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UNCOMPENSATED WURM EXTINCTIONS. 6. FINAL COMMUNICATION: THE CRISIS OUTSIDE THE OLD WORLD

Некомпенсовані вюрмські вимирання. 6. Заключне: криза за межами Старого Світу. Пучков П. В.— Гострота кризи в Америці та Австралії обумовлена відсутністю довгої коеволюції мегафауни з гомінідами. Мисливська майстерність людей, що прийшли сюди вже на стадії неоантропу, зросла надто швидко і велетні-едифікатори не встигли виробити резистентності до антропічного пресу. Тому знищення велетнів та спричинена цим перебудова екосистем відбулися неспівставно швидше й раптовіше, ніж у Старому Світі. Звідси — набагато більший масштаб вторинних вимирань.

Ключові слова: Плейстоцен, вимирання, актуалізм.

Некомпенсированные вюрмские вымирания. 6. Заключительное: кризис вне Старого Света. Пучков П. В.— В Америке и в Австралии коэволюция «заинтересованных зверей» с «неискусными звероборцами» уложилась в несколько или, от силы, в несколько десятков тысячелетий. Этого хватило, чтобы потомки неопасных для крупной дичи первопоселенцев (собирателей литоральной зоны) переквалифицировались в искусных охотников и вышли из-под пресса хищников. Но гигантские фитофаги — эдификаторы сообществ не обрели за такой срок резистентности к промыслу. Скачкообразно возросши в числе, люди извели исполинов несопоставимо скорее, чем в Старом Свете. Несопоставимо скорее преобразовались и экосистемы. Вот почему размах вторичных вымираний оказался настолько значительней. Как и предсказал Дарвин, загадку вюрмских вымираний удалось решить по уяснению причины особой пригодности плейстоценовых экосистем для крупных млекопитающих. Эта причина — средообразующая роль гигантских фитофагов и крупнейших хищников. Она понята в ходе наблюдений за ныне живущими представителями указанных групп. Отсюда очевидна неоправданность попыток дискредитации принципов селекционизма и актуализма, ссылаясь на их мнимую неприменимость к плейстоценовым сообществам и их кризису.

Ключевые слова: плейстоцен, вымирания, актуализм.

Why was the crisis so pressing in America and Australia? In the Pleistocene gigantic herbivores (weighing more than 1000 kg) were essential for maintaining ecosystems on all continents (Putshkov, 1992a etc.) However due to the pre-Wurm absence of hominids the Wurmian megafauna of America and Australia had some special features:

1) **very low resistance of the giants** and other animals **to predation by man** (in the Old World this resistance was high because there hunting activities of man had grown slowly over a period of 3 milion years) (Jelinek, 1967; Martin, 1984; Putshkov, 1989b) *; 2) **the giants completely kept their ecological role** because there was no decrease of the number of species or of population densities (Kurten, Anderson, 1980; Savage, Russel, 1983; Martin, 1984) in comparison with the Eopleistocene. In the Old World this role of the giants tapered off towards the Wurm as species less resistant to man gradually became extinct, and in some parts of the Paleoarctic their role went down even more due to low population densities of the more resistant species that still existed (Putshkov, 1989b, 1993a, 1993b); 3) **the largest predators completely kept their stabilizing effects on ecosystems** (in the Old World, especially in the Palaeoarctic, it became

*Sources non-indicated in the reference of this final communication are referred in previous communications of this work (Putshkov, 1991b, 1992a, 1992b, 1993a, 1993b).

greatly reduced op. cit.); 4) the outcome of features 2 and 3 was that **far more animals that in the Old World continued to depend vitally on the impacts of gigantic herbivores and/or on these of the largest predators; 5) many herbivores were dependent on pyrophobic vegetation** as natural fires were rare due to high densities of gigantic grazers (in the Old World fires, being induced by man, became more frequent) (op. cit.).

By all these reasons the Wurm (Wisconsin) megafauna of America and Australia was incomparably more vulnerable to direct and indirect action from «modern» man (i. e. *Homo s. sapiens*) than of Africa and Eurasia. After reaching America and Australia man consisted an entirely new factor that led to a quick and drastic crisis. Man-induced changes concerning primary production consuming, predation and competition relationships lasted only for several thousand years in the beginning of the second half (Australia) or at the very end of the Wurm (America). Far more species became extinct here than in Africa or Eurasia. But why didn't the crisis burst out immediately after man had appeared there?

Man came to America some 25—40 thousand years ago or even earlier. However the human population up to 12 500 yrs B. P. was scarce and was represented by unspecialized hunters-gatherers; their tools were of mid- or even early Palaeolithic type (MacNeish, 1976; etc.). At first glance it seems preposterous that people (contemporaries of well skilled «elephant killers» of Eurasia!) certainly belonging to *H. s. sapiens* for such a lengthy time (12 000 yrs or more!) existed at a so low level. In senses of technical development, hunting skills and ecological role they stood far behind certain *H. erectus* of the Mindel that lived hundreds of thousands of years earlier. Considering this some authors tend (Mossiman, Martin, 1975; Martin, 1984: Haynes, 1984; West, 1986; etc.) to deny the presence of man in America earlier than 13 thousand yrs ago, although this is against the evidence.

Really here we don't have any contradictions. The first people that colonized America didn't hunt on large animals being specialized on gathering food within the intertidal zone (Gruhn, 1988). This way of life could have existed without the invention of new technologies or the improvement of hunting skills. Living in such a way people (would they be *H. erectus* or *H. sapiens*) gradually lost their hunting habits. Precisely such gatherers populated America in the middle (or early?) Wurm moving down along the Pacific coast. They quickly occupied the shelf zone nowadays flooded by the sea in both North and South America and later formed hordes that moved inland (op. cit.). Being out of contact with skilled hunters of Eurasia these people could hardly become in a short time once again qualified hunters. Poor hunting skills and predation pressure (see lower) kept the human population at low level. Both these factors considered were responsible for the time gap between the appearance of man in America and the beginning there of uncompensated extinctions. While these factors were in force the killing of gigantic herbivores by men was a rare event and occurred only sporadically (MacNeish, 1976; etc.). This kind of hunting could enrich the populations of giants with individuals resistant to predation by man only if it had lasted for hundreds of thousands of years, as it lasted in the Old World (Putshkov, 1992b, 1993a, 1993b). In America this stage lasted hardly more than 15—30 thousand yrs; man (already belonging to *H. s. sapiens*) too quickly gained control over predators. Here this process was accelerated but went on in the same way as in the Old World (Putshkov, 1989a, 1989b, 1993a).

Improved hunting techniques and the gaining of control over predators led to a sharp increase (much sharper that in the Old World) of the human population. Settlements ageing 10—12 thousand yrs B. P. largely outnumber more ancient ones and have been met over a much greater area (virtually all over the continent) (MacNeish, 1976; Haynes C., 1984; West, 1986). Regular killings of giants was a striking factor that very suddenly (we note again that in the Old World this was of not such a surprise) hit theit populations. Under fierce hunting pressure enhanced by the use of fire and more advanced weaponry (Krantz, 1970; Keram, 1979; Martin, 1984; Grühn, Bryan, 1984; West,

1986; Frison, 1989; etc.) and aggravated by inevitable «indirect death» (Jelinek, 1967; Vereshchagin, 1967; Putshkov, 1992b) the thriving populations of giants came to a crash over a period of several hundred years (West, 1986), or even over a shorter time, decades and years (Martin, 1984 etc.). There is no need in supposing that man exterminated the giants totally if we take into account that depauperated populations can just stochastically die off (Putshkov, 1992a). Due to the short contact of the «poorly skilled» hunters with the giants (even considering South American mastodons, *Megatherium*, glyptodons and *Toxodon* that were under lower hunting pressure) no resistant forms did evolve in the way recorded for their counterparts in the Palaeotropics (Putshkov, 1989b etc.). Concurrent with the suppression of the giants, the rapid reshaping of ecosystems took place. It was accompanied by secondary extinctions of many animals.

In Australia the crisis went on in a similar way. By raft or boat man came there some 40—55 thousand yrs ago (Lambert, 1991; etc.) and most likely also was trophically associated with the sea shelf. It seems that most extinctions occurred here about 33—40 thousand yrs ago (Merrilees, 1984; Murray, 1984; Martin, 1984; Flannery, 1989). If this is true we have here a much narrower gap between the peopling of the continent and the beginning of the crisis than in America. Probably it was easier for man to cope with Australian largest predatores (*Megalania, Pallimnarchus, Thylacoleo*) as well as with herbivorous marsupial giants than with their American countreparts (Martin, 1984; Putshkov, 1989b).

Now we can examine more precisely the fairly well documented North American extinctions.

Features of extinction in the Nearctic. Giants (more than 1 ton). The American mammoth (*Mammuthus jeffersoni*) started to disappear within ecological favourable areas some 15 thousand yrs ago. The extinction affected the animals in the worse peripheral parts of the range only later (Agenbroad, 1985). The fading away of mammoths was preceded everywhere by the appearance of Palaeoindians. In the North of Canada the Holarctic mammoth (*M. primigenius*) yet survived 7.6 thousand years ago (op. cit.). Clear evidence exists of man hunting mammoths and mastodons (*Mammut, Cuvieronius*) and this was the primary cause of their extinction (op. cit.; Irwin-Williams, 1997; Edwards, 1967; Martin, 1984; West, 1986; etc.). Giant sloths (*Eremotherium*) and tortoise-like glyptodons (*Glyptotherium*) probably were supressed both by hunting pressure and by environmental changes that took place after the extinction of proboscidians, in much the same way as in many African communities the hippopotamus and white rhinoceros are dependent on the elephant for creating suitable grazing areas (Kingdon, 1979). Even the browsing black and Sumatran rhinoceroses are faced with difficulties in the absence of the elephant (Schenkel, Schenkel-Hulliger, 1968; Strien, 1986).

Giants, climate and the enviroment. The question was thoronghly analysed in previous publication (Putshkov, 1988, 1989a, 1989b, 1991a, 1992a). Evidence has been presented there that notorious Pleistocene highly mozaic plant communities that «have no modern analogues» (Guilday, 1967, 1984; Lundelius, 1967 etc.; Guthrie, 1984, 1990; Graham, 1985 etc.; and others) were shaped mainly by extinct giants (as now by Palaeotropic pachyderms) and not by one or another of climatic agents as often claimed (op. cit.). Being extremely eurybiotic the giants withstood all pre-Wurmian climatic stresses. They prevented extinctions without replacement among the rest of the megafauna by shaping ecosystems in a way favourable for a rich species composition (Putshkov, 1992a etc.). Climatic changes indeed converted periglacial «mammoth steppes» into interglacial «cryophytic savannahs» in Eurasia and Alaska and altered the plant composition in «mosaic open woodlands» of East USA. But it were the proboscideans themselves that kept such ecosystems in regions climatically adequate for «usual» tundras, steppes, continuous taiga or deciduous forests hostile to many large mammals (op. cit.). Be-

sides their impact on vegetation giants favoured the smaller northern megafauna as powerful stampers of snow and breakers of frozen show-crust; «brutes and beasts» of semi-arid regions depended on «wells» diggen by giants (op. cit.). That's why the sudden supression of giants everwhere doomed to extinction a lot of smaller species.

Smaller (50—1000 kg) herbivorous megafauna. Such herbivores of ecotones and open habitats as sloths (*Megalonyx, Glossotherium*), horses, ovibovines (*Symbos, Bootherium*), certain deers (*Sangamona, Cervalces*), giant beavers (*Castoroides*) coexisted with extant forest-dwellers in East USA throughout the Pleistocene for there were vast plaids of meadows, grasslands and parklands intermingled by patches of open woodlands (Guilday, 1967, 1984; etc.). Such a situation was due to the feeding and other activities of mastodonts and mammoths (Putshkov, 1989b, 1991a). The supression of giants led to the overgrowth by dense, continuous, climax stage forests of the entire space except of small glades and narrow river-side meadows. Some of aforsaid herbivores couldn't exist under new conditions, others were outcompeted by extant deers that since then began to thrive. The giant spectacled bear (*Tremarctos floridanus*) probably also was dependent on plants abundantly growing in communities maintained by mastodons and glyptodons. After losing its predecessor of the grazing succession this bear failed to compete with the deers as a herbivore, and with the black bear as an omnivore (op. cit.). Its Neotropical counterpart (*T. ornatus*) also retreated from the plains (Hershkovitz, 1969) and survived in the Andes where a more complex mosaics of the vegetation is due to orography.

The replacement of various highly mozaic (Guilday, 1967, 1984; Guthrie, 1984; etc.). Pleistocene plant communities of the Midwest USA by **monotonous prairies** and of a diverse fauna of ungulates by countless herds of bison was caused by the extinction of mammoth. The feeding of proboscidians as now observed in Africa (Kingdon, 1979) on one hand, sets a limit (and a quite high one!) on the number increase of each ungulate species, and on the other creates a complex pasture mosaic consisting the basis for dividing the niche between many species. Activities of various ungulates led to even greater complexity of the plant community mozaics, i. e. areas occupied by herbaceous vegetation of various hight and species composition alternated with areas covered by shrubs, small patches of forests, and individual trees that could be «seeded» by the giants in the same way as this is going on nowadays in Africa (Owen-Smith, 1987). Owing to different competition abilities of various herbivores within different patches of the mosaic (Guthrie, 1984) the animals were «doomed» to coexistence and even to interdependence in view of grazing successions. The extinction of the mammoths «beheaded» these successions. In the absence of mammoths herbivores failed to «cut down» the grass fast enough to prevent it from drying up and coming easily set to fire. Spontaneous ignition was thus facilitated. Fires became more frequent also due to the hunting activities of man and his attempts to ameliorate grazing areas for the bison (Jelinek, 1967; etc.). Herbs, shrubs and trees susceptible to fire were destroyed. Easily resuming grasses were favoured. Natural aridization also promoted the spreading of grasslands. Nevertheless, this factor alone could neither monotonize prairie vegetation to such an extent nor be responsible for the marked boundary between the prairies and continuous forest present in the Holocene and absent in the Pleistocene (Guilday, 1967, 1984; Graham, 1985; etc.). Browsers and mixed browsers/grazers retreated to this boundary. Here only small populations vulnerable to any harmful influences could be maintained. The coexistence of open areas grazers was also hampered because of the simplification of grass community mosaics due to increasing fires, «beheading» of grazing successions and increasing monotonous effect induced by growing herds of bison (Putshkov, 1989b).

If the mammoths would have been supressed gradually as they were in Eurasia the spreading of new types of vegetation also should have been proceeded step by step (Putshkov, 1989b, 1993b). Herbivores, especially such flexible ones as horses, could have the time to adapt to the new conditions in various ways, including the rearrangement of grazing successions. However the giants were supressed too suddenly. It is no great surprise that a herbivore (primarily preadapted to the new environment)

In this case would rapidly multiply in large numbers. And that particular herbivore came out to be the bison. The bison made a better use of the monotonous vegetation of the prairies than other herbivores had done (Guthrie, 1984; Graham, Lundelius, 1984). Speculations on the toxic effect that the new diet had on other herbivores (op. cit.) seem to be misleading: simply from the very beginning they were less able to compete under conditions of a changing environment and couldn't keep pace with the moving events (Putshkov, 1989b).

Within the provoked by man harsh competition between herbivores the bison was favoured also by greater than horses or camels reproductive abilities (McDonald, 1984) and physical strength, a beneficial character (Kingdon, 1979, 1982; Mills, 1982; Berger, 1985) for interspecific interactions of grazers. After the mamoths had gone the bison became the main animal to be hunted by man and this only stepped up their numbers due to the effect of the «primitive under-kill» of fecund prey (Krantz, 1970; Putshkov, 1989b, 1992b). Man successfully supressed predators that competed with him and were causing more deaths of juvenile bison than man could inflict himself (op. cit.). Mainly mature individuals were hunted so in time more animals reached a reproductive stage and left an offspring. Numbers of bison increased to an extent made possible by the potentialities of the environment. Under these circumstances horses, camels, llamines, ovibovines and other herbivores were driven out. However, the extant pronghorn, a species rare in the Pleistocene (Graham, Lundelius, 1984), gained advantage. Grazing on dicots that vegetated after the feeding there of bisons (Guthrie, 1984) the pronghorn multiplied in numbers and displaced smaller relative taxa *(Stockoceros, Tetrameryx, Capromeryx)*.

Thus the 60 million herd of bison that was destroyed by the «pale faces» during the 19th century represented a peculiar «hunting monoculture» brought into being by the «redskins» some 10 000 yrs ago. The same didn't occur in the steppes of Eurasia because originally the changes were of gradual and later it was hampered by the failure of the bison to compete successfully with the local aurochs (Putshkov, 1993b).

In **regions** that **underwent severe aridization** hunting and frightening away of animals from watering and feeding places by man settled in oases could have been fatal even for fecund species (Jelinek, 1967). Here in some places the mammoth existed even longer than horses and most of the megafauna (Haynes, 1985; etc.). This is natural considering that elephants under severe drought conditions (unlike under milder ones — Kingdon, 1979; etc.) supress ungulates by driving them away from watering places and competing for food (Water..., 1968; Haynes, 1987; etc.). It doesn't contradict with the pivotal role of giants in the Wurm extinctions over 80 % of the Nearctic where conditions were semiarid or humid (McDonald, 1984; etc.).

In **mountains** the heterogenous environment maintains the mosaics of the vegetation quite independently from climatic or zoogenic influences. This is why competition of large herbivores here is not so narsh. However local disasters make individual or mass death of animals more frequent. For instance, mustangs enjoy splendid pastures in the mountains but quite often suffer there from snowstorms (Berger, 1983). Owing to the orography animals could be driven to death over a cliff and it would be surprising if humans or wolves that had multiplied after supressing the largest predators didn't operate in that way. Losses suffered here by horses and other herbivores had a greater effect than they had in the plains also due to smaller sizes of montane populations and their greater isolation. As soon as an inward flow of individuals being in excess in the plains ceased extinction became a matter of time. Mountainous grazing areas were then taken over by montane sheep and goats and forests were occupied by survived deers.

Large carnivores as a factor and object of extinction. Before man came Nearctic predators and their prey were in a state of a dynamic equilibrium. Prey was adapted to avoid key predators and predators were adapted to a fairly stable ratio of various prey. The key predators, car-

nivorous short-faced bears (*Arctodus spp.*), the lion (*Felis leo atrox*), the jaguar (*F. onca*), sabertooths (*Smilodon, Homotherium*), the dire wolf (*Canis dirus*), maintained the balance of both herbivores and smaller predators. Besides survived species, the latter ones included the cheetah (*Acinonyx trumani*) and the dhole (*Cuon alpinus*). Till the very end of Wurm the key predators also regulated human numbers (Putshkov, 1989b). After escaping from beneath their pressure people in quite a short time slaughtered most of the proboscideans. *Homotherium*, a specialized predator of juvenile and aged proboscideans (Kurten, Anderson, 1980) was deprived of its prey. The first victim of the secondary supression of many smaller herbivores was probably the cheetah. Now its African counterpart is more vulnerable than other large predators to growing shortages of prey (Simpson, 1978; Owen-Smith, 1989). Lions, leopards and hyenas often kill cheetah kitten and take away prey from the adults (Shaller, 1972; Guggisberg, 1975; etc.). It could be so that the American cheetah also could coexist with other predators only if the prey was abundant. Further deterioration of the resource was fatal for the short-faced bears, the lion and *Smilodon*. The jaguar was driven far to the south. The remaining prey was insufficient for these predators under the rapidly changing conditions of the environment and growing competition from man.

Before extinctions became a reality there could have been some kind of local short-time surplus of dominant predators when the human population had **already** increased and the largest carnivores were **still** numerous. So some kinds of prey couldn't stand against this **joint** attack (McDonald, 1984). Extinctions threatened not those species of prey that competed successfully (and thus were numerous) but those that were supressed and continued to decline. The remaining populations were poor in numbers and this made them even more vulnerable to predators as it is in unusually small herds of ungulates (Osborn, 1910; Sinclair, 1985). The «surplus» predators could prolong their existence by scavenging human refuse and by feeding on food of low quality (i. e. insects, small vertebrates, plants etc.) (Janzen, 1983; McDonald, 1984). In addition to the largest carnivores countless flocks of birds of prey (eagles, vultures and condors), both extinct and survived, also had an impact on the agonizing populations. Carcasses of large animals became rare and this forced them to more often attack juvenile of smaller ungulates and adult individuals of small extinct pronghorns (Steadman, Martin, 1984).

Wolves (*C. lupus*) were rare in the Pleistocene of the Nearctic (Kurten, Anderson, 1980); they were supressed by the largest carnivores. After the latter had faded away wolves rapidly multiplied. Millions of years herbivores existed in ecosystems where canids living in packs played a minor role. So it was an unexpectedness for facing a fierce offensive from the wolf. For much of the prey conditions became worse than under the sway of the former key predators. Nowadays similar relations can be seen in Asia where wolves have a heavy impact on deer and the goral in areas where tigers have disappeared (Kucherenko, 1985). Being able to predate a large variety of thriving prey (ranging from rabbits to bison) wolves kept up themselves in large numbers and could eradicate anywhere populations of less resistant prey. Probably wolves inflicted the last blow to the remaining populations of North American capybara, tapirs, horses, camels, llamas, extinct deers, pronghorns and ovibovines lowering their numbers to a level that made reproduction a problem (Putshkov, 1989b).

It is believed that omnivorous peccaries (*Mylohyus, Platygonus*) failed to compete with the black bear in habitats that changed due to the climate (Guilday, 1967; Kurten, Anderson, 1980), or, and this seems more possible, due to the disappearance of giant herbivores (Putshkov, 1989b). The bear could be favoured more than the peccary because

of its greater resistance to wolves. Wolves do attack black bears (Rogers, Mech, 1981) but possibly inflict them less losses than did earlier more stronger predators.

Becoming numerous wolves forced out other large canids. The dire wolf was abundant in the Pleistocene (Kurten, Anderson, 1980) but failed to successfully compete after the depletion of the «supply» of carcasses of large animals. It ranked below the grey wolf in brain volume and running abilities (op. cit.). The dhole failed for the same reasons as in Eurasia (Putshkov, 1993b).

Although extinctions in the Neotropics were of a great scale certain animals related to form extinct in the Nearctic (tapirs, llamas, peccaries, capybara, the spectacled bear) survived there. This could be due to the significant stabilizing effect (Terborgh, 1981) induced by the survived large felids. Contrary to my assumption (Putshkov, 1989b) here canids living in packs gained no advantages. The deteriorated diet together with environmental changes connected with the disappearance of the giants turned out to be fatal for the sabertooth, lion and short-faced bears, but not for the jaguar that underwent dwarfing (Kurten, Anderson, 1980) and, nevertheless, adapted to using efficiently the survived prey (Guggisberg, 1975). Successfull passing of the critical stage could probably be facilitated by less harsh than in the North direct competition with man because of a better supply of food alternative to the megafauna (Putshkov, 1993a). The jaguar and puma restrained canids and possibly caused the disappearance of the largest ones (*Protocyon, Canis dirus*). This could have taken place when packs desintergrated due to extinctions of many kinds of prey.

Other animals. In the African savannahs ungulates restrict the food resources of rodents (Sinclair, 1975). Numbers of rodents don't fluctuate here in such a catastrophic way as they do in so many ecosystems. May it be that notorious oscillations of murine rodents originated since the Wurm crisis? In anyway densities of murine rodents have risen in the Nearctic after the downfall of the megafauna; correspondingly have risen numbers of birds and mammals predating them, e. g. the bobcat (Kurten, Anderson, 1980; Steadman, Martin, 1984). Increasing numbers of lower rank predators within unbalanced ecosystems often leads to the extermination of less resistant prey (Diamond, 1984; Soule et al., 1988; etc.). Possibly the tiny pronghorns (*Capromeryx*) and an array of birds (among ducks, geese, gulls, cormorants, cuckoos, turkeys, passerines→Steadman, Martin, 1984; The Late Quaternary..., 1986) were eradicated by smaller predators continuing some time to be abundant after the repeated crashings of murine populations. Both prey and predators had to keep pace with the rapid changes of the habitats, food supplies, range of enemies and competitors. Probably several extinct rodents, lagomorphs, snakes, owls, hawks, the skunk, *Brachyprotoma*, the procyonid, *Bassariscus*, the felid, *F. amnicola*, (op. cit.; Kurten, Anderson, 1980) were outcompeted under novel conditions. May be the mentioned predators were more dependent than their competitors in years of low murine densities on the food remains of large carnivores or on dung-beetles, numbers and aggregations of which became scarce (2 beetle species even became extinct — Miller, 1983) when so many main producers of manure had disappeared. In the Palaeotropics these beetles consist a considerable part of the food of small carnivores (Janzen, 1976). Decreasing numbers and dispersed distribution of some large invertebrates (a result of gigantic herbivores ceasing their grazing activities) could have deprived the armadillo, *Dasypus bellus*, of food. Subsequent to the extinction of many large herbivores aggregations of blood-sucking insects should have thinned out. There might have been a change of the species composition. This could have been the cause of the extinctions of some passerine birds and chiropterans (Kurten, Anderson, 1980; Steadman, Martin, 1984). Megafaunal extinctions placed an end to the food resources of the vampire, *Desmodus stocki*, and a dozen of bird scavengers (op. cit.). Elephant tortoises were destructed by man (Martin, 1984; Late Quaternary..., 1986).

Wurm extinctions, selectionism and actualism.

The extinctions without replacement of American horses and so many other thriving «highly adapted» animals at the end of the Pleistocene embarassed selectionists (Darwin, 1953; Osborn, 1910; Grayson, 1984; etc.) but inspired catastrophists and adepts of the species senescence theory (Wolkenstein, Rass, 1987; etc.) Arguements of the latter are groundless (Putshkov, 1991a). But selectionist explanations were for a long time unconvincing, e. g. views on Wurm (Lujanian) extinctions in the Neotropics as a «natural correction» of the «faunistic disbalance» caused by the Pliocene invasion of North American forms (Simpson, cited from Keast, 1969). Of what kind was this surprising «disbalance» that it had to be corrected not earlier than over a time of 3 million years? The overkill models of Wurm mainland extinctions are applicable only to giants; the climatic ones are in glaring contradiction to facts (Putshkov, 1989a, 1989b, 1991b).

As Darwin predicted this problem couldn't be solved until the question wasn't cleared up on what global factors favoured the worldlide thriving of diversified sets of large quadrupeds. Though he thought that this factor had nothing to do with climatic zonality it was sought among climatic agents. Both Darwins suggestions were confirmed: Pleistocene ecosystems revealed to be very different from modern ones but the climatic explanations of these differences were insufficient or even delusive (Putshkov, 1989a, 1991b). It was even proclaimed (Sher, 1990) that the disconformity of the Pleistocene and modern ecosystem discredits the actualistic approach to Pleisticene biota. Such exagerration roots in disregard for existing evidence on biotic interactions. The factor was the megafauna itself. The major reason of the extraordinary suitability of Pleistocene ecosystems to megafauna was the shaping of the former by extinct giants. This idea was independently suggested in South Africa (Owen-Smith, 1987), Australia (Flannery, 1989) and USSR (Putshkov, 1988). Another important factor was the stabilizing effect of the largest predators (Putshkov, 1988, 1989a, 1989b, 1992a, 1993a, 1993b). The crisis everywhere began by the shifting of the balance between predators and man. Then ensued primary extinctions of giants (mostly by overkill) and secondary ones of other species (due to the transformation of ecosystems). The regional patterns of the crisis differed due to various subsidary biotic, social and abiotic reasons (op. cit.).

Considering all the existing evidence we inevitably arrive to conclusions that by no means are in any contradiction with selectionism or with actualism. Who knows if Darwin had worked in Africa for such a long time as he did in America the enigma of the Pleistocene megafauna environment and extinctions would be solved 160 years ago?

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Regret. Excellent works of W. Schule (1990, Ecol. Studies, 84; 1991, HOMO, **41**/3; 1992, Tropical forests in transition : 45) and T. May (1993, Natur und Museum, **123**/6) became known to me only when this work was already in imposition. So I couldn't use them here. Our views are similar in the Man-Giants-Vegetation part.

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