Lagomorphs from a Villafranchian sequence in Transbaikalia and their paleoenvironmental implications

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Accepted for publication: 10 May, 1995

ERBAJEVA M. A. 1996. Lagomorphs from a Villafranchian sequence in Transbaikalia and their paleoenvironmental implications. Acta zool. cracov. **39**(1): 131-135.

Abstract. A review of and new data on lagomorph remains of the Villafranchian (Late Pliocene-Early Pleistocene) from eight Transbaikalian localities are presented. Lagomorphs are represented at least by two archaeolagine leporids of the genus *Hypolagus* and by different species of the ochotonid genera *Ochotonoides* and *Ochotona*. Villafranchian environmental changes in Transbaikalia from woodland to arid open landscapes resulted in a significant reduction of lagomorphs towards the end of the Pleistocene.

Key-words: mammalian sequence, Lagomorpha, Leporidae, Ochotonidae, Villafranchian, Transbaikalia.

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I. INTRODUCTION

The record of lagomorphs in western Transbaikalia covers the time span from the beginning of the Late Pliocene to the Recent. Hares and pikas were important elements of the Villafranchian faunas of Transbaikalia (ERBAJEVA 1970; BAZAROV et al. 1976; AGADZHANIAN & ERBAJEVA 1983). They attained considerable abundance and diversity in this region during the entire Villafranchian. In this paper, new data on lagomorphs from the locality Udunga and a short review of the Villafranchian lagomorph faunal sequence are presented.

II. THE SEQUENCE OF LAGOMORPH FAUNAS

The fauna of Udunga

The stratigraphically oldest fauna with lagomorphs in western Transbaikalia is Udunga (Fig. 1), situated on the left bank of the Temnik river. Here, mammalian remains are rather abundant. A list of large mammals is given by SOTNIKOVA & KALMYKOV (1991) and KALMYKOV (1992). Lagomorphs are represented by *Hypolagus transbaikalicus* (ERBAJEVA), *H. multiplicatus* (ERBAJEVA), *Ochotonoides complicidens* (BOULE & TEILHARD) and *Ochotona*.

The lagomorph association at Udunga shows a predominance of leporids, rather abundant *Ochotonoides* and a few *Ochotona*. All lagomorph species under investigation were previously known from the locality of Beregovaya in Transbaikalia (BAZAROV et al. 1976).

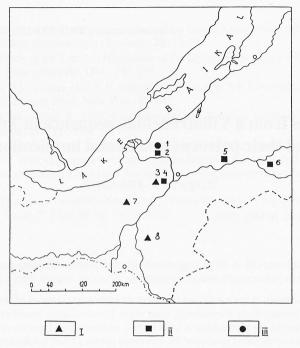


Fig. 1. Sketch map indicating the geographic position of the localities and their geological age. Villafranchian: I: Early, II: Middle, III: Late; 1: Zasuchino, 2: Itantza, 3: Tologoi 1, 4: Tologoi 2, 5: Dodogol, 6: Kudun, 7: Udunga, 8: Beregovaya.

F a m i l y L e p o r i d a e. These are represented by fragmentary mandibles and maxillae with teeth of all types and by isolated teeth.

Hypolagus multiplicatus from Udunga is characterized by slightly larger size than *Hypolagus transbaikalicus* and also differs from the latter in some dental characteristics. The P^2 of this species has two reentrant folds that are well-developed, medially positioned and rather shallow on the labial side (Fig. 2F). P^3 - M^2 have variably crenulated hypostriae, with the greatest development of the crenulations on P^3 - M^1 . On M^2 the crenulations of the hypostriae can be on both margins or one margin only (Fig. 2E). The P₃ of *Hypolagus multiplicatus* is characteristic of the archaeolagines. It is elongate and somewhat broad. It has a flattened anterolingual surface. The labial side of P₃ has a cement-filled, rather deep anteroexternal reentrant and a posteroexternal reentrant that extends about half-way across the occlusal surface (Fig. 2A).

The small P₃ of *Hypolagus transbaikalicus* distinguishes this species from *H. multiplicatus*. *H. transbaikalicus* has a P² with a single, deep anterior reentrant (Fig. 2D). The hypostriae on P^3-M^1 have variable crenulations that become reduced toward the back of the tooth rows, while on M^2 the crenulations are almost or completely absent (Fig. 2C). The P₃ is long, with a straight anterolingual surface. The labial side has two reentrants, of which the anteroexternal is shallow with little or no cement. The cement-filled posteroexternal reentrant is deep and extends almost half-way across the crown (Fig. 2B).

Both Hypolagus species from Udunga are conspecific with leporids from Beregovaya (Fig. 3A-F).

F a m i l y O c h o t o n i d a e. Ochotonoides complicidens is a large pika with a P₃ with a characteristically complex pattern. The P^2 of this pika has a main anterior median fold and a slighter inner grove. The P₃ is very complicated due to a trigonid with an anterior fold on the occlusal surface and a "plicated" border of the reentrant folds separating the trigonid from the

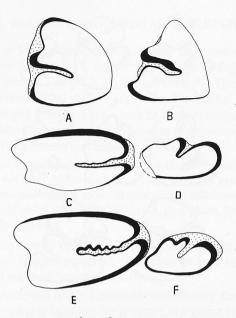


Fig. 2. Hypolagus multiplicatus: A: P₃, E: M², F: P²; Hypolagus transbaikalicus: B: P₃, C: M², D: P²; (from Udunga).

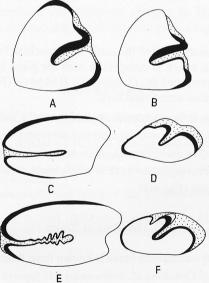


Fig. 3. Hypolagus multiplicatus: A: P₃, E: M², F: P²; Hypolagus transbaikalicus: B: P₃, C: M², D: P²; (from Beregovaya).

talonid by one to three plications (Fig. 4A, B, D, I). On the basis of the rodent association and the evolutionary stage of the voles, the geological age of Udunga is early Villafranchian.

The faunas of Tologoi and Beregovaya

Two other localities from this time are Tologoi and Beregovaya. The first includes 14 species of small mammals. The fauna of Tologoi 1 is somewhat younger than the fauna of Udunga and is

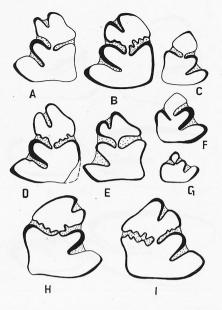


Fig. 4. Ochotonoides complicidens: A, B, D, I: P₃ (from Udunga); E: P₃ (from Zusuchino); H: P₃ (from Tologoi 1); Ochotona gromovi: C: P₃; O. sibirica: G: P₃ (from Beregovaya); O. tologoica: F: P₃ (from Tologoi 1).

defined as the next evolutionary stage of the early Villafranchian fauna. Pikas are represented by *Ochotonoides complicidens*, which is conspecific with the pikas from Udunga and Beregovaya (Fig. 4.H). *Ochotona* is represented by *O. tologoica* HABAEVA (Fig. 4F) and *O.* cf. *intermedia* ERBAJEVA. No leporid remains were found here.

The fauna of Beregovaya is the uppermost stage of the early Villafranchian fauna of Transbaikalia. It includes 23 species. In this fauna lagomorphs are represented by seven taxa. The leporids are represented by *Hypolagus multiplicatus*, *H. transbaikalicus* and Pentalagini gen. and the Ochotonids by *Ochotonoides complicidens*, *Ochotona gromovi* ERBAJEVA (Fig. 4C), *O. intermedia* and *O. sibirica* ERBAJEVA (Fig. 4G).

The fauna of Itantza

A middle Villafranchian mammalian fauna is known from Itantza. It includes the lagomorphs *Ochotona* cf. *intermedia* and *Ochotona* cf. *nihewanica*. No leporid remains were found here.

The faunas of Dodogol, Zasuchino, Kudun and Tologoi 2

Upper Villafranchian faunas are known from Dodogol, Zasuchino (second layer), Kudun and Tologoi 2 (middle stratum). The lagomorph faunas of this stage are rather rich in taxa. They include *Hypolagus* cf. *transbaikalicus*, *Ochotonoides complicidens* (Fig. 4E), *Ochotona* cf. *tologoica*, *O. bazarovi* ERBAJEVA, *O. zasuchini* ERBAJEVA and *O.* cf. *nihewanica* QIU. Towards the end of the Villafranchian *Hypolagus* and *Ochotonoides* disappeared, as well as most of the Villafranchian species of *Ochotona*.

III. PALEOENVIRONMENTAL IMPLICATIONS

Inspection of the list of lagomorph species shows that *Ochotona* is rare in the Udunga fauna, *Hypolagus* is absent from Tologoi 1, 2, Itantza, Kudun and Dodogol, while no *Ochotonoides* remains are known from Itantza, Tologoi 2, Kudun and Dodogol. These phenomena can probably be explained by past environmental differences in the Transbaikal area. In the Udunga fauna associations of both large and small mammals such as *Parapresbytis*, *Gulo*, *Lynx*, *Ursus*, *Capreolus*, *Orientalomys* and *Hypolagus* show a predominance of woodland species. The climate at the beginning of the early Villafranchian was humid.

The faunas of Tologoi 1 and Beregovaya indicate a climatic change to a continental and arid type towards the end of the early Villafranchian. Forest biotopes gradually became reduced and savanna-like forest-steppes and steppes became more widely distribution. At that time an adaptive radiation of ochotonids and voles, especially *Villanyia*, took place. Species characteristic of open landscapes dominate at Beregovaya.

With the change in the climate during the middle Villafranchian towards a cooler and more arid phase, grassland and steppes expanded. *Ochotona*, ground squirrels and *Villanyia* were predominant in the small mammal faunas of that time.

Among the late Villafranchian (Early Pleistocene) faunas only Zasuchino includes *Hypolagus* and *Ochotonoides*. This probably indicates the presence of a varied environment in Transbaikalia at the time. In the southern and eastern parts open landscapes were widely distributed while to the north woodland areas dominated.

Thus, during the Villafranchian environmental changes in Transbaikalia from woodland towards arid open landscapes resulted in a significant reduction of lagomorphs towards the end of the Pleistocene.

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