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The Geographic Ranges of *Martes* Species (Carnivora, Mustelidae) in the Middle Urals in the Late Pleistocene and Holocene

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Abstract—*Martes* mandibles from Late Pleistocene and Holocene sites in the Middle Urals were identified to the species level using discriminant analysis. As has been shown, sable lived there in the Late Pleistocene, with its geographic range covering all this area until the end of the 18th century; however, its range started to reduce towards the north and northeast in the early 19th century. Over 150 years, the southwestern boundary of the sable range shifted by 3° to reach the current position by the mid-20th century. The pine marten appeared in the Middle Urals in the Holocene no later than 8000 years ago and inhabits this territory at present.

Keywords: *Martes zibellina, M. martes*, mandible, species identification, geographic range, Middle Urals, Neopleistocene, Holocene

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INTRODUCTION

Two species of the genus *Martes* are now living in the Middle Urals—the pine marten *M. martes* L. 1758 and the sable *M. zibellina* L. 1758 (Marvin, 1969). *M. martes* lives over the entire area, while the southern boundary of the *M. zibellina* geographic range runs in the northeastern part of the considered region (Fig. 1a). Thus, the ranges of these two species overlap in the north of the Middle Urals. This raises the question formulated by Pavlinin (1963, p. 75) on which species, the sable or the pine marten, was the first to colonize the Urals and whether the current western boundary of the sable range is initial or, on the contrary, secondary. This question has not so far received a grounded answer. This is associated with the fact that this answer requires analysis of the changes in the geographic range boundaries reconstructed according to fossils, whereas a reliable species-level identification of bone fossils has been unfeasible until recently. Methods for identification of *M. zibellina* and *M. martes* have been developed for the skulls and genital bones (Novikov, 1956). However, the postcranial skeleton fragments and mandibles are prevalent in the fossils, and their species-level identification has not been elaborated or has been problematic (Paaver, 1965; Gasilin and Kosintsev, 2013). Fossils belonging to the genus *Martes* have been found in many Late Pleistocene and Holocene sites of the Middle Urals. Some studies have identified these fossils to the level of genus, as *Martes* sp. (Vereshchagin, 1982; Kosintsev, 1986, 1988, 1995, 1996, 2003, 2007; Varov and Kosintsev, 1996; Kosintsev and Vorob'ev, 2000; Kosintsev et al., 2000; Kosintsev and Orlova (Mamyachenkova), 2002; Petrov, 2003; Ulitko, 2003, 2005, 2006, 2012; Petrov and Kosintsev, 2005; Razhev et al., 2005; Fadeeva and Smirnov, 2008; Izvarin and Ulitko, 2009), while many researchers identified these fossils to a species level based on subjective estimates. Note that both *M. martes* and *M. zibellina* fragments were identified in the fossils (Kuz'mina, 1975, 1982, 2005; Serikov and Kuz'mina, 1985; Kosintsev, 1988, 1995; Varov and Kosintsev, 1996; Kuz'mina et al., 1999; Petrov, 2003; Petrov and Kosintsev, 2005; Ulitko and Shirokov, 2006; Fadeeva and Smirnov, 2008; Kosintsev and Plasteeva, 2009). Thus, it was not reasonable to use these identifications for an objective reconstruction of the *Martes* species history in the Middle Urals. A specialized technique for species-level identification of individual mandibles has been elaborated (Gasilin and Kosintsev, 2013), which allows the above formulated problem to be solved.

MATERIALS AND METHODS

In this work, we consider the Middle Urals not only as part of the mountain system between 59°15′ and

55°54′ N (Borisevich, 1971), but also with the Cisural and Transural regions. The fossils of *Martes* species in the Middle Urals have been found in three taphonomic types of sites, namely, zoogenic deposits in karst caverns, zoogenic–anthropogenic deposits in karst caverns, and cultural layers of settlements of ancient man. Over 4000 bone fossils of *Martes* species have been found in these sites. The overwhelming majority of these fossils belong to the cranial skeleton, mandible fragments being most numerous. Skulls are less frequent. Most of the fossil bones are fragmented.

The skull is the best object for species differentiation of both the *Martes* species and other mammals. It is known that the *M. zibellina* cerebral cranium is more elongated as compared with that of *M. martes*; its tympanic bullae are more oblong in the longitudinal direction, so that the distance between them in the carotid foramens does not exceed half the bulla length from its anterior end to the posterior edge of the lateral occipital process; the *M. zibellina* mammillary processes do not project over the acoustic foramen edges (Novikov, 1956); and the anterior edge of the horizontal plate of palatine bone has a spina nasalis caudalis, absent in *M. martes* (Pavlinin, 1963). The shape of the p3 outer edge is also of diagnostic value, being concave in *M. martes* unlike *M. zibellina* (Pavlinin, 1963). However, these characteristics are as a rule insufficient for a species-level identification of the skull fragments typically found as fossils. The penile bones (*os penis*) of these species are also easily distinguishable (Novikov, 1956); however, they are most rarely found among fossils. Typically, the mandibles remain of the entire cranial skeleton. These bones are rather solid; in addition, they are paired structures and, thus, are better preserved and more frequently found as compared with skulls. In this work, we used mandibles to identify subfossil remains of the genus *Martes*. Their species-level identification was attempted earlier. The species was identified according to *M. zibellina, M. martes*, and *M. foina* mandibles using the graphical method (Paaver, 1965), and the *M. martes* and *M. foina* mandibles were distinguished by Gerasimov (1983, 1985) based on discriminant analysis.

In total, 436 mandibles of representatives of the genus *Martes* have been found in the sites of the Middle Urals, and 321 were analyzed, since the remaining specimens were considerably fragmented.

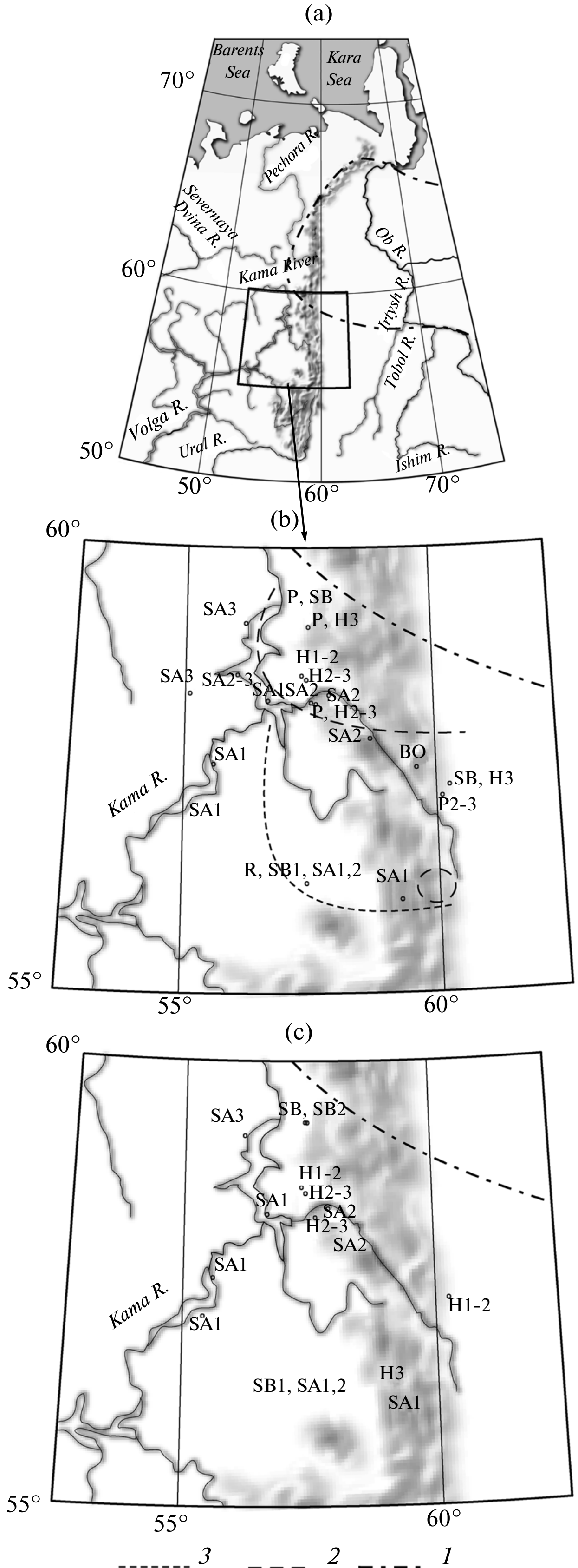

Fig. 1. The Late Pleistocene and Holocene sites with found fossil mandibles of *Martes* species and the change in the reconstructed western boundary of the *M. zibellina* geographic range in the Middle Urals in the recent past: (a) examined area; (b) sites with *M. zibellina* fossils; (c) sites with *M. martes* fossils; (*1*) current boundary of the *M. zibellina* geographic range; (*2*) boundary of the *M. zibellina* range in the 19th century; (*3*) boundary of the *M. zibellina* range in the 18th century; P, Late Pleistocene; H1-2, Early–Middle Holocene; H2-3, Middle–Late Holocene; and H3, Late Holocene (Subatlantic period 3). See text for common abbreviations.

Table 1. Classification of the *Martes mandibles* from the Upper Quaternary sites of the Middle Urals using discriminant functions

Period	Site	Coordinates		Identification results			Number of characteristics in model
		N	E	z	m	mz	
Late Holocene	Bazhukovo III Cave	56°32′	59°16′	0	1	0	17
	Bobylek Cave	56°23′	57°37′	0	0	2	21
	Bol'shoi Glukhoi Cave	58°16′	57°59′	17	2	3	10–21
	Kizelovskaya (Medvezh'ya) Cave	59°03′	57°36′	2	0	0	12–15
	Pershinskaya Cave	57°27′	61°27′	2	0	0	10–16
	Us'vinskaya Cave	58°41′	57°37′	7	1	1	16–21
SA 3	Rodanovskoe settlement	59°84′	56°19′	1	1	0	14–20
	Rozhdestvenskoe settlement	58°30′	55°13′	3	1	1	15–21
SA 2-3	Anyushkar (Kylasovso) settlement	58°53′	56°07′	1	1	1	21
SA 2	Bobylek Cave	56°23′	57°37′	5	9	4	10–21
	Bychki (Turistov) Cave	57°40′	58°54′	32	8	11	10–21
	Salamatovskoe settlement	58°30′	57°75′	6	13	3	10–21
	Telyachii Brod settlement	58°20′	57°47′	1	0	1	18–21
SA 1	Alten-Tau settlement	57°51′	55°54′	2	1	1	19–21
	Bobylek Cave	56°23′	57°37′	14	4	4	10–21
	Gremyachanskoe temple place	57°10′	55°36′	12	2	4	10–21
	Konetsgorskoe settlement	58°14′	56°29′	15	7	6	19–21
	Polovinnoe I settlement	57°56′	55°57′	1	0	0	16
	Severnyi Klyuch settlement	56°02′	59°34′	2	1	0	19–21
SB 3-SA 1	Zayurchim settlement	57°57′	56°01′	0	0	1	21
Middle–Late Holocene	Bol'shoi Glukhoi Cave	58°16′	57°59′	16	5	5	12–21
	Geologov I Cave	58°46′	57°44′	2	0	1	11–21
	Geologov III Cave	58°46′	57°43′	2	0	0	10–16
	Kotel Cave	58°01′	58°10′	3	0	0	21
	Rebristaya Cave	58°46′	57°44′	0	1	0	10–16
SB (1-3)	Bol'shaya Makhnevskaya Cave	59°27′	57°41′	2	1	0	10–17
SB 2	Bol'shaya Makhnevskaya Cave	59°27′	57°41′	1	1	0	14–21
SB 1	Bobylek Cave	56°23′	57°37′	7	5	0	11–21
AT	Pershinskaya I Cave	57°27′	61°27′	2	1	0	17–19
Early–Middle Holocene	Bobylek Cave	56°23′	57°37′	0	1	0	21
	Verkhnegubakhinskii Cave	58°53′	57°38′	1	0	0	10–16
	Lobvinskaya Cave	59°28′	60°04′	0	0	1	20
	Mariinskaya Cave	58°53′	57°37′	12	4	4	18–21
	Shigirskii peat bog	57°22′	60°10′	1	0	0	10–16
BO	Beregovaya II man site	57°49′	59°57′	1	0	0	21
Late Pleistocene	Bobylek Cave	56°23′	57°37′	0	0	1	13
	Bol'shoi Glukhoi Cave	58°16′	57°59′	3	0	0	6–9
	Dolgogo Kamnya III Cave	59°31′	57°41′	2	0	0	10–16
	Kizelovskaya (Viasher) Cave	59°05′	57°40′	3	0	0	8–21
	Tain Cave	59°25′	57°46′	8	0	0	11–21

z, *Martes zibellina*; m, *M. martes*; and mz, species not identified.

Various methods were used for dating the sites. Some of the sites were dated by the radiocarbon method. All the ancient man settlements and zoogenic–anthropogenic cave deposits were dated using archaeological techniques according to the implements found. Several sites in zoogenic cave deposits were dated according to the deposit lithology and stratigraphy. Eventually all the sites were divided into 13 chronological groups (Table 1): Late Pleistocene, 128–10.3 thousand years ago (TYA); Boreal period (BO), 9.3–8 TYA; Early–Middle Holocene, 10.3–2.6 TYA; Atlantic period (AT), 8–4.6 TYA; Subboreal period 1 (SB 1), 4.6–4.1 TYA; Subboreal period 2 (SB 2), 4.1–3.2 TYA; Subboreal period 1–3 (SB), 4.6–2.6 TYA; Middle–Late Holocene, 8–2.6 TYA; Subboreal period 3–Subatlantic period 1 (SB 3–SA 1), 3.1–2.6 TYA; Subatlantic period 1 (SA 1), 2.6–1.8 TYA; Subatlantic period 2 (SA 2), 1.8–0.8 TYA; Subatlantic period 3 (SA 3), 0.8–0.3 TYA; and Late Holocene, 2.6–0.3 TYA. The data on sable and pine marten distributions over the Middle Urals over the last 300 years were taken from written sources (Sabaneev, 1874, 1988a, 1988b; Kirikov, 1966; Marvin, 1969). These last three centuries are ascribed to the historical period. As was demonstrated earlier, various written sources, including the registers of collected tributes in furs, can be used for studying the history of fauna and the relative abundance of commercial species in the recent past (Kirikov, 1963).

In order to identify subfossil specimens, approximately similar samples of the recent right and left mandibles from different individuals were measured; they comprised *M. zibellina* specimens from the Northern Urals ($n = 91$; 41 females and 50 males) and *M. martes* specimens from Western Europe ($n = 52$; 25 females, 25 males, and 2 specimens of unknown sex) and the Urals ($n = 51$; 26 females and 25 males). Only adult mandibles were analyzed. All the examined fossils and recent specimens are deposited with the Zoological Institute (Russian Academy of Sciences, St. Petersburg, Russia) and the Institute of Plant and Animal Ecology (Ural Branch, Russian Academy of Sciences, Yekaterinburg, Russia).

Initially, 21 characteristics were measured for each recent and subfossil mandible specimens (Gasilin and Kosintsev, 2013). The fragmented subfossil mandibles allowed for only an incomplete set of measurements. All the specimens for which ten or more characteristics were measured were analyzed. The only exception was the four Late Pleistocene mandibles with only six to nine measured characteristics, since the sample for this period was small. The characteristics were measured accurate to 0.1 mm using electronic calipers.

The metric data for recent mandibles of these two species represented training samples in standard and stepwise (forward) discriminant analysis. To avoid the effect of the training sample size, the a priori probability of classification according to statistical models (discriminant functions) of 0.5 was set.

The statistical models for classification (identification) of whole mandibles were constructed using the complete set of characteristics and for the damaged mandibles, after initial selection of the characteristics measurable in these fragments. Stepwise discriminant analysis was applied to sets of characteristics for their reduction and further classification using the corresponding statistical models. In total, 40 such models were constructed. Before using the models for classification of subfossil specimens, they were validated in a stepwise manner. At the first stage, the models that allowed for at least 85% correct identification were selected, and at the second stage, test identification was performed with the help of training samples each comprising five recent mandible specimens not included in the training samples. In this work, we regarded the specimens as identified if the probability for their affiliation with one of the species was at least 0.85. All specimens of the test samples were correctly identified in the models.

In each model, all the mandibles (including whole specimens) that allowed for measurement of the characteristics included into this model were classified. As a result, both whole mandibles and the specimens damaged to different degrees were repeatedly (up to 14 times) classified in different models. The Statistica 6 software package was used for computations.

Systematic positions of *Martes* species in the Middle Urals. Currently, the pine marten ascribed to the subspecies *Martes* (*M.*) *martes uralensis* Kusnetzov 1941 lives in the Middle Urals (Aristov and Baryshnikov, 2001). The sable inhabiting the Middle Urals is ascribed to the subspecies *Martes* (*M.*) *zibellina zibellina* L. 1758 (Aristov and Baryshnikov, 2001). The extinct sable subspecies—*M. zibellina vereshchagini* Kuzmina 2005 (Kuz'mina, 2005)—is described based on the specimens from Kizelovskaya (Medvezh'ya) Cave. Kuz'mina (2005) dated the examined bone fossils and, correspondingly, the described subspecies to the Late Pleistocene. Our study using organoleptic examination (Vereshchagin, 1979) of the holotype and paratypes used to describe this subspecies dated these bone fossils to the Late Holocene. Thus, the extinct subspecies *M. zibellina vereshchagini* Kuzmina 2005 should be dated to the Late Holocene.

RESULTS AND DISCUSSION

Of 321 whole and fragmented (number of characteristics $n > 9$) subfossil mandible specimens, 57 specimens remained unidentified and formed the group *M. zibellina–M. martes*. For the remaining 264 analyzed mandible specimens, the species was identified (Table 1).

Late Pleistocene. Fossils of the genus *Martes* were found in 12 Late Pleistocene sites (Kuz'mina, 1975; Kuz'mina et al., 1999; Kosintsev and Vorob'ev, 2000; Kosintsev et al., 2000; Ulitko, 2003, 2005, 2012; Razhev et al., 2005; Ulitko and Shirokov, 2006; Kos-

Table 2. The ratios (%) of sable and pine marten pelts in the tribute in furs collected in the Middle Urals in the 17th century (according to Kirikov, 1966)

Region	Sable	Pine marten	Number of pelts
Middle and lower reaches of the Sos'va River	99.9	0.1	1607
Lyalya River basin	99.9	0.1	1057
Tura and Salda river basins	100.0	0.0	838
Tagil River basin	99.8	0.2	1068
Neiva and Mulgai river basins	98.0	2.0	248
Upper and middle reaches of the Rezh River	81.8	18.2	661
Upper and middle reaches of the Chusovaya River	72.7	27.3	1098
Upper reaches of the Ufa River	24.0	76.0	129

intsev, 2007; Fadeeva and Smirnov, 2008). Chronologically, these sites cover the overall Late Pleistocene from 128 to 10.3 TYA. Specimens from all these sites have been analyzed. In most of the sites, the specimens were considerably fragmented and inappropriate for species identification. Only 17 specimens fragmented to different degrees from five sites were satisfactory for analysis (Table 1). Of them, 16 specimens were identified to the species level as a sable. The most ancient specimens are the mandibles from the Tain and Bol'shoi Glukhoi Caves. The radiocarbon method dates the specimens from the Tain Cave as follows: OxA16961, 39.190 ± 0.360 TYA; OxA16965, 39.580 ± 0.360 TYA; OxA16962, 39.630 ± 0.360 TYA; OxA16963, 40.340 ± 370 TYA; and OxA16958, 47.600 ± 0.900 TYA (Pacher and Stuart, 2009) as well as one off-scale dating, 49.600 TYA. The following radiocarbon dates were obtained for the deposits in the Bol'shoi Glukhoi Cave: LE-4201, 33.900 TYA and GIN-8404, 38.200 ± 0.900 TYA (Svezhentsev and Shcherbakova, 1997) as well as one off-scale dating, over 64.400 TYA (Baryshnikov, 2007). Based on the radiocarbon dates and the accompanying mammalian fauna (Kuz'mina et al., 1999), the deposits in both sites can be dated to the first half of the Nev'yansk interglacial period of the Late Pleistocene (Karginsk or Middle Valdai interglacial period, first half of marine isotope stage 3), that is, 60–33 TYA (Mangerud, 1989; Araslanov, 1992). The deposits of the Kizelovskaya (Viasher) and Dolgogo Kamnya III Caves have no radiocarbon dates. Their ages were assessed according to the accompanying mammalian fauna (Fadeeva and Smirnov, 2008; Fadeeva et al., 2010). The deposits of the Kizelovskaya (Viasher) Cave cover the overall Late Pleistocene, 128–10.3 TYA. As for the deposits in the Dolgogo Kamnya III Cave, they are more precisely dated to the Nev'yansk interglacial period of the Late Pleistocene (Karginsk or Middle Valdai interglacial period, third half of marine isotope stage 3), that is, 60–24 TYA.

Analysis of the mandibles from the Late Pleistocene site in the Middle Urals has demonstrated that all the specimens belong to the sable, suggesting that only sable lived in the Middle Urals during the Late Pleistocene.

Holocene. The fossils belonging to the genus *Martes* in the Holocene sites are rather numerous but most nonuniformly distributed in time (Table 1). Eight sites are dated to the Early and Middle Holocene; 44 mandible specimens from these sites were analyzed. Six sites are dated to the Middle Holocene; 36 mandible specimens from these sites were analyzed. Finally, 17 sites are dated to the Late Holocene, and 217 mandibles found there were analyzed (Table 1).

Only one site was reliably dated to the Early Holocene, and only one sable mandible was found there (Table 1). In total, 23 mandibles found in the four sites dated to the Early–Middle Holocene were analyzed; of them, 13 mandibles were identified as sable and five, as pine marten. Of the four Middle Holocene sites, 13 sable and eight pine marten mandibles were identified. The Late Holocene is represented by 17 sites, from which 123 sable and 52 pine marten mandibles were identified (Table 1).

These data show that a large part of the most ancient pine marten mandibles belongs to the sites with rather a wide dating, spanning from the Early–Middle Holocene (10.3–2.6 TYA). The earliest finding with a narrow date is from the Pershinskaya Cave deposits, dated by the radiocarbon method to the beginning of the Atlantic period (Table 1), that is, to 8–7 TYA. Thus, the pine marten in the Middle Urals appeared no later than the beginning of the Atlantic period in the Holocene (Fig. 1c). The ratio of the sable to pine marten mandibles suggests an approximate ratio of these species in different periods. The pine marten fossils in the Early–Middle Holocene accounted for 26%; in the Middle Holocene, for 38%; and in the Late Holocene, for 30%. Thus, the pine marten abundance over the entire Holocene was approximately twofold lower as compared with the sable.

Historical time. The earliest data on the sable and pine marten distributions in the Middle Urals for this period are available in the registers for the tributes in furs collected in the 17th century (Kirikov, 1966). These records suggest that the sable and pine marten lived over the entire Middle Urals (Table 2). The ratio of sable to pine marten furs in the tributes allows for assessment of their approximate ratio in the hunting sample, and, presumably, their abundance in wildlife. Analysis of this ratio suggests that the sable in the 17th century was prevalent in almost the entire Middle Ural area. The sable abundance was lower than that of the pine marten only in the south of this region, in the upper reaches of the Ufa River (Table 2). The sable abundance in the southwest of the Middle Urals, in the Kungur forest–steppe, most likely was very low, as suggested by the fact that the tribute in fur in this area was counted in pine marten pelts rather than sable (Kirikov, 1966). In general, the pine marten abundance was rather high in the southern half of the Middle Urals from the upper reaches of the Ufa River (approximately 55°30′ N) to the Rezh River (approximately 57° N) and drastically decreased to the north, where it accounted for less than 1% of the hunted animals (Table 2).

In the 18th century, the sable geographic range according to written sources (Kirikov, 1966) covered the overall Middle Urals (Fig. 1b). However, its abundance considerably decreased and several areas appeared where this species was absent. In the 1730s, the sable disappeared in the forests near Yekaterinburg and Nev'yansk. According to P.S. Pallas (1786, 1788), *M. zibellina* was encountered to the south in the forests of the upper reaches of the Ufa River in the early 1770s but was already low in abundance. At the end of the 18th century and the first third of the 19th century, the southern boundary of the *M. zibellina* range shifted northward by 0.5°–1° (approximately to 56°30′ N), but this species still remained to the north in many sites of the Middle Urals (Kirikov, 1966). The southern boundary of the sable geographic range continued to shift to the north and northeast during the entire 19th century (Fig. 1b). This species completely disappeared on the western slope of the central and southern parts of the Middle Urals by the mid-19th century (Sabaneev, 1988b). In the second half of the 19th century, the sable range became disrupted. An isolated sable population remained in the southern part of the Middle Urals, in the upper reaches of the Ufa River (approximately, 55°30′ N) until the 1870s (Sabaneev, 1988, 1988a), while the southern boundary of its range was at 58° N, that is, approximately 300 km northward (Fig. 1b). In the first half of the 20th century, the sable range boundary shifted farther to the northeast to its current position at approximately 59°30′ N (Fig. 1b). Thus, the continuous southern boundary of the sable geographic range shifted from 56° to 59° N since the beginning of the 19th century to the mid-20th century, that is, by 3° over approximately 150 years. The pine marten range over this time span did not change, while its abundance in the Middle Urals increased considerably. In particular, the sable and pine marten in the 19th century were hunted in approximately equal amounts in the upper reaches of the Tagil River, where the share of the latter in the 17th century was less than 1% (Sabaneev, 1988). Currently, the pine marten population size in the area of its cohabitation with the sable is approximately two- to threefold higher (Marvin, 1969; Bakeev, Yu.N. and Bakeev, N.N., 1973; Polyzadov, 1973).

In the Late Pleistocene, the sable lived in the Middle Urals but the pine marten was absent, which, as we believe, is associated with specific features in the ecology of these species. During almost the entire Late Pleistocene, the forests in the Middle Urals were localized to the river valleys, while open (tundra–steppe) and semiopen (forest–tundra–steppe) landscapes were prevalent on a large part of the territory (Grichuk, 2002; Lapteva, 2007). The sable is associated with woods to a lesser degree than the pine marten (Yurgenson, 1933, 1956), and these landscapes for the sable were more favorable than for the pine marten. At the beginning of the Holocene, the forest zone started to develop in the Middle Urals (Khotinskii, 1977). The appearance of the pine marten in the Middle Urals was associated with this process. It is now impossible to date precisely when the pine marten appeared there, since fossils dated to the Early and Early–Middle Holocene are few. This is additionally complicated by the fact that the sable and marten are able to produce hybrids, referred to as kiduses (Portnova, 1941), which is most likely when one of the species has low abundance. In this case, the low-abundant species is the invading pine marten. These hybrids display the traits of both species and, depending on the set of characteristics in our models, can either be identified as one of parental species or remain unidentified. The earliest identified finding of the pine marten is dated to the beginning of the Middle Holocene, which suggests that the marten most likely started to colonize the Middle Urals in the Early Holocene.

The data described above demonstrate that the sable and pine marten lived in the overall Middle Ural area during most of the Holocene and the beginning of the recent past. The sable abundance was significantly higher as compared with the pine marten to the end of the 17th century. At the beginning of the 18th century, the sable population there started to decline, and its range decreased from the beginning of the 19th century. However, the pine marten range did not change, while its abundance increased, at least since the mid-19th century. These changes in the sable and pine marten populations took place against the background of the changes in the natural environment in the Middle Urals. Since the 18th century, the metal industry has intensively been developed in this region, which entailed large-scale forest cuttings. Thus, the aboriginal forests over almost the entire area were replaced with secondary forests. Presumably, these changes were the major factor that caused the reduction in the sable abundance and the geographic range. Indirect confirmation for this hypothesis is the fact that the regions of Yekaterinburg and Nev'yansk—the largest centers of metal industry in the first half of the 18th century—were the first areas where the sable disappeared.

CONCLUSIONS

Analysis of the data on species-level identification of the *Martes* mandibles found in the Late Pleistocene and Holocene sites of the Middle Urals has demonstrated that the sable lived there in the Late Pleistocene. The pine marten appeared in this region no later than the beginning of the Middle Holocene, that is, 8–7 TYA. Since that time and until now, the pine marten geographic range there has not changed and covers the entire area of the Middle Urals. The sable geographic range occupied the entire Middle Urals during the Late Pleistocene, Holocene, and recent past until the end of the 18th century. However, changes in the sable range commenced as early as the 18th century and comprised several stages. Initially, since the first half of the 18th century, the range spottiness started to increase with the appearance of large areas where the sable disappeared. Since the early 19th century, the sable range started to decrease towards the north and northeast. The geographic range became fragmented in the mid-19th century, and isolated sable populations distant from the main range were observed (Fig. 1b). The sable range boundary continued to shift to the northeast in the late 19th–early 20th century to reach its current position in the mid-20th century (Fig. 1b). The relative abundances of the sable and pine marten changed concurrently. The sable fossils identified in the Holocene sites are twofold more abundant as compared with the pine marten (Table 1), suggesting a constantly higher population of the former species. Analysis of the data from written sources has demonstrated that the sable was still rather abundant in the 17th century throughout the Middle Urals except for the southernmost regions, where the pine marten was prevalent (Table 2). In the 18th century, a decrease in the sable population was recorded throughout this region (Kirikov, 1966). The pine marten abundance in the 17th century was relatively high in the southern part to approximately 57° N and drastically decreased farther to the north. The sable abundance and geographic range changed concurrently with an increase in the scale of cuttings of the aboriginal forests and their replacement by secondary ones. Since the early 18th century, intensification in forest cutting entailed a decline in the sable population and further reduction of its range. It is evident that the factors that cause the decrease in its range were not only its direct hunting for fur, but also the changes in the environment. On the other hand, the same factors have not had a considerable negative effect on the pine marten population, and its abundance has even increased. Note here that the disappearance of sable entailed an increase in the hunting load on the pine marten population, since to a certain degree it replaced the sable in the hunting structure. The increase it its population may be associated with the disappearance of the sable as a competitor, change in the forest types, or both factors. At least the changes in forest vegetation have not had any negative effect on the pine marten population. Thus, the sable and pine marten have responded differently to the same environmental changes.

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