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On the Composition of the Forage of the Large Herbivorous Mammals of the Mammoth Epoch: Significance for Palaeobiological and Palaeogeographical Reconstruction

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With 5 Figures and 1 Table

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Abstractum

In this paper the results of research of the gastrointestinal tracts of a fossil horse, a bison, and four mammothes are discussed, mammals that perished in Siberia in the past 53000—10000 years. The sediments in which the animals have been embedded are described too. The problem of Pleistocene extinction, mainly that of mammoth, is discussed in detail.

In der vorliegenden Arbeit werden die Untersuchungsergebnisse von Pflanzenresten aus dem Magen-Darmtrakt eines Pferdes, eines Bisons und von vier Mammuten, die im Verlaufe der letzten 53000 bis 10000 Jahre in Sibirien verendeten, diskutiert. Ebenso werden die Fundschichten beschrieben, in denen die Kadaver eingebettet waren. Das Problem des Aussterbens einiger Großsäuger im Pleistozän, insbesondere des Mammuts, wird eingehend erörtert.

В статье приведены результаты исследований растительных остатков из желудочно-кишечных трактов лошади, бизона, четырех мамонтов, которые погибли в Сибири в течение последних 53 — 10 тысяч лет, и отложений вмещавших погибших животных. Обсуждается проблема причин вычирания в плейстоцене некоторых животных и, в частности, мамонта.

1. Introduction

As is generally known, a frozen mammoth caracass with the well preserved gastrointestinal tract filled with plant remains was first discovered in Yakutia at the Beresovka river in 1900 (HERZ 1902). This time the Russian Academy of Sciences was sending an expedition to deliver the mammoth. The stuffed body is now on exhibition at the Zoological Museum of Leningrad.

At present, when a fossil caracass or a skeleton is doscovered in any part of the country, the Soviet Academy of Sciences and the Committee for the Investigation of the Mammoth and the Mammoth Fauna will organize integrated expeditions to the respective regions and will superwise the entire research. The Komarov Institute of Botany is in charge of the botanical research. This paper reports the results of the studies of the gastrointestinal contents of large herbivores which died in Siberia at different periods of the Pleistocene and the Holocene. The studies of the Institute also includes investigations of the deposits in which the fossil animals have been embedded.

Six fossil animals, a horse, a bison, and four mammothes (Fig. 1) with well preserved gastrointestinal contents have been found since 1968 in different regions of Siberia.

The vegetation cover is one of the basic factors characterizing habitat conditions of herbivors. There is a close relationship between the latter and the flora according to C. C. FLEROV (1965). A slight change in the patterns of vegetation which serves for as animal forage as well as of the mode of obtaining it has a dramatical effect on their structure. This makes herbivorous animals an ideal object for palaeogeographical reconstructions. The examination of the gastrointestinal contents of fossil animals and the deposits in which they are embedded is therefore of great theoretical and practical importance.

2. Materials and Methods

The gastrointestinal contents of six animals as well as the deposits in which they were embedded have been examined. Studies of this kind require a special technique. Samples for anatomo-morphological, palynological and carpological analyses were taken from the same portions of the gastrointestinal tract, which enabled us to compare the data obtained with different techniques and thus estimate the possibilities of each. Owing to this approach we were able to show that the percentages for the main plant groups, i.e. herbs, shrubs, and low shrubs as established on the basis of macro-remains in the stomach of the Selerikhan fossil horse (Fig. 2, left) approximate those for the same plant groups resulting from the pollen analyses (Fig. 2, right). This illustrates the true percentages of the above plant groups in the feeding of the animal. On the other hand, the palynological method provides a more comprehensive picture of plant taxonomic composition (UKRAINTSEVA 1977), owing to the fact that pollen appears to be least affected by the notion of gastric juice while the tissues of some plants, especially of forb meadow representatives, are almost completely diggested, which makes their identification practically impossible. The identification, if any, can only be achived up to the family rank. The carpological method provides effective results in identifying sedges (EGOROVA 1977), while their pollen cannot be so far identified even down to the genus rank. In addition, the differentiated research of the contents of the gastrointestinal tracts provides possibilities for reconstructing patterns of plant communities which served as pastures shortly before the animal died (Fig. 3).

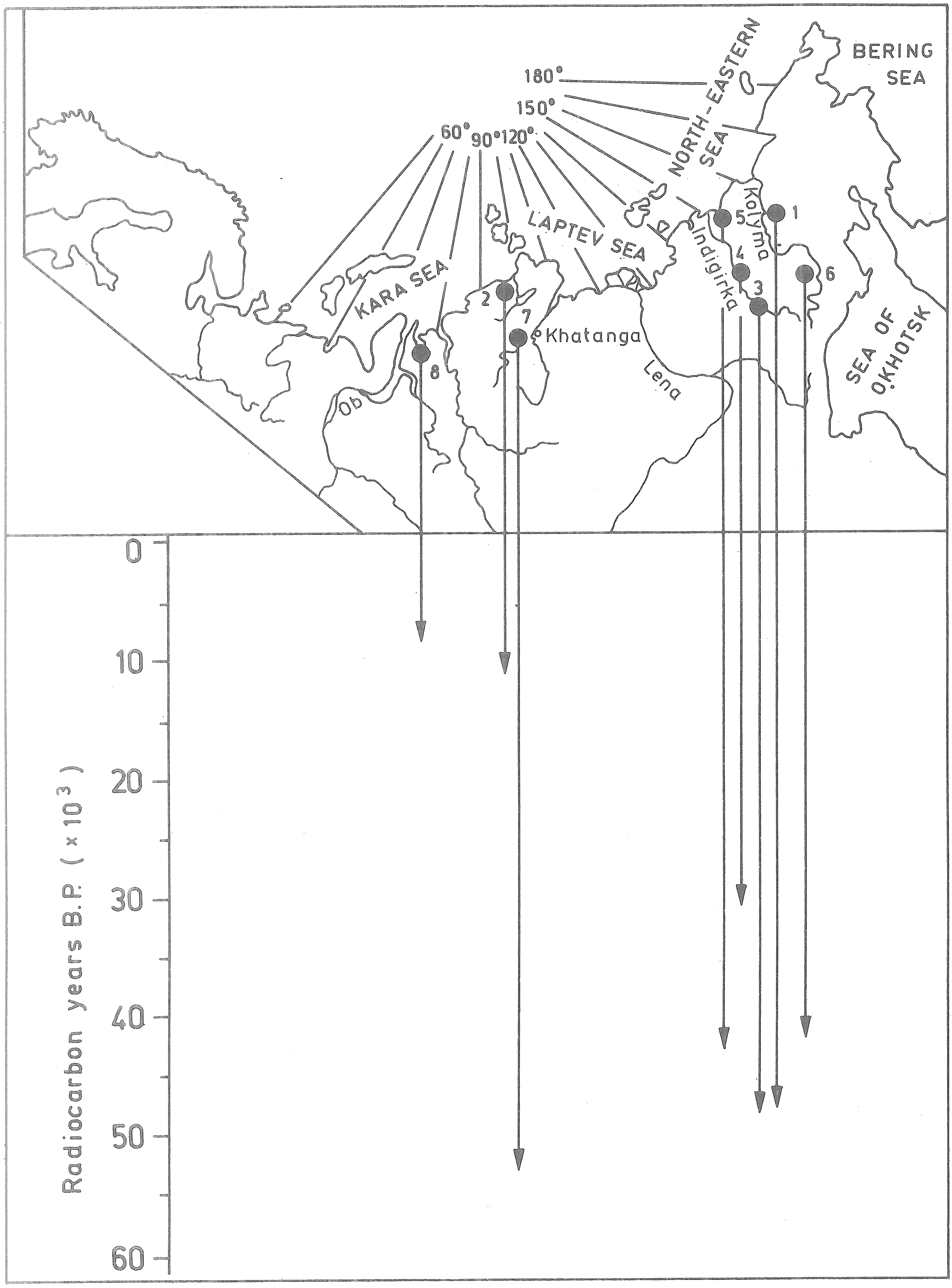

Fig. 1. Sites of frozen caracass and skeleton finds (or of their fragments)

1 — mammoth, Beresovka River, 1900; 2 — mammoth, NW Taimyr, 1948; 3 — horse, Selerikhan River, 1968; 4 — bison, Indigirka River, 1971; 5 — mammoth, Chandrin River, 1971; 6 — mammoth („Dima"), Kirgilyach River, 1977; 7 — mammoth, Large Forested Rassokha River, 1978; 8 — mammoth, Yuribei River, 1979

3. Results and Conclusions

The gastrointestinal contents of all the Siberian finds as well as the fossil plant-remains of the deposits in which the animals were embedded, have by now been fairly well examined. The macro-remains, the pollen, spores, fruits, and seeds have allowed a determination of plants on which the animals grazed shortly before they perished. Percentages in the gastrointestinal forage mass have also been established for the main plant groups — herbs, shrubs, low shrubs, and mooses. The composition of the macro-remains (SUKACZEV 1914; SOLONEVICH et al. 1977; UKRAINTSEVA et al. 1978; SOLONEVICH and VICHIREVA-VASIL'KOVA 1977) as well as of the pollen (TIKHOMIROV and KUPRIYANOVA 1954; KUPRIYANOVA 1957; TIKHOMIROV and KUL'TINA 1973; UKRAINTSEVA [KUL'TINA] 1977, 1982; UKRAINTSEVA et al. 1978) point to a dominant role of herbs in the forage of the representatives of the Mammoth Faunistic Complex. Shrub and low shrub branches and leaves of *Salix* ssp., *Alnus fructicosa*, *Betula exilis*, *Betula nana*, lower branches of some trees *(Larix*, *Betula*, *Chosenia)* also served as forage. It stands for reason, therefore, why the spectra of the gastrointestinal contents show shrub and low shrub pollen accounting for (2) 6—14%; pollen of wood plants making up no more than 4%. Pollen percentages for essential forage plants — grasses, sedges, and forbs — in the gastrointestinal tract spectra are variable in each animal (Fig. 4)[1]), which does not only reflect the role of a particular plant group in the food but also the pattern of plant communities in the area and their peculiarities.

Particularly noteworth in this respect are the results of the studies of the gastrointestinal contents of two animals: the Selerikhan horse (Fig. 1, 3) and the Chandrian mammoth (Fig. 1,5). These results, therefore, require a detailed discussion here. The horse gastrointestinal tract showed predominantly remains of herbaceous plants and their pollen (Fig. 2) — sedges, grasses, and forbs — being represented in practically equal percentage (Fig. 4,3). Along with the herbs the horse ingested moss stems, i.e. *Polytrichum strictum*, *Polytrichum* sp., *Rhutidium rugosum*, *Distichium capillaceum*, *Thuidium abietinum*, also *Bryum* sp., *Turtula ruralis*, *Sphagnum* sp., which occasionally occurred in the forage mass. Shrub branches (*Alnus fructicosa*, *Salix* ssp.), also low shrub branches *(Betula exilis*, *Betula nana)*, lower branches of some trees *(Betula platyphylla*, *Alnus hirsuta)* were also ingested. The variety of ecological plant groups the remains of which have been found in the horse tract (TIKHOMIROV and KUL'TINA 1973, EGOROVA 1977, SOLONEVICH and VIKHIREVA-VASIL'KOVA 1977, UKRAINTSEVA [KUL'TINA] 1977) testify that shortly before the animal died it grassed on a forest dry, shortgrass meadow, alpine-like steppe-meadow with *Carex bigelowii* (GEROD.) EGOR., *Kobresia filifolia* (TURCZ.) CLARKE, *Thalictrum fostidum* L., *Allium strictum* SCHRAD., *Selaginella sibirica* (MILDE) HIERON., *Stellaria jacutica* SCHISCHK., also on moist swamp meadows with *Kobresia* cf. *capilliformis* IVANOVA, *Polygonium scabrum* MOENCH, *Caltha palystris* L., *Juncus* sp., etc. The samples invariably contained pollen of spurce *Picea obovata*, pine *Pinus sylvestris*, birch *Betula* sp. ex sect. Costatae, alder *Alnus hirsuta*, although in insignificant amounts. Their present areas are over 1000 km south and southwest of the site of the fossil horse. The small pollen amount of the above mentioned trees in the tract content can be explained by the fact that the trees and shrubs had completed their flowering (most trees and shrubs flower in April—May). It was only the tree and shrub pollen which had sunk on other plants and also in the water that reached the horse tract, including a few distant elm and lime pollen grains. However, even this small amount of tree pollen is sufficient to indicate the presence of the above mentioned tree species in the vegetation of the region. These palaeobotanical data also suggests that during the period of 38590 ± 1120 years ago the climate of the adjacent areas was somewhat warmer and more humid than the climate at present, since large woody birch, spruce, and pine were among the forest components of the epoch.

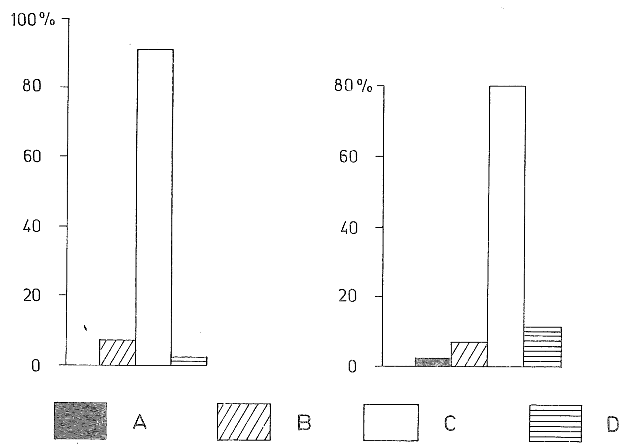

Fig. 2. Total composition of the gastrointestinal contents of the Selerikhan fossil horse

right — pollen and spores; left — macro-remains
A — trees; B — shrubs and low shrubs; C — herbs; D — mosses and ferns

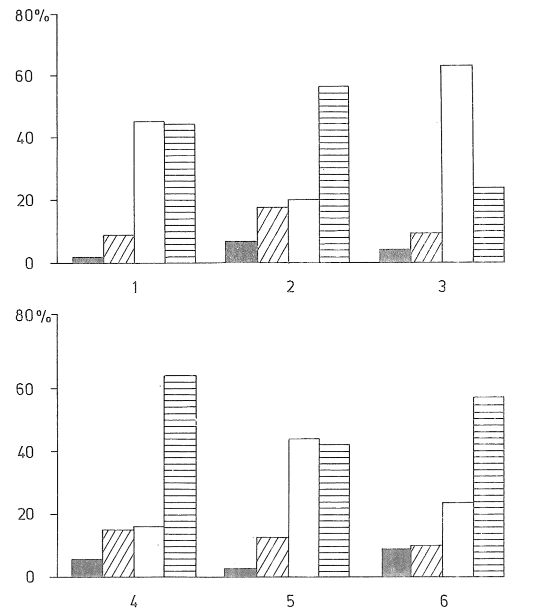

Fig. 3. Palynological spectra (total composition) of the gastrointestinal contents of the Yuribei mammoth and mammoth-embedding deposits

1 — stomach; 2 — mid-intestinal portion; 3 — colon; 4 — rectum; 5 — section 1, sample 15; 6 — section 1, sample 12, plant detritus under mammoth. Symbols as Fig. 2

[1]) Diagram 1 is based on data by L. A. KUPRIYANOVA (TIKHOMIROV and KUPRIYANOVA 1954), diagram 7 is based on results of palynological analyses of the sediments containing the mammoth remains (UKRAINTSEVA et al. 1981).

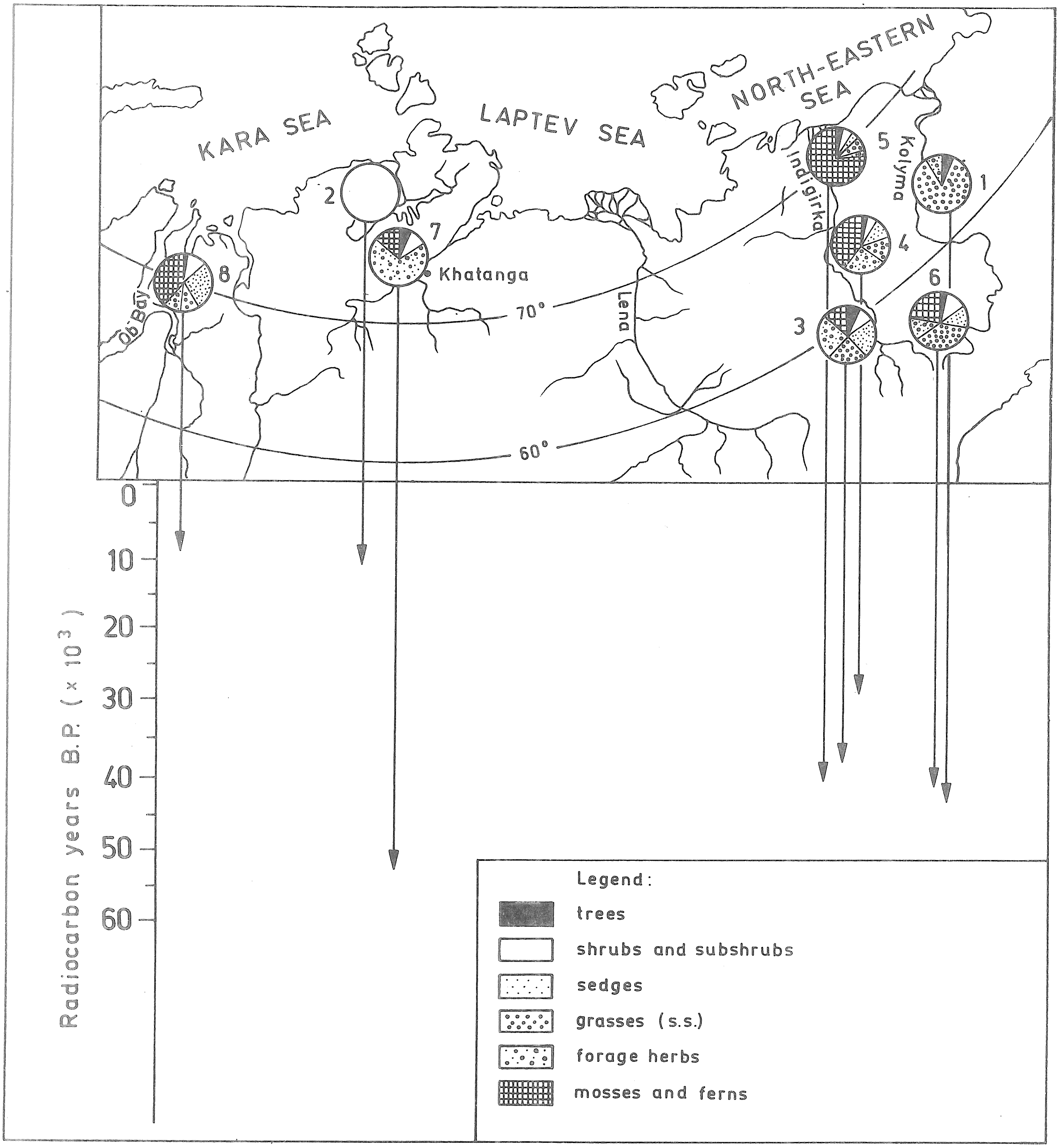

Fig. 4. Percentage of the main plant groups from Pollen and spores analyses of the gastrointestinal contents of herbivorous animals perished during the Upper Pleistocene and Holocene in different regions of Siberia

1 — mammoth, Beresovka River, 1900; 2 — mammoth, NW Taimyr, 1948; 3 — horse, Selerikhan River, 1968; 4 — bison, Indigirka River, 1971; 5 — mammoth, Chandrin River, 1971; 6 — mammoth („Dima") Kirgilyach River, 1977; 7 — mammoth, Large Forested Rassokha River, 1978; 8 — mammoth, Yuribei River, 1979

Abundance of moss remains, i.e. leaf and branch fragments as well as spores in the forage mass of the Chandrian mammoth (Fig. 4,5), bison (Fig. 4,4), and the Yuribian mammoth (Fig. 4,8) shows that the above mentioned plants although of little value forage (KOKSHINA 1961), were nonetheless ingested because being widespread in the given regions. The gastrointestinal tract of the Chandrian mammoth shows abundant more remains of 15—16 ecological related species (SOLONEVICH et al. 1977). Most frequent among them were the remains of *Polytrichum communis* HEDV., *Polytrichum strictum* SM., *Aulocomnium turgidum* WAHLENB.) SCHWAEGR., *Sphagnum angustifolium* C. JENS, *Sphagnum girgensohnii* RUSS., *Sphagnum* sp. ex sect. *Subsecunda*, *Sphagnum* sp. ex sect. *Palustria*. Remains of *Tomenthypnum nitens* (HEDV.) LOESKE and of some other five or six species, so far unidentified, have been found to be less abundant. Moss spores account for 76% (Fig. 4,5) of the total spore and pollen amount of the spectrum. The macro- and micro-remains (pollen and spores) in the tract contents of the animal indicate that sedges, cotton-grasses, low shrub and shrub branches and leaves (*Betula* sp., *Salix* ssp.), mosses and, occassionally, larch branches served as a source of its food. The quantities of larch needles, bark, remains of seed scales and pollen have been found to be very small. The animal was also grazing on different grasses and forbs whose soft epidermal tissues digest well, and their macro-remains are, therefore, only slightly, if at all, represented, while their pollen is present (*Dryas punctata*, *Valeriana capitata*, *Artemisia vulgaris*, *Pedicularis* sp., *Saxifraga* ssp., Caryophyllaceae).

It should be stressed that moss species composition as well as that of the main mass of macro-remains (sedges, cotton-grass), of pollen and spores bear witness of the swampy character of the area of the mammoth pastures, an area that was alternating with open light forests, and closed forests. The present-day vegetation of the Chandrian river basin is characterized by widespread bushy tundras, moss hummocky, marshy tundras as well as by sedge-hypnum swamps.

The data on the vegetation patterns of the region of the other animal caracasses are shown in table 1 suggesting that the excavated animals (individuals), at least the majority of them, existed when the environmental conditions were more favourable than (Berosovsky mammoth, Selerikhan horse, Chandrian mammoth, etc.), or very similar to the present conditions in the regions they died (Yuribian mammoth). As was determined by radiocarbon analyses (HEINZ and GARUTT 1964; ARSLANOV and CHERNOV 1977; ARSLANOV et al. 1980, 1981; SHILO and LOZHKIN 1981), at least eight of the nine animals in question perished during different relative warm periods of the Upper Pleistocene and Holocene (table 1). It should be mentioned here too that these are specific finds and it is due to them that we gat an admirable opportunity to have an idea of the environmental conditions of the Mammoth Faunistic Complex representatives.

However, a proper understanding of these conditions in a wider sense (i.e. considering the representatives of the Mammoth Faunistic Complex as species) can be gained if one views them on the background of global climatic changes in

Table 1. Data on the vegetation of the region of the animal caracasses

Fossil animal	^{14}C-dated time of perish	Pattern of reconstructed vegetation	Modern vegetation pattern of the find district
Mammoth Large Forested Rassokha River, 1978	> 53 170 yrs.	grass-forb and sedge-grass communities[9])	bush and low bush tundras, polygonal mires
Mammoth Terekhtikh River, 1971	44 540 ± 1870 yrs.	tundras, forest tundras (?)[10])	larch taiga
Mammoth Beresovka River, 1900	44 000 ± 3500 yrs.	larch taiga, occassionally with *Betula platyphylla*, *Betula pendula*, *Alnus hirsuta*, *Pinus sibirica*. Meadows, dry meadows, steppe like meadows[1])	larch taiga
Mammoth ("Dima") Kirgilyach River, 1977	41 000 ± 1100 yrs. 39 590 ± 870 yrs.	hypnum and cotton-grass swamps, bush and low bush tundras, larch taiga, occassionally with *Betula platyphylla*, grass-forb communities[6]) mountain (dry) tundras[7]), alpine bush and low bush tundras, larch forests along river valleys, mountain steppe like communities[8])	larch taiga, *Betula platyphylla* only on south slopes. Bushy tundras with *Betula exilis*
Mammoth Chandrin River, 1977	40 350 ± 880 yrs.	larch taiga, bush and low bush tundras, sedge and hypnum bogs[4])	bushy tundras, heavily paludified
Mammoth East Taimyr, 1948	11 450 ± 450 yrs.	bushy tundras forest tundras (?)[2])	cotton-grass tundras, sedge-grass tundras, polygonal tundras, "spotty" tundras
Mammoth Yribei River, 1979	9 730 ± 100 yrs.	flood plaine meadows, shrub moss meadows, sedge-cotton-grass tundras with *Betula exilis*[9])	bushy tundras with *Betula exilis*, *Salix* ssp., moss tundras, polygonal bogs
Horse Selerikhan River, 1968	38 590 ± 1120 yrs.	larch taiga with spruce and woody birch, grass-forbs meadows in the valleys and on the slopes[3])	larch taiga with *Betula platyphylla* on the south slopes, flood plaine meadows, mesoxerophytic conditions
Bison Indigirka River, 1971	29 500 ± 1000 yrs.	larch taiga, heavily paludified, grass-forb and sedge-grass communities[5])	larch taiga

[1]) SUKACZEV 1914; TIKHOMIROV and KUPRIYANOVA 1954; KUPRIYANOVA 1957
[2]) TIKHOMIROV 1950; ZAKLINSKAYA 1954
[3]) TIKHOMIROV and KULTINA 1973; EGEROVA 1977; SOLONEVICH et al. 1977; UKRAINTSEVA (KUL'TINA) 1977
[4]) SOLONEVICH et al. 1978
[5]) UKRAINTSEVA et al. 1978
[6]) BELAYA and KISLEROVA 1978
[7]) ABRAMOV and ABRAMOVA 1981
[8]) UKRAINTSEVA 1981
[9]) UKRAINTSEVA 1982
[10]) MEDVEDEV and FORENOVA 1977

the Upper Pleistocene and Holocene (Fig. 5). The Mammoth epoch, i.e. the life-time of mammoth as a species, as well as of the other representatives of the Mammoth Faunistic Complex, is characterized by a cyclic, fluctuating pattern of the environment, i.e. alternation of cold (glacial) and warm (interglacial) periods. By this is following that the mammoth and the other representatives of the complex having adapted to cold (glacial) epochs, had to exist under environmental conditions not suitable to their morpho-functional pretensions. Afforestation and paludification resulting from the warm and interglacial periods dramatically diminished the pasture area. The forage quality deteriorated: dominating among the plants were wet swamp habitat species, i.e. sedges, cotton-grasses, grasses, mosses which are less valuable than plants of dry habitats and meadow grasland with respect to protein, albumin, lipid and mineral contents (LARIN 1958), while green mosses, although abundant, do not appear to be a suitable kind of forage (KOSHKINA 1961). Sedges and grasses whose remains are found to be dominant in the gastrointestinal contents of the fossil animals in question, are practically of the same forage value. However, wet habitat sedges are significantly inferior to desert and mountain sedges both in their nutrional proporties and in the mineral content, particularly calcium content (LARIN 1958). Reduced quality of the forage during the warm Pleistocene and Holocene intervals diminished birthrate and increased mortality in the warm

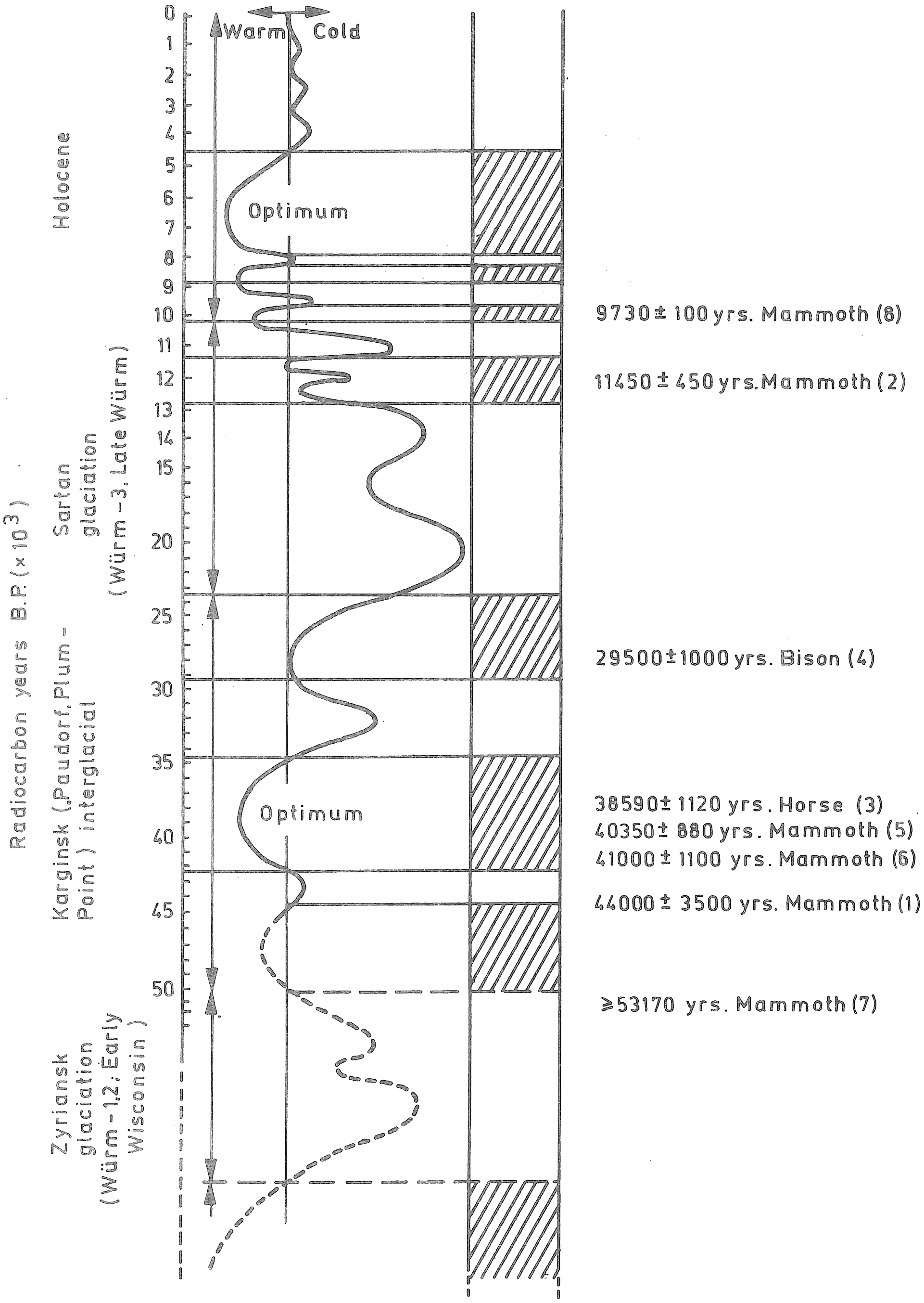

Fig. 5. Scheme showing the periods of the mass perish of large herbivorous animals of Siberia on the background of global climatic changes

periods, which invariably resulted in the decrease of the animals' total abundance. Genetically, such species as mammoth and wooly rhinoceros proved to be inadequately adapted to the warm epochs. The cyclic, fluctuating nature of the environment reduced the animals incapable of developing a species common strategy of adaption, since environmental fluctuations were sharp enough, while alternation of cold and warm rhythms was too rapid in terms of the geological time to allow a readjustment of the correlation mechanisms in the animal organisms. As a result, species of more narrow specialization, i.e. mammoth, wooly rhinoceros, appear to be extinct first, since their genetic possibilities of adaption to sharp changes in the environmental conditions proved to be most limited. Thus, mammoth extinction, as well as extinction of some of their "trabants", was due to set of causes which, in turn, resulted from the Pleistocene and Holocene fluctuating environment, alternation of cold and warm rhythms. The animals, as can be concluded, proved incapable of adapting to the drastic changes in the ecological conditions.

Summary

The majority of fossil animals discovered in Siberia is coming — according to C^{14}-dating — from warm-time deposits of the past 53000—10000 years. The essential part of plants, determined by results of research of the gastrointestinal contents of the fossil animals, give evidence that in these periods in Siberia forests, swamp communities of different types and swamps have been widely distributed. In dependence of this fact the favourable feeding-places have been reduced to a great extent. The types of the feeding-plants have been changed fundamentally too: sedge-grasses, cotton-grasses, grasses, and mosses became dominant. In the contents of basic food-elements (protein, albumin, and fat) as well as of minerals (calcium, calium, phosphor and others) these plants were distinctly poorer than those of dry places and meadows with various grass-communities essential for the large herbivorous animals.

These new palaeobotanical date allow conclusions as to the natural environment of the mammoth and its "sputniks" giving the possibility to solve the problem of Pleistocene extinction on a palaeobiological basis. The relative sudden extinction of the mammoth is undaubtedly explainable by a complex of causes. Our opinion, therefore, is that these causes should bee seen as a function of physical structure and the sum of natural processes in the Pleistocene, the cyclic alternation of the natural environment and the interaction of optimal cold periods and infavourable warm periods to cold-climate adapted animals. So the cold-climate adapted animals existed in the late Pleistocene mainly under natural conditions not suitable to their morpho-functional adaptions (altogether 2/3 of the time).

Zusammenfassung

Die Mehrzahl der in Sibirien entdeckten fossilen Tierkadaver stammt nach C^{14}-Daten aus Warmzeit-Perioden der letzten 53000 bis 10000 Jahre. Der Pflanzenbestand aus dem Magen-Darmtrakt der genannten Tierkadaver zeigt, daß in diesen Perioden in Sibirien vorherrschend Wälder, Sumpfgesellschaften verschiedenen Typus und Sümpfe weit verbreitet waren. Als Folge dieser Umstellung verschlechterten sich die für die Großsäuger günstigen Lebensbedingungen deutlich. Grundlegend veränderte sich auch das Nahrungsangebot: es herrschten Pflanzen feuchter und versumpfter Standorte vor — Riedgräser, Wollgräser, Gräser und Moose. In der Zusammensetzung der Grundnahrungselemente (Protein, Eiweiße, Fette) und im Mineralbestand (Calcium, Kalium, Phosphor und andere) waren diese Pflanzen bedeutend ärmer als diejenigen trockener Standorte und Wiesen mit vielfältigem Grasbestand, die für die herbivoren Großsäuger lebenswichtig waren.

Diese neuen paläobotanischen Daten erlauben nun, die Lebensbedingungen des Mammuts und der anderen assoziierten Großsäuger zu rekonstruieren und auf diese Weise an die Lösung des Problems des Aussterbens einiger Großsäuger im Pleistozän auf paläobotanischer Grundlage heranzugehen. So erscheint das verhältnismäßig schnelle Aussterben des Mammuts infolge eines Komplexes von Ursachen verständlich. Wir nehmen demzufolge an, daß diese Gründe durch den Verlauf der Naturprozesse im Pleistozän bedingt sind, durch den zyklisch schwankenden Charakter der Umwelt, durch die Wechselwirkungen der Dauer der für diese Tiere optimalen Kaltzeiten und ungünstigeren Warmzeiten. Diese kälteliebenden Tiere existierten also zumeist unter Bedingungen eines ihrer morphofunktionalen Anpassung nicht entsprechenden Milieus (insgesamt 2/3 dieser Zeit).

Резюме

Большинство из обнаруженных в Сибири ископаемых животных погибло, согласно данных C^{14} метода, в периоды потеплений в последние 53 — 10 тысяч лет. Состав растений, установленный в результате изучения содержимого их желудочно-кишечных трактов, свидетельствует, что в эти периоды на территории Сибири широкое распространение получали леса, различного типа заболоченные сообщества, болота. Площади кормовых угодий в связи с этим резко сокращались. Кардинально менялся и состав кормов: в них преобладали растения увлажненных и заболоченных местообитаний — осоки, пушицы, злаки, мхи, которые по содержанию основных питательных элементов (протеин, белки, жиры) и минеральному составу (кальций, калий, фосфор и др.) значительно беднее растений сухих местообитаний и лугового разнотравья, что было жизненно важно для крупных растениеядных животных.

Эти новые палеоботанические данные позволили составить представление об условиях обитания мамонта и его „спутников" и, таким образом, подойти к решению проблемы причин вымирания некоторых животных в плейстоцене на палеобиологической основе. То что относительно быстрое вымирание мамонта было вызвано комплексом причин не вызывает сомнений. Однако, эти причины, мы полагаем, были обусловлены структурой и ходом природного процесса в плейстоцене, циклическим, колебательным характером природной среды, соотношением длительности холодных, оптимальных для них, и теплых, пессимальны, ритмов; тем, что эти холодовыносливые животные большую часть времени (в сумме 2/3) существовали в условиях среды не соответствующих их морфофункциональным приспособлениям.

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