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Differentiation of three *Martes* species (*M. martes*, *M. zibellina*, *M. foina*) by tooth morphotypes

Différenciation des trois espèces de Martes *(*M. martes, M. zibellina, M. foina*) par morphotypes de dents*

Dmitriy Gimranov*, Pavel Kosintsev

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, 202, 8th March Street, 620008 Yekaterinburg, Russia

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ABSTRACT

We studied crown morphology of *Martes foina*, *M. martes*, and *M. zibellina* from different regions of the northern Eurasia and described its morphotypes. The following has been identified: three morphotypes for P3, eight morphotypes for P4, 16 morphotypes for M1, four morphotypes for i3, three morphotypes for p3, four morphotypes for p4, nine morphotypes for m1, and three morphotypes for m2. Morphotypes for P4, i3, m1, and m2 are described for the first time. Morphotype frequency is given for each species. It was found that 3 teeth (i3, m1, and m2) are enough for differentiation of the sable, stone marten, and pine marten. We used the above-mentioned dental patterns for species identification of the teeth belonging to the representatives of the genus *Martes* from archaeological sites of the southern Urals. *M. foina*, *M. martes*, and *M. zibellina* inhabited the territory under study in the Holocene. We have also given some consideration to the morphotypes of Tertiary and Quaternary members of the genus *Martes* and come to preliminary conclusions about evolutionary trends.

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RÉSUMÉ

Nous avons étudié la morphologie de la couronne de *Martes foina*, *M. martes* et *M. zibellina* de différentes régions du Nord de l'Eurasie et identifié ses morphotypes, comme suit : trois morphotypes pour P3, huit morphotypes pour P4, 16 morphotypes pour M1, quatre morphotypes pour i3, trois morphotypes pour p3, quatre morphotypes pour p4, neuf morphotypes pour m1 et trois morphotypes pour m2. Les morphotypes pour P4, i3, m1 et m2 ont été décrits pour la première fois. La fréquence des morphotypes est donnée pour chaque espèce. Il a été constaté que trois dents (i3, m1 et m2) sont suffisantes pour différencier la zibeline, la fouine et la martre. Nous avons utilisé les modèles dentaires précités pour l'identification des espèces de dents appartenant aux représentants du genre *Martes* des sites archéologiques de l'Oural du Sud. Il a été découvert que *M. foina*, *M. martes* et *M. zibellina* habitaient le territoire holocène étudié. En outre, nous avons considéré les morphotypes des membres tertiaires et quaternaires du genre *Martes* et sommes parvenus à des conclusions préliminaires quant aux tendances évolutives.

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* Corresponding author.
E-mail address: djulfa250@rambler.ru (D. Gimranov).

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1. Introduction

One of the most important fossils used for species identification is the skull, but an intact skull is a rare fossil. Palaeozoological material is usually represented by skull fragments, mandibles, and isolated teeth, not to mention the post-cranial elements. Therefore, identification of species-specific patterns on separate teeth is an important methodological issue. Odontologic studies are of particular importance for differentiation of fossil sibling species. In the family Mustelidae such species are the pine marten (*Martes martes* L., 1758), stone marten (*Martes foina* Erxl., 1777), and sable (*Martes zibellina* L., 1758).

The first researcher who described the differentiation in the tooth structure of the pine and stone martens was Miller (1912). Anderson (1970) compared odontologic data from different *Martes* species to characterize the evolution of the family Mustelidae. Variability of dental patterns within the genus *Martes* was fully described by Wolsan in his works (Wolsan et al., 1985, 1988, 1989) covering intraspecific, interspecific and geographic variability of certain cheek teeth (P1, P3, M1, p1, p3, and p4) of martens, but he gave no special attention to differentiation of species-specific patterns. Pavlinin (1963) described specific characters of the P3, P4 and M1 crowns of the sable and pine marten. Ognev (1931) graphically showed specific features of the P3, P4 and M1 in the genus *Martes*. Smirnov (1975) called attention to some differences in the occlusal surface of molars of these species. The sable, stone marten, and pine marten are usually differentiated by certain patterns of two teeth of the maxilla (P3 and M1).

The aim of our work is to find new species-specific teeth patterns for the sable, pine marten, and stone marten. Thus, the tasks of this study were to (1) identify and describe tooth morphotypes of the species under study, (2) estimate the frequency of the identified tooth morphotypes, (3) determine species-specific dental patterns, (4) use these dental patterns to identify fossil remains of the representatives of the genus *Martes*.

2. Material and methods

We studied samples of recent skulls and lower mandibles of three marten species (*Martes foina, M. martes, M. zibellina*) from various regions of Eurasia. The examined material belongs to collections from the Zoological Museum of the Moscow State University (Moscow), the Zoological Institute, Russian Academy of Sciences (St. Petersburg), and the Museum of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (Yekaterinburg). The geographical distribution of the studied samples is shown in Fig. 1.

Regions and the number of the studied specimens of the stone marten are as follows: western Europe ($n = 6$), eastern Europe ($n = 23$), the Caucasus ($n = 60$), central Asia ($n = 23$), specimens from unknown regions ($n = 8$). The sample contains 120 specimens.

Regions and the number of the studied specimens of the pine marten are: eastern Europe ($n = 430$), the Urals ($n = 420$), the Caucasus ($n = 140$). The sample contains 990 specimens.

The studied specimens of the sable are derived from the Urals ($n = 360$), Siberia ($n = 310$), Kamchatka ($n = 100$), the Far East of Russia ($n = 70$). The sample contains 840 specimens.

Not all teeth of three *Martes* species exhibit morphotypical variability. Morphotypes of P3, P4, M1, i3, p3, p4, m1, and m2 are described. These results were further used for identification of species-specific differences in the sable, pine marten and stone marten. A total of 10,520 teeth were described and analyzed, independent of sex (Table 1). Descriptions of occlusal surface and analysis of tooth morphotypes follow Vandebroek (1967); Hershkovitz (1971); Wolsan (1989); Baryshnikov and Potapova (1990); Baryshnikov et al. (2003); Szuma (2011), and Gimranov and Kosintsev (2012). Specimens with different morphotypes of the same element on either side of the tooth row (the number of such teeth in the samples did not exceed 1%) were excluded from the analysis. The significance of morphotype differences between the three marten species was determined using the Chi-square test (χ^2) (Table 1).

We studied 354 teeth of representatives of the genus *Martes* from seven archaeological sites from the southern Urals. The Yukalikulevo settlement (55°19′N, 58°25′E; Obydennov et al., 1994) is dated to the Bronze Age (Middle Holocene). Other sites are dated to the Iron Age and the Middle Ages (Late Holocene). These are: Atysh 1 (54°33′N,

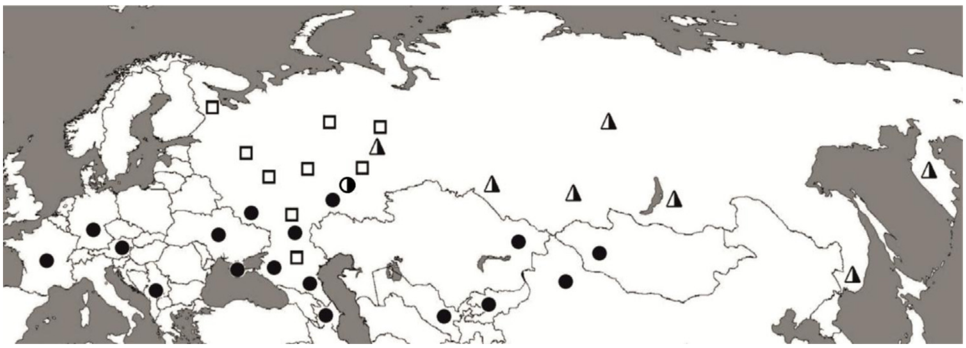

Fig. 1. Geographical distribution of the studied samples of the martens. ● – *M. foina*, □ – *M. martes*, ▲ – *M. zibellina*, ◑ – *fossil remains*.

Fig. 1. Répartition géographique des échantillons étudiés de martre. ● – *M. foina*, □ – *M. martes*, ▲ – *M. zibellina*, ◑ – restes fossiles.

Table 1
Quantity of teeth under study for each species.
Tableau 1
Quantité de dents à l'étude pour chaque espèce.

Teeth	SPECIES			Total
	M. foina	*M. martes*	*M. zibellina*	
P3	120	570	430	1,120
P4	120	660	530	1,310
M1	120	660	530	1,310
i3	120	660	430	1,210
p3	120	570	430	1,120
p4	120	660	530	1,310
m1	120	660	530	1,310
m2	120	930	780	1,830
Total	960	5,370	4,190	10,520

57°16′E; Yakovlev et al., 2005), Kalinovskaya [55°09′N, 57°24′E], Podpornaya (55°09′N, 57°24′E; Gimranov, 2009), the Serny Klyuch settlement (56°03′N, 59°36′E; Petrov, 2003), and the Tra-Tau settlement [55°50′N, 54°10′E]. At the Tashmurun site (52°58′N, 57°01′E; Kosintsev, 2003) the marten remains were found in layers dated to the Bronze Age, the Iron Age and the Middle Ages. Morphotypical characteristics of the marten teeth from the archaeological sites are given in Table 4.

To describe dental polymorphism, morphotypes of eight teeth were distinguished. Morphotypes P3 are characterized by lingual convexity of the crown base (Fig. 2):

A1 – no lingual bulge.

A2 – small lingual bulge.

A3 – noticeable lingual bulge.

Morphotypes P4 are distinguished by configuration of the tooth buccal side, position of the protocone, and the number of additional cusps on the protocone (Fig. 2):

A1 – a notch between the protocone and parastyle; the protocone is anterior to parastyle; concave buccal outline.

A2 – a notch between the protocone and parastyle; non-protruding protocone; concave buccal outline.

A3 – a notch between the protocone and parastyle; the protocone is anterior to parastyle; no buccal concavity.

A4 – a notch between the protocone and parastyle; non-protruding protocone; no buccal concavity.

B1 – no notch between the protocone and parastyle; the protocone is noticeably anterior to parastyle; no buccal concavity.

B2 – undeveloped protocone; concave buccal outline.

C – two-cusped protocone; concave buccal outline; the protocone is anterior to parastyle.

Morphotypes of the M1 are defined by several patterns, such as the shape of the crown on its lingual and buccal sides, the presence or absence of cusps on the occlusal surface, and the degree of the crest complexity (Fig. 2):

A1 – rounded lingual and buccal outline; the preprotocrista bears two small cusps.

A2 – straight lingual and rounded buccal outline; the preprotocrista bears two small cusps.

A3 – heart shaped lingual and rounded buccal outline; the preprotocrista bears two small cusps.

B1 – rounded lingual outline; a well-pronounced buccal groove between the paracone and metacone; the preprotocrista bears two small cusps.

B2 – straight lingual outline; a well-pronounced buccal groove between the paracone and metacone; the preprotocrista bears two small cusps.

B3 – rounded lingual outline; a well-pronounced buccal groove between the paracone and metacone; the preprotocrista bears two small cusps; the metaconule is present.

B4 – rounded lingual outline; a well-pronounced buccal groove between the paracone and metacone; no paraconule; the protocone forms a massive bulge.

C1 – rounded lingual and buccal outline; the preprotocrista bears two small cusps; the metaconule is present.

C2 – straight lingual and rounded buccal outline; the preprotocrista bears two small cusps; the metaconule is present.

C3 – straight lingual and rounded buccal outline; the preprotocrista bears two small cusps; two-cusped metaconule.

C4 – straight lingual outline; a shallow buccal groove between the paracone and metacone; the preprotocrista bears two small cusps; two-cusped metaconule.

D1 – straight lingual and rounded buccal outline; the preprotocrista bears two small cusps; the hypocone is present.

D2 – straight lingual and rounded buccal outline; the preprotocrista bears two small cusps; the hypocone and metaconule are present.

D3 – straight lingual and rounded buccal outline; the preprotocrista bears two small cusps; the hypocone and two-cusped metaconule are present.

D4 – straight lingual outline; a shallow groove between the paracone and metacone; the preprotocrista bears two small cusps, the hypocone and two-cusped metaconule are present.

E – straight lingual outline; a small buccal groove between the paracone and metacone; the preprotocrista bears three small cusps (Fig. 2).

Morphotypes of the i3 are distinguished by the degree of the distoconid development and the presence of the mesial cingulum and mesioconid. The terms distoconid and mesioconid follow Rabeder (1999) (Fig. 3):

A1 – massive distoconid (inferior in size to the main elevation).

A2 – the distoconid is undeveloped and represents a small cusp.

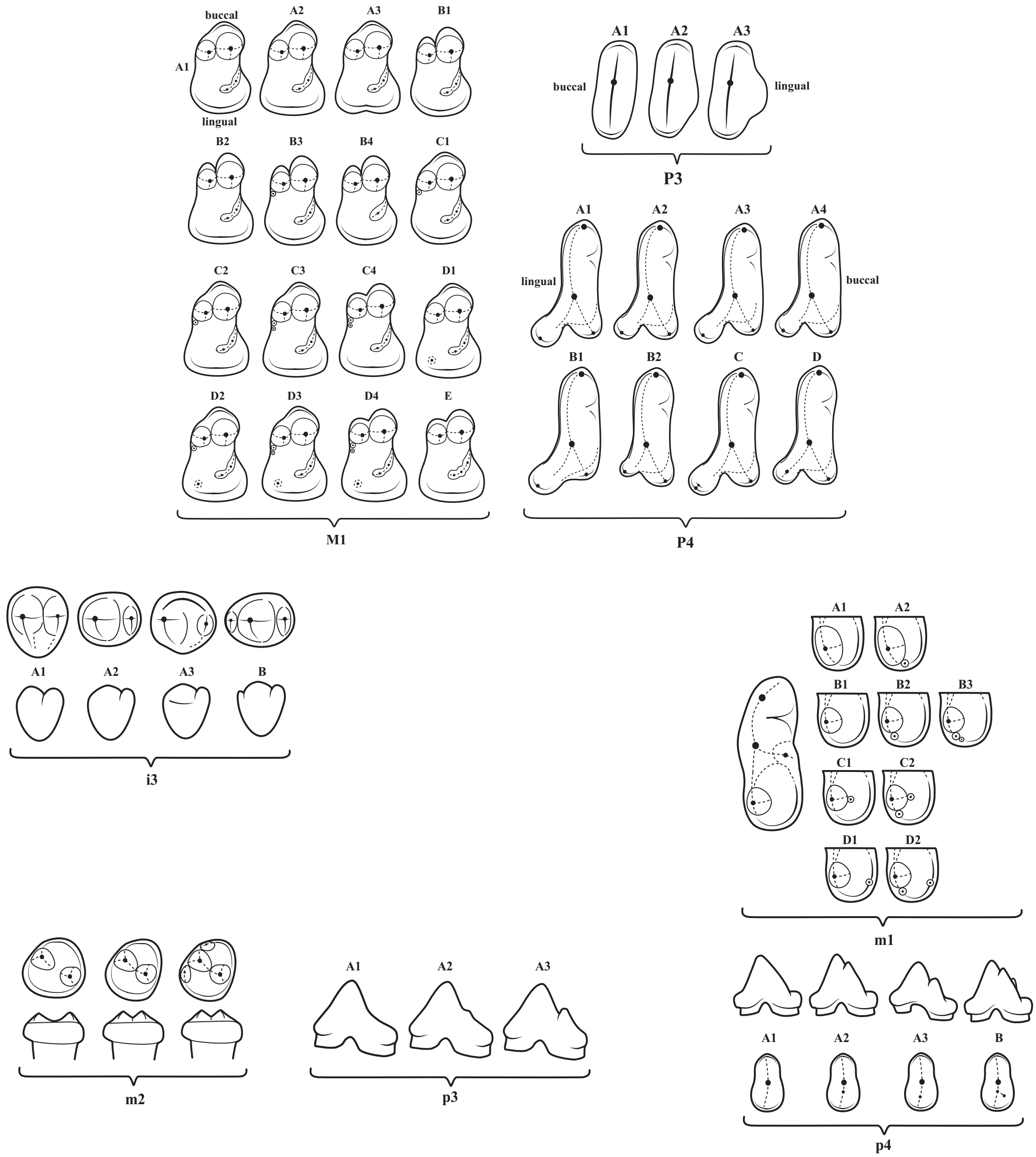

Fig. 2. Upper teeth morphotypes in *M. zibellina*, *M. martes* and *M. foina*.

Fig. 2. Morphotypes de dents supérieures chez *M. zibellina*, *M. martes* et *M. foina*.

A3 – the distoconid is undeveloped and represents a small cusp; a mesial cingulum is present.

B – the distoconid is undeveloped and represents a small cusp; a small-size mesioconid is present.

Morphotypes of the p3 are distinguished by the degree of an additional cusp development on the protoconid distal ridge (Fig. 3):

A1 – posterior accessory cusp is absent.

A2 – small posterior accessory cusp is present.

A3 – a well-developed posterior accessory cusp is present.

The identification of morphotypes of the p4 is based on the degree of a cusp development on the protoconid distal margin and on the presence of an additional cusp on the lingual side of the tooth (Fig. 3):

A1 – posterior accessory cusp is absent.

A2 – the posterior accessory cusp has highest position.

A3 – the posterior accessory cusp has lower position.

B – the posterior accessory cusp has highest position; an additional lingual cusp is present.

In m1, differences are based on the talonid occlusal surface. The morphotypes were differentiated on the basis of the hypoconid robustness and the presence, as well as relative position of additional cusps on the talonid (Fig. 3):

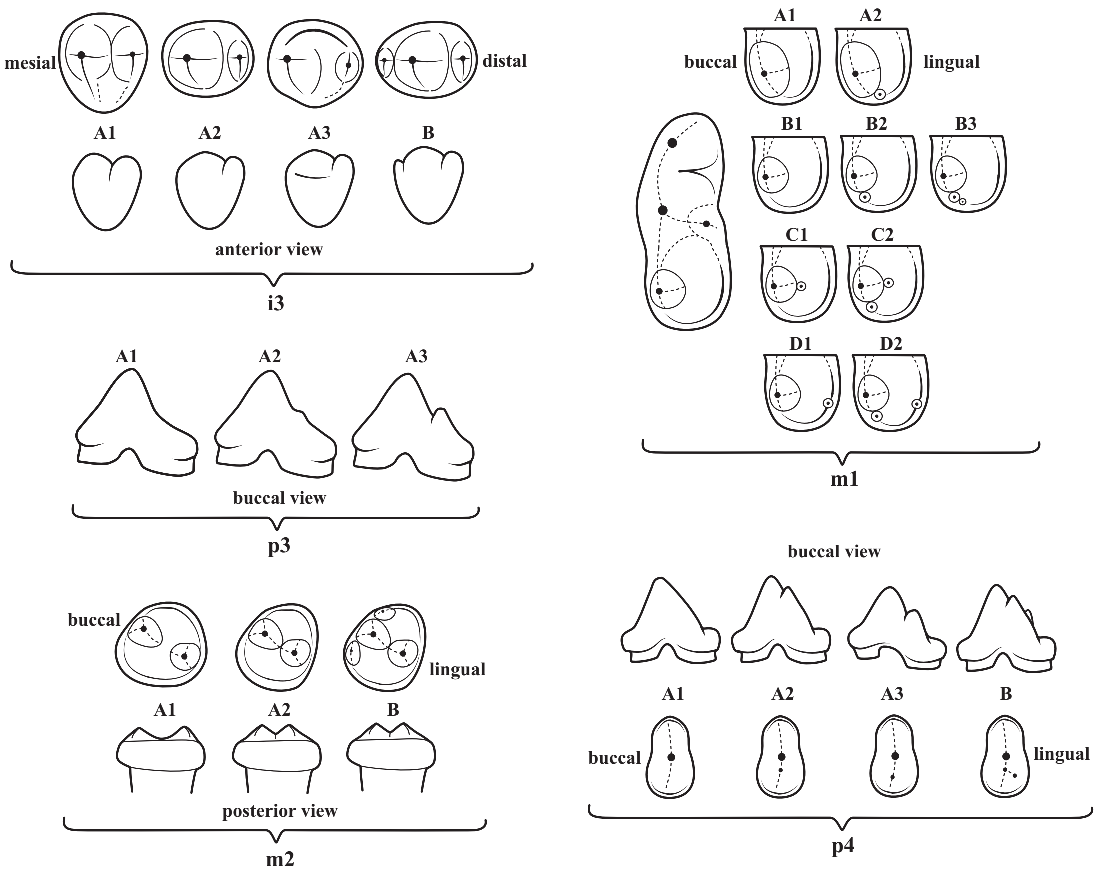

Fig. 3. Lower teeth morphotypes in *M. zibellina*, *M. martes* and *M. foina*.
Fig. 3. Morphotypes de dents supérieures chez *M. zibellina*, *M. martes* et *M. foina*.

A1 – the distinct massive hypoconid occupies approximately a half of the talonid basin.

A2 – the hypoconulid is adjacent to the massive hypoconid.

B1 – a small-sized hypoconid.

B2 – an additional element – hypoconulid – is adjacent to the hypoconid.

B3 – two-cusped hypoconulid.

C1 – an additional cusp – entohypoconid – is adjacent to the hypoconid in the talonid basin.

C2 – the hypoconulid and entohypoconid are both present.

D1 – the hypoconid is similar in size to those in groups B and C; the entoconid is present.

D2 – the hypoconulid and entoconid are both present.

Morphotypes of the m2 were identified according to relative position of the protoconid and metaconid, as well as the presence of the paraconid and hypoconid (Fig. 3):

A1 – the protoconid and metaconid are at considerable distance from each other.

A2 – closely-spaced protoconid and metaconid frequently forming a crest.

B – the protoconid, metaconid, paraconid, and hypoconid are present; the protoconid and metaconid are closely spaced.

3. Results

P3. A relatively simple shape of the tooth crown (morphotype A1) prevails in the stone marten and sable (Table 2). Dominance of morphotype A2 is typical of the pine marten. A complicated morphotype A3 is recorded only in *Martes martes* and *M. zibellina* (8% and 2% respectively). Differences in the morphotype frequency distribution between the three species are statistically significant (Table 3).

P4. Morphotype frequency distribution is similar in all three species (Table 2). Morphotypes A1 and A2 are dominant. Morphotypes A4, B1 and B2 are recorded in all the species, but appear in small numbers. Morphotype D occurs in *M. foina* and *M. zibellina* (2% and 15% respectively) and is not found in *M. martes*. Morphotype C appears exclusively in the sable population with frequency of 5%.

M1. Morphotype frequency distribution for this tooth is rather specific. Morphotypes of group B are observed only in the stone marten and not found in the pine marten and sable at all (Table 2).

Martes martes and *M. zibellina* are similar in their morphotype frequency distribution. Both species are dominated by morphotype A2, followed by quite numerous morphotype A1. Other morphotypes are rather rare.

Table 2
Morphotype frequencies for the teeth of three *Martes* species (%).
Tableau 2
Fréquences des morphotypes de dents chez trois espèces de *Martes* (%).

Tooth	Morphotypes	*M. foina*	*M. martes*	*M. zibellina*
P3	A1	97	19	82
	A2	3	73	16
	A3	0	8	2
	n	**120**	**570**	**430**
P4	A1	58	58	40
	A2	33	24	24
	A3	3	10	9
	A4	1	5	2
	B1	1	2	3
	B2	2	1	2
	C	0	0	5
	D	2	0	15
	n	**120**	**660**	**530**
M1	A1	0	32	21
	A2	0	55	62
	A3	0	1	1
	B1	48	0	0
	B2	17	0	0
	B3	32	0	0
	B4	3	0	0
	C1	0	3	0
	C2	0	5	1
	C3	0	0	1
	C4	0	0	1
	D1	0	3	7
	D2	0	1	1
	D3	0	0	1
	D4	0	0	1
	E	0	0	4
	n	**120**	**660**	**530**
i3	A1	62	7	2
	A2	32	80	3
	A3	4	7	94
	B	2	6	1
	n	**120**	**660**	**430**
p3	A1	83	84	71
	A2	15	12	26
	A3	2	4	3
	n	**120**	**570**	**430**
p4	A1	4	3	2
	A2	1	6	67
	A3	95	90	25
	B	0	1	6
	n	**120**	**660**	**530**
m1	A1	55	0	0
	A2	40	0	0
	B1	1	24	5
	B2	4	67	44
	B3	0	0	2
	C1	0	1	2
	C2	0	8	45
	D1	0	0	1
	D2	0	0	1
	n	**120**	**660**	**530**
m2	A1	14	91	1
	A2	83	9	96
	B	13	0	3
	n	**120**	**930**	**780**

Morphotypes C3, C4, D3, D4 and E have not been found in the pine marten, and the sable lacks morphotype C1.

i3. Each species has its own dominant morphotype (Table 2). Morphotype A1 is marked by the massive distoconid predominates in the stone marten (62%). The relatively simple morphotype A2 is typical of *M. martes* (80%). The most complicated morphotype A3 (94%), distinguished by the mesial cingulum, dominates in the sable. Differences in the morphotype frequency distribution between the three species are statistically significant (Table 3).

Table 3
Statistical estimation of significant morphotype differences between the three *Martes* species using Chi-square test (χ^2).
Tableau 3
Estimation statistique des différences significatives entre les morphotypes des trois espèces de *Martes* en utilisant le test du khi carré (χ^2).

Tooth	Species	Value χ^2 ($P < 0.0001$)	df
P3	*M. foina*	124.9	2
	M. martes		
	M. zibellina	79.4	2
	M. martes		
i3	*M. foina*	67.2	3
	M. martes		
	M. zibellina	152.7	3
	M. martes		
	M. foina	163.3	3
	M. zibellina		
m1	*M. foina*	181.1	5
	M. martes		
	M. zibellina	47.4	6
	M. martes		
	M. foina	182.0	8
	M. zibellina		
m2	*M. foina*	128.8	2
	M. martes		
	M. zibellina	163.1	2
	M. martes		

p3. The morphotype frequency distribution reveals similar patterns for all the species and agrees well with previously published data (Wolsan, 1989). Morphotype A1 is dominant (Table 2).

p4. The morphotype frequency distribution is different for all the species (Table 2). Morphotype A3 dominates in the pine and stone martens, while morphotype A2 prevails in the sable. The share of morphotype A1 is approximately the same in all the three species. Morphotype B does not occur in the stone marten, but is recorded in the pine marten and sable (1% and 6%, respectively).

m1. The frequency distribution of morphotype m1 is different for all the species (Table 2). Morphotypes of group A occur only in the stone marten. Morphotypes B3, D1 and D2 appear exclusively in the sable. Morphotypes C1 and C2 have not been found in the stone marten. Morphotypes of group B are mostly present in the sable and pine marten. Differences in the morphotype frequency distribution among the three species are statistically significant (Table 3).

m2. Morphotype A1 dominates in the pine marten (91%). The highest frequency of morphotype A2 is recorded in the sable and stone marten (Table 2). No morphotype B has been found in the pine marten. Differences in the morphotype frequency distribution are shown in Table 3.

4. Discussion

No species-specific patterns were found for P4 and p3. The analysis of the p4 structure showed that the position of the posterior accessory cusp is an additional dental feature used for differentiation of three marten species. Wolsan (1989) noted the presence of a cusp on the protoconid distal ridge of p4, but did not consider its position relative to the top of the tooth. Our morphotype scheme coincides with the scheme developed by this author only in description of morphotype A1 [or B1 in the terminology of Wolsan (1989)]. Our data with regard to the frequency of this morphotype support those published earlier by Wolsan (1989). The morphotypes A1, A2, A3 of P4, morphotypes A2, A3 of p4 and morphotypes A1 of p3 have been found in other Miocene-Pliocene members of the genus *Martes*, namely among *M. ginsburgi*, *M. laevidens*, *M. palaeosinensis*, *M. stirtoni* and *M. zdanskyi* which were described by Anderson (1970); Dehm (1950); Montoya et al. (2011); Rabeder (1976); Teilhard de Chardin and Leroy (1945); Wilson (1968), and Zdansky (1924). Within the group of Late Miocene martens, the only P4 of *Martes palaeosinensis* described by Zdansky (1924) resembles morphotype D. Following the description by Garcia and Arsuaga (1997), it can be concluded that the upper carnassial of Middle Pleistocene *M. martes* from Sierra de Atapuerca belongs to morphotype A1.

P3. The comparison of frequency distribution of morphotypes P3 in the three marten species shows that the pine marten can be differentiated from the sable and stone marten by the structure of this tooth. The specific pattern typical of the pine marten shows even outlines of the tooth crown base on the lingual side. The difference between the crown outline of P3 characteristic of the pine marten and the sable was pointed out by Pavlinin (1963). Smirnov (1975) recorded the presence of the bulge on the inner side of the tooth in all the Holocene pine marten skulls from the Sumgan-Kutuk cave (the southern Urals). Both specialists distinguished two forms of the tooth structure with and without bulge. We have obtained similar data for the pine marten and for the sable. We have compared our results with those obtained by Wolsan (1989). Whereas morphotypes A1 and A3 in our research correspond to Wolsan's A1 and A4, and our A2 to his A2 and A3, our data for the sable differ slightly from his results. We attribute this fact to different numbers of distinguished morphotypes. Morphotype frequencies of P3 in *M. foina* and *M. martes* are similar to published data (Wolsan, 1989). In accordance with the morphological description found in the works by Anderson (1970); Rabeder (1976); Teilhard de Chardin and Leroy (1945); Wilson (1968), and Zdansky (1924), morphotypes A1 and A2 have been demonstrated in Mio-Pliocene martens such as *M. palaeosinensis*, *M. stirtoni*, *M. wenzensis* and *M. zdanskyi*. We also recognized that all P3 of *M. palaeosinensis* described by Zdansky (1924) belong to morphotype A1.

M1. Wolsan (1988,1989) proved a deep groove between the paracone and metacone of M1 to be a reliable specific character for *M. foina*. We followed this characteristic to identify morphotypes of group B. The sable dentition also displays a similar element in the M1 crown. In our opinion, the groove is less pronounced in *M. zibellina* than in *M. foina*. We have found out that a rare morphotype C1 is typical only of the pine marten. Rare morphotypes C3, C4, D3, D4, and E appear exclusively in the sable.

The morphotypes of M1 distinguished by Wolsan (1989) can be compared with those defined in our paper. Unlike Wolsan (1989), we did not study the vertical groove on the buccal side of M1 in such detail. Despite the formal resemblance between our morphotypes and those defined by the researcher, they are different. The morphotypes must be compared as follows: C1 and C2 (sensu Wolsan) are similar to A1-A3, C1-C3, and D1-D3 (this paper), while C3 is congruent with B1-B4, C4, D4, and E. The comparison leads us to the conclusion that the data obtained by us for the pine marten and the sable are similar to those published by Wolsan (1989). Morphotype frequencies for the stone marten slightly differ from the published data, which we attribute to small numbers of the *M. foina* samples covered in this paper. We arrive at similar conclusions while comparing morphotypes of the M1 protocone section. Morphotype E2 (sensu Wolsan) corresponds to morphotype B4 (this paper), while the rest of the morphotypes described by us correspond to morphotype E1 (sensu Wolsan). Prior to comparing our results for the M1 protocone-hypocone section with the data published by Wolsan (1989), we made the following analogies: morphotype B (sensu Wolsan) corresponds to morphotypes A1-B4 (this paper); Dc = B3, C1 and C2; Dce = D2; De = D1. Morphotype frequencies of M1 obtained during our research in three *Martes* species are quite similar to frequency distribution of the D-morphotypes defined by Wolsan (1989). According to Anderson (1994), the earliest known marten is *M. laevidens* from the Early Miocene of Wintershof-West, Germany. In our classification, M1 of *M. laevidens* refers to morphotype A1. The same M1 morphotype (A1) is found in *M. lefkonensis* from the Late Miocene of the locality of Morskaya 2 in the Black Sea region (Sotnikova, 2013). More complicated morphotypes C2 and C3 have been found in other Tertiary members of the genus *Martes*: *M. ginsburgi*, *M. stirtoni* and *M. wenzensis* (Anderson, 1970; Montoya et al., 2011; Rabeder, 1976; Wilson, 1968). *Martes vetus* and *M. martes* from Middle Pleistocene of Europe, described by Rabeder (1976) and Garcia and Arsuaga (1997), also belong to complicated morphotypes similar to E and D2. The morphological pattern of M1 in fossil species such as *M. palaeosinensis*, *M. filholi* and *M. zdanskyi* has not been found among morphotypes characterized by us. These above-mentioned forms show advanced features of posterolingual part of M1. Some of these displayed a long postprotocrista and cusp-like metaconule. However, it must be noted that despite the lack of this morphotype in our collection, it was described for living martens by Pavlinov (1974).**i3.** All three marten species can be differentiated by the structure of occlusal surface of i3 (Table 3). The species-specific pattern is represented by the degree of the distoconid stoutness and the presence of the mesial cingulum.**m1.** The stone marten can be differentiated from the pine marten and the sable by the structure of the occlusal surface of the m1 talonid. The same is true for differentiation of the sable from two other species. The specific pattern typical of the stone marten is the hypoconid robustness. Rare morphotypes B3, D1 and D2 appear exclusively in *M. zibellina*. Following the description by Anderson (1970); Koufos (2011); Montoya et al. (2011); Rabeder (1976); Schmidt-Kittler (1995); Teilhard de Chardin and Leroy (1945); Sotnikova (2013); Wilson (1968), and Zdansky (1924), we have found morphotypes A1, A2, B1 and B2 in other Tertiary species of *Martes*, namely *M. filholi*, *M. ginsburgi*, *M. lefkonensis*, *M. palaeosinensis*, *M. woodwardi* and *M. zdanskyi*. The m1 of the Middle Pleistocene *M. vetus* described by Rabeder (1976) belongs to morphotype B1.**m2.** Analysis of this tooth shows that the pine marten can be differentiated from the sable and the stone marten. The protoconid and metaconid are in contact in the sable and stone marten, whereas no such contact is observed in the pine marten. We established morphotype A1 in all *Martes palaeosinensis* and *M. zdanskyi*. The only m2 of *M. palaeosinensis* described by Zdansky (1924) belongs to morphotype A2.

The morphotype distribution for the teeth of the representatives of the genus *Martes* from the archaeological sites of the southern Urals is given in Table 4. The teeth (m1 and m2) found in the Bronze Age layer of the Tashmurun site demonstrate morphotypes typical of *M. martes*, which proves that this species inhabited the southern Urals in the Middle Holocene. The pine marten also inhabited the territory under study in the Late Holocene, which is confirmed by morphotypical identification of the teeth (P3, i3, m1 [B1–B3], m2) from the sites of Atysh 1, Kalinovskaya, Podpornaya, and Tashmurun. At the Late Holocene sites of Atysh 1, Podpornaya, and Kalinovskaya we found teeth (P4 [D], p4 and m1 [C1–C2]) whose morphotypes are mostly typical of *M. zibellina*. A reliable finding of *M. foina* was discovered in the Podpornaya cave and is dated to the Late Holocene. It is a mandible fragment with p2, p3, p4 and m1 (morphotype A2). Its mental foramina are closely-spaced, which is typical of the stone marten (Aristov and Baryshnikov, 2001). The fact that *M. foina, M. martes*, and *M. zibellina* inhabited the southern Urals during different periods of the Holocene was proved earlier by the results of the mandible metric data analysis (Gasilin and Gimranov, 2010; Kosintsev and Gasilin, 2011). Marten hunting within the territory of Povolzhie and the southern Urals was also described in our previous paper (Gasilin et al., 2013). Not only do the results of the research prove that the three *Martes* species inhabited the southern Urals in the Middle and Late Holocene, but they also give evidence for

Table 4
Morphotype distribution for the teeth of the representatives of the *Martes* genus from the archaeological sites of the southern Urals.
Tableau 4
Répartition des morphotypes de dents des représentants du genre *Martes* des sites archéologiques de l'Oural du Sud.

Teeth	Morphotypes	Sites								Total NISP/%
		1[a]	**2**	**3**	**4**	**5**	**6**	**7**	**8**	
P3	A1	–	1	1	–	–	–	–	–	2/10.0
	A2	5	1	3	–	–	–	1	–	10/50.0
	A3	8	–	–	–	–	–	–	–	8/40.0
Total		**13**	**2**	**4**	**–**	**–**	**–**	**1**	**–**	**20/100**
P4	A1	8	1	–	–	–	–	1	1	11/37.9
	A2	2	2	–	–	–	–	1	1	6/20.7
	A3	7	–	–	–	–	–	–	–	7/24.1
	A4	3	–	–	–	–	–	–	–	3/10.3
	D	2	–	–	–	–	–	–	–	2/6.9
Total		**22**	**3**	**–**	**–**	**–**	**–**	**2**	**2**	**29/100**
M1	A1	1	–	–	–	–	–	–	–	1/4.8
	A2	9	5	–	–	–	–	1	1	16/76.2
	A3	1	–	–	–	–	–	–	–	1/4.8
	C2	2	–	–	–	–	–	–	1	3/14.3
Total		**13**	**5**	**–**	**–**	**–**	**–**	**1**	**2**	**21/100**
i3	A2	2	–	–	–	–	–	–	–	2/100.0
Всего		**2**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**2/100**
p3	A1	25	7	3	–	–	4	20	–	59/78.7
	A2	5	1	2	–	–	1	6	–	15/20.0
	A3	–	1	–	–	–	–	–	–	1/1.3
Total		**30**	**9**	**5**	**–**	**–**	**5**	**26**	**–**	**75/100**
p4	A1	4	–	–	–	–	–	–	–	4/5.2
	A2	25	5	–	–	1	–	–	–	31/40.3
	A3	1	6	7	1	1	7	19	–	42/54.5
Total		**30**	**11**	**7**	**1**	**2**	**7**	**19**	**–**	**77/100**
m1	A2	–	–	1	–	–	–	–	–	1/1.0
	B1	27	7	1	–	1	6	18	–	60/58.3
	B2	16	3	6	–	–	1	3	–	29/28.2
	B3	2	–	–	–	–	–	–	–	2/1.9
	C1	1	2	–	–	1	–	2	–	6/5.8
	C2	2	1	2	–	–	–	–	–	5/4.9
Total		**48**	**13**	**10**	**–**	**2**	**7**	**23**	**–**	**103/100**
m2	A1	14	–	2	–	–	2	6	–	24/88.9
	A2	3	–	–	–	–	–	–	–	3/11.1
Total		**17**	**–**	**2**	**–**	**–**	**2**	**6**	**–**	**27/100**
Total number of teeth		**175**	**43**	**28**	**1**	**4**	**21**	**78**	**4**	**354/100**

[a] 1 – Atysh1; 2 – Kalinovskaya; 3 – Podpornaya; 4 – SernyKlyuch; 5 – Tra-Tau; 6 – Tashmurun(BronzeAge); 7 – Tashmurun (IronAge,MiddleAges); 8 – Yukalikulevo.

understanding that local people hunted these species in the Bronze Age, the Iron Age, and the Middle Ages (Table 4).

Anderson (1970) and Wolsan (1988,1989) describe a general trend to progressive simplification of the morphological dental structure in *Martes*. Our analysis has confirmed their results. The material studied here has given evidence that the frequencies of simple morphotypes M1 are predominant over more complicated structures in living martens species. These conclusions are also confirmed by our analysis of the paleontological data indicating a long-term trend to simplification of morphological structure of the occlusal surface of the M1 during the *Martes* evolution. According to this point of view, morphotypes A1, B1 and B4 are the most advanced among the *Martes* members. The same can be observed in frequencies of the m1 morphotypes. However, it cannot be confirmed by the palaeontological data due to the paucity of fossils.

The evolution of the teeth of the family *Canidae* (which is probably true for all groups of Carnivora) follows two trends, namely hypo- and hypercarnivorous adaptations (Tedford et al., 2009; Van Valkenburgh et al., 2004). A similar situation is observed in the genus *Martes*. *Martes lefkonensis*, *M. ginsburgi* and *M. laevidens* demonstrate the trend to hypercarnivory, whereas *M. palaeosinensis*, *M. woodwardi* and *M. zdanskyi* tend to hypocarnivory. Extant *M. foina* tends towards a hypercarnivorous adaptation, while *M. zibellina*, by contrast, shows a tendency towards hypocarnivorous adaptations. *Martes martes* exhibits morphological traits representing mesocarnivorous adaptation.

5. Conclusion

The dentition analysis revealed that the martens have eight teeth (P3, P4, M1, p3, p4, i3, m1, and m2) that are characterized by morphotypical variability. Morphotypes of four teeth out of these eight (P4, i3, m1, and m2) are described for the first time. Peculiarities of the P3, M1, i3, m1, and m2 morphology afford grounds for confident differentiation of the three species. We have found that the sable and the stone marten can be differentiated by two teeth of the maxilla (P3 and M1 respectively), which confirms earlier results (Pavlinin, 1963; Smirnov, 1975; Wolsan, 1989). Species-specific patterns of three teeth of the mandible (i3, m1, and m2) are demonstrated for the first time. *M. foina* can be differentiated from the two other species by the massive distoconid of i3 (morphotype A1). *M. martes* can be distinguished by the small distoconid of the same tooth (morphotype A2). The mesial cingulum (morphotype A3) is a specific feature for *M. zibellina*. A massive hypoconid (morphotypes A1 and A2) of the m1 is a specific character of the stone marten. A distance between the protoconid and metaconid (morphotype A1) in m2 is typical of the pine marten. Some rare morphotypes appear exclusively in the sable. Morphotype C is rare for P4, while morphotypes C3, C4, D3, D4, and E for M1 and morphotypes B3, D1, D2 for m1. Morphotype C1 for M1 was recorded only once in the pine marten. Dental analysis of *Martes* remains from archaeological sites of the southern Urals has allowed us to conclude that *M. martes* inhabited this area in the Middle and Late Holocene. In the Late Holocene, this territory was also inhabited by *M. foina* and *M. zibellina*. For some time, all three species were hunted by the people living in this area. At the moment, only the pine marten inhabits the southern Urals (Aristov and Baryshnikov, 2001).

The fossil and recent *Martes* members show two directions of development of M1 and m1, namely the trend to hyper- and hypocarnivorous adaptations. We found that extant *M. foina* (unlike the two other species) demonstrates hypercarnivorous features. This apparently depends on its early separation from the ancestral form, which was also noted by Anderson (1994). Our results do not contradict molecular genetic data (Li et al., 2014; Stone and Cook, 2002). *Martes zibellina* has the most complicated teeth, showing a trend towards hypocarnivorous adaptation. Interestingly, some of the specific characters of the sable have been found among the Late Miocene marten – *M. palaeosinensis*.

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