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Primitive and derived features in the teeth of modern moose (*Alces,* Cervidae, Mammalia) from Eastern Siberia

Pavel A. Nikolskiy*[1] & Gennadiy G. Boeskorov[2]

ABSTRACT: Variability of evolutionary relevant teeth morphology of modern moose from Eastern Siberia has been studied in comparison with the European form. Primitive deviations have been revealed in Eastern Siberian sample, that is rare in the teeth of moose from Europe. The data suggest that "American" and "European" moose have been developing independently for a long time, which could resulted in differentiation of moose in to two species, *Alces alces* L., 1758 (Europe, Western Siberia) and *Alces americanus* Clinton, 1822 (North America, Eastern Siberia, Far East).

KEY WORDS: Moose, *Alces*, teeth, morphology, variability, Eastern Siberia.

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Архаичные и прогрессивные черты в строении зубов современных лосей рода *Alces* (Cervidae, Mammalia) из Восточной Сибири

П.А. Никольский, Г.Г. Боескоров

РЕЗЮМЕ: Изучена изменчивость эволюционно-значимых признаков зубов современных лосей из Восточной Сибири. Выявлены очень примитивные отклонения, которые крайне редко встречаются у лосей из Европы. Эти данные указывают на длительный период независимого развития «Американских» и «Европейских» лосей в условиях изоляции, что могло привести к дифференциации лосей на два вида — *Alces alces* L., 1758 (Европа, Западная Сибирь) и *Alces americanus* Clinton, 1822 (Северная Америка, Восточная Сибирь, Дальний Восток).

КЛЮЧЕВЫЕ СЛОВА: Лось, *Alces*, морфология, зубы, изменчивось, Восточная Сибирь.

Introduction

Recently the data have been published (Boeskorov, 1998, 2001) confirming K.K. Flerov's concept (Flerov, 1931, 1934) that the modern moose are divided into two species: the "European" elk/moose, *Alces alces* L., 1758 (Europe, West Siberia) and the "American" moose, *Alces americanus* Clinton, 1822 (North America, Eastern Siberia, Far East). Major recent studies on the systematics of *Alces* s.l. do not provide any evidence for this concept (Breda, Marchetti, 2005). In this regard, we studied the degree of premolars molarization variability in moose from Eastern Siberia, in comparison with corresponding variability in moose from Eastern Europe. Molarization of premolars occurred in the history of all deer (including moose) continuously but at different rates (Heintz, 1970; Vislobokova, 1994). Variability of evolutionary relevant features, which includes the degree of premolars molarization, reflects the previous evolutionary processes of the dental system of moose. Isolation, that probably lead to specific differentiation within *Alces*, could promote different ways of the premolars molarization in the isolated groups of moose. Thus, molarization peculiarities of the "American" moose could be an additional argument in favor of their taxonomic independence.

Material and Methods

The last lower premolar, p3 is the most suitable tooth for examination of molarization processes in moose. In phylogeny of deer, molarization in lower premolars progresses anteriorwards from p4 to p3 and p2. The p4 thus shows the strongest molarization degree comparable to m1, p2 is least molarized, and p3 has an intermediate condition between p2 and p4. All deviations in structure of p3 similar to p2 are considered primitive, whereas morphotypes approaching p4 are considered as derived (Fig. 1).

The following features of the p3 involved in molarization were studied (Figs 1, 2):

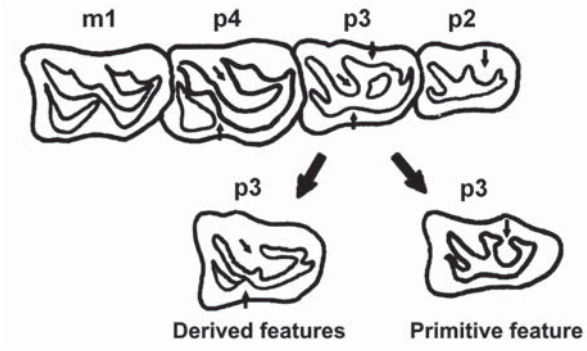

Fig. 1. Primitive and derived deviations in variability of the moose p3.

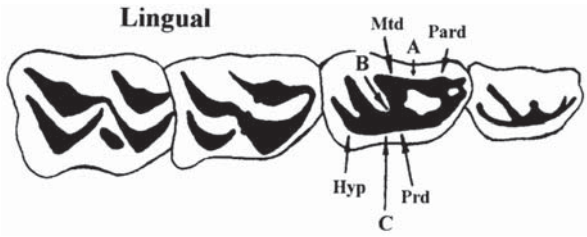

Fig. 2. Nomenclature of moose teeth elements: Prd — protoconid; Mtd — metaconid; Pard — paraconid; Hyp — hypoconid; A — connection of the metaconid with paraconid; B — connection of the protoconid with metaconid; C — connection of the protoconid with hypoconid.

1) Degree of development of tooth lobe that closes the second valley (lobe connecting metaconid and paraconid). Normally, this lobe in *Alces* completely seals the second valley.

2) Degree of development of tooth lobe that connects protoconid and metaconid. In the majority of *Alces* this lobe is well developed.

3) Degree of development of tooth lobe that connects protoconid and hypoconid. Usually, this lobe is well developed.

The development of the investigated features was classified into three categories determined by the degree of connection of conids by lobes (Fig. 3). The first category includes the teeth, on which the lobe connecting conids is well developed (no constriction), the second one houses premolars with a weakened connection between conids (clearly visible constriction, but the continuity of the lobe is not broken), and the third category comprises the teeth with a reduced connection between conids, they have the lobe cut by valley (Fig. 3).

We studied 32 p3 of *Alces* from Eastern Siberia, among which 25 teeth originated from various regions of Yakutia: central part (Gorny and Khangalass districts), south-west (Olyekminsk district), south (Aldan and Neryungri districts), north-east (Nezhnekolymsk district) and seven from the Irkutsk region.

105 p3 of *Alces* from Eastern Europe (Pechora-Ilych Nature Reserve, Eastern East European plain; Mordovian, Prioksky, and Oksky Nature Reserves, Central Russian Plain) have been used for comparison.

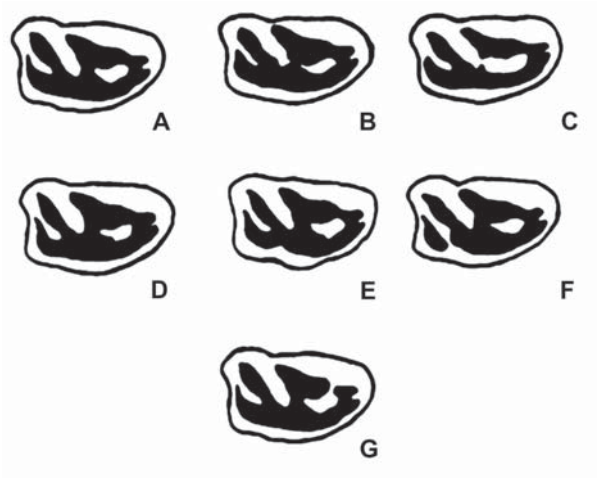

Fig. 3. Variants of the evolutionary significant features of moose premolars from Eastern Siberia. A–C — protoconid-metaconid connection; D–F — protoconid-hypoconid connection; G — metaconid-paraconid connection. A, D — connection well-developed; B, E — connection weakened; C, F, G — connection absent.

The teeth only of moderate and weak degree of wear were selected, because the features under study become indistinguishable on strongly worn teeth.

Results and discussion

Variability of the observed variants of evolutionary significant features of moose premolars from Eastern Siberia are represented in Fig. 3.

Frequency distribution of the features in the East Siberian sample are the following:

1) The lobe closing the second valley is well developed in 74% of cases, the connection between paraconid and metaconid is partially weakened in 13% of cases and *is absent* in 13% of observations (Fig. 4).

2) Connection between protoconid and metaconid is well developed in 52% of cases, it is partially weakened in 16% of cases and is absent in 32% of observations (Fig. 4).

3) Connection between protoconid and hypoconid is well developed in 74% of cases and it is partially weakened in 26% of cases. The cases of complete absence of this connection were not found (Fig. 4).

The frequency distributions of features in the East European sample of p3 are following:

1) The lobe closing the second valley (paraconid-metaconid connection) is well developed in 100% of cases.

2) Connection between protoconid and metaconid is well developed in 22% of cases, it is partially weakened in 46% and weak in 32% of observations (no one case with the absent connection observed).

Features	Development of the features		
	Connection well-developed	Connection weakened	Connection weak or absent
Lobe that closes the second valley	 74%	 13%	 13%
Protoconid-metaconid connection	 52%	 16%	 32%
Protoconid-hypoconid connection	 74%	 26%	 0%

Fig. 4. Frequency of derived and primitive features on p3 in the moose from Eastern Siberia.

3) Connection between protoconid and hypoconid is well developed in 65.5% of cases, partially weakened in 30% of cases, and weak in 4.5%. The cases of complete absence of this connection were not found.

The most noticeable feature of the East Siberian *Alces* is high frequency of morphotypes with the open second valley on the p3. Until now it was thought that the second valley on the p3 of Alceini had closed about 1 million years ago (Nikolskiy, 1995). In modern *Alces alces* from Eastern Europe (more than a hundred of teeth studied) no case of the open valley was found. As a rule, the second valley on the p3 of elk in Western Europe is also closed. Only a few cases of the fossil *Alces alces* p3 with an open valley are known (Maüser, 1990).

It was somewhat unexpected to reveal a relatively high frequency of "derived" p3, with a reduced lobe connecting protoconid with metaconid. But this feature occurs in the studied sample from Eastern Siberia not as frequently (48%) as in the sample of elk from Europe (78%). At the same time the weakened protoconid-hypoconid connection on the p3 of moose from the "American" group is slightly less frequent (26%) than in moose from the "European" group (34.5%). Thus, all derived features, indicating a relatively strong molarization of p3 are more common in moose of the "European" group compared to the "American" group.

It can be concluded that in the "American" group of moose (specimens from Eastern Siberia) primitive morphotypes occur more often than in the teeth of elk from Europe. High frequency of the primitive feature in teeth of the "American" group may indicate that they are closer to their ancestral form than the elk of the "European" group. This conclusion is in an excellent agreement with the mtDNA data. Although the worldwide study of the mitochondrial phylogeography of moose **does not support the existence of distinct eastern and western races**, levels of genetic variation and structure of phylogenetic trees identify *Asia as the origin* of all extant mitochondrial lineages (Hundertmark et al., 2002).

Odontological differences in these elk/moose groups agree with differences in their chromosome sets: the karyotype of the "European" moose (2n = 68) is most likely formed from the karyotype of "American" moose (2n = 70), moreover the latter group of moose may be more ancient, because the 70-chromosome karyotype is ancestral for the family Cervidae (Graphodatsky, 1991; Groves & Grubb, 1987; Boeskorov, 2001).These data indicate that the "American" and "European" elk/moose, apparently developed independently during some period of the geologic time, which may be a justification of Flerov's concept on differentiation of modern moose in two groups of the species rank, the "European" group (Europe, Western Siberia) and "American" one (North America, Eastern Siberia, Far East).

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