

# The genetics of the modern moose and a review of its taxonomy

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## Summary

The results of investigations on genetics and systematics of the moose are presented. New data from our own research and data from the literature on morphological variability, genetics, ecological and ethological features of the modern moose are discussed. Numerous data testify that differentiation among modern *Alces* has reached a specific level and they divided into two species: European moose *Alces alces* L. inhabiting Europe, Ural, and Western Siberia and American moose *A. americanus* Clinton inhabiting North America, Eastern Siberia, and the Far East. These species differ in chromosome numbers (European moose has  $2n=68$ , American moose has  $2n=70$ ), as well as in some eco-ethological features. In light of new data a revision of the systematics of the moose is carried out, and questions on phylogeny are considered.

## Samenvatting

De resultaten van onderzoek naar de genetica en de systematiek van de eland worden in dit artikel gepresenteerd. Gegevens afkomstig van eigen onderzoek en uit de literatuur over morfologische variatie, erfelijkheid, ecologische en gedragskenmerken van de moderne eland worden besproken. Veel gegevens ondersteunen het idee dat de differentiatie in de moderne *Alces* een soortspecifiek niveau heeft bereikt, en in twee soorten onderverdeeld kan worden: de Europese eland *Alces alces* L., voorkomend in Europa, de Oeral en west Siberië, en de Amerikaanse eland *A. americanus* Clinton, voorkomend in Noord Amerika, oost Siberië en het uiterste oosten van Rusland. Deze soorten verschillen in chromosoomgetal (de Europese eland heeft 68 chromosomen in de diploïde set, de Amerikaanse eland echter 70), maar ook in enkele eco-ethologische kenmerken. Aan de hand van nieuwe gegevens wordt een revisie ondernomen van de systematiek van de eland, en worden vragen betreffende hun fylogenie behandeld.

## Introduction

The moose is the largest representative of the family of deer. The original English name of *Alces alces* is 'elk', but nowadays the American name, 'moose', is usually used in scientific literature. It essentially differs from the other deer by its habitus: very massive but with a rather short

trunk, a strongly developed thorax, a large, elongated and hump-nosed head, a very large and massive upper lip, very large and wide ears, very long legs, and a long 'bell', which is a hanging outgrowth of skin under the throat. The antlers in the male project laterally from the head and are usually palmated (shovel-shaped expanded). The front part of the moose torso is more massive than the hind part (fig. 1).

The systematic position of the modern moose is under discussion. Within their huge Holarctic habitat, the moose is represented by a number of forms with various degrees of morphological isolation. The opinion prevails that Northern Eurasia and North America is occupied by one species - *Alces alces* L. -, which contains a maximum of eight subspecies: the European moose or elk (*A. a. alces*), the East-Siberian moose (*A. a. pfitzenmayeri*), the Manchurian or Ussuri moose (*A. a. cameloides*), the Buturlin's moose (*A. a. buturlini*), the Alaskan moose (*A. a. gigas*), the West-Canadian moose (*A. a. andersoni*), the East-Canadian moose (*A. a. americanus*), and the Yellowstone moose (*A. a. shirasi*) (Peterson, 1955, 1974; Sokolov, 1959; Heptner *et al.*, 1961; Wilson & Reeder, 1992; Geist, 1998). The first description of the moose as a species (*Cervus alces*) was made by



Fig. 1. Moose male. The Kolyma river basin. Photo by Yu. Labutin

Mannelijke eland in de vallei van de Kolyma rivier.  
Foto: Yu. Labutin

Karl Linné in 1758, based on the moose from Sweden as *Cervus alces*; gradually this name became used for other moose populations as well. In 1821 Gray attributed the species into the separate genus *Alces*. Since the description of the American moose as *Cervus americanus* Clinton 1822, a number of the researchers considered this a separate species, distinct from the European *A. alces* (Miller, 1899; Seton, 1910; Lydekker, 1915; Anthony, 1928). An interesting detail is that during the 20th century several times moose were imported in England from Canada; some experts (Rolfe, 1983) even identified them with the extinct giant deer, or Irish elk, *Megaloceros giganteus*. Unfortunately Linné himself never saw the American moose.

Based upon some morphological features of the moose, Flerov (1931, 1934) revealed some differences between moose from Europe and North America, and concluded that East Siberian moose are closer to the latter than to European moose. He proposed two separate moose species: *A. alces* L., inhabiting Scandinavia, part of Eastern Europe, and Siberia westward of the Yenisey river, and *A. americanus* Clinton, inhabiting North America, Siberia eastward of the Yenisey, and the Far East. Although some scholars agreed with this (e.g. Vereshchagin, 1949), Flerov later stated that the observed differences did not exceed subspecies level (Flerov, 1952). Nevertheless, his earlier opinion had large influence and many Russian mammalogists considered the moose from East and Northeast Siberia to belong to the American moose (Bobrinsky *et al.*, 1944; Gromov *et al.*, 1963; Baryshnikov *et al.*, 1981). It was agreed upon that the American moose probably differ from European ones at a species level (Gromov *et al.*, 1963; Chernyavsky & Domnich, 1989) or subspecies level (Groves & Grubb, 1982). Subsequently, differences in chromosome numbers, and in a number of other genetic, ecological and ethological features were found between the European and North American moose. For a long time the morphologic and genetic differences between the European and American moose attracted the attention of the specialists and were discussed in some monographic works (Filonov, 1983; Bubenik, 1986; Chernyavsky & Domnich, 1989; Danilkin, 1999). Nevertheless, the question on the number of species and subspecies of modern moose remains till now unsolved.

In order to solve this problem we started research on the systematics, genetics and morphological variability of the moose in 1992. In this article we present our analysis on the differentiation in

genetic material of the European, Siberian, the Russian Far Eastern and American moose; part of our results has already been published (Boeskorov, 1996a, 1996b, 1997, 1998; Boyeskorov, 1999). Results from our morphological and palaeontological studies will appear in the next two issues of *Cranium* (2004).

## Material and Methods

For the study of karyotypes of moose from central and northeast Yakutia (Eastern Siberia), four males and one female were shot in the Sakha region (Kolyma river basin, Gorny district, and Khangalassky district; see Boeskorov, 1997). The chromosomes were studied in short-term cultured cells of bone marrow, with the use of standard methods of staining (Ford & Hamerton, 1956) and silver-staining (Howell & Black, 1980). Heterochromatin regions of the chromosomes of a Kolyma river basin male were revealed by C-banding (Sumner, 1972). The polymorphism of DNA markers was studied by Udina (Udina *et al.*, 2002) in seven moose muscle samples collected by us in Yakutia.

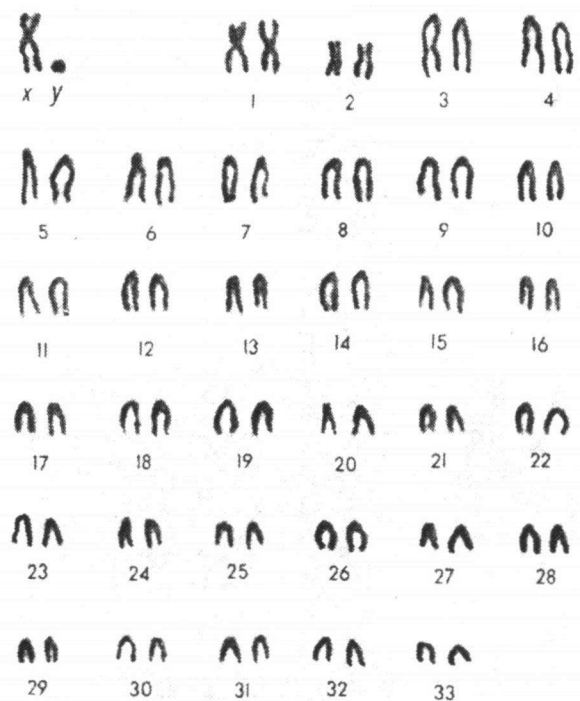


Fig. 2 Karyotype of a moose male from the south of Western Siberia, Altai mountains (after Grafodatsky & Radjabli, 1988).

Het karyotype van een mannelijke eland uit het zuiden van West Siberië, Altai gebergte (naar Grafodatsky & Radjabi, 1988)

## Genetics of the moose

### Karyological data

Karyological studies of moose in Europe and North America began in the 1960s. These studies demonstrated that moose from these regions differ in chromosome number: moose from Scandinavia and Finland had 68 chromosomes in the diploid set (Aula & Kääriäinen, 1964; Nes *et al.*, 1965; Gustavsson & Sundt, 1968), whereas moose from northeastern Canada and northwestern USA had 70 chromosomes (Hsu & Benirschke, 1969). These distinctions were until recently considered as an intraspecific dimorphism of *A. alces* (after Orlov & Bulatova, 1983). Similar results were obtained for moose from other parts of its geographic range: moose with  $2n=68$  occur also in Finland (Gripenberg *et al.*, 1986), Western

Siberia and Altai (fig. 2; Grafodatsky & Radjabli, 1985; 1988), the Saratov district (A. Belyanin, pers. comm.), and moose with  $2n=70$  occur also in Alaska (Rausch, 1977) (fig. 3; table 1). In addition, karyotypes of moose from the extreme northeast of Asia (the Kolyma river basin) and from Central Yakutia were found to be identical to those of American moose ( $2n=70$ ) (Boeskorov, 1996a, b; 1997; Boeskorov *et al.*, 1993) (fig. 4).

The basic number of chromosome arms of all moose is identical ( $NFa = 70$ ). Among the autosomes of European and Altai *A. alces* two pairs of bi-armed chromosomes are present, whereas North American and East Siberian moose had only one bi-armed pair. The X-chromosome is large and submetacentric in all moose; the Y-chromosome is usually the smallest acrocentric

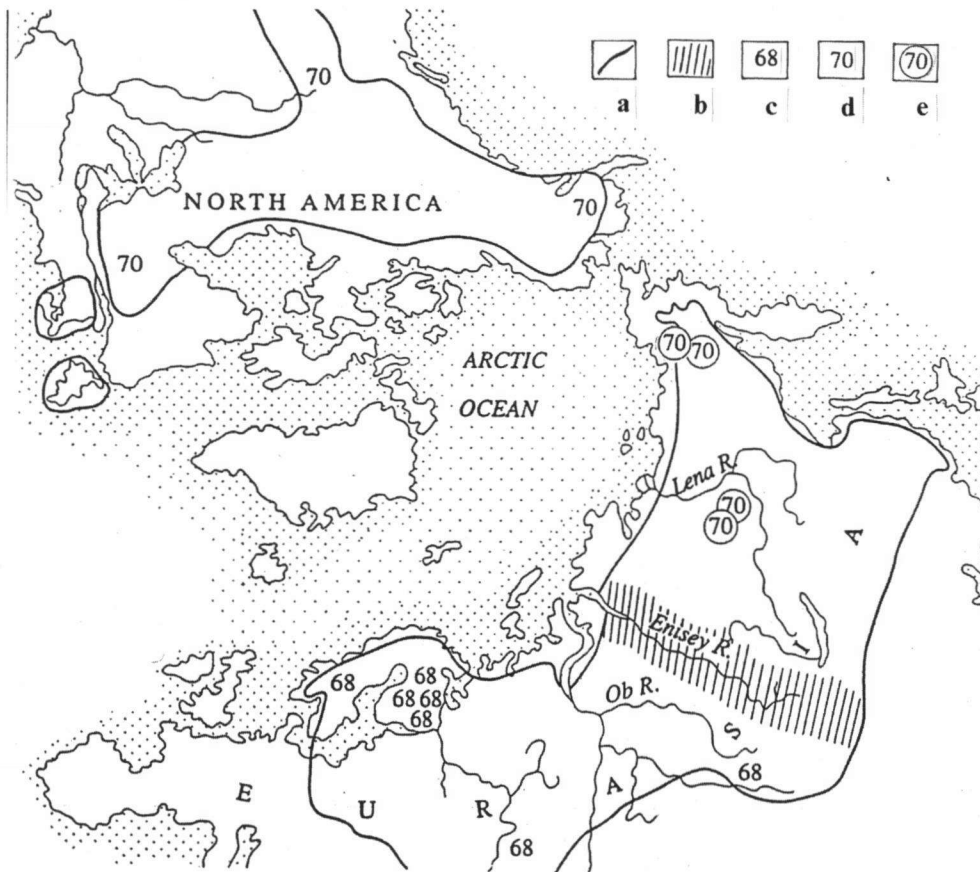


Fig. 3 Geographic differences in moose chromosome numbers (after Boeskorov, 1997. a = the modern area of genus *Alces* (acc.to: Peterson, 1955, 1974; Filonov, 1983); b = the hypothetical border between the European and American forms of moose; c = "68", findings of the European chromosomal form; d = "70", findings of the American chromosomal form; e = "(70)", chromosome numbers in East and North-East Siberian moose (data of the author)

Geografische verschillen in chromosoomgetal van eland (naar Boeskorov, 1997). a = huidige verspreidingsgebied van het geslacht *Alces* (volgens Peterson, 1955, 1974; Filonov, 1983); b = de denkbeeldige grens tussen de Europese en Amerikaanse vormen van eland; c = "68", vondsten van de Europese chromosomale vorm; d = "70", vondsten van de Amerikaanse chromosomale vorm; e = "(70)", chromosoomgetallen in Oost en Noordoost Siberische eland (gegevens van de auteur)

chromosome. In Finland and Scandinavia a few individuals are found with a meta- or submetacentric Y-chromosome (Aula & Kääriäinen, 1964; Gustavsson & Sundt, 1968; Gripenberg *et al.*, 1986).

The karyotype of moose from the Kolyma river basin has a large amount of C-heterochromatin (Boeskorov *et al.*, 1993) (fig. 4), which is also characteristic for European and West Siberian moose (Grafodatsky & Radjabli, 1985; Gripenberg *et al.*, 1986). All acrocentric chromosomes

Table 5 Diploid chromosome sets in moose from different geographic regions. The number of animals studied is not indicated.

Diploide chromosoomparen in elanden van verschillende geografische streken. Het aantal bestudeerde dieren is niet aangegeven.

Region	Number of animals karyotyped	2n	Reference
Sweden	6	68	Gustavsson & Sundt, 1968
Norway	+	68	Nes <i>et al.</i> , 1965
Finland	218	68	Aula & Kaariäinen, 1964; Gripenberg <i>et al.</i> , 1986
Russia, Saratov district	1	68	A. Belyanin (pers. comm.)
Western Siberia, Altai	5	68	Grafodatsky & Radjabli, 1985
Eastern Siberia, Central Yakutia	3	70	Boeskorov, 1997
North-Eastern Siberia, middle stream of the Kolyma river	1	70	Boeskorov <i>et al.</i> , 1993
North-Eastern Siberia, lower stream of the Kolyma river, near Chersky village	1	70	Our unpublished data
USA, Alaska	+	70	Rausch, 1977
North-Eastern Canada	1	70	Wurster & Benirschke, 1967; Hsu & Benirschke, 1969
North-West of USA, Montana	1	70	Wurster & Benirschke, 1967; Hsu & Benirschke, 1969

have expressed pericentromeric C-heterochromatin blocks that sometimes amount to half and more of the total chromosome length. At the same time, C-heterochromatin blocks seem to be lacking on the pairs of bi-armed autosoms and on the X-chromosome of the Kolyma moose. In the moose from Finland these blocks are visible on certain chromosomes (Gripenberg *et al.*, 1986). Moose from Altai had no heterochromatin blocks on the X-chromosome and the second pair of bi-armed autosomes (Grafodatsky & Radjabli, 1985). Thus, it seems that the Altai moose has an intermediate variant of heterochromatin distribution between European and East Siberian moose (the latter belongs to the American group). The Y-chromosome in all investigated moose is completely heterochromatic.

The nucleolar organizing regions of chromosomes (NOR's) in moose from Yakutia are present in teleomeric regions of the four largest chromosomes from the first, and second or third autosome pairs (fig. 4) (Boeskorov, 1997; Boeskorov *et al.*, 1993). By number and, apparently, on localization of NOR's the Kolyma and central Yakutian moose do not differ from Finnish *A. alces* (Gripenberg *et al.*, 1986) and Altai moose (Grafodatsky & Radjabli, 1985). A similar number and localization of NOR's is found at the majority of the investigated deer species of the genera *Rangifer*, *Cervus* and *Dama* (Grafodatsky *et al.*, 1990). The stability of this karyotype, which is characteristic for different genera of deer, has apparently an ancient nature, and may reflect features of the ancestral karyotype of the family Cervidae.

Karyological data testify a high level of differentiation among moose: they can be divided on chromosome number: European (2n = 68; Europe, Western Siberia) and American (2n = 70; North America, Russian Far East and Eastern Siberia) (fig. 3, table 1). This dimorphism of chromosome number is not present within these two forms, for example, the karyotypes of more than 200 individuals in Finland all contain exactly 68 chromosomes (Gripenberg *et al.*, 1986).

The difference in chromosome number of the European and American moose is explained by fusion of two acrocentric autosome pairs into two large metacentrics (Grafodatsky *et al.*, 1990; Gripenberg *et al.*, 1986; Groves & Grubb, 1982). Proceeding further from this, it is possible to assume that European-West Siberian moose with 2n=68 originally originated from the East Siberian-American moose with 2n=70. Thus, the latter

should then be more ancient, since the karyotype with  $2n=70$  is considered ancestral for the family Cervidae (Groves & Grubb, 1982; Grafodatsky *et al.*, 1990).

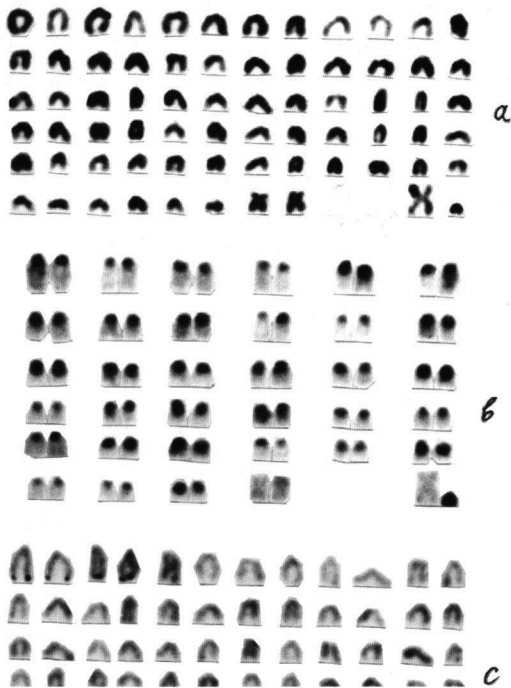


Fig. 4 Chromosome number of a moose male from the Extreme North-East of Asia (the Kolyma river basin, near Zyryanka village). a = routine staining; b = C-banding; c = AgNOR-staining

Chromosoomgetal van een mannelijke eland uit het meest noordoostelijke deel van Azië (het dal van de Kolyma rivier, vlakbij het dorp Zyryanka). a = standaard kleuring; b = C-band patronen; c = zilverkleuring (AgNOR)

Differences in chromosome number between closely related forms are factors for subsequent genetic isolation (Vorontsov, 1958; Ayala, 1975; Timofeeff-Ressovsky *et al.*, 1977; Orlov & Bultova, 1983), and they can provide evidence for specific differences between these forms.

#### Electrophoretic mobility of proteins

The first electrophoretic investigations of blood proteins in moose showed a complete absence of electrophoretically determined genetical distinctions between European and North American moose (Nadler *et al.*, 1967; Wilhelmson *et al.*, 1978).

Further electrophoretic research of twenty biochemical loci carried out on a large number of moose from Scandinavia and Canada, revealed a low level of differentiation between them. The

genetic distance between these moose is  $D=0.0602$  (Reuterwall & Ryman, 1979; Reuterwall, 1980), which is less than that between reindeer (*Rangifer tarandus tarandus*) and caribou (*R. t. caribou*) ( $D=0.174$ ; Baccus *et al.*, 1983), but larger than that between European red deer (*C. elaphus elaphus*) and American wapiti (*C. e. canadensis*) ( $D=0.0248$ ; Dratch & Gyllensten, 1985).

#### Analysis of DNA polymorphism

During the last years molecular genetic research of moose DNA structure has been carried out. Though in general it was noted that moose have a low level of genetic variability, interesting results came out which have a large value for the systematics and phylogeny of these animals.

Research of mitochondrial DNA structure of representatives of all four North American subspecies of moose has shown the absence of variability of this feature (Cronin, 1992), which phenomenon testifies to the presence of the "effect of the founder" (Cronin, 1992) in *Alces* history of North America and confirms the opinion that the moose moved from its refuge in Alaska into North America after the last ice sheet had melted in the beginning of the Holocene (Geist, 1987; Kurtén & Anderson, 1980).

The study of a major histocompatibility complex (MHC) through analysis of nuclear and mitochondrial DNA of Scandinavian and Canadian moose has shown that the low genetic variability is characteristic for them as a whole (Mikko & Andersson, 1995). These researchers investigated the variability exon-2 of a gene DRB-1 and found distinctions in an allelic set of a locus DRB-1 between Swedish and Canadian moose. Among the revealed 10 alleles of DRB-1, 7 and 4 alleles among Swedish and Canadian moose, respectively, were specific and only one allele was shared between continents. Nevertheless, the variability of this gene appeared to be low, which was explained by loss of the variability, probably due to a selection response on one or several preferred haplotypes MHC, or to a 'bottleneck-effect' during evolution, which took place before the division into different subspecies. Research of a fragment of a mitochondrial DNA control region (D-loop) has shown distinctions between moose from Scandinavia and Canada: mtDNA of the former contained an insertion of 75 nucleotides (Mikko & Andersson, 1995).

Recently, the study of DNA polymorphism shows a more complicated picture among the Old and New World moose. The most distinctions are found between North American and European



moose, and the absence of the 75-bp insertion in mtDNA in the former is a reliable marker to distinguish them from the latter (studied in Scandinavia, Eastern Europe, Ural and western Siberia). Among moose from Eastern Siberia, the Russian Far East and Manchuria, however, a high level of mtDNA polymorphism was found. Many specimens (about 45 %) from these regions also lack the 75-bp insertion and belong to American haplotype, but the remaining specimens have the insertion and belong to the European haplotype or to a separate Asian haplotype, which differs from the European haplotype in some other mtDNA features (Hundertmark *et al.*, 2002; Udina *et al.*, 2002). The absence of Asian-like haplotypes on the European territory and in western Siberia corresponds to the geographic distribution of moose karyotypes ( $2n=68$  and  $2n=70$ ). A variable picture similar to the mtDNA variants was revealed in the study of MHC polymorphism of moose from Europe, Siberia and the Russian Far East (Udina *et al.*, 2002). As in the work by Mikko and Andersson (1995), it appeared that European and North American moose differ in their set of DRB1 alleles, but among Yakutian and Ussurian moose three alleles typical for *A. a. americanus* and three alleles typical for Swedish moose were found. These complicated data show that most DNA differences exist between European and North American moose. Moose from Eastern Siberia (*A. a. pfitzenmayeri*) and from the south of the Far East (*A. a. cameloides*) represent the highest genetic variation and probably represent the oldest moose populations (Hundertmark *et al.*, 2002; Udina *et al.*, 2002), although this high genetic diversity of the Yakutian and Manchurian moose could as well be the result of ancient hybridization between European and American moose (Udina *et al.*, 2002).

Similar results on moose mtDNA variation were obtained by Lister & Pijlen (1998). The low mtDNA variation made them suggest a "star phylogeny" and a recent "bottleneck" effect among moose (Lister & Pijlen, 1998; Hundertmark *et al.*, 2002). Lister & Pijlen (1998) consider the aberrant *A. a. cameloides* "to be a recently derived and reduced moose, rather than a relict ancestral form", which opinion is not shared with later studies (Hundertmark *et al.*, 2002; Udina *et al.*, 2002).

## Ethological features

### Sound signalization

The acoustic signals in mammals are supposed to be genetically inherited (Nikolsky, 1992). The distinctions in the sound signal system between European and American moose once again evidently testify that these groups of moose are essentially diverged from each other.

Males of European (*A. a. alces*) and American moose (*A. a. gigas*) make different sounds during the rutting season (Lent, 1974; Bogomolova *et al.*, 1984). In the European moose, these signals resemble grunting, while the Alaskan moose make deep, resonant sounds followed (or sometimes preceded) by nonvocal sound resembling suction. Cries of female American moose (*A. a. americanus*, *A. a. gigas*), unlike European, are longer and probably louder, and have a higher average frequency and demonstrate a wider range of both frequency and temporal variations (Lent, 1974; Bogomolova *et al.*, 1984).

Among red deer *Cervus elaphus* two groups of subspecies are distinguished on morphological grounds, as is the case with moose: the western, or elaphoid group, and the eastern, or wapitoid group (also known as maral's group). The level of divergence between these groups approaches that of the specific divergence, or even reaches it. Representatives of these groups are also well diagnosed on sound signals which males make during the rutting season (Nikolsky, 1984).

### Helmintological data

At present more than sixty species of helminths (worms) are known in moose. Many of them occur throughout the complete geographic range of the genus. Others are recorded only in the eastern part of the geographic range of the moose (Eastern Siberia and the Far East; for example the cestode *Moniezia expansa*, and the nematodes *Acantospiculum cervipipedis*, *Parabronema skrjabini*, *Spicalopteragia schulzi*, and *Alceffilaria abramovi*). Again others are found only in the western part of the geographic range: the fluke *Parafasciolopsis fasciolaemorpha*, and the nematodes *Setaria labiato-papillosa*, *Bunostomum trigonocephalum*, *Fasciola hepatica*) (Pryadko, 1976; Filonov, 1983; Zheleznov, 1990). These differences provide indirect evidence for the rather ancient differentiation of the genus *Alces* into two large groups.

### Pheromones

Between Norwegian and North American moose distinctions in the composition of sexual pheromones are found (after Bubenik, 1986).

## Taxonomic diagnostics of *A. alces* and *A. americanus* and their subspecific systematics

Numerous data testify that the differentiation among modern *Alces* has reached a high level and that they can be divided into two large groups: European moose (Europe, Ural, Western Siberia) and American moose (North America, Eastern Siberia, and the Far East). Representatives of these groups differ in chromosome numbers (European moose have  $2n=68$ , American moose have  $2n=70$ ), as well as in morphological (pelage colour, body and skull proportions, non-metrical features of skull and antlers) and some ecological and ethological features.

In contrast with these differences, only low levels of genetic differentiation between European and American moose were found in studies of electrophoretic mobility of proteins and DNA markers (see above). Examples of unequal rates of molecular, chromosomal and morphological evolution are, however, not rare among mammals. There are more cases that show that different ungulate species that can be distinguished by morphological and genetic features yet have a low level of genetic distances as determined by electrophoretic mobility of proteins. For example, a very low level of genetic differences was found between the American buffalo (*Bison bison*) and domestic cattle (*Bos taurus*), which even belong to different genera according to the prevailing opinion (Baccus *et al.*, 1983). Among cervids a low level of differentiation ( $D=0,149$ ) was found between mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) (Baccus *et al.*, 1983), a comparatively low genetic distance ( $D=0,390$ ) was found between American wapiti (*Cervus elaphus* spp.) and sika deer (*C. nippon mantchuricus*) (Emerson & Tate, 1993), etc. On the other side, there are some cases in which closely related forms (for example, subspecies), which have a low level of  $D$ , yet have a high level of DNA differentiation. For example, the genetic distance between European red deer (*C. elaphus elaphus*) and American wapiti (*C. e. canadensis*) is smaller than that between the European and American moose ( $D=0,0248$ ; Dratch & Gyllensten, 1985). However, these same *Cervus elaphus* subspecies differ significantly in mitochondrial DNA markers, therefore it was suggested to consider them as two separate species: *C. elaphus* and *C. canadensis*, based upon their differences in morphology, behaviour and DNA

markers (Lister & Pijlen, 1998). The European bison (*Bison bonasus*) and American bison (*B. bison*), being undoubtedly separate species, differ at the same time only slightly in some DNA markers (Miyamoto *et al.*, 1989; Morris *et al.*, 1994; Sipko *et al.*, 1997). The same scenario is also revealed between some other closely related species of ungulates: *C. elaphus* and *C. nippon*, *Capreolus capreolus* and *C. pygargus*, *Bos taurus* and *B. indicus* (Potapov *et al.*, 1998). Such examples are not restricted to ungulates.

In our view, the sum of differences clearly demonstrates that the divergence between European and American moose has reached a specific level. The clearest evidence for this is the existence of differing chromosome sets. Such a differentiation between related forms are due to factors of genetic isolation which, in turn, create effective post-zygotic factors of reproductive isolation (Vorontsov, 1958; Ayala, 1975; Timofeeff-Ressovsky *et al.*, 1977). Modern moose consists thus of two distinct species: *Alces alces* L. (inhabiting Scandinavia, parts of Eastern Europe, the Ural and Western Siberia) and *A. americanus* Clinton (inhabiting North America, Eastern and North-Eastern Siberia and part of the Russian Far East).

The forms that are genetically spoken the most far removed from each other are North American and Scandinavian populations of *Alces*. The Siberian and Russian Far Eastern moose may have traces of hybridization between the two species. This is indicated by the Altai *A. alces* on the basis of its chromosome heterochromatin distribution. Furthermore, among the East Siberian and Russian Far Eastern *A. americanus* some individuals are present with the European variant of mitochondrial DNA.

### *Alces alces* Linnaeus, 1758 – European moose, or elk

1758. *Cervus alces* Linnaeus, Syst. Nat. (10th ed.) 1: 16.

1827. *Cervus coronatus* Lesson, Man. Mammal.: 356.

1837. *Alces machlis* Ogilby, Proc. Zool. Soc. London (1836): 135.

1843. *Alces palmatus* Gray, List Mamm. Coll. Brit. Mus.: 182.

1860. *Alces jubata* Fitzinger, Naturg. Säugeth. 4: 86.

**Holotype.** Unknown. Sweden, Vänersborg.

**Characters.** Karyotype consists of 68 chromosomes. Colouring of trunk and head rather monotonous, brown and dark-brownish. The lower part of limbs is light grey, whitish. Nasal mirror (rhinarium) is elongated, ellipsoid. Nasal cartilages are moderately developed; top of the

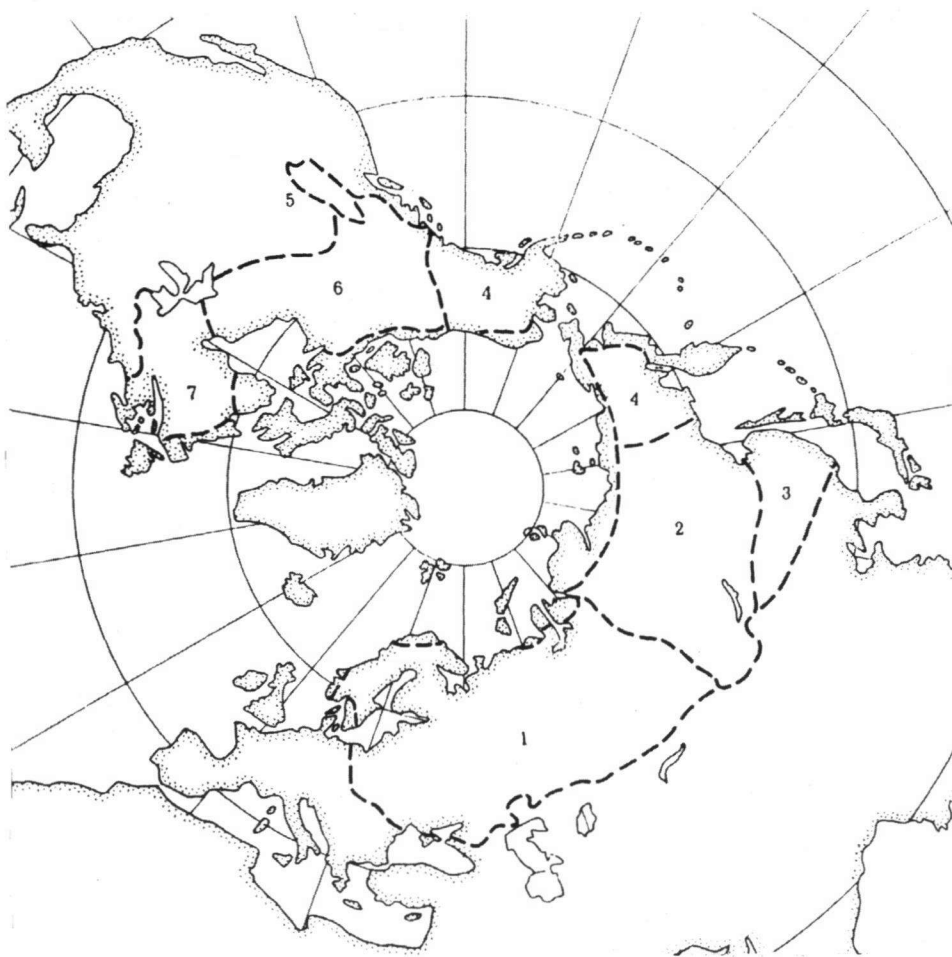


Fig. 5 Moose species and subspecies distribution at present. 1 = *Alces alces alces*, 2 = *A. americanus pfizenmayeri*, 3 = *A. a. cameloides*, 4 = *A. a. gigas*, 5 = *A. a. shirasi*, 6 = *A. a. andersoni*, 7 = *A. a. americanus*

Huidige verspreiding van elandsoorten en -ondersoorten. Voor verklaring van de nummers, zie Engelstalig onderschrift

muzzle forms an almost straight line, nose height is almost equal to width or slightly exceeds it. Upper (nasal) processes of the premaxillary bones are spoon-like widened.

**Description.** Large, medium and small-sized moose. Mature bulls reach a withers' height of 190 to 200 cm, body length of 260 to 275 cm, live weight upto 500 or even 600 kg. Comparatively short rostrum. Antlers with broad, undivided single palm or deer-shaped (without palm) prevail. Antlers spread usually about 100 cm, but sometimes reach 135 cm. Width of antler shovel (palmation) is 20 to 30 cm. Antler beam comparatively short, usually 5 to 10 cm.

**Distribution.** Scandinavia, part of Eastern Europe, Ural, Western Siberia (including Altai) eastward approximately till the Yenisey river.

Till the 20th century the species contained two living subspecies, but at present only one remained.

***Alces alces alces* Linnaeus, 1758 - European moose, or elk**

1913. *Alces machlis uralensis* Matschie, Beroff. Inst. Jagdkunde. Neudamm 2: 155. "Southern Urals". Type specimen in Zoological Museum of Humboldt's University, Berlin.

1913. *Alces machlis meridionalis* Matschie, Beroff. Inst. Jagdkunde. Neudamm 2: 156. "Samarskaya guberniya". Type specimen in Zoological Museum of Humboldt's University, Berlin.

1915. *Alces alces tymensis* Zykowsky, Arch. Naturg. 80, 9: 42. "Tomsk district, the Tym river". Type specimen in Zoological Museum of Humboldt's University, Berlin (?).

1915. *Alces alces alces* Lydekker, Cat. Ungulate Mamm. Brit. Mus. (Nat. Hist.) 4: 232.



Holotype. Unknown. Sweden, Vänersborg.

Characters. Upper processes of the premaxillary bones are widened spoon-like, and do not come into contact with the nasal bones.

Description. A large to medium-sized moose. Antlers with broad undivided palm or deer-like antlers prevail. Condilobasal skull length usually 530 to 560 mm.

Remarks. In spite of the fact that West Siberian moose are a little larger than East European moose, they do not differ significantly.

Distribution. Scandinavia, Finland, Poland (whence it comes into East Germany, Czechia and Austria), Baltic countries, Russia (wood zones of the European part, Ural and Western Siberia (including Altai), north of Kazakhstan) and the western part of Mongolia (fig. 5).

#### ***Alces alces caucasicus* Veretschagin, 1955 - Caucasian moose**

1955. *Alces alces caucasicus* Veretschagin, Zool. Journal 34, 2: 461.

1956. *Alces alces caucasicus* Naniev, Scientific papers of the North Osetian State Pedagogical Inst. 20.

Lektotype. ZIN 23615 (male), skull without lower jaw. Northern Osetia, Makhchet district, Digo-rized cave, Uruk river. ZIN RAS, St.-Petersburg.

Remarks. Got extinct at the beginning of the 20th century, so information on this moose is based on the bone material only.

Characters. Upper processes of the premaxillary bones are spoon-like, very wide and long and practically reach the nasal bones. Antlers are deer-like.

Description. Medium and small-sized moose. Condilobasal skull length is 520-540 mm.

Distribution. Forests of the foothills of the Northern Caucasus, part of Transcaucasia (shore of the Black Sea).

#### ***Alces americanus* Clinton, 1822 - American moose**

1822. *Cervus americanus* Clinton, Letters on Nat. Hist. and Inst. Resources of New York: 193.

1835. *Alces americanus* Jardine, Nat. Library 21 (Mammalia: deer, antelope, camels, etc.): 125.

1867. *Cervus cameloides* Milne-Edwards, Ann. Sci. Nat., Zool. 7: 377.

1899. *Alces gigas* Miller, Proc. Biol. Soc. Wash. 13: 57.

1902. *Alces bedfordiae* Lydekker, Proc. Zool. Soc. London 1: 109.

1910. *Alces pfizenmayeri* Zykowsky, Wild und Hund 16: 807.

Holotype. Unknown. "Country north of White-stone" (probably in western Adirondak region), New York.

Characters. Karyotype consists of 70 chromo-

somes. Colouring of trunk and head mainly brown and dark-brown. Different parts of the body differ in colour from light-brown to almost black. The colour of the lower part of the limbs ranges from light-brown to dark-brown or grey. Nasal mirror is widened in the upper part and pear-shaped. Nasal cartilages are strongly developed; top of the muzzle is humped, nose height exceeds sufficiently its width (almost 1,5 times). Upper processes of the premaxillary bones are wedge-like narrowed.

Description. Large, medium and small-sized moose. Mature bulls reach a withers' height of 220 cm and more, body length of 300 cm and more, live weight to 600 kg and more. Comparatively long rostrum. Antlers with broad, divided (double) palm prevail; anterior (brow) palm is separated from the main palm. Only for Ussurian moose the deer-like antlers are characteristic. Antlers spread usually more 100 cm, sometimes even 150 to 160 cm, with a recorded maximum of 200 cm. Width of antler shovel (palmation) is 20 to 40 cm. Antler beam comparatively long, usually 9 to 11 cm.

Distribution. Forest zone of North America, Eastern Siberia west-ward to the Yenisey river basin, Russian Far East, north and east Mongolia, north-eastern China.

Remarks. Among American moose upto seven subspecies were described: three in Eurasia and four in North America. We agree with six subspecies, and consider moose from the extreme North-East of Asia and Alaska consubspecific with *A. a. gigas*. The treatment of four subspecies in North America is rather traditional, and it is more likely that there are not sufficient differences between *A. a. americanus* and *A. a. andersoni* to treat them as two subspecies (Grubb & Gardner, 1988). Nevertheless we have not enough cranial material of these subspecies, and therefore consider them for the time being as separate subspecies.

*A. americanus* includes the following six subspecies, which are considered according to their geographical distribution in Eurasia and North America (fig. 5):

#### ***Alces americanus pfizenmayeri* Zykowsky, 1910 - East Siberian, or Yakutian moose**

1910. *Alces pfizenmayeri* Zykowsky, Wild und Hund 16: 807.

1911. *Alces machlis yakutensis* Millais, The Field 118: 113.

Holotype. Unknown. Eastern Siberia, Yakutia, the Aldan river basin.

**Characters.** Antler palmation is divided into two parts, the anterior (brow) palm is divided into one to three branches. Antler length is 90 to 110 cm. Condilobasal skull length usually is 540 to 565 mm.

**Description.** A large-sized moose. Mature bulls reach a withers' height of 190 to 205 cm, body length of 265 to 290 cm, live weight of 400 to 500 kg. Antlers spread 100 to 110 cm, width of antler shovel (palmation) is 20 to 30 cm, antler length is usually approximately 100 cm.

**Distribution.** Eastern Siberia west-ward to the Enissey river basin, northeast-ward to the Chersky ridge, Western Transbaikalia, Northern Mongolia, partly Manchuria (?) (fig. 5).

***Alces americanus cameloides* Milne-Edwards, 1867 - Ussurian (Manchurian) moose**

1867. *Cervus cameloides* Milne-Edwards, Ann. Sci. Nat. Zool. 7: 377.

1902. *Alces bedfordiae* Lydekker, Proc. Zool. Soc. London 1:109.

1928. *Alces alces bedfordi* "Lydekker" Bobrinskoi, Field Guide to Game Animals: 95. Ussuriysky (Primorsky) kray (region). Specification of the name and type locality for *Alces bedfordiae* Lydekker.

1940. *Alces alces cameloides* Allen, Mamm. China and Mongolia, Am. Mus. Nat. Hist. 11, 2: 1205.

**Holotype.** Unknown. China, Heilongjiang ("Manchuria").

**Remarks.** Till present for moose from the south of the Russian Far East (Shikhote Alin), North-Eastern China and the extreme east of Mongolia, which all belong to one and the same subspecies, subspecific names as *A. cameloides*, and *A. bedfordi* are used. *Alces bedfordiae* was described in 1902 by Lydekker based on a skull with deer-like antlers. This material probably originated from Eastern Siberia. In 1928 Bobrinsky partly changed the name of this form of moose and has specified the type locality: Ussuriysky kray (Ussurian region), but this change and specification have no value (Heptner *et al.*, 1961), and *A. a. bedfordiae* and *A. a. bedfordi* can be nothing more than synonyms for *A. a. cameloides*.

Some morphological features of this moose are closer to those of European moose (short rostrum, deer-like antlers) but other diagnostic features (narrow edges of upper processes of premaxillary bones, dark body pelage, grey or light-brown colour of legs) show that Manchurian moose belong to the American group. The karyotype of this subspecies is not known yet, but most probably it belongs to the American species based upon some molecular-genetic markers of DNA (Udina & Danilkin, 1998; Udina *et al.*, 2002). **Characters.** Smallest and most dark-colored

subspecies in Eurasia. Antlers are deer-like shape, without palmation. Antler length is 80 to 90 cm. Condilobasal skull length is 505 to 545 mm. **Description.** Small- to medium-sized moose. In Primorie region mature bulls reach a withers' height of 170 - 190 cm, a body length of 230 to 280 cm, live weight of 250 to 400 kg with an average of 300 kg. In Manchuria this moose may be smaller. The average body length of two males from Great Qingan was 230 cm at a withers' height of 165,5 cm (Wang & Liu, 1989). A dark colour for body and head is characteristic. Antlers spread 80 to 100 cm; adult males have three to five tines. Rostrum is comparatively short.

**Distribution.** The south of the Russian Far East (Shikhote Alin), North-Eastern China (Manchuria) and the extreme east of Mongolia (Great Qingan) (fig. 5). In the adjacent territories (Lower Amur river, Eastern Transbaikalia) and sometimes in the main area hybrids with *A. a. pfizenmayeri* were noted. They usually have large body sizes and deer-like antlers.

***Alces americanus gigas* Miller, 1899 - Alaskan moose**

1899. *Alces gigas* Miller, Proc. Biol. Soc. Wash. 13: 57.  
1904. *Alces americanus gigas* Osgood, N. Am. Fauna, 24: 29.

1915. *Alces alces gigas* Lydekker, Cat. Ungulate Mamm. Brit. Mus. (Nat.Hist.) 4: 237.

1982. *Alces alces buturlini* Chernyavski et Zhelesnov, Bulletin of the Moscow Society of Naturalists. Biol. Department 87, 5: 28.

**Holotype.** No 86166, male. "North side of Tustumena Lake, Kenai Peninsula, Alaska" (U.S. National Museum).

**Remarks.** A long time ago it was already supposed that the largest moose with antlers characterised by a huge shovel, living on both sides of the Bering strait (in the extreme North-east of Asia and in Alaska) belong to one and the same subspecies: *A. a. gigas* (Kulagin, 1932; Yegorov, 1972). However, others (Chernyavsky & Zheleznov, 1982) assigned the Eurasian population to a separate subspecies (*A. a. buturlini*), based upon their larger body and skull size in respect to Alaskan *A. a. gigas*, which really are smaller in many parameters (Peterson 1955; Franzmann *et al.*, 1978). From the middle of the 20th century onwards a decrease took place in the size of *A. a. gigas* because of intensive hunting pressure (Chernyavsky & Domnich, 1989). Earlier very large sizes of Alaskan moose, not smaller than *A. a. buturlini*, were noted: withers' height to 230 cm, and a living weight of 800 kg (Seton, 1910; Stone, 1924 - after Peterson, 1955; Anthony, 1928). Chernyavsky & Zheleznov

(1982), comparing data of a small sample of skulls from the upper stream of the Yukon river (data given by Youngman, 1975), noted that their sizes were smaller than those of moose from Kolyma and Anadyr region. Our craniometric parameters of moose from the extreme Northeast of Asia and Alaska show that they have very similar parameters (Boeskorov, 1998; Boeskorov & Puzachenko, 2001). This allow us to consider the subspecies *A.a.buturlini* invalid. In our view they belong with the moose of Alaska and the Yukon river basin to the subspecies *A. a. gigas*.

**Characters.** Very large antlers with long and wide palmation separated into two parts. Anterior (brow) palm is divided in four to six branches. Large number of tines per antler: ten to fifteen. Antler length usually exceeds 110 cm. Condilobasal skull length is 570 to 600 mm.

**Description.** Largest living moose. Mature bulls usually reach a withers' height of 200 to 220 cm or more, body length is 280 to 330 cm, live weight 500 to 600 kg or more. Representatives of the modern Alaska-Yukon population are smaller in size (size decrease took place due to intensive hunting) than those of the Eurasian population. Nevertheless, the former are the largest subspecies in North America. Mature bulls usually reach a withers' height of 190 to 210 cm, body length is 270 to 320 cm, live weight 400 to 600 kg. Antlers spread 120 to 150 cm, with a maximum upto 200 cm; width of antler shovel (palmation) is 30 to 40 cm.

**Distribution.** In North America: wood areas of Alaska, western Yukon, northwest of British Columbia. Extreme Northeast of Asia: basins of the rivers Indigirka, Kolyma, Anadyr, Penzhina. In the recent past (down to the beginning of the 20th century) they were distributed more widely: in the west up to the Lena river, in the south upto the Aldan river (fig. 5).

***Alces americanus andersoni* Peterson, 1950 - Northwestern moose, or West Canadian moose**

1907. *Alces columbae* Lydekker, Field 9:18.

1950. *Alces americana andersoni* Peterson, Roy. Ont. Mus. Zool., Occ. Pap. 9: 1.

1952. *Alces alces andersoni* Peterson, Roy. Ont. Mus. Zool. and Paleo., Contrib. 34: 24.

**Holotype.** No 20068, male, complete skeleton and skin. "Section 27, Township 10, Range 16, Spruce-wood forest reserve (15 mi. E. Brandon), Manitoba". Royal Ontario Museum of Zoology and Palaeontology.

**Characters.** Differ from other North American forms chiefly in cranial details, especially with respect to the shape of the palate (relatively wider

than *A. a. americanus* and narrower than *A. a. gigas* and *A. a. shirasi*) (after Peterson, 1955).

**Description.** A large to medium-sized moose. Mature bulls reach a withers' height of 180 to 200 cm, body length of 255 to 275 cm, live weight of 350 to 550 kg. Antlers spread usually 90 to 115 cm, width of antler shovel (palmation) 20 to 30 cm, number of tines 8 to 12. Condilobasal skull length 545 to 580 mm.

**Distribution.** Northern Michigan and Minnesota, western Ontario, westward to central British Columbia, north to eastern Yukon Territory and Mackenzie Delta, Northwest Territories. In the northwestern part of its area hybrids with *A. a. gigas* occur, which therefore have larger sizes (fig. 5).

***Alces americanus shirasi* Nelson, 1914 - Yellowstone moose**

1914. *Alces americanus shirasi* Nelson, Proc. Bio. Soc. Wash. 27: 72.

1952. *Alces alces shirasi* Peterson, Roy. Ont. Mus. Zool. and Paleo., Contrib. 34: 23.

**Holotype.** No 202975. "Snake River, Lincoln County, Wyoming". U.S. National Museum.

**Characters.** Probably the smallest of all North American moose. Nelson (1914) noted: "A medium form with nasal aperture relatively wide. Colouration of pelage along the back averages paler than other North American forms". However, Bubenik's data (1986) do not confirm the paler coloration, and the systematic status may need revision.

**Description.** A medium-sized moose. Mature bulls reach a body length of 255 to 275 cm, and a live weight of 300 to 450 kg. They have relatively small hoofs. Antlers are probably the smallest in North America. Condilobasal skull length is 535 to 550 mm.

**Distribution.** Western Wyoming, eastern and northern Idaho, western Montana, northward into southwestern Alberta and southeastern British Columbia (fig. 5).

***Alces americanus americanus* Clinton, 1822 - Eastern moose, or East Canadian moose**

1822. *Cervus americanus* Clinton, Letters on Nat. Hist. and Inst. Resources of New York: 193.

1901. *Alces machlis americanus* Lydekker, Great and Small Game of Europe, etc.: 46.

1924. *Alces americana americana* Miller, U.S. Natl. Mus., Bull. 128: 490.

1952. *Alces alces americana* Peterson, Roy. Ont. Mus. Zool. and Paleo., Contrib. 34: 28.

**Holotype.** Unknown. "Country north of White-stone" (probably in western Adirondack region),

New York.

**Characters.** Narrow palate relatively to length of upper tooth row (after Peterson, 1955).

**Description.** A large to medium-sized relatively dark moose. Mature bulls reach withers' height of 180 to 190 cm, body length of 250 to 290 cm, live weight of 350 to 450 kg. Antler spread is about 100 cm, width of antler palmation 20 to 30 cm, number of tines seven to nine. Condilobasal skull length is 540 to 560 mm.

**Remarks.** Probably there are no significant differences between *A. a. americanus* and *A. a. andersoni*; they may represent one subspecies.

**Distribution.** From Maine and Nova Scotia westward through Quebec to central Ontario (fig. 5), where it apparently intergrades with *A. a. andersoni*. Introduced into Newfoundland, where it is now established (after Bubenik, 1986).

## Conclusion

Analysis of karyological data indicates that the forms from which later the European-West-Siberian and the East-Siberian-American moose originated, probably stood apart already at the Late Pleistocene. The level of differentiation between modern European and American moose, based upon molecular-genetic markers of DNA, has allowed to estimate the time of their divergence at more than 100 thousand years ago (Mikko & Anderson, 1995) or somewhere between 75 and 150 thousand years ago (Udina *et al.*, 2002). Thus, the divergence of *Alces* into two species apparently occurred at the end of the Middle - beginning of the Late Pleistocene. Which species of moose is the most ancient is difficult to say on the basis of paleontological finds. The presumably earliest remains of late Middle Pleistocene true moose are found from Western Europe up to Eastern Siberia. At the same time genetic data testify that the East-Siberian - American moose most likely are more ancient than European moose. The karyotype with  $2n=70$  is considered as ancestral for the family Cervidae; the similar chromosomal set of *A. americanus* is therefore more probable the archaic set, which was transformed into the  $2n=68$  chromosomal karyotype of *A. alces* as a result of Robertsonian fusions (Groves & Grubb, 1982; Grafodatsky *et al.*, 1990). In Eastern Siberia and the Russian Far East the largest variety of haplotypes of mitochondrial DNA is revealed, which might indicate that this region was the closest to the place of origin and evolution of modern *Alces* (Hundertmark *et al.*, 2002; Udina *et al.*, 2002). In our opinion, the

stronger differentiation of the American moose (five or six subspecies in Eurasia and North America) than of the European moose also testifies the more ancient origin of the former.

Based upon the lack of variation in mitochondrial DNA restriction fragments in North American moose it can be concluded that this population must be relatively young and that moose entered North America from Northeast Asia during the late Wisconsinan (Cronin, 1992). At the same time there is a fossil yearling bull mummy from Little Eldorado Creek, Alaska (AMNH, AM 274-4002), which is radiocarbon dated 33,000 y. BP (after Guthrie, 1990b). This mummy probably belongs to *Cervalces latifrons* or to stag-moose *Cervalces* sp. (Guthrie, 1990a, 1990b), but more likely to true moose, *Alces* (Boeskorov, 2001). This makes it possible that true moose inhabited Alaska more than thirty thousand years ago, nevertheless, we consider that the time when *Alces* penetrated into North America is till now unclear. In our opinion the differentiation of modern North-American moose into three or four subspecies could not have taken place during ten thousand years. For example, the two amph-Berian populations of *A. a. gigas* still have not reached a subspecific level of differentiation notwithstanding their ten thousand years of morphological isolation from each other (Boeskorov, 2001).

## Acknowledgments

The author thanks the following persons for discussion of the material and valuable remarks: Prof. N.N. Vorontsov, Dr. N. A. Formozov, Dr. I. A. Vislobokova, Dr. E. A. Lyapunova, Prof. A. A. Nikolsky, Dr. P. A. Nikolsky, Dr. A. V. Sher, and Dr. I. Yu. Baklushinskaya. The author is deeply grateful for help with the collections to Dr. J. Alexander, Mr. A. K. Antonov, Dr. G. F. Baryshnikov, Dr. Yu. M. Dunishenko, Prof. K. Heissig, Dr. R. Hütterer, Dr. U. Joger, Dr. R. Kraft, Dr. V. F. Lyamkin, Dr. R. MacPhee, Mr. J. Oppermann, Dr. I. Ya. Pavlinov, Prof. G. Storch, Prof. M. Stubbe, Dr. A. N. Tikhonov, and Dr. E. I. Zholnerovskaya. We are extremely grateful to Dr. Yu. V. Labutin, Dr. Ya. L. Volpert, Mr. I. I. Semenov, and others who helped us during the collecting of material in the field. Finally, the author brings cordial gratitude to his wife M. V. Shchelchkova for her constant help in my work and the editing of the manuscript.

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