dwelled' woodlands and woodland/savanna landscapes are the mosaic complex of plaids with tree-stands and herbage of various heights, density and species composition. Here coexist ungulates that do not live together in the absence of elephants. Different carnivores also easily coexist due to the diversity of prey items and increased landscape ecotone diversity. Megafauna is the most diverse there, where the ecosystem effects of elephants are modified by those of hippos and both rhinos (Owen-Smith, 1987). Elephant 'wells' also strongly contribute to the maintenance of the megafaunal diversity (Sect. 8.4.4.). Elephants restrict the density of certain ungulates, such as gray duiker (*Sylvicapra grimmia*), bushbuck (*Tragelaphus scriptus*), lesser kudu (*T. imberbis*), eland, etc., through trophic competition and partial destruction of their preferable habitats. Even in this case their activity leads to the increase of the diversity of the ecosystem as a whole (Owen-Smith, 1989). Only the abnormally high density of elephants leads to the transformation of savannas or bushlands to treeless grasslands with the corresponding impoverishment of the megafaunal set and then — to catastrophic die off of elephants (Sect. 2.4.).

#### 8.4.6. Pachyderms and the moist jungles

The outlined evidence (Sect. 8.4.1.— 4.) does not concern humid tropical forests, where there are relatively few large mammals. The megafauna would be even less representative there, but for elephants. Without elephants, glades that appear due to the falls of the old trees or due to the dying out of the old bamboo stands, are disappearing very fast. Due to extremely favorable temperature and moisture conditions, saplings quickly become large trees, inaccessible for browsing. The light loving shrubs and herbage disappear due to the overshadowing. Marches between glades are often difficult for ungulates due to the interlacement of overground roots, undergrowth, fallen branches and hanging lianas (Wagner, 1987).

Tropical forest with elephants is a quite another matter. Glades are linked with each other by paths, cleared from all hindrances up to the elephant height or higher (beasts tear off many lianas). The vegetation of glades is eternalized on those stages of succession that are more suitable for the feeding of elephants and other herbivores. Undergrowth is retained in the condition of so-called 'elephant-tangles'. These are dense thickets that are nonetheless well fit for the browsing, being cut in every direction by the dense network of paths. Glades are numerous: new ones appear, whereas the old glades are still under existence. Elephants even widen glades by uprooting small trees and debarking the large ones (up to enormous emergents). The debarked trees are doomed to be ruined by termites. Forest becomes more light and patchy to the profit of many its dwellers (Short, 1981). In Africa vegetation of elephants glades is used by gorillas, okapis, yellow-backed duiker (*Cephalophus silvicultor*), dwarf antelopes (*Neotragus batesi*), bongo (*Taurotragus eurycerus*), red buffaloes (*Bubalus caffer nanus*), giant forest hog (*Hylochoerus meinertzhageni*) (Kingdon, 1979, 1982; Owen-Smith, 1989). The four last species can not live in the primary forest without considerable glades at all. If the man-made clearings are not taken into account, it is only in 'elephant-tangles' that buffaloes are capable to create by their browsing and grazing activity patches of herbaceous vegetation. These patches are necessary for them, as well as for the mentioned bongos and hogs, whose grazing prepares the pasture for dwarf antelope (Kingdon, 1979, 1982).

Elephants raise the ecosystem diversity of tropical forests not only by the maintaining of the successional plots, but also by the shaping of the species composition of the climax vegetation. This shaping is the result of the different resistance of different plants to elephant browsing as well as to the role of pachyderms in the spreading of seeds. Elephants are unique or even optimal distributors of seeds for 30% of the climax trees of the Tai forest (Ivory Coast). Fruits of the most of these trees are eaten by monkeys, rodents, bats and ungulates, but these animals can not spread their seeds, or do it rather inefficiently (Alexandre, 1978).

The repeated grazing by Asian elephants maintains most of the Ruguna park monsoon forest (Ceylon) in the state of peculiarly deformed tree stands no higher than 5 m. Dense branches of these trees feed not only elephants but also deer (*Cervus axis*, *C. unicolor*) and buffaloes (*Bubalus b. arnee*) using the network of elephant paths. Near watering places trees and bushes disappear due to intensive trampling and browsing. They are replaced by grass that completes the ratios of all four mentioned herbivores (Mueller-Dombois, 1972). In India gaurs (*Bos gaurus*) like to go after elephants, eating numerous branches, broken by giants (Krishnan, 1970). In Malaysia elephants destroyed two palm species, considered as pests of silviculture. The first is quickly proliferating bertam (*Eugeissona triste*) that forms dense monospecific stands. The second one is baya (*Oncosperma horrida*), with trunk, densely covered with horrendous thorns. Elephants fall it down by pressing with their forehead, and then press out the mild edible core out of trunk with legs. Movements are so precise that all spines are breaking without doing any harm to beasts. Due to elephants these palms of the great competitive ability could not oust many other trees (Hubback, 1941).

Sumatran rhinos (*Dicerorhinus sumatrensis*) in the absence of elephants have difficulties in the maintaining of the network of their feeding and walking paths. If the latter are present, the rhinos make



far more paths than necessary for their proper use. Rhino reposes at the wide elephant path, and then carves the crossing and collateral paths itself, breaking through dense and, frequently, thorny undergrowth with evident pleasure. Paths of the two pachyderms are used by deer, tigers, hog-badgers, peacocks and other animals (Strien, 1986). On Java paths of smaller one horned rhino (*Rhinoceros sondaicus*) for long centuries were used by people and animals. Then the modern human roads were paved over them (Penny, 1987).

#### 8.4.7. Pachyderms and other environment making factors

Besides pachyderms many other factors work over the vegetation of the Paleotropical ecosystems. These are climate, relief, soils, fires, hurricanes, carnivores and ungulates other than pachyderms, rodents, locusts, ants, termites, tsetse flies, other animals, microorganisms and other agents. All of them are very important (Guilday, 1967; Hester, 1967; Hirst, 1975, Kingdon, 1979, 1982; Wagner, 1987; Wilson, 1987; Terborgh, 1988, etc.), though none is the primer cause of the special fitness of African pastures to the megafauna. It is sufficient to remind that overall diversity of Australian and South American organic world is high, whereas their megafaunal sets are strikingly poor. The diversity of relief and climatic types there is comparable with the African one. Fires are blazing in grasslands and savannas of these two continents as, or even more frequently and intensively (Kreulen, 1979; Flannery, 1989) than in Africa. It indicates once again that fires, in spite of the wide-spread opinion, are not the prime cause of the increased suitability of African pastures for the sustaining of rich large mammals communities. True enough, even in Africa, beyond the narrow zones of the intensive hippopotamus feeding, the grazers activity is usually insufficient to prevent frequent fires. Due to this, and, to a lesser extent, to the setting of fires by man, fires play such an outstanding role in modern savanna ecology. Fires largely contribute to the increase of the productivity of pastures. Nevertheless their role in the maintenance of the plant communities mosaicity and the coexistence of rich sets of large and medium sized browsers and grazers, is secondary in comparison with that of elephants (Laws, 1970, 1971; Hirst, 1975; Kingdon, 1979, 1982; Putshkov, 1989a, 1992a; Schule, 1990, 1992a). All American and Australian savannas are completely abiotically driven. In Africa the 'elephant-driven' savannas occupied probably most of savanna zone (the purely abiogenic savannas are mainly those of the Great Rift regions) (Owen-Smith, 1989).

The South American shrub and low trees associations (chako, caatinga, some types of serrados) are inhospitable for large herbivores due to their impenetrability, low accessibility of browsing and low quantity of the herbage (Martin, 1984; Guidon, 1987, etc.). They resemble the African bushlands, after the exclusion of elephants and black rhinos. Even elands, being introduced in Brazil, have converted the impenetrable shrubs and low trees thickets of an experimental plot to the open woodland with rich herbaceous storey (they efficiently broke branches, placing them between horns and then — turning the head) (Perry, 1972). As if sneering over the generally correct principle of the unsuitability of the closed rainforest for large terrestrial herbivores, the largest Neotropical herbivores — tapirs live in selva and not in pampa.

#### 8.5. Large herbivores in modern ecosystems beyond the Old World tropics

The environmental impacts of large herbivores are by no means exclusively Paleotropical phenomena. Not only domestic ungulates, whose density is abnormally high due to the protection by man, but also the wild ones, influence noticeably over the species composition and other characteristics of plant communities as well on these of small animals [Ungulates..., 1975].

For instance, reindeer in tundras, digging their food from under condensed or crusted snow, make snow crumbly. Due to this ptarmigans (*Lagopus mutus*) also get the possibility to find their snow covered food — frozen berries, etc.. (Formozov, 1990). A lot of birds of steppe and forest zones also seek considerable part of their winter food at plots, where snow is raked by ungulates (ibid.).

The traditional utilization of pastures in steppe zone is based over the grazing of sheep after horses or cattle. The fact that sheep find enough of food after larger ungulates, while the latter have nothing to

eat after the sheep grazing is not a unique reason for such a practice. Pastures that were not grazed by horses and cows in May and June, become profusely covered by ripe ears of feather-grasses (*Stipa capillata*, *S. sareptana*) in autumn. The long and sharp awns of the feather-grasses seeds screw deeply into skin and muscles of sheep, tormenting or even killing them. Horses and cows eat the unripe feather-grasses ears, thus preventing the mass appearance of dangerous seeds (Bykov, 1957). During winter grazing on snow covered pastures, sheep get access to fodder going after horses or cattle, whose snow-raking possibilities are by far superior to these of sheep (Formozov, 1990).

Many of herbs of the temperate forest zone would be ousted by other plants, if it were no 'ploughing' activity of wild swine that creates for these herbs favorable soil conditions. They 'plant' seeds of maples, ashes, oaks, elms, tramping them in the 'ploughed' soil. Due to this their sprouting becomes more successful (Bulakhov, 1975). Paths, made by large cervids or bison in forest zone, played an outstanding role in the life of these and other large animals in feebly disturbed areas. Spruce (*Picea*) have competitive superiority over fir (*Abies*), being far less actively eaten by Eurasian cervids (Walter, 1982).

Tapirs and other Neotropical ungulates influence the undergrowth and climax tree-stands composition of the rainforest, eating fruits, seedlings and saplings of certain trees more intensively than those of other trees (Terborgh, 1988; Dirzo & Miranda, 1990).

There are the many other cases of the noticeable environmental effects of various non-Paleotropical large herbivores. Nonetheless due to the absence of pachyderms, their impact is only a pallid shadow of the environmental impact of Paleotropical megafaunas.

### 8.6. The actualistic models for Wurm extinctions

Arguing against the 'key herbivores Wurm extinctions' model, Guthrie (1990b: 50) states that 'vegetation changes' that took place 'due to overhunting' of modern pachyderms 'have not resulted in a wave of secondary extinctions predicted by the keystone model. Diverse large mammals communities now flourish in the many game parks and extensive private holdings that lack elephants. In regions where black and white rhinos were extirpated the many decades ago, other herbivore species have not become extinct'.

However this judgment is no more than 'demi-truth'. The most important part of the evidence has not been taken into account. The genuine reasons of non-extinctions cases are not analyzed (Sect. 8.7.). Quite numerous local and regional secondary extinctions cases are completely disregarded.

To take an example, the climate of western Kenya and of the adjacent parts of Ethiopia, Somali and Tanzania has not changed during the last 200 years. Correspondingly there were no climate-induced changes of the season of plant growth that are considered by some climatists as decisive factor of the Pleistocene crisis (Sect. 5.5.). But till the end of XVIII century the previous savanna/open bushland mosaics have been replaced here on the territory equal to that of Roumania by the uniformly dense and thorny bushland-nyika (Thornbahn, 1984). It was the outcome of the extermination of elephants by Wambisha hunting tribes. Wambisha sold the tusks to Arabs and then to Europeans. Without elephants all the savanna biome has been gone, with most of its browsers, grazers and Wambisha themselves (ibid.). Till the end of a century at the present territory of Tsavo park (that is placed in this zone) remained only rare black rhinos, dik-diks and lesser kudu that largely used paths of rhinos and war-paths, maintained by massai. Also remained kobs, inhabiting the riverside reeds. And, at last, the meager maneless lions, those famous Tsavo man-eaters that greedily attacked the Indian railway workers (Guggisberg, 1975; Beard, 1989). In 1948 the park was founded. Starting from the mid-fifties the severe protection of elephants has been installed. Only few years were sufficient for the giants to restore the former savanna/open bushland mosaics. All the set of the East African megafauna has been returned (ibid.). Around the park and anthropocenoses the same nyika still dominates (Thornbahn, 1984).

At Chluchluwe reserve (Natal) elephants were exterminated about one century ago. Fires and restricted trees-felling could only slow down the encroachment of shrubs and forests. Populations of many ungulates were growing at the beginning, because lions, hunting dogs and chitas were exterminated in a line with the elephants. But then an implacable decrease of numbers of white and black rhinos,

zebras, kudus, bushbucks began. Stenbok (*Raphicerus campestris*), klipspringer (*O. oreotragus*) and reedbuck (*Redunca arundinum*) have been completely disappeared (Owen-Smith, 1989). In the return nyala (*Tragelaphus buxtoni*) that was previously rare, has turned to be highly competitive under new conditions and increased in number (ibid.).

In Chobe valley (Botswana) during few decennies of the absence of elephants, dense bushes relentlessly encroached over savanna in spite of repeated artificial burnings. In the line with it were decreasing the numbers of zebras, giraffes, stenboks, gnus, elands, roane and other antelopes, as well as these of all large predators. Chita has been extinct completely. Only return of elephants has give an opposite direction to the process (Simpson, 1978).

At Kafue (Zambia) and Kasungu (Malawi) parks the density of elephants and rhinos is low due to continuing poaching. They can not stop the offensive of the bush. No ungulate species has become already extinct, but most of them are represented by small herds, living over the small herb covered areas. Probably their extinction is only a matter of time (Owen-Smith, 1989). At Kruger-park (South African Republic) density of elephants is too low for the maintenance of open habitats. Due to this, populations of antelopes, living in ecotones (roane, sable and sessebi — *Damaliscus korrigum*) are in the state of constant depression (ibid.).

More than 90% of elephants, rhinos and hippos of Ugandan parks (Kabalega, Ruvenzori, etc.) were killed by poachers and soldiers of Idi Amin till 1978. Only few years were necessary for the conversion of grasslands and savannas spaces to dense forests of acacias and spurge-trees. Most of smaller ungulates were put on the verge of extinction due to difficulties of feeding and locomotion and, partially, to fires that became catastrophic, due to many standing dead trees (and/or dried tall grass in other habitats) (Hatton & al., 1982; Edroma, 1989). On the other hand the elephant and rhino poaching has been cut off in Zimbabwe during the war of 1972-1980 years, for poachers were killing by both armed forces (guerillas and Rhodesian army). The elephants became numerous and converted the immense space, previously covered with dense bushlands and forests in grasslands/open bushlands mosaics, rich in big game. But the further increase of elephant numbers would be harmful to other game (Hallagen, 1981).

The local disappearance of other big game after the extermination of elephants and rhinos has been registered also for many districts of Sumatra. The overgrowing of pachyderms paths drastically diminishes the mobility of deer, tigers, dholes and sun bears (*Helarctos malayanus*), as well as the chances for the survival of their populations (Strien, 1986). Life for Sumatran rhinos also became difficult without elephants. Number and space of rhinos feeding areas with early stages non-climax vegetation decrease, distances between them become longer. Rhino can repose on the broad elephant path no more. Only wild boars (*Sus scrofa s.l.*, *S. barbatus*) feel themselves well in jungles lacking elephants.

It is not merely megafauna, who suffers due to disappearance of giants from ecosystems. But hosts of invertebrates and small vertebrates, living in ecotones or linked with non-climax vegetation, usually did not become extinct. Even drastically diminished spaces of glades, forest edges, etc., are usually sufficient for the persistence of the viable populations of 'Little Things' (Wilson, 1987).

### 8.7. What prevents the 'pachyderms demise caused' secondary extinctions ?

The recent secondary extinctions cases prove in the most spectacular way that it is an impact of giants, and not this of climate that makes Paleotropical ecosystems so hospitable for the rich megafauna. But there are many cases, when there were no secondary extinctions after the extirpation of pachyderms. However these examples lose their persuasiveness, if the reasons, aiding lesser ungulates to survive, were considered. Some of African parks (e.g., Serengeti) are situated in

regions, where grasslands and/or savannas are maintaining due to soils conditions and/or other abiotical reasons, independently from the presence of elephants (McNaughton, 1985; Owen-Smith, 1989). But this is not the most important part of the answer.

It should be particularly emphasized that consequences of the removal of elephants from the historical and modern time ecosystems were/are considerably diminished by the forest or bushland clearing actions of 'man the agriculturer'. Animals largely use paths and roads that are maintained, but not too frequented by humans, feed on the man-made clearings, the man-burned spaces and abandoned fields (Guilday, 1967; Kingdon, 1982; Owen-Smith, 1989, etc.). Often it allows to maintain the sufficiently large ungulate populations, giving the illusion that the demise of giants does not lead to secondary megafaunal extinctions. The Paleolithic and later hunters surely tried to prevent such extinctions too, first of all with the elaborated system of burnings (Hester, 1967; Flannery, 1988; Schule, 1990, 1992a, etc.). But their possibilities in this field were not comparable with these of the 'civilized' man, as proves, e.g., the case of Wambisha hunters of XVIII-early XIX century in Kenya (Sect. 8.6.).

Other decisive circumstance is that Holocene large mammals are more resistant to the temporary decrease of density or even to the extirpation of pachyderms than were the Pleistocene ones, notably in America and Australia. The former are the descendants of animals that had been living for many thousand years (or even for about 3 million of years as in Africa) in ecosystems, exhibited to the disturbances, inflicted by man, including the man-made oscillations of number of pachyderms. This question has been considered previously (Putshkov, 1989a,b; 1992b, 1993a,b, 1994).

### **8.8. Deductions concerning the role of giant herbivores in modern ecosystems**

The increased, in the comparison with other regions, diversity of large (50-1000 kg) mammals in Paleotropical ecosystems seems to be caused mainly by the presence here of few gigantic (over 1 ton) phytophagans. They, notably elephants, strikingly improve the existence conditions for smaller megafaunal species, radically transforming the milieu due to their normal locomotive, feeding, water procuring and social behavior. Actively counteracting to unfavorable climatogenic environmental changes (complete forestation, other forms of landscape monotonization, droughts), they benefit not only themselves, but also many other animals. Speaking figuratively giants 'doom' plant communities to increased productivity and mosaicity, to the lowered density of trees-stands, to the abundance and large sizes of ecotonal and non-climax areas. These features are the same that were proper to dominant Pleistocene mainland plant communities (and probably to most of previous Cenozoic ones) (Putshkov, 1992a). The exclusion of giants from ecosystems leads to extinctions among smaller megafauna, similar to those that took places at the end of Wurm. Certain kinds of the man-induced environmental effects could decrease the unfavorable consequences of the extirpation of giants, partially or completely preventing secondary extinctions.

## **9. THE PREHISTORIC EQUILIBRIUM MECHANISMS**

The 'keystone removal concept' cogently explains the 'paradox of prehistoric pastures'. Extinct giants (proboscideans, rhinocerotids, the largest edentates, diprotodontids, etc.), like modern pachyderms, considerably modified the environment by treading paths through thickets, digging 'wells' in semiarid countries, stamping on snow and breaking frozen snow-crust in northern regions.

Crushing and eating trees, they created and perpetuated the glades, open woodlands, parklands and savannas in regions, climatically suitable for the monotonously dense scrubs or forests. At some other regions they 'planted' certain trees and cropped the grass thus preventing the accumulation of dried plant mass and, consequently, decreasing the frequency and intensity of fires. In this way they often maintained savanna conditions in regions, abiotically suitable for treeless grasslands. The giants were the leaders of grazing and browsing successions. Smaller herbivores modified the effects of giants (Owen-Smith, 1987, 1989, Putshkov, 1989a,b, 1991a, 1992a,b, 1993a,b, 1994; Schule, 1990, 1991, 1992a).

Vegetation reacted to the feeding, fertilizing, trampling and seed propagation activity of giants and smaller herbivores by the increase of the productivity of pastures as well as by the raising of its local mosaicity. Increase of the productivity of plant communities took place due to the expansion of plants with better developed aptitude to compensatory growth in response to repeated feeding and fertilizing of soils. Such plants under conditions of the intensive, but naturally regulated, multispecies grazing and/or browsing, efficiently competed with plants of poor quality but with well-developed chemical defenses. The repeated visits of giants and other herbivores to feeding patches have led to the 'eternalization' of their vegetation in the non-climax stages, which are (and were) the best habitats for the majority of large and medium-sized land mammals. The activity of different large herbivores led to the increased mosaicity (patchiness) of the vegetation. The increased zoogenic mosaicity, in its turn, was a factor that diminished the competition of herbivores; this facilitated their coexistence (Putshkov, 1989a; 1992a). The well-being of numerous representatives of the megafauna on all continents relied upon the aforementioned activity of gigantic herbivores (*ibid.*; Owen-Smith, 1987; Flannery, 1989; Schule, 1990, *etc.*; Maslov & Antipina, 1994, 1995).

Another important biotic agent of the Pleistocene equilibrium were the largest predators (Putshkov, 1989a; 1993a,b, 1994). They regulated the number of herbivores, thus preventing the monopolization of resources by prey species with higher competitive ability. Maintaining certain proportions between different prey species, top carnivores exerted the potent indirect influence on vegetation, small vertebrate and invertebrate species composition. So puma and jaguar, controlling the number of peccaries, tapirs, deer, howlers, largely contribute to the maintenance of the biotic diversity in Neotropical rainforest communities (Terborgh, 1988, *etc.*).

Were the giant herbivores also controlled by predators? Some biotists (Owen-Smith, 1987, 1989; Schule, 1990, 1991, 1992a) prefer the negative answer, other (Putshkov, 1989a, *etc.*) — the positive one. The former opinion issues out of the fact that modern tigers, lions and hyenas do not control the number of pachyderms. According to it numbers of prehistoric giants were restricted mostly by diseases and natural catastrophic events. Damage to vegetation has been decreased due to regular large scale migrations of proboscideans too.

The second position is based over the circumstance that certain extent of the human predation on pachyderms is the obligatory element of equilibrium in the Holocene Paleotropical ecosystems. The cessation of human control has led in Tsavo and several other African parks at sixties and seventies to fast proliferation of elephant and hippo populations beyond the ecological capacity of the environment. The giants' impact that was up to this moment beneficial, becomes, especially during droughts, destructive to both plant and large mammal communities, including the giants themselves (Sect. 2.4.). Epizooties and natural disasters are too irregular phenomena for the prevention of such course of affairs. It is difficult to imagine that in prehistoric ecosystems numbers of proboscideans and other giants have been oscillated similarly to these of lemmings or other voles. Even more difficult to believe that such, inevitably frequently, stressed ecosystems, were the appropriate place for the prosperity of rich megafaunal sets. Migrations are only subsidiary measure, working only in concert with not only efficient, but constantly acting mortality factors. Inventing pachyderms, nature was obliged to invent the efficient pachyderms-killers as well.

Such specialized young pachyderms hunters were larger species of saber-toothed cats — *Megantereon* (= *Machairodus*, part), *Smilodon*, and *Homotherium* (= *Machairodus*, part) (Kurten, 1968; Kurten & Anderson, 1980). The latter probably attacked proboscidean calf from the ambush, disemboweled it with a single blow of terrible fangs, then ran away, escaping adult proboscideans and returned, when the latter parted from the dead calf (ibid.). Saber-tooths were seconded with less specialized large predators, whose giant-killing potentialities could also be not negligible. According to some data (McKay, 1973) tigers in Burma killed up to 25% of elephant calves in the first half of XX century. Even adult elephants are sometimes killed by tigers (Singh, 1972). Among black rhinos lions and spotted hyenas mostly kill half-grown individuals, no more protected by their mothers. It allows to think that Neogene and Pleistocene top carnivores killed enough of young giants, for the preventing of the degradation of Old and New World plant communities. In Australia the same 'work' on marsupial giants (diprotodontids, palorchestids) was executed by enormous monitors and land crocodiles.

Nevertheless the losses of giants from non-human predators never were so important, as to undermine the decisive giant herbivores' impact on ecosystems. Saber-tooths numbers were dependent from these of young and sick pachyderms (Krantz, 1970). The possibilities of 'non saber-toothed' predators were restricted: it was hard for them to kill calves or subadult pachyderms near the herd or mother sufficiently fast as to have enough time for the safe retreat.

Largest predators also maintained the diversity of prey species by the suppression of subdominant predators, potentially more destructive for some victims. So the Far East ghorals and sikas fall in number in the absence of tigers. The tigers keep the density of these ungulates at high level because they persecute wolves fiercely; tigers being absent, proliferated wolves kill much more ghorals and sikas than tigers do. The role of largest carnivores in ecosystems stabilization became even more important, when hominids have learned to kill giant herbivores. Biped hunters were potentially dangerous for the 'Pleistocene Equilibrium'. On one hand they killed pachyderms more efficiently than saber-tooths and ousted the latter in the Old World well before Wurm. On the other hand their population density was dependent not on this of pachyderms, but on the wide range of interchangeable food resources. Preventing the overproliferation of hominids and humans (mostly women and children), big cats, hyenas, bears and dholes slowed down or prevented the overexploitation of pachyderms, thus ensuring the maintenance of the 'prehistoric equilibrium' (Putshkov, 1989a,b, 1993a).

In Neogene and Pleistocene the impacts of giant herbivores and top predators over ecosystems were even far stronger than in modern Palearctic, because there was no, or only minimal human intervention. The sets of giants in Pleistocene ecosystems were often richer than in modern Palearctic ones. In many cases they included 2, 3 or more species of proboscideans. Together with various numbers of species of other giants, they created even more patchy plant communities than those, created by modern pachyderms. This environment was even more fit for diversified lesser megafauna. Probably the feeding successions and other interdependencies of herbivores were then significantly more rigid than in modern African savannas.

Activity of giants has corrected the climatogenic stresses of communities, making them less pernicious for most of other megafauna in the just the same way, as elephants maintain now the megafaunal diversity under very different physico-geographical conditions (Sect. 8.4.). This activity served as the ecosystem protective mechanism against climate-induced changes. The efficiency of this mechanism is evident out of the following facts. Only during the last 2 million of years there were more than twenty major global climatic oscillations; some of them were of greater scope and/or celerity than the oscillations of the final Wurm/early Holocene (Sect. 3.17; 6.3.; 6.4.). They resulted in spectacular alternation of Glacials and Interglacials, stadials and interstadials, arids and pluvials, but not in mass megafaunal extinctions without replacement.

So the Prehistoric Equilibrium was based on the interdependencies of largest herbivores, largest predators, other megafauna and plant communities. The combined ecosystem impact of top herbivores and top predators minimized the consequences of numerous pre-Wurm climatogenic stresses for ecosystems and efficiently prevented the crash of the megafaunal communities (Putshkov, 1989a,b, 1992a, etc.). There were regional particularities of Pleistocene Equilibrium mechanisms (ibid.; Schule, 1990, 1992a; Owen-Smith, 1989; Flannery, 1989). They could be considered here only concerning the mammoth-biome.

## 10. MAMMOTHS MAINTENANCE OF THE MAMMOTHS' BIOME

### 10.1. Two views on ecological impacts of mammoths

According to one of them the principal cause of the maintenance of mammoths' ecosystems were mammoths themselves. During pre-Holocene warmings mammoths or, in earlier times, their ancestors (*M. trogontherii*, *M. meridionalis*), seconded with other herbivores, converted zonal vegetation of forest or tundra type to open woodland, parkland or criophytic savanna state. Open or nearly open areas covered with luxuriant meadow and/or steppe-like vegetation persisted because mammoths, like modern elephants, prevented the expansion of trees both by direct and indirect influences. During coolings climatic and biotic causes of deforestation acted in concert, but for pastoral productivity and mosaic plaid structure of plant communities the 'megaherbivory factor' still remained more important. Only when mammoths and rhinos had gone, the more modern biomes have been established (Owen-Smith, 1987; Putshkov, 1989a, 1989b, 1993b, etc.; Schule, 1990, etc.; Maslov & Antipina, 1994, 1995). These views are an application to mammoth biome of the global model of an panbiotic concept that is based on ecological effects of modern herbivores, notably elephants (Sect. 1.4.—6.; 8).

However R.D.Guthrie argues that it could be no valid analogy between 'unusual ecological effect' of such abnormal 'grazer-turned-browser' beasts as are African elephants and that of normal 'strict grazers' as were woolly mammoths and rhinos. The woolly giants 'did not rely on browse for the dry winter season', never '...made significant use of woody plants, especially the birch, alder, spruce, larch and pine that were taking over the northern steppes as mammoths became extinct ...'. So the giants '... could not have held back the mesic forests by direct action.' Also '... it is unreasonable to assume that ...' it could be done due to '... some unknown secondary effect' of mammoths activity. How could mammoths maintain the '... biome of succession grasses ...' if their predominant diet were 'arid grasses' of genera that were not '... early colonizers but climax groups'? Being 'strict grazers' they could only accelerate the demise of their grassland habitats, when climate became favorable for woods or moist tundra. Even this influence could be only of minor importance, for population density of northern pachyderms was 'considerably beneath that of the African model' (Guthrie, 1990b: 50, 51).

Nevertheless these assertions are rather misleading for only part of a very important evidence has been considered.

First, there are proofs of vast use by mammoths of plants that at any rate could not be considered as 'arid grasses' up to birch, larch, current, mosses, etc. (Sect. 3.15.1.). Herbaceous and woody plants of mesic and humid habitats were also largely eaten by Siberian horses and bison (Yurtsev, 1976; Filina & Filin, 1980; Ukrainseva, 1985, 1993, etc.). Then it is ignored that under the same regional climate both non-climax and climax plant-communities would be strikingly different in absence or presence of giant herbivores seconded by other gregarious ungulates.

Such neglecting is queer. Guthrie (1990a: 205-207) acknowledges himself that tundras and boreal forests are not mere products of climatically driven temperature and humidity. Taiga and tundra plants maintain themselves their favorite communities. They resist to evaporation thus retaining the soils under cold and hyperhumid conditions. Under these conditions spruce and other plants of spruce forests and tundras have decisive advantages over the meadow grasses. The latter need drier and richer soils. Meadow vegetation could not grow under spruce forest due to overshadowing and increased humidity and acidity of soil (mainly because of the decomposition of needles) (ibid.; Rabotnov, 1993, 1996). Spruce and other bushy and herbaceous spruce forests plants are low palatable or even toxic for

herbivores. So these plants exclude some cold adapted herbivores from spruce forest ecosystem (Guthrie, 1990a: 205-207).

Other full-grown boreal and temperate trees also determine to various extent the herbaceous storey composition. The weakest is this influence in peculiar scattered larch stands of vast regions in central and, partially, northern Yakutia (Sect. 3.4.).

Stating that only climatic aridization could shift the odds and replace taiga and tundra with grasslands, Guthrie (1990a: 208-215) glaringly contradicts with the facts that experimental fertilizing of northern soils with nitrogen, phosphorus and potassium fertilizers leads to ousting of mosses and sedges by meadow grasses and forbs (ibid.: 200-205). Grazing is favorable for meadow plants too (ibid.). Probably Guthrie does not pay to these facts much attention because extant ungulates (mooses, other deer, bison, bighorn sheep) do not drive taiga and tundra communities to zonal grasslands state. On the contrary — their ranges and population density largely depend on the resources of the restricted azonal habitats such as riverside or alpine meadows, glades, riverside willow thickets, etc. (ibid.; Guthrie, 1990b). But there is a tremendous difference between ecological effects of mammoths and these of extant northern herbivores. Moreover — effects of smaller herbivores in ecosystems with mammoths were different from those in the ecosystems without them (Putshkov, 1989a, 1989b, 1992a, 1993b).

## 10.2. Grazers and trees

The clear-cut grazing adaptations of woolly mammoths and rhinos (as well as these of horses, hemionus, bison, yak, musk-oxen, bighorn sheep, saiga and reindeer) could by no means be considered as signs of their harmlessness to woody vegetation.

The division of herbivores to browsers and grazers and their relations with plants in nature are not always so simplistic as in some of extinctions models. Pure browsers and pure grazers are rare. For most ungulates the mixed diet is optimal, at least at some seasons (Geptner & al., 1961, Kingdon, 1979, 1982; Penny, 1987, etc.). Though so called strict grazers (horses, many bovids) could live and proliferate without browse, they often do not spare the seedlings when meet them. Due to various reasons determining the trophic behavior, grazers of different or even of the same species could either favor the propagation of woody vegetation by oppressing the grass, or impede it by eating or trampling the seedlings.

So hippopotamus (as well as white rhinos, zebras, gnu and some other antelopes, cattle, sheep and goats) often accelerates the forestation by its grazing activity (Kingdon, 1979, 1982; Owen-Smith, 1987, 1989, etc.). On the other hand in places, subjected to the intensive grazing by numerous behemoths '... dense gallery woods will hardly ever form, existing woods may become more open or even disappear' due to '... wide mouth of hippopotamus works like a lawn mower, cropping not only grass but also young trees' (Schule, 1992: 49). Some Mediterranean islands and Madagascar were largely deforested by hippos that colonized them (ibid.). Hippos are thought to be responsible for creating the riverside meadows during Interglacials in West Europe (Turner, 1975; Stuart, 1976; Stuart & Hibbard, 1986).

'Hypsodont grazers with high-crowned teeth ... like goats, camels or horses ... are more efficient destroyers of woody vegetation than brachyodont ... woodland ungulates.' The former 'chew nearly anything, and they can feed from the ground, not only from fairly near the canopy like real browsers. Tree seedlings have little hope of surviving hungry grazers. Browsers would do them only little damage during their first years' (Schule, 1990: 278). Normal succession of a beech/oak forest in Germany after its felling (foxglove dominated lawn; raspberry-canes; birch wood; climax beech/oak forest) is prevented if grazing by domestic ungulates commences at earliest stage. In this case *Agrostis* dominated grassland installs and no forest reappears (Walter, 1982). The contribution of domestic sheep and goat in a matter of deforestation of many territories is too well known (Dorst, 1968), as well as their dual effect in forest fire profilaxis. Goats, horses, asses, and even llamas reduce the danger of conflagration and fire intensity in Spanish dehesas and regenerating French maquis, eating up grass and undegrowth. But 'the reverse of the coin is that not one young tree will grow as long as the donkeys are present' (Schule, 1990: 278). The renewing of the massive New Forest in England during XVII-XX centuries was several times ceased for decades due to combined activity of two hypsodont 'strict grazers' (ponies and cattle) and one brachyodont 'grazer/browser' (red deer) (Connell, 1975). In a word there are no grazing specializations that prevent browsing. It is the opposite thing (that is to be mixed browser/grazer in spite of the manifest morphological adaptations for browsing) that is more difficult, though not impossible (e.g., red deer).

The said on ungulates with even more reasons should be applied to elephants, as well as to woolly mammoths and rhinos (Sect. 3.15.). Macrorests of woody plants are almost invariable present in the digestive tracts of the frozen carcasses of Siberian mammoths, rhinos, horse and bison (ibid.). In the preceding context such presence gets much greater significance than it seems considering the quantitatively small share of woody plants compared to the bulk of the eaten grasses and sedges. It



means that animals did not neglect woody vegetation even during the warm season. In winter the share of the browse should be much greater.

### 10.3. Mammoths, spruce and other trees

Even if mammoths indeed recurred to feeding on large trees relatively rare, it worth noting that pachyderms and ungulates destroy saplings and full-grown trees not only by feeding but due to other aspects of their ethology too. Mammoths, much as the modern elephants, should destroy many trees in the course of their sexual behavior, simply out of pleasure, to clear the paths, etc. (Sect. 8.4.2.). Rhinos (to a lesser extent also wisents and stags) are also known as breakers of young trees simply for sake of physical exercises (Kingdon, 1979; Penny, 1987, etc.).

Certainly woolly mammoths were not as potent destroyers of adult trees as modern African and extinct straight-tusked (*Paleoloxodon antiquus*) elephants. The two latter species are/were better adapted to tree crushing activity due to their pointed, slightly or moderately curved tusks and stronger dorsal and hind quarter parts musculature. But the stunted trees (especially those growing on permafrost soils with a thin seasonal thaw layer) in many taiga regions were also not as mighty 'adversaries' as trees of climatically milder areas. Even more important are the slower tempos of the regeneration of boreal forests (both of low or tall trees types) than those of temperate and tropical ones. Being once destroyed by fire, pests or storm (with or without the help of mammoths), taiga trees needed many years to grow, ousting the non-climax plants. Under favorable climatic conditions struggle with other plants is easy for adult spruces, real edificators of the climax dark-needled taiga forests (Sect. 10.1.). For the seedlings of spruce, not to speak about seedlings of trees with less developed antiherbivore properties, the situation is more complicated even now. It was far more difficult at the times of mammoths.

Mammoths should inflict heavy damage to seedlings and saplings with their high crowned cheek teeth and two-pointed tip of the trunk, so well adapted for grazing on even very low plants. In this way they prevented the forestation of their pastures. Feeding of mammoths, horses and bison on larch, birch, willow and alder is proven, though part of specimens probably or surely belongs to dwarf forms (Sect. 3.15.1.4.). Such discrimination may seem important for climatic extinctions models. But for a feeding animal there are no differences between dwarf adult birches or bush alders and seedlings or saplings of tree alders and birches.

There are no reliable direct proves of the feeding of mammoths and their satellites on spruce and pine (ibid.). What is more, it is plausible that spruce has been feebly eaten by extinct large herbivores (May, 1993), being unwillingly eaten by the living ones (Geptner & al., 1961; Walter, 1982, etc.). But it was not necessary to eat little spruces for preventing the spread of the continuous spruce forest. For the destruction of many young spruces the repeated mammoths browsing on birches would be sufficient. It is known that needles of spruce and cedar pine that resist in winter to frosts of -40 degrees centigrade or more, are damaging by night frosts of -7 degrees centigrade in warm seasons (Walter, 1982). Birches and asps protect spruce seedlings and saplings from the belated spring or even summer frosts (Rabotnov, 1996, etc.).

Even more important was the circumstance that mammoths pasture activities caused a rapid recycling of nutrients in ecosystems. Eating up enormous quantity of plant biomass, mammoths and their satellites abundantly fertilized the soil with their dung and urine. Under such conditions grasses and herbs, rapidly growing on fertile soils and resisting to herbivores much more by rapid compensatory growth than by deterrent substances (McNaughton, 1984; Guthrie, 1990a,b), obtained the advantage. They ousted slowly growing plants, including spruce seedlings, that could realize their odds (well protection with toxic antiherbivory compounds) only on poor unfertilized soils. Due to all this the steppe-like plant-communities installed

under the drier and the meadow-like ones — under the wetter climatic conditions (Putshkov, 1989a).

Rather demonstrative is the fact that at the north-east of the Central Europe spruce forests transform to speckled alder ones due to regular pastoral activities of domestic cattle (Ellenberg — cit. by May, 1993). In boreal and temperate forest zones of Siberia and European Russia meadows resist to forestation due to repeated grazing. Seedlings and saplings are directly damaged due to eating and trampling by herbivores and are oppressed by competition from grasses and herbs that have ability to quick compensatory growth (Shennikov, 1964).

#### 10.4. Other impacts of mammoths and their satellites on vegetation

The similar situation was in climatically treeless tundras, where mammoths acted in favor of meadow grasses and forbs against bushes, mosses and lichens, these 'masters' of the present-day tundras. It is extremely significant that in modern typical tundras small patches of mesic meadows appear not only due to local abiotic conditions (*e.g.*, steep well-drained plots on southern slopes of hills that receive enough of the warmth in warm season, etc.). They occur also on the monotonous moss-covered flats in places with high lemmings density, around Arctic foxes burrows, on tops of hillocks, where birds of prey repeatedly dine and repose, as well as near the human settlements. In other words tundra meadows often have zoo- or anthropic origin. They appear everywhere, where soil gets organic fertilizers as garbage and excrements (Matveyeva & Chernov, 1992: 43). Dense and highly productive grasses and forbs develop there, oppressing mosses and lichens. At Pleistocene such meadows should be inevitably dominant vegetation type in all areas, climatically fit for present-day typical and bushy tundras, because everywhere soils were copiously fertilized with urine, excrements and corpses of mammoths and other large animals.

These meadows nourished the immense herds. Climatists are right saying that either mammoths and their satellites, or their foes, cave lions and hyenas, have not lived in taiga and tundra of the Holocene type. But they are wrong paying no attention to the reverse of the coin: these 'mammoth steppes' or criophytic savannas (meadows, woodland/meadows, parkland/meadows, etc.) existed during previous warmings at the places of the present-day taiga and tundra due to mammoths and other large animals feeding, trampling, seed dispersal, fertilizing and other activities.

Mammoths were the principal force of the maintaining of their biome that created and perpetuated the immense zoogenic meadows. Due to them other grazing and grazing/browsing ungulates had high population densities and could freely migrate through woodland and brushy spaces by meadow corridors (Owen-Smith, 1989; Putshkov, 1989b, 1993b). And these herbivores in their turn reinforced and modified the ecosystem impact of giants (Putshkov, 1989a, 1992a, etc.), as do now various herbivores in elephants dominated ecosystems (*ibid.*; Kingdon, 1979, 1982; Wagner & Schneiderova, 1984; Wagner, 1987, etc.). It is well known that not only overgrazing, but also undergrazing leads to degradation of meadows in different forest zone regions (*e.g.*, Abaturon, 1975). Seeds of many meadow and steppe grasses and herbs are spreading on and inside the large animals (Shennikov, 1966; Janzen, 1984). Large herbivores are the better agents for the spreading of seeds of herbs and grasses of disturbed places. Grasses and herbs, covered with excrements, mostly die, giving place for young plants, rapidly growing from the dung. In the best position for the germination and consequent growth are seeds that had been dug to the earth by dung-beetles. Moving over considerable distances, large herbivores restored the plants that disappeared locally due to various reasons. These phenomena have largely contributed to the maintenance of the local species diversity, richness, high mosaicity and productivity of pastures (Janzen, 1984;

Putshkov, 1989a). Various species of herbivores were to the different extent efficient as feeders on different woody and herbaceous plants, more or less efficient propagators of their seeds.

Changing feeding places, large herbivores could even raise the productivity of plant communities, growing in abiotically unfavorable habitats, with nutrients, brought in their bellies. Going from one fertile pasture to another, or to salt-licking, other mineral-licking or watering places, they regularly fertilized 'barren lands' with their urine and manure. These changed soil conditions lead to more rich composition of soil microflora and fauna. It is significant that there are soil oribatid mites that became extinct not after the 'tundra-steppe crash', but after the extinction of mammoths (Putshkov, 1989a). Due to richer soil fauna and microflora, richer vegetation could vegetate, thus bringing further changes of soil regime. Some seeds were brought and 'planted' by herbivores (trampling on feces laying on sandy soil, or soil, wetted by rain or melted snow), some were brought by other agents to a place 'prepared' by herbivores. At last the 'barren land' became a satisfactory pasture, at least for some of large phytophagans. Due to this, even Subarctic and Arctic steppoids (Sect. 3.15.1.3.) became, probably, productive enough for saigas and horses, if not for mammoths.

Effects of herbivores on vegetation and their interactions between each other were modified also by influence of predators, first by that of the largest ones (Putshkov, 1989a,b, 1992a, 1993a, b, etc.). The combined action of various megafaunal species explains the notorious mosaicity of the ecosystems of mammoth' and other Pleistocene biomes much more convincingly (ibid.) than an appeal (Guthrie, 1984, 1990a, 1990b; Graham & Lundelius, 1984, etc.) to climatic causes.

### **10.5. Mammoths impacts on snow cover**

Mammoths and other herbivores created not only highly patchy (mosaic) vegetation but increased mosaicity of snow cover qualities too (Putshkov, 1989a, 1989b, 1992a, 1993a). In part it was a sequence of vegetation patchiness: woods with deeper and 'crumblier' snow were interspersed with open areas, maintained by herbivores, with more condensed and shallower snow. Enormous spaces were covered with snow raked or shoveled by mammoths' tusks, rhinos' horns, hooves of horses, bison and reindeer herds. A patchwork of wider and narrower paths was trampled. Feeding and moving mammoths, rhinos, large herds of bison and horses broke the frozen snow crust over immense spaces. Other herbivores could largely graze over the fields, where snow-crust was smashed by mammoths. They could also browse over branches or even trees that had been broken by giants. Herbivores and carnivores had the possibility to use giants-made paths and roads. Now Far Eastern deer, boars and tigers use automobile roads, thus evading frozen snow crust and deep snow areas. It was mammoth herds that prepared in Pleistocene roads for cave lions. In a word due to mammoths many other large mammals got the better chances to overwinter (ibid.).

In regions with climatically driven thick snow cover and humid soils, activities of mammoths could create satisfactory conditions only for them and for the other beasts of sufficient high mild soil and snow cover tolerance. That is why the interglacial range of saiga and, to a lesser extent, that of musk-oxen, dwindled to greater extent than ranges of mammoths, woolly rhinos, horses and bison (Sect. 3.17.; 6.1.). But in regions with climatically driven thin snow cover, so wide-spread even now in taiga and tundra zones of Eastern Siberia, snow-scraping and frozen snow crust smashing activities of mammoths could create satisfactory conditions even for saigas and hemionids. These animals, together with other ungulates, were the members of feeding successions headed by mammoths. Saigas and reindeer could coexist not only using patches, where vegetation was different due to abiotic

(Sect. 3.10.) and biotic reasons. They also could graze side by side (or, more probably, saiga after deer) on short grass lawns that appeared out of the tall or moderately tall grass meadows, previously grazed by mammoths and their satellites (Baryshnikov & Krakhmalnaya, 1994). It's pity that we can not guess the details of symbiotic and antagonistic relations (antipredatory behavior and pasture utilization) that existed in mammoth biomes as they exist now among the megafauna of African savannas (Sinclair, 1975, 1985; Kingdon, 1979, 1982; Wagner, 1987).

The subterranean ice-veins in loess were the main water resource under the most crioarid stadials conditions in East Siberia. Mammoths broke out with their tusks the pieces of such ice. Crumbs of this ice, remaining after the work of giants, were used for drinking by other animals (Tomirdiario, 1991).

### 10.6. How numerous were the mammoths ?

The evaluation of mammoths number is a delicate matter. It tends to increase magnificently, when climatists are sure that the 'paleoecological riddle' — the fitness of Periglacial Pleistocene ecosystems to 'big game' could be explained exclusively by the climatic causes. It grows even more, when they refute the possibility of the prehistoric overkill (e.g., Bgatov & al., 1989: 27). But when the alternative, non-climatic, explanation of the 'riddle' appears, number of mammoths hastily dwindles ... .

At any rate the population density of animals that were as resilient to natural factors as proves the exposed evidence and as unmolested by man as states climatistic doctrine, it could not be too much beneath the ecological capacity of ecosystems. Presence in mammoths ecosystems of such carnivores as cave lion, doubled in many regions by cave hyena and/or other large carnivores (Vereshchagin & Baryshnikov, 1980a, 1983, etc.), proves that 'big game' populations were large enough to exert an environmental impact, comparable to the pressure of Palaeotropical megafauna on their surroundings. Supposition that absence of mane by cave lions (*Felis leo spelaea*, *F. l. atrox*) proves that victims were scarce (Guthrie, 1990a) is not convincing. These extinct races that were to some extent intermediate between modern lions (*F. l. leo*), tigers and jaguars (Vereshchagin, 1971b) could have no manes simply because they still had not acquired this secondary masculine character.

## CONCLUSION

So even the most modernized climatic versions of the Late Wurm extinctions in North Eurasia and Americas are inconsistent with the evidence. The same is true for the climatic versions of Pleistocene extinctions of large mammals in Paleotropical and Australian regions (Putshkov, 1989a, 1989b, 1993a,b). Everywhere the giants were among the most euryoecic forms that perfectly resisted to multiple major long-and short-time climatic oscillations — a recurrent feature of the Pleistocene and Pliocene climate. Only such climatic stresses could extirpate them that were deadly for most other mammals (ibid.). The brilliant examples of such climate-induced megafaunal extinctions are the disappearances of African savanna biome from the territory of Sahara due to its aridizations about 40 kyr BP and 4-5 kyr BP (Reed, 1970; Klein, 1984). It is true that here climatic changes chased away elephants, together with most of other megafauna and biped hunters (Guilday, 1967). But these were the regional extinctions that extirpated hosts of small mammals, birds, reptiles, amphibians, invertebrates, plants as well, except for the deserticolous ones. Elephants would be completely extinct only if all the Africa became the desert of Sahara (not that of North Namib! — Giraffes ..., 1981) type. Wurm/early Holocene climatic stresses were neither stronger, nor more rapid than

certain of the previous ones. Hence they could not be considered as the primer cause of the extinctions of giant herbivores and, consequently, as that of the crisis as a whole.

Climatic models are correct in a very important point: ecological capacity of the Pleistocene continental communities for megafauna was far superior than that of the Holocene ones. However, the origin of these differences was not of climatic, but of biotic reasons. The most important was the role of largest herbivores. They transformed the environment in a way, favorable for them, and for most of other megafauna. So notorious 'mammoth steppes' and 'parklands' were in literary sense creating and maintaining by mammoths.

The 'prehistoric equilibrium' has been based on the interdependencies of largest herbivores, largest predators, other megafauna and plant communities. The combined ecosystem impact of top herbivores and top predators minimized the consequences of numerous pre-Wurm climatogenic stresses of ecosystems and efficiently prevented the crash of the megafaunal communities (Putshkov, 1989a,b, 1992a, etc.). The biotic mechanisms of the man-induced upset of the 'prehistoric equilibrium' have been discussed previously in many details (*ibid.*, 1991a,b, 1992a,b,c, 1993a,b, 1994) and could not be considered here.

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## SUPPLEMENTS OF VESTNIK ZOOLOGII

**THE VERTEBRATE ANIMALS OF BLACK SEE RESERVATION (ANNOTATED LIST OF SPECIES)** / T. I. Kotenko, T. B. Ardamatckaja, V. I. Pinchuk, A. G. Rudenko, Z. V. Selunina., P. V. Tkachenko Eds. dr. I. A. Akimov. — Vestnik zoologii. — 1996. — Suppl. № 1. — 48p. — Bibl. 86. (In Russian)

The papers of this publication present the results of several years research on vertebrate animals fauna of reservation which have saved the unical Black See wetlands of Ukraine with rare and disappears plant associates, plants and animals species from international lists. The recent count of species is 432: 70 for pisces, 4 for amphibians, 9 for reptiles, 302 for birds (145 - nested) and 47 for mammals. 70 species of vertebrate are from the Red Book of Ukraine.

**Key words:** vertebrates, fauna, taxonomy, Black See, Ukraine.

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**THE KEYS FOR IDENTIFICATION OF TENTACULOUS INFUSORIA (CILIOPHORA, SUCTORIA) OF THE UKRAINIAN FAUNA** / I. V. Dovgal — Vestnik zoologii. — 1996. — Suppl. N 2. — 42 pp. — Bibl. 35. (In English)

This paper is the guide for identification of tentaculous infusoria of the regional fauna, including 88 species. Besides the keys for identification, the information about the main methods of suctorians investigation, significant diagnostic characters, papers that might be useful for identification of suctorians and diagnoses of all taxa is also included. The genus *Praethecacineta* Matthes was moved to the subclassis *Exogenea* Jankowski and included in the order *Metacinetida* Jankowski in range of new family *Praethecacinetidae* fam. n.

The work is based on the own materials of the author. The diagnoses and figures of that species, which are absent in own materials are referred by literary data. The manual may be useful for zoologists, hydrobiologists, ecologists, teachers and students of biological specialities.

**Key words:** tentaculous infusoria, fauna, keys for identification, Ukraine.

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**TERRESTRIAL LOCOMOTION APPARATUS OF TETRAONIDAE AND OTHER GALLIFORMES. MORPHO-ECOLOGIC CHARACTER** / I. A. Bogdanovich. — Vestnik zoologii. — 1997. — Suppl. N 3. — 152 pp. — Pict. 127 — Tabl. 14 — Bibl. 35. (In Russian)

The gross morphology of the skeletal and muscular system of the hind limbs of all Tetraonidae genera was compared with that of other galliform and some other birds. Muscle activity was monitored by electromyography and cinematography, emphasizing also the feeding behaviour. The tetraonids show a complex of peculiar features, including a particular wide and low pelvis, short legs, weak pelvic muscles, long muscular bellies and short tendons etc. Such features indicate that tetraonids are the galliforms with least cursorial adaptation. But the same features may considered as adaptive with respect to the ability of tetraonids to move on branches while foraging. Other morphological patterns facilitate terrestrial locomotion in most tetraonids. The well developed bending capacity of the femoral and tarsometatarsal joints allow the supporting foot to remain under the center of gravity and maintain balance during the supportive phase of locomotion; heavy foot pads passively dampen some reaction forces. The combination of these and some other morphological patterns allow tetraonids to be equally effective for both arboreal and terrestrial feeding. Use of biomorphologic method (comparative morphology, functional analysis and comparative ecology) allow some taxonomic and phylogenetic suppositions.

**Key words:** locomotor apparatus, function, adaptation, tetraonids.

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WERE THE MAMMOTHS KILLED BY THE WARMING ? (TESTING OF THE CLIMATIC VERSIONS OF WURM EXTINCTIONS) / Putshkov P. V. — Vestnik zoologii. — 1997. Suppl. N 4. — 76 pp. — Bibl. 293.

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