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History, evolutionary development and systematics of marmots (Rodentia, Sciuridae) in Transbaikalia

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ABSTRACT. New materials on extinct marmots of Western Transbaikalia, the Middle Pliocene *Marmota tologoica* Ivanijev, 1966 and Middle Pleistocene *M. sibirica nekipelovi* Erbajeva, 1966 are described.

KEY WORDS: evolution, biostratigraphy, *Marmota*, Transbaikalia, Pliocene, Pleistocene.

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История, эволюционное развитие и систематика вымерших сурков (Rodentia, Sciuridae) Забайкалья

М.А. Ербаева

РЕЗЮМЕ. Описаны новые материалы по вымершим суркам Западного Забайкалья - среднеплиоценовому *Marmota tologoica* Ivanijev, 1966 и среднеплейстоценовому *M. sibirica nekipelovi* Erbajeva, 1966.

КЛЮЧЕВЫЕ СЛОВА: эволюция, биостратиграфия, *Marmota*, Забайкалье, плиоцен, плейстоцен.

Introduction

The recent marmots of the genus *Marmota*, the history of which can be traced since the Miocene, have Holarctic distribution. The most early reliable fossil remains of marmots, close to the North American *M. vetus* (Marsh, 1871), are known from the Early and Upper Miocene beds of Zaissan Depression (Eastern Kazakhstan). These beds are referred to the Akzhar and Sarybulak formations (Shevyreva, 1968). Marmot remains have been found also in Mongolia in the Ulan-Tologoi locality in the Middle Miocene fauna with a dominance of ochotonids of the genus *Alloptox* and various jerboas (Devyatkin, 1981).

In North America this group of rodents is known from the end of the Middle Miocene. The most ancient taxon, *M. vetus* was described from the Clarendonian. Another Miocene species, *M. minor* Kellog, 1910 was found in the Early Hemphillian (Black, 1963). Based on the Miocene records of marmots in North America Koenigswald (1990) supposed that Eurasian marmots are the New World immigrants. Paleontological and karyological data permit us to consider that marmots have an Asian origin that is in accordance with the opinion by Gromov *et al*. (1965). These authors, basing on the analysis of paleontological data and the studies of recent marmots of the world fauna, considered that one of the centers of origin of this group was Central Asia. However, as it was noted by Bibikov (in Gromov *et al*., 1965), the question on assessing initial landscape as a place of formation of ancient marmots is still disputable. There are various points of view related to this question. Thus, according to the opinion by Bazhanov (1947) and Andrushko (1955), appearance of ancient marmots in the evolutionary history of rodents was connected with the development of plain steppes; they penetrated into mountains significantly later. Zimina points to Hamilton's supposition that marmots initially were forest animals and colonized woodless territories later.

Dental terminology is after Gromov *et al*. (1965: fig. 13) with some additions taken from Black (1963). The teeth and skull measurements are given in mm. A stratigraphic scale according to which the border between the Pliocene and the Pleistocene is at the level of 1.8 Ma is accepted here.

Brief characteristics of Transbaikalian mammal fauna and landscapes in the Pliocene and Pleistocene

At present two species, Mongol marmot or tarbagan *M. sibirica* Radde, 1862 and Barguzin subspecies of the black-cap marmot *M. camtschatica doppelmayri* Birula, 1922 inhabit the Transbaikalia. The history of marmots of the genus *Marmota* in the given region begins in the Middle Pliocene (early Villafranchian).

The most ancient remains of marmots in the Western Transbaikalia are known from the Middle Pliocene localities Tologoi 1 (Vereshchagin *et al*., 1960) and Beregovaya (Ravskii *et al*., 1964). They were found within the limits of the recent range of *M. sibirica*. Marmots were not numerous in the Pliocene fauna. They were the elements of the Hipparion fauna of the

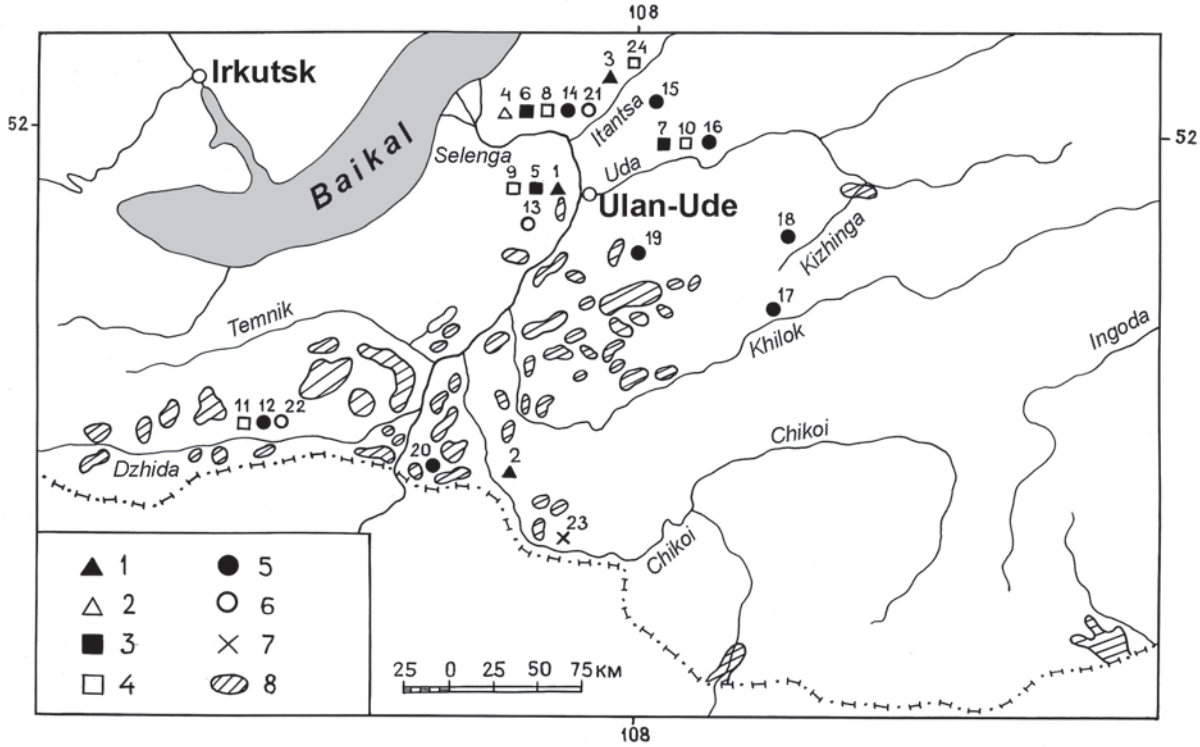

Figure 1. Recent distribution of Recent *Marmota sibirica* and fossil marmot localities in Western Transbaikalia.
1 — Middle Pliocene; 2 — Late Pliocene; 3 — First half of Middle Pleistocene; 4 — Second half of Middle Pleistocene; 5 — First half of Late Pleistocene; 6 — Second half of Late Pleistocene; 7 — Holocene; 8 — Recent range of *M. sibirica* (after Shvetsov, 1978: fig.37).
Localities: 1 — Tologoi 1; 2 — Beregovaya; 3 — Khalzanovo; 4 — Klochnevo I; 5 — Tologoi 2.4; 6 — Zasukhino II_3; 7 — Dodogol 3; 8 — Zasukhino II_4; 9 — Tologoi 2.6; 10 — Dodogol 4; 11 — Tsezhe; 12 — Mikhailovka; 13 — Tologoi 3.3; 14 — Zasukhino X; 15 — Ingiskhan; 16 — Dodogol 5; 17 — Ust'-Obor; 18 — Novokizhinginsk; 19 — Varvarina Gora; 20 — Ust' Kyakhta 17; 21 — Zasukhino IX_5; 22 — Botsi; 23 — Malaya Kudara; 24 — Zyryansk.

Chikoi complex that included *Petenyia hungarica* Kormos, 1930 *Beremendia fissidens* (Petenyi, 1864), *Hypolagus multiplicatus* Erbajeva, 1976, *H. transbaicalicus* Erbajeva, 1976, *Ochotonoides complicidens* (Boule & Teilhard, 1928), *Ochotona gromovi* Erbajeva, 1976, *Ochotona sibirica* Erbajeva, 1988, *Orientalomys sibiricus* Erbajeva, 1976, *Sicista pliocaenica* Erbajeva, 1976, *Cricetinus* cf. *varians* Zdansky, 1928, *Villanyia eleonorae* Erbajeva, 1975, *Mimomys minor* Feifar, 1961, *M.* cf. *reidi* Hinton, 1910, *Prosiphneus praetingi* (Teilhard, 1942), *Canis* cf. *chihliensis minor* Teilhard & Piveteau, 1930, *Nyctereutes* cf. *sinensis* (Schlosser, 1903), *Hyena* cf. *licenti* Pei, 1934, *Euryboas* sp., *Felis* (*Lynx*) *shansius* Teilhard, 1945, *Acinonyx sp*., *Hipparion houfenense* Teilhard & Young, 1931 and others (Vangengeim, 1977; Bazarov *et al*., 1976). The species composition of the fauna shows that landscapes of Western Transbaikalia were rather mosaic. However, forest-steppe landscapes of savanna type were prevailing. Climate was arid and moderately warm, but not sharply arid (Ravskii *et al*., 1964).

The population of marmots was extremely low in the fauna of the Itantsa complex of the Middle Pliocene time (middle Villafranchian). Only single fossil records of these animals are known in this period. Ground squirrels dominated among rodents. They were represented by the species of the subgenera *Urocitellus* and *Spermophillus* and composed up to 60% of total number of small mammals. True horses of the genus *Equus* for the first time appeared in the fauna of the Itantsa complex as well as the voles of the genus *Clethrionomys* and jerboas among rodents. Landscapes continue to be mosaic, steppe-like pine forests with a mixture of cobnut, oak and elm. Amidst herbaceous vegetation wormwood dominated, fat-hen, Gramineae, Compositae and others occurred. On the mountain' foothills the mountain steppes and forest steppes were widely distributed (Belova, 1985).

Fossil remains of marmots of the Early Pleistocene in the Western Transbaikalia are unknown. It is related, perhaps, to the taphonomic conditions of localities or to the incompleteness of fossil record, or marmots were actually extremely rare at that time in Transbaikalia. However, remains of *Marmota* sp. have been found southward in Northern Mongolia in the Early Pleistocene fauna in the locality Nalaikha (bed 6). A marmot was found together with remains of *Ochotona* sp., *Spermophilus* sp. and *Allactaga* sp. Faunal composition of this site and palynologic data evidence for distribution of motley grass meadow steppes and woodless areas on the slopes of valleys at this time (Zhegallo *et al*., 1982).

Extending cooling and aridization of climate resulted in a wide distribution of dry steppes and semi-deserts at the territory of Western Transbaikalia in the Middle Pleistocene. Fauna of mammals of this time was represented by Tologoi complex, including two species of the genus *Ochotona*, *Marmota sibirica nekipelovi* Erbajeva, 1966, *Spermophilus (Urocitellus) gromovi* Erbajeva, 1966, *Allactaga sibirica transbaicalica* Erbajeva, 1966, *Eolagurus simplicidens* (Young, 1934), *Ellobius tancrei* Blasius, 1884, *Meriones unguiculatus* Milne-Edwards, 1867, *Lasiopodomys brandti* (Radde, 1861), *Myospalax wongi* (Young, 1934), *Microtus gregalis* (Pallas, 1779), *Microtus fortis* Büchner, 1889, *Equus sanmeniensis* Teilhard & Piveteau, 1930, *Coelodonta tologoijensis* Beljaeva, 1966,*Spirocerus* cf.*peii* Young, 1932 and others. Faunal composition and quantitative proportion of the species indicate dominance of inhabitants of dry steppe and semi-desert landscapes, although the representatives of desert and meadow-steppe habitats were also present. The climate at that time was rather dry and continental.

In the Late Pleistocene due to the further extending of climate continentality periglacial arid steppes became widely distributed, which appeared to be the most favorable for marmot habitat. At this time fossil records of marmots are known everywhere on the vast territory of Western Transbaikalia (Fig. 1). The data on periglacial expansion of marmots in the Eastern Europe are provided in works of Zimina & Gerasimov (1970) and Gerasimov & Zimina (1973).

Humidification and warming of climate at the end of the Pleistocene resulted in decrease of open areas and developing of forest-steppe landscapes of the recent type. In the Holocene related to the decrease of open areas and developing of forest-steppe landscapes of the modern type the northern border of the *M. sibirica* range shifted significantly to the south up to 52º N which is its current limit (Fig. 1).

Review of extinct marmots of Transbaikalia

Two extinct species were described previously in the fauna of Western Transbaikalia: a Middle Pliocene marmot *M. tologoica* Ivanijev, 1966 from the Tologoi 1 locality (Ivan'ev, 1966) and a Middle Pleistocene *M. sibirica nekipelovi* Erbajeva, 1966, known from the Dodogol 3 locality (Erbaeva, 1966). During the last 30 years a rich material on this group was gathered in the territory of Western Transbaikalia. Preliminary analysis of this material showed that several taxa of subspecies rank of *M. sibirica* and, possibly, of *M. camtschatica* could be distinguished. Detailed investigation of these taxa is the task of the nearest future. Fossil remains of marmots are represented mostly by fragments of low jaws and postcranial bones and isolated teeth. Almost complete skeletons are met rarely. Distribution of fossil records of marmots in Western Transbaikalia is shown in Fig.1. Analysis of these materials allows us to study morphological changes in the structure of the skeleton and dentition in time and to trace the development of this group of mammals in the Western Transbaikalia from the Middle Pleistocene till Recent. New Pliocene and Middle Pleistocene materials of better preservation than known before allow us to give more detailed morphological description and to specify diagnosis both of Tologoi and Nekipelov's marmots from the localities Tologoi 1 and Dodogol 3.

Institutional abbreviations. GI — Geological Institute of the Siberian Branch of the Russian Academy of Sciences, Ulan–Ude; ZIN — Zoological Institute of the Russian Academy of Sciences, Saint-Petersburg.

Order Rodentia Bowdich, 1821

Family Sciuridae Fischer, 1817

Genus *Marmota* Blumenbach, 1779

Marmota tologoica Ivanijev, 1966

Fig. 4A—C.

Marmota tologoica sp. nov.: Ivan'ev, 1966: 174.

Holotype. ZIN 82783, deformed skull with incomplete tooth row. Collector L.N. Ivan'ev.

Type locality. Tologoi 1, Western Transbaikalia; red beds of Chikoi Formation, Middle Pliocene.

Revised diagnosis. A marmot similar in size with a recent *M. sibirica*. The skull is comparatively narrow, posterior incisor foramens are deep, sagittal ridge short and low even in old individuals. The central ridge in P3 is not wide and does not reach the lingual crown edge; anterior cingulum is poorly pronounced or absent, the platform of the anterior cingulum is absent.

Material (GI collection). Two imperfect skulls, fragments of the left dentary with p4–m1, right dentary with m1–3. Isolated teeth: single left P3, P4, M3 and right M1, M2; two right p4 2; three left dP4. Single fragments of humerus and ulna. Collectors M.A. Erbaeva and N.V. Alekseeva, 1993.

Description. Skull. The total length is 100; the length from the upper incisor alveolus to the occipital condyle is 83.

The axial skull is not massive, comparatively wide in postorbital area. The zygomatic arches as can be judged from the remaining left arch were rather widely arranged. The dorsal profile of the skull is flattened. The upper incisors are not massive, comparatively wide without a longitudinal fissure on the anterior surface. They are directed vertically down and inclined somewhat backward to the diastema region. The frontal bone is short and wide. The upper edges of the orbit are comparatively high lifted over the frontal bone. The supraorbital processes are not massive, slightly acute, their tips somewhat lowered. Parietal bones are elongated, their ridges are comparatively long, and they have lyriform contours and joining together at a small distance from the occipital bone form a short and low sagittal ridge. In the area of conjunction of parietal bones and occipital the powerful lambda ridge is formed. The auditory bullae are not large, their length exceeds the width. Suborbital tuber of the maxillary bone is rather large, stretching forward outside posterior edge of the large infraorbital foramen that has a form of equilateral triangle. Incisor foramens are of a small size. The palate bone is long, the distance between P3 significantly exceeds that between M3. Foramens on the palate bone are very small. Choanae in the anterior part are significantly wider than in posterior.

Dentition. Upper teeth are comparatively large, low crowned. Thus, alveolar length P3–M3 23.4, crown length

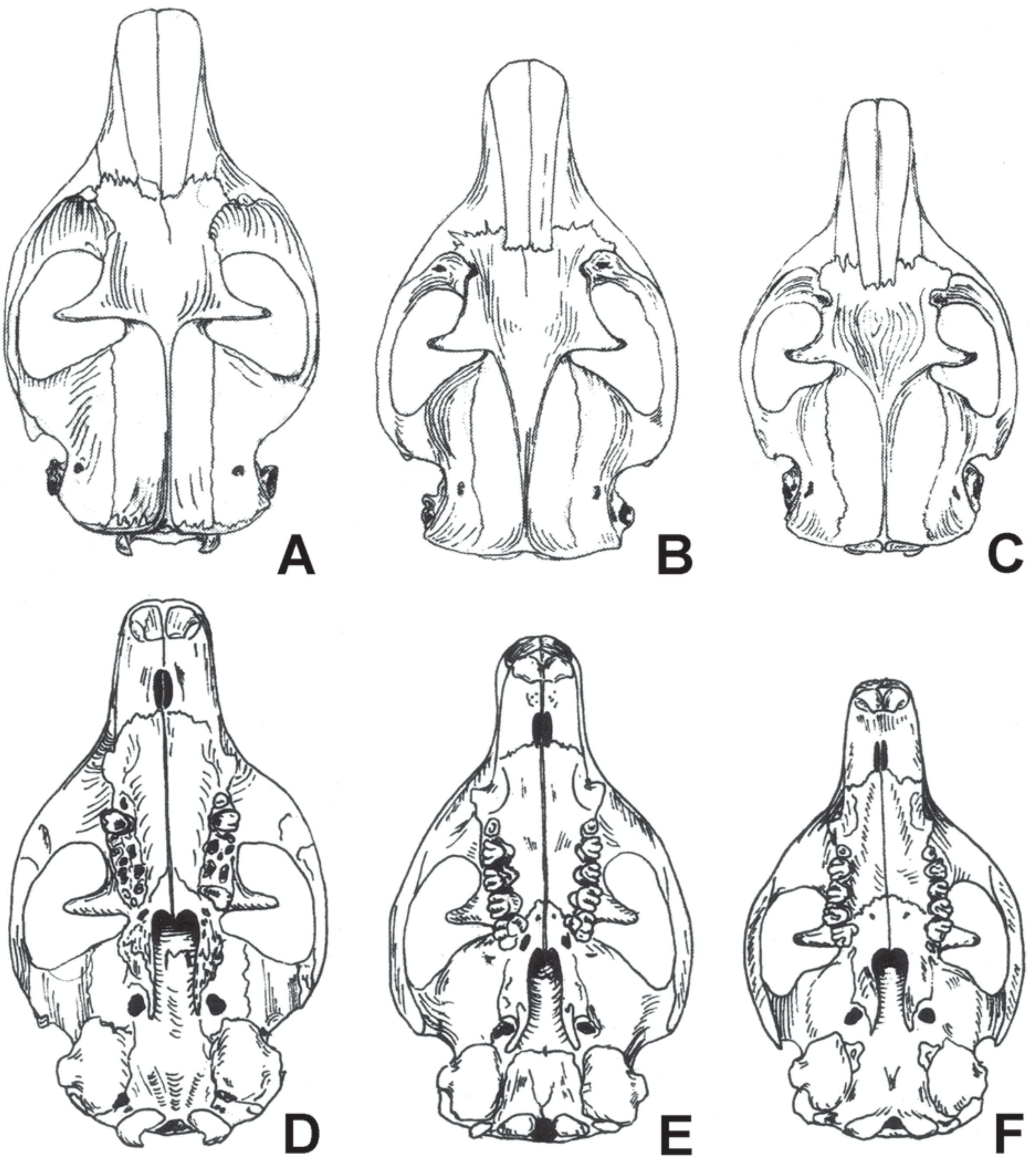

Figure 2. Skulls of Middle Pleistocene *Marmota sibirica nekipelovi* Erbajeva, 1966 from Dodogol 3 (A, D), Recent *M. sibirica sibirica* Radde, 1862 (B, E) and *M. camtschatica doppelmayri* Birula, 1922 (C, F) in dorsal (A, B, C) and ventral (D, E, F) views.

P3–M3 22.0. P3 as well as other teeth is large, with one cusp, posterior cingulum large, its platform wide and along the inner edge of the tooth continues to the anterior half of the tooth. On the posterior ridge (metastyle) P4, M1 and M3 have two metaconule separated to a different degree; posterior and anterior cingula of these teeth are rather well developed. The base of M3 is significantly narrower (Fig. 4A) than anterior margin and elongated both in *M. tologoica* and recent *M. camtschatica doppelmayri*. Posterior ridge of this tooth (metastyle) is long, goes parallel to the anterior ridge from the lingual edge of the tooth towards the labial edge, and then at the level of the middle of the crown the ridge turns backwards almost on 90º and goes to the posterior edge of the tooth. Metaconule remains in a form of an elongated narrow islet. Posterior cingulum of this tooth is small. According to the personal communication of G.I. Baranova, the holotype

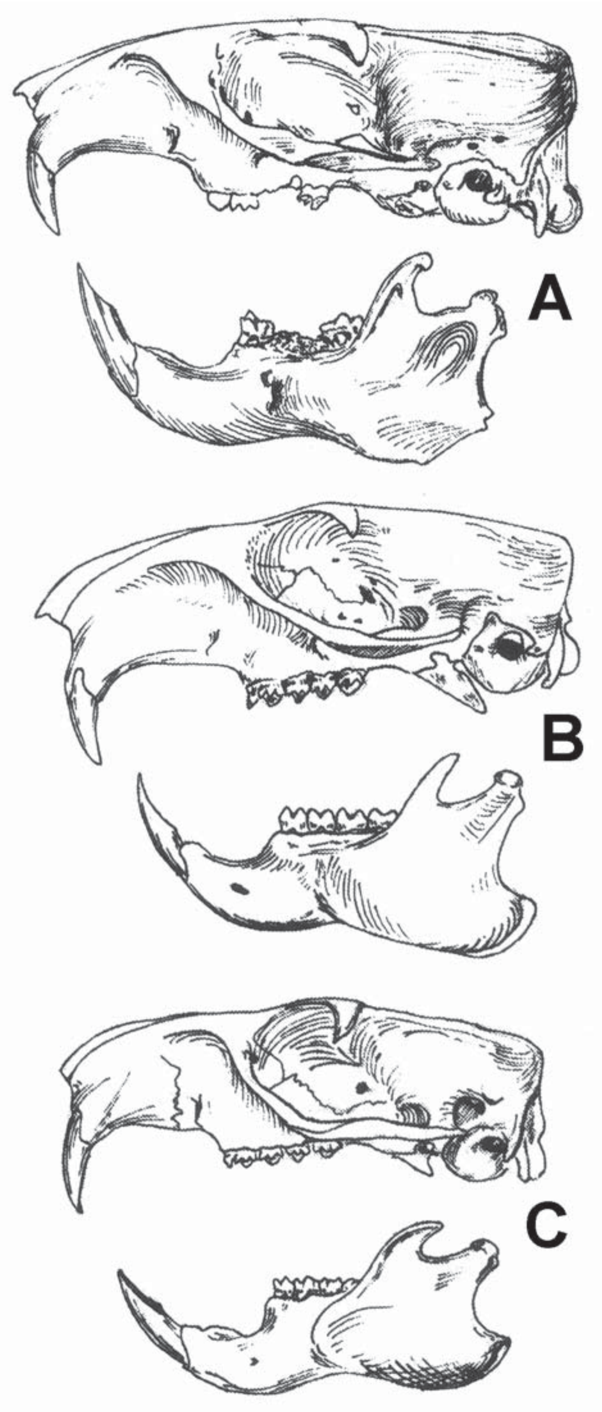

Figure 3. Skulls of Middle Pleistocene *Marmota sibirica nekipelovi* Erbajeva, 1966 from Dodogol 3 (A), Recent *M. sibirica sibirica* Radde, 1862 (B) and *M. camtschatica doppelmayri* Birula, 1922 (C) in lateral view.

on M3 has "metastyle clearly directed to the labial edge but not backwards". This character of the holotype should be checked in the future. Here the additional description of *M. tologoica* is based on new material at author's disposal.

p4, possibly, belongs to semi-adult individuals, cusps of both teeth are not worn, and according to classification of Mashkov & Kolesnikov (1990) marmots with teeth wear of this type are referred to the group that survived only one winter (yearlings). The length of the tooth exceeds its width. At the anterior edge of the tooth there is clearly pronounced cusp that connecting with metaconid and paraconid forms a shallow funnel-shaped depression. Metalophid on this tooth same as with m2 and m3 is not developed, but the hypoconid is well developed; it projects significantly labially. On the lingual crown edge there is clearly pronounced but not high mesostylid present as well in m1 and m2. On m1 there is a poorly pronounced metalophid formed by short ridges that pass from the paraconid and metaconid to the middle of the tooth. The latter do not join each other but form a shallow depression of trigonid that connected with talonid.

Comparison and remarks. *M. tologoica* shows some similarity in size and structure of the skull with a recent *M. sibirica* that allowed Gromov (in Gromov *et al*., 1965) to suppose that the extinct *M. tologoica* is, probably, ancestral form of the recent *M. sibirica*. The study of the new material that is significantly better preserved than the holotype allowed us to carry out more detailed morphological analysis and to discover unexpectedly in a Pliocene form characters typical of *M. camtschatica doppelmayri* (Figs. 2C, F; 3C). These are well developed post-incisor depressions in the palate, poorly developed central ridge in P3 that goes up to the middle of the tooth's width and practically total lack of anterior cingulum and platform. Unlike the extinct Tologoi marmot in the Recent *M. sibirica* the central ridge of this tooth goes along the whole its width from the outer to inner surface. *M. tologoica*, *M. camtschatica doppelmayri* (Fig. 4D) and *M.* aff. *camtschatica* from the Zasukhino II_3 locality (Fig. 4E) show significant similarity also in the structure of M3.

These data evidence for that in the Transbaikalian fauna of the Middle Pliocene occurred marmots, which were morphologically more close to the Transbaikalian *M. camtschatica* but not the steppe species, *M. sibirica*.

It could be supposed that the ancestral forms of *M. camtschatica doppelmayri* that now inhabits the mountains of Northern Baikal initially inhabited plains and later in the Pleistocene due to the gradual elevation of Baikal ridges became mountain-dwellers. Perhaps initially it were not high mountains and then more high and gradually they became widely distributed along Baikal ridges. It could be also supposed that Transbaikalian Pliocene marmot from the Tologoi 1 locality could be ancestral form for both recent Transbaikalian forms. In the fauna of the beginning of Middle Pleistocene (locality Tologoi 2.4) isolated teeth of extinct marmots possessing individual characters typical both of *M. sibirica* and *M. camtschatica* and forms with mixed characters have been found. It could be supposed that at the end of the Pliocene – beginning of Pleistocene in relation to dramatic changes of environment and climate an essential change in biota took place. The latter in its turn caused adaptive radiation of many mammals, including Pliocene marmots. Divergence in marmot group, possibly, had taking place that resulted later in formation of Transbaikalian recent forms. In early studies (Byalynitskii-Birulya, cited after Ognev, 1947) morphological similarity of *M. camtschatica doppelmayri* and *M. sibirica* was emphasized. Occurrence of common endoparasite species in *M. sibirica* and *M. camtschatica doppelmayri* may serve as an indirect evidence for their relationships (Nekrasov *et al*., 1996).

Geological age. Middle Pliocene (early Villafranchian).

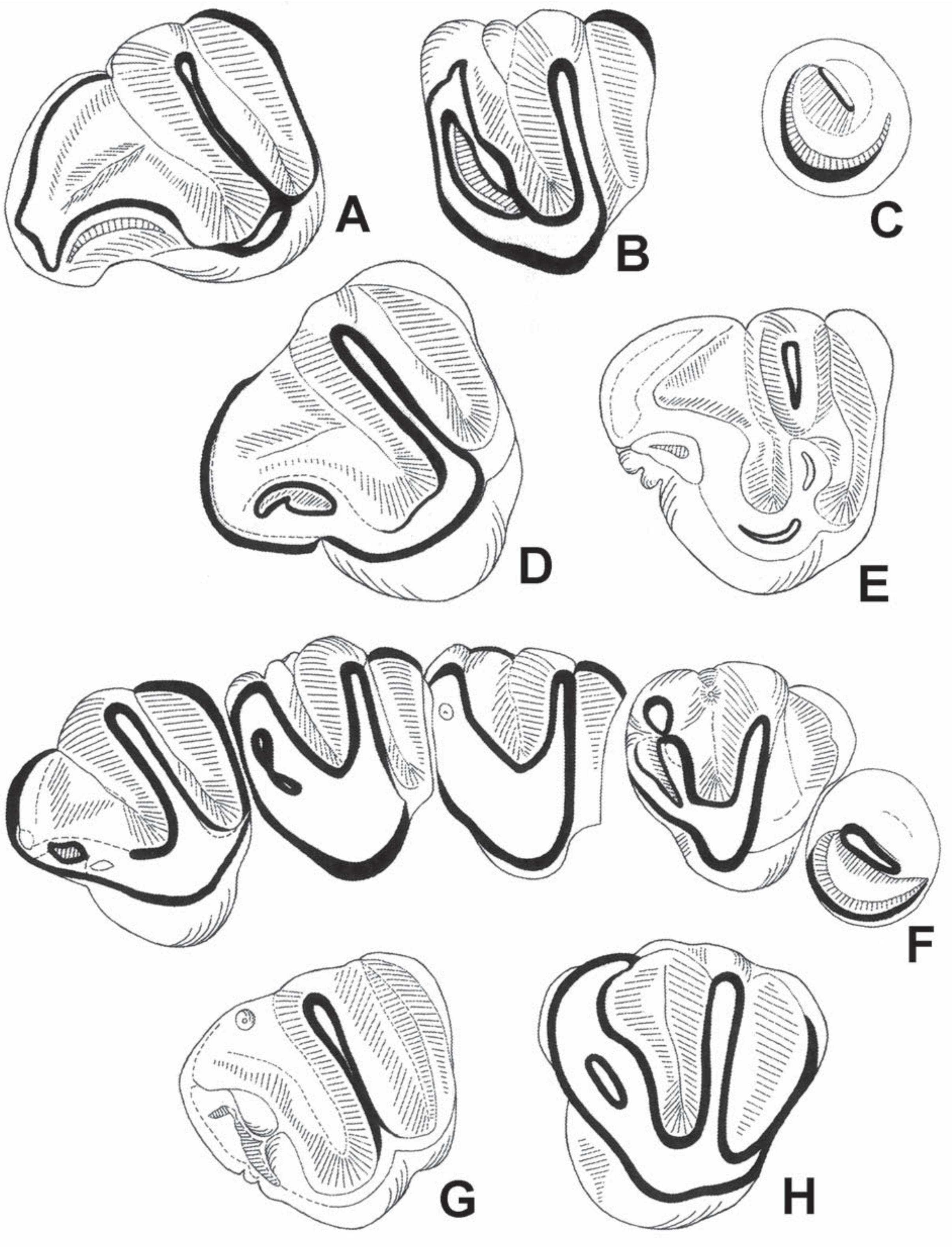

Figure 4. Right upper dentition of Middle Pliocene *Marmota tologoica* Ivanijev, 1966 (A — P3, B — M1, C — M3) from Tologoi I, Recent *M. camtschatica doppelmayri* Birula, 1922 (D — M3), Middle Pleistocene *M.* aff. *camtschatica* from Zasukhino II_3 (E — M3), Middle Pleistocene *M. sibirica nekipelovi* Erbajeva, 1966 from Dodogol 3 (F — P3-M3), Middle Pleistocene *M.* cf. *sibirica* from Tsezhe (G — M3), and Recent *M. sibirica* (H — M3) in occlusal view.

Marmota sibirica nekipelovi Erbajeva, 1966
Figs. 2A, D; 3A.

Marmota sibirica nekipelovi sp. nov.: Erbaeva, 1966: 96.

Holotype. ZIN 51350, right dentary fragment with complete toothrow. Collector M.A. Erbaeva, 1963.

Type locality. Dodogol, Western Transbaikalia; Middle Pleistocene.

Revised diagnosis. Distinguished by large size among all Transbaikalian marmots both extant and extinct. Post incisor foramens are poorly developed. The sagittal ridge is long and high. Metastyle on M3 is located under an angle to the anterior ridge and goes backwards parallel to the posterolingual edge of the tooth. P4 has a well developed anterior intermediate cusp and funnel-form depression.

Material (GI collection). Two left dentaries, three fragments of maxilla with a various number of teeth, isolated teeth, almost complete skull with a completely worn teeth (according to classification of Mashkov & Kolesnikov (1990) correspond to an individual of eight or more years old), dentary, postcranial bones. Dodogol 3 locality. Collectors M.A. Erbaeva and N.V. Alekseeva, 1993.

Description. The axial skull (Fig. 2A, D) is of large size, rather massive, with wide zygomatic arches, narrow in postorbital area. Condylobasal length is up to 106. The dorsal profile of the skull is flattened (Fig. 3A), its occipital part is located almost perpendicular to the surface, in the base of the skull only occipital condyles project backwards. The massive upper incisors with marks of longitudinal grove on the anterior surface directed vertically downwards and somewhat inclined backwards to diastema part. The nasals are long, their width at the base at the border with frontal bone almost twice less than in the anterior part. The frontal bone is wide and short. The upper edges of the orbit are lifted and the tips of supraorbital processes are slightly dropped. Supraorbital processes are thin, pointed. Parietal bones are long and comparatively narrow, their outer edge go practically parallel. Parietal ridges are dramatically narrowing backwards and at the distance of one quarter of the parietal bone length uniting and form a long and high sagittal ridge. In the area of connection of parietal and occipital bones a powerful lambda ridge is forming. The outer part of auditory processes of temporal bone strongly dropped down. Occipital bone in its middle part above the occipital foramen is concave, the edges of jugular processes arranged almost at one level with a lower edge of bullae. The auditory bullae are not large; their length exceeds the width, auditory foramens are large. Infraorbital tubercle of maxilla is large, distinguishes beyond posterior edge of large infraorbital foramen, which has a form of equilateral triangle. Incisor foramens are of small size. Palate bone is long, the distance between P3 significantly exceeds such between M3. Foramens on the palate bone are of small size. Unlike in recent *M. sibirica* choanae in the anterior part are wider than in the posterior half (Fig. 2D, E).

Dentary has a relatively short and high incisive portion. The dorsal edge of the incisive portion is elevation at the symphysis and forms a small depression dorsally. The lower incisors are relatively narrow transversely and elongated in anteroposterior direction. On the labial dentary side under m1 at the anterior border of masseteric fossa there is a quite large tubercle. The dorsal margin of large and wide condylar process is placed below the relatively high and vertically oriented coronoid process. The condylar head is medially deflected and bears a small depression at the base laterally. The angular process is relatively weakly rotated medially. The angular incisura is shallow.

Dentition. The teeth are comparatively high crowned. P3 is large, in young individuals slightly two-cusped, the inner cusp is small and located under the outer. The cusps fuse with attrition forming a wide central ridge (Fig. 4F). P3 lacks anterior cingulum; the posterior cingulum is well developed and a wide posterior platform is present. P4 as well as other teeth is of large size, its anterior cingulum is narrow, rather well developed anterior platform is present. Posterior cingulum and platform are rather well developed. Metaconule on P4-M2 is rather well separated. On the occlusal surface of M3 there are two ridges, posterior of them (metastyle) goes under an angle to the anterior and parallel to posterolingual edge to the base of the tooth. Unlike *M. tologoica* and *M. camtschatica doppelmayri*, the posterior half of M3 in *M. sibirica nekipelovi* is comparatively short, not so elongated in anterior-posterior direction and significantly wider. Posterior cingulum is poorly pronounced. p4 is of large size, in young individuals the length of the teeth exceeds the width, and not to the same degree in adults. The anterior intermediate cusp of this tooth connecting with paraconid and metaconid forms a rather pronounced funnel-like depression. Both m1 and m2 are slightly compressed in anterior-posterior direction. Metalophid on the m1 is well developed, it completely separates trigonid from the talonid and hypoconid strongly protrudes labially. The m3 is of large size, its anterior width significantly exceeds posterior.

Comparison and remarks. Differences of *M. sibirica nekipelovi* from the Recent Siberian marmot were pointed out in the original description. Discovery of an almost complete skull of this extinct taxon in the type locality revealed additional distinctions: its larger size, more wide frontal anteriorly, long nasal bones, wide anteriorly and narrow at the base. In the recent *M. sibirica* (Fig. 2B) edges of the nasal bones are weakly broadened anteriorly and goes parallel, especially in the posterior one third. Moreover, the extinct taxon has a long and high sagittal crest (Fig. 2A), which is significantly shorter and lower in the Recent species (Fig. 2B). Among the extinct Pleistocene marmots from Western Transbaikalia the closest to *M. sibirica nekipelovi* in size and some morphological characters is the Middle Pleistocene marmot from Zasukhino II_3 and Ust'-Obor. These differs from the former by subtle details. Thus, marmot from Ust'-Obor has a massive and wide skull, large-sized orbits, wider frontal bones and massive, weakly pointed supraorbital processes.

Middle Pleistocene marmot remains are known from some other localities in Western Transbaikalia (Fig. 1). It can be supposed, that during this time the formation of Recent species began: *M. sibirica* and *M. camtschatica doppelmayri*. In the Late Pleistocene Zasukhino X locality, located north to Ulan-Ude, remains of marmots with the prevailing characters of *M. camtschatica doppelmayri* were found. In marmots lived more south, known from the localities Dodogol 4 on Uda River, Tsezhe in Dzhida District (Fig. 4G), Malaya Kudara and Ust' Kyakhta 17 in the south of Transbaikalia, characters of *M. sibirica* prevailed. However, every of these forms preserve some characters characteristic for *M. camtschatica doppelmayri*.

In Western Transbaikalia marmots were mostly distributed in Late Pleistocene, when periglacial environments were established there as in other parts of Eurasia. In Eastern Transbaikalia marmot remains are not known. In this period dry woodless wormwood steeps were widely distributed. Zonal steeps reached Yakutia in the north (Giterman & Golubeva, 1965). Palynological data indicate predominance of the pollen of not-woody plants in the deposits of this time. Especially abundant were xerophytes: wormwood, saltbush, ephedra, cereals, and Compositae. Scant distribution had dwarf birch (Ravskii *et al*., 1964). Possibly, this time was the most favorable for marmots, because they range at that time covered vast territory from the Itantsa River valley (localities in the vicinity of Zyryansk settlement and Zasukhino 5, 6) in the north, country between the rivers Chikoi and Khilok in the east and Dzhida River valley in the south-west. In this region there are numerous localities with marmot remains (Fig. 1). In the Southern Transbaikalia most records of the extinct marmots is within the Recent range. It is worthy to point that marmot remains from Zyryansk locality in Itantsa River valley in the structure of p4 is most similar with *M. sibirica*. This form is referred preliminary as *Marmota* cf. *sibirica*. It is probably that this region was the northern limit of *M. sibirica*. This species did not penetrate the Barguzin Depression, which was inhabited by other representatives of open steppe and semi-desert landscapes, such as Siberian jerboa, Brandt's vole, steppe lemming, and Daurian pika. These species occurred much north than marmot, up to N 54°. These observations support data by Giterman & Golubeva (1965) who noticed that zonal dry steppes in the Late Pleistocene were distributed much further to north relative to their modern limits, which is also indicated by paleobotanical data (Vipper, 1962). Uplift of circum-Baikal mountain ranges in Pleistocene, possible, divided formerly united territory of Transbaikalian steppes, spread to Barguzin depression on the north.

Marmot remains from the Late Pleistocene locality Zasukhino 6 on Itantsa River by structure of p4 are close to *M. camtschatica doppelmayri*, differs from the latter, however, in more massive dentary and larger size. This type of dentary occur in some marmot specimens, close to *M. sibirica*, from the archeological site Ust' Kyakhta 17. A distinct feature of marmots from this locality was a great variability in the structure of dentary and especially in the structure of p4. Perhaps, Late Pleistocene marmots of Western Transbaikalia preserved some archaic characters of Pliocene taxa, common to both *M. sibirica* and *M. camtschatica doppelmayri*. It should be mentioned, that among Holocene forms of *M. sibirica* also some specimens with archaic characters occur.

Conclusion

Analysis of the paleontological materials from Transbaikalia showed that common tendencies in the marmot evolution include progressive development of hypsodonty in dentition, shortening of upper and lower teeth, decreasing of the postorbital constriction in the skull, increasing of the body size during the Pleistocene and its decreasing towards the modern time, with alveolar length of the upper tooth row being almost unchanged (Tab. 1). The oldest marmot from Tologoi I locality differs from the Late Pleistocene forms by smaller size of the skull. However, all Transbaikalian forms, having sufficient differences in the skull size, are very similar in the length of tooth row and proportions of cheek teeth and incisors. Thus, alveolar length of the upper tooth row in the Pliocene marmot from Tologoi 1 is 21.5-23.4, in Dodogol's form is 21.8, in marmots from Ust'-Obor and Zasukhino is 24.0 and 23.7 respectively, and in the Recent species it is 23.2 in average. These taxa do not differ sufficiently in the zygomatic breadth, in the relative length of frontal bones and interorbital space. Possibly, this was connected with live in similar landscapes during the Pleistocene.

A morphometric analysis of skulls, dentaries and teeth of marmots from the Pleistocene localities and its comparison with the Pliocene and Recent taxa allowed to establish that during the marmot evolution in Transbaikalia was a tendency to increase the absolute body size in the Middle and Late Pleistocene and decrease this parameter in the Holocene and Recent time. The similar regularity was observed on the representative material on Brandt's vole, which was on of the dominant species in the faunas of Middle and Late Pleistocene and was distributed in Transbaikalia as wide as marmots.

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Table 1. Skull and dentary measurements of Transbaikalian marmots (*Marmota*).

Measurements, mm	Taxa							
	M. sibirica		*M. camtschatica*		*M. tologoica*		*M. sibirica nekipelovi*	
	n	lim	n	lim	n	lim	n	lim
Condylobasal length	5	85–102	4	85–88	2	100*	2	106
Length from upper incisor alveolus to occipital condyle	5	82–100	4	81.5–84	1	83*	2	92, 93
Interorbital width	5	21–27	4	22.3–23	1	20.8	2	24, 24.5
Length of frontal	5	18.5–22	4	15–16	1	22.3	2	20.5, 25.5
Width of upper incisor	5	2.5–4.0	4	3.56	1	3.3	2	4.2, 4.4
Alveolar length of P3–M3	5	22–23.2	4	20–20.5	1	23.4*	2	21.3–21.8
Crown length of P3–M3	5	20.5–22	4	18–18.5	1	22*	2	21
Length of P3	5	3–3.2	4	2.6	2	3-3.3	2	3.2
Width of P3	5	3.2–3.4	4	2.6–2.7	2	2.8, 2.9	2	3.4, 3.5
Length of P4	5	5–5.2	4	4–4.2	1	4.7	1	5.2
Width of P4	5	4.8–5	4	4–4.2	1	4.5	1	5
Length of M1	5	4.8	4	4	3	4.4–4.7		
Width of M1	5	3.8–5.2	4	4–4.1	3	4.2–4.6		
Length of M2	5	4.7–4.9	4	4	2	4.4–4.8		
Width of M2	5	5.3–5.8	4	4–4.5	1	4.7		
Length of M3	5	5–6	4	5	4	5.2–5.6	1	5.7
Width of M3	5	4.8–6	4	4.5	3	4.7–4.8	1	5.5
Width of lower incisor	5	3.6–4	4	3.3–3.6			3	4.4–4.5
Crown length of p4–m3	5	20–21	4	17–19			2	21, 23.5
Length of p4	5	4.7–4.8	4	4–4.4	2	4.5, 5	4	5–5.4
Width of p4	5	4.6–4.8	4	3.8–4.2	2	4.3	4	4.3–5
Length of m1	5	4–4.3	4	3.7–4.1	1	4.3	1	4.6
Width of m1	5	4.8–5	4	3.8–4.2	1	4.5	1	4.3
Length of m2	5	4.5–4.6	4	3.7–4.4	1	4.8	3	4.5–5
Width of m2	5	5–5.8	4	1–4.2	1	4.8	2	4.8–5.2
Length of m3	5	5.3–5.7	4	4.5–4.8	1	5.3	4	5–5.8
Width of m3	5	5.5–6	4	4.5–4.6	1	2	4	5–6.5

* approximately.

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