# Notes on the genus *Ochotona* in the Middle East (Lagomorpha: Ochotonidae)

Poznámky k rodu *Ochotona* na Blízkém východě (Lagomorpha: Ochotonidae)

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**Abstract**. New records of *Ochotona* from Iran and Turkey are reported. The finding of a bone remain of the Recent age (from the Eagle owl pellet) from Turkey represents the first record of the genus and family in this country and extends the range of the genus in the Middle East by approximately 600 km to the northwest. All new records from Iran belong to *O. rufescens* (Gray, 1842), the only known species in the region. Based on the comparison of the Persian material, the pikas from the Zagros and Kopetdag Mts are similar in size and probably do not represent two different subspecies. The newly reported pikas of the Recent age from the Armenian Highlands of Turkey and Iran slightly differ from those inhabiting the rest of Iran and are reported as *O. cf. rufescens*.

# INTRODUCTION

Only one species of ochotonid lagomorph, the rufescent or collared or Afghan pika, *Ochotona rufescens* (Gray, 1842), is known to occur in the Middle East (i.e. the region comprising Arabia, Iran, and the Asian part of Turkey). Its distribution range covers the mountainous areas of Afghanistan, north-western Pakistan, Iran and south-western Turkmenistan (Ellerman & Morrison-Scott 1951, Gromov & Erbaeva 1995). Concerning the Middle East proper, the Afghan pika has been reported to reach the mountains of Iran.

TAGHIZADEH (1964) and LAY (1967) summarised the distribution of the Afghan pika in Iran. LAY (1967: 151) using the data by BLANFORD (1876), MURRAY (1884), and MISONNE (1956) and his new records, suggested that: "the rufescent pika inhabits all of the mountainous regions of Iran". However, the westernmost Persian record of pika came from the vicinity of Agbolagh Morched, Kurdistan (LAY 1967), in the central Zagros Mts, and represented also the westernmost Recent record of the species. No records have been reported from the western Elborz Mts, the Talysh Mts or from Armenian Highlands, i.e. from all the mountains of the northwestern part of Iran (see Fig. 1 and/or TAGHIZADEH 1964: 25, Fig. 12). The last new records of the Afghan pika from Iran were referred by DE ROGUIN (1988) and OBUCH & KRIŠTÍN (2004), including the easternmost Persian record of the species, from Mount Taftan, Baluchestan.

Although the talus/steppe-dwelling pikas (sensu Smith et al. 1990) are known to be regularly distributed in the mountains from Iran and Turkmenistan to the east, several records of Ochotona have been mentioned from Transcaucasia. However, at least some of them actually are the records of fossil or sub-fossil bone fragments found in cave deposits, and their species affiliation is often not fully convincing. Sosnihina (1947, 1948) reported findings of Ochotona from Armenia; a lower jaw of sub-fossil age from a gorge of the Čirahan River and other bones from the vicinity of the Aknalič Lake. She identified these bone remains to come from pellets of the Eagle owl (Bubo bubo) and specifically attributed both records to O. rufescens according to the geographically nearest known species. Another Armenian records of pikas of sub-fossil age were reported by Dal' (1954, 1957) from caves of the Urcskij Range. However, Dal' (1957)

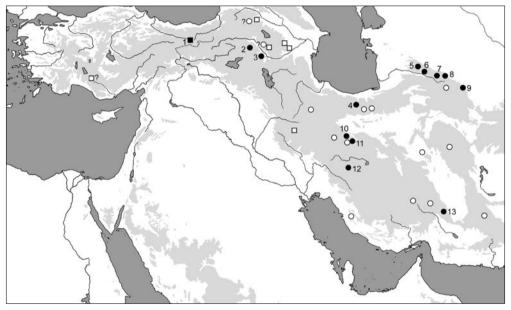


Fig. 1. Records of *Ochotona* in the Middle East and Transcaucasia; numbers correspond with the sites numbered in the list of new records (see the text); squares – fossil or sub-fossil records (of the Upper Bi-harian-Toringian age), circles – Recent records, closed symbols – new records, open symbols – literature data (based on Sosnihina 1947, 1948, Coon 1951, Dal' 1957, Gadžiev & Aliev 1966, Lay 1967, de Roguin 1988, Montuire et. al. 1994, and Obuch & Krištín 2004). For the extralimital data on occurrence of *Ochotona rufescens* in Turkmenistan see Sokolov et al. (1994: 59, Fig. 18), in Afghanistan see Hassinger (1973: 34, Fig. 6), and in Pakistan see Roberts (1997: 310, map 80).

Obr. 1. Místa nálezů pišťuchy (*Ochotona*) na Blízkém východě a v Zakavkazí; čísla odpovídají číslování lokalit v textu (kapitola New Records); čtverce – fossilní, nebo subfossilní nálezy (stáří svrchní bihar až toring), kroužky – recentní nálezy, plné symboly – nové nálezy, prázdné symboly – literární údaje (podle Sosnihiny 1947, 1948, Coona 1951, Dal'a 1957, Gadžieva & Alieva 1966, Laye 1967, de Roguina 1988, Montuireové et. al. 1994 a Obucha & Krištína 2004). Extralimitní rozšíření pišťuchy rezavé (*Ochotona rufescens*) v Turkmenii viz Sokolov et al. (1994: 59, Fig. 18), v Afghanistanu viz Hassinger (1973: 34, Fig. 6) a v Pakistanu viz Roberts (1997: 310, map 80).

placed his own and Sosnihina's records, vernacularly named as an Armenian pika ('armenijska-ja piščuha'), into morphological proximity of *Ochotona eximia* (Khomenko, 1914), described from the Upper Miocene site of Taraklia in Moldavia. Vereščagin (1959) summarised these Transcaucasian records of Armenian pikas as of the Holocene age and considered the 'species' to be extinct in the Recent.

Vekua & Šidlovskij (1958) reported on a record of a large sized ochotonid from the Mousterian, Middle Palaeolithic, of Georgia (Copi Station, Marneuli Dist., E Georgia). Later, based on an additional material from this site, Vekua (1967) described the respective pika as a new species, *Ochotonoides transcaucasica* (now included in the genus *Ochotona*, see below). Another pika species from Transcaucasia, *Ochotona azerica*, is reported from the Acheulean/Mousterian deposits of the Azyh Cave, Azerbaijan (Aliev 1969, Gadžiev et al. 1979). A second Azerbaijan record of *Ochotona* was published by Gadžiev & Aliev (1966) from Taglar, also of the Mousterian age.

All the above mentioned published records of *Ochotona* from Transcaucasia are reported to be of fossil to sub-fossil age (the Upper Biharian-Toringian age *sensu* Fejfar & Heinrich 1983; the Akhalkalaki-Akhstyr faunal units *sensu* Baryshnikov 2002). However, some Transcaucasian records were mentioned to come from the Eagle owl pellets but without specifying their age, i.e. whether they come from fresh pellets or from deposits of bones from supposed owl pelleting places.

VINOGRADOV & GROMOV (1952) suggested possible occurrence of *O. rufescens* in Armenia, based on findings of pika bones in Eagle owl pellets in the Daralegezskij Range, Mikojan [= Ehednadzor] District. Šidlovskij (1976: 72) mentioned: "remains of lower jaws of pikas have been found in the last years in southern Armenia, in the Eagle owl pellets in a cave near the village of Amagu in the Sarajbulagskij Range and in Georgia, on the eastern slope of the Džavahetskij Range (Dmanisi Dist.)" [translated from Russian].

Probably based on these reports, Hoffmann (1993) and Hoffmann & Smith (2005) mentioned Armenia among the countries inhabited by *O. rufescens*. On the other hand, Russian authors (i.e., Ognev 1940, Gureev 1963, 1964, Erbaeva 1988, Sokolov et al. 1994, Gromov & Erbaeva 1995, Pavlinov et al. 1995, Pavlinov & Rossolimo 1998) did not mention any Recent representative of the genus *Ochotona* from Transcaucasia. Moreover, Gureev (1981: 73) wrote in the paragraph concerning *O. rufescens*: "obviously, this species or a species close to it existed in the Caucasus at the end of the Pleistocene" [translated from Russian]. Thus, the occurrence of pikas in Transcaucasia and adjacent regions of the Middle East in the Recent remains indefinite.

Here, we report new findings of *Ochotona* from several parts of the Middle East in attempt (1) to draw the Recent distribution range of the genus in the region of southwestern Asia, and (2) to evaluate morphologic characteristics and systematic status of particular populations of the Middle East.

#### MATERIAL AND METHODS

Erbaeva (1988), Sen (1998), and Čermák (2004). Dimensions and drawings were made using binocular microscope. Measurements are given in millimetres and ratios in percentages.

For comparative purposes, the morphometric characteristics of *O. pusilla* (Pallas, 1768), *O. pallasi* (Gray, 1867), *O. rutila* Severtzov, 1873, *O. macrotis* (Günther, 1875), and *O. roylei* (Ogilby, 1839) provided by Ognev (1940), Gureev (1964), and Erbajeva (1988) were taken into account. The studied material is deposited partly in the collection of the second author (JO), partly in the collection of the Department of Zoology, National Museum, Prague (NMP).

# **NEW RECORDS**

## Turkey

- 3 km SE of Güzyurdu, small cave in a mountain pass, sub-fossil deposite 2A\* (Gümüşhane Prov; 39° 54' N, 39° 34' E, ca. 2300 m a. s. l.), 15 September 1995, isolated right M¹ and a fragment of left maxilla of *Ochotona* cf. pusilla collected, leg. I. Horáček.
- Ishak Paşa Sarayi, 6 km E of Doğu Bayazit, rock outcrop (Ağri Prov.; 39° 31' N, 44° 08' E, ca. 1950 m a. s. l.), 1 October 2002, right mandible of *Ochotona* cf. rufescens (NMP 90157) from a pellet of *Bubo bubo* collected, leg. J. Obuch.

#### Iran

- Bastam, 10 km W of Qarah Ziya'oddin, archaeological site (Azerbaijan Gharbi Prov., 38° 53' N, 44° 58' E, ca. 1250 m a. s. l.), 30 September 1998, right mandible of *Ochotona* cf. rufescens (NMP 90156) from a pellet of *Bubo bubo* collected, leg. J. OBUCH.
- rocks above Gazanak (Mazandaran Prov., 35° 55' N, 52° 15' E, ca. 1650 m a. s. l.), 15 May 1997, remains of three inds. of *Ochotona rufescens* from pellets of *Bubo bubo* (one left and three right mandibles, two maxillar fragments) collected, leg. J. OBUCH.
- 5. 3 km E of Tangeh, 10 km SW of Raz (Khorasan Shamali Prov., 37° 54' N, 56° 56' E, ca. 1200 m a. s. 1.), 12 May 1997, several colonies of *Ochotona rufescens* observed, five individuals caught, an adult male (NMP 90153 [S+A]), sub-adult male and a female (NMP 90154, 90155 [A]) collected, leg. P. Benda, J. Sádlová & R. Šumbera.
- 6. Qarloq, 15 km W of Bojnurd (Khorasan Shamali Prov., 37° 30' N, 57° 26' E, ca. 890 m a. s. l.), 12 May 1997, remains of five inds. of *Ochotona rufescens* from pellets of *Bubo bubo* (four left and five right mandibles, fragments of five skulls) collected, leg. J. OBUCH.
- 7. two rocky valleys ca. 2 and 5 km E of Emam Qoli, ca. 30 km N of Quchan (Khorasan Razni Prov.; 37° 22' N, 58° 32' E, ca. 1710 m a. s. l.), 11 May 1997, remains of 30 inds. of *Ochotona rufescens* from pellets of *Bubo bubo* (30 right and 30 left mandibles, remains of 16 skulls), leg. J. OBUCH; several colonies of *O. rufescens* observed, one individual caught, leg. J. SADLO; 25 May 2006, colonies of *O. rufescens* observed, leg. A. REITER (cf. Fig. 2).

<sup>\*</sup>Güzyurdu 2A: surface layer of a loamy debris infilling of a narrow karstic fissure in a small rock overhang ca. 3 km SE of the Güzyurdu village which provided the following assemblage (MNI): 1 ind. of *Bufo* cf. *viridis*, 1 *Rana* cf. *temporaria*, 1 *Lacerta* sp., 1 Aves indet., 1 *Erinaceus* sp., 1 *Spermophilus* cf. *xantho-prymnus*, 1 *Apodemus* cf. *uralensis*, 3 *Mesocricetus* cf. *brandtii*, 2 *Cricetulus migratorius*, 1 *Allactaga* cf. *williamsi*, 1 *Arvicola* cf. *terrestris*, 4 *Chionomys nivalis*, 7 *Microtus* cf. *obscurus*, 2 *Microtus* cf. *subterraneus*, 3 *Spalax* sp., 1 *Ochotona* cf. *pusilla*, 1 *Lepus* sp. The sample obtained from the lower layer of the infilling was of a similar composition (except for *Ochotona*, *Spalax*, and *Erinaceus*). The bones exhibit signs of fossilisation and undoubtedly are not of the Recent age. Tentatively, the assemblage is considered to be of the Holocene age (I. HORÁCEK in litt.). The accompanying species do occur in a wider surroundings of the site even recently (cf. e.g. Kryštufek & Vohralík 2001).

- 8. dry valley ca. 5 km S of Mina, ca. 25 km SW of Dargaz (Khorasan Razni Prov.; 37° 18' N, 58° 58' E, ca. 1075 m a. s. l.), 22–23 May 2006, a colony of *Ochotona rufescens* observed, leg. A. Reiter.
- 9. rocks 12 km E of Bazangan, 18 km NNW of Mazdavand (Khorasan Razni Prov., 36° 17' N, 60° 33' E, ca. 650 m a. s. l.), 11 May 1997, remains of 16 inds. of *Ochotona rufescens* in pellets of *Bubo bubo* (14 right and 16 left mandibles, fragments of 9 skulls) collected, 8 October 2002, remains of 11 inds. of *O. rufescens* from pellets of *Bubo bubo* (7 right and 11 left mandibles) collected, leg. J. OBUCH.
- 10. wadi under Emam Sadeh, ca. 12 km W of Kashan (Esfahan Prov., 33° 59' N, 51° 17' E, ca. 1130 m a. s. l.), 6 April 2000, a fragment of a left mandible of *Ochotona rufescens* from a pellet of *Bubo bubo* collected, leg. J. OBUCH.
- 11. Deh Zireh, 25 km NNW of Natanz (Esfahan Prov., 33° 46' N, 51° 42' E, ca. 850 m a. s. l.), 27 April 1996, remains of five inds. of *Ochotona rufescens* from pellets of *Bubo bubo* (three left and four right mandibles, remains of one skull) collected, leg. J. OBUCH.
- 12. Qamishlu, ca. 40 km W of Shahreza (Esfahan Prov., 32° 02' N, 51° 29' E, ca. 2200 m a. s. l.), 28 April 1996, remains of one skull and two mandibles (right and left) of *Ochotona rufescens* from a pellet of *Bubo bubo* collected, leg. J. OBUCH.
- 13. 5 km NE of Deh Bakri, ca. 40 km W of Bam (Kerman Prov., 29° 05' N, 57° 56' E, ca. 1930 m a. s. l.), 7–8 April 2000, remains of two inds. of *Ochotona rufescens* from pellets of *Bubo bubo* (two left mandibles and one right mandible, fragments of one skull) collected, leg. J. OBUCH.



Fig. 2. A valley at Emam Qoli, ca. 30 km N of Quchan, Kopetdag Mts, northeastern Iran. Rocky slopes represent a typical habitat abundantly dwelled by *Ochotona rufescens* (photo by A. Reiter). Obr. 2. Horské údolí nedaleko Emam Koli, asi 30 km na sever od města Kučan, pohoří Kopetdag, severovýchodní Írán. Skalnaté svahy údolí vytvářejí biotop hojně obývaný pišťuchou rezavou (*Ochotona rufescens*) (foto A. Reiter).

#### NOTES ON BIOGEOGRAPHY

New records of *Ochotona* of the Recent age from the Middle East come from five sub-regions (see Fig. 1); (1) northeastern Iran, the range of the Kopetdag Mts along the border with Turkmenistan [records Nos. 5–9]; (2) southeastern Iran, the easternmost extent of the Zagros Mts in the Kerman Province [13]; (3) central Iran, central parts of the Zagros Mts and northern part of the Qohrud Range [10–12]; (4) central Iran, central part of the Elborz Mts [4]; (5) the border region of Iran and Turkey, the eastern part of the Armenian Highlands [2, 3].

Most of the new records come from Iran, where they cover mainly the known distribution range as described by Lay (1967). They come from all main mountainous areas of the Iran Plateau, including the central Persian mountains (Zagros Mts, Elborz Mts, Qohrud Mts) as well as the southeasternmost parts of the Zagros system, the Jebal Barez Mts, bordering the Baluchestani deserts. Records from the latter area were given already by Lay (1967) and DE ROGUIN (1988). Only one record has been published before from the Persian side of the Kopedag Mts (Akhlamad, Khorasan Razni Prov.; MISSONE 1956). Newly reported data suggest the occurrence of *O. rufescens* in the whole main range of these mountains, similarly as it is known from the Turkmen part of the region (Sokolov et al. 1994).

The new records of pikas from the border area between the northwestern corner of Iran and eastern Turkey [2, 3] are of particular significance because the extant representatives of the family had not been reported from this region before (see e.g. Lay 1967, Kumerloeve 1975). In Turkey, the finding at Ishak Paşa Sarayi represents the first record of the genus and family in this country (Kumerloeve 1975, Krystufek & Vohralík 2001). The pika jaw was obtained from a pellet of the Eagle owl, at the site where material from pellets had been collected at least three times before, during visits in April 1996, April 1997, and September 1998, and no remnants of *Ochotona* were found. The Recent age of this finding is therefore undoubted and possible confusion with fossil or sub-fossil material is unlikely. Concerning the Iran side of the region, one pika record comes from Bastam, an archaeological site used as a rest place by the Eagle owl. These records shift the known Recent distribution range of the genus *Ochotona* some 600 km to the northwest and verify the Recent distribution of this genus in the Caucasus region (see the Introduction chapter). Moreover, they suggest that the records from Transcaucasian countries formerly considered as of rather uncertain age may also be of the Recent age (see Fig. 1).

The other Turkish finding of *Ochotona* [record No. 1] comes from a sub-fossil deposition and its interpretation as an extant occurrence of pika in central Anatolia is irrelevant.

#### NOTES ON MORPHOLOGY

The ochotonid material collected in various parts of the Middle East is quite homogenous in morphology and dimensions. It is represented by a large sized pika (alveolar length  $P_3$ – $M_3$ : X=9.33, n=27; alveolar length  $P^2$ – $M^2$ : X=8.97, n=14) with a relatively long and low mandible (MR: X=59, n=27). The lower incisors extend to below the area between  $P_4$  and  $M_1$ . The posterior mental foramen is located ventrally to  $M_3$ , or even more posteriorly. The skull is narrow. Frontal bones with well-developed crests form the a narrow interorbital region. The relatively short rostrum possesses a large preorbital foramen of the triangular type. Nasal bones are wider anteriorly than posteriorly. The incisive-palatal foramen is not closed.

Third lower premolars (P<sub>3</sub>; 9 specimens), the most characteristic teeth, are available almost only in non-adult stages; based on the morphology, they belong to not overwintered animals younger than 4 months (*sensu* Lissovsky 2004). These permanent teeth are worn, nevertheless

they still retain their conical structure. So, occlusal dimensions and morphology of the tooth (the main diagnostic features) are not stable during conversion of the crown to its definitive prismatic state, therefore evaluation of demonstrative conclusions is difficult. Differences between occlusal and root morphologies are shown on Fig. 3 (1–4, 1a–4a). Only in one tooth, a well developed lingual fold divides the posteroconid and forms a three-segmented juvenile appearance of the tooth (Fig. 3: 5).

Owing to the hypselodont teeth, the alveolus of  $P_3$  corresponds in its shape with occlusal outline of  $P_3$ , therefore the ratios of visible structures of both alveolus and  $P_3$  are the same and their comparison possible (see ČERMÁK 2004). According to morphology of the available  $P_3$ 

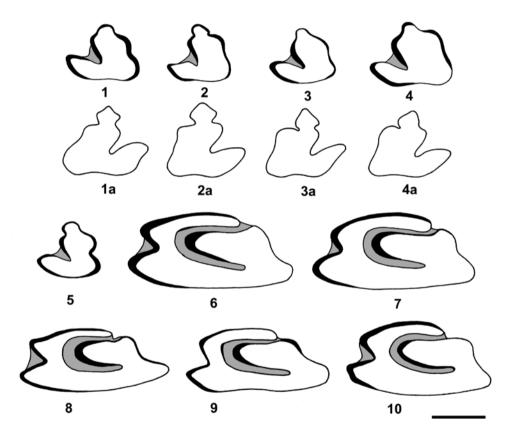


Fig. 3. Morphology of  $P_3$  (non-adult) and  $P^3$  teeth in *Ochotona rufescens* from Iran; all teeth are figured as left specimens (1–2, 5–6, 9–10 are reversed); 1–10 – occlusal views, 1a–4a – root views; scale bar – 1 mm.

Obr. 3. Morfologie třenových zubů (P<sub>3</sub> – nedospělí jedinci; P<sup>3</sup>) u pišťuchy rezavé z Íránu; všechny zuby jsou zobrazeny jako levé (1–2, 5–6, 9–10 jsou stranově převráceny); 1–10 – okluzální pohled, 1a–4a – kořenový pohled; měřítko – 1 mm.

Legend / legenda: P<sub>3</sub>: 1–3, 1a–3a, 5 – Emam Qoli, 4, 4a – Bazangan; P<sup>3</sup>: 6–8 – Emam Qoli, 9 – Qarloq, 10 – Bazangan.

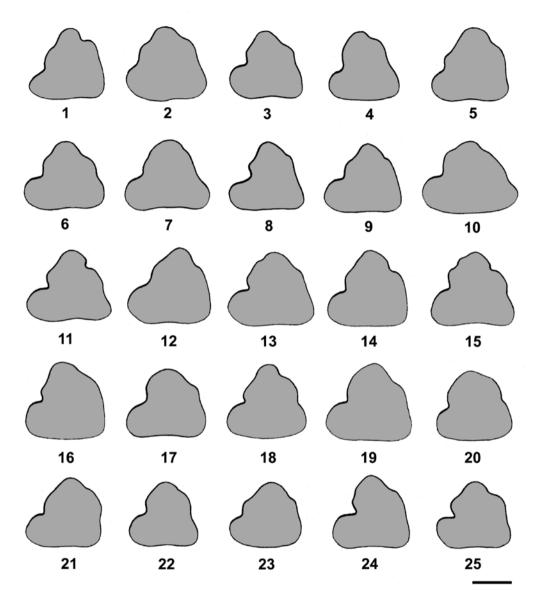


Fig. 4. Morphology of  $P_3$  alveoli in *Ochotona* from the Middle East (Iran, Turkey); all alveoli are figured as left specimens (1–4, 8, 9, 21–23, 25 are reversed); scale bar – 1 mm.

Obr. 4. Morfologie alveolů třetího třenového zubu (P<sub>3</sub>) u pišťuchy rezavé z Blízkého východu (Írán, Turecko); všechny alveoly jsou zobrazeny jako levé (1–4, 8, 9, 21–23, 25 jsou stranově převráceny); měřítko – 1 mm.

Legend / legenda: 1 – Ishak Paşa Sarayi, 2 – Bastam, 3, 4 – Qarloq, 5 – Gazanak, 6–12 – Emam Qoli, 13–19 – Bazangan, 20–22 – Deh Zireh, 23 – Qamishlu, 24–25 – Deh Bakri.

alveoli (L×W =  $1.80\times2.00$ , OR =  $1.55-2.00\times1.70-2.30$ ; n=33), the tooth is almost triangular (Fig. 4). The posteroconid is large and long (the relative length is determinable from entoconid protrusion on the lingual side of  $P_3$  alveolus – see Fig. 4). The anteroconid is small (PR of  $P_3$  alveoli: X=74, n=33), rounded, often with asymmetrical position. The  $P^2$  is (according to the shape of alveoli, n=6) oval, in its shape, its lingual side is almost straight. The  $P^3$  (Fig. 3: 6–10) is trapezoidal in the occlusal outline (L×W =  $1.27\times2.61$ , OR =  $1.08-1.44\times2.04-3.00$ ; n=7). The mesial hypercon of  $P^3$  is relatively large (mean of hyperconal width is 1.51); its width is quite variable. There is also often an additional protrusion on the anterior part of the  $P^3$  metacon (Fig. 3: 6–8).

All the above mentioned features of the compared material are characteristic for *Ochotona rufescens* and fall clearly within the known variation range of the species (see e.g., Ognev 1940, Erbaeva 1988). At the same time, it differs from the other species inhabiting the surrounding regions. The studied ochotonids from the Middle East, as well as all specimens of *O. rufescens*, are well distinguishable from *O. pusilla* by their much larger size, and from all of the other known

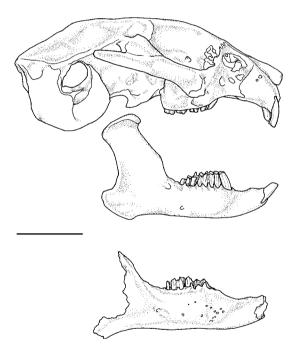


Fig. 5. Skull and mandible of *Ochotona rufescens* from the Kopetdag Mts., NE Iran (NMP 90153) (above) and mandible of *O.* cf. *rufescens* from Ishak Paşa Sarayi, E Turkey (NMP 90157) (below); scale bar – 5 mm.

Obr. 5. Lebka a spodní čelist pišťuchy rezavé (*Ochotona rufescens*) z pohoří Kopetdag, severovýchodní Írán (NMP 90153) (nahoře) a spodní čelist pišťuchy *O.* cf. *rufescens* z letoviska Ishak Paşa Sarayi, východní Turecko (NMP 90157) (dole); měřítko – 5 mm.

species by their much smaller  $P_3$  anteroconid; the mean PR of  $P_3$  alveoli of geographically close species (i.e., *O. pallasi*, *O. rutila*, *O. macrotis*, and *O. roylei*) falls within the range from 62 to 65. These species differ also from the pikas from Iran in many skull features: e.g., in their closed incisive-palatal foramen (*O. pallasi* and *O. rutila*), in their distinctly wider interorbital part (*O. rutila*, *O. macrotis*, and *O. roylei*), or in their presence of foramina in the frontal bones (*O. macrotis* and *O. roylei*), etc. (see Ognev 1940, Gureev 1964 and Erbaeva 1988 for details).

Based on the above discussed dimensions and morphological characters, the pikas from Ishak Paşa Sarayi (Turkey; record No. 2) and Bastam (NW Iran; No. 3) correspond very closely with O. rufescens and fall clearly into its variation range. Nevertheless, they differ in certain respect. These specimens are somewhat larger than other Persian pikas under study (Figs. 5, 6). However, taking into account the small size of the sample, it is difficult to evaluate the actual meaning of the difference. It seems possible either that (1) Ochotona from the border region of Iran and Turkey falls within the variation range of populations from northeastern and central Iran, while accidentally only the larger individuals were available for comparison, or (2) these western pikas are actually larger than Ochotona from northeastern and central Iran. However. the second possibility does not have to imply the existence of a separate taxon, as there could also be a cline increase in body size in pikas from east to west (the phenomenon known in such geographical arrangement in other mammals, e.g. bats, see Benda & Horáček 1995). In P<sub>3</sub> anteroconid proportions, the pikas from Ishak Pasa Sarayi and Bastam lie at the upper margin of variation at the Persian pika samples; PR of P<sub>3</sub> alveoli are 83 and 81, respectively. However, as there are no mandibles or additional dentition available (particularly P<sub>3</sub>), it is quite difficult to make a more conclusive comparison and taxonomical identification of the pikas from the region at the border between Iran and Turkey. Thus, we assign these specimens tentatively to O. cf. rufescens.

Using the available material from Iran, the expected differences in body size between populations from northeastern Iran (the Kopetdag Mts, an area of occurrence of *O. rufescens regina* Thomas, 1911) and central Iran (central parts of the Zagros Mts, an area of occurrence of *O. r. vizier* Thomas, 1911) were not proved (Fig. 6).

In any case, based on both morphological and metric characteristics, all the other Persian samples surveyed in this paper can be referred to *O. rufescens*, with an exception of the material from Emam Sadeh (record No. 10), where the lack of available features does not allow a precise species assignment. However, taking into account the geographical position of the locality, it seems very probable that the mandibular fragment belongs also to that species.

#### NOTES ON PALEONTOLOGY

The fossil record of *O. rufescens*, including the fossils placed in close proximity of this species, is quite poor to date (Erbaeva 1988). The ochotonid remains, almost identical with the extant *O. rufescens*, known from the Acheulean Palaeolithic site of Sel' Ungur, Kirghizia, slightly differ from the Recent species by their longer diastema and wider P<sub>3</sub> (Erbaeva 1988). Besides the ochotonid from Kirghizia, some large sized pikas referred to *O. rufescens* have been reported from Transcaucasia (see above). Unfortunately, no detailed characteristics of these specimens are available in the literature, and a relevant comparison is difficult. Dal' (1957) placed the Armenian findings into proximity of *Ochotona eximia* (Khomenko, 1914) based on the size and morphological similarities in P<sub>3</sub> and mandible. In his opinion, these ochotonids represent an Upper Tertiary relic derived from a heterogeneous group of species from the "*eximia-gigas*"

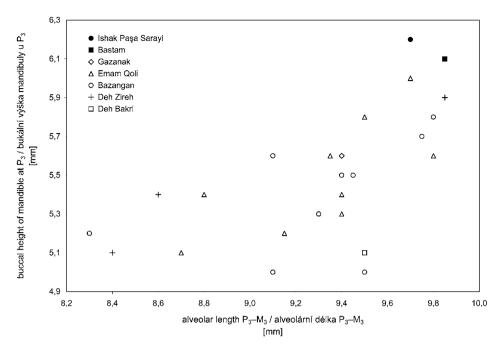


Fig. 6. Scatter plot of the alveolar length of the lower tooth-row  $(P_3-M_3)$  against the buccal height of the mandible at  $P_3$  in the samples of *Ochotona* coming from the Middle East (Iran, Turkey); only adult specimens were used.

Ôbr. 6. Srovnání alveolarní délky dolní zubní řady (P<sub>3</sub>–M<sub>3</sub>) proti bukální výšce spodní čelisti u třetího třenového zubu (P<sub>3</sub>) jedinců pišťuch z Blízkého východu (Írán, Turecko); použity byly rozměry pouze dospělých jedinců.

range (for details see Argyropulo & Pidopličko 1939, Agardžanjan & Erbaeva 1983, Erbaeva 1988, Erbajeva 1994, and Sen 2003), According to Averianov & Baryšnikov (1992), findings from the Čirahan River and Urcskii Range are likely to belong to Ochotona transcaucasica. This species was first described by VEKUA (1967) from the Copi Station, Georgia, and due to its large size and general structure of P<sub>3</sub> as Ochotonoides transcaucasica, i.e., belonging to a fossil genus, which was known that time from China and Hungary (see Boule & Teilhard De Chardin 1928, Teilhard de Chardin & Young 1931, Teilhard de Chardin 1940, and Kretzoi 1962). With more fossil evidence at hand, Erbaeva (1988) assigned the pika from the Copi Station to the genus Ochotona. In spite of very similar morphology (small and rounded anteroconid in P<sub>3</sub>, posterior mental foramen in mandible below M<sub>3</sub>, etc.), this species differs from the ochotonids under study by its larger size; OR of the P<sub>3</sub>-M<sub>3</sub> length is 11.00-12.00 in O. transcaucasica (Vekua 1967) compared to 8.30–9.85, n=27, in the studied ochotonids of the Middle East. Ochotona transcaucasica was also reported from the Azih cave in Azerbaijan; the available teeth are very close in size and morphology to those of pika from the Copi Station (Markova 1982, Erbaeva 1988). A smaller pika form found at the Azih cave is referred to Ochotona azerica (ALIEV 1969, GADŽIEV et al. 1979). This pika is of a similar size (OR of P<sub>3</sub>-M<sub>3</sub> length: 8.7-9.5) as O. rufescens presented in this paper, nevertheless it has a more robust mandible and a larger anterokonid of P<sub>3</sub> (Erbaeva 1988).

Besides the large sized ochotonids from the Middle East, a small sized form was found at the Güzyurdu 2A site in central Turkey (for details see New Records). Poorly preserved remains do not allow a precise species assignment. Nevertheless, in its size (L×W of the available M<sup>1</sup> is 1.28×2.44), the pika from Güzvurdu 2A resembles rather O. pusilla than O. rufescens: OR of L×W of M<sup>1</sup> is  $1.15-1.45 \times 2.00-2.40$ , n=20 in the extant O. pusilla in contrast to 1.50-1.85× 2.60–3.15, n=11 in the studied O. rufescens. According to the shape of alveolus, the mesial hyperloph of P<sup>3</sup> is relatively wide and flat; its width is approximately 75 per cent of the tooth width. Based on body size, we assign tentatively the material from Güzyurdu 2A to O, cf. pusilla. A similarly sized pika, referred to Ochotona sp., was reported by Vekua et al. (1981) from the Toringian site of Bronzovaja in western Georgia; according to its size, it is also placed into systematical proximity of O. pusilla (Vekua et al. 1981, Averianov & Baryšnikov 1992). A pika of an uncertain taxonomical position, referred to Ochotona sp., is known from the Middle Pleistocene (the Lower Toringian) site of Emirkaya-2 from the south of Central Anatolia (Montuire et. al. 1994). Its P<sub>3</sub> shares transitional features between O. pusilla and O. rufescens, and therefore this pika is considered to be an early representative of the former species by some authors (e.g., Montuire et. al. 1994, Erbajeva 2001), by others it is referred to the latter species (e.g., Averianov 2001).

Because of the limited data on fossil record, phylogenetic relationships of the taxa under study with other extant species are not yet clear. Nevertheless, from the morphological point of view it can be mentioned that *O. rufescens* as well as the large sized fossil ochotonids from Transcaucasia and *O. pusilla* share archaic dental features (i.e., P<sub>3</sub> with small and rounded anteroconid, wide confluence between anteroconid and posteroconid, shallow proto- and paraflexid, rounded P<sup>2</sup> with a short anteroflexus) and their dentition is much less differentiated than in other extant species.

Phylogenetic relationships within the genus *Ochotona* reconstructed using the mitochondrial gene for cytochrome *b* (Niu et al. 2004) do not support the current subgeneric classifications (see Allen 1938, Ellerman & Morrison-Scott 1951, Erbaeva 1988, Erbajeva 1994, and others). Niu et al. (2004) recognised five groups; they placed *O. rufuscens* into the Surrounding Quinghai-Tibet Plateau group, i.e. into phylogenetic proximity of the rock-talus-dwelling species (*O. macrotis, O roylei, O. iliensis, O. himalayana, O. rutila, O erythrotis, O. gloveri, O. brookei,* and *O. muliensis*) and intermediate types between the talus- and steppe-dwelling species (*O. ladacensis, O. forresti* and *O. koslowi*). The species divergence occurred most probably in the Early Pleistocene and was closely related to the uplifting of the Quinghai-Tibet Plateau and subsequent climatic changes. Due to the relatively stable environment, the differentiation was not so strong within the Central Asian group, including *O. pusilla* (Niu et al. 2004). Based on fossil remains, the structure of teeth, and molecular data, *O. pusilla* represents a very distinct and ancient species, which is often considered to be a relic of the Late Pliocene (Erbajeva 1994, Niu et al. 2004).

## **SOUHRN**

V příspěvku jsou prezentovány nové nálezy pišťuch (12 recentních a 1 subfosilní) z území Turecka a Íránu. Většina recentních nálezů, řazených zde do druhu *Ochotona rufescens* (Gray, 1842) – pišťucha rezavá, pochází z horských oblastí Íránu, naše nálezy většinou spadají do dosud známého areálu rozšíření tohoto druhu. Nález kosterních pozůstatků pišťuchy ve východním Turecku představuje první recentní nález

v této zemi a významně posouvá hranici dosud známého areálu rozšíření rodu (i celé čeledi Ochotonidae) na Blízkém východě. Nálezy ve východním Turecku a severozápadním Íránu (Arménská vysočina) spadají morfometricky do variační šíře pišťuchy rezavé, přesto se liší od studovaných pištuch z Íránu větší velikostí a trochu odlišnou morfologií třetího třenového zubu. Nicméně vzhledem k nepočetnému materiálu z Arménské vysočiny je věrohodné srovnání problematické a studované pišťuchy jsou provizorně determinovány jako O. cf. *rufescens*. Nově nálezený subfosilní jedinec pišťuchy ze střední Anatolie je výrazně menší než předešlé pištuchy a jedná se s největší pravděpodobností o pišťuchu stepní – O. pusilla (Pallas, 1768), rozšířenou v současné době nejblíže v Předkavkazí. Uvedené nálezy byly též morfologicky srovnány s ostatními pišťuchami regionu, a to jak v kontextu neontologickém, tak paleontologickém.

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#### REFERENCES

- AGADŽANJAN A. K. & ERBAEVA M. A., 1983: Pozdnekajnozojskie gryzuny i zajceobraznye territorii SSSR [Late Cenozoic Rodents and Lagomorphs of the territory of the USSR]. Nauka, Moskva, 189 pp (in Russian).
- Argyropulo A. I. & Pidopličko I. G., 1939: Predstaviteli Ochotonidae (Duplicidentata, Mammalia) v pliocene SSSR [Representatives of Ochotonidae (Duplicidentata, Mammalia) in the Pliocene of the USSR]. Dokl. Akad. Nauk SSSR, 24(7): 723–728 (in Russian).
- ALIEV S. D., 1969: Fauna Azyhskoj paleolitičeskoj stojanki [Fauna of the Palaeolithic Azyh Encampment]. Candidate Dissertation Thesis, unpublished. Institute of Zoology, Baku, 30 pp (in Russian).
- ALLEN G. M., 1938: Mammals of China and Mongolia. Natural History of Central Asia. Vol. XI, Part 1. The American Museum of Natural History, New York, xxv+620 pp.
- AVERIANOV A., 2001: Pleistocene lagomorphs of Eurasia. Deinsea, 8: 1–13
- AVERIANOV A. A. & BARYŠNIKOV G. F., 1992: Plejstocenovye zajci (rod *Lepus*, Lagomorpha) Bol'šogo Kavkaza [Pleistocene hares of the genus *Lepus* (Lagomorpha) in the Greater Caucasus]. *Trudy Zool. Inst. RAN*, **246**: 4–28 (in Russian).
- Baryshnikov G. F., 2002: Local biochronology of Middle and Late Pleistocene mammals from the Caucasus. *Russ. J. Theriol.*, 1: 61–67.
- Benda P. & Horacek I., 1995: Geographic variation in three species of *Myotis* (Mammalia: Chiroptera) in South of the Western Palearctics. *Acta Soc. Zool. Bohem.*, **59**: 17–39.
- Blanford W. T., 1876: Eastern Persia, an account of the Journeys of the Persian Boundary Commission 1870–71–72. Volume II. The Zoology and Geology. London, vii+516 pp, 28 pls.
- Boule M. & Teilhard de Chardin P., 1928: Le Paleolithique de la Chine (Paleontologie). Arch. Inst. Paleontol. Humaine (Paris), 4: 1–102, 20 pls.
- COON C. S., 1951: Cave Explorations in Iran 1949. University Museum, Univ. of Pennsylvania, Philadelphia, 125 pp.
- ČERMÁK S., 2004: A new ochotonid (Lagomorpha) from the Early Pleistocene of Slovakia. N. Jahrb. Geol. Paläontol. Monath., 2004: 662–680.
- Dal'S. K., 1954: Paleofauna nazemnych pozvonočnych iz peščer Urcskogo chrebta [Paleofauna of terrestrial vertebrates from caves of the Urcskij range]. *Izv. Akad. Nauk ArmSSR*, 7(2): 61–71 (in Russian).
- Dal' S. K., 1957: Zakavkazskaja piščuha [Transcaucasian pika]. *Mater. Izuč. Fauny ArmSSR*, **3**: 17–26 (in Russian).

- ELLERMAN J. R. & MORRISON-SCOTT T. C. S., 1951: *Checklist of Palaearctic and Indian Mammals 1758 to 1946*. British Museum (Natural History), London, 810 pp.
- Erbaeva M. A., 1988: Piščuchi kajnozoja (taksonomija, sistematika, filogenija) [Cenozoic Pikas (Taxonomy, Systematics, Phylogeny)]. Nauka, Moskva, 224 pp (in Russian).
- Erbajeva M. A., 1994: Phylogeny and evolution of Ochotonidae with emphasis on Asian ochotonids. In: Tomida Y., Li C. K. & Setoguchi T. (eds.): Rodent and Lagomorph Families of Asian Origins and Diversification. Natl. Sci. Mus. Monogr., Tokyo, 8: 1–13.
- Erbajeva M. A., Montuire S. & Chaline J., 2001: New ochotonids (Lagomorpha) from Pleistocene of France. *Geodiversitas*, 23: 395–409.
- Fejfar O. & Heinrich W.-D., 1983: Arvicoliden-Sukzession und Biostratigraphie des Oberpliozäns und Quartärs in Europa. In: Heinrich W.-D. (ed.): Wirbeltier-Evolution und Faunenwandel im Känozoikum. Schriftenr. Geol. Wissensch., 19–20: 61–109.
- Gadžiev D. V. & Aliev S. A., 1966: Piščuha (*Ochotona* sp.) iz mus'terskich otloženij Taglarskoj peščeri [A pika (*Ochotona* sp.) from the Mousterian deposits of the Taglar cave]. *Učen. Zap. Azerb. Gos. Med. Inst.*, **20**: 18–21 (in Russian).
- Gadžiev D. V., Gusejnov M. M., Mamedov A. V. & Širinov N. Š, 1979: Kratkie rezul'taty kompleksnyh issledovanij Azyhskoj drevněpaleolitičeskoj stojanky [Short results of the complex researches of the Lower Palaeolithic site of Azyh]. *Izv. Akad. Nauk AzSSR*, 3: 10–16.
- Gromov I. M. & Erbaeva M. A., 1995: *Mlekopitajuščie fauny Rossii i sopredelenyh territorij. Zajceobraznye i gryzuny [The Mammals of Russia and Adjacent Territories. Lagomorphs and Rodents*]. Zoologičeskij Institut RAN, Sankt-Peterburg, 522 pp (in Russian).
- Gureev A. A., 1963: III. Otrjad Lagomorpha zajceobraznye [III. Order Lagomorpha lagomorphs]. Pp.: 218–243. In: Gromov I. M., Gureev A. A., Novikov G. A., Sokolov I. I., Strelkov P. P. & Čapskij (eds.): *Mlekopitajuščie fauny SSSR*. Časť 1 [Mammals of the Fauna of the USSR. Part 1]. Izdateľ stvo Akademii Nauk SSSR, Moskva & Leningrad, 639 pp (in Russian).
- Gureev A. A., 1964: Fauna SSSR. Mlekopitajuščie. Tom III, vypusk 10. Zajceobraznye (Lagomorpha) [Fauna of the USSR. Mammals. Volume III, Number 10. Lagomorphs (Lagomorpha)]. Nauka, Moskva & Leningrad, 276 pp (in Russian).
- GUREEV A. A., 1981: Otrjad Lagomorpha Brandt, 1855 zajceobraznye [Order Lagomorpha Brandt, 1855 lagomorphs]. Pp.: 60–74. In: GROMOV I. M. & BARANOVA G. I. (eds.): *Katalog mlekopitajuščih SSSR. Pliocen–sovremennost'* [Catalogue of Mammals of the USSR. Pliocene–Recent]. Nauka, Leningradskoe otdelenie, Leningrad, 456 pp (in Russian).
- HASSINGER J. D., 1973: A survey of the mammals of Afghanistan resulting from the 1965 Street Expedition (excluding bats). *Fieldiana Zool.*, **60**: i–xi+1–165.
- HOFFMANN R. S., 1993: Order Lagomorpha. Pp.: 807–827. In: WILSON D. E. & REEDER D. M. (eds.): Mammal Species of the World. A Taxonomic and Geographic Reference. Second Edition. Smithsonian Institution Press, Washington & London, 1206 pp.
- HOFFMANN R. S. & SMITH A. T., 2005: Order Lagomorpha. Pp.: 185–211. In: WILSON D. E. & REEDER D. M. (eds.): *Mammals Species of the World. A Taxonomic and Geographic Reference. Third Edition. Volume 1*. The Johns Hopkins University Press, Baltimore, xxxv+743 pp.
- Kretzoi M., 1962: Fauna und Faunenhorizont von Csarnóta. *Jahresb. Ungar. Geol. Inst.*, **1959**: 297–395.
- Kryštufek B. & Vohralík V., 2001: Mammals of Turkey and Cyprus. Introduction, Checklist, Insectivora. Knjižnica Annales Majora. Zgodovinsko društvo za južno Primorsko, Koper, 140 pp.
- Kumerloeve H., 1975: Die Säugetiere (Mammalia) der Türkei. Veröff. Zool. Staatssamm. München, 18: 69–158.
- Lay D. M., 1967: A study of the mammals of Iran resulting from the Street Expedition of 1962–63. *Fieldiana Zool.*, **54**: 1–282.
- Lissovsky A. A., 2004: Contribution to age determination of pikas (Lagomorpha, Ochotonidae, *Ochotona*). *Russ. J. Theriol.*, **3**(1): 43–48.

- LÓPEZ-MARTÍNEZ N., 1974: Taux taxonomique d'evolution dans l'ordre des Lagomorphes (Mammalia). Bull. Soc. Géol. France, 16: 422–430.
- MARKOVA A. K., 1982: Mikroteriofauna iz paleolitičeskoj peščernoj stojanky Azyh [Micromammals from the Palaeolithic cave of Azyh]. *Paleontol. Sbor.*, **19**: 14–28 (in Russian).
- MISONNE X., 1956: Notes sur les Ochotones de l'Iran. Bull. Inst. Roy. Sci. Natur. Belg., 32(54): 1-7.
- Montuire S., Sen S. & Michaux J., 1994: The Middle Pleistocene mammalian fauna from Emirkaya-2, Central Anatolia (Turkey): systematics and paleoenvironment. *N. Jahrb. Geol. Paläontol. Abhandl.*, **193**(1): 107–144.
- Murray J. A., 1884: Additions to the present Knowledge of the Vertebrate Zoology of Persia. *Ann. Mag. Natur. Hist.*, ser. 5, **14**: 97–106.
- Niu Y. D., Wei F. W., Li M., Liu X. M. & Feng Z. J., 2004: Phylogeny of pikas (Lagomorpha, *Ochotona*) inferred from mitochondrial cytochrome *b* sequences. *Folia Zool.*, **53**: 141–155.
- OBUCH J. & KRIŠTÍN A., 2004: Prey composition of the little owl *Athene noctua* in an arid zone (Egypt, Syria, Iran). *Folia Zool.*, **53**: 65–79.
- Ognev S. I., 1940: Zveri SSSR i priležaščih stran. Tom 4. Gryzuny [Mammals of the USSR and Adjacent Countries. Part 4. Rodents]. Izdatel'stvo Akademii Nauk SSSR, Moskva & Leningrad, 616 pp (in Russian).
- PAVLINOV I. Ja. & ROSSOLIMO O. L., 1998: Sistematika mlekopitajuščih SSSR. Dopolnenija [Systematics of mammals of the USSR. Additions]. *Sbor. Trud. Zool. Muz. MGU*, **38**: 1–190 (in Russian).
- Pavlinov I. Ja., Borisenko A. V., Kruskop S. V. & Jahontov E. L., 1995: Mlekopitajuščie Evrazii. II. Non-Rodentia. Sistematiko-geografičeskij spravočnik [Mammals of Eurasia. II. Non-Rodentia. Systematic and geographic review]. *Sbor. Trud. Zool. Muz. MGU*, **33**: 1–333 (in Russian).
- ROBERTS T. J., 1997: The Mammals of Pakistan. Oxford University Press, Karachi, 252 pp.
- DE ROGUIN L., 1988: Notes sur quelques mammifères du Baluchistan iranien. Rev. Suisse Zool., 95: 595–606.
- SEN S., 1998: Pliocene vertebrate locality of Çalta, Ankara, Turkey. 4. Rodentia and Lagomorpha. Geodiversitas, 20: 359–378.
- Sen S., 2003: Lagomorpha. Pp.: 163–178. In: Fortelius M., Kappelman J., Sen S. & Bernor R. L. (eds.): *Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York, 448 pp.
- SMITH A. T., FORMOZOV N. A., HOFFMANN R. S., ZHENG C. L. & ERBAJEVA M. A., 1990: The pikas. Pp.: 14–60.
  In: CHAPMAN J. A. & FLUX J. E. C. (eds): Rabbits, Hares and Pikas. Status Survey and Conservation Action Plan. International Union for the Conservation of Nature, Gland (Switzerland), 168 pp.
- Sokolov V. E., Ivanickaja E. Ju., Gruzdev V. V. & Geptner V. G. 1994: *Mlekopitajuščie Rossii i sopre-delenyh regionov. Zajceobaznye [Mammals of Russia and adjacent regions. Lagomorphs*]. Nauka, Moskva, 272 pp (in Russian).
- Sosnihina T. M., 1947: O nahoždenii kostej piščuhi (*Ochotona* sp.) v Armjanskoj SSR [On the finding of pi-ka's (*Ochotona* sp.) bones in Armenian SSR]. *Dokl. Akad. Nauk Arm. SSR*, 7(2): 77–78 (in Russian).
- Sosnihina T. M., 1948: Pol'za i vred filina v sel'skom hozjajstve Armjanskoj SSR [Utility and harm functions of the Eagle owl in the agriculure of Armenian SSR]. *Dokl. Akad. Nauk Arm. SSR*, *Biol. Selsko-Hozjajst. Nauky*, **1**(3): 271–281 (in Russian).
- ŠIDLOVSKIJ M. V. 1976: Opredelitel' gryzunov Zakavkaz'ja (izdanie vtoroe) [Key to Identification of Glires of Transcaucasia (Second Edition)]. Mecniereba, Tbilisi, 256 pp (in Russian).
- Taghizadeh F., 1964: *The Harmful Rodents of Iran and their Control*. Ministry of Agriculture, Tehran, 109 pp (in Farsi, with a summary in English, paginated separately: 10 pp).
- Teilhard de Chardin P., 1940: The fossils from Locality 18 near Peking. *Paleontol. Sinica*, N. S. C, 9: 1–101, 3 pls.
- TEILHARD DE CHARDIN P. & YOUNG C. C., 1931: Fossil mammals from northern China. *Paleontol. Sinica*, S. C, 9(1): 1–87, 10 pls.
- Vekua A. K., 1967: Novyj predstavitel' Lagomyidae iz paleolita Gruzii [A new representative of Lagomyidae from the Palaeolithic of Georgia]. *Soobšč. Akad. Nauk GSSR*, **15**(1): 139–143 (in Russian).

- Vekua A. K. & Šidlovskij M. V., 1958: Pervaja nachodka piščuhi (*Ochotona*) v paleolite Kavkaza [The first finding of pika (*Ochotona*) from the Palaeolithic of the Caucasus]. *Soobšč. Akad. Nauk GSSR*, 21(3): 285–288 (in Russian)
- Vekua A. K., Gabelaja C. D. & Mushelišvili A. T., 1981: Paleolitičeskaja fauna pozvonočnych iz peščer Zapadnoj Gruzii [The Palaeolithic vertebrates from caves of western Georgia]. *Peščery Gruzii*, 9: 38–50 (in Russian).
- Vereščagin N. K., 1959: Mlekopitajuščie Kavkaza. Istorija formirovanija fauny [The Mammals of the Caucasus. The History of Forming of the Fauna]. Izdatel'stvo Akademii Nauk SSSR, Moskva & Leningrad, 704 pp (in Russian).
- VINOGRADOV B. S. & GROMOV I. M., 1952: *Gryzuny fauny SSSR* [Glires of the Fauna of the USSR]. Izdatel'stvo Akademii Nauk SSSR, Moskva & Leningrad, 298 pp (in Russian).