

Rudimentary small upper premolars in the Northern bat, *Eptesicus nilssoni* (Vespertilionidae, Chiroptera)

Tatyana V. Fadeeva & Sergei V. Krusko

ABSTRACT. A case of presence of the upper small premolar in the genus *Eptesicus* is being described. Members of this genus were thought to be invariable in having no small premolars in upper toothrows. However, nine partial skulls of northern bats with traces of upper small premolars were excavated from cave deposits of Perm' Territory. One additional specimen with abnormal dental formula was found in the collection of the Zoological Museum of Moscow University. The presence of the small premolars in at least some individuals represents a primitive trait which puts *E. nilssoni* apart from the more advanced members of its genus.

KEY WORDS: *Eptesicus*, northern bat, tooth formula, small premolar, cave deposits.

Tatyana V. Fadeeva [fadeeva.tatyana@mail.ru], Institute of Plant and Animal Ecology of RAS Ural Branch, ul. 8th of March 202, Ekaterinburg 620144, Russia; Sergei V. Krusko [krusko@zmmu.msu.ru], Zoological Museum, Moscow State University, ul. Bolshaya Nikitskaya 6, Moscow 125009, Russia.

Рудиментарные верхние малые предкоренные зубы у северного кожанка, *Eptesicus nilssoni* (Vespertilionidae, Chiroptera)

Т.В. Фадеева, С.В. Крускоп

РЕЗЮМЕ. Описывается случай наличия верхних малых предкоренных зубов у представителя рода *Eptesicus*. Предполагалось, что у видов этого рода малых предкоренных в верхнем зубном ряду не бывает никогда. Однако в пещерных отложениях Пермского края было найдено девять фрагментарных черепов северных кожанков с явными следами наличия у них верхних малых предкоренных. Еще один экземпляр с необычной зубной формулой был обнаружен в коллекции Зоологического музея Московского государственного университета. Наличие малых предкоренных зубов, по крайней мере, у части особей представляет собой примитивную черту, противопоставляющую *E. nilssoni* прочим более продвинутым видам рода.

КЛЮЧЕВЫЕ СЛОВА: *Eptesicus*, северный кожанок, зубная формула, малый предкоренный зуб, пещерные отложения.

Introduction

The number of premolars and degree of their reduction are commonly used as genus- or species-specific diagnostic characters for Vespertilionid bats (Bobrinskii *et al.*, 1965; Tate, 1942; Corbet & Hill, 1992; Pavlinov *et al.*, 1995; Borisenko & Krusko, 2003; Smith & Xie, 2008). Because the reduction of the number of teeth occurred independently in different evolutionary lineages of vespertilionids (Menu, 1987), the value of this character complex in phylogenetic reconstructions is doubtful. However, dental formulas can still be instrumental in characterizing certain genera. In particular, the genus *Eptesicus* (sensu Simmons, 2005) is defined by the constant absence of both small upper premolars (P2 and P3) (Corbet & Hill, 1992) and, until recently, no exceptions to this were documented.

A recent excavation of the subfossil material from the Upper Pleistocene and Holocene cave deposits in the western Ural Mountains recovered numerous bat skeletal fragments, including many skulls of the northern bat, *Eptesicus nilssoni*. Amongst these remains, several skulls were found possessing well-developed alveoli of the small upper premolars in one or both sides of upper jaws. One additional skull of *E. nilssoni* with the same archaic feature was later found in the collection of the Zoological Museum of Moscow State University. This study aims to describe our unusual findings.

Material and methods

Subfossil bat remains were found in deep parts of the four natural caves situated in Alexandrovsk District, Perm' Territory, about 15–20 km north-east from the town of Yayva, between villages Skopkortnaya

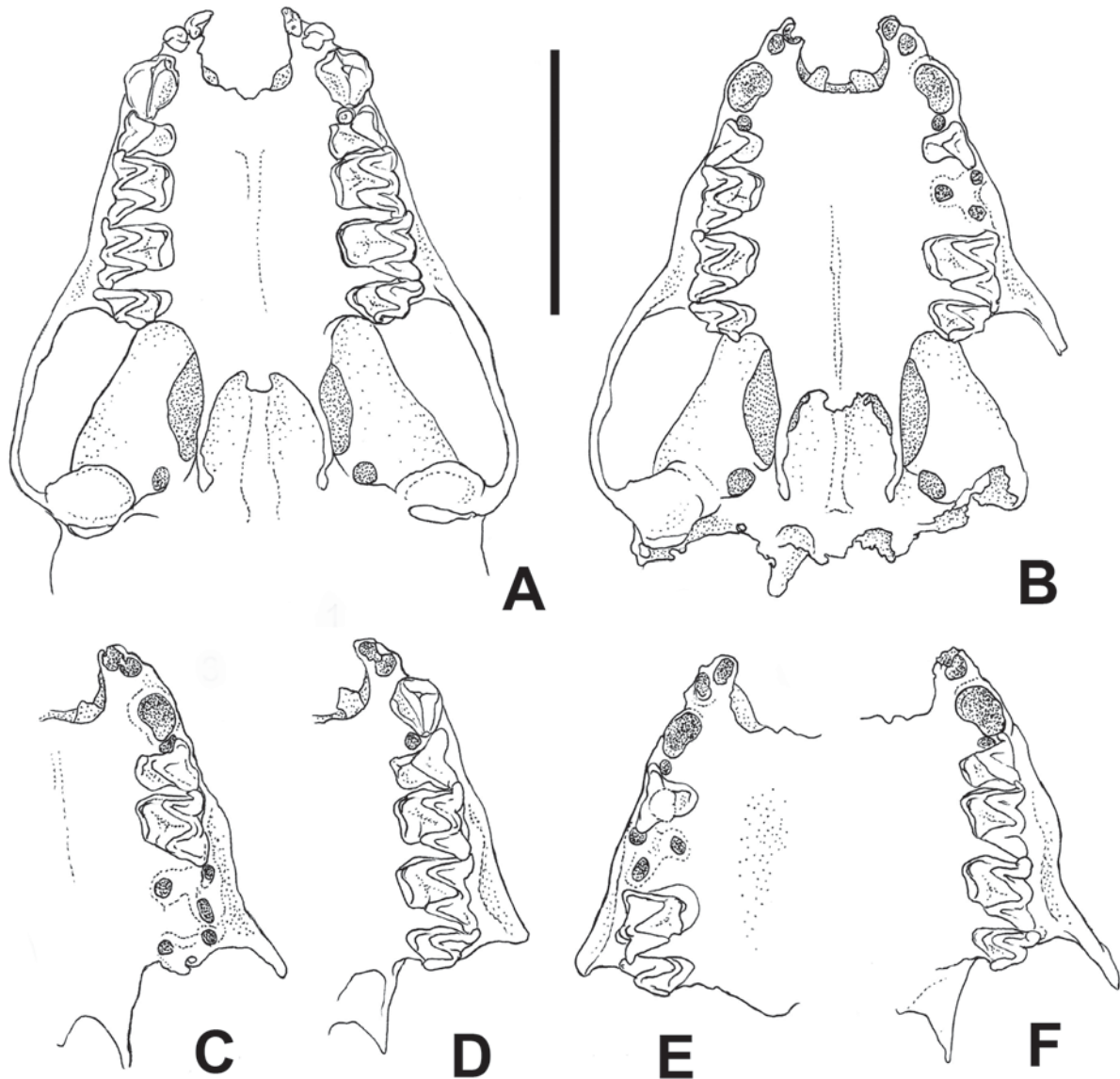


Figure 1. Upper jaws of *Eptesicus nilssoni* with traces of the small upper premolar (P2): A — adult male, captured in Nizhny Novgorod Region, with P2 in the left toothrow (ZMMU S-162550); B–F — premolar alveoli in subfossil skulls from Perm' Territory: E and F — P2 present only in one side (right and left, respectively, as shown), B, C and D — P2 positioned symmetrically of (for C and D only left jaws shown). Scale bar equals 5 mm.

(59.383° N, 57.818° E) and Kamen' (59.491° N, 57.447° E). The age of these deposits as determined by radiocarbon dating is $3\ 628 \pm 86$ years for Bolshaya Mahnevsкая Cave (layer 1.40–1.47 m), $6\ 121 \pm 127$ for Mahnevsкая Ledyanaya Cave (both analysis were made in the A.N. Severtsov Institute of Ecology and Evolution), $16\ 470 \pm 560$ years (upper part of bone containing layer) for Tain Cave (analysis was made in Siberian branch of Russian Academy of Sciences); Sokol'ya Cave (layer 0.0–0.35 m) was not dated yet, but presumably belong to the Late Holocene.

Subfossil remains of *E. nilssoni* were found in association with at least five other bat species: *Myotis*

brandtii, *M. mystacinus*, *M. daubentonii*, *M. dasycneme* and *Plecotus auritus*, however, they dominate in proportion. The number of identified *E. nilssoni* remains totals 664 (14 in Sokol'ya Cave, 11 in Tain Cave, 69 in Mahnevsкая Ledyanaya Cave, and 570 in Bolshaya Mahnevsкая Cave). Identification of excavated skull fragments was made based on published identification manuals and comparison with extant bat skulls preserved in the collection of the Zoological Museum of Moscow University (ZMMU). All subfossil material is housed at the Laboratory of Historical Ecology, Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences.

Results and discussion

A total of nine *Eptesicus* skulls with P2 alveoli were found in all four caves: six in Bolshaya Mahnevskaia Cave and one in each of the remainder caves. Alveoli of P2 in two of these specimens were found on the left side only (Fig. 1F); in one case alveolus of P2 could be seen only on the right side (Fig. 1E); in four cases the position of the alveoli is symmetrical. Only one side of the rostral fragments was retained in two cases. In most specimens the alveolus of P2 was visibly displaced internally from the median of the toothrow. In these cases the canine and P4 were observed to be or extrapolated to have been in close contact, which is typical for *Eptesicus*. However, in four specimens the displacement of P2 alveolus was minimal (Fig. 1B, C), suggesting that the small premolar may have been visible from the buccal side of the toothrow. This corresponds to a stage of its reduction found in some recent *Pipistrellus* and *Hypsugo*.

During the comparison of our subfossil material with the ZMMU collection, an additional anomalous skull was found: an adult male captured in the Ichalki protected area, Perevoz District of the Nizhny Novgorod Region. This specimen possesses a small but well developed P2 in its left tooth row (Fig. 1A). The tooth is conical in shape, rounded in occlusal view, about 0.3 mm in diameter and is almost identical to the same teeth in *Arielulus* and *Hypsugo*.

Members of the genus *Eptesicus* sensu Simmons (2005), i.e. including “*serotinus*” and “*fuscus*” species groups with their most possible relatives, are generally characterized by having only one premolar (P4) in each upper tooth row (Dobson, 1876; Corbet & Hill, 1992). By contrast, some other taxonomically proximate genera possess upper small premolars as a facultative feature subject to intraspecific variation between populations or even between individuals within one population. These genera include *Hypsugo*, *Arielulus*, and *Neoromicia*. The latter two were sometimes synonymized with *Eptesicus* (Koopman, 1993; Volleth & Heller, 1994), although recent molecular data (Hooper & Bussche, 2003), confirm their valid generic status. Within *Eptesicus* proper, no small upper premolars were described, even as rudiments (Hill & Harrison, 1987; Corbet & Hill, 1992). The only alternate idea was expressed by Menu (1987), however without explanation of any concrete examples. Amongst taxa closely related to *Eptesicus* based on DNA sequence data, only *Ia io* has greatly reduced small upper premolars (Bates & Harrison, 1997).

The proportion of northern bats with anomalous dental formula averaged ca. 1.4 percent amongst subfossil material (1.1–9% for different caves). A comparable result was obtained for extant material — about 1.5% (1 out of 67 processed). This leads to suppose that the presence of P2 is a very rare but not an extraordinary case for *E. nilssoni*. This, combined with other archaic morphological traits, makes this species unique

within its genus and challenges its sister position to *E. serotinus* inferred from mtDNA (Mayer & Helversen, 2001), calling for a more thorough revision.

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