

A review of the systematics of Pliocene and Pleistocene moose, part 2

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Summary

This paper is the second part of the article on the evolution and the systematics of the moose. Data from the literature on morphological variability and genetics of the moose and new data from our own research are discussed. New data on fossil broad-fronted moose (*Cervalces*; see part 1) and true moose (*Alces*) is submitted. The former and *Libralces* (part 1) are no direct ancestors of *Alces* (part 2). In light of new data, a revision of the systematics of the moose is carried out, and questions on phylogeny are considered.

Samenvatting

Dit artikel is het tweede deel van de publicatie over de evolutie en de systematiek van de eland. Gegevens uit de literatuur over morfologische variatie en erfelijkheid van de eland en gegevens van eigen onderzoek worden besproken. Ook worden nieuwe gegevens van de fossiele hert-eland *Cervalces* (deel 1) en van fossiele ware eland *Alces* (dit deel) 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 phylogenie behandeld.

FAMILY CERVIDAE GRAY, 1821

Subfamily Alcinae Jerdon, 1874

Genus *Alces* Gray, 1821

Type species. *Cervus alces* Linnaeus, 1758.
Present, Europe.

Diagnosis. Antler beam of average length or short (length always less than circumference). Braincase is rather narrow and higher than in *Cervalces*. The facial portion of the skull is long, and the rostrum is strongly elongated. Nasal bones are short; their length is less than that of the dental row. The upper (nasal) processes of the premaxillary bones usually do not reach the nasal bones. The area between the antlers bears a pronounced cone-like prominence. The orbits are almost on a level with the frontal vault.

Species composition. At least two species are recognised: *A. alces* (Linnaeus, 1758), early Late Pleistocene - present, Western Eurasia; *A. americanus* (Clinton, 1822), early Late Pleistocene - present, Eastern (?) Eurasia, end of the Late Pleistocene (Wisconsinan) - present, North America.

Alces sp.

Remains of true moose (*Alces*) are found in deposits from the late Middle Pleistocene onwards. Finds of *Alces* sp. in the Netherlands (Erdbrink, 1954) belong to that period. Some moose remains from the Middle Pleistocene

sediments of the Ob river (Krasny Yar) are attributed to true moose (Alexeeva, 1980). Moose bones found in morrain on the Kola peninsula probably belong to the Middle Pleistocene (Gromova, 1965; Vereshagin, 1967). To the late Middle Pleistocene (Tasovskoe glaciation) true moose are assigned in connection with a periglacial (tundra-steppe) fauna at the Lower Tunguska river (Vangengeim, 1977).

Pavlov (1906) described an adult true moose skull found at the Kama river in the vicinity of Mysy village under the name "*Alces savinus* Fisch." (fig. 19p). This skull may belong to a Khasarian fauna of the Middle Pleistocene (Gromova, 1965), though its stratigraphic position requires a re-examination (Sher, 1986). The skull shows characteristics of *Alces*: a long rostrum and short nasal bones. Its upper processes of premaxillary bones are widened, as in modern European moose. The antler beam is long, though much shorter than in broad-fronted moose; antlers are close to the deer-like type with only a few tines. An original feature of this moose is a well-expressed tine on the right beam (fig. 19p). The development of an additional tine on the beam is not characteristic for modern moose: a similar formation is not found in modern *Alces*, nor by Vereshchagin (1949; among 136 pairs of antlers), nor by us (among more than 300 pairs of antlers). Apparently, there was an original early Pleistocene *Alces* for which the presence of an additional tine on the beam was characteristic. Similar

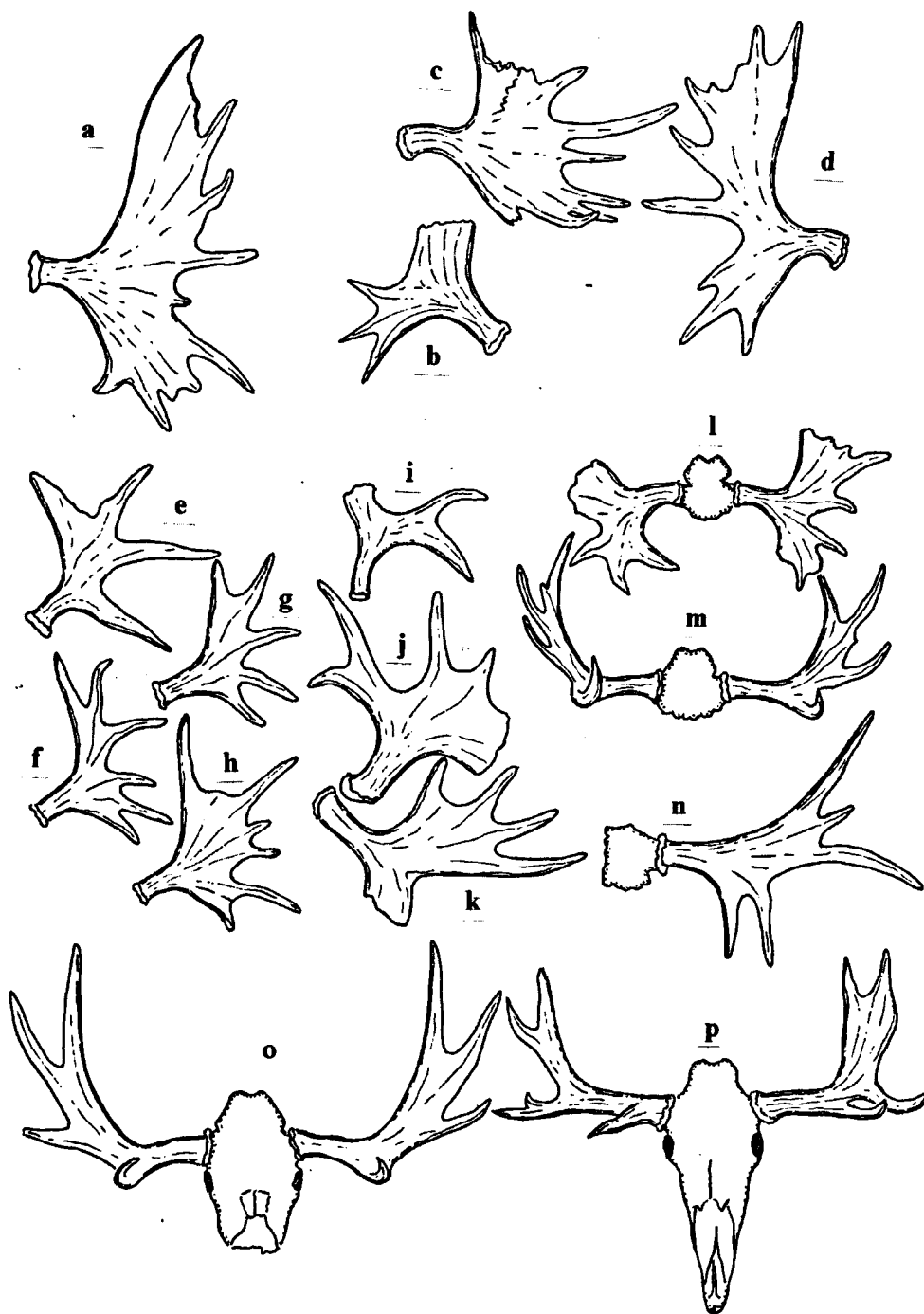


Fig 19 Antlers of the fossil and subfossil *Alces* from Western and Eastern Europe: a - Germany, Schussenried, Late Würm (Kahlke, 1956, after Sher, 1971); b - specimen at PMM, Germany, Bavaria, Holocene; c - AMNH 27772, Denmark, Holocene; d - specimen at PMM, Austria, Brück, Holocene; e - k - "*Alces palmatus*", Romania, Pleistocene (after Macarovici, 1961); l, m - Western Ukraine, Pleistocene (after Vereshchagin, 1967); n - North-East of Russia, the Kichmenga river, Pleistocene (?) (after Vereshchagin & Russakov, 1979); o - "*Alces fossilis*", near Moscow, vicinity of Mytishchi, Late Pleistocene-Holocene and p - "*Alces savinus*", middle stream of the Volga river, late Middle Pleistocene (?) (both - after Pavlow, 1906).

Geweien van fossiele en subfossiele *Alces* uit West- en Oost-Europa: a - Duitsland, Schussenried, Laat Würm (Kahlke, 1956, naar Sher, 1971); b - stuk uit PMM, Duitsland, Beieren, Holoceen; c - AMNH 27773, Denemarken, Holoceen; d - stuk uit PMM, Oostenrijk, Brück, Holoceen; e - k - "*Alces palmatus*", Roemenië, Pleistoceen (naar Macarovici, 1961); l, m - West Oekraïne, Pleistoceen (naar Vereshchagin, 1967); n - Noordoost Rusland, Kichmenga rivier, Pleistoceen (?) (naar Vereshchagin & Russakov, 1979); o - "*Alces fossilis*", omgeving van Moskou, nabij Mytishchi, Laat Pleistoceen-Holoceen en p - "*Alces savinus*", middenstroom van de Wolga, laat Midden Pleistoceen (?) (beiden naar Pavlow, 1906).

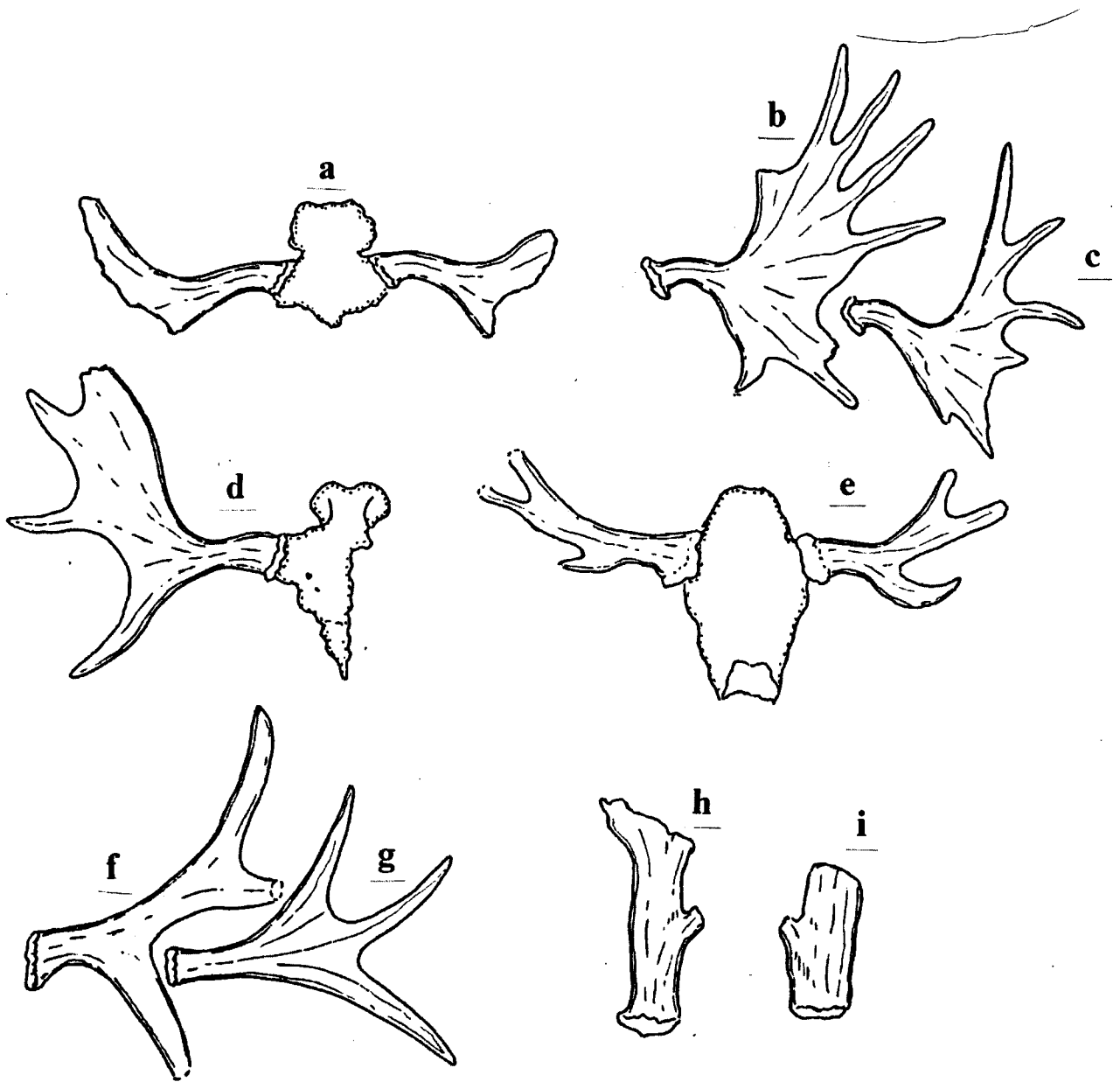


Fig 20 Antlers of the fossil and subfossil *Alces*: a - specimen at GM RAS, near Moscow, vicinity of Mytishchi, Holocene; b, c - GM RAS, Eastern Europe, Holocene (?); d - ZM MSU, vicinity of Moscow (?), Pleistocene-Holocene; e - Stavropol district, near Caucasus region, Holocene (after Vereshchagin, 1949); *A. alces* cf. *caucasicus*: f - lower stream of the Don river, Sarkel fortress, Middle Ages, g - Krasnodar district, the Urup river, Holocene (both - after Vereshchagin, 1959); h, i - *Alces* sp., Western Siberia, Krasny Yar, Pleistocene (after Alexeeva, 1980).

Geweien van fossiele en subfossiele *Alces*: a - stuk in GM RAS, omgeving Moskou, nabij Mytishchi, Holoceen; b, c - GM RAS, Oost-Europa, Holoceen (?); d - ZM MSU, nabij Moskou (?), Pleistoceen-Holoceen; e - Stavropol district, nabij de Kaukasus, Holoceen (naar Vereshchagin, 1949); *A. alces* cf. *caucasicus*: f - benedenstroom van de Don, Sarkel kasteel, Middeleeuwen, g - district Krasnodar, Urup rivier, Holoceen (beiden naar Vereshchagin, 1959); h, i - *Alces* sp., West Siberië, Krasny Yar, Pleistoceen (naar Alexeeva, 1980).

antler beams of true moose were found by Alexeeva (1980) in the Pleistocene sediments of Western Siberia (fig. 20h-i). Vereshchagin (1959; 1967) described the skull of fossil or subfossil moose from Cis-Caucasia with rudimental brow tines (fig. 20e). Pleistocene *Alces* had, on average, longer antler beams than modern moose (Vereshchagin, 1967).

True moose were widespread in Eurasia until the beginning of Late Pleistocene (see above). Probably, during this period their differentiation into two forms, the European and the East-Siberian, began. The latter later gave rise to the North American moose. It is difficult to say where exactly this process took place. In Late Pleistocene deposits, true moose remains are found from Western Europe up to the Russian Far East and Japan (after Kahlke, 1999). Many finds testify that they were distributed more widely than at present (see fig. 6 of part 1).

A high variation in antler shape was typical for Pleistocene *Alces* (especially in western regions). Four antler types are recognized: shovel-shaped antlers with undivided palmation, shovel-shaped antlers with bi-partite palmation, deer-like antlers, and antlers with an additional tine on the beam. In our opinion, this undoubtedly testifies the existence of a differentiation

process among moose. The wide, bi-partite palmation and elongated antler beam is characteristic for the East-Siberian moose of the Late Pleistocene. Most probably, the American moose evolved in Eastern Siberia.

Alces cf. *alces* and *A. alces* L., 1758 - moose of the European type and the European moose

Cervus (Alces) fossilis H. V. Meyer, 1832.

Alces palmatus Gray, 1843.

Alces leptcephalus Push, 1846.

Material and locality. Separate antlers and fragments: PMM 1955, Western Germany, Baden-Württemberg, Markt-Schwaben; PMM 1950/92, Bavaria, Taufkirchen (fig. 19b); PMM 1974/253, Bavaria, Künzing; PMM specimen without number, Austria, Bruk, Markt Grafing, (fig. 19d); AM 27772, Denmark, AMNH (fig. 19c); GM 1823 and GM 1824, Eastern Europe (?), GM RAS (fig. 20a, c). Skull fragments with antler parts: ZM 1411, vicinity of Mytishchi Sity (fig. 20a); ZM specimen without number, vicinity of Moscow (?), ZMMSU (fig. 20d); GM 1829 (?), vicinity of Kostroma Sity, the Nerekhta river and GM specimen without number, Tiraspol (?).

Geological age. The beam of the left antler PMM 1974/253 is found in the Pleistocene

Table 14 Sizes of fossil and subfossil *Alces* antlers (in mm); in case of multiple specimens, the averages are given. Notes: * - after specimens from Paleontological Museum of Munich (Germany) and AMNH (USA); ** - after specimens from Zoological Museum MSU and Geological Museum RAS, Moscow.

Maten van fossiele en subfossiele elandgeweien (in mm); het gemiddelde is gegeven in het geval van meerdere geweien. Opmerkingen: * - naar geweien in het Paleontologisch Museum van München (Duitsland) en AMNH (USA); ** - naar geweien in het Zoologische Museum MSU en het Geologische Museum RAS, Moskou.

Parameter	<i>Alces alces</i>		<i>"Alces savinus"</i>	<i>A. cf. americana</i>	<i>A. americanus</i>		
	West Germany and Denmark, Q4,	East Europe, Q3-Q4	Moscow district, Q3-Q4	The Ob river, Q3-Q4	North-East Asia, Verkhoyansk Mnts, the Sartang river, Q3 (?)	Chersky village, Q4	Alaska, Q3-Q4
	n=4*	n=5**	PIN RAS	ZIN 155-895	VMN	CMN	AMNH
Antler spread	ca.1000	ca. 1000	ca. 1700	1640	1430	1200	1200, 1340
Palmation width	217.5	191	ca. 400	right - 400; left - 420	right - 360	300	337.3 (n=11)
Maximal antler length	914.3	902	ca. 1200	left - 1260	left - 1040	1050	1260 (n=4)
Circumference of the beam	154.8	169	right - 220; left - 215	right - 210; left - 214	right - 190; left - 190	right - 205; left - 200	183.4 (n=9)
Beam length	98.8	129	right - 225; left - 215	right - 120; left - 114	right - 150; left - 140	right - 155; left - 150	128.6 (n=11)
Number of tines per antler	7.8	6.2	12 - 14	15	14	10	10.8 (n=9)

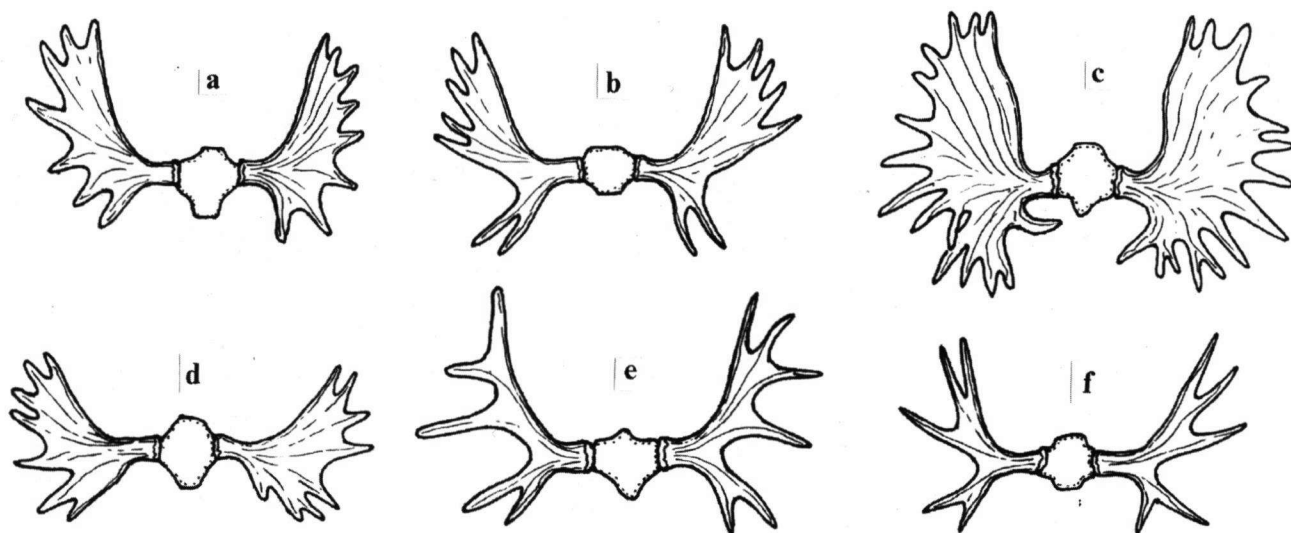


Fig 21 Antler shape in European moose: a – from a specimen at KM, Norway; b– from a specimen at MK, Sweden; c, d – Western Siberia, Vasyuganie, Demyanka river (after Kaplanov, 1948); e – Estonia (after Buturlin, 1934); f – from a specimen ZM 51087, ZM MSU, Tverskaya district

Geweivorm in Europese eland: a – naar een stuk in KM, Noorwegen; b– naar een stuk in KM, Zweden; c, d – West Siberië, Vasyuganie, Demyanka rivier (naar Kaplanov, 1948); e – Estonië (naar Buturlin, 1934); f – ZM 51087 in MSU, district Tverskaya

gravel sediments at a depth of five to ten metres. The strong mineralization of the specimens from ZMMSU and GM RAS testifies that they belong to the Late Pleistocene or Early Holocene period. AM 27772 and ZM 1411 are found in peat-bogs and are probably of Holocene age. The other antlers from Germany and Austria belong to the Holocene.

Description and comparison. The antler fragment PMM 1974/253 from Bavaria has a rather long (13.5 cm) and massive beam (circumference in the middle is 19 cm, circumference above the burr is 21 cm). The massivity index (circumference by length) of the antler beam of 110% proves that this specimen undoubtedly belongs to *Alces*. The beam of PMM 1974/253 is longer than in modern European moose. PMM 1974/253 has a long antler as the brow tine is 28.5 cm. Furthermore, it has a wide and, apparently, undivided palmation. The size of the occipital part of skulls from the Late Pleistocene - Holocene of Eastern Europe is characteristic for *Alces* (see table 2 of part 1), and their antler sizes are close to those of modern *A. alces* (table 14), however, antler beams of the former are slightly longer. The parameters of antlers and beams of Holocene moose from Western Europe practically do not differ from those of modern European moose (tables 14 and 15). In

general, the Late Pleistocene and Holocene moose from Western and Eastern Europe had antlers with a wide, undivided palmation and long tines (figs. 19, 20), which is also characteristic for modern *A. alces* (fig. 21a, c). Only some antlers have a palmation with the tendency to become divided into two parts (fig. 19d, j-l). Furthermore, antlers close to the deer-like type occur (fig. 19m, o-p; fig. 20e-f), which is also characteristic for European moose.

***Alces cf. americanus* - moose close to the American moose**

Material and locality. “*Alces savinus*” Fischer, skull with antlers, without number (?), Moscow district, PIN RAS (fig. 22a); skull fragment with antlers ZIN 155-1895, the Ob river, ZIN RAS (fig. 22b). Mandible fragments, Yakutia: YIGS 4411, the Adycha river; YIGS 4759, the Lena river delta.

Geological age. The skull of “Savin’s moose” was found in a peat bog at the Ruta river in the Moscow district (sixty miles from Moscow), and most likely is from the Holocene period. Vereshchagin (1967) paid attention to the strong mineralization of this specimen and proposed a Late Pleistocene age for the “Savin’s moose”. The label on ZIN 155-1895 tells that it was found at the Ob river. The age of this exhibit is

Table 15 Sizes (in mm; mean in case of multiple specimens) and massivity index (in %) of true moose antler beams. 1 - length; 2 - circumference of the burr; 3 - circumference above the burr; 4 - circumference at midpoint; 5 - horizontal diameter. n.n. = no number.

Maten (in mm; gemiddelde in het geval van meerdere stukken) en massiviteitsindex (in %) van geweistokken van ware eland. 1 - lengte; 2 - omtrek van de rozenkrans; 3 - omtrek boven de rozenkrans; 4 - omtrek halverwege; 5 - dwarsdoorsnede. n.n. = geen nummer.

Sizes and index	<i>Alces alces</i>		<i>"Alces savinus"</i>	<i>A. cf. americanus</i>				
	Germany and Denmark, Q4	Eastern Europe, Q3-Q4	Moscow district, Q3-Q4	Ob river, Q3-Q4	Aldan river, Mamontova Gora, Q3		Kolyma, Duvanny Yar, Q3	Bolshaya Chukochiya river, Q3
	PMM, AMNH, n=4	ZMMSU, GM, n=5	PIN RAS, n.n.	ZIN155-1895	YIGS 631	YIGS 778	YIGS, MM, n=5	YIGS 3380
1	98.8	129	225	120	102	95	105	90
2	239	233	-	285	270	250	225	250
3	173	176.8	250	230	225	210	167	180
4	154.8	169	220	210	187	180	152.6	165
5	48.3	49.2	-	-	56	57	47.8	48
3:1	207.7	130.8	111.1	191.7	220.6	221.1	172	200

unknown. However, based upon its rather strong mineralization, the Zoological Museum almost certainly will admit it as a fossil. Probably this exhibit originates from the Late Pleistocene or the beginning of the Holocene. Mandibles are found together with bone remains of characteristic representatives of the Yakutian Mammoth fauna: *Mammuthus primigenius*, *Equus lenensis*, *Bison priscus*, *Rangifer tarandus*. Based upon this circumstance, and also upon the rather strong mineralization of the YIGS 4411 and 4759, the specimens can be attributed to the Late Pleistocene.

Description and comparison. The "Savin's moose" is a remarkable exhibit, now in the exhibition of the Paleontological Museum of PIN RAS. It was originally described as "*Cervus (Megaloceros) savinus*" (Fisher von Waldheim, 1834); later as "*Alces savinus*" (Rouillier, 1846). Though the "Savin's moose" was already well-known and studied (Vereshchagin, 1967; Vereshchagin & Russakov, 1979), we re-studied it, and found some interesting results.

Skull and antlers of the "Savin's moose" are very large. In size they are only comparable to the largest modern moose, which lives in north-east Siberia and Alaska and belongs to the subspecies *A. a. gigas*. Condilobasal length of the "Savin's moose" skull was not less than 63 cm, width in cheek bones near 24 cm, skull height in the nasion point 16 cm, length of the nasal bones 13.6 cm, length of the upper tooth

row 15.5 cm. Antler sizes of this moose are given in tables 14 and 15. Extremely interesting is the fact that although this specimen originated from Eastern Europe, it seems to be related to the modern moose of Northeast Siberia and Alaska by several features. Primarily, these are its craniometric parameters. Additionally, it has very large antlers, a very wide shovel (palmation) with the tendency to become divided into two parts. It possesses many tines and very long, massive antler beams. The upper processes of the premaxillary bones, especially the right one, are wedge-shaped narrowed (see fig. 4e of part I). This is characteristic for American moose ("American" morphotype, after Boeskorov, 1998) and very seldom occurs in European moose. Besides, in this specimen one of the right shovel tines is directed downwards, which among modern moose is found only in *A. a. gigas* (Bubenik, 1986; our data). The combination of such an amount of typically American moose features indicate that 'Savin's moose' must be a representative of the American group.

The second specimen is equally interesting, and until now undescribed: a skull with antlers on exhibit in the Zoological museum ZIN RAS (fig. 22b). The sizes of the preserved posterior part of the skull are large: the greatest occipital width is 17.2 cm. The occipital heights from the lower and upper edges of the foramen magnum are 12.8 and 9.7 cm, respectively. The width of occipital condyles 10.1 cm. The antlers of this

specimen are very large (tables 14 and 15). The majority of parameters of these antlers (spread, length of antler, width of palmation, circumference of beam) is much larger than those of the modern European moose that occupy in partic-

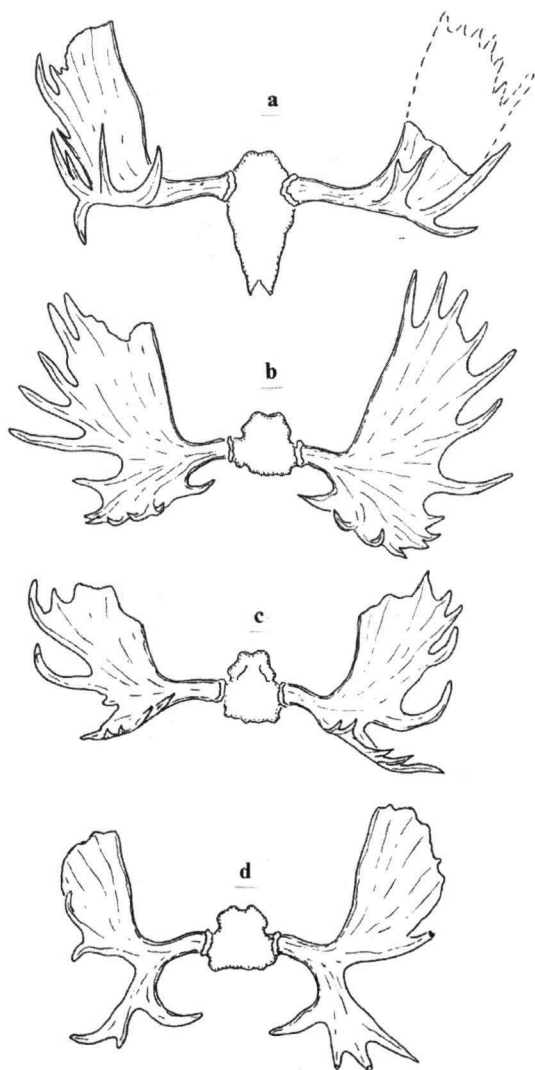


Fig 22 Antlers of the fossil and subfossil moose relative to *A. americanus*: a - "*Alces savinus*", specimen without number at PIN RAS, Moscow district, Pleistocene-Holocene; b - ZIN 155-1895 (ZIN RAS), Ob river, Pleistocene-Holocene; c - specimen without number at VMN, Verkhoyanie, Sartang river, Late Pleistocene (?); d - specimen without number at CMN, lower stream of Kolyma river, Chersky village, Holocene.

Geweien van fossiele en subfossiele eland vergeleken met *A. americanus*: a - "*Alces savinus*", stuk zonder nummer in PIN RAS, district Moskou, Pleistoceen-Holocene; b - ZIN 155-1895 (ZIN RAS), de Ob, Pleistoceen-Holocene; c - stuk zonder nummer in VMN, Verkhoyanie, rivier Sartang, Laat Pleistoceen (?); d - stuk zonder nummer in CMN, benedenloop van de Kolyma, Chersky dorp, Holocene.

ular the basin of the Ob river. The antlers correspond to the largest antlers of moose from northeast Siberia and Alaska. The antler shape of ZIN 155-1895 with the characteristic lengthened shovel with the tendency to become divided into two parts is also typical for modern amphi-Beringian populations of moose.

Except for "Savin's moose", some antlers of Pleistocene moose from Western Ukraine and Middle Volga region are extremely similar to antlers of modern Kolyma and Alaska moose (Vereshchagin, 1967; Vereshchagin & Russakov, 1979). This has led to the conclusion that "...in the Pleistocene the geographical variability of moose populations was other than nowadays" (Vereshchagin & Russakov, 1979: 40). In my view, however, it seems more likely that during the Late Pleistocene, the American moose had a much wider distribution in Eurasia than today. As it is more adapted to a cold climate than the European moose, it may have occupied Western Siberia and even parts of Eastern Europe. Mandibles YIGS 4411 and 4759 have similar basic sizes as modern *Alces* (jaw height, premolar length, sizes of most teeth; see tables 4 and 6 of part 1), but, at the same time, have some original features as well. A very large molar length is characteristic for both these specimens: for YIGS 4411 it is a large length of the teeth row, and for YIGS 4759 it is the large sizes of M3, similar to *Cervalces* (see table 3 of part 1). Among the true moose only fossil, subfossil and modern *A. americanus* from Alaska and the extreme northeast of have more or less similar sized teeth (see tables 4 and 6 of part 1), which doubtlessly correlates with their very large skulls.

Alces americanus Clinton, 1822 - American moose

Material and locality. North-east Asia. Skull fragments with antlers: VMN, without number, found in 1996 in Verkhoyansk mountains at the Sartang river (fig. 22c); without number, found in the 1990ties at Chersky village, ChMN (fig. 22d). Occipital parts of skulls: YIGS 4291, Chukotka, the Malyi Anuyi river, Krassivoye locality; YIGS two specimens without numbers, northern Yakutia (?); MM 8121 and MM two specimens without numbers, Duvanny Yar locality. Mandibles: MM 7099 and MM, one specimen without number, the Kolyma river. MAE, three mandible fragments, without numbers, southwestern Yakutia, the Oleykma river basin, Ulakhan Segelennyakh, Late Holo-

cene human settlement. Antler fragments: YIGS 631 (see fig. 15c of part 1) and YIGS 788, the Aldan river, Mamontova Gora locality; YIGS 3208, 6395 and one specimen without number, MM 7313 and MM 7754 (see fig. 15d of part 1), Duvanny Yar; YIGS 3380, the Bolshaya Chukochiya river (see fig. 15e of part 1), YIGS one specimen without number, northern Yakutia (?); MM one specimen without number, the Batamai river; IRMN 6645 and one specimen without number, Irkutsk district, near-Baikal region.

Alaska. Skulls: AMNH 106-7527, Ester Creek (see figs. 17c and 18f of part 1); AMNH 368-1426, Fish Creek; AMNH 485-4734, Hunter Creek (see fig. 18g of part 1). Skull fragments: AMNH 327-5020, 383-2037, 508-1489 (see fig. 18h of part 1), 615-1107 and 615-1108 (see fig. 18i of part 1), vicinity of Fairbanks. Antler fragments: AMNH 252-1939, Eldorado Creek (see fig. 12a of part 1), AMNH 4772, 5269, 5291, 252-4442, 276-5295, 292-5273, 292-5293, 292-9143, 348-8487, 420-1360, vicinity of Fairbanks (fig. 23). Mandibles: AMNH 616, 276-5283 (see fig. 8a of part 1), 368-1426, 485-4734, 583-2162, 583-2167, 584-2161, vicinity of Fairbanks. Metatarsals: AMNH 34586, 368-1426, 368-1426/1, 586-2310, vicinity of Fairbanks. Mummified corpse AMNH 274-4002, Little Eldorado Creek (fig. 24).

Geological age. The skull fragment with antlers from the Sartang river obviously belongs to the Late Pleistocene, because it was found on a depth of 2.5 m together with bones of *Mammuthus primigenius* of a late type. The antlers from Chersky village were found at a depth of two metres, so are attributed to the Holocene. YIGS 4291, YIGS 3380, MM 7754 and MM 8121 all originated from the Edoma formation (Icy Complex) sediments of the Late Pleistocene and they were found together with bones of the characteristic representatives of this period: *M. primigenius* of the late type, *Coelodonta antiquitatis*, *Equus lenensis*, *Bison priscus* cf. *occidentalis*, *Rangifer tarandus*. The radiocarbon age of specimen MM 7754 from the Duvanny Yar locality (see fig. 15d of part 1) is 12,250 ± 70 y. BP (GIN - 11025). YIGS 631 and YIGS 788 from the Mamontova Gora locality were described by Russanov (1968), and attributed to the Late Pleistocene, because they were found in the Late Pleistocene loess-like sediments. The mandibles from the Oleykma river basin were found in the settlement Ulakhan Segelennyakh layers of the Eneolithic period (1,500 - 1,000

years ago). The remainder of the described moose remains from Yakutia have no geological dating but their mineralisation allows for an attribution to the Late Pleistocene - beginning of Holocene. The material of the true moose from the AMNH belongs to the Rancholabrean, according to the museum catalogue. Bone remains of Alaskan moose are mineralized and their colour ranges from light to dark brown, and can be attributed to the final Late Pleisto-

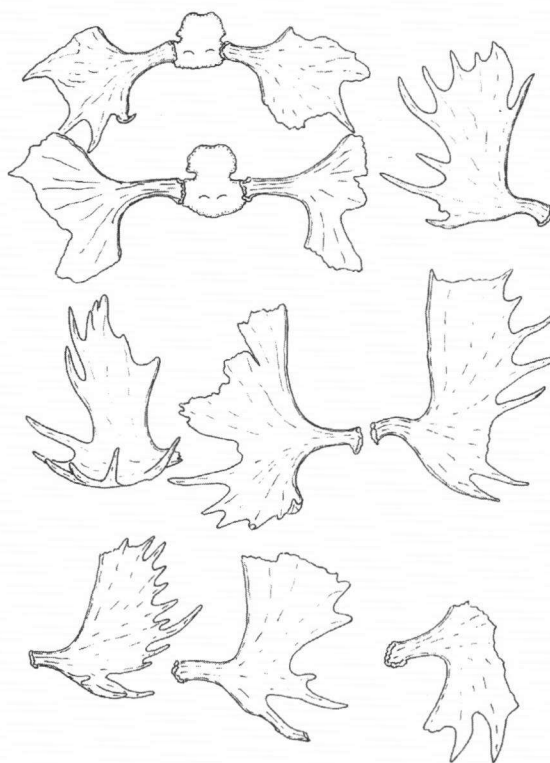


Fig 23 Fragments of the fossil and subfossil antlers of *A. americanus* from Alaska (coll. AMNH)

Fragmenten van fossiele en subfossiele geweien van *A. americanus* uit Alaska (coll. AMNH)

cene - beginning of Holocene. The moose mummy (AMNH 274-4002) is dated 33,000 ± 750 y. BP (Guthrie, 1990b).

Description and comparison. The measurements of the fossil and subfossil remains of moose skulls from the northeast Asia fall within the variation of modern moose living in the territory of Yakutia, but are closer to the parameters of the largest living subspecies: *A. a. gigas*. Fossil and subfossil moose from Alaska are outstanding by their greatest sizes (see table 2 of part 1). The mandible sizes also testify that fossil and subfossil *Alces* from Yakutia belong to the large form. However, Alaskan moose surpass them in sizes (see table 4 of part 1). For

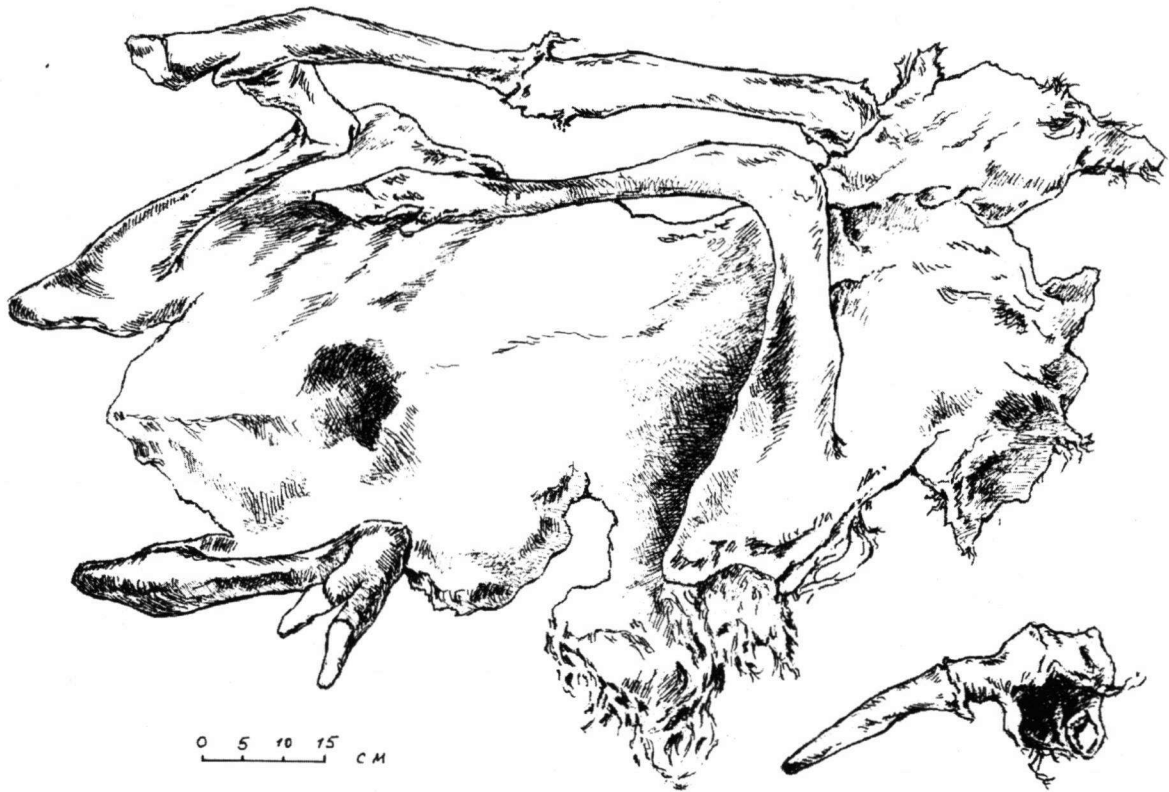


Fig 24 Late Pleistocene *A. americanus* mummy (AMNH 274-4002) found in 1940 on Alaska, Little Eldorado Creek.

Laat-Pleistocene *A. americanus* mummie (AMNH 274-4002) gevonden in 1940 in Alaska, Little Eldorado Creek.

Late Pleistocene and Holocene *A. americanus* the lengthening of molars is characteristic. The sizes of teeth of the Yakutian moose fall within the variation of modern *A. a. pfizenmayeri* and *A. a. gigas*; the sizes of teeth of Alaskan moose surpass the parameters of the latters (see table 6 of part 1 and table 16 of this part).

The mummified corpse of the young moose from the Little Eldorado Creek (fig. 24) was earlier attributed to *Cervalces latifrons* or stag-moose *Cervalces* sp. (Guthrie, 1990a, 1990b). Nevertheless, our research has shown that this specimen has characteristics of *Alces*: a cone-like prominence between the antlers and lengthened hoofs. Absolute age of this find ($33,000 \pm 750$ y. BP) is evidence for the penetration of true moose into Alaska prior to the Wisconsinian glaciation.

The best preserved antlers from Sartang and Chersky (fig. 22c-d) and Alaska (fig. 23) have the clearly expressed form (long and wide, bi-partite shovel with many tines) and large sizes (table 14), characteristic for modern *A. a. gigas* from the Northeast of Siberia and Alaska. The remainder of described antler remains of

the Late Pleistocene and Holocene *A. americanus* represents only beams with the beginning of a shovel-shape expansion. It is remarkable that many of them had a bi-partite shovel. The sizes of these beams are given in tables 14 and 15, and it is obvious that the rather long and massive antler trunk is characteristic for these moose. The massivity index of the beam always exceeds 100%. The Late Pleistocene and Holocene moose from Eastern Siberia and Alaska are closest to modern *A. a. gigas* by their beam length. As Bubenik noted, the morphotype of the latter moose (large body and skull, long rostrum, huge spread of antlers with many tines) developed under conditions of thin northern taiga and taiga-tundra of the northeast Siberia and Alaska. In the snow-free period, these moose prefer semi-open to open landscapes. Their regular penetrations into the tundra zone are noted, and in Alaska the moose is even called "tundra-moose" (Bubenik, 1986). Apparently, this type of moose is close to the Late Pleistocene moose, which was part of the Mammoth fauna in a significant part of Northern Eurasia. During the Late Pleistocene, it

migrated to Alaska through the Bering Land Bridge.

Alces sp. from the Pleistocene of Eastern Siberia, and also fossil and subfossil *A. americanus* from Alaska have very large metatarsals, which are in size closest to those of modern moose from the Northeast of Siberia (see table 9 of part 1).

Conclusion

Analysis of paleontological data indicates that the evolutionary lineage of the broad-fronted, long-beamed moose, known from the beginning of the Late Pliocene of Eurasia, apparently got extinct in Eurasia by the beginning of the Late Pleistocene, and in North America by the beginning of the Holocene.

Libralces gallicus, the earliest known representative of this lineage was replaced by *Cervalces latifrons* in the Early Pleistocene. Remains of an intermediate form combining the features of *L. gallicus* and *C. latifrons* are found in the Kolyma lowlands (Sher, 1971; 1986; Nikolsky, 1996). Large broad-fronted moose with long massive antler beams disappeared during the Middle Pleistocene of Eurasia. In this period a new, smaller form of *Cervalces* appeared. On average, it had a long and rather thin antler beam, and was described as the separate subspecies *Alces latifrons postremus* (Vangengeim & Flerov, 1965). Later, it was moved to the genus *Cervalcus* (Sher, 1986). The chronological and morphological hiatus between *C. latifrons* and the *postremus*-form allow us to consider the latter as the separate species *Cervalces postremus*. This species was widely distributed in Eastern Siberia.

After the dispersal into North America, it apparently gave rise to the American stag-moose, *Cervalces scotti*. In Eurasia *C. postremus* was the

last representative of the genus *Cervalces*. Presumably it became extinct at the beginning of the Late Pleistocene.

The salient features of the broad-fronted moose (see the diagnosis) are traced in this evolutionary lineage from the Late Pliocene to the end of the Pleistocene. In my view, until now there is no convincing evidence in favor of a direct phyletic link between *Cervalces* and true moose *Alces*. The latter differ significantly from broad-fronted moose and stag-moose in the above mentioned features (see the diagnosis). The evolutionary tree of moose is shown in figure 25. Most likely the evolutionary lineage of true moose developed in parallel with that of broad-fronted moose, starting as early as the end of the Late Pliocene or the beginning of the Pleistocene. However, remains of a real ancestral form of *Alces* have not been found yet.

Paleontological data to the present time testify that a fully-developed true moose already existed by the late Middle Pleistocene. Their evolution took place in the central and northern altitudes of Eurasia, which gave rise to a number of adaptations and features of *Alces*: large body sizes, characteristic for deer of northern altitudes, features of a body structure with high withers, lengthened metapodials, enlarged basic area of the hoofs, promoting locomotion in hilly bogs, wind-fallen wood and deep snow. The large weight of the nasal cartilages and the strongly developed upper lip serve as an adaptation to preliminary heating of air, but also to grasp foliage from branches and marsh plants (Flerov, 1952; Vereshchagin, 1967).

Apparently, already at the beginning of the Late Pleistocene, a radiation among *Alces* took place. This is testified by finds of *Alces* antler remains with the various forms peculiar to modern moose together with unique finds with an addi-

Table 16 Sizes (in mm; mean values) of lower jaw teeth of the modern moose (genus *Alces*).

Maten (in mm; gemiddelden) van de onderkaaskiezen van de huidige elk (geslacht *Alces*).

Species and subspecies	P ₂		P ₃		P ₄		M ₁		M ₂		M ₃	
	length	width	length	width	length	width	length	width	length	width	length	width
<i>Alces alces alces</i> , Tambov district (Nikolsky, 1996)	-	-	22.5	15.8	25.6	17.1	-	-	26.5	20	-	-
<i>A. americanus pfizenmayeri</i> , Central and Southern Yakutia, n= 10	18	13.4	24.2	16.5	28.3	18.7	28.4	19.7	29.4	20.5	40	20
<i>A. a. gigas</i> , Extreme North-East Asia, n= 10	19.5	14.2	24.5	17	28.7	19.7	28.2	20.6	30.6	22.5	40.5	21.5

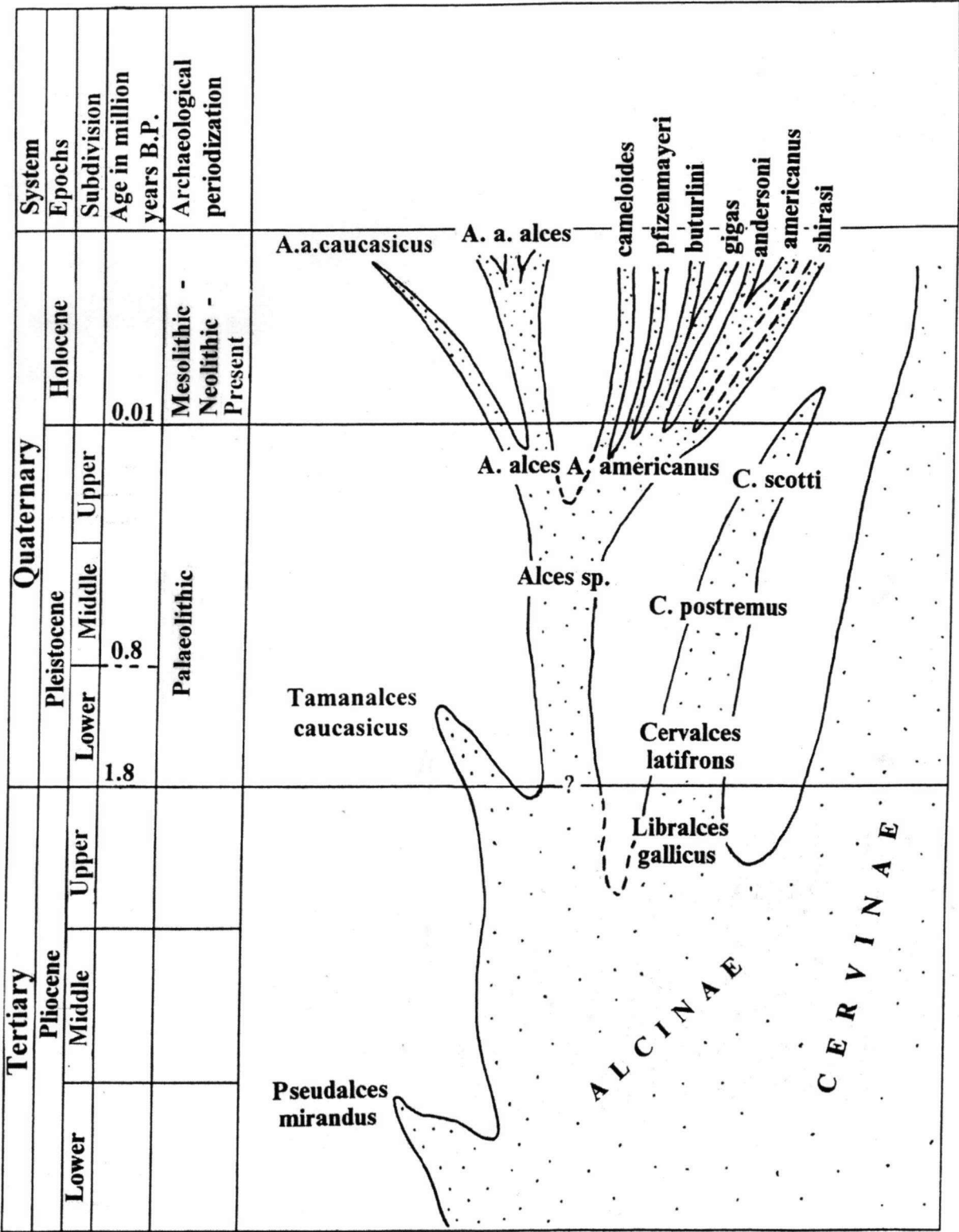


Fig 34 Evolutionary lineage of Alciinae / Evolutielijn van de Alciinae.

tional line on a beam. The forms from which later the European-West-Siberian and the East-Siberian-American moose originated, probably stood apart at that time. The level of differentiation between modern European and American moose on the basis of molecular-genetic markers of DNA has allowed to estimate the time of their divergence at more than 100,000 years (Mikko & Anderson, 1995) or at 75,000 to 150,000 years (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.

On the basis of palaeontological finds, it is difficult to say which species of moose is the most ancient. 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. It is therefore most probable that the similar chromosomal set of *A. americanus* is the archaic set. It 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 Far East the largest variety of haplotypes of mitochondrial DNA is revealed. This 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 my view, 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.

East-Siberian moose is more adapted to a cold climate than European moose; the former was widely distributed among the Mammoth fauna of Eurasia, west-ward to Western Siberia and even Eastern Europe. In the Late Pleistocene, populations of this moose were not numerous, as can be derived from the rare finds of *Alces* bone remains at Mammoth fauna sites and at Paleolithic settlements. This is explained by the fact that open, steppe-like landscapes were not suitable for them. Remains of modern moose found *in situ* (the Aldan river, Mamontova Gora locality; after Russanov, 1968), and also radiocarbon dating (Taimyr Peninsula; after Sulerzhitsky & Romanenko, 1997) and findings at Late Paleolithic sites (Vangengeim, 1977; Mochanov, 1977; Lazarev *et al.*, 1998) evidently

testify that this animal occupied Eastern Siberia, including its northern part at least from the Karginian interglacial of the Late Pleistocene (more than 40,000 years ago). But remains of *Alces* found in the late Middle Pleistocene of the Lower Tunguska river (Vangengeim, 1977) allows to assume that true moose inhabited the larger part of Eastern Siberia at least from the beginning of the Late Pleistocene.

Earlier, it was supposed that *Alces* probably entered North America from Asia at the beginning of the Wisconsinan, about 100,000 years ago (Hibbard, 1958) or even before the Sangamonian interglacial (less than 250,000 and more than 100,000 years ago) (Guthrie, 1966). But until now no radiocarbon dated *Alces* remains have been found in North America that are older than the beginning of Holocene (Alaska 8,740 ± 70 y. BP and 5,380 ± 55 y. BP, after Guthrie, 1990b; Manitoba 7,848 y. BP and 5,950 ± 40 y. BP, after Brownlee *et al.*, 2002). Guthrie (1990b) suggests that *Alces* penetrated into North America quite recently: between the end of the last interglacial (24,000 y. BP) and the end of the maximum of the glaciation (14,000 y. BP) or even at the beginning of the Holocene (Guthrie, 1995). Based upon the lack of variation in mitochondrial DNA restriction fragments in North American moose, it can be concluded that the population must be relatively young and 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 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. However, the time when *Alces* penetrated into North America is unclear until now. We do know that it must have taken place before the end of the Late Pleistocene or the beginning of Holocene, because the differentiation of modern North-American moose into three or four subspecies could not have taken place in ten thousand years only. For example, the two amph-Beringian populations of *A. a. gigas* still did not reach a subspecific level of differentiation although they were morphologically isolated from each other for ten thousand years (Boeskorov, 2001).

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