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A new extinct ochotonid genus from the late Pleistocene of the Russian Far East

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Abstract

A new genus, *Tonomochota* n. gen., and three new species, *T. khasanensis* n. sp., *T. sikhotana* n. sp., and *T. major* n. sp. of Ochotonidae are described from late Pleistocene cave deposits in the Russian Far East. The description of the new genus was based on thirty-two isolated lower third premolar from the sediments in the Sukhaya and Tetyukhinskaya caves. The new genus was primarily established based on the following characteristics: the triangular anteroconid of the lower third premolar always has a labial fold filled with cement; lingual fold of the anteroconid of the lower third premolar with or without cement; the re-entrant fold(s) on the anteroconid is directed laterally. All of the three new species differ significantly from each other in the size of the lower third premolar.

Keywords: New genus; New species; Late Pleistocene; Far East Russia; Sikhote-Alin; Cave

1. Introduction

Historically, the Ochotonidae family included two extant subfamilies: Sinolagomyinae Gureev, 1960 and Ochotoninae Thomas, 1897. At the end of the Miocene, all taxa of Sinolagomyinae disappeared from all continents (Erbajeva, 1988, 1994, 2007); towards the end of the Pliocene, all representatives of Ochotoninae also became extinct with the exception of the genus *Ochotona*, which is now the only living genus of the ochotonids. In the majority of Ochotonidae fossil species, identification and description were mainly conducted using the most informative lower third premolar (p3) (for example, Cai, 1989; Erbajeva et al., 2003; Čermák, 2007, 2010; Fostowicz-Frelik, 2008; Zhang and Kawamura, 2008; Čermák and Rekovets, 2010; Angelone et al., 2017).

In the South Far East of Russia, the fossil remains of mammals have mainly been found in caves and archaeological sites. All fossil bone remains of ochotonids previously discovered (pre-2012) in the Primorsky Krai (Far East of Russia) belong to the species *Ochotona hyperborea* (Pallas, 1811) (Erbajeva, 1988; Panasenko and Tiunov, 2010). However, material obtained in 2012−2016 from palaeontological excavations in two caves in Primorsky Krai included isolated teeth that belonged to Ochotoninae but did not belong to *Ochotona*. The Ochotoninae subfamily is characterised by the following structural features of p3: (1) a well-defined anteroconid with a rounded or more or less triangular outline and (2) the presence of an opposite shallow lingual fold (paraflexid) and deep labial fold (protoflexid) (Sen, 2003). Currently, there is no clear consensus on the composition and size of Ochotoninae; however, we follow the classification of Čermák (2010), in which Ochotoninae includes five genera: *Bellatonoides, Ochotona, Ochotonoma, Pliolagomys*, and *Ochotonoides*. Given this classification, the ochotonid fossils we discovered in 2012−2016 do not belong to any of these genera. Our fossil findings can be attributed to the late Pleistocene complex of animals, as previously demonstrated and by the accompanying fauna (Kosintsev et al., 2016). Based on these data, we have identified a new fossil genus, *Tonomochota* n. gen., and three new species, *Tonomochota khasanensis* n. sp., *Tonomochota sikhotana* n. sp., and *Tonomochota major* n. sp., which are described below.

2. Geological setting and dating

The limestone Sukhaya Cave is located 3−5 km from the Barabash Village in the north-western part of the Manchurian-Korean

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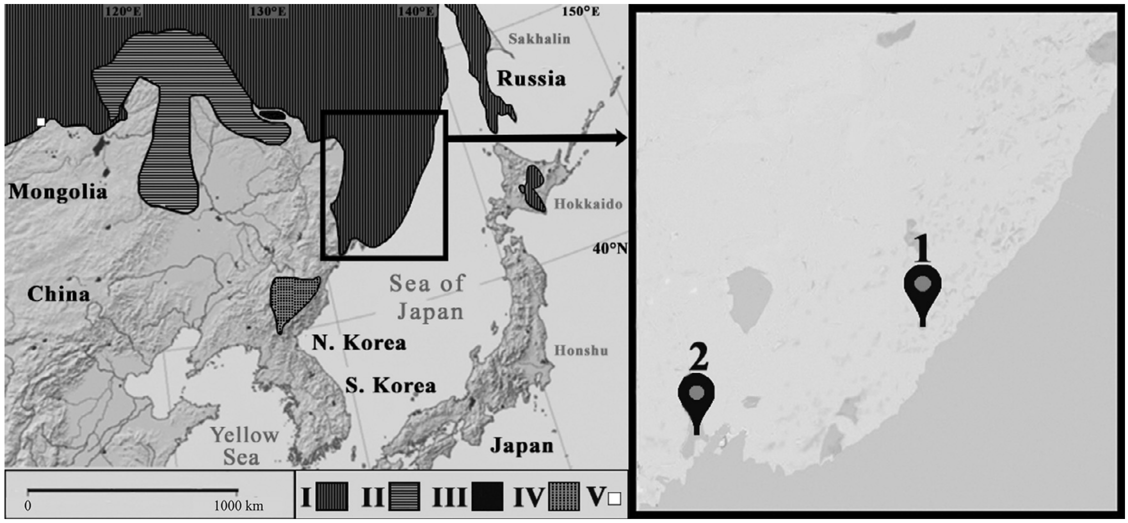

Fig. 1. The current distribution of species of the genus *Ochotona* in the Far East and the location of caves. Symbols: I − *O. hyperborea*; II − *O. mantchurica*; III − *O. coreana*; IV − *O. alpina*; V − *O. hoffmani*; 1 − Tetyukhinskaya Cave; 2 − Sukhaya Cave.

Mountains. This is a horizontal cave 21 m long. The entrance to the cave is located at an altitude of 126 m above sea level. The pit was laid in the far part of the cave in front of a narrow passage filled with clay and going deep into the rock. To date, material from the Sukhaya Cave has been found mainly in the upper layers of sediments. A brief description of the lithological layers is given in the caption of Fig. 2. The four accelerator mass spectrometry (AMS) dates proposed for the bones from the Sukhaya cave were as follows: 24440 ± 90 years, NUTA2-1527; 25570 ± 90 years, NUTA2-1529; 48400 ± 1700 years, UCIAMS-211763; and 51300 ± 2500 years, UCIAMS-211762 (Kosintsev et al., 2020). These dates correspond to the boundaries of marine isotope stage (MIS) 3 to early MIS 2. In general, the deposits of the Tetyukhinskaya and Sukhaya caves have been formed over a long period and can be attributed to a rather broad time interval (MIS 5−MIS 2) during the late Pleistocene.

The limestone Tetyukhinskaya Cave is located in the mid-part of the Sikhote-Alin near Dalnegorsk City. The entrance to the cave is located at an altitude of 410 m above sea level. The depth of the cave is 31.5 m, the total length of the described part of the cave is 490 m. Six pits were dug, four of them were placed in the entrance grotto. All pits in the entrance grotto were dug to the rocky bottom. Most teeth belonging to one of the new species were found in pits laid in the entrance grotto. Despite some disturbance of the deposits, the sequence of layers can be fairly well traced in the profiles of the pit walls. Separate teeth were found at different depths, but the highest concentration of teeth was recorded at a depth of 20−50 cm in the second and third lithological layers. A brief description of the lithological layers is given in the caption of Fig. 3. From an isolated tooth of an Asian black bear (found at a depth of 40−50 cm), a radiocarbon date of 39874 ± 133 BP (NSK−850, UGAMS−21786) was obtained using AMS (Kosintsev et al., 2016). Of all the radiocarbon dates obtained in this cave, this one is the furthest from the present day. This date corresponds to the boundary of the Hasselo Stadial and the Hengelo Interstadial, or the middle of MIS 3 of the late Pleistocene sub-epoch (Blockley et al., 2012).

3. Material and methods

All of the fossil teeth of the ochotonids described here were collected in the Russian Far East from sediments in the

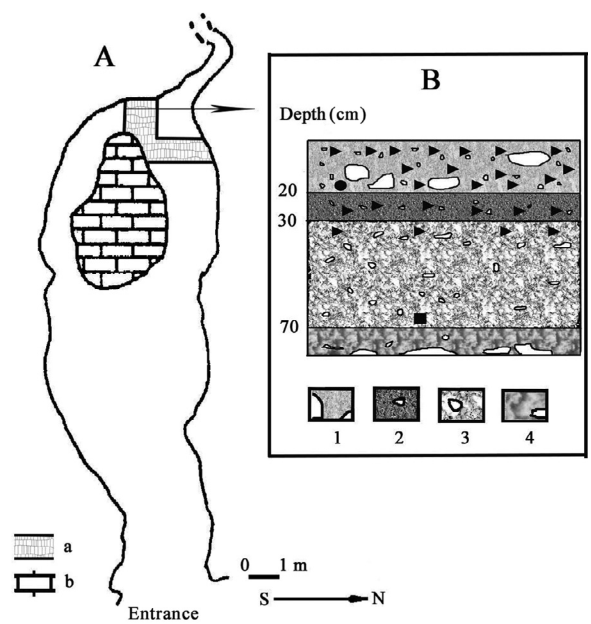

Fig. 2. Plan of the Sukhaya Cave (A) and sketch of a section of the south wall of the pit (B). Symbols: a − fossil site; b − limestone monolith. Lithological layers: 1 − brownish heavy loam with large stones; 2 − brownish clay with small stones; 3 − brown-fawn clay with small stones; 4 − yellowish-brown clay with large stones in the lower part of the lithological layer. Black circles − areas in which separate teeth of *Tonomochota sikhotana* n. sp. were found; black triangles − areas in which separate teeth of *Tonomochota khasanensis* n. sp. were found; black square − the location of the individual tooth of *Tonomochota major* n. sp.

Tetyukhinskaya Cave (Middle Sikhote-Alin, 44°35′N, 135° 36′E) and in the Sukhaya Cave (43°09′N, 131°28′E) (Fig. 1). The accumulation of bone remains in these caves occurred as a result of the vital activity of predatory animals and birds, which used the caves as a dwelling or temporary shelter. The excavation was carried out in arbitrary levels (spits), approximately 10 cm. All recovered bone and teeth material was wet-sieved (mesh size: 1 mm) in the field, and further work was conducted in the laboratory. All of the teeth are currently kept as a part of the fossil collection (prefixed with RPRV) of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences.

The excavations in the Sukhaya Cave were carried out in 2016. Twenty-seven isolated p3 teeth belonging to the three aforementioned new fossil species of ochotonids were found in a pit that was laid out in the entrance grotto. In addition to the third lower premolar, many other teeth were found. After all the material has been processed, these additional teeth will be identified.

The excavations in the Tetyukhinskaya Cave were conducted periodically between 2012 and 2015. Seventeen teeth of the new species were collected: five p3, four P3, two P4, three M1 and three m2. Several teeth were also extracted from the dump of sediments that were left after the work of speleologists who were engaged in expanding the low passages of the cave.

The dental terminology used in this paper was mainly adapted from López Martínez (1986), Fostowicz-Frelik (2008) and Čermák (2009). All of the tooth measurements are reported in millimetres. Only non-juvenile specimens (according to Lissovsky, 2004) were included in the metric comparison. The photographs of the teeth were taken with a SteREO Discovery.V12 stereo microscope and stacked using CombineZM software (Hadley, 2008). The final illustrations were post-processed for contrast and brightness using Adobe® Photoshop® software.

The linear discriminant function analysis was used to classify tooth. In the analysis, 9 measurements were used as independent variables, shown in Fig. 4 for 25 isolated third lower premolars (p3) of *Tonomochota khasanensis* n. sp. and one premolar *T. sikhotana* n. sp., which were found from the sediments in the Sukhaya Cave. Nine p3 of *Ochotona hyperborea* and five p3 of *T. sikhotana* n. sp. from the sediments of the Tetyukhinskaya Cave were also included in the analysis. The grouping variable was the species. The *T. major* sample is an outlier, so it has been removed from the analysis. All of the

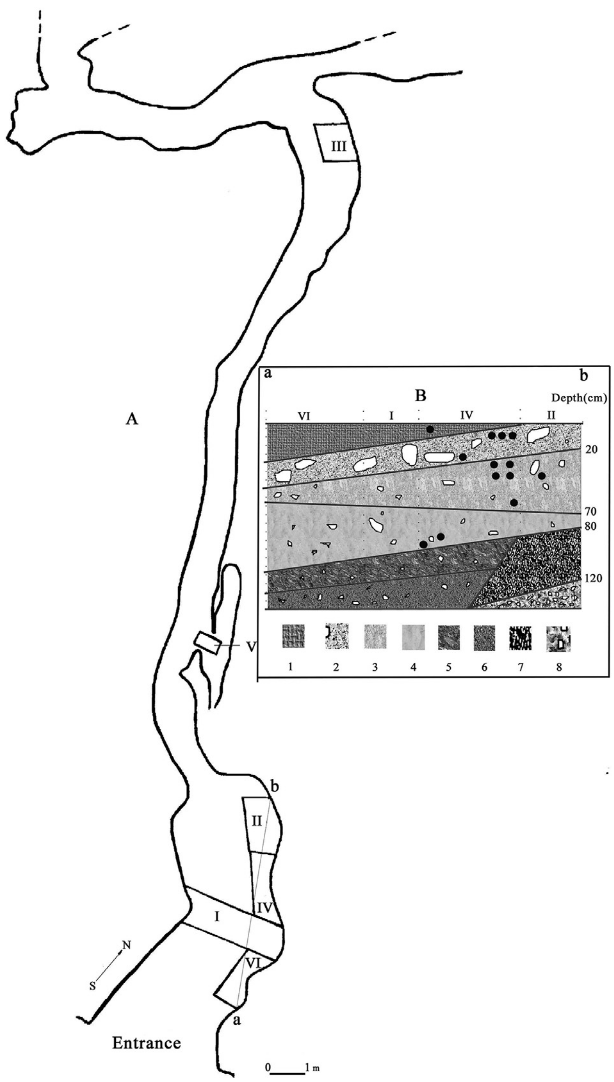

Fig. 3. Plan of the first part of the Tetyukhinskaya Cave (A) and sketch of the section pit along the ab line (B). Symbols: I−V − pit numbers. Lithological layers: 1 − greyish-brown uniform medium loam; 2 − brown medium loam with large stones; 3 − brownish heavy loam with small stones; 4 − brown medium loam with small stones; 5 − yellowish-brown light loam with small stones; 6 − tan light loam with small stones; 7 − yellowish clay with small stones; 8 − dark yellow raw clay with lots of small stones. Black circles − areas in which separate teeth of *Tonomochota sikhotana* n. sp. were found.

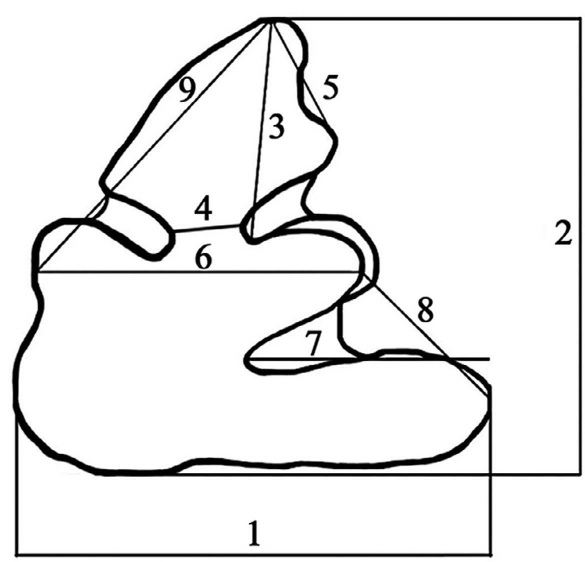

Fig. 4. Occlusal view of p3 and the measurements that were taken. 1 − tooth width; 2 − tooth length; 3 − anteroconid length; 4 − isthmus width; 5 − distance between the most nasal and labial points of the of the anteroconid; 6 − distance from the metaconid to the protoconid; 7 − distance between the most labial point of the hypoconid and the deepest point of the hypoflexid; 8 − distance from the protoconid to the hypoconid; 9 − distance from the metaconid to the apex of the anteroconid.

calculations were performed in Systat 12.00.08 (https://www.systat.com/) and Statistica® 13.

3. Systematic palaeontology

Order Lagomorpha Brandt, 1855
Family Ochotonidae Thomas, 1897
Subfamily Ochotoninae Thomas, 1897

Genus *Tonomochota* n. gen.
Type species: *Tonomochota khasanensis* n. gen. n. sp.
Etymology: Anagram of the generic name Ochotonoma.
Type locality: Sukhaya Cave, in the north-western part of the Manchurian-Korean Mountains, in the Khasansky district of Primorsky Krai, Russia.
Diagnosis: Small, medium to large-size ochotonids. The triangular anteroconid of p3 always has a labial fold filled with cement. A lingual fold with or without cement. The re-entrant fold(s) on the anteroconid is directed laterally.
Differential diagnosis: New genus differs from *Ochotona* by the presence of one or two lateral folds that are filled with cement on the anteroconid of p3. In representatives of *Ochotona*, this cement-filled fold is usually absent. Although some fossil species of *Ochotona*, such as *Ochotona lagreli, Ochotona chowminchevi* and some specimens of *Ochotona antiqua*, may rarely have folds on the anteroconid of p3, they are shallow and generally not filled with cement (Sen, 1998; Erbajeva et al., 2006; Čermák and Rekovets, 2010). In representatives of the genus *Ochotonoma* and *Ochotonoides*, the lateral folds are deeper and directed anterolabially and anterolingually. The new taxon differs significantly from *Ochotonoides* by the lack of plications in the para- and protoflexids. Furthermore, *Tonomochota* differs from the genus *Pliolagomys* by the anteroconid-posteroconid connection, which is much more labial in *Pliolagomys*; consequently, the paraflexid is deeper and the protoflexid is shallower. The p3 of *Pliolagomys* generally lacks cemented folds on the anteroconid. The species of *Pliolagomys* are larger than those of *Tonomochota*. The genus *Bellatonoides* is characterised by a labially-located and rounded anteroconid that is delimited by a deep labial fold (i.e., protoflexid) and a shallow lingual fold (i.e., paraflexid). The anteroconid without anteroflexids. The isthmus between the anteroconid and posteroconid is wide.
Occurrence: South of the Russian Far East. Late Pleistocene sub-epoch.

Tonomochota khasanensis n. sp.
(Figs. 5, 6)

Etymology: The name is derived from the Khasansky district of the Primorsky Territory, in which the Sukhaya Cave is located.
Type locality: Sukhaya Cave, in the north-western part of the Manchurian-Korean Mountains, in the Khasansky district of Primorsky Krai, Russia.
Holotype: RPRV–SukC–08, a right p3 (Figs. 5D, 6D).
Age: MIS 3, late Pleistocene.
Other material: Collected together with the holotype: 12 left p3 and 12 right p3 (Figs. 5A–C, E–Y, 6A–C, E–Y).
Diagnosis: Small-sized ochotonid. The triangular anteroconid of p3 has a labial fold that is filled with cement. As a rule, the anteroconid also has a lingual fold, with or without cement. Mesoflexid is often present.
Description: This is the smallest species in this genus (Table l). The occlusal surface of p3 has a triangular shape. The ratio of width to length varies from 0.83 to 1.08, with an average of 0.98 (n = 25). The triangular anteroconid of p3 has a labial fold filled with cement. Eight of the 25 examined specimens had a lingual fold with cement, 4 specimens had a fold without cement, and 13 specimens lacked this fold. In most specimens, this fold does not reach the occlusal surface. The width of the isthmus between anteroconid and posteroconid is about one-fifth of the distance from the metaconid to the protoconid (Fig. 4, Table 1). The mesoflexid is variable: it was deep (one specimen), shallow (six specimens), marked (five specimens), or absent (13 specimens).

Tonomochota sikhotana n. sp.
(Figs. 7–9)

Etymology: The name is derived from the Sikhote-Alin ridge of the Primorsky Territory, in which the Tetyukhinskaya Cave is located.
Type locality: Tetyukhinskaya Cave, in the mid-part of the Sikhote-Alin near to Dalnegorsk City, in the Dalnegorski district of Primorsky Krai, Russia.
Holotype: RPRV–TetC–07, a right p3 (Figs. 7D, 8D).
Age: MIS 3, late Pleistocene.
Other material: Collected together with the holotype: one left p3 and three right p3; two left P3 and two right P3; two right P4; two left M1 and one right M1; one left m2 and two right m2 (Figs. 7A–C, E, 8A–C, E, 9). Sukhaya Cave: one right p3 (Figs. 7F, 8F).
Diagnosis: Medium-sized ochotonid. The triangular anteroconid of p3 has one small labial fold filled with cement. This crease may taper to the upper edge of the tooth and may not be visible on the occlusal surface, but it is always clearly visible from the lateral surface.
Description: Medium-sized. p3, as the most informative tooth, plays an important role in identifying the ochotonid species. The occlusal surface of p3 has a triangular shape. The length of p3 is greater than the width (Table 1). The ratio of width to length varies from 0.86 to 0.95, with an average of 0.90 (n = 6). The anteroconid p3 of *T. sikhotana* n. sp. (six specimens) always has a small labial fold filled with cement. It sometimes does not reach the tooth surface, as in RPRV–TetC-08 and RPRV–SukC–04 (Figs. 7E, F, 8E, F). However, this fold is always present and is continuous along the shaft. Four of the six specimens examined had a lingual fold with cement (two-thirds of the lower part of this crease were filled with cement), one specimen had a fold without cement, and one specimen lacked this fold. In most specimens, this fold does not reach the occlusal surface. The width of the isthmus between the anteroconid and posteroconid is about one-quarter of the distance from the metaconid to the protoconid (Fig. 4, Table 1). The mesoflexid

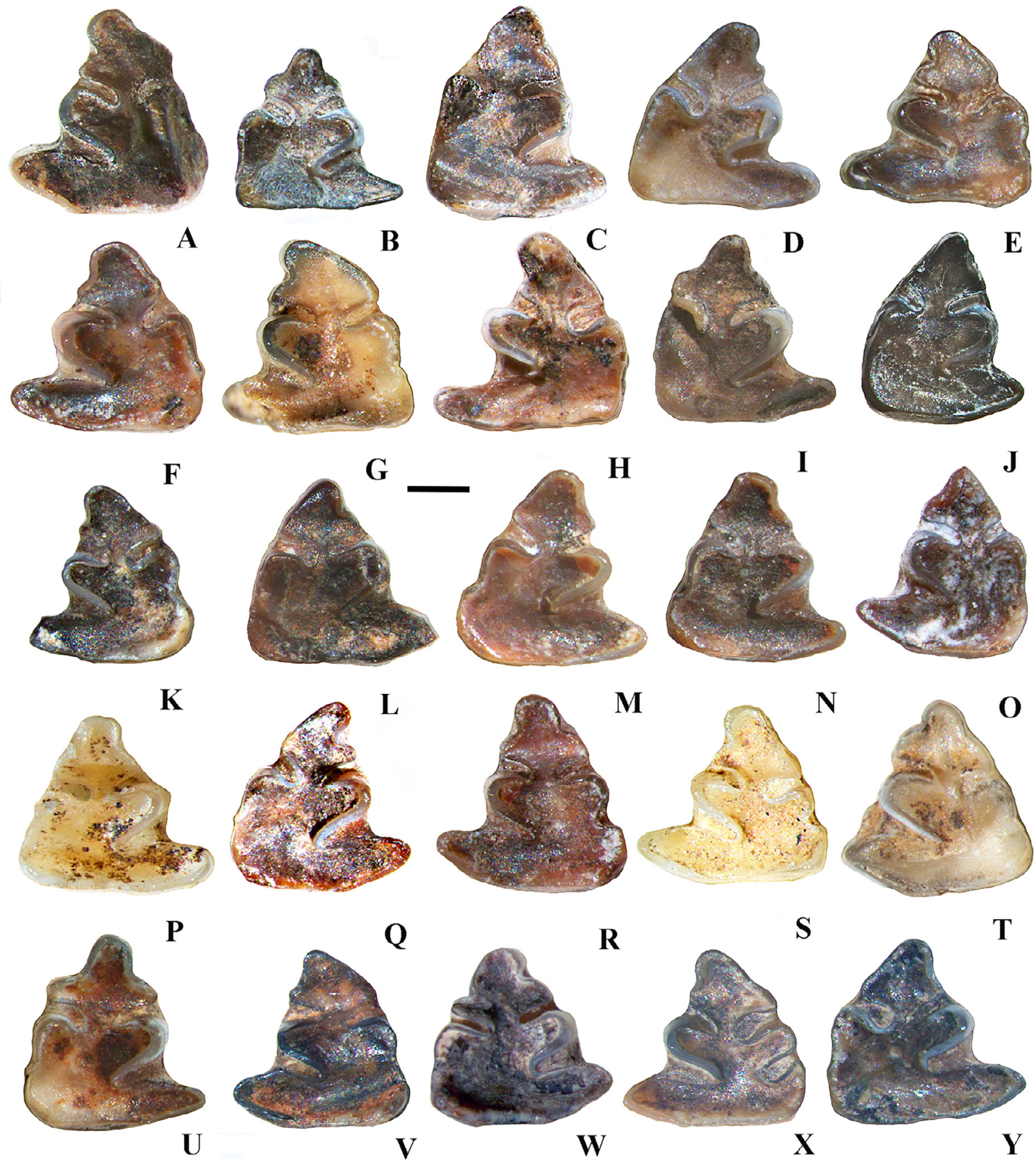

Fig. 5. Occlusal views of p3 of *Tonomochota khasanensis* n. sp. (A) RPRV–SukC–05, a left p3; (B) RPRV–SukC–06, a right p3; (C) RPRV–SukC–07, a right p3; (D) RPRV–SukC–08, a right p3; (E) RPRV–SukC–09, a left p3; (F) RPRV–SukC–10, a left p3; (G) RPRV–SukC–11, a left p3; (H) RPRV–SukC–12, a left p3; (I) RPRV–SukC–13, a right p3; (J) RPRV–SukC–14, a right p3; (K) RPRV–SukC–15, a left p3; (L) RPRV–SukC–16, a right p3; (M) RPRV–SukC–17, a right p3; (N) RPRV–SukC–18, a right p3; (O) RPRV–SukC–19, a left p3; (P) RPRV–SukC–20, a right p3; (Q) RPRV–SukC–21, a right p3; (R) RPRV–SukC–22, a left p3; (S) RPRV–SukC–23, a left p3; (T) RPRV–SukC–24, a left p3; (U) RPRV–SukC–25, a right p3; (V) RPRV–SukC–26, a left p3; (W) RPRV–SukC–27, a right p3; (X) RPRV–SukC–28, a left p3; (Y) RPRV–SukC–29, a right p3. Scale bar = 0.5 mm.

was small (five specimens), with cement in the middle part; however, one specimen did not have this fold.

The teeth other than p3 are less important when identifying ochotonid species. The occlusal outline of P3 is trapezoidal (Fig. 9A–D). It has an anterior loph that covers about 60% of the tooth width. A U-shaped paraflexus begins at about one-quarter and ends at one-third of the tooth width from the buccal side. The hypoflexus is rather short, narrow and filled with cement. The upper molariform teeth, P4 and M1, consist of two lophs separated by a deep hypoflexus, which is filled with cement. The enamel of the lophs is thicker on the anterior borders than on the posterior borders (Fig. 9E–I). The m2 is formed by two lophids (trigonid and talonid) joined with cement. The widths of the trigonid and talonid are the same. The antero-buccal wall of the trigonid is weakly concave to form the protoflexid (Fig. 9J–L).

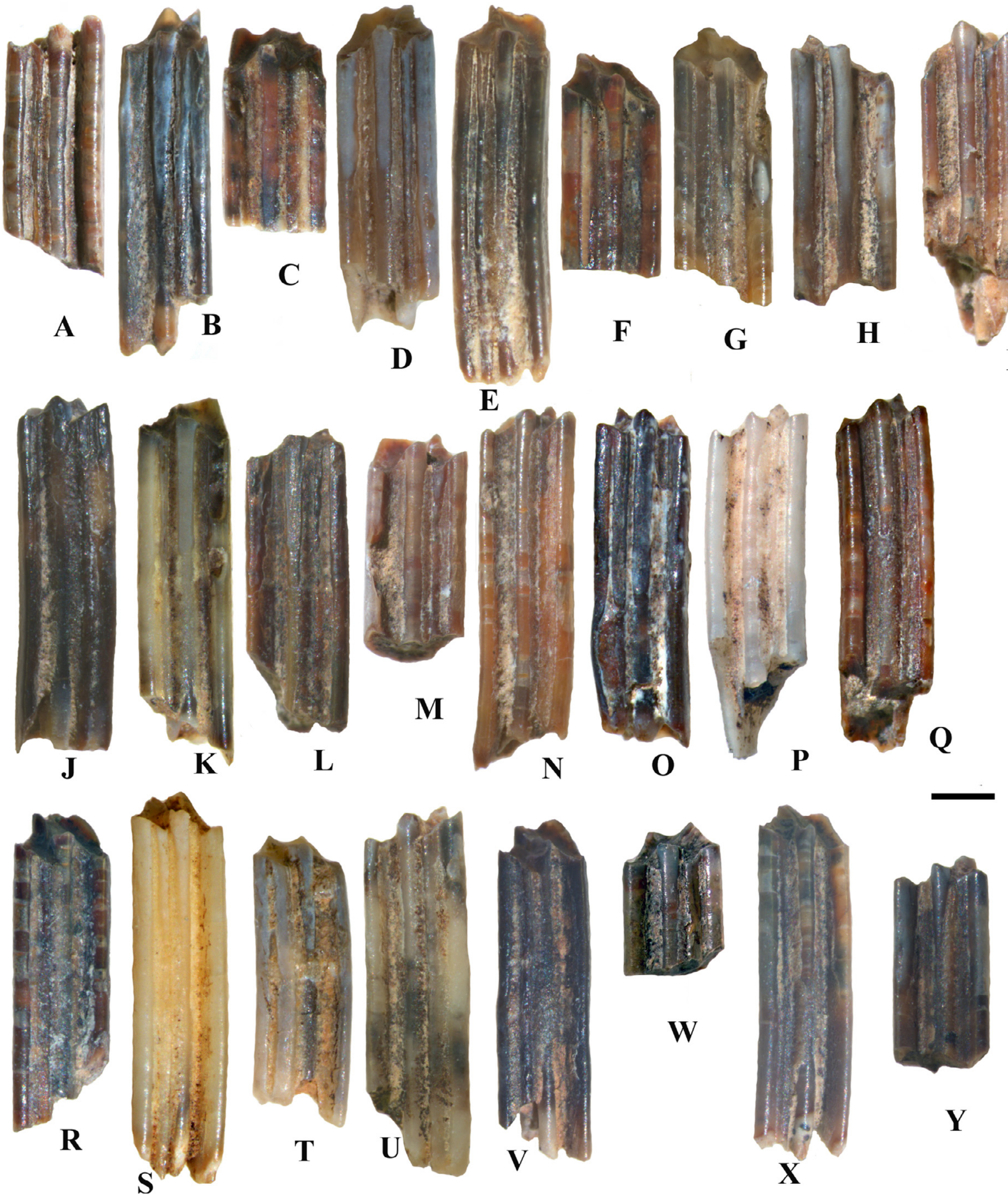

Fig. 6. Labial views of p3 of *Tonomochota khasanensis* n. sp. (A) RPRV−SukC−05, a left p3; (B) RPRV−SukC−06, a right p3; (C) RPRV−SukC−07, a right p3; (D) RPRV−SukC−08, a right p3; (E) RPRV−SukC−09, a left p3; (F) RPRV−SukC−10, a left p3; (G) RPRV−SukC−11, a left p3; (H) RPRV−SukC−12, a left p3; (I) RPRV−SukC−13, a right p3; (J) RPRV−SukC−14, a right p3; (K) RPRV−SukC−15, a left p3; (L) RPRV−SukC−16, a right p3; (M) RPRV−SukC−17, a right p3; (N) RPRV−SukC−18, a right p3; (O) RPRV−SukC−19, a left p3; (P) RPRV−SukC−20, a right p3; (Q) RPRV−SukC−21, a right p3; (R) RPRV−SukC−22, a left p3; (S) RPRV−SukC−23, a left p3; (T) RPRV−SukC−24, a left p3; (U) RPRV−SukC−25, a right p3; (V) RPRV−SukC−26, a left p3; (W) RPRV−SukC−27, a right p3; (X) RPRV−SukC−28, a left p3; (Y) RPRV−SukC−29, a right p3. Scale bar = 1.0 mm.

Tonomochota major n. sp.
(Fig. 10)

Etymology: From the Latin 'major' (big).
Type locality: Sukhaya Cave, in the north-western part of the Manchurian-Korean Mountains, in the Khasansky district of Primorsky Krai, Russia.
Holotype: RPRV−SukC−30, a right p3 (Fig. 10).
Age: MIS 3, late Pleistocene.
Diagnosis: Large-sized ochotonid. The triangular anteroconid of p3 has a deep labial fold filled with cement.
Description: Large-sized. The occlusal surface of p3 is triangular-shaped. The length of p3 is slightly larger than the width (Table 1). The ratio of width to length is 0.93. The width of

Table 1
Measurements (mm) of *Tonomochota khasanensis* n. sp., *T. sikhotana* n. sp., T. *major* n. sp., and *Ochotona hyperborea* (upper and lower teeth). Abbreviations: n − number of specimens; SD − standard deviation; 1−9 − as in Fig. 4; 1/2 − ratio of width to length of the anteroconid; 4/6 − ratio of width of the isthmus to distance from the metaconid to the protoconid.

Tooth	Measurement	*Tonomochota sikhotana* n. sp.			*Tonomochota khasanensis* n. sp.			*Tonomochota major* n. sp.		*Ochotona hyperborea*		
		n	mean ± SD	min−max	n	mean ± SD	min−max	n	min−max	n	mean ± SD	min−max
p_3	1	6	1.61 ± 0.07	1.52−1.71	25	1.46 ± 0.09	1.23−1.58	1	2.27	9	1.34 ± 0.06	1.24−1.41
	2		1.79 ± 0.08	1.66−1.89		1.48 ± 0.08	1.28−1.65		2.45		1.29 ± 0.04	1.23−1.35
	1/2		0.90 ± 0.03	0.86−0.95		0.98 ± 0.06	0.83−1.08		0.93		1.04 ± 0.03	1.00−1.09
	3		0.86 ± 0.06	0.80−0.94		0.66 ± 0.06	0.52−0.76		1.25		0.57 ± 0.04	0.51−0.62
	4		0.32 ± 0.03	0.28−0.37		0.22 ± 0.03	0.17−0.26		0.44		0.19 ± 0.05	0.12−0.29
	5		0.66 ± 0.07	0.56−0.75		0.51 ± 0.06	0.41−0.64		0.82		0.45 ± 0.04	0.37−0.49
	6		1.16 ± 0.05	1.11−1.24		1.02 ± 0.06	0.91−1.17		1.77		0.96 ± 0.08	0.83−1.03
	7		0.81 ± 0.06	0.69−0.88		0.73 ± 0.06	0.62−0.82		1.34		0.68 ± 0.08	0.52−0.78
	8		0.67 ± 0.07	0.56−0.78		0.60 ± 0.04	0.51−0.71		0.90		0.57 ± 0.04	0.49−0.61
	9		1.21 ± 0.10	1.10−1.34		0.97 ± 0.06	0.84−1.07		1.75		0.90 ± 0.10	0.77−1.05
	4/6		0.27 ± 0.02	0.25−0.30		0.21 ± 0.03	0.16−0.26		0.25		0.20 ± 0.06	0.12−0.29
P^3	1	4	2.61 ± 0.29	2.37−2.91	–	–	–	–	–	–	–	–
	2		1.25 ± 0.08	1.16−1.35								
P^4	1	2	2.35 ± 0.10	2.28−2.42	–	–	–	–	–	–	–	–
	2		1.31 ± 0.03	1.29−1.33								
M^1	1	3	2.21 ± 0.28	1.89−2.42	–	–	–	–	–	–	–	–
	2		1.27 ± 0.08	1.19−1.32								
m_2	1	3	1.80 ± 0.04	1.77−1.85	–	–	–	–	–	–	–	–
	2		1.67 ± 0.07	1.61−1.76								

the isthmus between the anteroconid and posteroconid is one-quarter of the distance from the metaconid to the protoconid (Fig. 4, Table 1). The hypoflexid and the protoflexid are narrow and deep. The paraflexid in the holotype extends first transversely, and then it suddenly turns posteriorly. The anteroconid has labial and lingual folds filled with cement. These folds are continuous all along the shaft.

4. Discussion

The three new *Tonomochota* species are each significantly different from the other in terms of the size of p3. The third lower premolar *T. major* n. sp. is almost 1.5 times larger than the other two new species in all respects. *T. sikhotana* n. sp. larger than *T. khasanensis* n. sp. Specifically, the length of the tooth, the length of the anteroconid, the width of the isthmus and the distance from the metaconid to the top of the anteroconid (Fig. 4) do not overlap in these species (Table 1). The width of the isthmus between the anteroconid and posteroconid is about one-quarter of the distance from the metaconid to the protoconid in *T. sikhotana* n. sp., in contrast to *T. khasanensis* n. sp. in which this ratio is about one fifth. A discriminant function analysis based on all 9 tooth measurements was 100% accurate in assigning independently identified individuals to the correct species (Wilk's = 0.08, R = 0.95, $\chi^2 = 82.15$, $p < 0.01$). A scatter plot of the first and second canonical roots showed clear discrimination of the three species (Fig. 11). The analysis showed that measurements 2, 3, 4, 5 and 9 (Fig. 4) playing an important role in the discrimination between *T. sikhotana, T. khasanensis* and *Ochotona hyperborea*.

In the soft sediments of the Tetyukhinskaya Cave, bone remains of the northern pika were also found. This species currently inhabits the north of Primorsky Krai. Other species of this genus (Lissovsky et al., 2007, 2008), living in adjacent territories to the west and south (Fig. 1), are close in morphology to *O. hyperborea* and have similar p3 sizes and structures. *T. khasanensis* n. sp. is closest to *O. hyperborea* in terms of p3 size (Table 1). However, the structural features of the occlusal surface of p3 clearly distinguish the fossils of the northern pika teeth collected in this cave from those of the new species.

The bone remains of the following small mammals were also found in the caves: Siberian flying squirrel (*Pteromys volans*), Eurasian red squirrel (*Sciurus vulgaris*), Siberian chipmunk (*Eutamias sibiricus*), Korean field mouse (*Apodemus peninsulae*), brown rat (*Rattus norvegicus*), greater long-tailed hamster (*Tscherskia triton*), zokor (*Myospalax psilurus*), grey red-backed vole (*Craseomys rufocanus*), northern red-backed vole (*Clethrionomys rutilus*), wood lemming (*Myopus schisticolor*), reed vole (*Alexandromys fortis*), Maximowicz's vole (*A. maximowiczii*), tundra vole (*A. oeconomus*), and Mongolian vole (*A. mongolicus*).

When these fossil ochotonid species were extant, the fauna included forest species and species that occurred mainly in

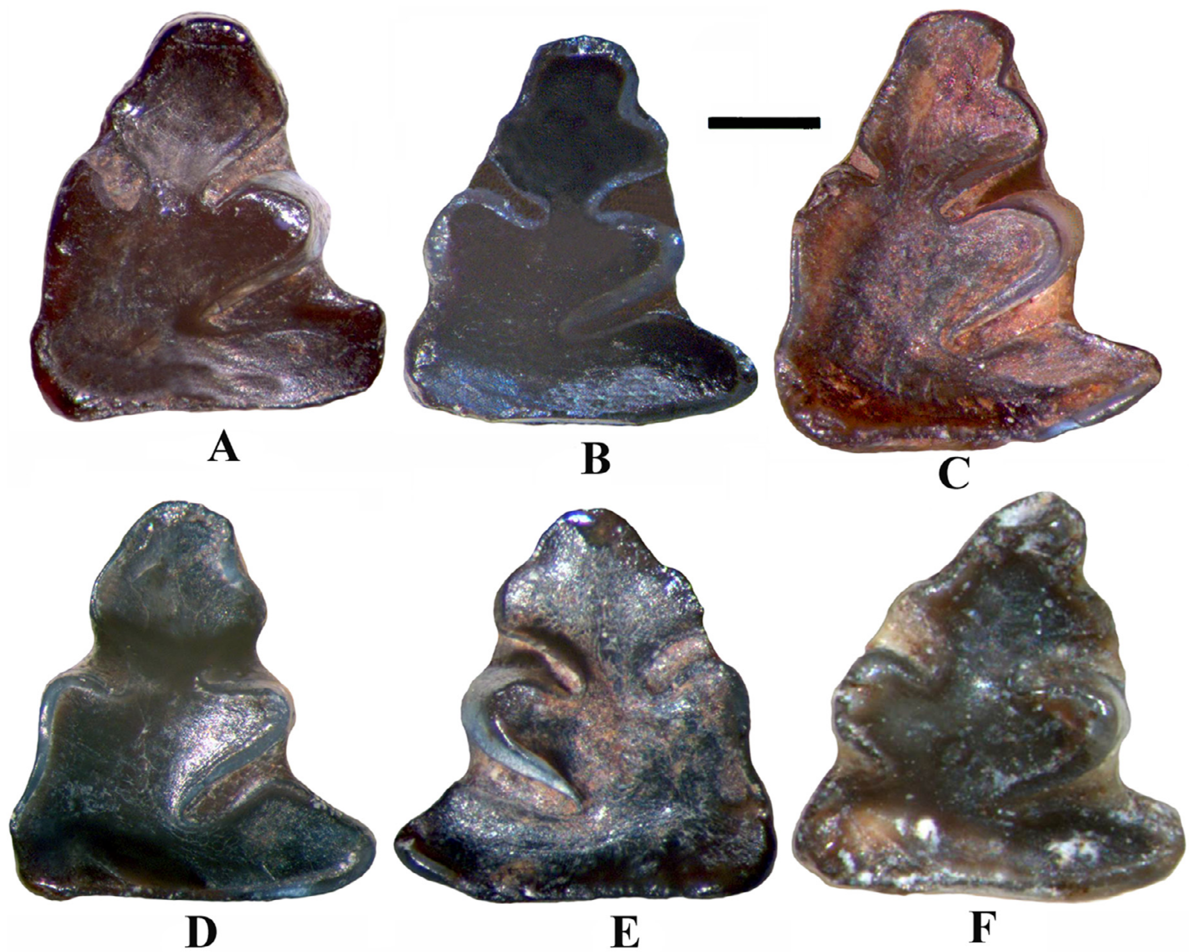

Fig. 7. Occlusal views of p3 of *Tonomochota sikhotana* n. sp. (A) RPRV−TetC−04, a right p3; (B) RPRV−TetC−05, a right p3; (C) RPRV−TetC−06, a right p3; (D) RPRV−TetC−07, a right p3; (E) RPRV−TetC−08, a left p3; (F) RPRV−SukC−04, a right p3. Scale bar = 0.5 mm.

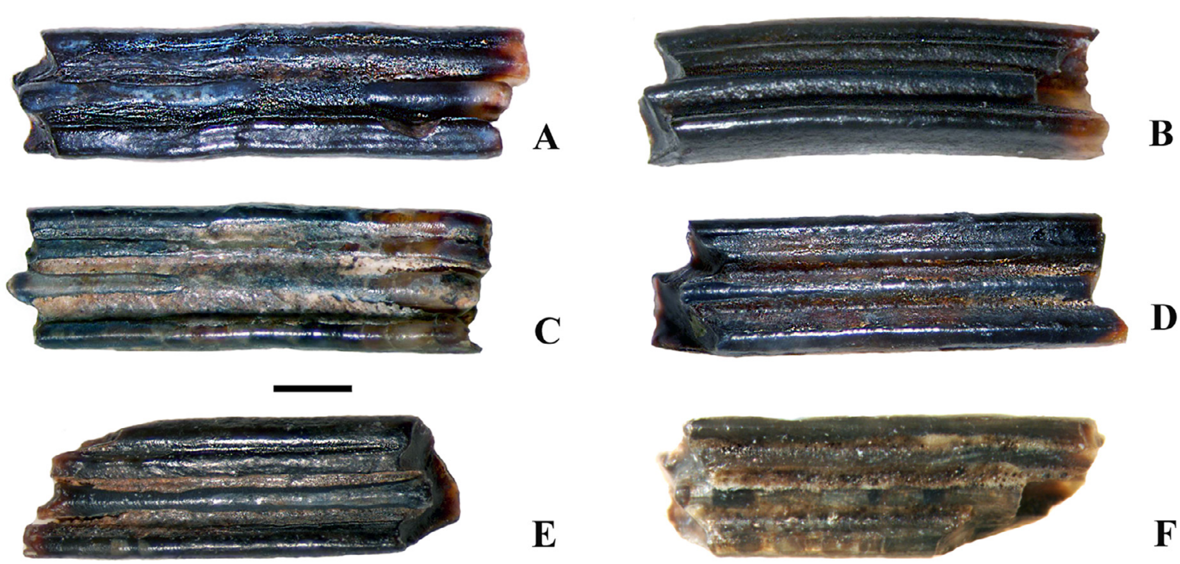

Fig. 8. Labial views of p3 of *Tonomochota sikhotana* n. sp. (A) RPRV−TetC−04, a right p3; (B) RPRV−TetC−05, a right p3; (C) RPRV−TetC−06, a right p3; (D) RPRV−TetC−07, a right p3; (E) RPRV−TetC−08, a left p3; (F) RPRV−SukC−04, a right p3. Scale bar = 1.0 mm.

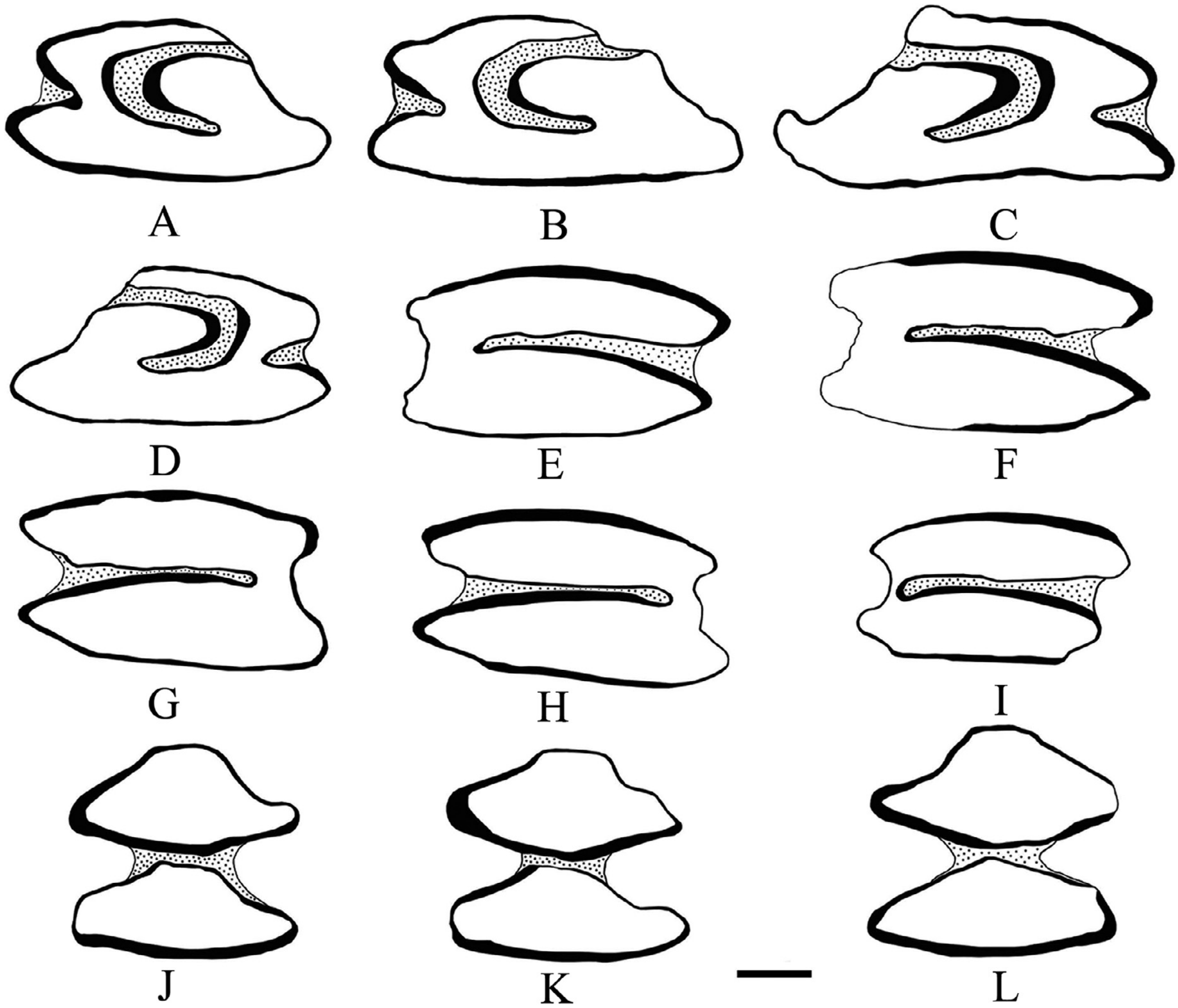

Fig. 9. Upper and lower cheek teeth (occlusal view) of *Tonomochota sikhotana* n. sp. (A) RPRV−TetC−09, a left P3; (B) RPRV−TetC−10, a left P3; (C) RPRV−TetC−11, a right P3; (D) RPRV−TetC−12, a right P3; (E) RPRV−TetC−13, a right P4; (F) RPRV−TetC−14, a right P4; (G) RPRV−TetC−15, a left M1; (H) RPRV−TetC−16, a left M1; (I) RPRV−TetC−17, a right M1; (J) RPRV−TetC−18, a right m2; (K) RPRV−TetC−19, a right m2; (L) RPRV−TetC−20, a left m2. Scale bar = 0.5 mm.

open spaces; they show the distribution of savannah-like landscapes, typical on the outskirts of the mammoth steppe. It can be assumed that the Sikhote-Alin refugium not only allowed some mammal species, including those long-extinct throughout the rest of the territory (Tiunov et al., 2016), to survive unfavourable periods (Kosintsev et al., 2016) but was also the centre of speciation (Tiunov and Gimranov, 2020). Erbajeva et al. (2006) has stated that many of the fossil species of ochotonids may have had a limited distribution; indeed, the bone remains of two of the three new species described here were found only in the southernmost cave, i.e., the Sukhaya Cave.

It should be noted that two teeth (Figs. 5P, S, 6P, S) belonging to *T. khasanensis* n. sp. have a Holocene preservation by colour and their organoleptic characteristics. Thus, ochotonids belonging to the genus *Tonomochota* were perhaps alive relatively recently in the Far East of Russia. The sufficiently high diversity within the endemic genus is primarily associated with a significant mosaic of living conditions in their territory in the late Pleistocene−Holocene time. During this time, forests and rocky landscapes existed in the intermontane basins and there was widespread development of savannah-like landscapes and coastal lowlands, which significantly increased during the period of sea retreat. Of great importance, in our opinion, is the fact that the Sikhote-Alin ridge actually became an island during the periods of marine transgression. In other periods, it was surrounded by plains and low-lying areas, which also created a certain level of isolation. Perhaps this, as well as the climatic characteristics of the Pacific coast, created the specific conditions that facilitated the speciation and allowed individual species to survive here for a relatively long period of time.

The fossil material from the Sukhaya Cave has not yet been fully processed. It is likely that subsequent studies of the fossil fauna of the Sikhote-Alin will include a number of similar discoveries.

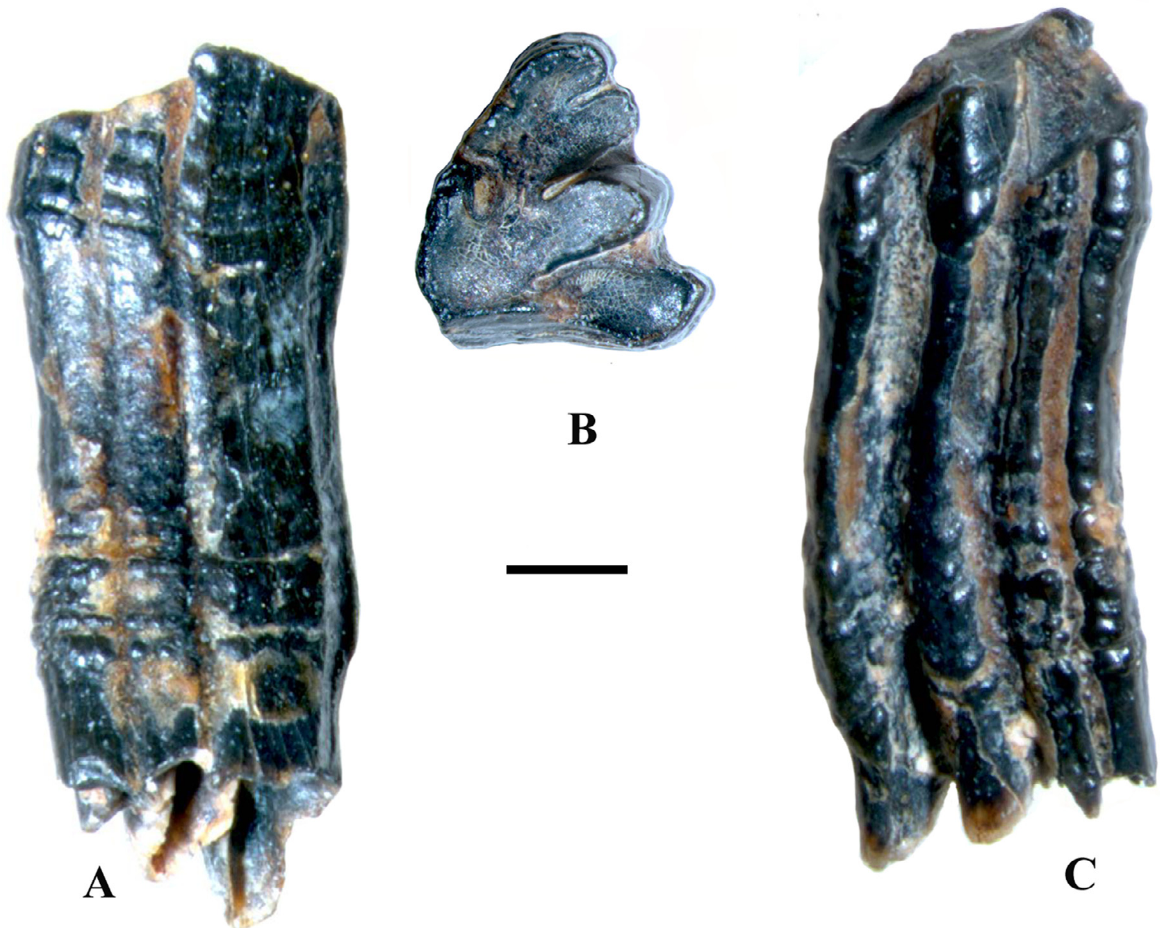

Fig. 10. Lingual (A), occlusal (B) and labial (C) views of p3 (RPRV−SukC−30) of *Tonomochota major* n. sp. Scale bar = 1.0 mm.

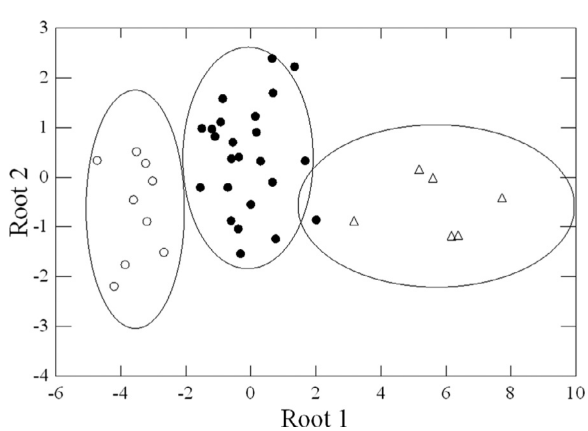

Fig. 11. Scatter plot for the nine morphometric measurements of the teeth (p3) analyzed. The circles drawn represent 85% confidence ellipses. Open circles − *Ochotona hyperborea*; solid circles − *Tonomochota khasanensis* n. sp.; open triangles − *T. sikhotana* n. sp.

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