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BIODIVERSITY OF VERTEBRATES AND THE DEVELOPMENT STEPPE SPACES IN THE NEOPLEISTOCENE OF KAZAKHSTAN (CENTER OF EURASIA)

Annotation. This work examines how shifts in regional and global climatic regimes during the Neopleistocene influenced both the development of steppe landscapes and the structure of fossil vertebrate diversity across the territory of Kazakhstan. Reconstruction of paleoenvironments and climate dynamics was based on palynological datasets from deposits of varying facies, which made it possible to trace transformations in vegetation and landscape conditions throughout sediment accumulation. The Neopleistocene interval was marked by alternating phases of cooling, including advances of mountain glaciations, and intervals of climatic moderation accompanied by increased humidity. On lowland territories, the effects of glacial phases expressed themselves more distinctly through intensified cooling and moisture growth. These environmental transitions shaped ecological niches and directly affected faunal composition, generally leading to a reduction in species richness through successive stages of the Neopleistocene. By the close of the Pleistocene, most representatives of the mammoth complex had disappeared, while only a limited group of taxa (saiga, moose, carnivores, brown bears, rodents) persisted and later formed the basis of the modern vertebrate fauna.

Keywords: Neopleistocene; vertebrate diversity; palynological indicators; climatic evolution; steppe landscapes.

Introduction

According to P.A. Tleuberdina [14], the Neopleistocene constitutes the final and geologically shortest phase of Earth’s history, characterized by profound natural and climatic reorganizations. Although brief in duration, the Quaternary is the interval during which modern geomorphological structures took shape and when the major climatic phenomena—most notably the Ice Age—exerted significant influence on terrestrial biota and the emergence of modern vertebrate communities, including humans. During this time, orogenic uplift in Alpine-type geosynclinal regions continued, while large-scale oscillatory movements of the lithosphere intensified contrasts in relief. The combined effects of cooling and tectonic activity facilitated the formation of extensive ice sheets at high latitudes. Faunal assemblages from this period consistently reflect a markedly

continental climate regime, with progressive cooling and aridization toward its end. These conditions stimulated the expansion of steppe and desert zones at the expense of earlier savanna-like environments.

Kazakhstan, owing to its central position in Eurasia and considerable physiographic heterogeneity, preserves a rich record of vertebrate evolution spanning numerous geological epochs. Over the last century, studies of the Quaternary faunas (Neopleistocene epoch) have documented substantial shifts in taxonomic composition, including changes in the distribution of proboscideans, the palaeogeographic history of the fossil saiga, the diversity of Pleistocene equids and rhinoceroses, as well as numerous Cenozoic rodents and ungulates as discussed by K.Zh. Zhilkibaev [10], Zazhigin [11], Tleuberdina and Kozhamkulova [12], and Tleuberdina with Nazymbetova [13,14].

Materials and methods of research

Paleoenvironmental and paleoclimatic reconstructions were undertaken using the principle of actualism and comparative analysis of palynoflora and paleofaunal datasets. Variations in the composition of spores and pollen extracted from deposits of differing facies provide evidence of climatic oscillations during the accumulation of Neopleistocene strata. Palynological data from the works of L.N. Chupina [1] and E.V. Chalykhyan [2] formed the basis for reconstructing vegetation dynamics. Information on early vertebrate findings derives from classical publications by Yu.A. Orlov [3], V.A. Teryaev [4], E.I. Belyaeva [5,6], and I.A. Vislobokova [7]. Since the 1960s, extensive contributions by B.S. Kozhamkulova (1969–2017) have significantly advanced knowledge regarding Kazakhstani Quaternary vertebrate diversity [8,9].

Research results

During the Neopleistocene, the principal mountain structures within Kazakhstan continued their development. Climatic variability throughout the epoch manifested through alternating glacial advances in mountainous regions and intervals characterized by moderate temperatures and partial increase in moisture availability. In lowland territories, glacial phases produced more pronounced cooling and humidity shifts. While the general structure of vegetation—forests, forest-steppe, steppe, desert—remained recognizable, the relative proportions of these biomes were altered: forested areas gradually contracted, open landscapes expanded, and tree species diversity became progressively limited, especially across plains. These transformations created preconditions for gradual faunal restructuring through different stages of the Pleistocene [13].

By the terminal Pliocene (Eopleistocene), Kazakhstan’s zonal landscape distribution already resembled in many ways its present configuration. By the end of the Apsheronian, mountain systems of southeastern Kazakhstan had reached elevations exceeding 5,000 m, contributing to the initiation of local glacial systems, including the semi-permanent Khan-Tengri glaciation [13,15]. Climatic cooling in the latter half of the Late Pliocene induced significant shifts in soil–vegetation zonation, which in turn affected mammalian communities. According to B.S. Kozhamkulova [16,17], the fauna of this interval consisted of carnivores such as *Canis cf. chihliensis*, *Hyaena cf. brevirostris*, *Homotherium*; proboscideans including *Archidiskodon gromovi*; equids of the *Equus (Allohippus) stenonis* group; rhinocerotids of the genus *Dicerorhinus*; and a suite of artiodactyls, including *Cervus cf. elaphus*, *Leptobos cf. etruscus*, *Gazellospira*,

Procapra gutturosa, *Gazella subgutturosa*, and *Ovis ammon*. The composition of this assemblage indicates a strongly continental climate, with aridification and cooling contributing to the widening of steppe and desert belts. Vegetation underwent multiple reorganizations during the Neopleistocene, reflecting recurring climatic fluctuations [14].

As the Neopleistocene progressed, the early phase of the epoch was characterized by a moderately humid, yet thermally restrained climate. Steppe landscapes with isolated patches of mixed forest predominated across much of the territory, while swampy areas were widespread in eastern regions. Increased humidity promoted the expansion of tree taxa such as *Betula*, *Pinus*, and *Populus*. However, during the second half of the early Neopleistocene, conditions shifted toward increased aridity, leading to a reduction in arboreal diversity. During the wetter interval of the epoch's first half, the mountain glaciation expanded considerably; once it achieved its maximum extent, the regional climate became distinctly colder and drier. The subsequent warming phase triggered glacial recession, strengthening erosional and depositional processes in mountain valleys.

These broader climatic oscillations were directly accompanied by faunal transitions. In the early Neopleistocene, mammalian assemblages gradually gave way to proboscideans of the genera *Archidiskodon* and *Palaeoloxodon*, taxa adapted to forested habitats near water bodies, where they fed on shrubs, leaves, and woody vegetation. Various rhinocerotids the large-bodied *Elasmotherium sibiricum* and species of *Dicerorhinus* occupied steppe environments with tall grasses and meadow vegetation. The broad-faced elk *Alces latifrons* was restricted to northern regions dominated by swampy forests. The steppe biome was inhabited by fast-running equids such as the Zussenborn and Mosbach forms, while bison, pronghorns, early asses, and camelids were characteristic of open and semi-desert territories. Many of these ungulates likely engaged in seasonal migrations. Taken together, these faunal elements demonstrate the emergence of communities increasingly adapted to steppe landscapes [1, 10, 14, 17].

During the Middle Neopleistocene, tectonic activity intensified across Kazakhstan, and mountain ranges approached their modern elevations. Climatic conditions during the first half of this interval were relatively favorable, fostering a more diverse arboreal cover alongside mesophytic meadow associations. The second half of the Middle Pleistocene, however, brought a pronounced cold phase associated with the peak of the Samara glaciation in Western Siberia. This cooling event caused a substantial southward displacement of vegetation belts. Palynological evidence shows a marked increase in taxa typical of dark coniferous taiga, while steppe communities shifted from wormwood-dominated assemblages toward mesophilic grass–cereal steppes and cereal–maral-steppe groupings enriched with *Ephedra* [2, 14].

Overall, this period reflects a gradual climatic cooling which, following an earlier phase of increased moisture availability, initiated the development of dry steppes and desert landscapes. According to Tleuberdina and Kozhamkulova (2009) [12], faunal assemblages became dominated by organisms adapted to open habitats, including *Mammuthus chosaricus* and the forest elephant *Palaeoloxodon*. The same environments supported the large-horned bison *Bison priscus gigas*, the giant deer *Megaloceros giganteus ruffi*, and the saiga *Saiga tatarica*. The camel *Camelus knoblochi*, like its modern relatives, inhabited arid desert tracts. As aridization strengthened, the genera

Archidiskodon and *Palaeoloxodon* eventually disappeared, while the mammoth proved capable of adapting to the increasingly severe climate. During the Late Neopleistocene, the mammoth complex dominated much of Eastern Europe and the Trans-Ural region. These faunas were characteristic of the cold tundra–steppe environments typical for the non-tropical Northern Hemisphere. In Kazakhstan, vegetation successions during this period progressed from cereal–grass communities with *Chenopodiaceae* to combinations of cereal–chenopod and wormwood-dominated assemblages, later replaced by mixed cereal–grass landscapes enriched with *Ephedra* and *Artemisia*. The culmination of powerful tectonic movements in the terminal Pleistocene resulted in renewed mountain uplift and increased humidity, promoting the expansion of valley glaciers.

According to Chupina (1974, 1981), the second half of the Late Pleistocene was dominated by arid conditions, especially during the colder phases. Dry steppes and semi-desert zones were prevalent, whereas warming episodes facilitated the development of meadow and forest-steppe patches. This interval corresponds to the distribution of the woolly mammoth, *Mammuthus primigenius Blum.*, which reached Kazakhstan in the late Middle Pleistocene and survived here almost until the end of the Late Pleistocene. Its remains are widespread throughout the country except for the Mangystau region. As noted by Kozhamkulova and Pak (1988), the mammoth fauna of Kazakhstan included *Coelodonta antiquitatis*, *Bison priscus mediator*, *Bos primigenius*, *Camelus knoblochi*, saiga, equids (horses and kulans), *Ovis ammon*, cave and brown bears, the cave lion *Panthera spelaea*, wolf, fox, hare, and various small mammals and birds. Representatives of this faunal complex occupied nearly the entire northern part of Kazakhstan.

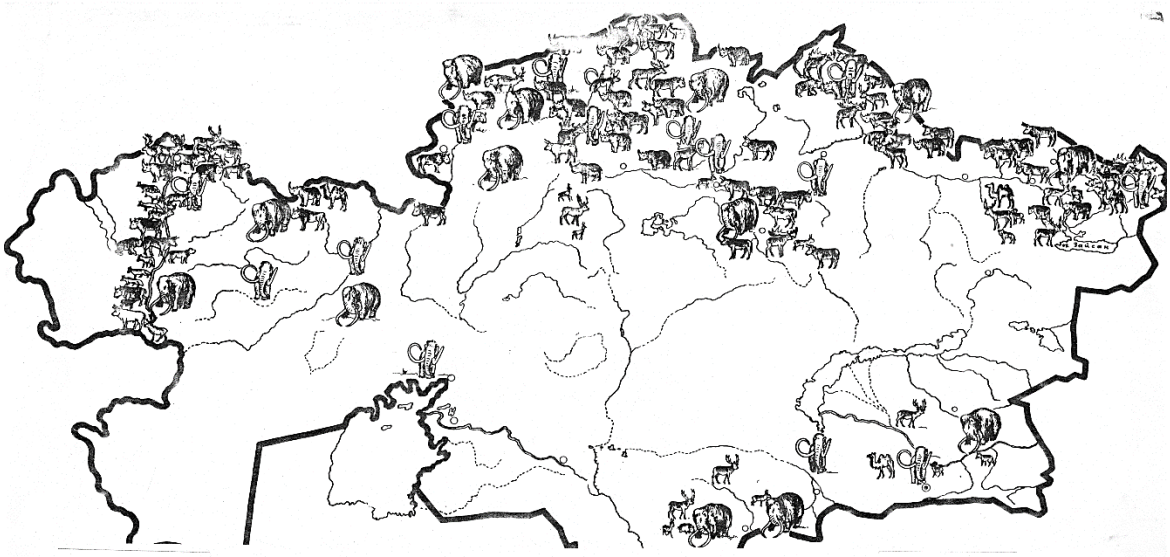

Figure 1 - Map of distribution of mammoth fauna elements in Kazakhstan (according to B.S. Kozhamkulova [10].

Conclusion

In the Holocene, when some periods of humidification were noted, a steppe developed that was similar to its modern counterparts, and the vegetation composition included numerous representatives of mesophilic and xerophilic plant groups. In the

south, as the climate became drier, the role of both xerophilic plants and desert associations increased. In the early Holocene, the climate remained similar to that of the late Neopleistocene [19]. Accordingly, landscapes with the corresponding fauna have been preserved: tarpan, kulan, Knobloch camel, short-horned bison, primeval tur, reindeer, moose, etc. Judging by the spore-pollen spectra from the youngest sediments, after the Middle Holocene aridization, a gradual general humidification of the climate occurs, which continues to the present, it should be noted that of the Holocene species, eight of which are no longer found in Kazakhstan [20].

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Тлеубердина П.А.

ОМЫРТҚАЛЫ ЖАНУАРЛАРДЫҢ БИОӘРТҮРЛІЛІГІН МЕН ДАЛА КЕНІКТІКТЕРІНІҢ ДАМУЫ ҚАЗАҚСТАННЫҢ НЕОПЛЕЙСТЛЦЕН КЕЗЕҢІНДЕ (ЕУРАЗИЯ ОРТАЛЫҒЫ)

Андатпа. Осы зерттеудің мақсаттарына сәйкес, Қазақстан аумағындағы неоген дәуірінің әртүрлі кезеңдерінде жалпы климаттық жағдайлардың өзгеруінің далалық кеңістіктердің дамуына, сондай-ақ жойылып кеткен омыртқалылардың биоәртүрлілігінің құрамына әсер ету процесі қарастырылды. Бүкіл кезең бойы климаттың ауытқулары байқалады, кейде тауларда мұздық дәуірлердің басталуымен, кейде климаттың жұмсаруымен және ішінара ылғалдануымен көрінеді. Жазықтарда климаттың ылғалдануы мен таулардағы мұздықтар кезіндегі салқындау айқын байқалды. Бұл климаттың континенталдануын және салқындау мен аридизацияның жалғасуын көрсетеді, бұл тегістелген кеңістіктерде айтарлықтай аумақта далалар мен шөлдердің пайда болуына ықпал етті. Ландшафттық-климаттық жағдайлардың өзгеруінің бұл процесі омыртқалылардың биоәртүрлілігін сақтау үшін экологиялық орындардың дамуына ықпал етіп қана қоймай, сонымен қатар неоген дәуірінің әр кезеңіндегі омыртқалылардың түрлік

алуандылығының азаюын да көрсетеді. Неоген дәуірінің соңына қарай мамонт фаунасының көптеген түрлері жойылып кетті, тек киік, бұлан, құлан, қасқыр, түлкі, қоңыр аю, қоян және кеміргіштер ғана қазіргі фаунаның негізін құрады.

Кілт сөздер: Неоплейстоцен; биоалуантүрлілік; полинофлора; климаттық жағдайлар; дала кеңістігі.

Тлеубердина П.А.

БИОРАЗНООБРАЗИЕ ПОЗВОНОЧНЫХ И РАЗВИТИЕ СТЕПНЫХ ПРОСТРАНСТВ НЕОПЛЕЙСТОЦЕНА КАЗАХСТАНА (ЦЕНТР ЕВРАЗИИ)

Аннотация. В соответствии с целями данного исследования был рассмотрен процесс влияния изменений общих климатических условий на освоение степных пространств и на состав биоразнообразия ископаемых позвоночных в разные периоды эпохи неоплейстоцена на территории Казахстана. Для реконструкции палеосреды и климатических условий метод анализа данных о спорах и пыльце из разных фаций отложений позволил нам проследить, как менялась ландшафтно-климатическая ситуация в процессе формирования неоплейстоценовых отложений. На протяжении всего периода наблюдались колебания климата, выражавшиеся в наступлении ледниковых периодов в горах, а также в смягчении и частичном увлажнении климата. На равнинах увлажнение климата и похолодание в периоды оледенения гор были более выраженными. Этот процесс трансформации топографических и погодных условий также способствовал формированию экологических ниш, которые не только использовались для поддержания биоразнообразия животных, но и демонстрировали снижение видового разнообразия животных в течение каждого периода эпохи неоплейстоцена. В конце плейстоцена большинство мамонтовых животных вымерло (исключение составляли сайгаки, лоси, волки, лисы, бурые медведи и грызуны), которые сформировали позвоночных современной фауны.

Ключевые слова: Неоплейстоцен; биоразнообразие; палинофлора; климатические условия; степные пространства.