

TAXONOMIC POSITION OF Alcinae Jerdon, 1874  
AND THE HISTORY OF THE GENUS Alces Gray, 1821

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**Abstract:** Previous classifications of deer rely entirely on skeletal features. The present paper shows that classification of cervids should include anatomical, morphological and behavioural characteristics in order to provide a broad based phylogenetic hypothesis for the group. For this reason a revised classification is proposed here. All available characteristics indicate that Alcinae belongs in the family Odocoileidae. The evolutionary history of Alcinae is reviewed including the questionable relationships of Cervalces to Alcinae and Libralces as possible propagul of Norwegian moose. The development of the 3-palmated antlers of the stag moose and reasons for cranial, external and behavioural peculiarities of tundra and taiga moose are discussed. A new view on moose invasions to North America is presented.

Alces 22 (1986)

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CLASSIFICATION OF MOOSE

Most taxonomists classify cervids using features established by BROOKE (1878). This include (a) retention of distal (telemetacarpal) or proximal (plesiommetacarpal) parts of the lateral metapodia, branches of the skull to reach, or

not to reach, the nasal bones, and (c) on the length of, and progress in, ossification of the vomer, which separates the posterior nasal cavity into 2 distinct chambers (Fig.1).

Due to the long distal remnants of metacarpals, and despite its very short nasal bones and long vomer, moose are classified as a telemetacarpal cervid group which in present classification belongs under the subfamily Odocoileinae (Brooke 1878, Frick 1937, Haltenorth 1963, Heintz & Poplin 1981, Simpson 1945).

However, there are paleontologists who argue that all pristine cervids were probably only plesiommetacarpal, with short vomer and intermaxillary bones joint with the nasal bones. They consider the reduction of the lateral metapodia a secondary and repeated adaptation during deer evolution. Therefore, the telemetacarpal cervids have no evolutionary integrity and moose and roe deer (genus Capreolus) are phyletically connected with plesiommetacarpals, i.e. with the subfamily Cervinae (Azzaroli 1981, Flerov 1952, Thenius 1980, Sher 1986).

I can not share this latter view. First of all Frankenberger (1959) and Slaby (1962) show conclusively, although plesiommetacarpal cervids are younger than telemetacarpals, that there is no evidence of their development from telemetacarpal cervids. Frankenberger (ibid.) in his conclusion assumes that the process of metacarpal reductions was not an **archallaxis** as suggested by Severtzow (1949), but by **deviation** from an intermediary stage

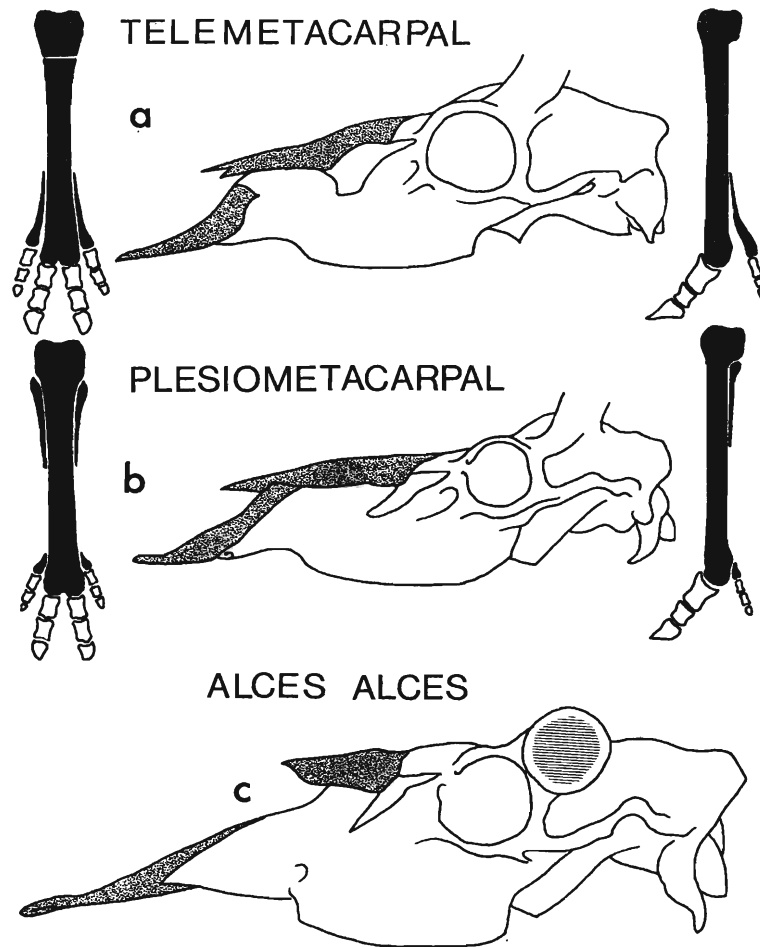


Fig. 1. CRANIAL AND METAPODIAL CHARACTERISTICS OF DEER

(a) telemetacarpal conditions (b) plesiometacarpal conditions (c) nasal and praemaxillar bones

found in many pristine eupecorans (Webb and Taylor 1980). [Gould 1977: "Archallaxis, Severtzow's term for addition of a new feature during early period of embryonic morphogenesis, usually causing a major alteration of subsequent ontogeny. Deviation, DeBaer's name....Early embryological stages of related forms are very similar. As development proceeds from general to special ontogenic paths of related animals diverge gradually during embryology"].

However, the taxonomical integrity of plesiometacarpals and telemetacarpals as two phyletically distantly related groups is expressed also by other than skeletal features.

For example, all telemetacarpals terminate the replacement of permanent teeth within 18 months, i.e. 10 months earlier than plesiometacarpals. The only exception is the plesiometacarpal muntjac (*Muntiacus* sp.), a cervoid (antlered ungulate) of Miocene origin. Therefore I do not consider muntjacs as phyletically related to other living cervids (Bubenik 1982a).

The karyotypes provide additional evidence. According to Grippeberg *et al.* (1983) and Grippeberg and Nygren (1986) the karyotype of Swedish moose is arranged in the same way as the karyotype of the reindeer (*Rangifer*) with the exception of only three small acrocentric pairs. An additional a large metacentric pair, precedes the smaller submetacentric pair. The American moose lacks this metacentric chromosome (Wurster and Benirschke 1968). The number of acrocentrics is 66 and the total chromosome number is 70. The homologies in form,

size and banding pattern of the chromosomes between moose and reindeer indicate a close relationship between the two species, and there is no doubt that reindeer and caribou are typical telemetacarpals.

Only the telemetacarpal roe deer and pudu deer (Pudu sp.) have no tarsal glands. The mazama deer (Mazama) may or may not have them. All of those genera are very primitive, probably Miocene deer. All other telemetacarpals of later origin have tarsal glands, and most of them [it is uncertain for the South American genera Blastocerus and Dorcelaphus] urinate on these glands. This is an important social gesture, which cannot be omitted as a taxonomical characteristic. The females are mostly multiparous. All telemetacarpals have a rumen with two blind chambers, in contrast to all plesiometacarpal cervids, except the cervoid muntjac, which have a rumen with 3 blind chambers (Bubenik 1956a, 1982a, 1984).

In telemetacarpals the first antler set appears within the first 5 months of life, in plesiometacarpals (except the muntjac) when they are almost 1¼ year old (Bubenik 1966). Except for Rangifer, the shaft is long (Bubenik 1982b). Sprouting, i.e. development of tines from the cortex, instead of splitting the beam's tip by branching [common in Rangifer in any subsequent antlers (Bubenik 1956b)] is limited to the prong (Bubenik 1982b). In plesiometacarpal cervids the shaft is short and sprouting was observed only in first antlers of red deer (Bubenik and Munkacevic 1967).

In telemetacarpals the multiparous female monopolizes

the male; in plesiometacarpals the male monopolizes as many, mostly uniparous females as he can herd and defend (Bubenik 1985).

#### EVOLUTIONARY HISTORY OF DEER

Based on the fact that many behavioural cues are more typical than anatomical (McDougal 1928; Wickler 1972), I must conclude that telemetacarpals are an integral group, which have evolved sometime in Middle Miocene from the **holometacarpal** [with complete metacarpals] cervoids of the Late Miocene, like e.g. Cervocerus (Zdansky 1927), or some Middle Miocene pseudocervicorn dicrocerids (Bubenik 1982a, Schlosser 1924, Zdansky 1925). Therefore, the cranial differences in moose and roe deer contrary to other telemetacarpal deer are secondary adaptations and not leading taxonomical cues as presumed by Flerov (1952).

There is no doubt that the plesiometacarpal cervids originated during the Lower Miocene somewhere in Eurasia and with a "high probability" within Inner Asia. The plesiometacarpal cervids evolved only in Eurasia. Why only few pristine telemetacarpals lineages with less elastic genetical programs remained in Eurasia is still obscure. The elastic ones invaded America at the beginning of Pliocene, 2½ million years ago (Thenius 1980). However, it is questionable, if some **pliocervines**, a term coined by Khomenko (1913) for the very primitive plesio- and holometacarpal deer of Lower Plio-

cene, e.g. Cervocervus, Cervavitus, and Pavlodaria (Thenius 1980, Vislobokova 1980, Zdansky 1925), might also be ancestral to North American deer.

In my view the term pliocervine is confusing. I consider the very primitive pliocervines of Khomenko (1913) as typical **miocervids**, close to the propaguls of the Middle-Upper Miocene. Using the miocervid muntjac as a model, I conclude that all miocervids were adapted to the warm Miocene climate (Hambrey and Harland 1981, Kowalski 1971, Webb 1983) by polyestrous breeding, independent on antler cycle. The timing of the latter might be individually tuned (Bubenik 1986b).

The next evolutionary step related to the more temperate climate of the Pliocene, was the **pliocervids**. They are monoestrous short-day breeders with endogenous antler cycle, whose antler core may survive velvet shedding for an unspecified period. From this group survived all Asiatic plesiometacarpals, from telemetacarpals the roe deer (Capreolus), and all South American except the Hippocamelus. The white-tailed deer (Odocoileus virginianus) is the most adaptable pliocervid, capable to mimic a pleistocervid in northern latitudes (Bubenik, A. 1986b).

The youngest and most specialized are the **pleistocervids** (Bubenik 1986b). They evolved under the severity of the hostile Pleistocene winters as large runners. In order to calve in spring, as an optimal season, they became irreversibly short-day breeders with antler growth cycle concurrent with the period of highest quality of vegetation.



Table 1. **PROPOSAL FOR RECLASSIFICATION OF CERVOIDS**

Infraorder:	<b><u>Eupecora</u></b> Webb and Taylor, 1980. All pecora, except si- necorn ones.
Superfamily:	<b><u>Cervoidea</u></b> Simpson, 1931. All eupecoran with frontal bone appendices.
Family:	<b><u>Antilocapridae</u></b> Gray, 1866. Cervoids with perennial protuberances, but deciduous hornsheat instead of velvet.
Infrafamily:	<b><u>Pseudocervoidae</u></b> , (n.if.) Extinct pseudocervicorns, with perennial appendages in North America and Eurasia.
Infrafamily :	<b><u>Cervoidea</u></b> (n.if.)= Cervoidea Hay, 1930 Cervids with deciduous antlers.
Family:	<b><u>Muntiacidae</u></b> , (n.f.) [polyestrous miocervids with long pedicles and long tusks (BUBENIK 1982a).
Family?*	<b><u>Capreolidae</u></b> Brookes, 1828. Pliocervids, rank questio- nable. Presently a tribe <u>Capreolini</u> of <u>Odocoileinae</u> (SIMPSON 1945).
Family:	<b><u>Odocoileidae</u></b> , n.f. Telemetacarpal pliocervids and pleistocervids
Subfamily	<b><u>Odocoileinae</u></b> Pocock, 1923. Miocervids, pliocervids and pleistocervids explicitly of the American continent.
Subfamily:	<b><u>Rangiferinae</u></b> Pocock, 1923. Telemetacarpals with antle- rogenesis independent of testicular androgens, and tines which can develop by accessoric "sprouting" instead of branching.
Subfamily:	<b><u>Alcinae</u></b> Jerdon, 1874. Telemetacarpals with skull characteristics closer to plesiometacarpals, long limbs and horizontal pedicles.
Family:	<b><u>Cervidae</u></b> Gray, 1821. Plesiometacarpals pliocervids and pleistocervids with an annual antler cycle with many extinct subfamilies.
Subfamily:	<b><u>Cervinae</u></b> Baird, 1857, Plesiometacarpals plio- and pleistocervids of Old World, except <u>Cervus e.</u> <u>canadensis</u> .

\*\*\*) The taxonomic position of the roe deer, genus Capreolus Frisch, 1775, is still not clear. It has telemetacarpal metapodia but a more plesiometacarpal skull. Its rumen has 2 blind chambers, but tarsal glands are not developed. The implantation of ova is delayed. In many regards it seems to be a very early pliocervid. It might be almost a "living fossil", the last lineage of an extinct family Capreolidae Brokes, 1828.

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#### CLASSIFICATION OF ALCINAE

Moose evolved also as a pleistocervid (Bubenik, *ibid.*), and remained for a very long time in Eurasia. Here it evolved far behind the general framework of American telemetacarpals which, of course, makes its classification difficult.

At present all moose are classified either to a tribe Alcini Simpson (Simpson 1945), or a subfamily Alcinae Jerdon, 1874 (Frick 1937, Haltenorth 1963, Heintz and Poplin 1981, Sher 1986, Thenius 1980).

I agree with those who ascribe all moose the rank of a subfamily within the telemetacarpal deer. Then of course, the systematics must change: the Odocoileinae Pocock, 1923, became a subfamily representing only the New World telemetacarpals. The only family name as the next higher taxon in the classification of telemetacarpal (s.s.) cervids [including Alcinae and Rangiferinae] remains the Odocoileidae Brookes, 1828. Hence, logically the plesiometacarpal Cervidae Gray, is a family which includes as subfamily the Cervinae Baird, 1857, and others which are extinct. The Muntiacidae should be considered also as a family for reasons explained elsewhere (Bubenik 1982a). In order to place all cervoid eupecoran under the superfamily Cervoidea Simpson, 1931, some

infrafamilies are inevitable. For the true cervicorn deer with an annual antler cycle I propose terms like: Cervoidae, (= Cervoidea Hay, 1930). The proposal of a new classification is presented in Table 1., and as far concerns the members of odocoileidae, are shown in the dendrogram [Fig. 2].

Opinions on phyletic relationships in Alcinae are not unanimous (Azzaroli 1981, Heintz and Poplin 1981, Sher 1986). Sher (*ibid.*) considers the oldest ancestors of all Alcinae to be the specimens discovered in the Late Pleistocene layers of the Near-the-Azov-Sea region, and the Middle Villafranchian of Tadjikistan - USSR (Vislobokova 1980) resp. These specimens were aged 2.5 to 2 million years old (Bajgusheva 1971).

However, the first well defined genus of Alcinae is the broad-fronted Libralces (Azzaroli 1952) from the Late Villafranchian of S n ze - France, about 1.8 million years ago. That huge animal with large and specially shaped antlers is distinguished from present-day moose by different dentition and limbs, and by long nasal bones. It was ascribed to the type L. gallicus. It is not identical with the poorly identified giant moose which lived between the Late Pliocene and Early Pleistocene (1.2 to 0.5 million years in Eastern Siberia (high latitude of Yakutia). The another latifrons moose from the very end of the Pliocene and Early Pleistocene, ascribed to the so called broad-fronted moose Alces latifrons, Johnson 1874, [Fig. 3] is known from the Trans-Bajkal area USSR (Vangengeim 1977). According to Sher (1986) that moose seems to be the most abundant from France



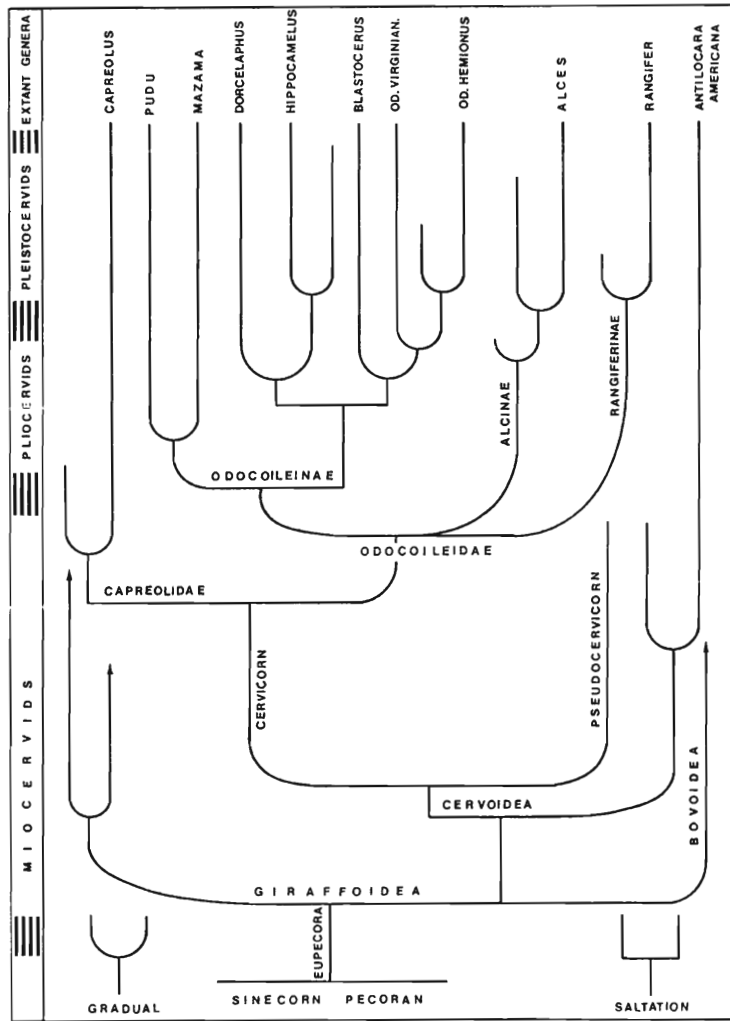


Fig 2. DENDROGRAM OF TELEMETACARPAL DEER

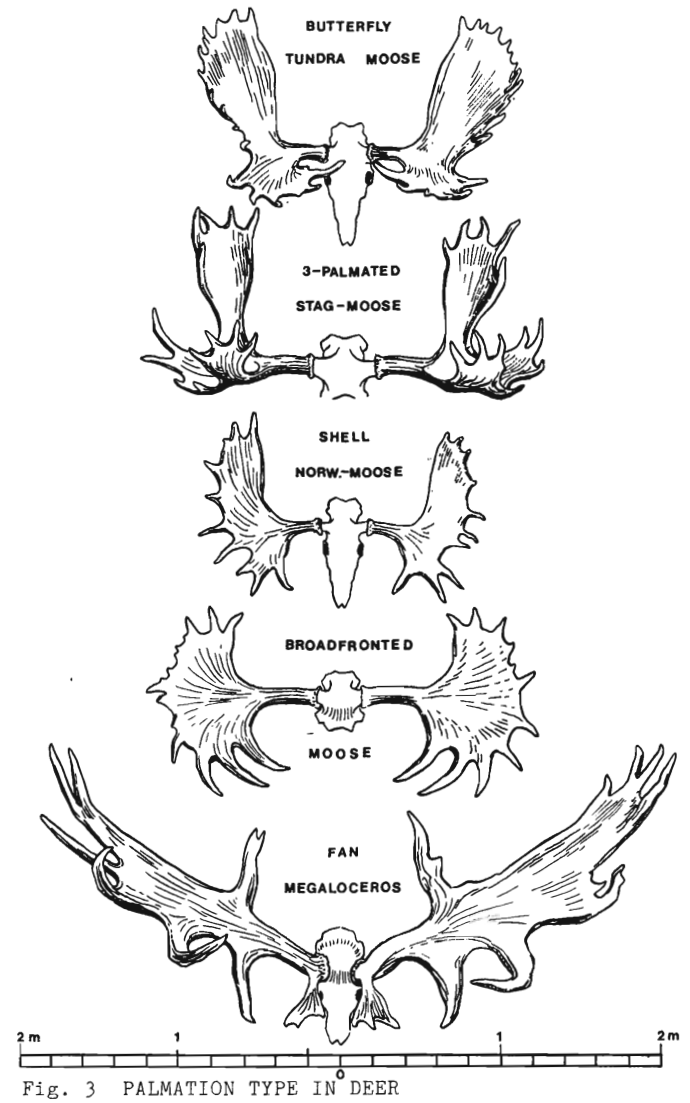


Fig. 3 PALMATION TYPE IN DEER

and the British Isles to the lowest beaches of the Kolyma River and Kamchatka ( $0^{\circ}$  to  $165^{\circ}$  W and  $45^{\circ}$  to  $71^{\circ}$  N). The youngest of the broad-fronted moose and the last of its line is considered to be A. latifrons postremus Flerov 1965, from Kamchatka (Vaskovskii 1966). It may have become extinct during the maximum glaciation of Siberia, i.e. in the first half of Middle Pleistocene, called Riss [Table 2]. In Europe, the broad-fronted moose may have disappeared a little later, i.e. during the Riss-Würm period (Kahlke 1976).

EPOCH	EUROPE	ASIA	DATE
HOLOCENE	P O S T G L A C I A L		10,000
LATE PLEISTOCENE	WÜRM GL	WISCONSIN GL	40,000
	RISS-WÜRM IGL		
	RISS GL	SANGAMONIAN GL	.1 MA
	MINDEL-RISS IGL		
MIDDLE PLEISTOCENE	MINDEL GL	ILLINOIAN GL	.25 MA
		YARMOUTHIAN IGL	
	GÜNZ-MINDEL IGL	KANSAN GL	.5 MA
	GÜNZ GL	CROMERIAN IGL	
		NEBRASKAN GL	1 MA
EARLY PLEISTOCENE	DANUBIAN GL? TIGHLIN WARM		2.5-3 MA
PLIOCENE			5 MA
MIOCENE			25 MA
OLIGOCENE			37 MA

Table 2. GLACIALS and INTERGLACIALS

Vereshchagin (1967) and Heintz and Poplin (1981) speculate that the youngest subspecies of broad-fronted moose might be a transition stage to the true moose A. alces. Azzaroli (1981) and Sher (1986) disagree with this. They do not accept the possibility that an ancestral species might survive with its direct descendant. In other words the broad-fronted moose must have died out prior to the Riss-Würm period. However, a coexistence between a propagul and its descendant is generally accepted (Stanley 1979) and indeed, also documented in the Cervus e. angulatus Beninde, 1936. This elaphoid deer was considered to have been extinct for about 400,000 years, but Meunier (1984) has shown that it is identical with the extant red deer of Spain.

Heintz and Poplin (1981) consider A. φarnutorum Laugel, 1862, the relatively small moose from the boundary between the Late and Middle Pleistocene of GDR as the ancestor of our present moose. Sher (1986) disagrees and considers this moose as some intermediate stage between A. gallicus and A. latifrons.

Finally Vereshchagin (1949, 1955) described from the Caucasus, a moose (A. caucasicus) which died out in the 19th century A.D. It has slightly elongated nasals, and premaxillary bones so mighty that they almost reach the nasals. This is very interesting in respect to the peculiar shape of the premaxillary bones of the moose around the Great Lakes of North America, as will be discussed later. All other eurasiatic genera and species of huge fossil deer

[Alces maeoticus, Paleotragus, Bretzia pseudalces, Tamanalces, Pseudalces] are no longer considered to be relatives of moose (Heintz and Poplin 1981, Thenius 1980).

In America, according to the present classification, only two genera of moose are known: the extinct stag-moose Cervalces Scott, 1885, and extant Alces Gray, 1821. The Cervalces differs from Alces in skull characteristics. In contrast to its European relatives, the American stag-moose has the three-palmated antler construction [Fig. 3]. However, the Cervalces from Beringia (SHER 1986) was also three-palmated. Therefore, it is of interest that some antlers of recent moose from Mongolia [Collection Chr. Oswald, Ebersberg-Oberlaufing GFR] and my few records from Alaska show some attempt to develop three palms from a dorsal side of the main palm [Fig. 4]. This of course, may be a pure coincidence or effect of some other factors on antler development in this part of the world. In any event, it may support Azzaroli's view (1981) that the "queer" palmation of the North American Cervalces, is a feature acquired relatively late and is of subgeneric value.

Sher (1976) and Azzaroli (1979, 1981) seem to favour the congenity of Libralces and A. latifrons, and recommend to assigning both to the genus Cervalces Scotti. However, just recently Azzaroli [pers. comm. June 1985] expressed doubts as to whether Cervalces, due to cranial differences is affiliated with Alces.



Fig. 4. BEGINNING OF 3rd PALM FROM 2nd (?) DORSO-LATERALLY TWISTED TINE

AGE	EUROPE	ASIA	N. AMERICA
HOLOCENE	ALCES <u>alces</u>		
UPPER PLEISTOCENE	ALCES <u>latifrons postremus</u>		CERVALCES?
MIDDLE PLEISTOCENE	ALCES <u>latifrons</u>		
LOWER PLEISTOCENE	<u>A. cornutorum</u>		
	ALCES <u>gallicus</u> -2 MA		

Fig. 5. EVOLUTION OF ALCINAE [Heintz & POPLIN 1981]



I share the view of Heintz and Poplin (1981) who accept the genus Alces as the only representative of Alcinae and consider the phyletic connection with Cervalces as possible.

Tracing down all moose-like cervids and taking in account their special characteristics, I hypothesize that their propaguls must develop by saltation and not by gradual evolution [Fig. 5]. However, the subsequent evolution seems to be gradual, and in accord with the hypothesis of predictability of species diversity (Slobodkin and Sanders 1969), because the rate of extinction follows the gradual increasing of the severity of moose habitats during the Pleistocene. If that conjecture is correct then Alcinae have developed in accord with Goldschmid's (1940) "hopeful monsters" hypothesis.

The hypothetical transformation of broad-fronted moose into the shell- or butterfly-palmated moose, which should have happened during the Pleistocene (Vereshchagin 1967, Sher 1986) seems less probable. According to Stanley (1979), not a single valid example of phyletic transition from one genus to another is known during the Pleistocene.

Using mostly the classification and description of Flerov (1952), Peterson (1955) and Sher (1986), [except the later's view that moose belong to plesiometacarpal deer], the extinct and extant genera of Alcinae can be described as follows: [For more synonyms see Flerov 1952, Peterson 1955].



**Infrafamily Cervoidae**, n.f. = Cervoidae Hay, 1930

**Family Odocoileidae**, n.f.

**Subfamily Alcinae** Jerdon, 1874

**Genus Cervalces** Scotti, 1885

Face not as long as in Alces. Premaxillary bones rather short, with strong ascending branches contacting nasals. The latter are over-hanging the nasals. The orbits are situated much below the roof of the forehead. The braincase is broad and low. The antlers are always with a clearly expressed shaft, which may exceed 350mm.

**Subgenus Libralces** Azzaroli, 1952

The shaft varies from 200 over 350mm long; palmation is rather weakly concave.

**Cervalces (Libralces) gallicus** Azzaroli, 1952\*)

[\*]for detailed synonymy see Azzaroli (1979)]

Animals of a medium size; the skull is low, the facial skull is slightly inflated, the shaft is over 500 mm long and wave-like curved. The presence of the upper canines is suggested.

Middle (?) to Upper Villanfranchian in Europe. Sher (1986) includes here also the form from the Middle Villafranchian of USSR, [Liventsovka, Kumertau (S-Ural)], but he is not sure if in the future they will not be separated from Cervalces.

**Cervalces (Libralces) latifrons** Johnson, 1874\*)

\*) According Sher (1986), except A. a. caucasicus Ver. 1949, which is subfossil.

Very large animal, the skull has an inflated facial part, with an antler spread around 2.5 m and a shaft up to 500 mm long, occasionally slightly curved.

Epi-Villafranchian-Mindel in Eurasia, and in the north of North America. The specimens from Kolyma and Alaska are conventionally included here, but their taxonomy is not yet quite clear. In the future the Cromerian and Mindelian forms may be differentiated into separate taxa by beam lengths.

**Cervalces (Libralces) postremus** Vangengeim and Flerov, 1965

The shaft is of medium length (250 to 350 mm). No other features are known. Taxonomical position unclear. Mindel-Riss, Riss (?), Riss-Würm of Eurasia.

**Genus Cervalces (Cervalces) scotti** Lydekker, 1898**Subgenus Cervalces** Scott, 1885

Originally large animals, but towards to the end of the Middle Pleistocene the facial part of the skull became more moose-like (Sher 1986). Simultaneously the body was smaller and antler spread narrower. This process seems to be faster in Eurasia than in North America, where the genus was isolated by the inundation of Beringia.

The shaft is of medium length (+ 350mm), main palms are concave and divided into 2 parts, and the brow palm is

separated. Brow-palm and "middle-palm" protrudes forward-upward with 4 to 5 points on each side [formulated by Bubenik].

The characteristics of the genus and subgenus are the same. The Early Middle Pleistocene in Asia, Middle Pleistocene of North America, south of the Great Lakes.

**Genus Alces** Gray, 1821

1821: Alces Gray, Med. Repos. 20: 307

Distribution: Middle Pleistocene, Late Pleistocene up to present time in boreal and subarctic zones of Eurasia; from Late Pleistocene (Wisconsin) to recent in North America.

Characteristics: Skull measurements of all species can be found in Peterson (1955). Their statistical significance was not tested and overlappings seems quite possible. Sentences in "---" are quotations from Peterson (ibid.).

In eupecoran the definition of coat colours by standards is impossible. The colouration pattern can be mono- or dimorphic and in general depends in both sexes on the age and sexual gland activity (Bubenik, et al. 1977, Bubenik, G. and A. Bubenik, 1985). In this regard nothing is known for the corresponding holotypes.

The face is strongly elongated, the premaxillary bones are very long but their posterior edge is wedged into the maxillae, not reaching the nasal bones. Nasal bones are short, protruding over the nasal cavity. The upper edge of the orbits is situated at the level of the concavity of the



profile of the frontal bones. The skull is narrower and higher than in Cervalces; the nose is particularly high. It is convex in a horse-like manner.

The shaft is short, 100 to 150mm. A single palm [shell-type] is more common in Europe and Western Siberia. From here eastward up to North America the double palmated ["butterfly"] antler type prevails [Bubenik 1973].

**Alces alces alces** Linnaeus, 1758

European Moose

1758: Cervus alces Linnaeus, Syst. Nat., 10th ed. 1:66.

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

It is generally accepted that the holotype established by Linnaeus 1758 is the genotype for all extant moose, (PETERSON, 1952, 1955).

Type locality: Sweden

Presumed distribution: Europe and West Siberia.

Characteristics: A medium size moose not over 190 cm high and 275 cm long. Live weight of mature bulls not over 500 kg. The overall colouration pattern in winter is grey or greyish brown. Face of the bull is as grey as that of cows (Flerov 1952, Hermansson and Boethius 1975, Skuncke 1949). Legs are whitish-yellow, the bell is small. The shell-shaped antlers [Fig. 3] is the prevalent construction type in Norway antlers (Bubenik, pers. record, J. Lykke, pers. comm. 1985), otherwise also butterfly palmation occur. The posterior edge of

the premaxillary bones does not reach the nasalia (Fig. 6 c).

Altogether, I found 22 synonyms for the European moose. This suggests a great local diversity in Europe and Western Siberia, and/or to use of specimens of different maturation and social status. It is my view that the distribution of that subspecies is not well established. It should be confirmed whether or not the moose of Poland and Ukraine belongs to the Fennoscandian race.

**Alces alces caucasicus** Vereshchagin, 1955

1949: Alces alces caucasicus Vereshchagin. Zool. Zhurn. 34 (2): 1955.

1959: A. a. caucasicus, Vereshchagin. Mlekopitajushchie Kavkaza. AN USSR Leningrad.

Holotype No 2-23615 (male), No 7-23620 (female) ZIN AN USSR Leningrad.

Distribution: The forests of the foothills of Northern Caucasus), reed-areals of lower Don River, Kuban and Terek lowland and probably that of Colchis. Extinct since 19th century A.D.

Characteristics: Medium size moose. The premaxillary bones are full developed (Fig. 6a) and reach up to the rim between nasalia and maxillary bone. In contrast to the northern moose of European USSR the facial part is very narrow, brachyodont dentition, palms not well developed.

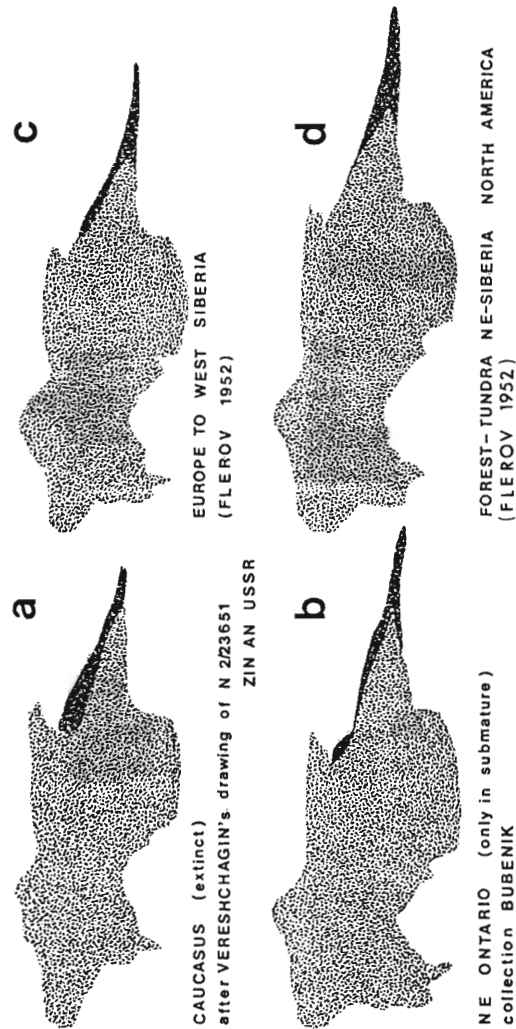


Fig. 6. PREMAXILLARY BONES IN ALCES

Alces alces cameloides Milne-Edwards, 1867

Manchurian Moose

1867: Cervus cameloides Milne-Edwards, Ann. Sci. Nat. Zool. ser. 5, 7:377

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

Holotype in Moscow Mus. Nat. History (Kaplanov 1948)

Type locality: Unknown, probably the basin of Ussuri River.

Distribution: According Dr. Ma Harbin (pers. comm. 1985): Eastern part of the Province of Heilongjiang, called also the Northern Qingan. By and large between the Amur and Sungari River, both sides of Inner Mongolia and Manchuria, and Sichote Alin Mountains in Ussuri USSR.

Characteristics: It is described as the smallest moose, about 250 - 276 cm long and 172 -195 cm high, live weight about 320 kg, max. 400 kg, antler construction cervicorn. The mane is very large, winter coat of torso is almost black, but legs are whitish; the bell is small, cheek hair is long (ABRAMOV 1954, KAPLANOV 1948).

This moose may be important for understanding the history of the black moose of the North American taiga. In a previous paper (Bubenik, 1973) I shared the view with the late Prof. V. G. Heptner [person. comm. 1956] that the Manchurian moose may be a primitive one. Now, I have changed my mind and am inclined to accept the assumption that that moose is a product of regressive gradualism or a reverse recapitulation (Alberch et al. 1979).

Alces alces pfizenmayeri Zukowsky 1910

Siberian Moose

1910: Alces pfizenmayeri Zukowsky, Wild u. Hund, 16 (11): 807.

1931: Alces alces pfizenmayeri Flerov, Comptes rendus de l'Acad. des Sci. de l' USSR: 73

Holotype Mus. of Nat. Hist. Berlin (?)

Type specimen Moscow Mus. Nat. Hist.

Type locality: probably Upper Lena and Indigirka River USSR (Pfizenmayer 1928/29).

Distribution: East Siberia north of Outer and Inner Mongolia, Amur River and Ussuri USSR (Heptner and Nasimovich 1974).

According to the antlers collected by Chr. Oswald, Ebersberg 1985, the moose of Inner Mongolia cannot be considered as representative for A. a. pfizenmayeri (Bubenik, A. unpubl.) and its classification deserves further study.

Characteristics: A huge moose, close in dimensions to the Alaskan one. Body length around 300 cm. Shoulder height 225-240 cm (?), live weight of bulls 570 - 655 kg. Winter coat greyish as in European moose, legs dark as the torso (!), bell is larger than in Europe (Heptner and Nasimovich 1974). Nasal processes of the premaxillary bone extending further up the rim of nasal aperture. Flerov (1962) did not recognize the Siberian moose as a subspecies, but rather as synonymous with Alces alces americana Clinton (1977), which is certainly erroneous. The very frequent longitudinal ridge

on the dorsal side of the main palm can occasionally split and becomes to a dorsal tine as has been shown in Fig. 4.

Alces alces gigas Miller, 1899

Alaskan Moose

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

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

Type specimen U.S. National Museum, no. 86166

Type locality: North side of Tustumena Lake, Kenai Peninsula, Alaska.

Distribution: from the Kivalina River in NW Alaska south and east to the Yukon, to northern British Columbia, and to the Northwest Territories in the forest-tundra. The southward distribution is limited by dense taiga and humid climate (Bubenik, A. own records, Hall 1973).

Characteristics: Moose as large as Siberian: Winter colouration different from Fennoscandian, Manchurian, North American woodland moose, and probably also from Siberian moose: upper part of the neck, shoulder and upper part of torso pale or light brown, sometimes almost ochraceous. Prime bull's face very dark, prime cow's face brown. Torso and lower part of neck dark, with bluish glister. Front legs dark, hind legs with white "stockings". Bell mostly fan-shape. However, prime bulls with a tailed-bell also occur. Antlers of butterfly type. Skull very long, convex nose, occiput high, palate relatively high, premaxillary

bones long, however, reduced in height (Fig. 6d). Orbital angle about 32° (Bubenik and Bellhouse 1980).

Alces alces shirasi Nelson, 1914

Yellowstone Moose

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

1952: Alces alces shirasi Peterson, Roy. Ont. Mus. Zool. and Paleo., Contrib. no. 34: 23

Type specimen: U.S. Natl. Museum, no. 202975

Type locality: "Snake River, Lincoln County, Wyoming".

Distribution: "Western Wyoming, eastern and northern Idaho, western Montana, northward into southwestern Alberta and southeastern British Columbia. Occasionally occurrence in extreme northeastern has been reported by Durrant 1952". Since late 1970 introduced from Wyoming (Bubenik, A. own records).

Characteristics: "A medium form with nasal aperture relatively wide. Colouration of pelage along the back averages paler than other north American forms". However, the description and slides I received from J. Peek (pers. comm. 1986) do not confirm the paler coloration. Prime bulls in winter coat seems not to differ from other dark moose along the Great Lakes. According to Peterson (1955) the upper edge of the premaxillary bones does not reach that of maxillary ones. Probably the smallest of all American moose.

Alces alces andersoni Peterson, 1950

Northwestern Moose

?1907: Alces columbae Lydekker, Field, 9: 18a (British Columbia?)

?1915: Alces columbae Lydekker, Zool. Rec. 44: Mamm., Brit. Mus. Nat. Hist.) 4: 236 (Ontario?)

9852: Alces alces andersoni Peterson, Roy. Ont. Mus. Zool. and Paleo. Contrib. no. 34: 24

Type specimen: "Adult male (skin and complete skeleton) no. 20068, Royal Ontario Museum of Zoology and Paleontology.

Type locality: Section 27, Township 10, Range 16, Sprucewood forest reserve (15 mi. E. Brandon) Manitoba.

Distribution: Northern Michigan and Minnesota, western Ontario, westward to central British Columbia, north to eastern Yukon Territory and Mackenzie Delta, Northwest Territories."

Characteristics: "A medium-size form differing from other North American forms chiefly in cranial details, especially with respect to the shape of the palate (relatively wider than americana and narrower than gigas)". According to figures in Flerov (1952) and (Peterson 1955), the nasal processes of the premaxillary bones are so much regressed that they end far below the rim of nasal aperture. However, my own collection of skulls from NW Ontario [where andersoni and americana should intergrade, (Peterson, ibid.)], show clearly that in submature specimens (under 4 years of age) the premaxillary bones consist from two, not



connected parts: the upper reaches up to the nasal rim and fuses with the maxillary bones at the age of 4 to 5 years. Thenafter only the lower part of the premaxillary bones is visible [Fig. 6b]. If this occurs also in the shirasi and americana moose should be investigated. Orbital angle over  $40^\circ$  (Bubenik and Bellhouse 1980). Colour of the winter coat depends on maturity stage and rank. The coat of prime, high ranking bulls is almost black. The face of those bulls is black just between the antlers, that of cows is brown. Postprime bulls have brown face, face of postprime cows becomes dark (Bubenik, *et al* 1977).

Alces alces americana Clinton, 1822

Eastern Moose

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

1852: Alces alces americana Peterson, Roy. Ont. Mus. Zoo. and Paleo. Contrib. no. 34: 28

Type specimen: Unknown.

Type locality: "Country north of Whitestown" (probably in western Adirondack region) New York".

Distribution: "From Maine and Nova Scotia westward through Quebec to central Ontario where it apparently integrates with A. a. andersoni. Introduced into Newfoundland where it is now established".

Characteristics: "A medium-size relatively dark race with a narrow palate relative to length of toothrow".



ECOLOGY AND DISPERSAL IN PAST

The dispersal must have begun somewhere between the Pyrenees and Azov Sea within the Early Pleistocene, 2.5 - 1.8 million years ago, during the Villafranchian (Heintz 1970). By the end of the Miocene, the climate in Europe became so dry and cool that the dense forest was gradually replaced with parkland-savannahs and steppes (Hambrey and Harland 1981, Janis 1982). With the opening of the landscape, ungulates grew bigger, and optical cues gained in importance. Among those, the accentuation of the head pole by horns and antlers proved to be the most purposeful and in part facilitated visual and olfactory communication in addition to being a tool in social interactions (Bubenik 1982c).

When the glaciation periods began, the cool winters became a problem for the polyestrous pliocervids. Those who could adapt their breeding and antler cycle to hostile winter conditions, like roe deer, mi-lu deer (Elaphurus davidianus) or Thorold's deer [genus Przewalskium], survived. The others died out or migrated through the Mediterranean area and from the steppes of China into India and Southeastern Asia (Thenius 1980, Bubenik *et al.* in prep.).

From the phyletic view, suddenly, many niches became vacant, many others appeared. It was a period in which many deer isolates [small, spatially isolated populations] developed probably by **quantum speciation** [chromosomal rearrangement leading to changes in growth gradients or

ontogenic sequences ] a population **flush** [a release of bizzare variability within a small founder population (Stanley 1979)]. The result was the **hopeful monsters** (Goldschmidt 1940) [chromosomal, pleiotropic rearrangements which produces by saltation many deleterious, but some "hopeful" higher taxa] like megalocerini [the giant elk *Megaloceros* sp. [Fig. 3] (Reynolds 1929), or the gigantic elk [*Cervus major*, n. sp.] (Barbato and Petronio 1986), and of course, the *Alcinae* .

As mentioned before, they all must be well established short-day breeders (Bubenik 1986b) with antler growth during the vegetation period and calving in spring.

All those giants began to spread into the vacant niches of the now open country. Moving westward they reached Spain, eastward they had to split their ways. Those which probably liked more mild climates went south of the Alps and remained in the Mediterranean space. Others, which favoured cooler climates and were incapable of crossing the Pamir [De Vos pers. comm. 1985] and the Himalayas, proceeded up into Central and Eastern Siberia and China.

The eastward progress was favoured by the fact that Europe became glaciated earlier than Siberia [THENIUS 1980]. The endless steppes of Siberia with riparian forests enabled extremely fast movement toward the northeast up to the outmost corner of Siberia. [Fig. 7,8,9].



Fig. 7. PRESUMED ROUTE OF MOOSE DISPERSAL DURING PLEISTOCENE



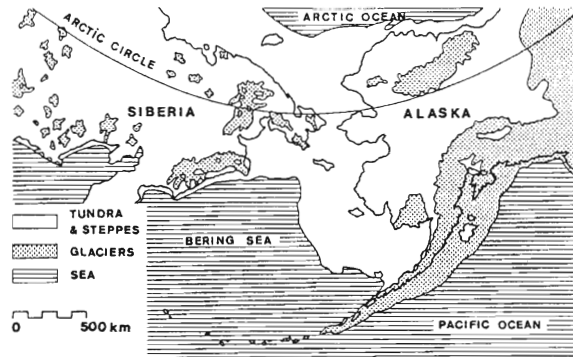


Fig. 8. BERINGIA DURING WISCONSIN [THENIUS 1980]

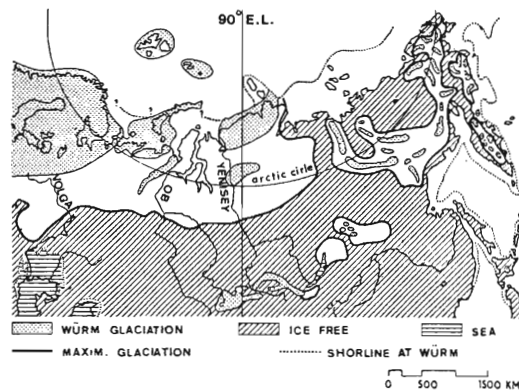


Fig. 9. GLACIATION OF EURASIA DURING PLEISTOCENE [FRENZEL 1960 after THENIUS 1980]

Here, all migration was stopped, since the next glaciation did not consume enough water for the sea level to drop below the bottom of the landbridge between Chukotsk Peninsula [USSR] and Alaska, called Beringia [Fig. 7,8,9].

The timing of the many ups and downs in the history of Beringia is connected with the different duration and different spread of periods of glaciation. Due to that, there were many periods of invasion of ungulates. Some were long, others short; some brought lineages with relatively closed developmental programs (Mayr 1974), others with elastic taxa, responding by saltation to new living conditions.

Among the first ungulates were the pristine *Odocoileinae* (FRICK 1937). They crossed into Beringia during the Matuyama magnetic epoch (Opdyke 1977) just prior the Pleistocene, some 2½ million years ago, at a time when the propaguls of moose appeared in Europe.

#### Late Pliocene to Middle Pleistocene

Because any quantum speciation presupposes optimum adaptation to new living conditions [Stanley 1979], it is worth speculating which changes the pristine *Alcinae* experienced, or to which they were exposed, and how they adapted in order to cope so successfully with the environment (Guthrie 1966, 1967, 1968, Hopkins 1959, Kahlke 1956, 1971, Khan 1970, Kurtén and Anderson 1980, Sher 1986, Thenius 1962, 1980).

The incomplete knowledge of climate and ecological conditions from this epoch allows only the conclusion that the zone of distribution can be characterized as arid steppe, steppe-tundra and tundra with braided rivers and riparian bushes, or a highland tundra.

However, I do not agree with Sher's (1986) assumption that the archaic moose was adapted to a wide range of temperatures. That seems very unlikely to me. My view is based on the very narrow range of critical temperatures of moose in summer [+14 to +20° C] and very wide in winter [-30 to +4° C] (Renecker and Hudson 1986). There is no reason to suggest that the summer critical temperature [above which the moose is losing heat in order to thermoregulate properly] of the broad-fronted moose should be different.

Between 1.0 and 0.7 million years ago (beginning of Middle Pleistocene) the archaic broad-fronted moose, Cervalces (Latifrons) of the Lower Pleistocene, was well established throughout the Eurasiatic continent except the most NE corner, the Chukotsk Peninsula. It's spread over Yakutia may be slowed down or stopped by the extremely cold climate of the Riss-glaciation. Further migration was not possible until a new, warmer interglacial at the Middle Pleistocene freed the land from a permanent ice shield. The next forward thrust of ice, less than 500,000 years ago [Cromerian period] again dropped the sea level in the Bering Strait so much that the Beringia, or the so called Bering-Chukchi platform reappeared and enabled the migration to Alaska. It was then,

when Cervalces crossed the Beringia and began its descent towards the Great Lakes (Peterson 1955).

The great antler spread of the broad-fronted moose Cervalces latifrons points to an inhabitant of open landscapes. Despite we know that at that period the forest-savanna formations were much thinner than at present, the suggestion of Sher (1986) that the archaic Cervalces could be also related to arboreal vegetation seems to me less probable, unless antlers with palms punctured during the velvet period are found, as it is the case in recent woodland moose (Bubenik 1986a).

Relying on fossil evidence (Peterson 1955, Sher 1986) and the progress in regression of the vertical width of premaxillary bones (Fig. 6a,b,c,d), the alces-moose may have invade Alaska twice. Their lineages were specialized, or they adapted to climatic severity experienced during migration, or when waiting for the re-emergence of Beringia. This might explain why the North American moose has some close relatives in Asia and why the moose of the forest-tundra is different from those of the taiga.

The almost ½ million years that Cervalces scotti spent in North America were long enough to allow speciation towards the tripalmed antler construction. The rate of the gradual evolution seems to be much faster in the northern latitudes than under the temperate climate of Villafranchian. For example the polar bear needed only 20,000 years to separate from its brown progenitors (Kurtén 1964), whereas about ½

million years were necessary for subspeciation for the Croizetoceras deer in Spain (Brunet and Heintz 1984).

The extinction of Cervalces in North America during the end of the Pleistocene [10,000 yrs ago] or later (Harington 1984), is considered to be directly connected with the extinction of all broad-fronted moose in Eurasia, rather than due to a direct competition with Alces. However, there might be another factor involved. Descending towards the boreal and subboreal forest and forest-steppe zone, the stag-moose invaded habitats occupied over 1½ million years by deer of the genus Odocoileus. One of them, the white-tailed deer (Odocoileus virginianus), can be infested by Paraelaphostrongylus tenuis, parasitic round worm mortal for moose when it penetrates into the brain. This is the case in populations around the Great Lakes (Saunders 1973).

In contrast, this parasite is generally non pathogenic in white-tailed deer (Anderson 1965). Hence, the infected white-tailed deer populations protect their home ranges against ruminant competitors, especially the moose (Saunders 1973). That knowledge tempts one to speculate that white-tailed deer populations infested with the brain worm might have contributed directly to the fast extinction of Cervalces towards the Neogene of North America (Harington 1984).

Reasons for the much faster extinction of broad-fronted moose in Eurasia are not known. It is interesting that towards the end of the Middle Pleistocene in some solitary regions of western Europe, the first typical Alces had

appeared. The niches where it evolved must have had very special umwelts (Bubenik 1984) under which pressure the peculiar skull characteristics and antler construction were developed, before the moose had spread over Eurasia.

Finally, it has to be said that there is also not unanimity concerning the number of subspecies of the genus Cervalces scotti. Khan (1970) considers only two: the C. scotti, and C. roosevelti, with the latter one the C. borealis should be synonymous; in his opinion the C. alaskanensis might rather belong to the subgenus Libralces. In contrast Kurtén and Anderson (1980) recommended attributing all Cervalces of North America to only one species C. scotti.

#### THE EXTANT MOOSE OF NORTH AMERICA

There are two different habitats in which the moose lives: the northern, characterized as forest-tundra and the southern where the boreal taiga prevails (Rowe 1959). That overlapping of the distribution exists, within the perimeter of which both moose meet is, of course, only natural. Also panmixia cannot be excluded (Peterson 1955), but if it exists on large a scale is still questionable.

Alces invaded North America first together with wapiti during Illinoian glacial or just before the Sangamonian interglacial [less than 250,000 and more than 100,000 years ago] (Guthrie 1966). The Sangamonian interglacial opened the

way south. The alces-moose reached the Great Lakes and finally spread from one ocean to the other. The second invasion of alces-moose came in Late Pleistocene, during the Wisconsin glaciation, about  $\pm$  40,000 year ago (Guthrie 1966, Kurtén 1971). However, at this time a great part of North America was covered by ice cap [Fig. 10] and the invading moose was cut off in the Northwest of Alaska in the harsh forest tundra.

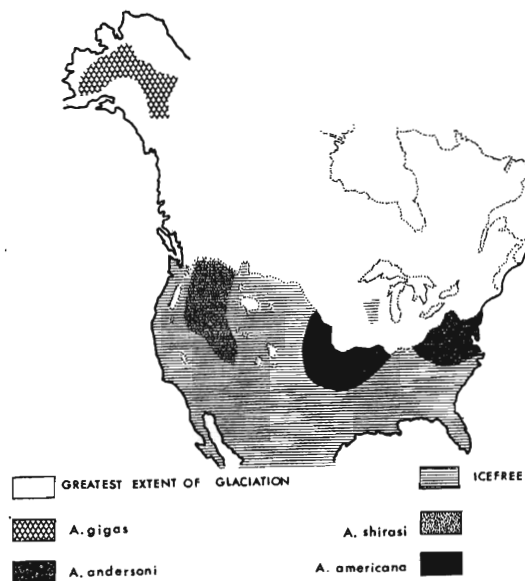


Fig. 10. DISTRIBUTION OF MOOSE DURING THE PEAK OF WISCONSIN [PETERSON 1955, THENIUS 1980].

However, during every glacial period when Beringia emerged, the climate on both sides of the Bering Strait was more severe than it is presently. Summers were too short and too cold to support forest vegetation, the snowfall was thin and patchy (Hopkins 1959, 1967). The speciation of the limb bones (Flerov 1952, Sher 1971), may be adaptations to facilitate moving on a very soft ground, and perhaps also in deep snow as is characteristic of recent moose habitats (Sher 1986).

The forest tundra and dense taiga of North America are characterized not only by different height and density of vegetation that moose has to penetrate, but also by different climatic conditions. By and large, the forest tundra has a vegetation which is mostly lower than the level of moose eyes, unlike the taiga which limits the visibility from 20 to 100 meters at most (Bubenik 1986a). Movement in forest tundra is easy, whereas in taiga it can be difficult. The taiga north of the Great Lakes is sometimes so dense that moose can move only on traditional trails and along the shores of lakes.

In the forest tundra of North America the air is very dry throughout the winter; there are long, almost windless periods, snow depth is low and crusting is infrequent. Therefore in view of the lower limit of the winter critical temperature (Renecker and Hudson 1986, Schwartz *et al.* 1984) thermal losses must be low in comparison to the relatively wet taiga. Snow depth of 120 cm and more and dangerous crust

are frequent. By and large, the habitat is energetically costly. The tundra moose experiences also [dependent on latitude] annually about 4 months of 24 hr daylight, and the same period of 24 hr darkness. It would be worth knowing, if these long periods without light-zeitgeber are capable to induce in moose endogenous periodicity of activity and more effective physiological processes with better food utilization, as known for other animals (Aschoff 1979).

The southern moose is considered as little bit smaller than the northern ones (Gasaway *et al.* 1986, Peterson 1955), but the most intriguing may be the colour of its coat. By and large, the winter coat of the "taiga" moose is, except for the white legs, almost uniformly dark. In mature, well conditioned animals it is black. In contrast, the "tundra" moose of Alaska has a light brown neck and upper torso, shoulders are very pale, almost ochraceous. The lower part of torso is very dark with a bluish shimmer. Outer sides of the front legs are dark. Both colouration patterns differ at least from that of the greyish coat of moose between Fennoscandia and east Siberia. Similarities exist only in the colouration of legs. Fennoscandian, Manchurian and all moose of North America have whitish legs. About the colour of the Siberian tundra I was unable to gather reliable information. According to Peterson (1955) the shirasi-moose "along the back averages paler than other North American forms". However, according to the description I received from Peek (see *A. shirasi*) that is not common.

The black coat may be the result of adaptation to the energetically costly taiga habitat. It provides not just an optical camouflage, but might also be advantageous for thermo-regulation. Using the experience from studies with different coat colour in goats (Finch *et al.* 1980), I assume that the dark coat under the shaded light of the taiga may also provide about a 30% gain in heat by radiation and convection in comparison to a grey coloured coat. In contrast, its heat losses should be similar to any other colour. If this could be confirmed, I would speculate that the dark colour developed in Siberia, when the first *Alces*-moose reached its NE-corner, long ago before Beringia reemerged. It might have waited there for over one hundred thousand of years or more, exposed to the very humid and severe climate of the Okhotsk Sea.

When the invasion occurred, the way down to the Great Lakes was open. However, the next invasion of moose brought the continental moose of the Siberian tundra. It might have reached the Beringia when it was above the sea level.

#### Moose in the Late Pleistocene of Eurasia

In Eurasia the Late Pleistocene is characterized by the true moose of the genus *Alces*. However, it seems highly probable that the temperate climate between Riss-Würm was unsuitable and during this time the moose is known only in Central Europe. Here the parkland steppe-forest still

prevailed, whereas eastern Europe was covered by mediterranean hardwood forest (Sher 1986). Later on, during Würm (2nd glacial of Upper Pleistocene), i.e. in the Upper Paleolithic [Fig. 7], the moose was common in western, central and eastern Europe, expanding towards the Balkan Peninsula, Caucasus and the southern Ural. However, it was still absent or very rare in the wooded areas of Trans-Ural, western Siberia and Altai. In contrast, it was more abundant farther to the north-east on the waterfront of the Ob River and in south Yakutia than in south Siberia and north Yakutia. In Kamchatka moose appeared much later, to the boundary between Late Pliocene and Holocene (Aleksejeva 1980), and was rather numerous in Primorie.

Interesting is the inconsistency of appearance and fluctuation of density of moose during the Würm [last glaciation 100,000 years]. Tseitlin (1979) presumes that the moose was driven out of its home ranges everytime the cryoxerotic habitat reached its peak. As soon as the climate became milder, the moose returned. In contrast, Sher (1982) is convinced that the moose was permanently present in these zones. However, its densities fluctuated, dependent on abundance of browse. Support for Tseitlin's hypothesis is provided by the fact that since the late 1950's moose reoccupied the original arctic tundra of NW of Alaska, following the reestablishment of shrub-coniferous vegetation along the shores of Kivalina and Kikpuik River in the coastal region of the Chukchi Sea [Bubenik A., own observ.].

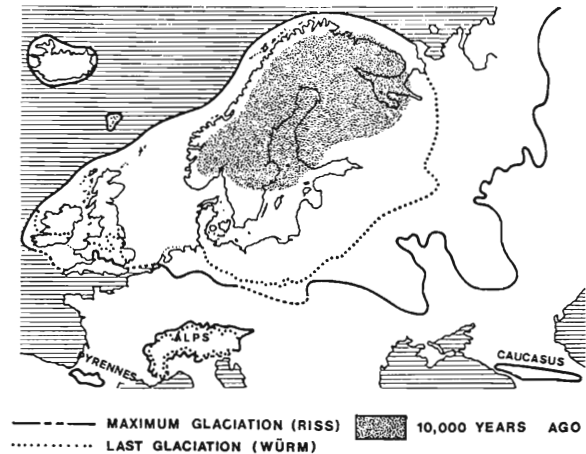


Fig. 11. GLACIATION OF EUROPE DURING PLEISTOCENE [THENIUS 1980].

The dispersal of moose from western Europe towards the north and east is not documented well as far it concerns the speciation in antler construction and shape, which seems to go along with climate and coat colouration (BUBENIK 1973, 1986a). Moose invaded northern Europe following the retreat of the ice cap [Fig. 11]. Due to the Gulf Stream, the Atlantic coast became deglaciated much sooner than the eastward regions. Because of this the Atlantic area may have been invaded by moose at the beginning of Holocene [Table 2], thousand years earlier before moose settled around the Gulf of Bothnia. That separation may be long enough to provide differentiation in speciation. It may be that since

that time the antlers of the atlantic populations have been predominantly shell-type [H. Haagenrudd, J. Lykke, pers. comm. 1985].

In contrast, the Baltic moose carries, in part, the "butterfly" antlers. That type of construction becomes more prevalent eastwards and dominates in North America (Bubenik, 1973).

Why the shell-type antler prevails in Norway has not been investigated. Nevertheless, it is hard to believe that Norway and Sweden were almost simultaneously invaded by moose with 2 different palmation types, coming so to say from one population. Therefore, I am inclined to the following hypothesis of Rausing (pers. comm. 1984). The butterfly antlered moose may have arrived in Sweden via Finland, or somewhere from central or eastern Europe after the Baltic region was freed from ice [Fig. 7,11]. If that is correct, then the butterfly antlers (Bubenik 1973, Pfizenmayer 1928/29) may be a direct adaptation to continental climate, or indirectly affected by continental environment. However, after the ice cap disappeared from Fennoscandia some 3,000 years ago [Lykke pers. comm. 1985], the Atlantic and Baltic moose became sympatric. Why they did not hybridize completely, is very interesting.

According to Sher (1986) the moose of continental Eurasia experienced dramatic population cycles between the Middle and Early Holocene [about 10,000 years ago] many times, in periods of thousands or hundreds of years. Sometimes it was

so abundant that on the excavation sites its bones represented in one horizon up to 70% of all wild animals, and in the next drops to less than 1 %, rarely more than those of roe deer and brown bear (*Ursus arctos*). A similar trend is evident at present in Fennoscandia where moose density increased about ten-fold of the level present only 30 years ago.

A similar trend is recorded from the European USSR, where moose again resettled the Caucasus. Population explosion of moose in Poland may be the cause of the westward migration and resettlement of inundation forests of southern Bohemia (Z. Henzl, pers. comm. 1986). These recent increases in moose density in Europe at least, cannot be attributed solely to any dramatic climatic changes or management policy, and the reasons are not entirely known. E. M. Addison (pers. comm. 1986) expressed the opinion that major impact in this regard must have come from changes in land and moose management in Sweden. But such changes cannot be registered in the European part of the USSR, where the moose density is also rising.

#### Moose in the Pleistocene of North America.

The history in North America is no more obscure than in Eurasia. Unfortunately we do not have reliable records of the fluctuations of moose density in North America occurred on the scale known from Eurasia. We have virtually no evidence about moose densities before the white man arrived and before

intensive colonization around the Great Lakes began, 100 or more years ago. From the accounts collected by Thompson-Seton (1953), the accuracy of which may be questioned, the highest average densities 60 to 80 years ago were not above 2 to 4 moose/km<sup>2</sup> or 6 to 10/ square mile. These densities are low in comparison with Sweden during the peak of the moose population explosion in 1982-84, with 6 - 8 moose/km<sup>2</sup> or 15.5 to 16.6/ square mile in some parts of the country. This disparity in the amplitude of oscillation of moose densities between North America and Europe is great and in my view the large fluctuations seen in Europe would not occur in North America where forest successions followed a quite different pattern than in Europe.

The timing of climatic and phytocenological changes in Eurasia and North America was not synchronous, which may explain the diversity in dispersal of density pattern of moose. Its relative low limit of the upper level of the critical temperature (Renecker and Hudson 1980) may be the monitor of its dispersal and its differentiation in the taiga of North America.

When the pale tundra moose invaded Alaska, some 40,000 years ago, the stag-moose (*Cervalces*) and the dark taiga-moose were well established around the Great Lakes. However, when the tundra-moose crossed into Beringia it entered in a tundra and forest tundra refugium, from which the way southward was closed by the Wisconsin ice cap [Fig. 10].

The tundra and forest tundra as well is a very stable,

relatively dry ecosystem. Its stability does not afford any further specialization of its inhabitants. This may be the reason why, after the Wisconsin period, the Alaskan tundra-moose, *Alces a. gigas*, had moved southward only as far, as the tundra and forest tundra did.

During the  $\pm$  70,000 years since the dark moose invaded the taiga, its dispersal and the plant communities comprising its habitat experienced dramatic changes in space and time with the approach of the Wisconsin glaciation. The northern fringe of taiga was pushed down to the Great Lakes (Flint 1948). However, the climate remained relatively mild with a very narrow tundra zone (Bryson, *et al.* 1970). Being kept isolated and forced to stay in the taiga for  $\pm$  40,000 years it adapted so much to the climate and dense habitat that it never tried to occupy the forest tundra. That may be the reason why it still hesitates to go far away from the forest edge and stay in openings of large clear-cuts and wind blows [McNicol and Gilbert 1978, Todesco, *et al.* 1986].

The various rates of forest succession, the different density of trees with different palatability for moose as food and shelter may exert a very strong selective pressure on moose around the Great Lakes. In my view, it may reach differentiation above the subspecies level.

The speciation and dispersal of the dark moose may have been affected also during the interglacials, when only the Laurentide and Cordilleran ice shields persisted and the central continental section was again ice free (Peterson



1955). In those intermediate climates, only the centrally located populations could expand northwestward. Albeit, at the same time the ice sheets still restricted the expansion westward and eastward [Fig. 10].

The enforced occupation of very special niches during the Wisconsin may have led to subspeciation found by Peterson (1952, 1955) leading in the Southwest to the development of *A. a. shirasi*, in the central area of *A. a. andersoni* and in the Maritimes of *A. a. americana*.

Finally the forests north of the Great Lakes became different from those south of their shores. The character of Maritime forests developed quite differently from forests as far as the Rockies. In the Rockies, close to the tree line the forest remained a northern taiga. This alpine formation proceeds very far to the south and may be the reason why moose are still there.

In light of this information I hypothesize that the history of extant moose of North America may have developed as follows:

The first moose which crossed the Beringia probably between Illonian glacial [200,000 years] and Sangamonian interglacial [100,000 yr], might be the more primitive, dark moose from Ussuri, adapted to the humid climate and dense taiga of the east coast of the Okhotsk's Sea by having smaller body size, short shafts of antlers, more parallel oriented palms and serial monogamous breeding strategy (Bubenik 1986a). The North American taiga might have been

suitable to that moose throughout the Great Lakes Districts and Maritimes, where it could cool itself during the hot summer days. After the retreat of the ice shield, its movement to the North was restricted by the very slow progress of reforestation of the deglaciated areas and of course, by the climate, a boreal taiga could sustain (Bryson 1966, 1974, Bryson, et al. 1969, 1970,). In the alpine regions of the Rockies, moose could occupy the more southerly range without being exposed to high ambient temperatures and free from competition with white-tailed deer.

Without attacking the taxonomical validity of the dark moose subspecies of Peterson (1952) I would recommend to reexamine the cranial parameters he used [palate and nasal bones width and skull length], and the shape of the premaxillary bones too. The reason being the recognized susceptibility of cranial changes, particularly of male cervids in relation to the infrastructure of the population (Bubenik and Bellhouse 1980) and habitat (Schonewald-Cox, et al. 1985) on the one hand, and on the other to be sure that these differences are statistically significant.

In contrast, the Alaskan tundra moose, as the last invader did not need to speciate more and is still close to the Siberian one.

Based on the present incomplete knowledge of all taxonomic characteristics of moose, it seems to me that the group *Alces* may be rather a super-genus or a ring-genus Stanley (1979), with 2 genera or superspecies respectively. The one which

is phyletically older might be the woodland or taiga moose. The tundra (strictly forest tundra) moose appears evolutionary younger:

The phyletical age difference can be followed in the progress of development of the premaxillary bones [Fig. 6a,c]. As Flerov (1952) indicated, the distance between the nasal and premaxillary bone is much greater in the tundra moose [*A. a. pfizenmaeyri* and *A. a. gigas*] than in the Fennoscandian and for all in the Caucasian moose. The developmental progress towards long but low premaxillary bones is still preserved in specimens of the taiga moose, at least of that of NW Ontario, i.e. north of Lake Superior [Fig. 6b]. That "interpremaxillar" bone is in my view just the distal residue of the upper part of the premaxillary bone, which may have lost its connection with the proximal part when the maxillary bone grew forward. This conclusion shared also by Vereshchagin (pers. comm. 1986).

If this conclusion is correct, then the dark American taiga moose is an intermediate stage between the extinct *Alces caucasicus* on the one hand, and the Fennoscandian on the other. Therefore, the tundra moose of Yakutia and North America must be the youngest of the lineage. Logically, the dark moose of the North American taiga must have invaded the continent before the tundra moose arrived.

## CONCLUSION

From all the data presented it is evident that the extant moose have specialized either for the woodland or forest-tundra habitat. The body size, pelage colouration and antler shape on the one hand, and the behavioural features on the other may represent adaptive processes.

The main question is, what level of speciation these differences represent. According the valid classification all extant moose are considered as subspecies. In this classification the differences in chromosome numbers (Gripenberg 1984), the divergence of some 20 enzymatic loci (Reuterwall and Ryman 1979), and the different composition of sex pheromones (Bubenik *et al.* 1979, Dombalagian 1979) between North American and Norwegian moose gives evidence that at least the North American populations reached a speciation close to species level. Differences in the pelage colouration, behavioural patterns, and antler shape must also be considered. However, attempts to use antler-size as criterion for separation of the *gigas* and *andersoni* moose (Gauthier and Larsen 1985) are not justifiable.

It is my view that the presently known differences of taxonomical features at least between the grey woodland moose of Fennoscandia, the dark taiga moose of North America and the forest-tundra moose of NE Siberia and North America are of such magnitude that it is difficult to ascribe them the subspecies level.

I am fully aware that in some cases it would be difficult to prove my arguments. Genetic purity of the Fennoscandian moose in the present day cannot be expected. The changes of climatic conditions during the Holocene, hunting pressure in general and habitat changes during the last 100 years influenced by man have certainly enforced fluctuations, migrations and hybridizations on a very large scale.

We do not have enough reliable data on taxonomical features of the Ussuri dark moose and tundra moose as well. Nevertheless, I am offering for consideration some questions which may lead to reclassification of extant moose:

Alces Gray, 1821 = (Alce Frisch, 1775), is a genus or super genus?

Alces a. alces Linnaeus, 1758, is it a true subspecies or a hybrid between the originally atlantic or Norwegian moose and the continental moose of European mainland? Or in other words:  
Did these two populations represent two subspecies or not.

Alces a. camelooides Milne-Edwards, 1867, is it a true subspecies or a regressed race, evolutionary very close to the dark moose of the taiga of North America?

Alces a. shirasi Nelson, 1814

Alces a. americana Clinton, 1822

Alces a. andersoni Peterson, 1950

Are they true subspecies or phenotypes, which skull parameters reflect only infra-structural and/or environmental conditions as has been demonstrated in other deer?, or is it a gradualisation on, or below subspecies level?

Alces a. gigas Miller, 1899, is it a subspecies or species? and how close it is related to

Alces a. pfizenmayeri Zukowski, 1910.

In the event that my suggestions regarding the specialization of extant Alces should be proved, how should the reclassification appear and which names should be used?

#### ACKNOWLEDGEMENT

I am very much obliged to Dr. Sher, Moscow, who let me quote his paper in press, presented 1984 in Uppsala, with all references on which I have to rely. I am very thankful for suggestions given me by Dr. E. Heintz, Paris, and Dr. A. Azzaroli, Florence, Dr. E. Addison, Maple, Dr. N.K. Vereshchagin, Moscow and the two anonymous reviewers, who kindly revised the manuscript and helped to improve it. Very valuable information concerning Norwegian moose I received from Dr. J. Lykke, Vuku and Dr. H. Haagenrud, Vadso. A great help in this study were the slides of antlers of Mongolian and Ussuri moose and antler collection of Mr Chr. Oswald,

Ebersberg-Oberlaufing, he brought from China, and his connection to Dr. Ma, Harbin. Both of them belongs my deep gratitude. Last but not least I must highly appreciate the clerical work done by my wife Mary.

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