A review of the systematics of Pliocene and Pleistocene moose, part 1

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Summary

The results of investigations on the evolution and the systematics of the moose are presented. New data from our own research and data from the literature on morphological variability and genetics of the living moose are discussed. In addition, new data on fossil broad-fronted moose (*Cervalces*) and true moose (*Alces*) is submitted. The former genus and *Libralces* appear not to be direct ancestors of *Alces*. Based upon the new data a revision of the systematics of the moose is carried out, and questions on philogeny are considered.

Samenvatting

De resultaten van onderzoek naar de evolutie en de systematiek van de eland worden in dit artikel gepresenteerd. Gegevens afkomstig van eigen onderzoek en uit de literatuur over morfologische variatie en erfelijkheid van de huidige eland worden besproken. Daarnaast worden nieuwe gegevens van de fossiele hert-eland *Cervalces* en van fossiele ware eland *Alces* gepresenteerd. *Cervalces* en *Libralces* blijken geen directe voorouders te zijn van *Alces*. Aan de hand van nieuwe gegevens wordt een revisie ondernomen van de systematiek van de eland, en worden vragen betreffende hun stamboom behandeld.

Introduction

The moose, one of the largest terrestrial animals of the Northern Hemisphere and an important hunting object, has a large economic importance in Norway, Sweden, Finland, in many regions of Russia, the USA and Canada. The original English name of *Alces alces* is 'elk', but nowadays the American name, 'moose', is usually used in scientific literature. The moose is the largest representative of the family of deer. 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. This characteristic constitution causes also a peculiar way of movement, with a quick, round trot, a pliable step, at which the trace of the hind limbs blocks a trace of the front limbs. The lengthened limb bones, in particular the metapodials, give it a high step, which promotes movement on tracks that are almost impassable for other deer: hillocky bogs, swamps, wind-fallen wood and deep snow.

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 at most 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*), 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 on its own (*Cervus alces*) was made by Karl Linné in 1758, based on the moose from Sweden; gradually this name became used for other moose populations as well. In 1821 Gray attributed the species to a separate genus: *Alces*. Since the description of the American moose as *Cervus americanus* Clinton 1822, some considered it a separate species, distinct from the European *A. alces* (Miller, 1899; Seton, 1910; Lydekker, 1915; Anthony, 1928). An interesting detail is that during the 19th century several times moose were imported to England from Canada; some experts (e.g. Rolfe, 1983) even identified them with the extinct giant deer, or Irish elk, *Megalo-*

ceros giganteus. Unfortunately Linné himself never saw the American moose.

Based upon some morphological features of the moose, Flerov (1931, 1934) indicated 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 Yenissey river, and *A. americanus* Clinton, inhabiting North America, Siberia eastward of the Yenissey, and the Russian 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). The consensus at the moment is that the American moose differs from European mooses at species level (Gromov *et al.*, 1963; Chernyavsky & Domnich, 1989) or semi-species 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. Although morphologic and genetic differences between the European and American moose were discussed several times (Filonov, 1983; Bubenik, 1986; Chernyavsky & Domnich, 1989; Danilkin, 1999), the question on the number of species and subspecies of modern moose remained unsolved till now.

In order to solve this problem we started research on the systematics, caryology and morphological variability of the moose in 1992. In this article we present our analysis on the differentiation of the European, Siberian, the Russian Far Eastern and American moose; part of our results has already been published (Boeskorov, 1996, 1996a, 1997, 1998; Boyeskorov, 1999). To solve some controversial points in the philogeny of the moose, we included material of fossil and subfossil *Alces* and of the extinct broad-fronted moose *Cervalces*.

Material and Methods

Fossil and subfossil remains of *Alces* and fossil broad-fronted moose *Cervalces* were studied in: Yakut Institute of the Geological Sciences Siberian Division of the RAS at Yakutsk (YIGS), Mammoth Museum of Yakutsk (MM), GM, PMM, American Museum of Natural History of New York (AMNH), IRMN, VMN, museums of natural history in Betenkes (MB) and Chersky (CMN) and in the Museum of East-Yakutian United Mine-Geological organization at Khandyga (MEYUMGO). Some fossil and subfossil remains of *Alces* were found by us during work on the Rebrovo outcrop (the Laptev strait seashore, 1995) and Duvanny Yar outcrop (lower stream of the Kolyma river, 1995, 1997, 1999). Of fossil and subfossil *Alces* we studied 19 complete skulls, 14 lower jaws, 25 antler fragments, and 4 metatarsals; of *Cervalces* we studied 13 partial skulls, 8 lower jaws, 31 antler beams and 6 metatarsals.

Skull measurements were made following Sokolov (1959) with some additions. We measured the skull parameters as given in figure 1. The lower jaw parameters are: 1. total length (from the front edge of the jaw, without teeth, up to back edge of mandibular angle; 2. coronar length of the tooth row; 3. alveolar length of the tooth row; 4. length of premolar row; 5. length of molar row; 6. length of diastema; 7. height from the lower edge of the mandibular angle to the coronar process; 8. height of the mandible ahead P_2; 9. height of the mandible behind M_3. Measurements of antlers (spread, length of antler, width of palmation) was carried out according to the rules of the International Union of the Hunters. Only antler tines longer than 5 cm were taken into account. Length of antler beam (shaft) was measured from the burr prior to the beginning of palmation, and beam circumference was measured above the burr and at midpoint (fig. 2).

Evolutionary history of moose

Fossil and modern moose are attribted to a separate subfamily: Alcinae Jerdon, 1874 (Frick, 1937; Haltenorth, 1963; Sher, 1986; Vislobokova, 1990). The origin of this subfamily lies somewhere in the Early Pliocene (5,5 - 4,1 million years ago). To this period the original *Pseudalces mirandus* Flerov, 1962 belongs, which was described from the Ciscaucasia (Kosyakinsky quarry, near Stavropol). This ancient 'pseudo--moose' had a skull with an elevation between the basements of the antlers. Its antler beams were directed laterally, backwards and slightly

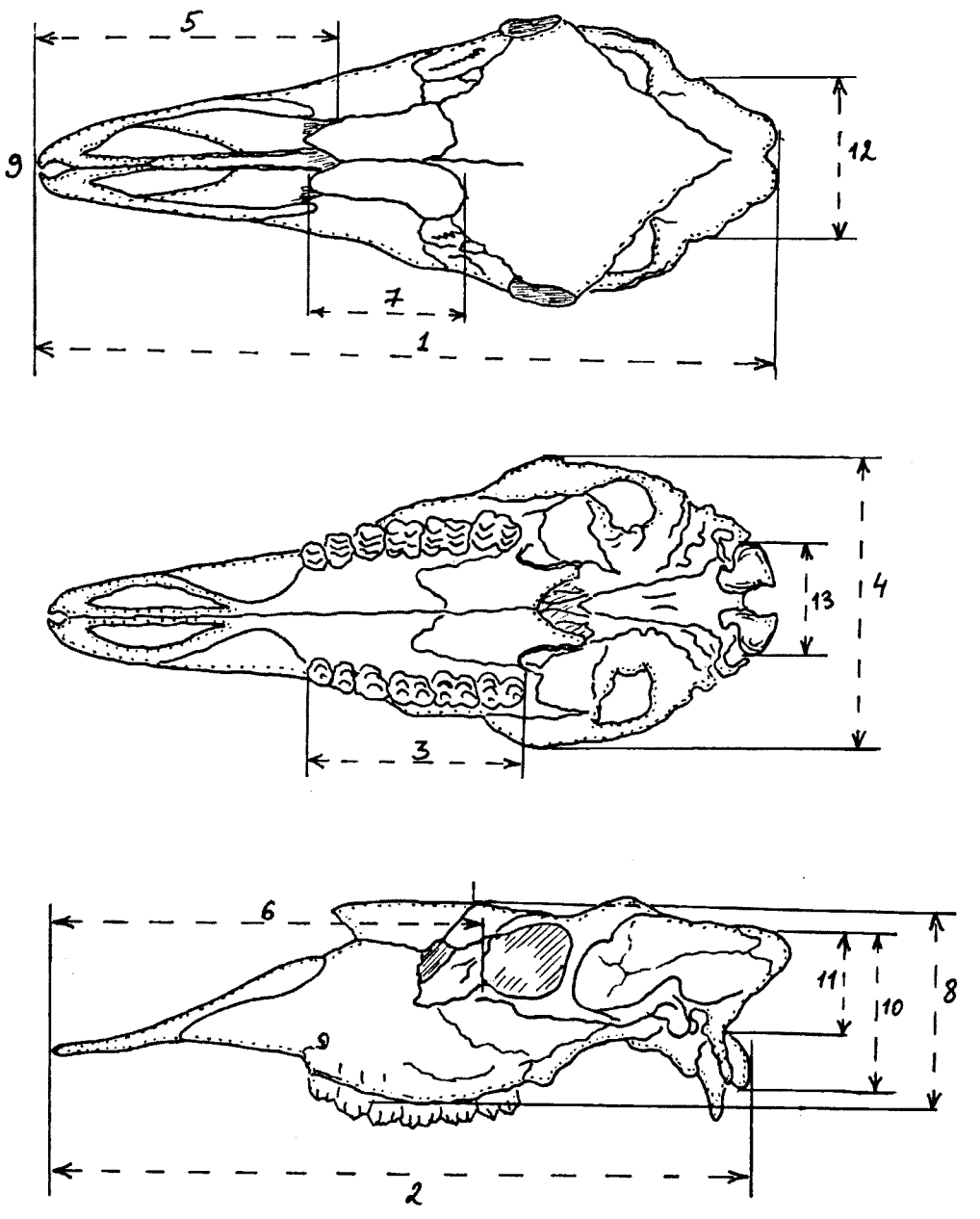

Fig 1 Measurements of a moose skull. 1 - length; 2 - condilobasal length; 3 - upper cheek tooth row; 4 - width of cheek bones; 5 - rostrum length (from front edge of intermaxillar bones to connecting point of nasal bones and maxillar bones); 6 - orbito-facial length; 7- length of nasal bones; 8 - skull height in the nasion point (from the posterior edge of the nasal bones perpendicularly to the skull axis to the lower edge of the maxillar bone, without teeth); 9 - rostrum width; 10 - occipital height from the lower edge of foramen magnum; 11 - occipital height from the upper edge of foramen magnum; 12 - maximum occipital width; 13 - width of occipital condyles

Metingen aan de elandschedel. 1 - lengte; 2 - condilobasale lengte; 3 - rij bovenkaakskiezen; 4 - breedte ter hoogte van de jukbeenderen; 5 - snuitlengte (gemeten van voorste punt van de intermaxillare beenderen tot het contactpunt van de neusbeenderen met de kaakbeenderen); 6 - orbito-faciale lengte; 7 - lengte van de neusbeenderen; 8 - schedelhoogte in het nasion-punt (gemeten van de achterrand van de neusbeenderen loodrecht op de schedelas tot de onderrand van het kaakbeen, zonder gebitselementen); 9 - snuitbreedte; 10 - achterhoofdshoogte vanaf de onderrand van het achterhoofdsgat; 11 - achterhoofdshoogte vanaf de bovenrand van het achterhoofdsgat; 12 - maximale achterhoofdsbreedte; 13 - breedte van de achterhoofdsknobbels

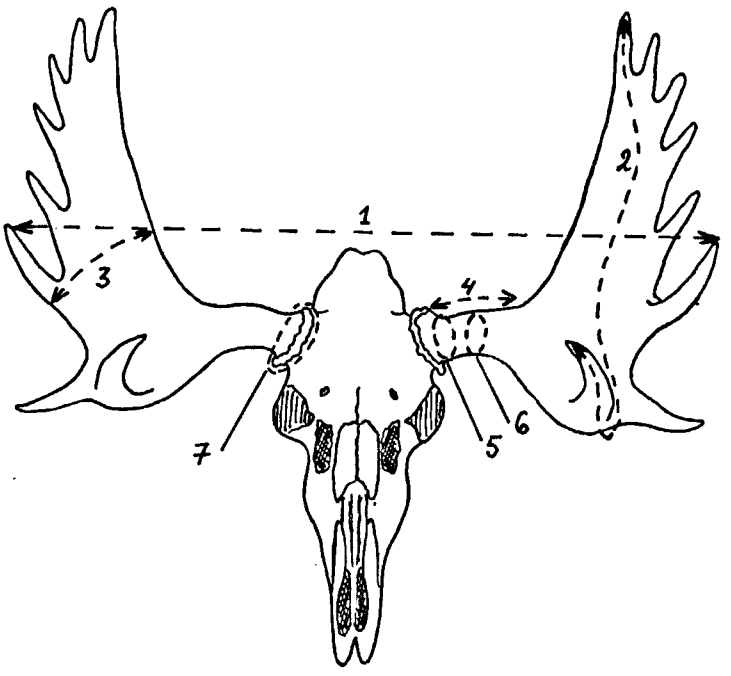

Fig 2 Scheme of measurements of moose antlers. 1 - spread; 2 - maximal antler length; 3 - shovel (palmation) width; 4 - beam (shaft) length; 5 - circumference of beam above the burr; 6 - circumference of beam at midpoint; 7 - circumference of burr

Schema van metingen aan elandgeweien. 1 - spreiding; 2 - maximale gewei-lengte; 3 - palmatie-breedte; 4 - stok-(schacht-)lengte; 5 - omtrek van de stok (schacht) boven de rozenkrans; 6 - omtrek van de stok halverwege; 7 - omtrek van de rozenkrans

upwards (Vislobokova, 1990). However, it might be that *Pseudalces* was not the oldest genus of Alcinae, but of the giant deer Megacerini and most probably presents a dead ending branch of the subfamilia Cervinae (Flerov & Shevyreva, 1963). Remains of Alcinae gen. indet. were found in the Late Pliocene (3,4 to 2,5 million years ago; Early-Middle Villafranchian) deposits of Transbaikalia, Udunga (Vislobokova *et al.*, 1995).

The first well-defined genus of Alcinae is the broad-fronted moose *Libralces*. It was described from the Late Pliocene (Late Villafranchian) fauna of Sénèze (France) as *Libralces gallicus* (Azzaroli, 1952). This species had an unusual habitus for moose: relatively small withers' height (about 1,4 m), and a very long (up to 1 m) but thin and S-shaped, curved antler beam. The palmation of its antlers was minimal, the skull was low and wide with very thick bones, the nasal bones were long and reached the premaxillary bones (fig. 3a; characteristic feature for the representatives of the subfamilia Cervinae), the M1 and sometimes the M2 had the *Paleomeryx* fold. Nevertheless, this oldest genus of Alcinae also shows the characteristic features that are observed during the whole evolutionary lineage of the subfamilia. These constant features are, amongst others, horizontally diverged antler beams without tines and ending in palmation, specific structure of teeth and limb bones, and telemetacarpals. Late Pliocene and Early Pleistocene remains of *Libralces* were also found in other sites of Western Europe (England, Germany). In the former USSR the oldest remains of *Libralces* were found in the Chaprov fauna from the Liventsov quarry in the region near the Asov Sea, dated about 2,5 million years (Bajgusheva, 1971) and in the Middle Villafranchian Kuruksay fauna from Tadjikistan (Vislobokova, 1988).

Vereshchagin (1957) described another representative of ancient moose: *Tamanalces caucasicus* from the Tamanian fauna of the latest Pliocene or Early Pleistocene from Taman peninsula (Tsymbal), but this taxon may be considered invalid.

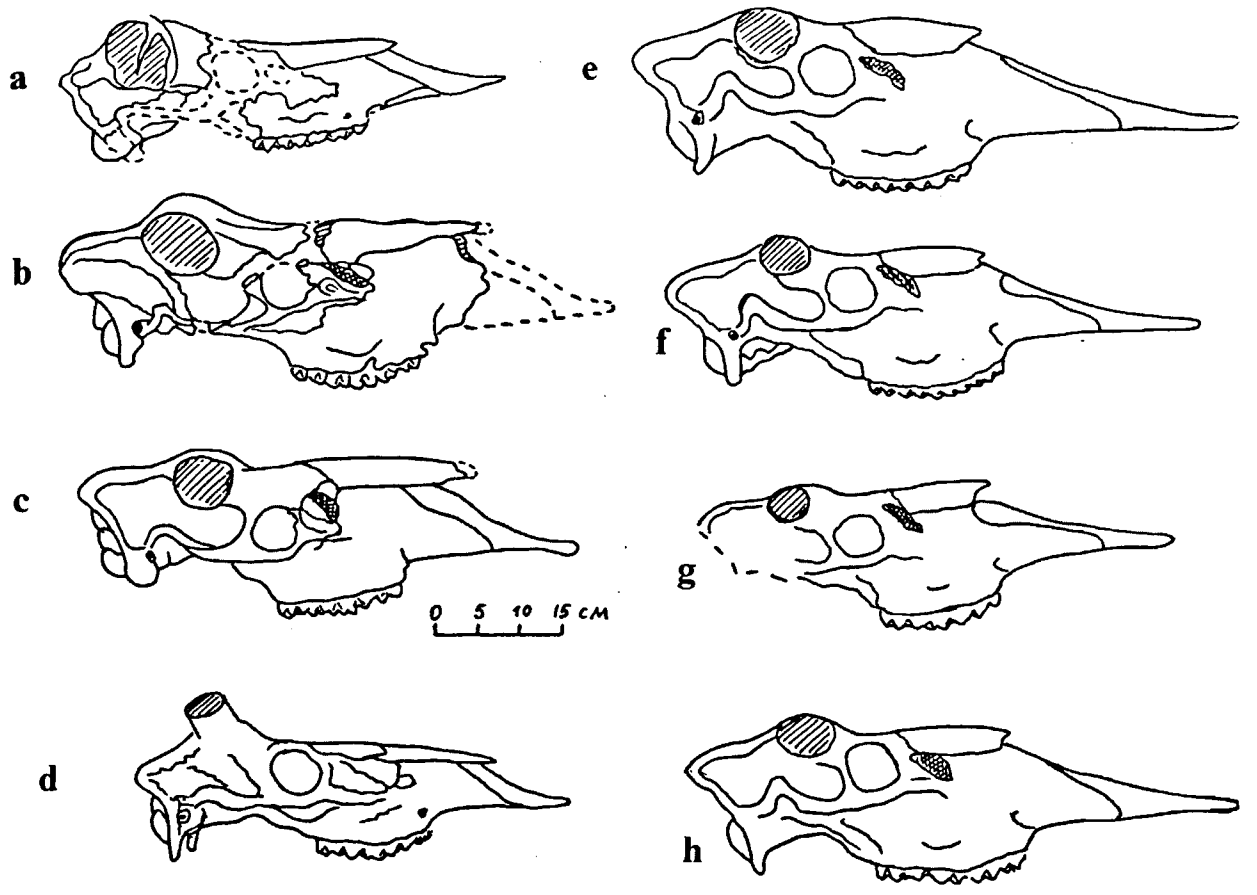

Fig 3 The skull lateral view: a – *Libralces gallicus*, Sénèze; b – *C. latifrons*, Süssenborn; c – *C. scotti*, New Jersey, Mount-Hermon (after Sher, 1986); d – *Cervus elaphus* (after Sokolov, 1979); e – *"Alces savinus"* (after Rouillier, 1846 and from a specimen in the PIN RAS); f – *Alces alces*; g – *A. alces caucasicus* (after Naniev, 1956); h – *A. americanus*

De schedel in zij-aanzicht: a – *Libralces gallicus*, Sénèze; b – *C. latifrons*, Süssenborn; c – *C. scotti*, New Jersey, Mount-Hermon (naar Sher, 1986); d – *Cervus elaphus* (naar Sokolov, 1979); e – *"Alces savinus"* (naar Rouillier, 1846 en een schedel in PIN RAS); f – *Alces alces*; g – *A. alces caucasicus* (naar Naniev, 1956); h – *A. americanus*

From the Early Pleistocene of the Forest Bed (Norfolk, England) the giant broad-fronted moose *Alces latifrons* was described (Johnson, 1874). Numerous finds of this moose revailed its close similarity with *Libralces*: long nasalia that contact the premaxillary bones (fig. 3b), horizontally projected long antler beams, etc. On the other hand, *A. latifrons* differs considerably from *Libralces*: the antler beam of the former is shorter (up to 0,6 m) but sufficiently more massive, the facial length of the skull is longer, and the former lacks upper canines and the *Paleomeryx*-fold in its molars. The giant broad-fronted moose has a very large skull and postcranial skeleton: it is the largest form among fossil and living Cervidae and its withers' height probably exceeded 2,5 m and its body weight was about 1000 kg. The huge antler spread of this moose points to an inhabitant of open landscapes (fig. 4a). The *latifrons* form is distinguished from the true moose *Alces* by some features: very long antler beam and nasalia, shape of nasalia, contact between nasal and premaxillary bones, large occipital width, etc. These significant differences favours the identification of *latifrons* as a representative of the genus *Cervalces*, not of *Alces* (Azzaroli, 1981; Sher, 1986; Vislobokova, 1990; Boeskorov, 2001).

However, there is no accordance on the generic systematics of the subfamilia Alcinae. Vislobokova (1990) agrees with Azzaroli (1952) that *Libralces* is a separate genus, and considers three genera within Alcinae: *Libralces*, *Cervalces* and *Alces*. But later Azzaroli himself (Azzaroli, 1981;

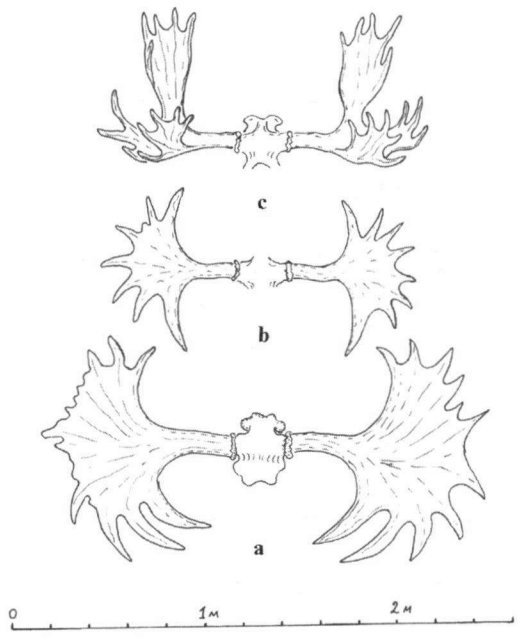

Fig 4 Shape and sizes of *Cervalces* antlers: a – *C. latifrons* (after Bubenik, 1986); b – *C. postremus* (restored); c – *C. scotti* (after Bubenik, 1986)

Vorm en afmetingen van *Cervalces* geweien: a – *C. latifrons* (naar Bubenik, 1986); b – *C. postremus* (hersteld); c – *C. scotti* (naar Bubenik, 1986)

followed by Sher, 1986) included all broad-fronted moose into a single genus *Cervalces* with two subgenera: *Cervalces* sensu strictu and *Libralces*, and considered the true moose *Alces* as the other genus of Alcinae. Others consider the differences in skull structure and antler features between broad-fronted moose and true moose insignificant and proof of gradual evolutionary changes; therefore they join all moose into the undivided genus *Alces* (Heintz & Poplin, 1981; Kahlke, 1990; Lister, 1993). We disagree with this opinion, and consider *Cervalces* and *Alces* to be different on the generic level.

Giant broad-fronted moose *Cervalces latifrons* were widely distributed over Northern Eurasia: west-ward to the British Isles and east-ward to the lower stream of the Kolyma river (fig. 5) (Vangengeim, 1961, 1977; Vereshchagin, 1967; Sher, 1971, 1986; Vislobokova, 1990). In Siberia the oldest remains of this moose belong to the end of the Pliocene or the beginning of the Pleistocene. An antler fragment similar to that of *C. latifrons* was found in Western Siberia (Irtysh river, Podpusk village) in sediments correlated with Upper Villafranchian (Vislobokova, 1986, 1996). Remains of *C. latifrons* and *C.* cf. *latifrons* were found in Early Pleistocene deposits of Transbaikalia in the faunas of Kloch nevo (Kozhamkulova, 1974; Vangengeim, 1977; Sher, 1986) and Zasukhino (Vangengeim & Sotnikova, 1981). In the North-East of Siberia, the Kolyma lowland, the oldest remains of broad-fronted moose were found in the Olyerian fauna (1,2 – 0,5 million years ago) (Sher, 1971, 1986). *C. latifrons* remains were also found in the sediments at Adycha , which is correlated to the Late Pliocene-Early Pleistocene (Anonymous, 1987). Early Pleistocene – early Middle Pleistocene remains of *C.* cf. *latifrons* were also found in North America in the Old Crow fauna, analogous to the Olyerian fauna (Harington, 1978 in Sher, 1992).

In the Quaternary sediments of Northern Eurasia (mainly in Eastern Siberia) antler fragments are found with the original proportions: comparatively long (20 to 35 cm) but slender (circumference 14 to 17 cm) antler beams. An analysis of the concomitant geological conditions and fauna reveals that at least the majority of these finds belong to the late Middle Pleistocene (Russanov, 1968; Sher, 1986). The new subspecific name *Alces latifrons postremus* was suggested for this moose with relatively long but gracile antler beams (Vangengeim & Flerov, 1965). Others (Sher, 1986; Bubenik, 1986; Boeskorov, 2001) consider *postremus* a separate species of the broad-fronted moose: *Cervalces postremus*. This moose was the last form of broad-fronted moose in Eurasia, and is either considered as the ancestor of the true moose *Alces* (Heintz & Poplin, 1981), or as the initial form of the American stag-moose *Cervalces* (Azzaroli, 1981). Guthrie (1990b: 112) considered that "sometime during the last glaciation, Eurasian *Cervalces latifrons* underwent rapid evolutionary changes toward anatomically modern moose (*Alces alces*)". However, the hypothesis that broad-fronted moose were the ancestors of modern moose was already rejected in an early stage (Soergel, 1912), based upon the irreversibility of evolution. He argued that it is impossible to fit the shortening of antler beams from the broad-fronted moose to the true moose into a single evolutionary lineage, as it would mean a reversal of the hypertrophy developed in the former ones. Furthermore, the shortening of the beam in *Alces* is accompanied by the appearance of a new character: the expansion of an antler palmation. Vereshchagin (1967: 10), in our

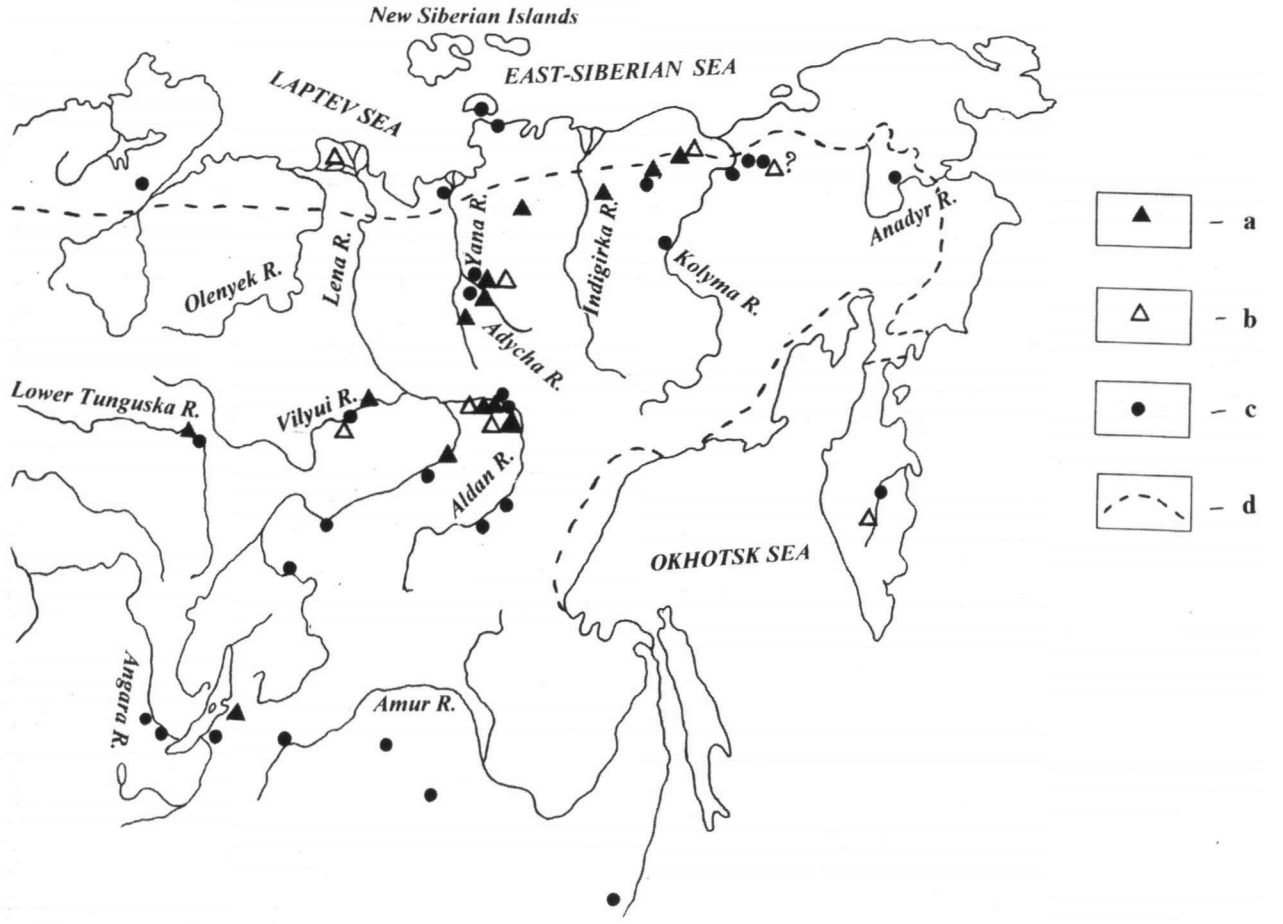

Fig 5 Finds of fossil remains of moose in Eastern Siberia and the Russian Far East: a – broad-fronted moose *Cervalces latifrons*; b – Siberian broad-fronted moose *C. postremus*; c – true moose *Alces*; d – northern limits of the present-day distribution of *A. americanus* in Eurasia

Vondsten van fossiele resten van eland in Oost Siberië en verder naar het oosten: a - breedhoofd-eland, *Cervalces latifrons*; b - de Siberische vorm, *Cervalces postremus*; c - ware eland *Alces*; d - noordelijke grenzen van huidige verspreiding van *A. americanus* in Eurasia

opinion, fairly considered: ".... hypothesis that the broad-fronted moose was the direct ancestor of the modern moose is doubtful. Most likely, the former one occupied in moose lineage about the same position, what in the proboscidean lineage - mammoth in relation to the Indian elephant... It is hard to believe in a transformation of high specialized long-beamed antlers of the broad-fronted moose during the first half of the Pleistocene into the short-beamed antlers of the modern moose ". Thus, Azzaroli's assumption (Azzaroli, 1981) that *C. postremus* was ancestral to the American stag-moose *Cervalces scotti* seems to us most plausible.

Remains of *Cervalces*, close to the Scott's stag-moose, are found in North America's Middle Pleistocene sediments. During the Late Pleistocene *C. scotti* was widely distributed in this continent and existed here prior to the beginning of the Holocene (after Churcher & Pinsof, 1987). Stag-moose had the characteristic *Cervalces* skull with long nasal bones, which contact the premaxillary bones, an antler beam of average length and massivity, and an antler shovel divided into two or three parts.

It is supposed that some facial skull and antler shape of unclear form *Alces brevirostris* Kretzoi from the Middle Pleistocene of Hungary indicate a connection between *C. latifrons* and *A. alces* (Vörös, 1985, after Kahlke, 1999).

Remains of the true moose (*Alces*) are found in deposits dated from the late Middle Pleistocene onwards. *Alces* sp. finds from the Netherlands, Kola peninsula, southeast of Western Siberia, and the Enissey river basin may belong to that period (Erdbrink, 1954; Gromova, 1965; Vereshchagin, 1967; Alexeeva, 1980; Sher, 1986). As the finds testify, in the beginning of the Late

Pleistocene modern moose were already widely distributed in Eurasia.

Although substantial research has been carried out on the fossil moose of Eastern Siberia and the Russian Far East (Vangengeim, 1961; 1977; Vangengeim & Flerov, 1965; Russanov, 1968; Sher, 1971, 1986), many aspects of their systematics, evolutionary relations and distribution are still unclear. In order to solve these questions, we studied material of fossil and subfossil moose in various museums. We examined not only new, undescribed collection material, but also specimens described by earlier authors, because measuring of certain antler dimensions (for example, beam length) is rather subjective and consequently comparison of such parameters becomes difficult. For this purpose we investigated material earlier described by Fisher & Rouillier (1846) on exhibit in the Paleontological Museum of RAS (Moscow): the so-called *Alces savinus* G.Fisher, 1834 (Savin's moose), and also material investigated by Pavlow (1906) as *Alces fossilis* H. v. Meyer, 1832, stored in the Geological Museum of RAS and some other collection specimens. Finally, we found some more fossil *Alces* remains during the field expeditions of the Mammoth Museum.

FAMILY CERVIDAE GRAY, 1821

Subfamily Alcinae Jerdon, 1874
Genus *Cervalces* Scott, 1885

Libralces Azzaroli, 1981
Alces Heintz, Poplin, 1981

Type species. *Cervus americanus* Harlan, 1825 [= *Cervalces scotti* (Lydekker, 1898)], Pleistocene of North America.
Diagnosis. Rostral part of skull extends forward much less than in *Alces*. The wide nasal processes of the premaxillary bones make contact with the nasal bones. Nasal bones are elongated, longer than the upper dental row. The cerebral section of the skull is wide and low. The ratio of cranium height from the lower edge of foramen magnum to maximal occipital width is usually less than 70%. A small prominence is present between the antlers. The orbits are much lower than the roof of the forehead. The antler beam is long or of average length (length always exceeds beam circumference), and is slightly bent.
Species composition. At least three species are recognised: *C. latifrons* (Johnson 1874), Late Pliocene (Late Villafranchian) to early Middle Pleistocene of Eurasia and Alaska (?), *C. postremus* (Vangengeim et Flerov 1965), late Middle Pleistocene of Eurasia, and *C. scotti* (Lydekker 1898), Middle to end of Late Pleistocene, North America.
Differential diagnosis. Differs from *Libralces* in longer facial part of the skull, longer and higher nasal aperture, absence of upper canines and the *Paleomeryx*-fold, and in the prominence of nasal bones. Differs from *Alces* in longer and relatively thinner antler beam (its length always exceeds the circumference), in the position and form of the upper processes of the premaxillary bones, in a broader occipital area, in shorter rostral part of the skull, longer nasal bones, and in a considerably smaller prominence between the antlers.

Cervalces latifrons Johnson, 1874 - broad-fronted moose

Alces latifrons Johnson, 1874
? *Cervalces alaskensis* Frick, 1937
Libralces reynoldsi Azzaroli, 1953

Material and locality. A fragment of a neurocranium with a right antler beam, MB without number, Adycha river, Ulakhan Sullar outcrop, found in 1978. Fragments of antlers: two specimens without numbers, MB and VMN, YIGS 4437, all from Ulakhan Sullar; YIGS 62, Aldan river, Khara-Aldan outcrop (fig. 6a); MB without number, Adycha river, Oskhordokh outcrop, found in 1994 (fig. 7e). A fragment of the frontal part of a skull with left antler beam, YIGS 4412, Oskhordokh (fig. 6f). Mandibles: YIGS 4403-4405 (fig. 7a-b) and one without number, private collection, all from Oskhordokh; without number, Ulakhan Sullar. Fragments of metatarsal bones: MM 8034 and VMN without number, both from Ulakhan Sullar; MB without number, Oskhordokh.

Geological age. YIGS 4403-4405, 4412 and 4437 are found in deposits of the Adycha site, dated Late Pliocene - Early Pleistocene (Anonymous, 1987). YIGS 4403-4405 are found together with remains of Early Pleistocene representatives: *Archidiskodon* sp., *Trogontherium* cf. *cuvieri*, *Canis* cf. *variabilis* (Kotov *et al.*, 1976). Earlier remains of broad-fronted moose were also found in these outcrops together with Early Pleistocene *Mammuthus trogontherii*, *Equus* (*Plesippus*) cf. *verae*. YIGS 4437 is found together with *Bison priscus* and *Rangifer* cf. *tarandus*. Antler frag-

Table 1 Sizes of the neurocranium (in mm) of broad-fronted moose and stag-moose (genus *Cervalces*). 1 - skull height from the lower edge of foramen magnum; 2 - skull height from the upper edge of foramen magnum; 3 - maximal occipital width; 4 - width of occipital condiles; 5 - width of the skull at the constriction behind the antlers. Q1 - Early Pleistocene; Q2 - Middle Pleistocene; Q3 - Late Pleistocene; Q4 - Holocene.

Maten van de hersenschedel (in mm) van breedhoofd-eland (*latifrons*) en van hert-eland (geslacht *Cervalces*). 1 - schedelhoogte vanaf de onderrand van het achterhoofdsgat; 2 - schedelhoogte vanaf de bovenrand van het achterhoofdsgat; 3 - maximale achterhoofdsbreedte; 4 - breedte van de achterhoofdsknobbels; 5 - breedte van de schedel ter hoogte van de insnoering achter het gewei. Q1 - Vroeg Pleistoceen; Q2 - Laat Pleistoceen; Q4 - Holoceen.

		Cranium height 1	Cranium height 2	Cranium height 3	Cranium height 4	Cranium height 5	Cranium height 6	Index: 1:3
Cervalces latifrons	Moldavia, Kolkotova Balka, Q1 (David *et al.*, 1990)	-	100	240	-	-	-	-
	Ulakhan Sullar, without No, VMN	146	106	209	118	-	>120	69,9
	Oskhor-dokh, YIGS 4412	-	-	-	-	-	136	-
C. postremus	Yakutia, Q2 Verkhnevilyuiskoye, YIGS 1277		-	-	-	-	125	-
C. scotti	Alaska, Q3, AMNH 342-2426	122	82,4	184	105,2	119	107	66,3
	Alaska, Q3, AMNH 627-6546	119	81	167	103	114	>100	71,3
	Alaska, Q3, AMNH 101-5090	115	72	>170	-	114	>105	<67,7
	Alaska, Q3, AMNH 712-1342	-	-	>170	87,3	122	-	-
	Alaska, Q3, AMNH 198-5899	115,4	83,1	166	100,1	112	>110	69,5
	Alaska, Q3, AMNH 16250	118	70,1	182	97	113	>110	64,8
	New Jersey, Q3-Q4, AMNH 107678	124	83	178	96,4	113,5	>120	69,7

Table 2 Average sizes of neurocranium (in mm) in true moose (genus *Alces*). Measurements: 1 - skull height from the lower edge of foramen magnum; 2 - skull height from the upper edge of foramen magnum; 3 - maximal occipital width; 4 - width of occipital condiles; 5 - skull width at the constriction behind the antlers; 6 - distance from the burr to the midpoint of the frontal bone. Note: * measurements from photo.

Gemiddelde maten van de hersenschedel (in mm) van ware eland (geslacht *Alces*). Maten: 1 - schedelhoogte vanaf de onderrand van het achterhoofdsgat; 2 - schedelhoogte vanaf de bovenrand van het achterhoofdsgat; 3 - maximale achterhoofdsbreedte; 4 - breedte van de achterhoofdsknobbels; 5 - schedelbreedte ter hoogte van de insnoering achter het gewei; 6 - afstand van de stok tot middelpunt van het voorhoofdsbeen. Opmerking: * maten genomen van foto.

Measurements	*Alces*	cf *Alces*	*Alcesamericanus*					*Alces americanus*, modern	*Alces americanus*, modern
	Eastern Europe, Q3-Q4, GM RAS, ZMMSU, n=4	Western Siberia, Q3-Q4 (Alexeeva, 1980)	Yakutia, Q4, without number, YIGS, n=2	Yakutia Kolyma, Duvanny Yar, Q3, MM 8121	Yakutia Lower Kolyma, Q3-Q4, without number, n=2	Chukotka, MalyiAnyui, Q3, YIGS 4291	AM 1067527	Central Yakutia, *A.a.pfizenmayeri*, n=7	Extreme North-East of Siberia, *A.a.gigas*, n=9
1	121	135	126,5	129	127,3	123	136	120,.8	125,.2
2	86,2	80	84	82	83,5	85	100	82,3	86,3
3	168	180*	173,8	162	175,5	170	181	159,.6	169,8
4	101,7	104*	99,5	104	105,5	99	103	96,6	98,6
5	93	109	101,5	-	102	105	105	102,4	106,1
6	-	-	99,5	-	101	99	104	92,7	100,1
Index 1:3	72,3	75	72,8	79,6	72,5	72,4	75,1	74,8	73,3

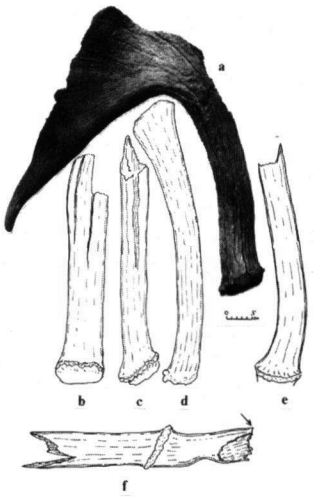

Fig 6 Fragments of antlers of the broad-fronted moose *C. latifrons*: a - Aldan river, Khara-Aldan, YIGS 62; b, c - Adycha river, Oskhordokh, after Lazarev & Tomskaya, 1987; d - *C.* aff. *latifrons*, Bolshaya Chukochiya river, after Sher, 1971; e - Adycha river, Oskhordok, specimen without number, MB; f - skull fragment with part of antler beam, Adycha river, Oskhordok, YIGS 4412 (the area of the frontal elevation is marked with an arrow)

Fragmenten van geweien van breedhoofd-eland, *C. latifrons*: a - Aldan rivier, Khara-Aldan, YIGS 62; b, c - Adycha rivier, Oskhordokh, naar Lazarev & Tomskaya, 1987; d - *C.* aff. *latifrons*, Bolshaya Chukochiya rivier, naar Sher, 1971; e - Adycha rivier, Oskhordokh, stuk zonder nummer uit MB; f - schedelfragment met een gedeelte van de geweistok, Adycha rivier, Oskhordokh, YIGS 4412 (het gebied van de opbolling aan de voorzijde is aangegeven met een pijl)

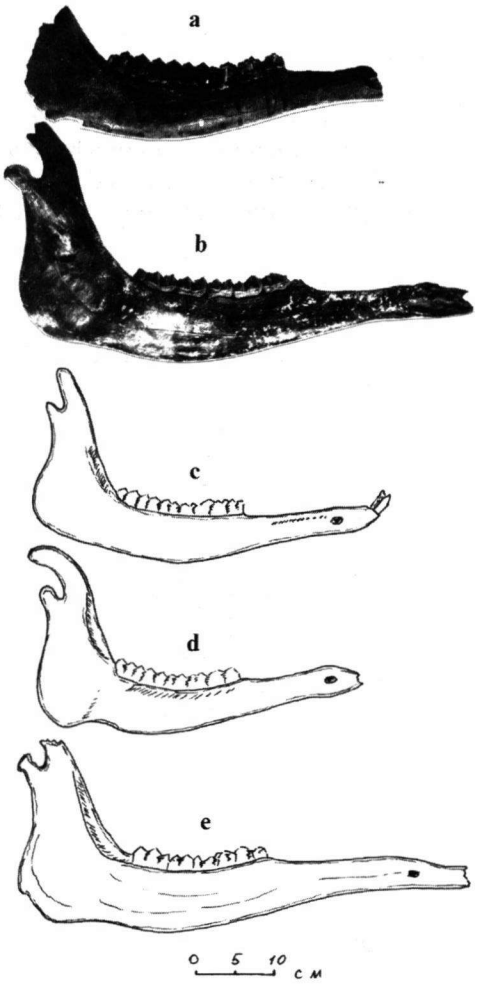

Fig 7 Mandibles of Alcinae. *C. latifrons*, Adycha river, Oskhordokh: a - YIGS 4403, b - YIGS 4404; *C. scotti*: c - AMNH 107678, New Jersey, Mount-Hermon, d - AMNH 198-5899, Alaska, Engineer Creek; e - *A. americanus*, AMNH 276-283, Alaska

Onderkaken van Alcinae. *C. latifrons*, Adycha river, Oskhordokh: a - YIGS 4403, b - YIGS 4404; *C. scotti*: c - AMNH 107678, New Jersey, Mount-Hermon, d - AMNH 198-5899, Alaska, Engineer Creek; e - *A. americanus*, AMNH 276-283, Alaska

ment YIGS 62 from Khara-Aldan, described earlier by Russanov (1968), belongs to the Early Pleistocene.

Description and comparison. All material of *C. latifrons* is strongly mineralized, coloured brown to dark - brown. Traces of transport by water flow are not revealed by the described remains.

The skull fragment from Ulakhan Sullar is represented by occipital, parietal and partial frontal parts with a preserved right antler beam. The specimen is very large (table 1). On skull fragment YIGS 4412 part of the frontal bone from antler basement to the sutura frontalis and part of the left antler beam are preserved (fig. 6f). In YIGS 4412 and in the previous specimen the distance from the burr (coronet) up to the middle of forehead (sutura frontalis) is larger (table 1) than in true moose *Alces* (table 2). For broad-fronted moose the small elevation at the middle of the forehead is characteristic (fig. 6f). Skull remains of *C. latifrons* are poorly known, but it is noted that broad-fronted moose had a larger occipital width than *Alces* (after Vislobokova, 1990). The specimen from Ulakhan Sullar, which has a smaller occipital width than *C. latifrons* from Moldavia, however, surpasses this parameter in true moose. Broad-fronted moose reliably differ from *Alces* in occiput height and in width of the occipital condyles (tables 1 and 2), in mandible size (tables 3 and 4) and in teeth (tables 5 and 6). It is obvious that *C.*

latifrons had a much larger skull than Pleistocene and modern *Alces*. The lower molars of *C. latifrons*, too, are much larger than those of *Alces* (tables 5 and 6). Having undoubtedly larger jaws than the true moose, *C. latifrons* preserved some original proportions: a relatively elongated dentition (about 39%) than *Alces* (33-37%), higher jaw and dental sections, and a shorter diastema (fig. 7; tables 3 and 4). The lower molars of the broad-fronted moose always have labial pillars, increasing the masticatory surface. These pillars are not always present in *Alces*. These specific features allowed the broad-fronted moose to chew more rigid nutrition. It is interesting to note that Flerov (1979: 22) noted in bisons two similar types of lower jaw constitutions (in translation): "The inhabitants of open steppe landscapes, whose feeding consists of rough forage (mainly grasses), are characterized by high dental section of the lower jaw, and are thus capable to maintain a large pressure while grinding firm vegetation. The symphyseal section is high and wide. The molars have additional strengthening formations, counteracting wear. The second type of lower jaw constitution is characteristic for forest bisons, eating mild forest grasses, branches, leafs and barks of trees and bushes. For them the low dental section and molars without strengthening formations are peculiar; symphyseal section is narrowed and low.". In our opinion, a similar division in lower jaw types is seen in broad-fronted and true moose. *Cervalces*, inhabitant of open landscapes, apparently mainly ate rigid steppe grasses, and also leafs and branches of bushes. True moose obviously were always more connected with forests and bushes, and branches and water-paludous green prevailed in their diet; and the herbaceous plants remained a minor food source. The specalization of feeding behaviour of true moose promoted lengthening of the facial section of the skull during evolution. Lengthening of the foremost section of the skull and the

Table 3 Sizes of mandibles (in mm) in broad-fronted moose and stag-moose (genus *Cervalces*). Length of 1 - mandible; 2 - tooth row, coronar; 3 - same, alveolar; 4 premolar row; 5 - molar row; 6 - diastema. Height 7 - from the coronar process; 8 - ahead P_2; 9 - under the middle of M_1; 10 - behind M_3.

Maten van onderkaken (in mm) van breedhoofd-eland (*latifrons*) en hert-eland (geslacht *Cervalces*). Lengte van 1 - onderkaak; 2 - tandenrij, over de kronen; 3 - idem, langs de tandkassen; 4 - rij valse kiezen; 5 - rij ware kiezen; 6 - diasteem. Hoogte 7 - vanaf coronair uitsteeksel; 8 - net vóór P_2; 9 - net onder midden van M_1; 10 - net achter M_3.

	Cervalces latifrons						*C. cf. latifrons*	*C.* sp.,Q3	*C. scotti*, Q3-Q4	
	Yakutia, Adycha river, Oskhordokh, Q1-Q2				Yakutia, Ulakhan Sullar, Q1-Q2	Transbaikalia, Q1	Western Siberia, Ob river, Q1- Q2	Alaska	Alaska	New Jersey
	YIGS 4403	YIGS 4404	YIGS 4405	without number, private collection	without number, VMN	Kozhamkulova, 1974	(Alexeeva,1980)	AM 1085745	AM 1985899	AM 107678
1	-	510	-	-	485	-	-	460	400	442
2	196	198	-	186	-	-	177,5	179	152	162
3	201	202	-	-	204	190	-	183	154	164
4	88	88	85	82	-	84*	76,5	75	63	73,5
5	111	108	-	104	-	109*	103,2	105,.5	89	95
6	-	185	-	-	-	-	-	174	144	163
7	-	251	-	-	257	-	-	226	223	221
8	49,3	51	55	55,5	-	-	-	43	43	48
9	64	65	-	-	64.2	-	-	53	59	60,3
10	80	85,5	-	-	-	-	72,9	71,4	73	74,7
Indices:										
4:5	79,3	81,5	-	78,9	-	77,1	72,0	71	70,8	77,5
2:1	-	38,8	-	-	near 40	-	-	38,9	38	36,7
6:1	-	36,3	-	-	-	-	-	37,8	36	36,9
7:1	-	49,2	-	-	near 50	-	-	49,1	near 50	50

diastema promoted increase of mouth cavity and, accordingly, has enabled them to improve manipulation of the tongue for grabbing branches and twigs (Gogina, 1979; after Vislobokova, 1990).
In various lines of deer an evolutionary shortening of the premolar row is observed. At the same time the premolar row remains rather long in moose (Vislobokova, 1990). We found a rather high index of premolar length in *C. latifrons* and modern *Alces*. At the same time, it appears to be slightly lower in fossil and subfossil *Alces* (table 4). Premolars are molarized in *C. latifrons*, as well as in *Alces*: the P3 valley between paraconid and metaconid is closed. A P3 of an archaic broad-fronted moose is described from the river Bolshaya Chukochiya, which has a deep valley between these conids (Nikolsky, 1996). For the P4 of broad-fronted moose and of *Alces* the fifth molarization degree after Heintz is characteristic: protoconid is fused with entoconid, and hypoconid is separated (after Vislobokova, 1990).
Antler beams of *C. latifrons* from Yakutia and from other parts of the geographic range are similar in size and proportions (table 7). Broad-fronted moose has very large antlers (spread 2 to 2,5 m) with a long beam (apparently, up to 0,6 m) (fig. 4a). The massivity index of their antlers is 42 to 82%, i.e., the circumference of an antler beam is always less than its length (contrary to *Alces*, where this index is more than 100%). Similar antler dimensions and proportions are characteristic for Early Pleistocene *C. latifrons* from the huge territory of Northern Eurasia, ranging from Western Europe up to Eastern Siberia (table 7). The antler beam of this

Table 4 Sizes of mandibles (in mm) and proportion indexes (%) in true moose (genus *Alces*). Length of 1 - mandible; 2 - tooth row, coronair; 3 - tooth row, alveolar; 4 - premolar row; 5 - molar row; 6 - diastema. Height of the mandible 7 - from the coronair processes; 8 - height ahead P_2; 9 - height under the middle of M_1; 10 - height behind M_3.

Maten (in mm) en verhoudingen (in %) van onderkaken van ware eland (geslacht *Alces*). Lengte van 1 - onderkaak; 2 - tandenrij, over de kronen; 3 - tandenrij, langs de tandkassen; 4 - rij valse kiezen; 5 - rij ware kiezen; 6 - diasteem. Hoogte 7 - vanaf het coronair uitsteeksel; 8 net vóór P_2; 9 - net onder midden van M_1; 10 - net achter M_3.

	Alces. cf. *americanus*, Yakutia, Q3		*A. americanus*, Yakutia Q3 - Q4			*A. americanus* Alaska, Q3-Q4							*Alces alces*, modern	*A. americanus*, modern	
	Adycha, Oskhordokh, YIGS 4411	Lena delta, YIGS 4759	Kolyma, Q3-Q4,MM 7099	Kolyma, Q4, without number	Olyekma basin, 1000 - 15000 years B.P., MAE, n=3	AM 583 2167	AM 4854 734	AM 616	AM 27652 83	AM 5832 162	AM 5842 161	AM 36814 26	Western Siberia, n=9	Eastern Siberia, n=14	North-East of Siberia, n=12
1	-	-	472	492	-	485	470	482	520	502	501	510	453,8	468,4	486,4
2	180	167	155,5	163,2	160,7	171	-	173	157	169	168	177	159,1	161,1	167,5
3	74	171	159	168	162,6	174	167	175	161	172	172	179	-	164,7	168
4	100	70,5	69	73	69,2	69,5	70,5	74,5	68	68	69	74	66,4	68,5	69,6
5	-	100	91	94	94,2	98	96	101	93	84	99	103	81	81,8	88,3
6	-	170	199	201	-	205	190	193	224	210	208	202	-	181	192
7	49	-	210	226	-	219	215	234	238	236	237	240	211,4	213,2	220,7
8	59,5	44	47	53	-	55	49	54	54,3	58	53	52	-	47,1	49,7
9	-	-	64,5	63	-	58	50,5	63	66,8	63	62	60	-	56,2	60,2
10		-	67	72	-	72	60,5	73,2	79	72	70	71	-	66	70,3
4:5	74	70,4	75,7	77,7	73,2	70,8	73,4	73,8	73,1	81	81	71,9	82,7	82,9	80,3
2:1	-	-	32,9	33,2	-	35,3	35,5	35,9	30,2	33,7	33,5	34,7	35,3	35,1	35,2
6:1	-	-	42,2	40,9	-	42,3	40,4	40	43,1	41,8	41,5	39,6	-	38,7	39,1
7:1	-	-	44,5	45,9	-	45,2	45,8	48,5	45,8	47	47,3	47,1	45,9	45,3	45,1

moose is slightly curved, in contrast to *Libralces gallicus*, which has an S-shaped beam. Sher (1971) describes an antler fragment of broad-fronted moose from the Olyerian deposits at the river Bolshaya Chukochiya, which has a more thin and curved beam than *C. latifrons* (fig. 6d; table 7). This observation, and also the weak molarization degree of the P3 of the Olyerian moose, allows to consider it as an archaic form, probably intermediate between *L. gallicus* and *C. latifrons* (Sher, 1971; 1986; Nikolsky, 1984). The antler fragment from Oskhordokh (fig. 6e; table 7), too, has a bent beam.
Metatarsals of broad-fronted moose are large and slender. Metatarsals of *C. latifrons* are much larger than those of *Alces*, but have similar proportions (fig. 8, tables 8 and 9). Sher (1971) noted some metatarsal features on the basis of which broad-fronted moose can be distinguished from *Alces*.

Remarks on systematics. The broad-fronted moose remains from Yakutia investigated by us does practically not differ from the earlier described *C. latifrons* remains from Europe and Siberia.
The original feature of *Libralces, Cervalces latifrons* and *C. scotti*, as it was already noted above, are the long nasal bones, which come into contact with the upper processes of the premaxillary bones (Azzaroli, 1952, 1981; Sher, 1986) (fig. 3a-c; fig. 9d-f). This feature puts them together with deer of the subfamily Cervinae: *Cervus, Megaceros, Rangifer, Capreolus*, etc. (fig. 3d; fig. 9c), and also distinguishes them from the true moose *Alces* (fig. 3e-h; fig. 9d-f). At the same time broad-fronted moose and true moose

Table 5 Sizes (in mm) of lower jaw teeth of the broad-fronted moose and stag-moose (genus *Cervalces*)

Maten (in mm) van onderkaakskiezen van de eland met breed voorhoofd (*latifrons*) en van hert-eland (geslacht *Cervalces*)

	P_2		P_3		P_4		M_1		M_2		M_3	
	length	width	length	width	length	width	length	width	length	width	length	width
Cervalces latifrons												
Western Siberia, Villafranchian (?) (Alexeeva 1980)	27	17,3	29,8	22	-	-	-	-	-	-	-	-
Transbaikalia, Q1 (Kozhamkulova 1974)	-	-	-	-	-	-	-	-	34	25	48	26
Yakutia, Adycha, Oskhordokh,Q1(?),YIGS 4403	24	18,5	31,1	21	32	23	33	24	37	25	48	23,3
YIGS 4404	23,2	-	29,4	21	33,3	25,2	31	26,1	35,7	27,2	46	27,1
YIGS 4405	21,3	14,8	30,2	19,7	36,5	23,7	-	-	-	-	-	-
Yakutia, Adycha, Ulakhan Sullar, Q1(?), MB n.n..	-	-	-	-	-	-	-	-	-	-	47	23,5
C. cf. latifrons												
Western Siberia, Q1-Q2(?) (Alexeeva 1980),	20,1	13,1	23,6	17,5	28,5	20,3	28,05	22,8	30	24,8	45,5	24,3
Q2-Q3(?), Alaska, AMNH 527-4102	22	15	29	20,1	35	24	34	24	37	25,4	46	23,4
C. aff. latifrons												
Yakutia, Bolshaya Chukochiya, Late Villafrancian (Nikolsky 1996)	-	-	29	19	34	23	-	-	36	24	-	-
C. postremus(?)												
Adycha, Oskhordokh, Q2(?): YIGS 4406	-	-	-	-	-	-	-	-	-	-	43,6	22,5
YIGS 4436	-	-	-	-	-	-	-	-	36,3	23,2	44	24,5
C. scotti												
New Jersey, AMNH 107678	21,7	15,5	28	18,4	30,6	20,5	30,2	20,7	31	21,1	41,3	19,5
Alaska, AMNH 1985899	19	12,3	23,4	16,6	26,8	18,8	28,2	21,4	30,2	20,5	39	20,1

share many general features, which unite them into a uniform subfamily Alcinae and distinguish them from Cervinae: a horizontal location of antler beams, antler shape, wide forehead that is inflated in the frontal sutura region, choanal height, constitution of the temporal region, telemetacarpality, etc. (after Vislobokova, 1990). The name *Cervalces* ('deer--moose') is appropiate, since it reflects features of both moose and deer.

One of the basic features of *Cervalces* (the combination of long nasal bones, which come into contact with the upper processes of the premaxillary bones) is never found in *Alces*. Sher (1986) and Lister (1993) demonstrated that subfossil Caucasian moose *A. alces caucasicus* has long and very wide upper processes of the premaxillary bones, which come into contact with the nasal bones (fig. 3g; fig. 9e); this feature unites the Caucasian moose with *Cervalces*, not with *Alces*. For Lister this observation proves the affiliation of the broad-fronted and true moose into one genus *Alces*. At close consideration it also becomes clear that the short rostral section, as well as the nasal and premaxillary bones of *Cervalces* are extremely similar to those of the Cervinae (fig. 3d; fig. 9c). For all *Alces* a lengthened rostral section and short nasal bones are characteristic. In addition, the shape of the nasal bones in *Alces* differs completely from that in *Cervalces* and deer. The upper processes of the premaxillary bones in *Alces* are long and thin, with an expansion at the end in the European moose (fig. 10a-d). The specified features of the rostral part of the modern moose skull are unique.

"All these features lead to a significant increase of the dimensions of an osteal nasal foramen

Table 6 Sizes (in mm) of lower jaw teeth of the fossil and subfossil true moose (genus *Alces*)

Maten (in mm) van onderkaakskiezen van fossiele en subfossiele ware eland (geslacht *Alces*)

	P_2		P_3		P_4		M_1		M_2		M_3	
	length	width	length	width	length	width	length	width	length	width	length	width
Alces cf. *alces*, Western Siberia, Q3-Q4 (Alexeeva, 1980), mean.	17,5	13	22,9	13,3	27,5	20	25,8	21,5	28,1	22,9	40,1	22,8
A. sp., Yakutia, Q3(?)												
Adycha, Oskhordokh, YIGS 4411	21	16	27,1	20	28,7	21	28	21,2	31,3	21,4	-	-
Lena delta, YIGS 4759.	17,5	13,6	25,2	17	29	19,4	28,3	20,2	31,5	22	43,3	22
A. cf. *americanus*, Q3												
Adycha, Ulakhan Sullar, YIGS 4435	-	-	27,4	17	-	-	-	-	30,5	21,7	40,2	21,5
Adycha, Kyra Sullar, YIGS 4959	-	-	25	16,8	28	19,5	28	20	29	20,4	40	19,4
Rebrovo site, no number	-	-	-	-	-	-	31,4	24,3	-	-	-	-
Alazeya, YIGS 5614	-	-	-	-	-	-	-	-	-	-	38,5	16,4
Ynykchan, no number, MEYUMGO	-	-	23	18	28,7	21	-	-	-	-	-	-
Kolyma, MM 7099.	18,7	14,5	23,4	18,6	28	19,8	28,1	20,9	32,8	23,6	40,3	22,8
A. americanus, Q4												
Olyekma river, Ulakhan Segelennyakh, Neolithic	-	-	-	-	-	-	-	-	32,3	24,2	42,7	21,5
Olyekma river, Ulakhan Segelennyakh, Early Iron Age, MAE, 1000-1500 y.B.P., MAE	18,1	13,8	23,7	17	29,1	19,5	26,1	20,5	29,5	20,9	40,6	20,8
Kolyma, no number	19,5	13,2	24,3	17,5	28	21	26,3	20,2	30	24	41,5	22,2
A. americanus, Alaska, Q3-Q4												
AMNH 583-2167	18	13	25	18,5	29	21,2	29	22,5	32,2	23	44,7	21,6
AMNH 616-6015	21,6	16	25,4	20	30	23,2	27,2	22	31	23	47,1	22
AMNH 276-5283	18	13	24,2	18	28,5	20,7	28	22	31,5	23,4	43,2	22,3
AMNH 276-5285	19,6	15,6	25	20	30,2	20,8	29,6	22,3	33,3	22,1	44,2	23
AMNH 473-3436	20,1	15,6	24,3	18	28,4	20,4	31,1	23	32	24,2	45,4	23
AMNH 584-2161	19,9	15,5	23	17	28,5	20	28	22	30,7	23	43,8	21

Fig 9 Metatarsal bones of moose from Yakutia: a – *C. latifrons*, Adycha river, Oskhordokh; b – *Alces* sp., Adycha river, Ulakhan-Sullar; c – *Alces* sp., Sartang river (after Lazarev & Tomskaya, 1987)

Middenvoetsbeenderen van eland uit Yakutië: 1 - *C. latifrons*, Adycha rivier, Oskhordokh; b – *Alces* sp., Adycha rivier, Ulakhan-Sullar; c – *Alces* sp., Sartang rivier (naar Lazarev & Tomskaya, 1987)

Table 7 Sizes (in mm) and proportion (in %) of antler beam of the broad-fronted moose. 1 - beam length; 2 - circumference of burr; 3 - circumference of beam above the burr; 4 - horizontal diameter of beam

Maten (in mm) en verhouding (in %) van geweistangen van de eland met breed voorhoofd (*latifrons*). 1 - lengte van de stang; 2 - omtrek van de rozenkrans; 3 - omtrek van de stang boven de rozenkrans; 4 - stangdoorsnede

Sizes	*Cervalces latifrons*, European part and Ural					*Cervalces latifrons*, Eastern Siberia								*Cervalces* aff. *latifrons*
	Germany, Mosbach	Germany, Süssenborn	Moldavia, Tiraspol		Ural	Eastern Siberia, Q1	Adycha river, Oskhordokh, Q1 (?)			Adycha river, UlakhanSullar, Q1			Aldan river, Khara-Aldan, Q1,	Bolshaya Chukochiya river, Q1
	Kahlke, 1956, 1960	Kahlke, 1956	David, 1965	Vereshchagin, 1967	Yakhimovich, 1965	Vangengeim, 1961	Lazarev & Tomskaya, 1987	YIGS 4412	MB n.n.	YIGS 4437	VMN n.n.	MB n.n.	YIGS 62	Sher, 1971
1	382	354	340	440	429	350	-	280	550	250	390	365	440	520
2	300	282	351	-	222	313,3	307,5	312	330	345	-	-	340	305
3	223	223	280	224	180	243,3	121,5	230	275	-	250	230	254	220
4	67	70	94	-	62	-	68	70	-	57	-	-	74	60
3:1	57,9	69,2	82,3	51	42	78	73,4	82	50	-	64	63	57,7	42,3

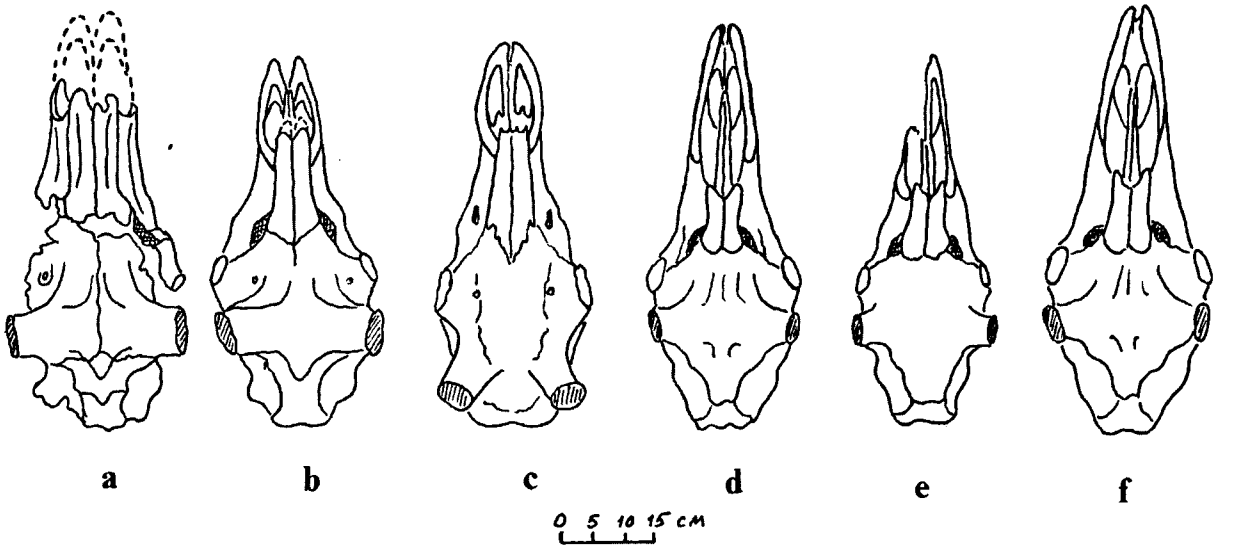

Fig 10 Skulls in top view: a - *C. latifrons*, Süssenborn; b - *C. scotti*, New Jersey, Mount-Hermon (both after Sher, 1986); c - *Cervus elaphus* (after Sokolov, 1979); d – *Alces alces*; e - *A. alces caucasicus* (after Vereshchagin, 1949); f – *A. americanus*

Schedels gezien van boven; voor soortnamen en vindplaats, zie Engelstalig onderschrift

Table 8 Measurements (in mm) and indices (in %) of metatarsal bones of broad-fronted moose and stag-moose (genus *Cervalces*). 1 - length; 2 - width of proximal end; 3 - transversal diameter of proximal end; 4 - width of distal end above trochlea; 5 - transversal diameter of distal end; 6 - width of shaft at midpoint.

Maten (in mm) en verhoudingen (in %) van middenvoetsbeenderen van de eland met breed voorhoofd (*latifrons*) en hert-eland (geslacht *Cervalces*). 1 - lengte; 2 - breedte aan bovenuiteinde; 3 - dwarsdoorsnede door bovenuiteinde; 4 - breedte van onderuiteinde; 5 - dwarsdoorsnede door onderuiteinde boven de rollers; 6 - breedte van de schacht in het midden

Measurements	*Cervalces latifrons*, Q1						*Cervalces* aff. *latifrons*, Q1	C. cf. *latifrons*, Q1		C. cf. *postremus*, Q2	*C. scotti*, Q3
	Tiraspol	Adycha				Yana	Bolshaya Chukochiya	Alaska		Maly Anyui	New Jersey
		Oskhordokh		Ulakhan Sullar							
	Sher, 1971	Lazarev & Tomskaya,1987	MB n.n.	VMN n.n.	MM 8034	Lazarev & Tomskaya, 1987	Sher, 1971	AM 3731709	AM 4744649	Sher, 1971	AM 107678
1	464	475,5	445	-	-	ca. 500	ca. 500	468	-	ca. 460	448
2	ca. 64	59,7	-	-	-	64	71	67	-	72,5	62,4
3	74	67,7	-	-	-	72	74,5	72	-	72	64,7
4	92,7	76,9	84	93,6	93	-	89,7	76	95,3	65	76
	46	41	51,6	51	50	46,3	39,5	46	49	44	37,1
6	56,8	50	-	-	54	-	ca. 60	47	59,3	ca. 45	48,1
Indices											
2:1	ca. 14	12,5	-	-	-	ca. 13	ca. 14,2	14,3	-	15,7	13,9
4:1	20	16,1	16,1	-	-	-	ca. 17,9	16,2	-	-	17
6:1	10	8,6	8,6	-	-	ca. 9	ca. 8	9,8	-	9,6	8,3

which has no analogue in others cervids, and they are connected with the existence of a powerful system of nasal cartilages and a long mobile (proboscis-like) upper lip in the moose" (after Sher, 1986: 13). The rostral section of *Alces* is somewhat similar to that of the saiga-antelope *Saiga tatarica*, for which the ventricose proboscis-like muzzle is an adaptation to a habitat in boreal regions with a continental climate (Sokolov & Zhirnov, 1998). Probably a similar constitution of the front of the moose muzzle indicates its origin in the boreal part of Eurasia. The shape of the upper processes of the premaxillary bones of modern *Alces* was discussed above. The morphotype of the Caucasian moose in which the nasal bones come into contact with the premaxillary bones does not unite this moose with *Cervalces* at all, because there is no essential lengthening of the nasal bones in this case, and much more, the shape of the nasal bones is typical for *Alces*. Also the upper processes of the premaxillary bones of the Caucasian moose differ from those of the broad-fronted moose, stag-moose and deer. A similar morphotype as that of *A. a. caucasicus* is occasionally met among modern *A. alces*: among 504 investigated skulls of this species we found two similar specimens (fig. 10a).

Cervalces cf. *latifrons*

Cervalces alaskensis Frick, 1937

Material and locality. Collections of AMNH, Alaska. Antler beams: AMNH 30496 (holotype of *Cervalces alaskensis*), AMNH 30497, AMNH 365-4327 and AMNH 710-1491, vicinity of Fairbanks; AMNH 527-4127 (fig. 11b-d), AMNH 527-4128 and AMNH 433-3858, Cripple Creek. Metatarsals: AMNH 373-1709, Ester Creek; AMNH 474-4649, Livenhood Creek.

Geological age. The specified antler beams are referred to in the AMNH catalogue to Rancholabrean, that corresponds to the American geochronological scale with 480 - 10 thousand years BP (Repenning, 1980; Churcher & Pinsof, 1987) or 300 - 10 thousand years BP (after Martin & Steadman, 1999), so it includes part of the Middle Pleistocene and the Late Pleistocene. All materials are strongly mineralized and range in colour from almost black up to brown.

Description and comparison. The beams are very long and massive (table 10), their dimensions are close to those of Eurasian *C. latifrons* (table 7). They are slightly bent (fig. 11b-d), especially AMNH 30497, which beam is practically S-shaped (fig. 11c).
The dimensions of metatarsals from Alaska

Table 9 Sizes (in mm) and indices (in %) of metatarsal bones of true moose (genus *Alces*). 1 - length; 2 - width of proximal end; 3 - transversal diameter of proximal end; 4 - width of distal end above trochlea; 5 - transversal diameter of distal end; 6 - width of shaft at midpoint.

Maten (in mm) en verhoudingen (in %) van middenvoetsbeenderen van ware eland (geslacht *Alces*). 1 - lengte; 2 - breedte van bovenuiteinde; 3 - dwarsdoorsnede door bovenuiteinde; 4 - breedte van onderuiteinde boven de rollers; 5 - dwarsdoorsnede door onderuiteinde; 6 - breedte van de schacht in het midden.

Measurements	*Alces* sp.			*A. americanus*				*A.a.pfizenmayeri*	*A.a.gigas*
	Lower Tunguska river, Q3	Yakutia, Q3		Alaska, Q3-Q4				Central Yakutia	Extreme North-East Siberia
	Sher, 1971	Sartang river	Ulakhan Sullar	AM 34586	AM 3681426	AM 3681426/1	AM 5862310	modern, n=6	modern, n=7
1	410	422,6	418,3	433	420	422	429	391	410,3
2	49	57	54,5	52	61	59	58	50,6	56,4
3	54	55,7	57,2	57	63	59	63	55,7	59,3
4	65	70	64,8	68	73	71	73	64,3	69
5	39,5	44	43	44	44	46	50	42,2	45,5
6	34,2	33,7	31,4	34	36	36	37	32,4	33,7
Indices									
2:1	11,9	13,4	13,0	12	14,5	14	13,5	13,7	14,1
4:1	15,9	16,3	15,4	15,7	17,4	16,8	17	16,5	17,1
6:1	8,4	7,9	7,5	7,9	8,6	8,5	8,6	8,2	8,3

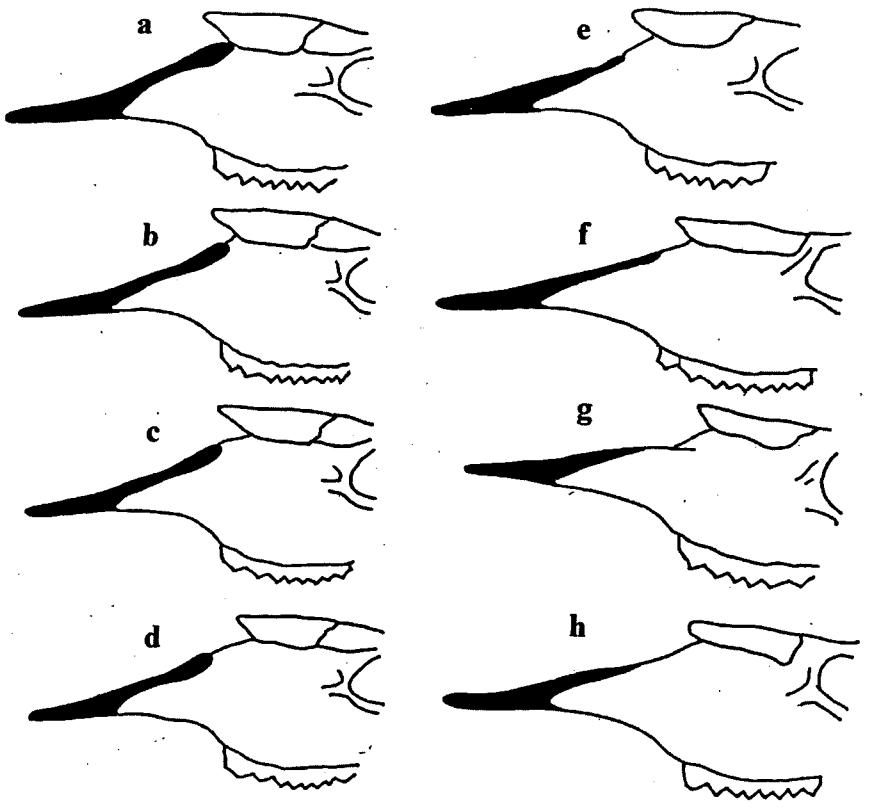

Fig 11 Shape of the upper process of the premaxillary bone in *Alces*: a - ZM 66317, Pechoro-Ilych Nature Reserve, coll. ZM MSU, Russia; b - MS 35551, Eastern Germany (?), coll. MS, Germany; c - ZIN 33726, St Petersburg district, coll. ZIN RAS, Russia; d - ZM 35273, Western Siberia, Malaya Sosva river, coll. ZM MSU, Russia; e - MS 494, Western Ukraine, coll. MS, Germany; f - no number, Norway, coll. KM, Germany; g - ZIN 32700, Canada, Ontario, coll. ZIN RAS, Russia; h - ZIN 12834, Eastern Siberia, Aldan river, coll. ZIN RAS, Russia

Vorm van het bovenste uiteinde van het premaxillare in *Alces*: a - ZM 66317, Pechoro-Ilych Natuurreservaat, coll. ZM MSU, Rusland; b - MS 35551, Oost Duitsland (?), coll. MS, Duitsland; c - ZIN 33726, St Petersburg district, coll. ZIN RAS, Rusland; d - ZM 35273, West Siberië, Malaya Sosva rivier, coll. ZM MSU, Rusland; e - MS 494, West Ukraïene, coll. MS, Duitsland; f -zonder nummer, Noorwegen, coll. KM, Duitsland; g - ZIN 32700, Canada, Ontario, coll. ZIN RAS, Rusland; h - ZIN 12834, Oost Siberië, Aldan rivier, coll. ZIN RAS, Rusland

Table 10 Sizes (in mm) and massivity index (=3:1, in %) of antler beams of *Cervalces* cf. *latifrons* from Alaska. 1 - length; 2 - circumference of burr; 3 - circumference above the burr; 4 - circumference at midpoint; 5 - horizontal diameter.

Maten (in mm) en massiviteitsindex (=3:1, in %) van geweistangen van *Cervalces* cf. *latifrons* uit Alaska. 1 - lengte; 2 - omtrek rozenkrans; 3 - omtrek boven rozenkrans; 4 - omtrek halverwege; 5 - dwarsdoorsnede.

Measurements and index	AM 30496, holotype of "*Cervalces alaskensis*" Frick, 1937	AM 30497	AM 3654327	AM 7101491	AM 5274127	AM 5274128	AM 4333858
1	380	405	320	370	340	260	320
2	320	250	275	230	300	280	340
3	241	228	241	224	249	252	244
4	209	193	224	197	224	222	238
5	68	56	75	65	69	72	76,3
3:1	63,4	56,3	-	60,5	73,2	-	76,3

exceed those of the true moose and of *C. scotti*, and come close to those of the broad-fronted moose from Eurasia (table 8).

Remarks. Remains of a moose close to *C. latifrons* were found in the Yukon river basin in Early Pleistocene fauna of Old Crow, which is similar to the Olyerian fauna (Harington, 1978 in Sher, 1992). Frick (1937), when describing a new species of stag-moose from Alaska ("*C. alaskensis*"), noted that the beam dimensions of this form are much larger than those of Scott's stag-moose. Antler remains of a large *Cervalces* from Alaska were under consideration and later it was supposed that they belonged to *C. latifrons* or a close form (Kurtèn & Anderson, 1980; Sher, 1971). Sher (1986) assumed that broad-fronted moose with long and bent antler beams from the Kolyma basin and Alaska are closer to the subgenus *Libralces* and belong to separate species. If this turns out to be valid, the name "*alaskensis*" has priority by rule, and will be re-installed. Apparently, remains of Alcinae from North America may revail useful new information. For example, the absolute age of one antler beam from Alaska (the Old Crow river), which parameters are close to those of *C. latifrons*, was dated 33.800 + 2.000 y. BP (Kurtèn & Anderson, 1980). In our opinion, this fact can testify the contemporaneous existence in Alaska of Scott's stag-moose and another, larger species of *Cervalces*.

Cervalces postremus Vangengeim et Flerov, 1965 - Siberian (?) broad-fronted moose

Material and locality. A skull fragment with part of an antler beam, YIGS 1277, Vilyui river, Verkhnevilyuiskoye locality, YIGS (fig. 12). Antler fragments: YIGS 45 (fig. 13c) and YIGS 64, Aldan river, Mamontova Gora locality; YIGS 135, Aldan river, Rossypnoye locality (fig. 13b); YIGS 970, 1310 (fig. 13d-e) and 1382, Vilyui river, Verkhnevilyuiskoye locality; YIGS 1762, Bolshaya Chukochiya; YIGS 4758, the delta of Lena river (fig. 13f); YIGS 6829, northern Yakutia (fig. 14b); VMN specimen without number, Adycha river, Ulakhan Sullar (fig. 14a). Mandible fragments YIGS 4406 and 4436, Oskhordokh, YIGS.

Geological age. The studied specimens of YIGS, No 45 and No 64 from Mamontova Gora, and No 135 from Rossypnoe were earlier described by Russanov (1968). He referred the material from Mamontova Gora to the late Middle Pleistocene, and YIGS 135, to the beginning of the Late Pleistocene (the Kazantsevo Interglacial). The locality Verkhnevilyuiskoe yielded specimens YIGS, Nos 970, 1277, 1310, and 1382. Deposits of the Middle and Upper Pleistocene

Table 11 Sizes (in mm) and massivity index (=3:1, in %) of antler beams of *Cervalces postremus* and C. aff. *postremus*. The antler from Ulakhan Sullar is at the Verkhoyansk Museum of Nature; the other antlers at YIGS. From Russanov (1968) the averages are taken. 1 - length; 2 - circumference of burr; 3 - circumference above the burr; 4 - circumference at midpoint; 5 - horizontal diameter. Holotype described and measured by Vangengeim & Flerov (1965).

Maten (in mm) en massiviteitsindex (=3:1, in %) van geweistangen van *Cervalces postremus* en C. aff. *postremus*. Het gewei van Ulakhan Sullar bevindt zich in het Verkhoyansk Natuurmuseum, de andere geweien in YIGS. Uit Russanov (1968) zijn de gemiddelde waardes genomen. 1 - lengte; 2 - omtrek rozenkrans; 3 - omtrek boven de rozenkrans; 4 - omtrek halverwege; 5 - dwarsdoorsnede. Het holotype is beschreven en gemeten door Vangengeim & Flerov (1965).

	Yakutia													Kamchatka
	Aldan river					Viluy river , Verkhnevilyuiskoye				Lena river delta	Northern Yakutia	Adycha river, Ulakhan Sullar	Bolshaya Chukochiya river	
	Russanov, 1968	Mamontova Gora			Rossypnoye									
		Holotype	YIGS 45	YIGS 64	YIGS 135	YIGS 970	YIGS 1277	YIGS 1310	YIGS 1382	YIGS 4758	YIGS n.n.	YIGS n.n.	YIGS 1762	Vaskovsky, 1966
1	294,6	280	225	265	190	185	173	215	205	220	185	180	270	278
2	213,8	235	195	290	-	230	195	-	-	-	206	205	260	-
3	174,2	160	155	198	150	147	140	160	184	155	156	146	170	157
4	-	-	144	161	143	140	142	154	173	153	143	130	157	-
5	53,5	50	42	49	45	43	44	46	54	44	46	-	47	54
3:1	60,8	57,2	68,9	74,7	78,9	79,5	70,8	74,4	89,8	70,5	84,3	81,1	63	56,5

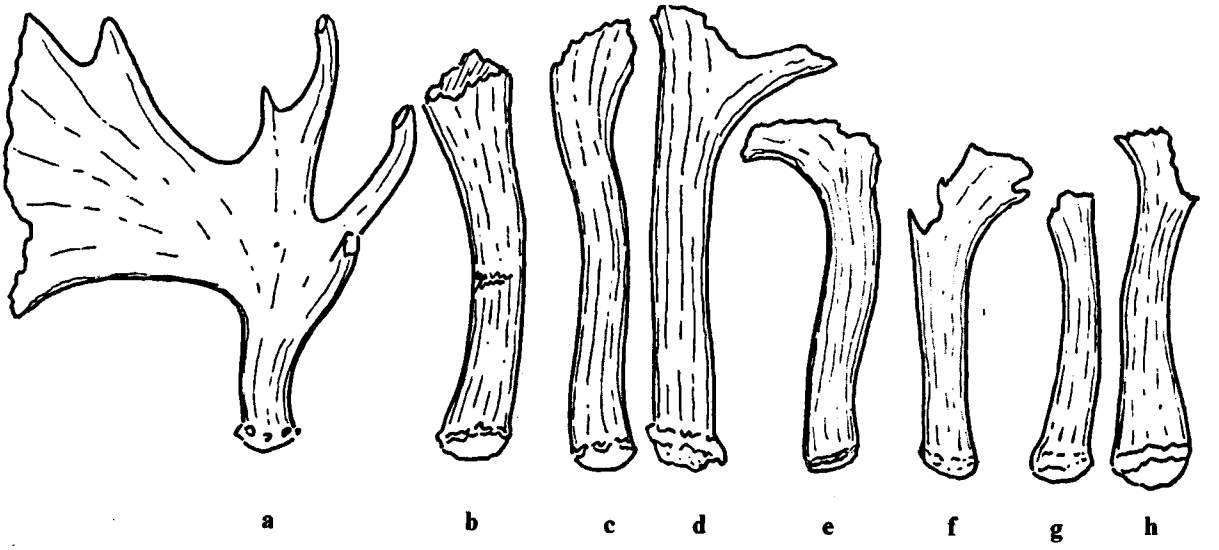

Fig 12 Fragments of Alcinae antlers from Alaska. *A. americanus*: a - AMNH 252-1939, Eldorado Creek (for comparison). *Cervalces* cf. *latifrons*: b - AMNH 527-4127, Cripple Creek, c - AMNH 30497, vicinity of Fairbanks, d - AMNH 30496, holotype of "*C. alaskensis*", vicinity of Fairbanks. *C. scotti* and *C.* cf. *scotti*: e - AMNH 276-6360, Banks-at-fox, f - AMNH 276-8309, Engineer Creek, g - AMNH 235-8130, Engineer Creek, h - AMNH 515-5170, vicinity of Fairbanks

Fragmenten van Alcinae geweien uit Alaska. *A. americanus*: a - AMNH 252-1939, Eldorado Creek (ter vergelijk). *Cervalces* cf. *latifrons*: b - AM 527-4127, Cripple Creek, c - AMNH 30497, omgeving van Fairbanks, d - AMNH 30496, holotype van "*C. alaskensis*", omgeving van Fairbanks. *C. scotti* en *C.* cf. *scotti*: e - AMNH 276-6360, Banks-at-fox, f - AMNH 276-8309, Engineer Creek, g - AMNH 235-8130, Engineer Creek, h - AMNH 515-5170, omgeving van Fairbanks

are exposed at this site (Lazarev, 1980). The fossil remains in question may belong to the late Middle or the beginning of the Late Pleistocene due to the co-occurrence with remains of *Mammuthus primigenius* Blum of the early type, *Bison priscus* Bojanus, *Equus orientalis* Russanov, and *E. lenensis* Russanov. Antler beam YIGS 1762 from the Bolshaya Chukochya River, found together with remains of *M. primigenius* of the early type, and *E. orientalis*, is most likely attributable to the late Middle Pleistocene. Though the age definition of other antlers is problematic, most remains of *C. postremus* from Yakutia can be dated to the Late Middle or the beginning of the Late Pleistocene. Earlier, this point of view was expressed by Russanov (1968), and Vangengeim (1977). Sher (1986) defined the biozone of this broad-fronted moose as the Middle Pleistocene (Mindel - Riss, Riss), and, likely, the beginning of the Late Pleistocene (Riss - Würm).

Description and comparison. Antler fragments are strongly mineralized, dark brown or grayish brown in colour. Antler beam is long, but relatively thin (figs. 23 - 25): beam length exceeds its circumference. The massivity index of the beam in *C. postremus* amounts to 50 to 90%, which is similar to values for *C. latifrons*. True moose of the genus *Alces* have shorter and relatively thicker antler beams (fig. 14) (Boeskorov, 1998), the massivity index of the beam always exceeds 100% (Sher, 1986; Boeskorov, 2001). Measurements of antler beams are listed in table 11. *C. postremus* has a thin antler beam of moderate length, contrary to *C. latifrons*, which has longer and much more robust beams (table 7) (Vangengeim & Flerov 1965; Russanov, 1968; Sher, 1971). *C. postremus* differs from *C. scotti* in the shape of the palmation (fig. 4). The former species (as well as *C. latifrons*) has an undivided, flat palmation, while Scott's stag-moose has a bi- or tripartite palmation, with its parts often lying in different planes. Besides, antler beams of *C. postremus* are slightly shorter and thinner than in *C. scotti* (table 12).

Specimen YIGS 1277 is the only presently known skull of *C. postremus*. It is noteworthy that the most important diagnostic area, the

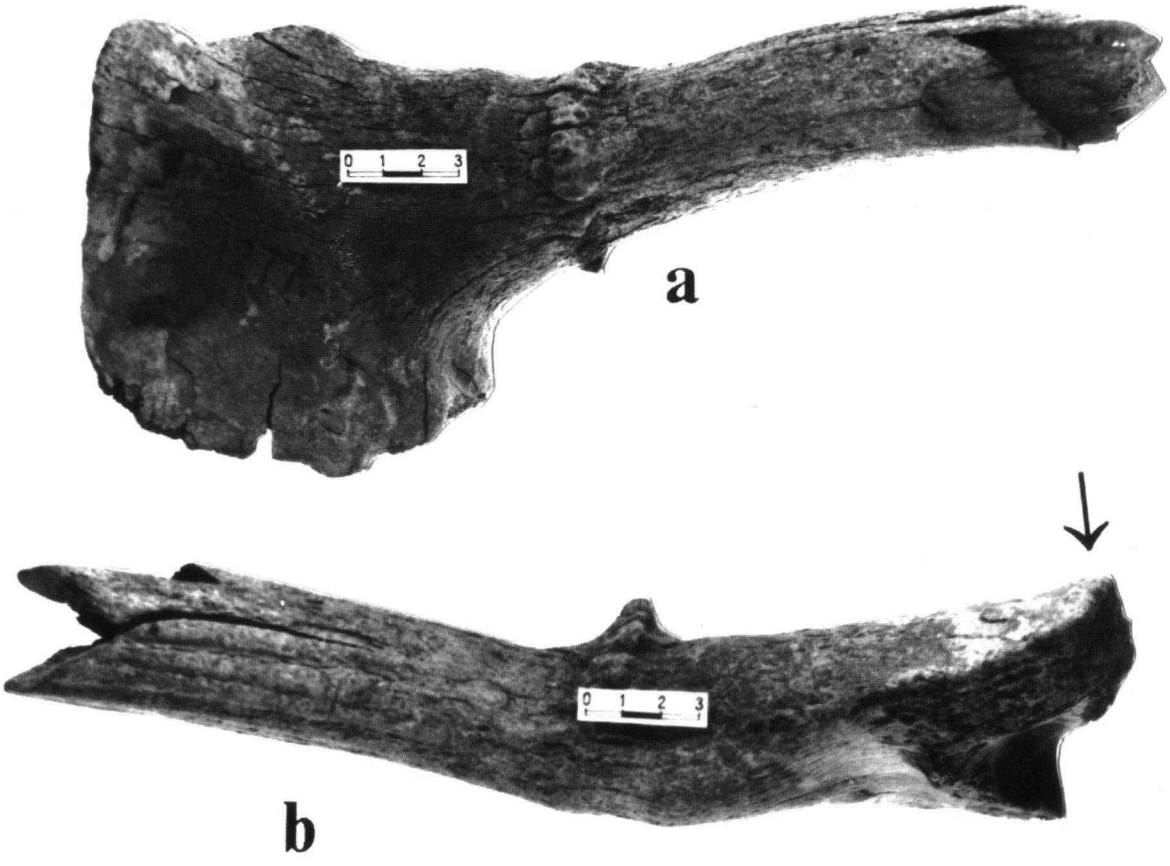

Fig 13 Skull fragment of *Cervalces postremus* from Verkhneviliuyskoye outcrop, the Viliuy river (YIGS 1277): a - view from above, b - posterior view (the area of frontal elevation is marked by an arrow). Scale bar 1 cm

Schedelfragment van *Cervalces postremus* uit Verkhneviliuyskoye ontsluiting aan de Viliuy rivier (YIGS 1277): a - gezien van bovenaf, b - gezien van achteren (het gebied van de opbolling aan de voorzijde is aangegeven met een pijl). Maatstreep 1 cm

basal part of the frontals(fig. 12b), is preserved. The antler beam of this specimen has the characteristic size and proportions of the "*postremus*" form (table 11). Moreover, an extensive distance from the burr to the midpoint of the frontal, and the weak frontal protuberance clearly confirm the attribution of this moose to the genus *Cervalces*. The distance from the burr to the mid-frontal (the fronto-parietal suture) in specimen YIGS 1277 is 12,5 cm, which is much more than in *Alces* (table 2). In fossil and subfossil true moose this parameter ranges from 9,6 to 10,4 cm, with a mean of 10,1 cm (n=6); recent forms show a range of 8,8 to 11,1 cm, with a mean of 9,69 cm (n=16).
The mandible fragments YIGS 4406 and YIGS 4436 are preliminary referred by us to *C. postremus*, since their molars have large dimensions, intermediate between *C. latifrons* and *Alces* (table 5); besides, the labial pillars are present, which is an obligatory feature for the ascription to *Cervalces*.

Remarks. Sher (1986) and Bubenik (1986) assumed that the form "*postremus*" is probably an independent species within the genus *Cervalces*. Sher (1986) and Lister (1993) argued that due to the lack of a skull of the "*postremus*" form, its attribution to *Alces* or *Cervalces* is obscure. The skull fragment YIGS 1277 clearly shows that "*postremus*", the younger broad-fronted moose, is not related to true moose and belongs to the genus *Cervalces*. This can already be concluded on the basis of antler beam morphology, because their proportions are characteristic for the lineage of broad-fronted moose (table 11). Besides, antler remains of *C. postremus* indicate a broad and undivided palmation with long tines (fig. 4b), similar to the

Table 12 Sizes (in mm) and massivity index (= 3:1, in %) of antler beams of the stag-moose *Cervalces scotti* and *C.* cf. *scotti* from Alaska (coll. AMNH). 1 - length; 2 - circumference of the burr; 3 - circumference above the burr; 4 - circumference at midpoint; 5 - horizontal diameter.

Maten (in mm) en massiviteitsindex (= 3:1, in %) van geweistangen van hert-eland *Cervalces scotti* en *C.* cf. *scotti* uit Alaska (coll. AMNH). 1 - lengte; 2 - omtrek rozenkrans; 3 - omtrek boven rozenkrans; 4 - omtrek halverwege; 5 - dwarsdoorsnede.

Measure-ments	AM 3422426	AM 2768309	AM 5155170	AM 2358130	AM 2766360	AM 2304231	AM 2758313	AM 1825414	AM 2297894
1	290	254	340	305	330	205	220	265	220
2	280	231	300	220	240	170	240	235	185
3	201	189	250	180	210	149	185	220	160
4	185	170	180	158	176	139	180	183	152
5	57,4	55,4	57	49,5	57	43	59	57	46,8
3:1	69,3	74,4	73,5	59	63,6	72,7	84,1	83	72,7

the morphology known for *C. latifrons*. There is a significant time gap between *C. latifrons* and *C. postremus*. Remains of the former species are common in deposits of the Early and early Middle Pleistocene of Northern Eurasia. The latter species is characteristic for the deposits of the late Middle Pleistocene of Eastern Siberia and the Russian Far East, whereas *C. latifrons* is already absent at this stratigraphic level (Baryshnikov *et al.*, 1981; Sher, 1986). The size of antler beams of the late broad-fronted moose is much smaller than known for *C. latifrons*, and almost no overlap is observed (fig. 15). The temporal and morphological discontinuity between *C. latifrons* and *C. postremus* clearly indicates that latter cannot be a subspecies of the broad-fronted moose, but represents an independent species.

Judging from its sites, *C. postremus* was widely distributed from Central Yakutia and the delta of the Lena River up to the Kolyma Lowland, the Western Chukotka, and Kamchatka (fig. 5). The area of *C. postremus* in Eastern Siberia was quite similar to that of *C. latifrons*. However, the younger broad-fronted moose obviously expanded still further to the east, and it is likely that in the late Middle Pleistocene *C. postremus* dispersed from the extreme northeast of Asia along the Beringian Bridge into North America to give rise to *C. scotti*. In Eurasia, the late broad-fronted moose, apparently, got extinct in the beginning of the Late Pleistocene. This process may have been influenced by moose of the genus *Alces*: being more adapted to a cold climate, they could displace *C. postremus*. Although the most reliable finds of *C. postremus* are known from Eastern Siberia (Yakutia) (Vangengeim & Flerov 1965; Russanov, 1968; Boeskorov, 2001), and Kamchatka (Vaskovsky, 1966), the actual distribution area of this moose was supposedly much wider. According to Alekseeva (1980), among the antlers of Pleistocene moose from the Krasnyi Yar locality (the Ob River region) there are specimens with a beam length up to 26 cm. This material may indicate *C. postremus*. Vereshchagin (1967) described a moose antler fragment from the Middle Pleistocene deposits of the Volga River region. Similar to *C. postremus*, this specimen is thin (the diameter above burr is 40,5 cm), and its beam has an average length (24 cm). Fossil moose antlers of the "*postremus*" type are known also from the eaerly Late Pleistocene of Ehringsdorf, Germany (Sher, 1986).

Cervalces sp.

Material and locality. Mandible AM 108-5745, Alaska, Engineer Creek (AMNH).

Geological age. This mandible is referred to in the AMNH catalogue to Rancholabrean, the period from Middle to Late Pleistocene. The bone is mineralized and has a dark brown colour.

Description and comparison. The dimensions of the described bone are presented in table 3. Proportions of this jaw (indices of dentition length, diastema length, height at coronar process) reveal that it belongs to *Cervalces*. At the same time the majority of parameters of AMNH 108-5745 is lower than in broad-fronted moose, though exceeds those of Scott's stag-moose. Probably this mandible belongs to an intermediate form between *C. latifrons* and *C. scotti*, close to *C. postremus*.

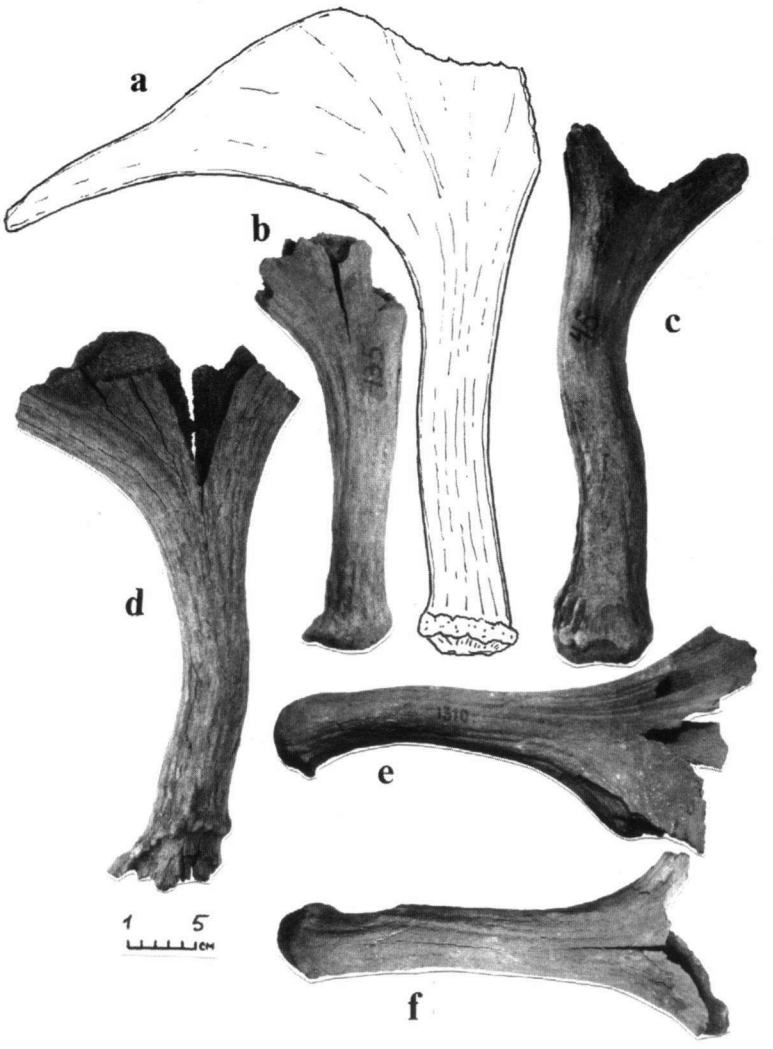

Fig 14 Fragments of antlers of *Cervalces postremus*. a - typical specimen, Mamontova Gora (after Russanov, 1968); b - YIGS 45, Mamontova Gora; c - YIGS 135, Rossypnoye locality; d, e - YIGS 970 and YIGS 1310, Verkhneviliuyskoye locality; f - YIGS 4758, the Lena river delta

Geweifragmenten van *Cervalces postremus*. a - karakteristiek exemplaar, Mamontova Gora (naar Russanov, 1968); b - YIGS 45, Mamontova Gora; c - YIGS 135, Rossypnoye vindplaats; d, e - YIGS 970 en YIGS 1310, Verkhneviliuyskoye vindplaats; f - YIGS 4758, delta van de Lena

Cervalces scotti Lydekker, 1898 - Scott's stag-moose

Cervalces roosevelti Hay, 1913
C. borealis Bensley, 1913

Material and locality. Collections of AMNH. A skull (fig. 16a), mandible (fig. 7c), metatarsal, AMNH 107678, New Jersey, Mount Hermon. Alaska: skull (fig. 16a) and mandible (fig. 7d), AMNH 198-5899, Engineer Creek; skull fragments: AMNH 101-5090 (fig. 17b) and AMNH 627-6546, both from Engineer Creek; AMNH 342-2426, Cripple Creek (fig. 17c); AMNH 712-1342 and AMNH 16250, vicinity of Fairbanks; mandible AMNH 108-5745, Engineer Creek; antler beams: AMNH 182-5414, 235-8130 (fig. 11g), 275-8313, 276-8309 (fig. 11f), Engineer Creek; AMNH 229-7894 and 515-5170 (fig. 11h), vicinity of Fairbanks; AMNH 230-4231, Eldorado Creek; N 276-6360, Banks-at-Fox (fig. 11e); AMNH 342-2426, Cripple Creek.

Geological age. Material of Scott's stag-moose is referred in the AMNH catalogue to the Rancholabrean; the geological age of this material is not exactly determined. All osteal remains of *C. scotti* are mineralized and range in colour from dark brown up to yellowish-brown. A similar degree of mineralization is also found in bones from the Early Holocene. The skeleton from

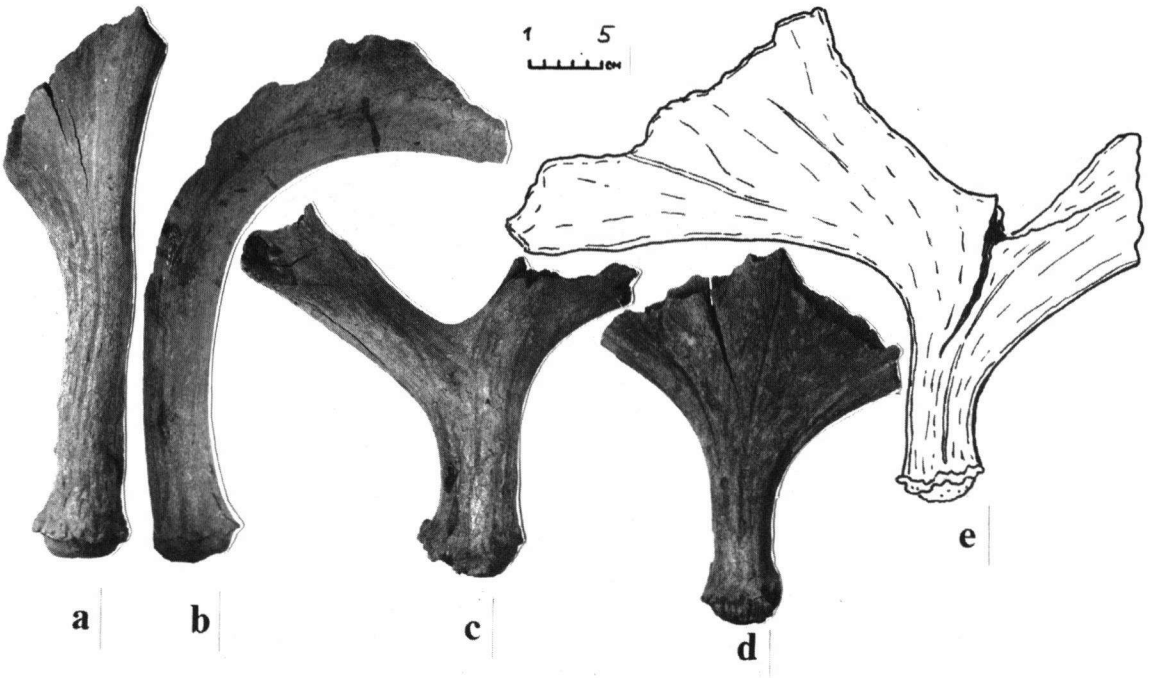

Fig 15 Antler fragments of *Cervalces postremus*. a – private collection, no number, Adycha river, Ulakhan-Sullar; b – YIGN, no number, Northern Yakutia. For comparison *Alces* cf. *americanus*: c - YIGS 631, Mamontova Gora; d - MM 7653, Kolyma river, Duvanny Yar; e - YIGS 3380, Bolshaya Chukochiya river (after Lazarev & Tomskaya, 1987)

Geweifragmenten van *Cervalces postremus*. a – privé collectie, zonder nummer, Adycha rivier, Ulakhan-Sullar; b – YIGN, zonder nummer, Noord-Yakutië. Ter vergelijk *Alces* cf. *americanus*: c - YIGS 631, Mamontova Gora; d - MM 7653, Kolyma rivier, Duvanny Yar; e - YIGS 3380, Bolshaya Chukochiya rivier (naar Lazarev & Tomskaya, 1987)

New Jersey AMNH 107678 was found in a post-glacial bog (Kurtèn & Anderson, 1980), so it probably belongs to the beginning of the Holocene. The skull with mandible AMNH 198-5899 is mineralized and also charred: it bears traces of burning by fire, most likely caused by prehistoric humans. According to recent data people penetrated into Alaska some 12.000 - 13.000 years ago (after Guthrie, 1990a); the geological age of this stag-moose can be determined as the end of the Pleistocene or the beginning of the Holocene. Our *C. scotti* material thus probably originated from this period.

Description and comparison. Though the skeleton of a stag-moose from New Jersey was investigated by Scott (1885) and Hay (1914), a detailed metrical description of its skull and mandible was never made. Our data on the metrical features of AMNH 107678 are given in tables 3 and 13. The skull of this specimen revealed distinctive features of stag-moose, which puts it together with the broad-fronted moose and distinguishes it from *Alces*: short rostrum, long nasal bones (which length exceeds the length of the upper dentition) (table 13), which come into contact with the upper processes of the premaxillary bones, etc. These features indicate that stag-moose and broad-fronted moose belong to a uniform genus *Cervalces* (Azzaroli, 1981).

Skull AMNH 198-5899 was not described yet. Its basic parameters are rather similar to those of a skull of *C. scotti* from New Jersey (table 13), which undoubtedly belongs to the same species and proves the existence of Scott's stag-moose in Alaska. Specimen AM 198-5899 is one of the few most informative remains of *C. scotti*, and allowed us, together with skull AM 107678, to test the reliability of some features with which stag-moose can be distinguished from true moose, and to add additional diagnostic features.

There seems to have been a synchronic existence at the end of the Late Pleistocene and, apparently, in the beginning of the Holocene in North America of two representatives of the subfamily Alcinae: Scott's stag-moose and American moose, which resemble each other significantly in many features of skull and post-cranial skeleton. This circumstance considerably

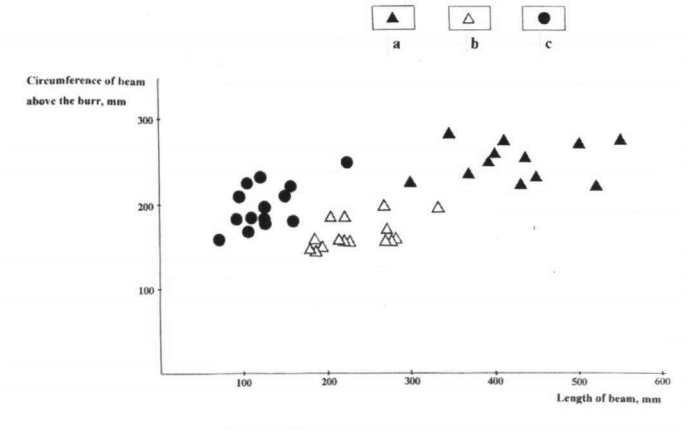

Fig 16 Sizes of antler beams of moose from the Pleistocene of Eastern Siberia and the Russian Far East: a - *Cervalces latifrons*; b - *C. postremus*; c - *Alces* sp. and *A.* cf. *americanus*

Maten van geweistangen van eland uit het Pleistoceen van Oost-Siberië en het verre oosten van Rusland: a - *Cervalces latifrons*, b - *C. postremus*, c - *Alces* sp. en *A.* cf. *americanus*

complicates the diagnostics of many fossil and subfossil bones of Alcinae in this territory, especially so because the rather rare finds consists mostly of neurocraniums, whereas *Cervalces* and *Alces* mainly differ in the nasal bones and the rostral part of skull.
For *Cervalces* a wide occipital part of skull is characteristic (after Vislobokova, 1990), together with a small height of the occiput (fig. 18) The height index of the occiput in broad-fronted moose is 69,9 %, and in *C. scotti* 64,8 to 71,3 %, with an average of 68,3 % (n=5) (table 1). In fossil and modern *Alces* the occipital part is higher, with an index of more than 70%) (table 2).
Moreover, we discovered that the transcornual width of the skull is more than in the true moose. In the former it is 11,2 to 12,2 cm, with an average of 11,54 cm (n=5); in the latter it is less than 110 mm. Even in the largest fossil and subfossil *Alces americanus* from Alaska this parameter varies between 10,2 cm and 10,65 cm, with an average of 10,51 cm (n=6) (table 2).
Cervalces, in contrast to *Alces*, had a more level intercornual area, without the pronounced, cone-like prominence (fig. 17).
The diastema of Scott's stag-moose was shorter than in true moose (table 3), thus the index of diastema length in the former is close to that in *C. latifrons*, which is less than 38%. In *Alces* the diastema is much longer, because of the general lengthening of the rostral part of skull, and here the index is higher than 38%; moose from Northeast Siberia and Alaska even reach indices higher than 39% (table 4).
For the stag-moose, as well as for broad-fronted moose, the rather large length of the lower dental row (index higher than 35%) and the height of the mandible at the coronar process (index higher than 49%) are characteristic (table 3). True moose have a relatively shorter dentition (index usually lower than 35%) and a lower mandible (index usually lower than 48%) (table 4).

Table 13 Sizes (in mm) of skulls of *Cervalces scotti* and *Alces* from Alaska.

Maten (in mm) van schedels van *Cervalces scotti* en *Alces* uit Alaska.

Species, coll. number, locality	Common length	Condilo-basal length	Upper tooth row length	Cheek bones width	Rostrum length	Orbito-facial length	Nasal bone length	Height at nasion point	Rostrum width
Cervalces scotti, Q3-Q4									
AMNH 107678, New Jersey	552	526	144	229	175	323	181	142	82
AMNH 198-5899, Alaska, Engineer Creek	500	-	139	215,3	-	-	155	144	-
Alces americanus, Alaska, Q3-Q4									
AMNH 106-7527, Ester Creek	614	584	152	232	282	386	122	152	85
AMNH 368-1426, Fish Creek	-	-	159	-	296	409	-	-	73
AMNH 485-4734, Hunter Creek	608	573	152	216	278	378	104	146	80

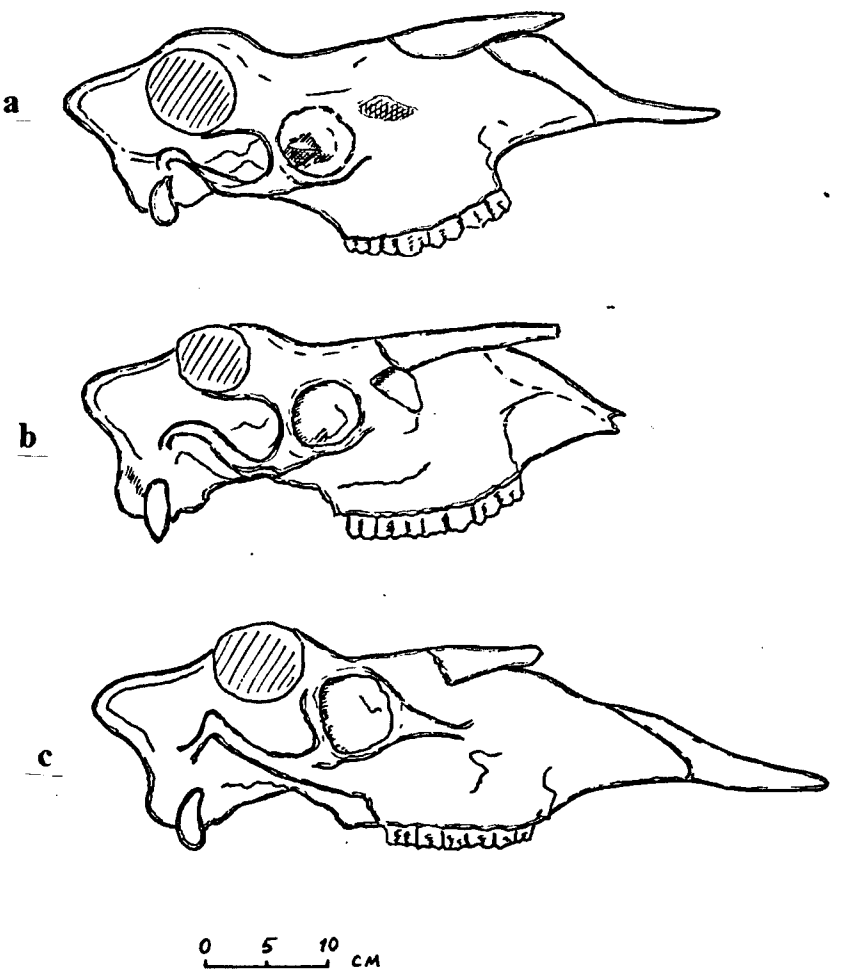

Fig 17 Skulls of Alcinae from the Late Pleistocene of North America. a – *C. scotti*, AMNH 107678, New Jersey, Mount-Hermon; b – *C. scotti*, AMNH 198-5899, Alaska, Engineer Creek; c – *A. americanus*, AMNH 106-7527, Alaska, Ester Creek

Schedels van Alcinae uit het Laat Pleistoceen van Noord-Amerika. a – *C. scotti*, AMNH 107678, New Jersey, Mount-Hermon; b – *C. scotti*, AMNH 198-5899, Alaska, Engineer Creek; c – *A. americanus*, AMNH 106-7527, Alaska, Ester Creek

The premolars to molars ratio in stag-moose, as in broad-fronted moose and true moose, varies highly (tables 3 and 4). *C scotti* has large tooth (table 5), and in the mandibles examined by us, the molars have labial pillars.

Antlers. *C. scotti* has large antlers with a long, but relatively thin beam and the original palmation divided into two or three parts, with many long tines (fig. 4c). A similar antler form is not found among other Alcinae. The spread of *C. scotti* antlers, apparently, is very large: the stag-moose from New Jersey, which is not even the largest specimen, has an antler spread of 1,62 m (Hay, 1914). Such dimensions of antlers testify that *C. scotti* did not inhabit dense woods.

Beam length in Scott's stag-moose varies from 30,9 to 41,7 cm (Churcher & Pinsof, 1987). The length of our antler beams from Alaska ranges from 20,5 to 34 cm, with an average of 26,99 cm (n=9) (table 12). The massivity index of the antler beam is less than the 100% that is in general characteristic for *Cervalces*, and varies between 59,0 and 84,1%, with an average of 72,5% (n=9), which is rather similar to the same parameter in *C. postremus* (table 11). The circumference of the antler beam of Scott's stag-moose at midpoint ranges from 13,9 to 18,5 cm, with an average of 16,92 cm (n=9), and thus slightly exceeds the value of this parameter in *C. postremus*.

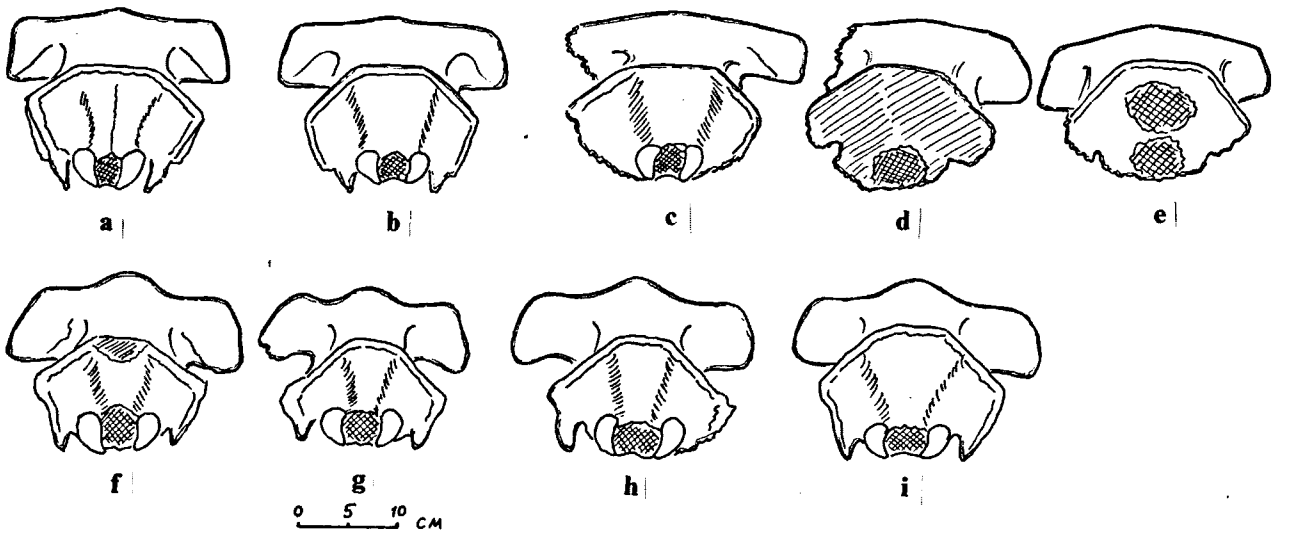

Fig 18 Occipital view of the Alcinae skulls from the North America. *C. scotti*: a - AM 107678, New Jersey, b - AMNH 198-5899, Alaska, Engineer Creek, c - AMNH 342-2426, Creeple Creek, d - AMNH 101-5090, Engineer Creek, e - AMNH no number, vicinity of Fairbanks. *A. americanus*, Alaska: d - AMNH 106-7527, e - AM 485-9734, f - AMNH 508-1489, g - AMNH 615-1108

Achteraanzicht van Alcinae schedels uit Noord-Amerika. *C. scotti*: a - AMNH 107678, New Jersey, b - AMNH 198-5899, Alaska, Engineer Creek, c - AMNH 342-2426, Creeple Creek, d - AMNH 101-5090, Engineer Creek, e - AMNH zonder nummer, omgeving Fairbanks. *A. americanus*, Alaska: d - AMNH 106-7527, e - AMNH 485-9734, f - AMNH 508-1489, g - AMNH 615-1108

C. scotti had body proportions generally similar to those of true moose: a rather short neck, long body, very long legs and a high body height (Scott, 1913; Hay, 1914; Sher, 1971); the skeleton from New Jersey has a withers' height not less than 1,81 m). Thus their metapodial length even exceeds the average parameters for *Alces* (Hay, 1914) (tables 8 and 9).

Scott's stag-moose remains in North America already originate from the Sangamonian interglacial (Middle Pleistocene) (Kurtèn & Anderson, 1980). However, the most reliable remains of this species are characteristic only for the Late Pleistocene, Late Rancholabrean (Martin & Steadman, 1999). Guthrie (1990b) provided two radiocarbon dates for remains of *Cervalces* (presumably, *C. scotti*) from Alaska (vicinity Fairbanks): 32.040 + 870 - 980 years BP (DIC-3090) and 25.330 + 200 y. BP (AA-3896). The youngest dates for *C. scotti* are 11.230 + 160 y. BP (New Jersey, Colombia; Harington, 1984), 10.950 + 150 y. BP (New York, Middleton; Buckley & Willis, 1970) and 10.230 + 150 y. BP (Ohio, Ansonia; Meltzer & Mead, 1985). Thus, the radiocarbon data testify that Scott's stag-moose lived in North America at least from 33.000 till 10.000 years ago, from the Middle Wisconsinan to the border between Pleistocene and Holocene. Dating on concomitant fauna allows for the extension of the existence till somewhere in the beginning of the Holocene (Churcher & Pinsof, 1987).

To be continued

For the genus *Alces* and the conclusion, see the next issue of CRANIUM (23, 1), scheduled for spring 2006.

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