ISSN 0031-0301, Paleontological Journal, 2022, Vol. 56, No. 1, pp. 97–105. © Pleiades Publishing, Ltd., 2022.
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Cave Bears (*Ursus Spelaeus* sensu lato) of the Urals

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Received June 8, 2021; revised June 10, 2021; accepted June 15, 2021

Abstract—The paper summarizes results of eighty years of studies of large (*Ursus* (*Spelaearctos*) *kanivetz* Vereshchagin, 1973) and small (*Ursus* (*Spelaearctos*) ex gr. *savini–rossicus*) cave bears in the Urals, including their biology, distribution, occurrence and extinction times, taxonomy and phylogeny, as well as interaction with humans.

Keywords: cave bears, *Ursus spelaeus*, *Ursus rossicus*, *Ursus savini*, *Ursus kanivetz*, the Urals, Late Pleistocene, morphology, distribution, biology

DOI: 10.1134/S0031030122010063

INTRODUCTION

Cave bears (*Ursus* (*Spelaearctos*) spp.) are a group of typical representatives of the Late Pleistocene (mammoth) faunal assemblage, widespread in Europe and northern Asia (Baryshnikov, 2007; Sher et al., 2011). Until the beginning of the 21st century two species of cave bears: the large cave bear *Ursus spelaeus* Rosenmüller, 1794 and the small cave bear *U. savini* Andrews, 1922, or *U. rossicus* Borissiak, 1930 were believed to exist in the Late Pleistocene of these regions (Kurtèn, 1995; Baryshnikov, 2007). At present, based on molecular data (Barlow et al., 2021), three species are recognized in the group of large cave bears: *U. spelaeus* and *U. eremus* Rabeder, Hofreiter, Nagel et Withalm, 2004 (common in Western Europe), as well as *U. kanivetz* Vereshchagin, 1973 (found in Central and Eastern Europe and in the Urals; Knapp et al., 2009; Rabeder et al., 2011; Stiller et al., 2014; Baryshnikov and Puzachenko, 2019, 2020). *U. savini* (Western Europe) and *U. rossicus* (Northern Caucasus, Eastern Europe, Urals, Altai, Western and Eastern Siberia) are recognized in the group of small cave bears (Borissiak, 1930; Spassov et al., 2017; Baryshnikov and Puzachenko, 2019, 2020; Barlow et al., 2021).

Large and small cave bears co-existed in the Urals in the late Pleistocene. At that time, the northernmost populations of both species existed here, and this was the eastern border of the range of the large cave bear. Here, their distribution ranges were the greatest length from north to south, more than 1300 km. They included areas with different geographical and climatic conditions. All this determines the importance of the Urals for studying the general problems of microevolution, phylogeography, ecology, and biology of large and small cave bears.

The cave bears of the Urals have been studied for over 80 years. A vast amount of data has been accumulated over this time, reflecting both specific and general issues of their biology, morphology, phylogenesis and interaction with humans. These data have been published in more than 160 papers and are summarized in this publication.

THE HISTORY OF STUDY OF CAVE BEARS IN THE URALS

E. Hoffman was the first to discover bones of cave bears in the Uninskaya Cave in the North Urals in 1847 (Hoffman, 1856), but they were identified to species only in the 20th century. The first scientific collections of cave bear bones were obtained during excavations of the caves of the South Urals by S.N. Bibikov in 1937 (Gromov, 1948).

Several stages can be distinguished in the history of the study of Uralian cave bears. At the first stage, which lasted from the late 1940s to the late 1980s, data on the locations of the bones of cave bears were accumulated. Dozens of localities were discovered and described in the North, Middle and South Urals (Gromov, 1948; Karacharovsky, 1951; Vereshchagin, 1957; Vereshchagin and Kuzmina, 1962; Guslitser and Kanivets, 1965; Kuzmina, 1971, 1975; Guslitser and Pavlov, 1987). At this time, variability and the taxonomic status of the cave bears inhabiting the Urals were assessed for the first time (Kuzmina, 1971; Vereshchagin, 1973). It was established that two forms of cave bears lived in the Urals: the large cave bear *Ursus spelaeus kanivetz* Vereshchagin, 1973 and the

small cave bear *Ursus uralensis* Vereshchagin, 1973 (Vereshchagin, 1973).

The second stage lasted from the late 1980s until the end of the 2000s. During this period, a focused study of the ecology of the Ural cave bears began (Kosintsev, 1988; Smirnov et al., 1990; Kosintsev and Vorobiev, 2001). The first radiocarbon dates obtained from the bones of cave bears appear (Kosintsev et al., 2003; Baryshnikov, 2007; Pacher and Stuart, 2009). The number of studies on the variability and taxonomy of Ural cave bears increased significantly (Vereshchagin and Baryshnikov, 2000; Baryshnikov and Foronova, 2001; Kuzmina, 2002; Baryshnikov, 2003, 2006, 2007; Sataev, 2006). Data on localities with remains of cave bears continued to be published (Smirnov et al., 1990; Sataev, 1995; Yakovlev et al., 2000; Ulitko, 2003; Kosintsev and Sataev, 2005; Razhev et al., 2005). By the end of this period, the morphological characteristics of the small cave bear were identified, and data on the sex and age composition of the populations of the large and small cave bears were obtained based on representative material from several localities of the Middle and South Urals.

The last stage began in the late 2000s and continues to the present. During this period, molecular genetic methods are actively used (Stiller et al., 2009, 2010, 2014; Knapp et al., 2009; Gretzinger et al., 2019; Knapp, 2019; Barlow et al., 2021). As a result of the analysis of nuclear DNA, taxonomic status was established, the divergence time of the phyletic lineages of small and large cave bears of the Urals was determined, and their morphological specificity was assessed. Multidimensional statistical methods are beginning to be widely used to study the variability of bears (Baryshnikov and Puzachenko, 2011, 2017, 2019, 2020; Baryshnikov et al., 2018, 2019). The first data on the interaction between humans and Uralian cave bears were obtained (Shirokov et al., 2011; Kotov et al., 2020; Gimranov et al., 2021a). Descriptions of new localities with remains of cave bears continue (Kosintsev et al., 2016; Fadeeva et al., 2019; Yurin, 2020; Danukalova et al., 2020; Gimranov and Kosintsev, 2020; Fadeeva et al., 2020; Gimranov et al., 2021b; Kosintsev et al., 2021).

CAVE BEAR OCCURRENCES IN THE URALS

Nearly all remains of cave bears in the Urals come from cave-type localities. There is only one open-type locality, the Bogdanovka site of the Middle Paleolithic in the South Urals (Shirokov et al., 2011), in which the remains of a small cave bear were found. No remains of cave bears were found in the Polar Urals (Bachura and Kosintsev, 2007).

Six localities (Figs. 1a, 1b) with bones of cave bears have been reported from the North Urals (Kuzmina, 1971; Kosintsev and Vorobiev, 2001). The northernmost location of the remains of the large cave bear is the Bolshaya Drovatnitsa Cave (63°57′ N; 57°37′ E) (Kuzmina, 1971). One locality for the small cave bear is known in the region, Medvezhiya Cave (62°05′ N, 58°05′ E) (Gimranov et al., 2021b). Finds of the bones of a cave bear in the Shaitanskaya Cave on the eastern slope of the North Urals (Kosintsev and Borodin, 1990) were not confirmed.

In the Middle Urals, there are 18 localities with bones of large cave bear and four localities with small cave bear (Figs. 1a, 1b). Finds of cave bears were previously reported in the Yazvinskaya and Pershinskaya caves (Kosintsev and Vorobiev, 2001) and the Bezymyanny Cave (Petrin and Smirnov, 1977; Kosintsev and Vorobiev, 2001). When revising these materials, we found that the bone remains from these localities actually belong to the brown bear.

In the South Urals, there are 28 localities with the remains of large cave bear and two localities with small cave bear (Figs. 1a, 1b). Previously, records of cave bears in the Beydinskaya and Uluir 2 caves (Yurin, 2011), Smelovskaya 2 Cave (Kuzmina, 2000; Kosintsev and Vorobiev, 2001; Kosintsev, 2007; Yurin, 2011) and Shulgan-Tash (Kapova) Cave (Kuzmina and Abramson, 1997; Kosintsev and Vorobiev, 2001). The revision of these materials showed that it is impossible to identify them beyond the genus *Ursus*. They could belong to either cave or brown bears.

Analysis of the geographical distribution of the records suggests that large cave bear was only present in localities on the western slope of the Urals, while small cave bear was found on both slopes (Fig. 1). There is no doubt that the Ural Mountains could not have been a physical obstacle to the passage of the large cave bear to the eastern slope, so its absence on the eastern slope has not been so far adequately explained. Both cave bear species are herbivorous animals (Naito et al., 2020), and therefore the sympatry of their ranges may indirectly indicate significant differences in their diets. It can be assumed that on the eastern slope of the Urals and further in Siberia, a number of the main food plant species of the large cave bear were absent, or the productivity of their cenopopulations was not high enough. This can also explain the limitation of the spreading of both species to the north.

TAXONOMY AND PHYLOGENY OF THE URAL CAVE BEARS

Currently, Ural cave bears are classified into two species: large *U. kanivetz* and small *U.* ex gr. *savini–rossicus*. They are readily distinguished by the structure of the baculum (Vereshchagin, 1973), in the size and proportions of the skull (Baryshnikov and Puzachenko, 2011), the lower jaw (Baryshnikov et al., 2018), cheek teeth (Vereshchagin and Baryshnikov, 2000; Baryshnikov and Puzachenko, 2019), 2020;

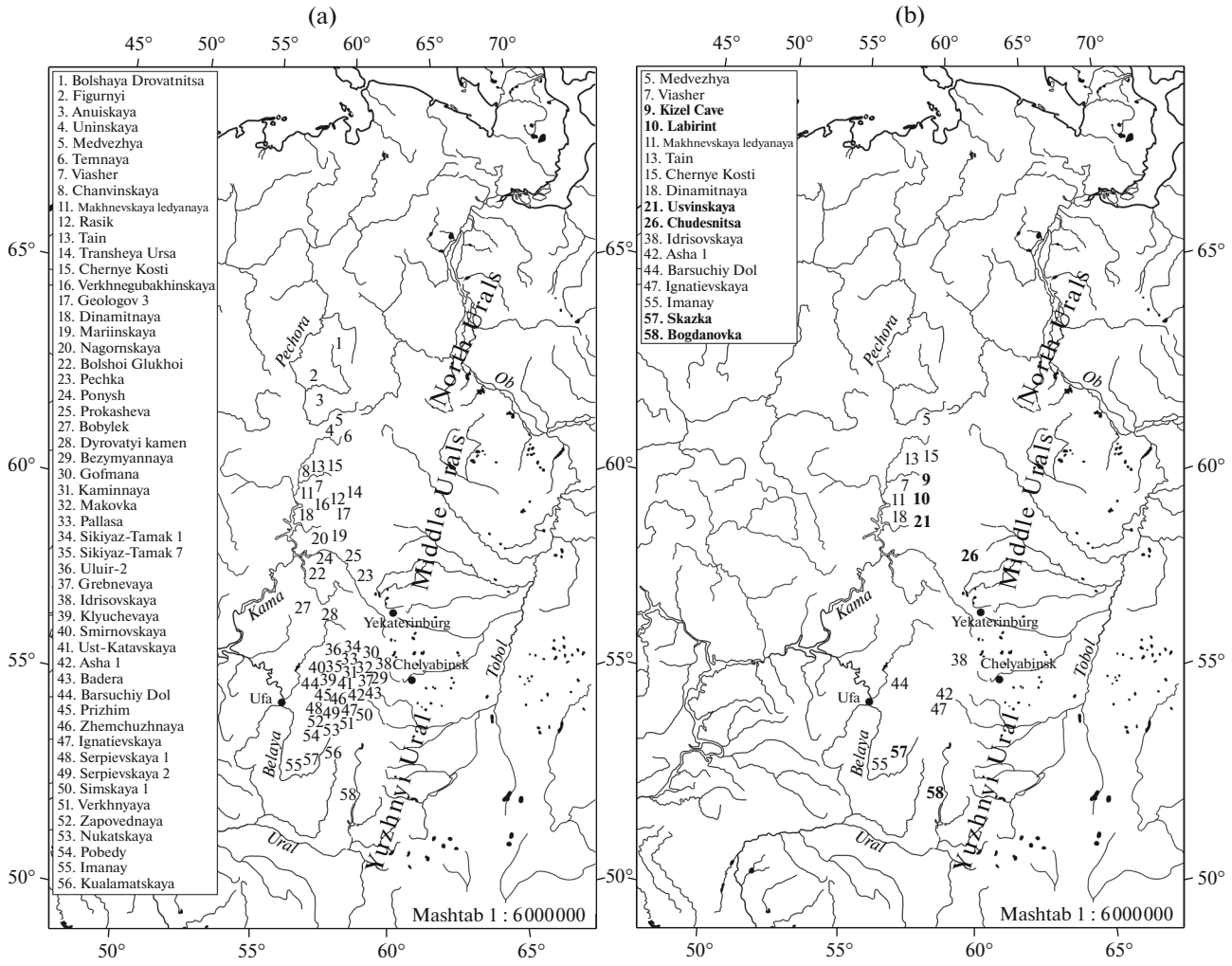

Fig. 1. Schematic map of the localities with the remains of cave bears in the Urals: (a) localities of the large cave bear, (b) localities of the small cave bear. Numbers and names of localities where the remains of only small cave bears were found are in bold italics.

Gimranov et al., 2021b) and metapodia (Baryshnikov and Puzachenko, 2017). The significance of these differences has recently been confirmed by nuclear DNA analysis (Barlow et al., 2021).

Over time, ideas about the taxonomic affiliation of cave bears from the Urals have changed several times. The first records were attributed to the large cave bear *U. spelaeus* (Gromov, 1948). All subsequent finds of large forms of cave bears were also attributed to this species. In 1973, a separate subspecies of the large cave bear *U. spelaeus kanivetz* was described based on materials from the Medvezhiya Cave (Vereshchagin, 1973). This name was used in subsequent publications (Baryshnikov, 1981, 2003, 2007; Abramov and Baryshnikov, 1990; Baryshnikov and Puzachenko, 2011). Later, the subspecies *U. s. bliznetshovi* Kuzmina, 2002 was described based on materials from Secrets Cave (=Tain Cave) (Kuzmina, 2002), which was later considered as a junior synonym of *U. s. odessanus* von Nordmann, 1858, along with *U. spelaeus kanivetz* (Baryshnikov, 2003). Subsequently, the status of *U. s. kanivetz* as a valid taxon was reinstated (Baryshnikov, 2007).

The study of mitochondrial DNA using samples from Medvezhiya Cave showed that the large cave bear from the North Urals belongs to the "*ingressus*" haplogroup (Knapp et al., 2009; Stiller et al., 2009), which was previously considered as a species in its own right *U. ingressus* Rabeder et al., 2004 (Rabeder et al., 2004). Later, this was confirmed by new studies of mitochondrial DNA in bears (Stiller et al., 2014; Gretzinger et al., 2019). The Medvezhiya Cave is a type locality of *U. spelaeus kanivetz* Vereshchagin, 1973. Thus, according to the International Code of Zoological Nomenclature, the latter name has priority, and the species should be named *U. kanivetz* Vereshchagin, 1973 (=*U. ingressus* Rabeder et al., 2004) (Baryshnikov and Puzachenko, 2017). Cave bears from the Bolshoi Glukhoi Cave in the Middle Urals and Serpievskaya Cave in the South Urals also

belong to the "*ingressus*" haplogroup (Stiller et al., 2009). Thus, all large cave bears of the Urals belong to *U. kanivetz*. Nuclear DNA analysis confirmed the genetic uniqueness and species status of the Ural large cave bear (Barlow et al., 2021).

The small cave bear from the Kizel Cave in the Middle Urals was originally assigned to *U. rossicus* Borissiak, 1930 (Vereshchagin, 1959), and later was identified as an independent species, *U. uralensis* (Vereshchagin, 1973). Later, this form was identified as either *U. rossicus uralensis* (Baryshnikov, 1981; Vereshchagin, 1982), or *U. rossicus* (Vereschagin and Baryshnikov, 2000; Baryshnikov and Foronova, 2001; Kuzmina, 2002; Kosintsev, 2003; Yakovlev et al., 2005). In 2003, the species *U. rossicus* Borissiak, 1930 was synonymized with *U. savini* Andrews, 1922, and the subspecies *U. r. uralensis* Vereshchagin, 1973, consequently, began to be referred to as *U. savini uralensis* (Baryshnikov, 2003). Over a number of subsequent years, the remains of the small cave bear from the territory of the Urals were attributed to *U. savini* Andrews, 1922 (Kosintsev and Sataev, 2005; Baryshnikov, 2007; Kosintsev, 2007, 2019; Shirokov et al., 2011; Sher et al., 2011; Kosintsev and Bachura, 2013; Kosintsev et al., 2016; Gimranov and Kosintsev, 2020; Fadeeva et al., 2020; Danukalova et al., 2020; Silaev et al., 2020). At the same time, other researchers continued to use the name *U. rossicus*, based, among other things, on molecular genetic data (Markova et al., 2008; Pacher and Stuart, 2009; Danukalova et al., 2009; Baryshnikov and Puzachenko, 2011, 2017, 2019, 2020; Fadeeva et al., 2011; Stiller et al., 2014; Baryshnikov et al., 2018; Bachura and Kosintsev, 2019; Knapp, 2019; Puzachenko et al., 2020; Barlow et al., 2021).

Until a revision of morphological and molecular genetic data on small cave bears of the Urals, Eastern and Western Europe, we assign the small cave bear of the Urals to the group *Ursus* ex gr. *savini–rossicus* (Kotov et al., 2020; Gimranov et al., 2021a, b; Pavlova et al., 2021). The small form of the cave bear from the Verkhnyaya Cave in the South Urals has an uncertain taxonomic position. It was identified as *Spelaearctos* cf. *rossicus* (Sataev, 1996), *S. rossicus* (Yakovlev et al., 2005) or *Ursus* (*Spelaearcos*) cf. *spelaeus deningeroides* Mottl, 1964 (R.M. Sataev, pers. comm.). Ultimately, it was concluded that a precise species identification was impossible, and this form was identified as *U.* (*Spelaearcos*) sp. (Sataev, 2008). Nevertheless, in a number of publications this find is included in the lists of faunas as *U.* cf. *deningeri hercynicus* (Danukalova et al., 2008), *U. savini* (Kosintsev et al., 2016), and *U.* cf. *deningeri* (Danukalova et al., 2020).

The interpretation of the phylogeny of the Ural cave bears was initially based on the results of morphological analysis. The large cave bear of the Urals, according to the results of multivariate analysis of the size of the skull (Baryshnikov, Puzachenko, 2011), the lower jaw (Baryshnikov et al., 2018), upper teeth (Baryshnikov, Puzachenko, 2019), lower teeth (Baryshnikov, Puzachenko, 2020) and metapodia (Baryshnikov and Puzachenko, 2017) is combined with other samples of the large cave bear (*U. spelaeus* s.l.). Based on analysis of tooth size, *U. rossicus* from Kizel Cave, along with bears from Krasnodar and southern Siberia, as well as *U. savini* Andrews, 1922 from the Bacton Forest Bed locality, were united into one clade, separate from *U. spelaeus* (Baryshnikov and Foronova, 2001). The combined sample of the small cave bear, including the sample of the Ural form, according to the results of the analysis of the sizes of the skull, lower jaw, teeth and metapodia (Baryshnikov and Puzachenko, 2011, 2017, 2019, 2020; Baryshnikov et al., 2018) forms an independent clade, separate from the other cave bears.

Recently, according to the results of mitochondrial DNA analysis, the following clades of bears have been reconstructed: "*U. spelaeus*", including "*spelaeus*", "*ladinicus*", "*eremus*", as well as the *U. kanivetz* (=*U. ingressus*) clade, including *U. rossicus* from the Urals (Stiller et al., 2014; Knapp, 2019). The latter is in poor agreement with morphological data.

Analysis of the nuclear DNA of bears from Europe and the Urals gave a completely different pattern of the phylogenetic relationships of cave bears (Barlow et al., 2021). Two clades were identified, one of which includes all the large cave bears (*U. spelaeus* s.l.) in Europe and the Urals, and the other only the small cave bear (*U. rossicus*) from the Kizel Cave in the Urals. The Ural small cave bear is a deeply diverged isolated phylogenetic lineage and the third large group of cave bears, along with the European (*U. spelaeus* s.l.) and Caucasian (*U. kudarenis* s.l.). Nuclear genome analysis confirms the validity of the taxon *U. kanivetz*, which is reconstructed as a sister group to the European *spelaeus* and *ingressus* lineages. The results of the analysis of the nuclear genome fully confirm the results of the morphological analysis (Baryshnikov and Puzachenko, 2011, 2017, 2019, 2020; Baryshnikov et al., 2018). Thus, the phylogeny of cave bears, constructed earlier based on the results of analysis of mitochondrial DNA, seems to be incorrect.

Recently, estimates of the times of divergence of different forms of cave bears have been obtained. The median estimate of the divergence of the Ural cave bear (*U. rossicus*) and the large cave bear (*U. spelaeus* s.l.) by nuclear DNA is about 880 thousand years ago, and the separation of *U. kanivetz* from the *spelaeus–ingressus* group, according to these data, took place about 400 thousand years ago (Barlow et al., 2021).

BIOLOGY OF URAL CAVE BEARS

The most representative data were obtained on the biology of the large cave bear. Based on samples from several localities, the sex and age structures of the part

of the population that died during hibernation were determined. Sex was determined using the size of the bones (Medvezhiya, Secrets Cave (=Tain Cave), Geologov 3 and Asha 1 caves) and canine (Ignatievskaya Cave). The ratio of males to females in Secrets Cave (=Tain Cave) Cave is approximately 1 : 3, in Medvezhiya, Geologov 3, and Ignatievskaya caves 1 : 2, and in Asha 1 it is 1 : 1 (Kosintsev and Vorobiev, 2001; Kuzmina, 2002). In all samples, except for the sample from Asha 1, the sex ratios significantly differ from the 1 : 1 ratio. Evidently, in most cases, females died during hibernation more often than males. This is explained on the basis of an analogy with the biology of the brown bear, in which pregnant females and females with cubs usually hibernate earlier than males and females without offspring, occupying the most convenient places for hibernation. Probably, this behavior was also characteristic of cave bears. If this is the case, then cave bears hibernated alone (or a female with cubs), and not in groups, otherwise the differences in the ratio of males and females would have been less pronounced (Kosintsev and Vorobiev, 2001).

The ratio of age groups was assessed using various criteria. In the samples from Secrets Cave (=Tain Cave) and Geologov 3 caves, it was determined by the size of bones and the accretion of epiphyses, as a result of which several age groups were identified (0–1 years, 1–2 years, 2–3 years, 3–4 years, over 4 years old). Both caves are dominated by individuals aged 1–2 and 2–3 years (58 and 75%, respectively), newborn individuals (0–1 year old) make up 9.5 and 2.3%, and adults (over 4 years old)—18 and 34% y. In the Ignatievskaya and Asha 1 caves, the age composition was determined by the degree of wear of the incisor crown (I1-2 and i1-2), for which seven stages of wear were identified (Smirnov et al., 1990). In Asha 1 Cave, the bears that had died were dominated by semi-adults (21%) and adults (63%). In the three ancient layers of the Ignatievskaya Cave, young (19–28%) and semimature (22–26%) individuals prevailed, while in the later layer, young individuals dominated (47%). The differences between the samples from the Ignatievskaya and Asha 1 caves are statistically significant (Smirnov et al., 1990), while the reasons for such significant differences in the age structure are unclear.

Parasitological analysis of coprolites of the large cave bear from Ignatievskaya Cave showed that it was infected by the nematode *Baylisascaris transfuga* Rudolphi, 1819 (Sivkova and Kosintsev, 2021), which is specific to the family Ursidae.

Less data on the biology of the small cave bear is available. Based on the analysis of bone sizes, it was found that the ratio of males to females in Imanay Cave is 3 : 1 (Gimranov and Kosintsev, 2020), and in Kizel Cave—1 : 2 (Vereschagin and Baryshnikov, 2000). The number of adults in Imanay Cave is 84% (Gimranov and Kosintsev, 2020), in Kizel Cave—52% (Vereshchagin, 1982). The first data on the age and season of death of single individuals of the small cave bear were obtained from recording structures in the teeth (Prilepskaya and Baryshnikov, 2019; Gimranov et al., 2021a).

The results of morphological analysis indicated that the diet of the small cave bear relied on grazing even more than the large cave bear (Vereshchagin, 1973), which was confirmed by the analysis of isotopic signatures C13 and N15 (Silaev et al., 2020). Pathological changes were noted on single bones of cave bears in the Urals (Kosintsev and Vorobiev, 2001).

The characteristics revealed of the biology of large and small bears in the Urals differ significantly not only between species, but also for individual studied paleopopulations. Such significant intraspecific differences have not yet been explained.

CHRONOLOGY OF CAVE BEARS IN THE URALS

The oldest remains of large and small cave bears in the Urals were found in the Ignatievskaya (excavation V, Bed 10) and Serpievskaya 1 (Bed 3) caves (Smirnov et al., 1990). They were part of the Serpievskaya Fauna, dating from the end of the Middle [end of the marine isotope stage (MIS) 6] or the beginning of the late (MIS 5e) Pleistocene (Fadeeva et al., 2019; Danukalova et al., 2020). Remains of both species were found in localities of the last interglacial (Mikulino, Kazantsevo, Eemian, MIS5e; Fadeeva et al., 2020). With the exception of the Serpievskaya fauna, the remains of cave bears in the Urals are found in faunas that include only species typical of the Late Pleistocene (mammoth) faunal assemblage (Kosintsev et al., 2016).

More precisely, the time of habitation and extinction of cave bears in the Urals makes it possible to determine radiocarbon dates. Before radiocarbon dates were obtained from the bones of cave bears, the extinction time was determined in the range of 104–120 ka BP (Vereshchagin, 1971; Kuzmina, 1971, 2002; Kosintsev and Vorobiev, 2001).

To date, 26 final radiocarbon dates and 11 transcendental dates have been obtained from the bones of large cave bear from localities of the Urals, and from the bones of small cave bear 14 radiocarbon dates and two dates beyond the method limit (Kosintsev et al., 2003; Baryshnikov, 2007; Pacher and Stuart, 2009; Kosintsev et al., 2020) were obtained. Among the dates obtained from the bones of large cave bear, there are several relatively late ones. Two dates from Viasher Cave (19550 ± 230, SOAN-4526; 22650 ± 670, SOAN-4515) and one from Verkhnyaya Cave (22750 ± 1210, LU-3714) (Kosintsev et al., 2003; Baryshnikov, 2007) coincide with the latest dates obtained from the bones of the large cave bear of Europe (Baca et al., 2016; Gretzinger et al., 2019). Probably, the extinction of the large cave bear

occurred synchronously throughout its entire range during the last glacial maximum (beginning of MIS 2, LGM). A much smaller amount of data were obtained for the bones of the small cave bear. All of them correspond to MIS 3 (Kosintsev et al., 2003; Gimranov and Kosintsev, 2020), and only one date from Kizel Cave (18 800 ± 340, IGAN-340) falls into MIS 2. According to samples from this cave, 11 more dates were obtained, all of which are older than 30 thousand years (Pacher and Stuart, 2009; Barlow et al., 2021).

Probably the most recent date is too late. This is indirectly confirmed by the fact that no small cave bear bones have been found in any of the numerous localities of the large theriofauna in the Urals dating from the MIS2 period. Thus, an analysis of the chronology of records of the large and small cave bears shows that at the end of the Middle Pleistocene (end of MIS 6?) And throughout most of the late Pleistocene (MIS 5–MIS 3), the large and small cave bears coexisted in the Urals.

HUMANS AND CAVE BEARS IN THE URALS

The previously stated assumption of the existence of systematic hunting for cave bears in the Paleolithic of the Urals (Kuzmina, 1971; Vereshchagin, 1973) was not confirmed. No bones of large cave bears were found at Paleolithic sites in the Urals (Kosintsev and Plasteeva, 2015), except for redeposited specimens (Guslitser and Kanivets, 1965). No traces of tools or artificial injuries were found on more than 50 thousand examined large cave bear bone remains from 52 localities. Of the 14 thousand bones of the small cave bear, only five bones (the Bogdanovka Mousterian site in the South Urals, Shirokov et al., 2011) showed traces of tools. In addition, a skull of a small cave bear with a hole punched by a stone tool was found in the Imanay Cave in the South Urals (Kotov et al., 2020; Gimranov et al., 2021a). Thus, in the Urals, there is only evidence of isolated cases of hunting, and only for the small cave bear.

CAUSES OF THE EXTINCTION OF CAVE BEARS IN THE URALS

Several reasons for the extinction of cave bears have been proposed: in particular, a change in the regime of spring floods, resulting, during early thaws, in water flooding caves and drowning sleeping animals, as well as a result of genetic degeneration of isolated populations (Vereshchagin, 1971, 1973, 1982). Extinction could have occurred as a result of several factors: morphofunctional overspecialization (pastoral specialization and low metabolic rate); the disappearance of the landscape of cold steppes at the beginning of the Holocene and a change in weather conditions; extermination by man and competition with him for "comfortable" caves (Vereshchagin, 1973).

The biocenotic factor could also be the cause of the extinction. Cave bears were zonal elements of the mammoth biota and became extinct as a result of its decay at the end of the Pleistocene. The mechanism of extinction is indicated, i.e., insufficient reproduction of populations as a result of increased mortality of immature individuals during hibernation. This explanation excludes both the anthropogenic factor and the factor of genetic degeneration (Kosintsev and Vorobiev, 2001).

Recently, to find out the reasons for the extinction of representatives of the "mammoth" fauna, the results of the analysis of ancient DNA are used in conjunction with data on the dynamics of climate, human activity and other parameters (Lorenzen et al., 2011; Murray et al., 2017; Knapp, 2019). At the same time, no such data are yet available for paleopopulations of bears in the Urals.

CONCLUSIONS

Research into Ural cave bears has been going on for over 80 years. During this time, more than 50 thousand bones of the large cave bear (*U. kanivetz*) from 52 localities and about 14 thousand bones of the small cave bear (*U.* ex gr. *savini-rossicus*) from 17 localities were collected and studied. Their joint habitation was established on the western slope of the Urals throughout most of the Late Pleistocene (MIS 5–MIS 3). It is shown that the large cave bear did not inhabit the eastern slope of the Urals.

Analysis of nuclear DNA, taxonomic independence was established and the divergence time of the phyletic lineages of the small and large cave bears of the Urals was determined. The morphometric characteristics of bones and teeth of both types were obtained. The age and sex variability of the sizes and proportions of a number of bones and teeth was studied. Estimates of the age and sex composition of the dead individuals were obtained in Kizel Cave, Secrets Cave (=Tain Cave) and Geologov 3 caves in the Middle Urals, as well as in Ignatievskaya, Asha 1 and Imanay caves in the South Urals. No evidence of the hunting of large cave bears by humans has been found. Isolated incidents of small cave bear hunting were revealed. The extinction in the Urals of the small cave bear occurred about 26 thousand years ago, and the large cave bear about 20 thousand years ago. It is noteworthy that the cave bears of the Urals have been studied differently. The large cave bear has been much better studied; there is much less data on the small cave bear. Large collections of remains of large and small cave bears from the caves Makhnevskaya Ledyanaya, Secrets Cave (=Tain Cave) and Geologov 3 in the Middle Urals, Barsuchiy Dol, Zapovednaya and Pobedy in the Southern Urals remain incompletely studied. The number of radiocarbon dates and amount of stable isotope data (C^{13}, N^{15}, O^{18}, $^{87}Sr/^{86}Sr$)

remain insufficient. The genetic diversity of the Ural cave bears also remains almost unexplored.

ACKNOWLEDGMENTS

The authors are grateful to the reviewers for their comments and recommendations, which made it possible to improve the quality of the publication and to discuss a number of controversial issues. We are grateful to the Museum of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences for the information provided.

FUNDING

The study was carried out with the financial support of the Russian Foundation for Basic Research in the framework of the scientific project no. 20-14-50162, and financial support from the Russian Science Foundation, project no. 20-74-00041.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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Translated by S. Nikolaeva