



The first fossil *Petaurista* (Mammalia: Sciuridae) from the Russian Far East and its paleogeographic significance

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Abstract

For the first time in the south of the Russian Far East in the Late Pleistocene cave deposits, fragments of the giant flying squirrel of the genus *Petaurista* were discovered. *Petaurista tetyukhensis* n. sp. is described based on a fragment of the upper jaw with two teeth and five isolated teeth from two cave locations. The main differences between the new species and living forms as well as other fossil species of the genus *Petaurista* are the absence of vertical groove on the lingual wall between the protocone and hypocone on M2, the absence of the anterior cross loph on the upper P4-M3, and the absence of mesoconids on lower, as a result of which the hypoflexid is not w-shaped. It is suggested that the Sikhote-Alin refugium allowed individual species to survive there during long unfavourable period of time and was the centre of speciation.

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Keywords: New species; Giant flying squirrels; Late Pleistocene; Refugium; Sikhote-Alin

1. Introduction

Among the materials obtained from the caves of Primorsky Krai (Russian Far East) during the 2012–16 paleontological excavations, isolated teeth of the representative of the genus *Petaurista* (Tiunov, 2016) were found. According to the degree of preservation, they are attributed to the Late Pleistocene complex of animals, as evidenced by the accompanying fauna (Kosintsev et al., 2016).

The giant flying squirrels, *Petaurista*, belong to the subfamily Sciurinae and are distributed currently from Pakistan and Nepal to East Asia, North Indochina and Southeast Asia (Thorington and Hoffmann, 2005; Smith and Xie, 2008; Jackson and Thorington, 2012; Ohdachi et al., 2015). According to the latest data, this genus includes nine species (Thorington et al., 2012). The nearest location of the modern representative of this genus *Petaurista leucogenys* is Honshu Island.

Fossil *Petaurista* first occurred in the Early Pleistocene localities of Chongqing and Anhui in southern China (Zheng, 1993; Jin et al., 2009). The northernmost find of *Petaurista* from the warm period of the Middle Pleistocene was at Zhoukoudian in North China (Young, 1934). For the Late Pleistocene, the main finds of this genus were in Japan and in China (e.g., Qiu et al., 1984). The Holocene occurrences of *Petaurista* included the southern Japanese islands and Hainan Island in southern China (Kawamura, 1988; Hao and Huang, 1998).

The northernmost find of a fossilized giant flying squirrel from the Late Pleistocene was on the mainland of East Asia, but they belong to another genus (*Aeretes melanopterus* (Milne-Edwards, 1867)), which is known from North China. These records in Beijing area from the Upper Cave and Tianyuan Cave at Zhoukoudian are of the late Pleistocene age, around 30 ky BP (Tong, 2007).

In this paper, a new species of *Petaurista* from the Russian Far East is reported. It represents the northernmost find of *Petaurista*, clarifying the existing idea of the paleolandscape environment and distribution of this genus in the Late Pleistocene in Northeast Asia.

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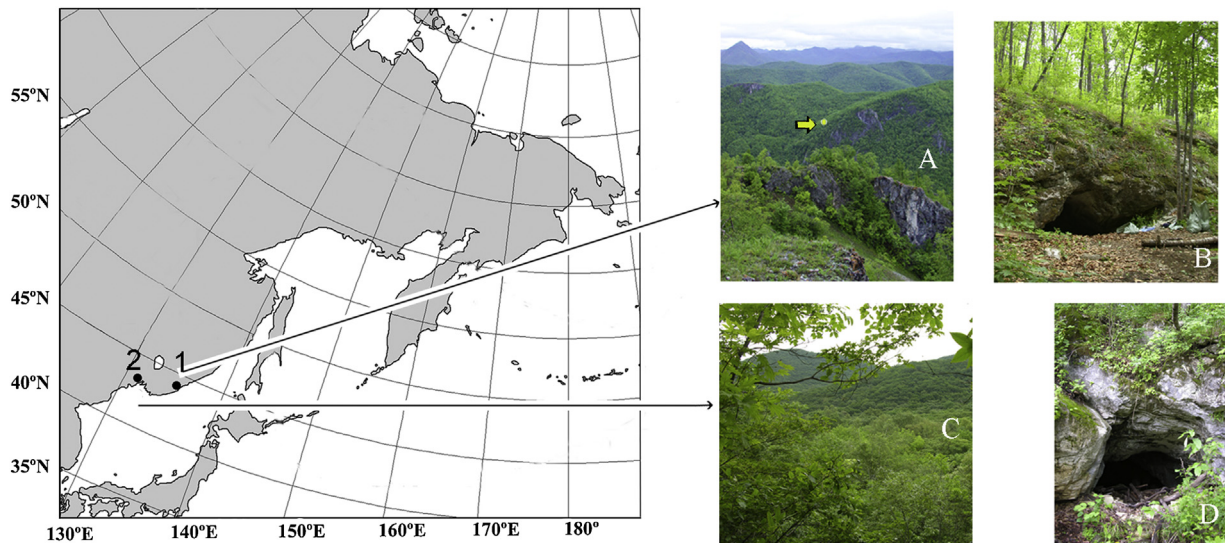


Fig. 1. Map of the location of the caves and the surrounding landscapes. 1 – Tetyukhinskaya Cave; A – the surrounding landscape; B – the entrance to the cave. 2 – Sukhaya Cave; C – the surrounding landscape; D – the entrance to the cave.

2. Materials and methods

All the fossil teeth of a giant flying squirrel described here were collected in the Russian Far East from sediments in Tetyukhinskaya Cave (Middle Sikhote-Alin, 44°35'N, 135°36'E) and 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, which used the caves as a dwelling or temporary shelter. Sediments were selected during excavation with a conditional horizon of 10 cm. The sediment samples taken in the field were screen-washed with 1.0 mm mesh size for microvertebrates.

Limestone Tetyukhinskaya Cave is located in the Middle Sikhote-Alin near Dalnegorsk city. Excavations were conducted periodically between 2012 and 2015. All the discoveries of *Petaurista* were made in pits laid in the entrance grotto. A fragment of the left upper jaw with two molars M1 and M2 was found at a depth of 10–20 cm. An isolated DP4 was found at a depth of 20–30 cm and an isolated lower molar m2 at a depth of 40–50 cm. From an isolated tooth of an Asian black bear (depth 40–50 cm), similar in preservation and colour to the *Petaurista* teeth, a radiocarbon date of 39874 ± 133 BP (NSK-850, UGAMS-21786) was obtained by accelerated mass spectrometry (AMS) (Kosintsev et al., 2016). This corresponds to the boundary of the stadial Hasselo and interstadial Hengelo or the middle of Marine Isotope Stage 3 (MIS 3) of the Late Pleistocene (Blockley et al., 2012).

Limestone Sukhaya Cave is located 3–5 km from the Barabash Village in the north-western part of the Manchurian-Korean mountains. Excavations were carried out in 2016. Isolated P4, m3 and M3 were found at a depth of 30–40 cm, 50–60 cm and 60–70 cm, respectively. Two fragments of horse teeth (*Equus* sp.) were isolated from the depth ranges 30–40 cm and 50–60 cm (Eq-Suh/2: UCSC ID SC17.AV073; Eq-Suh/5: UCSC ID SC17.AV075). The fragments were radiocarbon dated to be 51300 ± 2500 (Eq-Suh/2: UCIAMS-211762) and

48400 ± 1700 (Eq-Suh/5: UCIAMS-211763) uncalibrated years BP.

The materials are kept as a part of the fossil collection of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences. Registration of fossil materials used the following abbreviations: RPRV: R – Russia, PR – Primorye, V – Vladivostok; TetC – Tetyukhinskaya Cave; SukC – Sukhaya Cave.

The dental terminology used in this paper is mainly adapted from McKenna (1962) and Kawamura (1988). All tooth measurements are reported in millimetres. Photographs of teeth were taken with a SteREO Discovery.V12 stereomicroscope and stacked using CombineZM software (Hadley, 2008). The final illustrations were post-processed for contrast and brightness using Adobe® Photoshop® software.

3. Systematic palaeontology

Class Mammalia Linnaeus, 1758

Order Rodentia Bowdich, 1821

Family Sciuridae Hemprich, 1820

Subfamily Sciurinae Fischer de Waldheim, 1817

Tribe Pteromyini Brandt, 1855

Genus *Petaurista* Link, 1795

Petaurista tetyukhensis n. sp.

(Figs. 2, 3)

Etymology: The species is named after type locality. The old name of Dalnegorsk Town (Tetyukhe) is used.

Type material: Holotype, RPRV-TetC-01, Vladivostok, fragment of the upper left jaw with two teeth — M1 and M2 (Fig. 2).

Type locality: Tetyukhinskaya Cave, Middle Sikhote-Alin, the

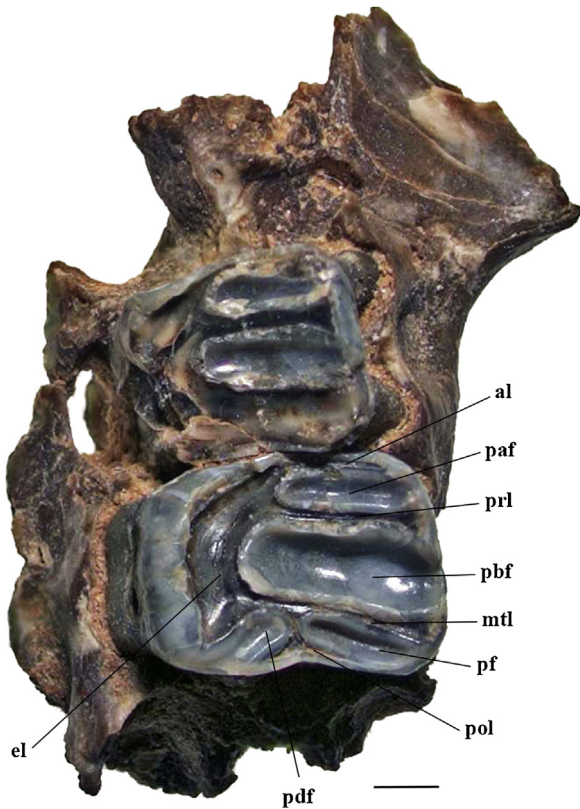


Fig. 2. Occlusal view of RPRV-TetC-01, the fragmentary maxillae of *Petaurista tetyukhensis* n. sp., holotype. Abbreviations: al, anteroloph; el, endoloph; mtl, metaloph; paf, paraflexus; pbf, posterobuccal flexus; pdf, posterolingual diagonal flexus; pf, postfossette; pol, posteroloph; prl, protoloph. Scale bar = 1 mm.

Dalnegerski Region of the Primorsky Krai, Russia.

Type horizon: MIS 3, Late Pleistocene.

Other materials: RPRV-TetC-02, left DP4 (Tetyukhinskaya Cave); RPRV-SukC-01, left P4 (Sukhaya Cave); RPRV-SukC-02, left M3 (Sukhaya Cave); RPRV-TetC-03, left m2 (Tetyukhinskaya Cave); RPRV-SukC-03, right m3 (Sukhaya Cave) (Fig. 3).

Diagnosis: On the lingual face of the protocone in the upper cheek teeth, the vertical groove on the lingual wall between the protocone and hypocone on M2 is absent. On the upper molars, the anterior cross loph is absent. On the lower cheek teeth, the mesoconid is missing. As a result, the hypoflexid is not w-shaped as in all other living and fossil squirrels.

Description and comparison:

DP4: The occlusal outline approximates a triangle with round corners. Its anterior- and posterior- lingual portions are heavily broken. The parastyle is elongated transversely to form the anterior ridge, which is well separated from the protoloph by the paraflexus. The protoloph is set parallel to the anteroloph. The paraflexus is as broad as the posterobuccal flexus. The metaconule is large and located in the middle of the metaloph. Nearby, closer to the lingual side, there is a shallow groove connecting the posterobuccal flexus and postfossette.

P4: The tooth has three roots. The lingual root is thicker and longer than the antero-buccal and postero-buccal roots. The enamel is thick and smooth. The occlusal outline is a rounded trapezoid. The parastyle is triangular in occlusal view and is connected to the protocone by the low anteroloph. Depressions on the lingual margin of the crown, surrounding the front and back of the base of the protocone, are well developed. The protoloph connects to the anterior part of the protocone and extends buccally to the paracone. The protoconule is distinct and situated on the buccal part of this loph, but never forms the anterior cross loph. The protocone and hypocone are almost merged but can be distinguished from each other by a faint groove on their lingual wall. The metaloph extends buccally from the hypocone to the metaconule and reaches the metacone. The posterior cross loph projects posteriorly from the metaconule to reach the posterior margin of the crown. The posterolingual diagonal flexus is deep and opens posteriorly. The postflexus of P4 perhaps can be isolated for a time by wear and has been converted to a fossette. The mesostyle is present at the buccal entrance of the posterobuccal flexus. It is triangular in occlusal view.

The fragment of the left maxilla preserves two teeth: M1 and M2. Both have three roots. The lingual root is thicker and longer than the antero-buccal and postero-buccal roots. The enamel is thick and smooth. It seems to be from an old individual as the surface of the crown of the teeth is severely worn.

M1: The lingual part of M1 is damaged. The posterior portion of the tooth is much planished. The occlusal outline and pattern of this tooth are basically identical with those of M2.

M2: The occlusal outline of the crown approximates a rectangle. Vertical groove on the lingual wall between the protocone and hypocone is absent. The parastyle merges with the anteroloph, forming a thin transverse ridge. The protoloph and metaloph are slightly thicker and run parallel to the anteroloph. The posterobuccal flexus is twice as broader as paraflexus. The posterolingual diagonal flexus opens postero-lingually, while the postfossette is a closed groove and extends postero-buccally in between the metaloph and the posteroloph. The posterior cross loph meets at right angles with the posteroloph, which forms the posterior wall of the crown.

Left M3: The tooth has three roots. The occlusal outline of M3 is a rounded rectangular. The parastyle and anteroloph are well merged to form a slender anterior transverse ridge. The protoloph is slenderer than the anteroloph but the same as the metaloph. The groove of the lingual wall of the crown is developed only opposite the hypocone. The postfossette is connected to the posterolingual diagonal flexus and is only in the early stages of wear. The posterior cross loph is weak. The posteroloph has two branches, one is lingual to the posterior cross loph, the other is buccal to the posterior cross loph, both of them form the posterior ridge of the tooth.

Left m2: The antero-lingual and postero-buccal portions of tooth are broken and its surface of the crown moderately worn. The occlusal outline of the crown of m2 approaches a trapezoid. The paraconid is connected to the anterolophid. The anterior valley between the paraconid and protoconid opens antero-buccally; the hypoflexid opens buccally and is not divided into two parts as in other species of *Petaurista*. The entoconid is con-

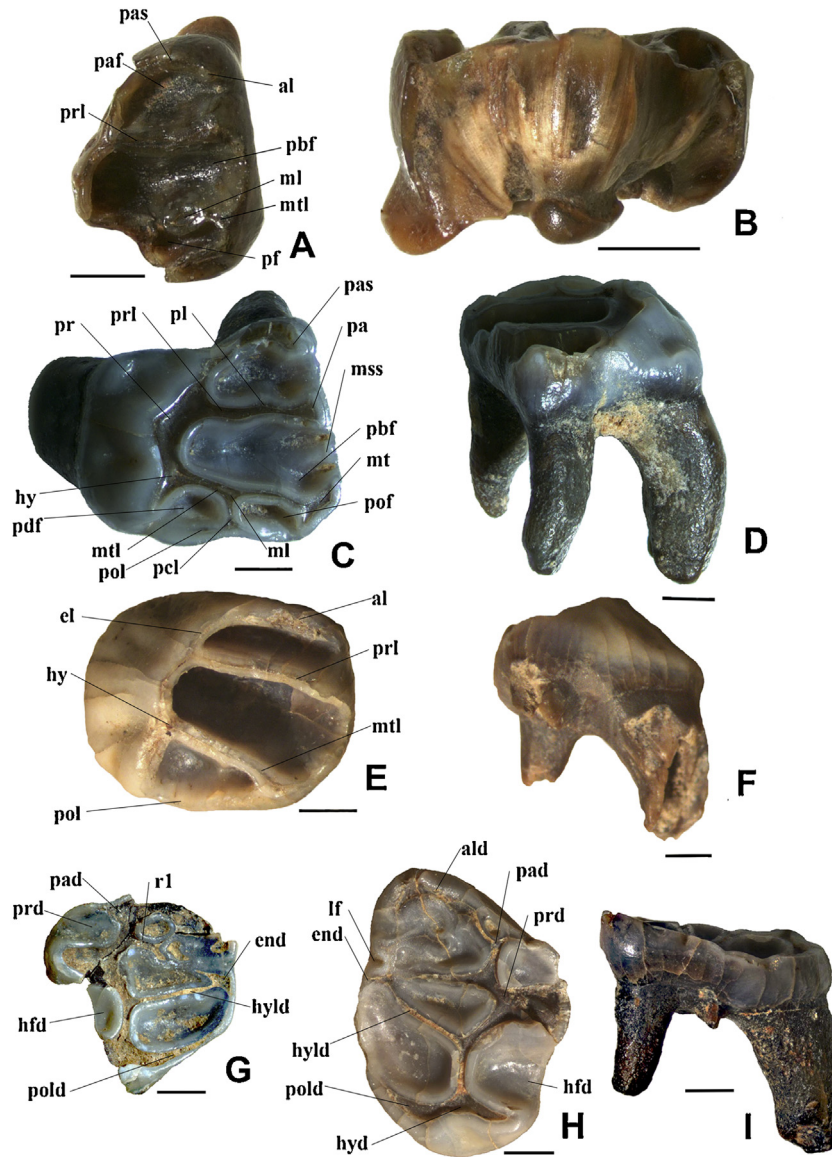


Fig. 3. Upper and lower cheek teeth of *Petaurista tetyukhensis* n. sp. (A, B) RPRV–TetC–02, left DP4; (A) occlusal view; (B) lingual view. (C, D) RPRV–SukC–01, left P4; (C) occlusal view; (D) antero-buccal view. (E, F) RPRV–SukC–02, left M3; (E) occlusal view; (F) anterior view. (G) RPRV–TetC–03, left m2, occlusal view. (H, I) RPRV–SukC–03, right m3; (H) occlusal view; (I) lingual view. Abbreviations: al, anteroloph; ald, anterolophid; el, endoloph; end, entoconid; hfd, hypoflexid; hy, hypocone; hyd, hypoconid; hyld, hypolophid; lf, lingual flexid; ml, metaconule; mss, mesostyle; mt, metacone; mtl, metaloph; pa, paracone; pad, paraconid; paf, paraflexus; pas, parastyle; pbf, posterobuccal flexus; pcl, posterior cross loph; pdf, posterolingual diagonal flexus; pf, postfossette; pl, protoconule; pof, postflexus; pol, posteroloph; pold, posterolophid; pr, protocone; prd, protoconid; prl, protoloph; r1, unnamed ridge. Scale bar = 1 mm.

nected with the hypolophid but separated from mesostylid and ridge r1.

Right m3: The tooth has four roots. The occlusal outline of the crown m3 is nearly triangular. The paraconid, protoconid, mesoconid and hypoconid are connected to each other to form a high and continuous ridge on the buccal side of the crown. This ridge (buccal ridge) is zigzag in the occlusal view, due to the deep intrusions of two buccal valleys. In front of the paraconid, there is a small fossetid. Opposite the paraconid on the lingual side, there are two small lingual flexids. The valley between the paraconid and protoconid opens buccally. As in m2, the hypoflexid is not divided into two parts. The paraconid is connected to the anterolophid. The ridge r1 is derived from the anterior arm of the protoconid and extends transversely. The entoconid is separated

from r1, the hypolophid and the posterolophid. The posterior wall of the crown is formed by the hypoconid and posterolophid.

The closest to the new species with respect to the size (Table 1) and the simple structure of the chewing surface of the teeth is *P. leucogenys*. The cheek teeth P4–M3 of the fossil species are similar to each other in size as in *P. leucogenys*. In other species of this genus, M3 is the smallest, and P4 is smaller than M1, with the exception of *Petaurista xanthotis*, in which P4 is the largest in this row. Postfossettes on P4, M1 and M2 in the *P. tetyukhensis* n. sp. and *P. leucogenys* only form a valley, not double pits as in the other species of this genus. The image of the chewing surface M3 of the new fossil species is similar to that of *P. xanthotis*. In comparison with other species, the image of the chewing surface M3 of the new species is the simplest.

Table 1
Measurements (in mm) of cheek teeth of *Petaurista tetyukhensis* n. sp. and *P. leucogenys*.

Tooth	Position	<i>P. tetyukhensis</i> n. sp.	<i>P. leucogenys</i> (from Kawamura, 1988)
DP4	Length	3.61	3.24–3.70
	Width		3.32–3.59
P4	Length	4.16	4.10–4.60
	Width	4.84	4.86–5.08
M1	Length	3.29	3.45–3.84
	Width		4.67–5.16
M2	Length	3.59	3.35–3.68
	Width	4.95	4.76–4.97
M3	Length	4.05	3.31–3.71
	Width	4.91	3.99–4.59
m3	Length	5.56	4.77–5.44
	Width	4.04	3.72–4.47

M3 of *Petaurista* sp. described by Kawamura (1988) from Japan is much smaller in size than in our new species. The extinct species of *Petaurista brachyodus* (Young, 1934), described from the fragment of the lower jaw with p4 and damaged m3 at the Middle Pleistocene sediments from Locality 1 of Choukoutien, is also much smaller in size. *Petaurista* sp., described by Hu and Qi (1978) based on an isolated M2 from Lantian, differs from our new species by well-developed anterior cross loph.

The main differences between the new species and living and fossil species of *Petaurista* are the absence of vertical groove on the lingual wall between the protocone and hypocone on M2, the absence of the anterior cross loph on the upper P4–M3 and the absence of mesoconids on lower, as a result of which the hypoflexid is not w-shaped.

4. Discussion

Global climate change that contributed to the periodic isolation of small populations in forest refugia has been proposed as a major influence on the processes of speciation in giant flying squirrels in southeast Asia (Mercer and Roth, 2003; Yu et al., 2006; Lu et al., 2013). High habitat heterogeneity in the region provided them with the necessary environmental backgrounds for rapid radiation (Yu et al., 2006). Previously, it was shown that the southern Primorye was a refugium of forest fauna during Late Pleistocene. The grey wolf (*Canis lupus*), raccoon dog (*Nyctereutes procyonoides*), red fox (*Vulpes vulpes*), brown bear (*Ursus arctos*), Asian black bear (*U. (Euarctos) thibetanus*), Asian badger (*Meles leucurus*), sable (*Martes zibellina*), wolverine (*Gulo gulo*), Eurasian otter (*Lutra lutra*), Eurasian lynx (*Lynx lynx*), leopard (*Panthera pardus*), tiger (*P. tigris*), steppe bison (*Bison priscus*), woolly rhinoceros (*Coelodonta antiquitatis*), wild boar (*Sus scrofa*), sika deer (*Cervus nippon*), red deer (*C. elaphus*), Siberian roe deer (*Capreolus pygargus*), Siberian musk deer (*Moschus moschiferus*), elk (*Alces alces*), and long-tailed goral (*Nemorhaedus caudatus*) were believed to live there (Gasilin et al., 2013; Kosintsev et al., 2016).

According to Kawamura (1988), in the warm periods of the Middle Pleistocene, giant flying squirrels advanced far north. It is likely that one of the populations survived in the inter-

mountain basins of the Pacific coast until the Late Pleistocene. Various forest vegetation was present in the Late Pleistocene and Holocene (Korotky et al., 2005). During the first Karginian optimum, taiga forests were the dominant type of vegetation (Shchetnikov et al., 2015), which provided habitat for giant flying squirrels. As a result of the Pleistocene climate aridification and the growing area of open landscapes, the forest fauna of the Sikhote-Alin and the East Manchurian mountains was periodically isolated. It was near the coast, under softer and more humid climactic conditions in intermountain hollows and high-growth forests, that the main habitats of species of this genus could be preserved. At the same time in the Late Pleistocene, this was the northernmost population of giant flying squirrels, and their habitat conditions were probably close to the habitat of modern *P. xanthotis*. This species occupies spruce forests at high elevations at about 3000 m asl in western China. It feeds mainly on young shoots and leaves, as well as pine nuts (Smith and Xie, 2008). Perhaps some similarity in the structure of the teeth of *P. tetyukhensis* n. sp. and *P. leucogenys* is evidence of close kinship of these species, and the similarity in the structure of M3 of the new fossil species and *P. xanthotis* may be due to the severe environmental conditions and the characteristics of food.

Despite a significant amount of research on the Late Pleistocene fauna in northeastern China, no species of the genus *Petaurista* has been reported so far. Thus, it can be assumed that the Sikhote-Alin refugium not only allowed some species of mammals, including those long extinct throughout the rest of the territory (Tiunov et al., 2016; Borodin et al., 2018), to survive the unfavourable conditions (Kosintsev et al., 2016), but also was the centre of speciation.

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