

**Shaped by the Ice Age**  
**Reconstructing the history of mammals in Finland during the**  
**Late Pleistocene and Early Holocene**

by

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*Academic dissertation*

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## **Abstract**

Finland is situated at the centre of the area covered by the Scandinavian Ice Sheet during the Late Pleistocene. The history of Finnish mammals provides an excellent opportunity to investigate immigration routes and the shaping of the mammalian fauna in a previously glaciated area. On the other hand, research has been complicated by the fact that the repeated glaciations have left behind a landscape practically devoid of fossil bearing deposits.

In Finland even Early Holocene faunal remains are scarce, due mainly to the poor preservation of bones in the acid soil. Only a few stray finds of subfossil bones of terrestrial mammals have been unearthed in Finland. The remains of marine mammals, embedded in clay or other marine or fresh water sediments, have survived better. Another source of palaeontological information are the refuse faunas, the burnt animal bones from prehistoric dwelling sites and hunting camps.

On the basis of these two types of data, an attempt has been made here to reconstruct the mammalian fauna during the last interglacial-glacial cycle in Finland.

So far no bone remains of terrestrial mammals of Eemian age have been discovered in Finland. A beaver dam deposit dated to the Eemian interglacial indicates, however, that mammals colonized the area during this period. The Weichselian glaciation that followed the Eemian interglacial was interrupted in Fennoscandia by an ice-free period or periods, as indicated by Finnish and Estonian mammoth remains of glacial age. Mammoth finds from Estonia show further that the glacial fauna did not go totally extinct at the beginning of the deglaciation period, but that at least some species re-colonized areas previously covered by the Scandinavian Ice Sheet. Mammoths still lived in Estonia and western Russia during the deglaciation period, about 10,000 BP.

During the deglaciation, the glacial fauna — including Arctic species such as the Arctic fox and the wild reindeer — did not spread from the southern coast into northern Finland, but went locally extinct. The area was subsequently colonized by the present fauna. The main immigration route for terrestrial mammals was directly from the east. The earliest finds indicate a faunal composition associated with young deciduous forests. The fauna developed rapidly into the modern boreal fauna, and no separate faunal periods can be detected.

Some carnivores, such as the wolf and the European lynx, which belong to the modern boreal fauna, have not been detected in the Finnish refuse faunas. The reasons for their absence may be sought in human hunting practices rather than faunal history. Remains of other carnivores, such as the red fox and the pine marten,

are relatively common in the Finnish refuse faunas.

The warm climate and the spread of mixed oak forests into Finland during the middle Holocene were not reflected in the terrestrial mammalian fauna. Southern species, such as the wild boar, the roe deer, and the red deer, which were common in adjacent areas, *e.g.* in Estonia and southern Sweden, did not colonize Finland during the warm period.

Seals immigrated into Finnish waters as soon as the ice sheet retreated, leaving the newly deglaciated area around the Baltic basin submerged. The pioneer species was the ringed seal, which entered the Baltic basin during the Yoldia stage, at the latest. The harp seal, which is no longer a resident species in the area, was part of the Baltic fauna at least from ca. 5,900 BP to 2,800 BP, *i.e.* for 3,000 radiocarbon years.

The thesis uses a deglaciation chronology based on uncalibrated radiocarbon years. A calibrated chronology is, however, briefly discussed and applied to the results at the end of the synopsis.

**Key words:** faunal history, Finland, mammals, mammoths, wild reindeer, seals, northern Baltic Sea

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**Acknowledgements**

**References**

**Papers I–V**

## Original publications

This thesis is based on the following papers, which are referred to in the text with Roman numerals, as well as some additional unpublished data:

- I Ukkonen, P. 1993. The post-glacial history of the Finnish mammalian fauna. *Annales Zoologici Fennici* 30:249–264.
- II Ukkonen, P., Lunkka, J.P., Jungner, H. and Donner, J. 1999. New radiocarbon dates from Finnish mammoths indicating large ice-free areas in Fennoscandia during the Middle Weichselian. *Journal of Quaternary Science* 14:711–714.
- III Lõugas, L., Ukkonen, P. and Jungner, H. Dating the extinction of European mammoths: new evidence from Estonia. *Quaternary Science Reviews*, in press.
- IV Rankama, T. and Ukkonen, P. 2001. On the early history of the wild reindeer (*Rangifer tarandus* L.) in Finland. *Boreas* 30:131–147.
- V Ukkonen, P. 2002. The early history of seals in the northern Baltic. *Annales Zoologici Fennici* 39, in press

## 1. Introduction

### 1.1. At the centre of the glaciation

Finland is situated at the centre of the area covered by the Scandinavian Ice Sheet during the Late Pleistocene, and in the vicinity of large periglacial centres of terrestrial mammals in Europe and Siberia. The history of Finnish mammals provides an excellent opportunity to investigate the shaping of the mammalian fauna in a previously glaciated area. However, the repeated glaciations have generated a landscape consisting of bedrock that is up to 3.2 billion years old and a sediment layer that is less than 20,000 year old. Practically no fossil bearing deposits have survived, which is problematic for research. Mammalian remains have been recovered mainly as stray finds in till or gravel, or in clay deposited on the ancient sea floor of the Baltic basin (Kurtén 1988; I).

Understandably enough, Finland has to date literally been a white spot on maps depicting the history of Pleistocene mammals. Sediments predating the Weichselian glaciation have been discovered in numerous locations throughout the country, mainly in western and northern Finland (Hirvas & Nenonen 1987), but so far, no mammalian bones have been discovered in interglacial or interstadial deposits. Stray finds from the last glaciation, the Weichselian, are more abundant, including remains of the woolly mammoth (*Mammuthus primigenius*), the wild reindeer (*Rangifer tarandus*), and the Arctic fox (*Alopex lagopus*; Kurtén 1988; I). These representatives of the glacial fauna lived in ice-free areas during warmer sub-stages. Their remains were originally picked up by the ice and subsequently redeposited in glacial or glaciofluvial minerogenic sediments.

In the marginal areas of the Scandinavian Ice Sheet — in Estonia, Latvia, Lithuania, northern Poland, Denmark, southern Sweden, coastal Norway, and western Russia — the sedimentological factors and geochemical environment have been relatively favourable for the survival of animal remains of pre-Holocene age. At the centre of the glaciation — in Finland, central Norway, northern Sweden and northwest Russia — even the Early Holocene faunal remains are scarce. The main cause for the scarcity of subfossils is seen in the poor preservation of bones in the acid soil of these areas, formed through the interaction of the acid bedrock, cold climate, high precipitation/evaporation rate, and vegetation dominated by coniferous forests. Only a few subfossil bones of terrestrial mammals have been found in Finland (Kurtén 1988; I). The remains of marine mammals, such as seals and harbour porpoises (*Phocoena phocoena*), which have been embedded in clay or other marine or fresh water sediments, have survived better.

The colonization of Finland by prehistoric people ca. 9,000 BP (Matiskainen 1996) leads, however, to the introduction of another source of palaeontological information: the burnt animal bones from prehistoric dwelling sites and hunting camps, referred to as refuse faunas. Heating made the bones more resistant to biological and chemical decomposition, and they can often be found in vast numbers at archaeological sites. The material recovered is not simple to analyse (I; Ukkonen 1996a), but it can, at its best, be employed in studies of faunal history.

The reconstruction of mammalian fauna in Finland during the last interglacial-glacial cycle, based as it is on the limited subfossil material, cannot be complete. Nevertheless, it might throw light on some important questions. The few pieces of evidence about the earlier fauna give us clues to how mammals colonized areas freed from ice during longer or shorter warm periods, such as the Eemian

interglacial, the ice-free periods within the Weichselian glaciation, and the present warm stage, the Holocene. They can even provide information about how the glaciation itself developed during the Late Pleistocene.

## 1.2. The Weichselian glaciation — key to faunal development

The last interglacial-glacial cycle (Fig.1) with its fluctuating climate and environment is the key to the faunal development in Finland and other areas previously covered by continental ice.

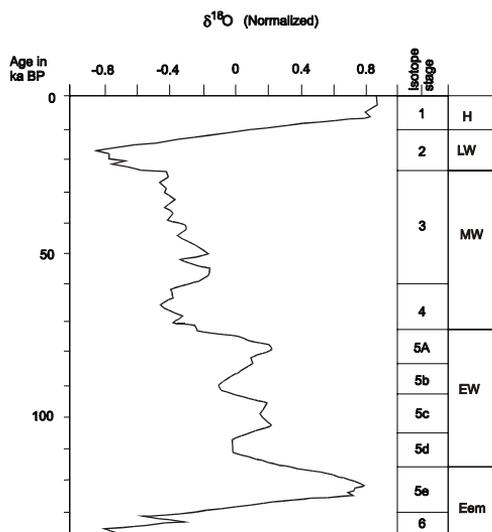


Fig. 1. The last interglacial-glacial cycle. EW = Early Weichselian, MW = Middle Weichselian, LW = Late Weichselian Substages, H = Holocene. Oxygen-isotope stages and curve (a proxy for the global ice volume) modified after Martinson *et al.* (1987).

Finland lies at the centre of the exposed Precambrian crust that forms the Fennoscandian Shield. In the east and south the shield dips under the Palaeozoic sedimentary rocks of the East European Platform. In Finland sedimentary rocks are found only in western Finland around and under the Gulf of Bothnia and in the Åland archipelago. Apart from some tills of Saalean age in Ostrobothnia, and Eemian organic and minerogenic deposits on the Finnish west coast and in Lapland (Donner 1995; Hirvas & Nenonen 1987) the bedrock is covered with glacial and glaciofluvial sediments of Weichselian and Early Holocene age.

A review of the geological and environmental data from Finland concerning the Eemian interglacial that preceded the Weichselian cold stage is given by Donner (1995; Fig. 2). Climatically, the Eemian was warmer than the present interglacial, and in Finland the limit of the temperate forest lay farther north than today. Trees typical of the mixed oak forest, such as *Ulmus*, *Corylus*, *Quercus* and *Carpinus*, were present as far north as Ostrobothnia (Eriksson 1993). In Lapland forests were dominated by *Betula* or *Pinus*, but *Alnus* and *Picea* were also present (see Donner 1995).

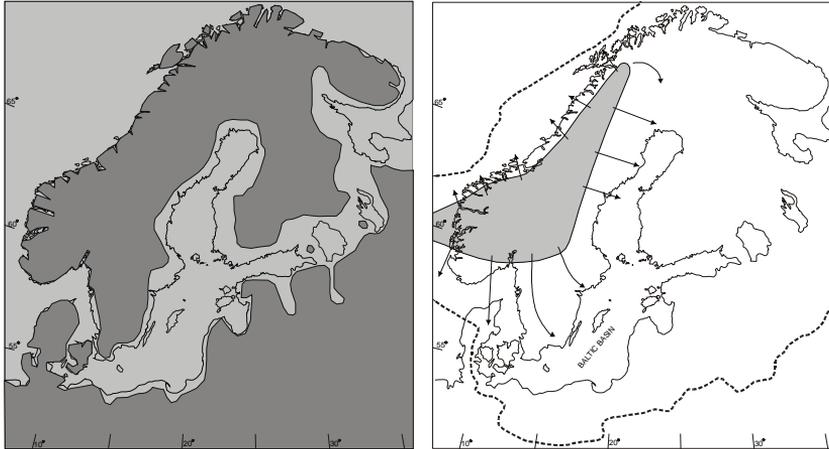


Fig. 2. The Baltic basin during the Eemian interglacial (after Donner 1995).

Fig. 3. The Weichselian glaciation. The dashed line indicates the extent of the Scandinavian Ice Sheet at the last glacial maximum. The centre of the glaciation in the Scandinavian mountains (shaded area; after Kleman *et al.* 1997), as well as the main ice flow directions (arrows) are indicated.

After the warm Eemian stage (*ca.* 115,000 y.a.), Fennoscandia was covered by continental ice. The extent and duration of the Scandinavian Ice Sheet during the Weichselian cold stage (Fig. 3) has recently been the subject of extensive research and discussion. Sites with deposits interpreted as deriving from an Early Weichselian interstadial have been found in northern Ostrobothnia and southern Lapland (see Donner 1995). Southern and western Finland may have been ice-free through the entire Early Weichselian (Lunkka *et al.*, in press). According to reconstructions based on geological observations (Andersen & Mangerud 1989) Finland, Sweden, apart from its southernmost regions, and most of Norway were glaciated during the Middle Weichselian. However, there is evidence of large ice-free areas in Fennoscandia during the Middle and Late Weichselian (II). The advance and retreat history of the Scandinavian Ice Sheet prior to its maximum extent is still poorly known, although several reconstructions of its growth and decay have been presented (Andersen & Mangerud 1989; Bauman *et al.* 1995; Donner 1995; Lunkka *et al.*, in press).

The following account of the final deglaciation of the Scandinavian Ice Sheet uses an uncalibrated radiocarbon chronology (see *e.g.* Eronen 1983; Lundqvist & Saarnisto 1995). A calibrated chronology and its applications to the results of the present research are discussed at the end of the synopsis.

After the glacial maximum *ca.* 18,000 BP the ice began to retreat from the south and southeast towards the Baltic basin and from the west and north towards the Norwegian mountains. The southern parts of Fennoscandia and the Baltic basin were deglaciated already during the Late Weichselian *ca.* 13,000-12,000 BP (Lundqvist & Saarnisto 1995) and large parts of the area were submerged beneath the waters of the Baltic Ice Lake (see Fig. 1 in IV). Dry land existed at this stage on the Norwegian west coast, in northwestern Russia (Svendsen *et al.* 1999; Saarnisto 2000b), and on the Kola Peninsula, where an ice cap had separated from the main ice sheet, leaving the coastal areas and a south-north corridor free of ice at the western edge of the peninsula (Lundqvist & Saarnisto 1995).

The ice retreat was halted for approximately a thousand years during the Younger Dryas (11,000 – 10,000 BP), an episode marked in Finland by the formation of the Salpausselkä end moraines (*e.g.*, Hyvärinen 1973). After the cold period the retreat of the ice was rapid and the present area of Finland was freed from ice in about a thousand years, by *ca.* 9,000 BP. After deglaciation southern and central Finland were inundated, leaving only a scattered archipelago above water. Supra-aquatic areas existed only in the easternmost parts of the country and in Lapland.

The vegetation succession in Finland after deglaciation was rapid. In southeastern Finland the late glacial sediments are characterized by abundant *Artemisia* pollen, but the amount of *Betula* began to rise soon after the commencement of deglaciation. By 9,000 BP the proportion of *Pinus* was already increasing in this area (Hyvärinen 1972), and during the following millennium pine became dominant throughout southern and central Finland.

### *The Baltic Sea*

The retreat of the Scandinavian Ice Sheet led to the formation of the Baltic Ice Lake during the Late Weichselian at *ca.* 12,600 BP (Björck 1995; Eronen 1983; see Fig 1 in IV). Unlike before, during the Eemian warm stage, there was no connection between the Baltic basin and the White Sea. A direct connection with the North Sea and the Atlantic Ocean was opened through Central Sweden around 10,300 BP. This was associated with a drop in the water level of the Baltic basin, and initiated the beginning of the Yoldia stage. The channel was a relatively narrow one, with a short-term saline water flow into the Baltic basin at around 10,000 BP (Björck 1995; Saarnisto *et. al.* 1999). The connection between the Baltic basin and the ocean was severed again at about 9,500 BP, following the glacio-isostatic land uplift, and the Baltic entered the Ancylus Lake stage (Björck 1995; Eronen & Haila 1982). At this stage water still covered the main part of southern and central Finland.

Around 8,200 BP, at the latest, the eustatic rise of ocean levels led to the opening of a new connection with the ocean through the Danish Straits. Fully brackish conditions were not established in the basin until after the so-called Mastogloia stage (see discussion in Hyvärinen 2000), around 7,500 BP (Eronen 1983), when the Baltic entered its Litorina stage. At the beginning of this stage the straits were significantly wider than today and the salinity of the basin was higher, *ca.* 10‰ in the southern, and *ca.* 8‰ in the northern parts of the Gulf of Bothnia, in contrast to the present *ca.* 6‰ and 2‰, respectively (see Segerstråle 1957).

### **1.3. The aims of the study**

In this thesis I present an overview of the mammalian subfossil finds and their interpretation as regards the early mammalian history in Finland (I), and how this picture can be completed by more detailed research on the glacial (II, III), and post-glacial (IV, V) fauna.

The study should be seen in a larger context. It aims to fill an obvious gap in the research of mammalian history in areas previously covered by the Scandinavian Ice Sheet. Extensive reviews already exist from Sweden (Liljegren & Lagerås 1993) and Denmark (Aaris-Sørensen 1988). Nevertheless, the last glacial period is not yet

sufficiently understood, especially in the northern and eastern parts of the area, where both faunal remains and research concerning them has been scarce. The present study is part of an ongoing research project that aims to summarize the existing data concerning the development of the mammalian fauna during and after the last glaciation in the area covered by continental ice during the cold periods. The ultimate goal is not only to describe what the response of the mammalian fauna has been to severe climatic and environmental changes, but also to gain a better understanding of the processes involved in the faunal dynamics (local extinction and re-re-establishment of mammalian populations) on a larger scale. This goal can only be reached through a broad synthesis of existing climatological, geological, botanical, and palaeontological data, and is not yet within reach. The purpose of the present study is to synthesise and critically evaluate the mammalian evidence as a first step towards this ultimate goal.

## **2. Bones from sediments and middens — Material and methods**

The reconstruction of the history of the mammalian fauna in Finland is based on two different kinds of subfossil material: geological finds and refuse faunas. Geological stray finds are found in sediments either *in situ* or redeposited in secondary locations after having been transported for short distances by the ice, icebergs, or rivers. Refuse faunas consist of subfossil bone fragments found in connection with archaeological excavations or surveys of prehistoric dwelling sites, cairns and cemeteries.

The two datasets differ as regards their taphonomy. The subfossil stray finds derive from mammals that died of natural causes at or near the locality where their remains were discovered. The displacement of the carcasses after death is here considered insignificant, if not otherwise stated. The archaeological finds, on the other hand, all derive from animals caught by prehistoric people, and the exact locations where they lived and died cannot be determined. Conclusions concerning the geographic distribution of the species are, however, based on the assumption that the refuse fauna of a dwelling site represents a biased sample of the fauna at or near the site during its occupation. The possibility of longer hunting trips needs, naturally, to be considered, especially in the case of seal bones found at dwelling sites in the inland, far away from the ancient shorelines.

### **2.1. Geological finds**

All geological stray finds reported from Finland are listed in the Appendix. The subfossils included in the present study have been recovered prior to this research project and described by other authors: Finnish mammoths by Holm (1904), Korvenkontio (1915), Malmgren (1874-1875), Metzger (1921), Okko (1949, 1953), Pearson *et al.* (1965), Ramsay (1897, 1900), and Rosberg (1901, 1924); Estonian mammoths by Indreko (1948), Lepiksaar (1937, 1992), Orviku (1933), and Paaver (1957); and seals from the Finnish coast by Forstén & Alhonen (1975, 1977), Korvenkontio (1936), Salmi (1944, 1948, 1949, 1963), and Sauramo (1936). Most of the finds have originally been dated by means of pollen and diatom analyses, shore displacement curves, etc. Of the finds discussed here only one reindeer antler (Siivonen 1975), three mammoth finds (Donner *et al.* 1979), and one beaver (*Castor*

*fiber*) skull (Ukkonen 1997) had been radiocarbon dated prior to this study.

## 2.2. Refuse faunas

The refuse faunas included in the present study represent more than 200 prehistoric sites and comprise *ca.* 25,000 identified mammalian bone fragments (Holocene fauna in general: 109 sites, 8777 bone fragments; the history of the wild reindeer: 61 sites, 6536 fragments; the history of seals: 155 sites, 14061 fragments; I, IV, V). The analyses of most of the archaeological bone assemblages have been carried out as part of the post-excavation routine of rescue excavation projects of the National Board of Antiquities. In addition, two recent interdisciplinary research projects, the *Ancient Lake Saimaa* project (Ukkonen 1996a, 1996b, 1996c), and the *Early in the North* project (Ukkonen 1997, manuscript), have resulted in a substantial body of information concerning the prey species exploited by the early inhabitants of Finland. Both projects were hosted by the University of Helsinki Department of Archaeology, and dealt with the history of human occupation in southeastern and northern Finland, respectively. Since the project *Early in the North* included an extensive dating programme, its results are of great importance especially regarding the history of the wild reindeer in Finland. Bones found at prehistoric sites that have been modified into artefacts have not been included in the study.

The majority of the bone identifications (referred to as osteological analyses) are unpublished and the reports can be found in the archives of the National Board of Antiquities Department of Archaeology in Helsinki. Refuse faunas have mainly been used for studies concerning the economy of prehistoric people (Ailio 1909; Edgren 1982; Forstén 1972, 1977; Forstén & Blomqvist 1977; Hiekkänen 1990; Karjalainen 1996, 1999; Kirkinen 1994, 1996; Kokkonen 1978; Lehtosalo-Hilander 1988; Lindqvist 1988; Matiskainen 1989; Matiskainen & Jussila 1984; Pesonen 1996a, 1996b; Rankama 1996; Rauhala 1977; Schulz 1996; Siiriäinen 1981, 1982; Sohlström 1992; Taavitsainen 1980; Torvinen 1999; Ukkonen 1996a, 1996b, 1996c, 1997, manuscript; Vikkula 1981). Prior to this study osteological analyses have been used in faunal history research by Kurtén (1988) in his overview of the Finnish fossil and subfossil finds, by Forstén & Alhonen (1975, 1977) in their seal studies, and by Forstén & Lahti (1976) in studying the postglacial occurrence of the beaver.

### 2.2.1. Identification

The bone fragments have been analysed morphologically by comparing them with modern vertebrate skeletons using the collection of the Zoological Museum in Helsinki as reference material. The osteological analyses have been carried out over the years by the author and several other osteologists (see App. in I, IV, V). The results of the osteological analyses are presented as lists containing the identified skeletal parts, their number and the species concerned. The analyses made by the individual osteologists are, in my opinion, relatively comparable. There are, of course, individual differences in the practices of analysis, mainly affecting the quantitative data.

Different seal species are difficult to distinguish from each other even when complete bones are available. A specific analysis of the archaeological bone material was carried out, in order to establish the feasibility of reliable species identification even of burnt and fragmented seal bones (V).

### 2.2.2. General problems associated with refuse faunas

There are some basic problems associated with the investigation of prehistoric sites in Finland. The most critical ones are the dating of the sites and the taphonomy, preservation, fragmentation and identification of the bones. These set special requirements on the interpretation of the results.

The most serious problem is the dating of the prehistoric sites. In coastal areas the settlement was typically of relatively short duration because of the retreating shoreline, but in the interior sites were often occupied repeatedly for longer or shorter periods. As a result of this the archaeological material is mixed, which makes it difficult to distinguish the different settlement stages and the bone remains associated with them.

Refuse faunas are produced by human activity. Hence, the finds do not represent the complete local fauna but merely the species hunted or consumed by man. This has to be borne in mind when interpreting the finds as evidence of faunal history or zoogeography. For instance, the absence of small mammals — bats, shrews, voles and mice — is readily understandable, but the absence of certain large carnivores, such as the wolf (*Canis lupus*), the Arctic fox, the wolverine (*Gulo gulo*) and the lynx (*Lynx lynx*), is more complicated to interpret.

Furthermore, the refuse faunas are not even fully representative of the prey originally taken by man. Hunting and butchering methods, tool making, the displacement of bones by scavengers, non-uniform preservation of bones of different species and of different skeletal parts — all of these factors change the anatomical and species composition of the material. Differences in excavation methods and finally problems relating to the osteological analysis itself result in data both qualitatively and quantitatively different from the original prey assemblage.

The preservation of bones is poor in the acid soil typical for most of Finland. Heating — cooking or burning — seems to improve their preservation considerably. The refuse faunas from the Finnish Stone Age dwelling sites consist almost exclusively of burnt bones. In the soil, different parts of the skeleton and bones of different species do not have equal resistance to decomposition. Small, compact bones of the distal parts of the limbs of mammals are far more resistant than thin or spongy bones, such as shoulder blades or vertebrae.

Shrinking and deformation caused by heating makes the identification of the bones difficult, but a far more serious problem arises from their fragmentation — the pieces seldom exceed 1 cm<sup>3</sup>. Due to the fragmentation, only a small portion of the excavated pieces can be identified. The identification quota varies for different parts of the skeleton and for different species and species groups. Carpal and tarsal bones of mammals, as well as the articular epiphyses of long bones, are the parts of the skeleton easiest to identify because of their characteristic shapes.

Species such as the red squirrel (*Sciurus vulgaris*), the beaver, and the Arctic hare (*Lepus timidus*) leave characteristic fragments that can be identified unequivocally. The bones of some species groups, such as canids, mustelids, and seals, have also very characteristic shapes, but their determination to the species

level is difficult. Larger species such as the European elk and the wild reindeer leave a large number of indeterminable fragments of the long bones, but only a few fragments with diagnostic features. This has an effect not only on the quantitative, but also on the qualitative results of the analysis.

Because of the problems connected with the taphonomy, preservation and identification of bones, both the species composition and their quantitative proportions in the data do not directly represent the original fauna. If a species is present in the refuse fauna of a site, it most probably was present in the surroundings of this site at its time of occupation. The absence of a species from the assemblage is, however, no proof of its absence from the local fauna or even from the list of species hunted by man.

### **2.3. Radiocarbon dating**

The present research project included an extensive dating programme of geological stray finds including Finnish and Estonian mammoths, seals found at the Finnish coast, and some reindeer antlers. The mammoth and seal bones were radiocarbon dated using the AMS technique, the reindeer antlers using the conventional technique. Isotope analyses ( $\delta^{13}\text{C}$ ) were made of all dated samples, and additionally of some seal bones. The Dating Laboratory of the University of Helsinki carried out all radiocarbon (AMS and conventional) and isotope analyses but one. One mammoth molar was dated at the Uppsala University.

The radiocarbon method cannot be used to date burnt bone fragments from prehistoric dwelling sites, since burning eliminates all collagen in the bones. A new method using the structural carbonate in the mineral fraction of the bone has been developed (Lanting *et al.* 2001), but this has not yet been applied to the Finnish material. Indirect methods have therefore been used for instance in dating archaeological reindeer and seal finds. The radiocarbon dates presented (BP; uncalibrated) derive from organic samples that can be reliably connected with the bone finds. Apart from radiocarbon dates, sites are dated using archaeological methods on the basis of artefact typology and shore displacement.

## **3. Results**

### **3.1. Pre-Holocene fauna**

Altogether 15 Finnish and Estonian (II, III) mammoth finds were dated (Table 1). The dates can be divided into three groups: 1) infinite ages (>37,000 BP), 2) ages older, and 3) ages younger than the Weichselian maximum (18,000 BP). Most of the Estonian mammoth finds and one Finnish one belong to the first group. The majority of the Finnish dates and one Estonian one form a continuous series from *ca.* 32,000 BP to *ca.* 22,000 BP and belong to the second group. Two Estonian finds and one Finnish one are younger than the last glacial maximum. The discussion about other pre-Holocene finds is based on literature.

Table 1. Mammoth remains from Finland and Estonia. Localities, stratigraphy, and AMS dates obtained in connection with the present research. All Finnish specimens are stored in the Finnish Museum of Natural History in Helsinki, except for the molar from Iijoki (Swedish Museum of Natural History, Stockholm), and the unlocated finds (modified after II and III).

Locality	Sediment	Dated Material	Date BP	Lab. nr.
<i>Infinite ages</i>				
Espoo, F <sup>1</sup>	Till	Molar	>43,000*	Hel-1076
Ihasalu, E <sup>2</sup>		Molar	>41,000	Hela-426
Tudulinna, E <sup>2</sup>	Gravel	Tusk	>40,000	Hela-419
Kunda, E <sup>3,4,5</sup>	Gravel	Tusk	>38,000	Hela-424
Kallaste, E <sup>5,6</sup>	Gravel	Molar	>38,000	Hela-421
Tahkumägi, E <sup>2</sup>		Bone	>38,000	Hela-422
Heimtäli, E <sup>2</sup>	Gravel	Tusk	>37,000	Hela-420
<i>Glacial ages older than the Weichselian maximum</i>				
Iijoki, F <sup>7,8</sup>	Sand	Molar	31,970±950	Ua-14190
Mooste, E <sup>2</sup>	Gravel	Molar	30,640±830	Hela-418
Haapajärvi, F <sup>9</sup>	Glaciofluvial sand and gravel	Tusk	28,740±670	Hela-294
Lohtaja, F <sup>10</sup>	Clay	Femur	24,450±385	Hela-295
Helsinki, Töölo, F <sup>8</sup>	Till	Premolar	23,340±350	Hela-282
Nilsia, Syväri, F <sup>8,11,12</sup>	Glacigenic gravel/till	Molar	22,420±315	Hela-281
<i>Glacial ages younger than the Weichselian maximum</i>				
Helsinki, Herttoniemi, F <sup>13</sup>	Holocene littoral clay/sand	Humerus	15,910±155	Hela-321
Puurmani, E <sup>5,6</sup>		Molar	10,200±100	Hela-425
Puurmani, E <sup>5,6</sup>		Molar	10,100±100	Hela-423
<i>Not dated</i>				
Tuulos, F <sup>14</sup>	Glaciofluvial	Humerus	(not relocated)	
Pohja, Brödorp, F <sup>15,16</sup>	Till	Costa	(not relocated)	
Kallaste, E <sup>4,5,17</sup>	Gravel	Tusk	soluble	

Original publications of the finds:

<sup>1</sup>Metzger 1921; <sup>2</sup>III; <sup>3</sup>Indreko 1948; <sup>4</sup>Lepiksaar 1937; <sup>5</sup>Lepiksaar 1992; <sup>6</sup>Paaver 1957; <sup>7</sup>Holm 1904; <sup>8</sup>Korvenkontio 1915; <sup>9</sup>Okko 1953; <sup>10</sup>Okko 1949; <sup>11</sup>Malmgren 1874-1875; <sup>12</sup>Ramsay 1900; <sup>13</sup>Pearson *et al.* 1965; <sup>14</sup>Rosberg 1924; <sup>15</sup>Ramsay 1897; <sup>16</sup>Rosberg 1901; <sup>17</sup>Orviku 1933.

\*conventional dating (Donner *et al.* 1979).

### 3.2. Holocene terrestrial fauna

The history of the post-glacial terrestrial fauna in Finland (I) is summarized in Table 2, which is based on refuse faunas from archaeological sites. The first colonizers appear to be species associated with young deciduous forests, such as the beaver, the Arctic hare, the European elk, and the red fox (*Vulpes vulpes*). These were followed by species associated with coniferous forests, such as the brown bear (*Ursus arctos*), the red squirrel, and the pine marten (*Martes martes*). Southern species, associated with mixed oak forests, such as the wild boar (*Sus scrofa*) and the roe deer (*Capreolus capreolus*) have been reported from Stone Age dwelling sites, but the identification of the fragments is equivocal.

Table 2. Terrestrial mammal finds from Stone Age cultural sites in Finland. I = 9,000-8,000 BP, II = 8,000-7,000 BP, III = 7,000-6,000 BP, IV = 6,000-5,000 BP, V = 5,000-4,000 BP, VI = 4,000-3,000 BP.

	I	II	III	IV	V	VI
<i>Canis familiaris</i> (dog)	X		X	X	X	
<i>Vulpes vulpes</i> (red fox)	X		X	X		
<i>Ursus arctos</i> (brown bear)		X	X	X		
<i>Lutra lutra</i> (otter)			X			
<i>Martes martes</i> (pine marten)			X	X		X
<i>Sus scrofa</i> (wild boar)*			?		?	
<i>Alces alces</i> (European elk)	X	X	X	X	X	
<i>Capreolus capreolus</i> (roe deer)*	X					
<i>Rangifer tarandus</i> (wild reindeer)		X	X	X	X	
<i>Sciurus vulgaris</i> (red squirrel)			X	X	X	
<i>Castor fiber</i> (beaver)	X	X	X	X	X	X
<i>Lepus timidus</i> (Arctic hare)	X		X	X	X	X

\* questionable identification

Special attention was paid to the history of the wild reindeer in Finland. The species is not among the earliest finds from archaeological contexts (I), at least not in the southern parts of the country (IV). All prehistoric locations that have yielded reindeer bone are shown in Fig. 4. The earliest indirect radiocarbon dates are included.

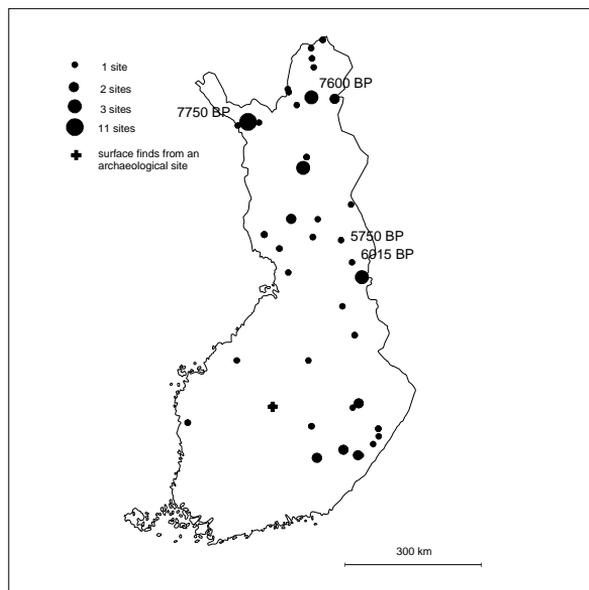


Fig. 4. The prehistoric occupation sites in Finland that have yielded reindeer bone. The earliest indirect radiocarbon dates are indicated.

### 3.3. Marine mammals

Subfossil remains of marine mammals found on the Finnish coast are listed in Table 3. Ten seal finds (V) were radiocarbon dated in connection with this study. Isotope analyses were made from all dated, and nine undated samples. The AMS-dates correspond fairly well with those previously estimated on the basis of the geological evidence from the locality, including pollen and diatom analyses of the sediment. The earliest date (9,505 BP) derives from a ringed seal (*Phoca hispida*). The harp seal (*Phoca groenlandica*) finds are relatively numerous, and the dates fall into the time interval between *ca.* 5,900 BP and 2,800 BP. Only one isolated find of the grey seal (*Halichoerus grypus*) has been reported so far from the Finnish coast.

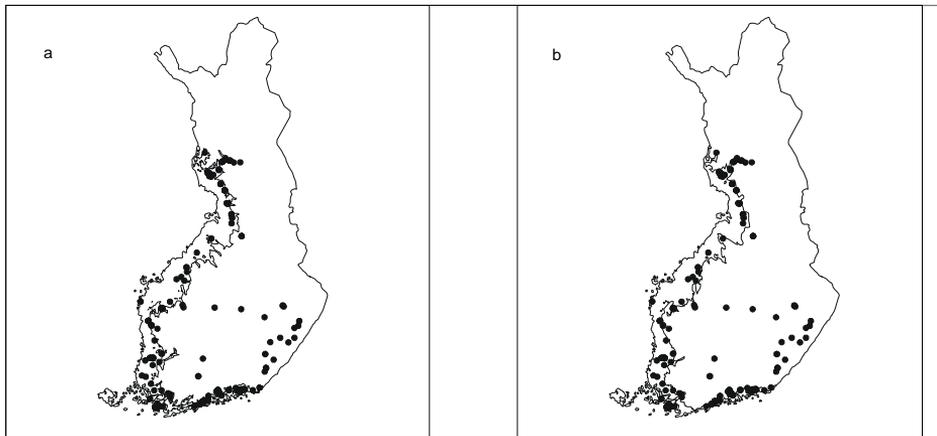


Fig. 5. The prehistoric sites in Finland with refuse faunas including seal bones. The coastlines: a) 7,500 BP, b) 6,500 BP are based on Eronen *et al.* (1995).

The prehistoric dwelling sites containing seal bones (V) concentrate at and below the 7,500 BP and 6,500 BP coastlines (Fig. 5). Several sites are also located in the inland, mainly in the area of the ancient Päijänne-Saimaa lake system.

Table 3. Subfossil stray finds of marine mammals found along the Finnish coast, the AMS dates and isotope values obtained in connection with the present research. NM = National Museum of Finland in Helsinki, ZM = Zoological Museum of the Finnish Museum of Natural History, University of Helsinki, GM = Geological Museum of the Finnish Museum of Natural History, University of Helsinki, Laihia = secondary school in Laihia, NOM = The Northern Ostrobothnia Museum in Oulu, SM = Satakunta Museum in Pori.

Locality	Museum	Assumed date	Date BP (AMS)	Lab.nr.	$\delta^{13}\text{C}$ PDB
<i>Phoca groenlandica</i>					
Närpiö <sup>1,2</sup>	NM 10087:2	Litorina	5890±70	Hela-441	-16.85
Espoo or Kirkkonummi <sup>3</sup>	ZM 6952	Litorina	5290±175	Hela-433	-16.41
Alatornio, Liekajoki <sup>3</sup>	ZM 6951	Litorina	4810±70	Hela-432	-16.26
Vaasa, Roparnäs <sup>4</sup>	ZM 6971	Litorina	2995±70	Hela-438	-16.90
Pietarsaari, Sundby <sup>5</sup>	ZM 6970	subboreal	2800±65	Hela-437	-16.50
Närpiö, Pjelax <sup>5</sup>	ZM 6966	subboreal	-	-	-15.87
Laihia, Ruto <sup>6</sup>	ZM 6973	Late Litorina	-	-	-16.75
Laihia, Potila <sup>5</sup>	Laihia	subboreal	-	-	-
Pori, Tuorsniemi <sup>4</sup>		Litorina	-	-	-
<i>Phoca hispida</i>					
Nurmo, It. Kimpimäki <sup>4</sup>	ZM 6978	Ancylus	9505±85	Hela-440	-19.77
Ylistaro, Rintamattila <sup>4</sup>	ZM 6972	Ancylus	8495±80	Hela-439	-19.72
Kovjoki (Uusikaarlepyy) <sup>4</sup>	ZM 6974	Yoldia/Ancylus	8270±80	Hela-434	-19.12
Ähtävä, Ylähtävä <sup>4</sup>	ZM 6945	Ancylus	8195±135	Hela-435	-19.25
Ilmajoki Palonkylä <sup>4</sup>	ZM 6968	Ancylus	-	-	-19.65
Lapua, Tiistejoki <sup>3</sup>	ZM 6953	Ancylus	-	-	-19.85
Ruukki <sup>6</sup>	ZM 6977	Ancylus	-	-	-18.39
Muhos, Honkalankylä <sup>4</sup>	ZM 6965	Litorina	5115±75	Hela-436	-15.93
Ylistaro, Kaukolankylä <sup>7</sup>	ZM 6976	Litorina	-	-	-16.57
Oulainen, Tiitjärvi <sup>3</sup>	ZM 6957	Litorina	-	-	-19.79
Oulujoki <sup>1,2</sup>	ZM 6980	Litorina	-	-	-18.36
Vähäkylä, Rekilänkylä <sup>8</sup>	ZM 6963	Litorina	-	-	-18.00
Kuivaniemi, Vakkurink. <sup>4</sup>	NOM	-	-	-	-
Ulvila, Harjunpää <sup>4</sup>	SM 16.400	Late Litorina	-	-	-
<i>Halichoerus grypus</i>					
Teuva <sup>9</sup>	ZM 6942	Early Litorina	-	-	-
<i>Phocoena phocoena</i>					
Tenhola <sup>10</sup>	GM	Litorina	-	-	-
Närpiö <sup>7</sup>	ZM	Late Litorina	-	-	-
Pori <sup>11</sup>	NM	Litorina	-	-	-

<sup>1</sup>Korvenkontio 1936; <sup>2</sup>Sauramo 1936; <sup>3</sup>Forstén & Alhonen 1977; <sup>4</sup>Forstén & Alhonen 1975; <sup>5</sup>Salmi 1963; <sup>6</sup>Salmi 1944; <sup>7</sup>Salmi 1949; <sup>8</sup>Salmi 1948; <sup>9</sup>Forstén 1979; <sup>10</sup>Metzger 1921; <sup>11</sup>Forstén 1975.

#### 4. Mammalian life during the Late Pleistocene and Early Holocene — Discussion

Each interglacial, including the Eemian and the present one, has had its own character as pertains to the development of the flora and fauna, although the warm periods show some general characteristics in common. Environmental changes derived from fluctuation of the temperature as well as the succession of the vegetation, shape the plant and animal life present in an area affected by continental ice. The species react to these changes independently, not as faunal complexes. The composition of the mammalian fauna in a specific area during each warm period is a result of several variables: the climate, the post-glacial shaping of the topography, immigration routes and barriers thereof, the evolution of the species and their adaptation to new conditions, and the distance from their glacial habitats beyond the ice border, to mention some of the most important factors.

The advance of the continental ice results eventually in the total depletion of plants and animals in the affected area. When the climate changes unfavourably, plants and animals retreat to more favourable environments, or, if the changes are very rapid, go locally extinct. This applies both to the interglacial flora and fauna when the temperatures fall, and to the glacial flora and fauna when the temperature regime rises.

#### 4.1. The Eemian interglacial

In Finland, no certain pre-Weichselian mammal remains have been reported. Aalto *et al.* (1989) report *ca.* 107,000 years old tree remains from Vimpeli and interpret them as an ancient beaver dam deposit. This is the only indirect evidence of the presence of mammals in Finland during the Eemian interglacial. The Eemian deposits found in different parts of the country (Donner 1995; Eriksson 1993; Grönlund 1991; Hirvas 1991) have not yet been studied thoroughly, and the recovery of mammalian bones in these sediments underlying till and gravel is still possible, even if the possibility seems remote. Recently, a cave filled with sediments of presumable Eemian age (field reports, National Board of Antiquities) was discovered in Karijoki on the Finnish west coast. No pre-Holocene bone remains have been recovered so far in this cave, called Susiluola (Ukkonen, unpubl.), but plans have been made to survey and excavate other similar caves with sediment fillings.

In Denmark, several fossil bearing deposits of Eemian age have been discovered and studied. The deposits contain *in situ* remains of the fallow deer (*Dama dama*), the red deer (*Cervus elaphus*), the steppe bison (*Bison priscus*), and the straight-tusked elephant (*Palaeoloxodon antiquus*; Aaris-Sørensen *et al.* 1990). Remains redeposited by the Weichselian ice include bones of the giant deer (*Megaloceros giganteus*) and the Merck's rhinoceros (*Dicerorhinus kirchbergensis*). A single bone of the harbour porpoise has been reported from Eemian marine deposits. The beaver has also apparently been part of the Danish Eemian fauna, since gnawed branches and stems have been found in freshwater deposits (Aaris-Sørensen *et al.* 1990).

In Sweden no Eemian deposits with vertebrate remains have been found so far (Liljegren & Lagerås 1993). In Norway, bones of seals, probably deriving from the harbour seal *Phoca vitulina* (Hufthammer 2001) have been found in Eemian or Early Weichselian deposits near Bergen.

The climate and vegetation prevailing during the Eemian interglacial would have offered favourable conditions for mammalian immigration into Fennoscandia. During at least part of the interglacial stage northern Fennoscandia was a large island separated from the European mainland (incl. Denmark) by the Eemian Sea, which was connected both with the Barents Sea and the Atlantic Ocean (Donner 1995). Liljegren and Lagerås (1993) have proposed that this limited the immigration of terrestrial mammals into the area. Mammals are, however, very successful in overcoming barriers, including larger bodies of water, which is demonstrated by the fact that at least the beaver appears to have spread into Finland during this period (Aalto *et al.* 1989; I).

## 4.2. Mammalian fauna during the Weichselian glaciation

### *The glacial fauna*

Mammalian remains of glacial age have been found in the entire area at intervals covered by the Scandinavian Ice Sheet during the Weichselian. The richest faunas derive from areas near the edge of the continental ice in Denmark, southern Sweden and coastal Norway. In the central, eastern and southeastern parts of the area — Finland, the Norwegian mountains, western Russia, Estonia, Latvia and Lithuania — the finds are scarce.

The advance and retreat history of the eastern sector of the Scandinavian Ice Sheet is not yet as well understood as that of its western edge (Mangerud 1991). Fennoscandia appears to have been ice-free for shorter or longer periods during the Weichselian Cold Stage. Between the cold periods, flora and fauna colonized the previously glaciated areas fairly rapidly (Aaris-Sørensen 1992).

### *Mammoths*

Mammoth remains (II) are relatively common in the entire area covered by the Scandinavian Ice Sheet during the cold stages. In Denmark, a total of 125 mammoth finds have been reported (Aaris-Sørensen *et al.* 1990), while the number in Norway is 19 (Bergersen 1991; Heintz *et al.* 1979), and in Sweden 30 (Liljegren & Ekström 1996).

In Finland remains of the woolly mammoth have been discovered at nine localities (Donner 1965), and 27 finds are reported from Estonia. Prior to the present study (II, III), only three Finnish and one Estonian mammoth h subfossil had been radiocarbon dated (Donner *et al.* 1979; Liiva *et al.* 1966). One of the Finnish samples had given an infinite age, and the two other samples strikingly young ages (*ca.* 15,500 BP and 25,200 BP; Donner *et al.* 1979). The latter dates puzzled geologists and palaeontologists since such young ages were not in accordance with the accepted view of the glacial history in Fennoscandia (see Lunkka *et al.*, in press). The Estonian find, a tusk fragment from a Mesolithic settlement site in Kunda, was originally dated at *ca.* 9,780 (Liiva *et al.* 1966).

Lepiksaar (1992) divided the megafaunal finds from the area around the Baltic basin in three age groups: 1) Eemian or Early Weichselian (very rare), 2) Weichselian interstadials, and 3) Late Weichselian. These can be employed when looking at the mammoth finds dated in connection with this study and earlier.

The majority of the dated Estonian mammoth finds (III), as well as the molar from Espoo in Finland (Donner *et al.* 1979; II), belong to the first age group. They probably date back to the Early Weichselian, but may be even older. Nearly all other Finnish finds and the molar from Mooste in Estonia belong to the second group. These are clearly interstadial in age (II, III). Several other Scandinavian mammoth finds have yielded similar dates (Aaris-Sørensen *et al.* 1990; Berglund *et al.* 1976; Heintz *et al.* 1979). Apart from the mammoths, one subfossil of another typical member of the glacial mammalian fauna, the wild reindeer, has been dated to this time period: an antler found in Tornio in northern Finland gave an age of *ca.* 34,300 BP (Siivonen 1975), indicating the presence of the species in Finland during the Late Middle-Weichselian interstadial.

The dates of the Finnish mammoth finds strongly suggest that Finland was ice-free for a relatively long period during the Middle and Late Weichselian (II), and that species belonging to the glacial fauna spread into the area. The same applies to other parts of Fennoscandia where Pleistocene mammals of similar age range have been discovered.

#### *Late mammoth populations*

The age of the mammoth humerus found in Herttoniemi in Helsinki (15,910 BP), is still an enigma. Unlike most of the mammoth remains in Finland this bone fragment was found between sand and clay, *i.e.*, embedded in marine sediments. The subfossils found in till have originally been picked up by the Scandinavian Ice Sheet and transported by the ice like erratics for a short distance (probably less than ten kilometres; *cf. e.g.* Perttunen 1977; Salonen 1986) as the Ice Sheet advanced southeastwards across Finland. Eventually the bone material has been deposited together with glacial sediments during the deglaciation. The Herttoniemi find must have a different kind of transport history and originate from outside Finland. One possibility is that the mammoth in question belonged to a population living in western Russia outside the ice border. Its remains could have been transported with icebergs into the Baltic basin and finally redeposited on the sea floor.

In Fennoscandia, as well as in Britain (Coope & Lister 1987), some mammoth finds have been dated at 13,000-12,000 BP, but no dates younger than 12,000 BP have been obtained. This has led Stuart (1991) to conclude that the woolly mammoth was extinct in Europe by 12,000 BP. The molars found in Puurmani, Estonia and dated at 10,200 BP (III) represent, however, a mammoth population living in northeastern Europe after the onset of the retreat of the Scandinavian Ice Sheet. The relatively young ages (*ca.* 13,000 BP) of mammoth remains from southern Sweden (Liljegren & Ekström 1996) and Denmark (Aaris-Sørensen *et al.* 1990) suggest that mammoths re-colonized recently deglaciated areas after the last glacial maximum. Here, the mammoth followed the retreating ice front very closely (Aaris-Sørensen 1992). This seems also to be the case farther north, *i.e.* in Estonia.

In northern Siberia, on Wrangel Island, mammoths survived far into the postglacial period (Vartanyan *et al.* 1993; Vasil'chuk *et al.* 1997). In western Russia, in Cherepovetz near the Rybinsk reservoir, a nearly complete mammoth skeleton found in gytja in 1942 was recently dated at *ca.* 10,000 BP (III). The area lies *ca.* 600 km east of Puurmani, where the two late/post-glacial mammoth molars were found.

On the basis of these finds it can be concluded — in contrast to some earlier views — that mammoths survived until or almost to the Pleistocene/Holocene boundary in Europe, at least in the northeastern parts of the area.

#### *Further glacial species*

In Denmark (Aaris-Sørensen *et al.* 1990) the Middle Weichselian terrestrial fauna includes, in addition to the woolly mammoth, also the giant deer, the wild reindeer, the saiga antelope (*Saiga tatarica*), the musk ox (*Ovibos moschatus*), the steppe bison, and the woolly rhinoceros (*Coelodonta antiquitatis*). From the Late

Weichselian Aaris-Sørensen (1988) reports finds of the giant deer, the wild reindeer, the elk, the wolf, the brown bear, the wolverine, the beaver and the Arctic hare, as well as some smaller mammals. At the very end of the period also the European bison (*Bison bonasus*), the aurochs (*Bos primigenius*) and the wild horse (*Equus ferus*) were parts of the Danish fauna.

Late Weichselian remains of the giant deer, the wild reindeer and the elk have also been reported from southern Sweden (Liljegren & Lagerås 1993; Liljegren & Ekström 1996) during the deglaciation period. The Swedish late glacial fauna includes also the polar bear (*Ursus maritimus*), the Arctic fox (Ronnie Liljegren, pers. comm.), the wild horse and the Arctic hare.

The Early and Middle Weichselian interstadial fauna of Norway (Hufthammer 2001) includes the polar bear, the wolf, the Arctic fox, the red fox, the otter (*Lutra lutra*), the wild reindeer, and the musk ox, as well as the ringed seal, the harp seal, the bearded seal (*Erignathus barbatus*), and some whales. The mammalian fauna recovered from the Late Weichselian, the deglaciation phase, resembles an arctic fauna, and includes bones of the wild reindeer, the ringed seal and the harp seal. The bird fauna, however, has a more boreal character (Hufthammer 2001). The youngest glacial find from Norway is an almost complete skeleton of a polar bear, dated at *ca.* 10,600 BP.

Lepiksaar (1992) has reported remains of the steppe bison and the woolly rhinoceros from Estonia and remains of the latter species from Latvia.

In Finland the only glacial mammal species recovered so far, apart from the woolly mammoth, are the interstadial wild reindeer (Siivonen 1975), and the Arctic fox, dated to the Younger Dryas (Kurtén 1966).

### *From glacial to post-glacial*

Towards the end of the glacial period several species of the European glacial fauna, such as the woolly mammoth, the giant deer, and the woolly rhinoceros, went globally extinct (Stuart 1991). In addition to that, species associated with arctic environments, such as the wild reindeer, the musk ox and the Arctic fox disappeared from southern Fennoscandia. Local extinctions are indicated also farther north, in Finland.

The skull fragment of an Arctic fox found in Tenhola in southwestern Finland (Kurtén 1966) has not been radiocarbon dated, but the pollen analysis of the sediment preserved in the skull cavities places the find in the Younger Dryas. The site lies between the Salpausselkä I and II end moraines, which would agree well with the suggested age (Kurtén 1966). The presence of this arctic species in the recently deglaciated archipelago near the border of the ice sheet suggests a southern immigration route for the early arctic fauna (I). In the light of the deglaciation history of the area (see Fig. 1 in IV) it is, however, questionable, whether arctic species, such as the Arctic fox and the wild reindeer, had any opportunity to immigrate farther north using this route before the climate became warmer and forests spread into the area (IV). More likely, these species experienced a local extinction at the beginning of the Holocene and the area was then colonized by boreal species, as indicated by the early post-glacial finds (I, IV).

### 4.3. Re-establishment of the mammalian fauna after the glaciation

Along with the deglaciation and the development of the vegetation suitable immigration routes were opened for the terrestrial fauna. Mammals were able to enter southern and central Finland either directly from the east or from the south through the Karelian Isthmus. Farther north two corridors existed already at an early stage of the deglaciation: one from the arctic northwestern Russia along the northern coast of the Kola Peninsula, a second one from Karelia along the eastern ice border. Apart from these eastern routes, it was possible for the mammals to migrate from central Europe through Denmark to southern Sweden, and — after the deglaciation — further north, or from the so-called North Sea Continent across to Norway and along the Norwegian west coast to the shores of the Barents Sea (Fig. 6).

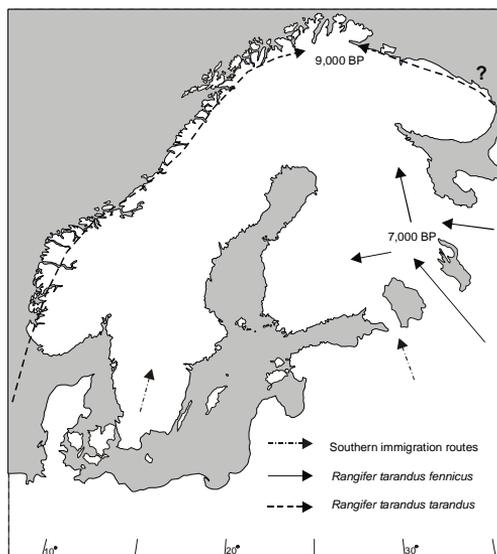


Fig. 6. Proposed immigration routes for the two subspecies (ecotypes) of the wild reindeer. The main part of the Finnish mammalian fauna probably used the eastern route. Possible southern immigration routes are indicated

A review of the Holocene history of the mammalian fauna in Fennoscandia and the Baltic countries has been presented by Lepiksaar (1986). More local data can be found in Aaris-Sørensen (1988), Daugnora & Girininkas (1995), Liljegren & Lagerås (1993), Lõugas (1997a), Paaver (1965), and Zagorska (2000). The following review concentrates on the Holocene history of the Finnish mammalian fauna.

#### 4.3.1. Terrestrial mammals – rapid development into a boreal fauna

As indicated above, the early postglacial terrestrial fauna in Finland reflects the rapid spread of birch and, later, coniferous forest into the area after the onset of the main deglaciation period. The earliest evidence of terrestrial fauna derives from Mesolithic dwelling sites in Lahti and Askola in southern Finland, and Hyrynsalmi

in northeastern Finland, all occupied *ca.* 9,000 BP (see Matiskainen 1996) and includes bones of the European elk, the beaver, the Arctic hare, and in Hyrynsalmi also the domestic dog (*Canis familiaris*) (I, IV; Matiskainen 1989). Later, the fauna was replenished by species associated with coniferous forests, such as the brown bear, the red squirrel, and the pine marten (I). It is evident that the species composition developed rapidly into that of the modern boreal fauna.

The evidence from the early settlement sites clearly contradicts the theory of early reindeer hunters — *i.e.*, that the first people who came to Finland after the retreat of the Weichselian Ice Sheet followed periglacial reindeer herds migrating from the south to the north as the glaciers melted (*e.g.* Huurre 1979). According to this theory, these herds entered the area from the southeast and retreated to the north as the postglacial climate became warmer and the environment in southern Finland became unsuitable for the species (Pulliainen & Leinonen 1990). The early Mesolithic refuse faunas of southern and central Finland do not suggest a tundra environment and fauna. Instead, they suggest that the first human settlers arriving in the area encountered a boreal forest environment and were already adapted to forest hunting.

Apart from the archaeological bone finds, only a few terrestrial subfossils of early and middle Holocene age have been encountered in Finland. These consist of some bones of a badger (*Meles meles*), dated on the basis of geological and pollen evidence at approximately 8,000-4,000 BP (Alhonen *et al.* 1987), the skeleton of an Arctic hare dated at the Ancylus Lake stage of the Baltic basin (Salmi 1948), and a beaver skull (Anonymous 1951), previously assumed to date back to the Litorina stage 6,000 – 7,000 years BP (Forstén & Lahti 1976), but later found to be much younger (2,670 BP; Ukkonen 1997).

### *Immigration routes*

The early history of the wild reindeer in Finland demonstrates the immigration routes of the mammalian fauna in general.

It has been previously proposed that the main route after the deglaciation would have been from the south through the Karelian Isthmus (I; Siivonen 1975). However, this is hardly the case for arctic species or species that we share with the eastern taiga. Immediately after the deglaciation a direct route existed from Siberia through eastern Karelia into the supra-aquatic areas in eastern and northern Finland. Southern and central Finland was inundated by the Baltic waters, leaving only a scattered archipelago above water. For the forest reindeer, and probably for a great part of the present mammalian fauna in Finland, this eastern immigration route is the most probable one when colonizing Finland (IV).

Another theory quoted in the literature relies on the proposed existence of ice-free areas in northern Norway during the last glacial maximum. According to this theory some plants and animals — including the wild reindeer — survived the last glaciation or its latest part there and colonized the northern parts of Fennoscandia from these refuges (Siivonen 1982). This theory is not supported by recent geological research, which indicates that during the glacial maximum the Scandinavian Ice Sheet terminated at the margin of the continental shelf off the Norwegian coast (Lundqvist & Saarnisto 1995; Mangerud 1991). This leaves no ice-free areas on the coast, and the few nunataks that probably existed were too small to support populations of at least larger mammals, such as reindeer (but see Fedorov &

Stenseth 2001).

The Norwegian coast may, nevertheless, be of importance to the colonization history of the wild reindeer and other arctic species in northern Fennoscandia. According to Hakala (1997) reindeer could have immigrated into southwestern Norway directly from the so-called North Sea Continent during the Late Glacial period and migrated northwards along the narrow coastal strip. There were ice-free areas on the west and north Norwegian coasts as early as 13,000 BP (see Hyvärinen 1997), and after a rapid postglacial immigration of plant cover (Birks *et al.* 1994) these were quite suitable environments even for larger mammals such as the reindeer (*cf.* Selsing 1986). Reindeer bone has been recovered for instance at Blomvåg on Blomøy island near Bergen (Lie 1986, 1990) in a fossil-bearing sediment dated to 12,700–12,200 BP (Mangerud 1977).

The arctic ecotype of the wild reindeer, the mountain reindeer, was present in northern Norway *c.* 11,500 BP (Hakala 1997) and, according to archaeological finds, in northernmost Finland at 7,750 BP at the latest — probably a thousand years earlier (IV).

The possibility of a contemporaneous expansion of the species into northern Finland from the east is not completely excluded by Hakala (1997). The glaciation history north and east of the White Sea indicates a potential immigration route along the northern coast of Russia to the Kola Peninsula and onwards to northern Norway (Saarnisto 2000b; Svendsen *et al.* 1999). The absence of subfossil reindeer remains *en route* (see Markova *et al.* 1995), however, makes this route for the moment impossible to verify. Another route along the south coast of the White Sea seems improbable in the light of the Late Glacial development of the hydrology.

The suggested northern immigration routes for the wild reindeer (Fig. 6) may be relevant also for other arctic species, for example the Arctic fox. The main colonization of Finland by mammals, however, probably took place from the east. The southern immigration routes *via* the Karelian Isthmus and central Sweden may have played a role, albeit a minor one, as seen today in the case of the roe deer (Cederlund & Liberg 1995; Kalela 1948).

### *The missing wolf and lynx*

Remains of terrestrial carnivores are rare in the Finnish refuse faunas. The red fox and the pine marten are relatively common, but some carnivores living in Finland today, for example the wolf, the Arctic fox, the wolverine and the lynx, are nearly absent from the reported finds.

Domestic dog is present already among the oldest finds, and in some samples (Ukkonen 1996a) it has been difficult to distinguish wolf and dog bones from each other. Recently, some bones from a Neolithic dwelling site Rusavierto in Saarijärvi have been identified as probable wolf bones (Nina Peltonen, pers. comm.). The above notwithstanding, wolf bones are extremely rare in the refuse faunas. This should, however, not be interpreted as the absence of this species from the fauna. The scarcity of wolf bones in the refuse faunas is more probably due to the human hunting strategies, for instance difficulties in catching certain large prey species, or the skinning of fur animals outside the dwelling sites. The same probably applies to the lynx, the wolverine, and smaller carnivores.

The absence of the Arctic fox from refuse faunas in northern Finland (Ukkonen 1997, manuscript) may perhaps not be explained through human hunting

strategies. Difficulties in distinguishing red and Arctic fox bones from each other may influence the data. It is, however, important to note that bones of the species are rare even in north Norwegian Stone Age dwelling sites (Frafjord & Hufthammer 1993).

It should be emphasized that bones of the brown bear are discovered regularly, if seldom, in refuse faunas. The species is relatively easy to catch in its winter den, and it was probably hunted both for its skin and for its meat.

### *Southern species*

The absence of evidence is no evidence of absence. Nevertheless, the total absence of certain southern game species, such as the red deer, the roe deer, and the wild boar, from the hundreds of excavated refuse faunas with thousands of identified bone fragments, is certainly suggestive. In adjacent areas, for example in southern Sweden (Liljegren & Lagerås 1993) and Estonia (Paaver 1965) these species are very common in local refuse faunas during the middle Holocene. Their absence from Finnish materials can therefore hardly be explained by a modest hunting pressure by prehistoric people, as in the case of the wolf or the European lynx.

Storå (2000) reports red deer remains from the prehistoric island dwellings sites Jettböle II and Källsveden in the Åland archipelago, but notes that the bones and antler were probably transported to the island for tool making purposes. They were most likely brought from the west, *i.e.* from Sweden (Jan Storå, pers. comm.).

Matiskainen (1989) reports one roe deer and one wild boar find from the Mesolithic Askola Settlement in southern Finland. The bone fragments are small and can, in my opinion, not be reliably identified as proposed by Jernvall (in Matiskainen 1989).

The reason for the absence of these species from the Finnish Holocene fauna is still to be discovered. Mixed oak forests resembling the modern habitats of these species in central Europe had spread to Finland by the middle Holocene, and the climatic and environmental conditions ought to have been more favourable for their dispersal than they are today. The answers may lie in smaller scale differences in the environment, such as the snow cover during the winter, or undergrowth in the forests.

#### 4.3.2. Marine mammals – the pioneers

The marine mammal species found as subfossil stray finds or among archaeological bone remains in Finland are the ringed seal, the harp seal, the grey seal and the harbour porpoise.

Prior to this study, the history of seals in the northern parts of the Baltic has been discussed by Ekman & Iregren (1984) on the basis of Swedish finds, and on the basis of Finnish finds by Alhonen & Forstén (1976), Forstén (1979), Forstén & Alhonen (1975, 1977), Korvenkontio (1936), Salmi (1944, 1948, 1949, 1963), Sauramo (1936) and Ylimaunu (2000). Ericson (1989) has discussed the distribution of different seal species in the Baltic from an archaeological point of view. In addition, an extensive archaeo-osteological study of seals and seal hunting in the Åland archipelago was recently published by Storå (2001).

A summary of the history of marine mammals in the Baltic area has been

given by Lepiksaar (1986). Zagorska (2000) and Daugnora (2000) discuss seals and seal hunting in Latvia and Lithuania, respectively. An extensive study on marine fauna in the central and southern Baltic and especially along the Estonian coast has been carried out by Lõugas (1997a). Danish finds of marine mammals have been discussed by Aris-Sørensen (1988), and southern Swedish finds by Liljegren & Lagerås (1993), and Lindqvist & Possnert (1997).

#### Ringed seal (*Phoca hispida*)

The first seal species to migrate into the Baltic basin after the retreat of the ice was the ringed seal (V). According to radiocarbon dates of subfossils found at the Finnish coast it was present in the northern Baltic at 9,500 BP at the latest, *i.e.*, from the very beginning of the Ancylus Lake stage of the basin.

The species probably entered the Baltic basin during the Yoldia Stage. However, the possibility of its immigration to the Baltic Ice Lake (Lindqvist & Possnert 1997) from the Atlantic Ocean through an earlier outlet in Öresund, or even from the White Sea indirectly through ice-marginal lakes and rivers, cannot theoretically be excluded.

Judged from both subfossil stray finds and archaeological data the ringed seal was very common in the northern parts of the Baltic during Prehistory, but did not necessarily dominate in the area, especially during the peak occurrence of the harp seal around 5,000 BP.

An isolated ringed seal population today resides in Lake Saimaa in southeastern Finland. The Lake Saimaa area was originally part of the Baltic Ice Lake and was isolated either directly from it or shortly after the beginning of the Yoldia stage (Saarnisto 1970). It is questionable whether the ringed seal could have entered the Saimaa area during this short interval (assuming they did not enter the Baltic basin until the Yoldia stage) and survived trapped in the water basins of the area when the connection to the Gulf of Finland was broken. During the Ancylus Lake stage the northwestern parts of the current Saimaa lake complex were part of the Baltic basin. At this stage the seals could have used a western route into Lake Saimaa from what is now the Gulf of Bothnia. Since the ringed seal is able to even swim up rivers, it could have entered Lake Saimaa as long as an indirect connection with the Baltic existed through large lakes in central Finland (V).

#### Harp seal (*Phoca groenlandica*)

The harp seal is an arctic species that currently does not inhabit the Baltic. The species did not enter the Baltic basin until the Danish Straits opened, offering a suitable (im)migration route for this pelagic species. All prehistoric dwelling sites that have yielded harp seal bones lie below the 7,500 BP shoreline (V) and are therefore probably younger than this.

The date of the harp seal stray find from Närpiö on the southern coast of the Gulf of Bothnia (5,890 BP) is the earliest so far from the northern Baltic (V). The stray find from Alatornio shows that the species had reached the northern end of the Gulf of Bothnia by 4,810 BP, at the latest. Similar dates of harp seals exist also from archaeological sites in this region. The earliest dated Estonian find is younger, 4,835 BP (Lõugas *et al.* 1996).

The youngest harp seal date from the Finnish west coast derives from a stray find from Pietarsaari and is 2,800 BP. The relatively late presence of the harp seal in the northern Baltic is also indicated by the skull found in a burial cairn of the “Lapp cairn” type in Kempele (Mäkivuoti 1985), archaeologically dated to the pre-Roman or Roman Iron Age. Harp seal remains have also been found in Iron Age contexts on the island Saaremaa in Estonia (Lõugas 1994). In the Åland archipelago the dominance of harp seals at dwelling sites decreases at the end of the Neolithic, but the species is still present in the fauna during the Iron Age (Storå 2000).

The harp seal was present in the northern Baltic for at least 3,000 radiocarbon years. The large number of both geological and archaeological harp seal finds disproves earlier views of the rarity of the species in the northern parts of the Baltic (Ekman & Iregren 1984; Storå 2001) and the alleged dominance of the ringed seal in refuse faunas (I).

The factors affecting the appearance of the harp seal in the Baltic and its subsequent disappearance cannot be inferred from the available data. It is doubtful whether the question can be solved on the basis of subfossil finds. Since ice conditions play a vital role in the life and breeding of seals, it might be profitable to approach the question from this angle. Changes in the salinity and fish diversity of the Baltic basin are often offered as an explanation (Forstén & Alhonen 1975; Lindqvist & Possnert 1997; Lõugas 1997a, 1998), but the confirmation or rejection of this hypothesis would require additional data both concerning the development of the salinity conditions and the ancient fish and harp seal populations in the Baltic.

The high abundance and the long presence of the harp seal in the northern Baltic suggest a stable residence in the area (Forstén & Alhonen 1975; Lindqvist & Possnert 1997) rather than just sporadic or even regular migrations (Lõugas 1997a, 1998; Salmi 1963). Recently, Storå (2001) has used epiphyseal fusion data and osteometry of archaeological harp seal finds to reach the conclusion that a breeding area existed near Gotland Island during the Subboreal Chron.

#### Grey seal (*Halichoerus grypus*)

Lindqvist and Possnert (1997) report grey seal finds from Gotland dated to the Ancylus Lake stage of the Baltic basin. If the dates are reliable, it means that the species must have entered the Baltic basin already during the Yoldia stage, since no suitable connection existed between the ocean and the Baltic basin during the Ancylus Lake stage. Lepiksaar (1986) and Lõugas (1997a) doubt the suitability of the narrow Närke strait as a migration route for this pelagic seal. The broader Danish Straits at the beginning of the Litorina stage seem a considerably more probable immigration route, as also discussed by Lindqvist & Possnert (1997). Moreover, the presence of this boreal species in the vicinity of the continental ice sheet seems questionable.

Although the grey seal has been common in historic times (Ylimaunu 2000), it is extremely rare in the Finnish subfossil faunas (V), as well as in the northern parts of the Baltic in general (Ekman & Iregren 1984; Ericson 1989). The single stray find from Teuva on the Finnish west coast is dated to the Litorina stage on the basis of stratigraphy (Forstén 1979). In the present study, grey seal was identified only in two refuse faunas from the south coast (V). In Estonia grey seal remains have been found in Early Neolithic contexts at several dwelling sites (Lõugas 1997a, 1997b), and also in the Bronze Age/Iron Age dwelling site Asva (Lõugas 1994). In

the Åland archipelago the earliest archaeological grey seal finds derive from Combed Ware sites dated to ca. 6,000 BP (Núñez & Storå 1991). At the later Pitted Ware sites the species is found only sporadically (Storå 2001). Grey seal is abundant only in the refuse fauna of the Bronze Age dwelling site Otterböte on the island Kökar in the Åland archipelago (Forstén 1977).

An interesting question is, whether the rarity of the grey seal during Prehistory should be explained through competition with other seal species, through environmental factors, such as the ice cover or food resources, or perhaps through a delay in the adaptation of the species in the new conditions it met in the Baltic Sea. The present grey seals in the Baltic Sea have different breeding habits than the grey seals in the North Sea and the North Atlantic. When and why this change took place may be a relevant question when studying the history of the grey seal in the Baltic Sea.

#### Harbour porpoise (*Phocoena phocoena*)

The harbour porpoise is today a regular visitor in the Baltic Sea. According to Forstén (1975) it has probably always been migratory in the area. All three stray finds reported from the Finnish coast (Forstén 1975; Metzger 1921; Salmi 1949) are assumed to be of Litorina age, and Forstén (1975) concludes that the species probably entered into the Baltic when the Danish Straits opened at the beginning of the Litorina stage, *i.e.* at the same time with other oceanic faunal elements, such as the harp seal (V).

In archaeological contexts harbour porpoise bones have been found at Jettböle in the Åland archipelago (H. Winge, archive notes), and at Jokiniemi in Vantaa (P. Ukkonen, unpubl. osteological analysis).

#### 4.4. Calibrating the history of mammals

In the account above only uncalibrated radiocarbon dates have been used both in summarizing the deglaciation chronology of Finland and the history of the Baltic basin, and in presenting and discussing the results of the present research project. However, a new calendar year chronology for the deglaciation with calibrated radiocarbon dates has recently been presented (Saarnisto 2000a; Saarnisto & Saarinen, in press; Lunkka *et al.*, in press). In the following, the post-glacial history of the Finnish mammalian fauna is summarized using calibrated radiocarbon years (cal BP).

The deglaciation of Finland began *ca.* 12,500 years ago and by *ca.* 10,200 y. a. the area was free from ice. So far, no mammalian finds have been connected with that period. The earliest post-glacial finds of terrestrial mammals in Finland derive from Mesolithic dwelling sites occupied *ca.* 10,000 y.a. The finds consist of species associated with young deciduous forests. During the following 1,000 years the fauna developed into the modern boreal fauna.

The main immigration route for the postglacial fauna was probably directly from the east. arctic species, such as the mountain reindeer, may, however, have spread to northern Finland from central Europe along the Norwegian coast, or from the northeast along the coast of the Kola Peninsula. The earliest indirect dates of reindeer remains in Lapland are *ca.* 8,500 years old, but the species was probably

present in the area already by 10,000 y.a. Reindeer remains from southern and central Finland are younger. The forest ecotype of the wild reindeer spread into Finland at *ca.* 8000 y.a., at the latest.

Marine mammals colonized the Baltic basin when the area was deglaciated and covered by the melt waters from the Scandinavian Ice Sheet. The ringed seal was present in the northern Baltic at 10,800 y.a., at the latest, *i.e.* from the very beginning of the Ancylus Lake stage (10,800 – 10,000 y.a.). The species probably entered into the Baltic during the Yoldia Stage (11,500 – 10,800 y.a.), but may have theoretically been part of the Baltic fauna since the Baltic Ice Lake (12,500 – 11,500 y.a.). The harp seal, which is no longer a resident species in the Baltic, was present in the area from 7000 y.a., at the latest, until at least 3,000 y.a., *i.e.* for 4,000 years. It did not enter the Baltic basin until the beginning of the Litorina Stage (10,000 y. a.) and the opening of the Danish Straits.

## 5. Conclusions

1. No bone remains of terrestrial mammals of Eemian age have been discovered in Finland, Norway or Sweden, so far. The presence and character of the mammalian fauna is, however, indicated by the beaver dam deposit found in Vimpeli, dated to the Eemian interglacial (I).

2. The Weichselian glaciation was interrupted in Fennoscandia by an ice-free period or periods. During these periods Finland was colonized by species of the glacial fauna including the woolly mammoth and the wild reindeer (II).

3. During the deglaciation period remnants of the glacial fauna re-immigrated areas previously covered by the Scandinavian Ice Sheet. A skull fragment of an Arctic fox found in southern Finland is dated to this period (I). In Estonia and western Russia mammoths lived as late as *ca.* 10,000 BP (III).

4. Arctic species, such as the wild reindeer, spread into northern Finland probably along the Norwegian coast from the south or along the coast of the Kola Peninsula from the northeast. The main immigration route for the Finnish fauna after the deglaciation, however, was directly from the east (I, IV).

5. The earliest finds of terrestrial mammals in Finland indicate a fauna associated with young deciduous forests. The fauna developed rapidly into the modern boreal fauna, and no separate faunal periods can be detected (I, IV).

6. Some carnivores, such as the wolf and the European lynx, which are part of the boreal fauna, have not been detected in the Finnish refuse faunas. The reasons for their absence may be sought in human behaviour rather than faunal history (I).

7. The warm climate and the spread of mixed oak forests into Finland during the middle Holocene were not reflected in the terrestrial mammalian fauna. Certain southern species, such as the wild boar, the roe deer, and the red deer, which were common in adjacent areas to the south and west, did not colonize Finland during the warm period (I).

8. Seals were the first mammals to immigrate into the area of Finland. The ringed seal was the pioneer species. It immigrated into the Baltic basin during the Yoldia stage of the Baltic, at the latest, and is still present both in the Baltic Sea and in Lake Saimaa. The harp seal was part of the Baltic fauna at least from 5,900 BP to 2,800 BP, *i.e.* for 3000 radiocarbon years. The grey seal is rare both as subfossil stray finds and in the refuse faunas (I, V).

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Appendix. Subfossil stray finds from Finland. Museums: GM = Geological Museum of the Finnish Museum of Natural History, Helsinki; ZM = Zoological Museum of the Finnish Museum of Natural History, Helsinki; ZM Oulu = Zoological Museum, Oulu; NM = National Museum, Helsinki; RM = Swedish Museum of Natural History, Stockholm; UC? = University collections, not relocated; St. P.? = St. Petersburg, not relocated; Laihia = Laihia secondary school; NOM = The Northern Ostrobothnia Museum, Oulu; SM = Satakunta Museum, Pori. *Previous dating* refers to dates mentioned in the original papers which are based on pollen and diatom analyses, shore displacement and the stratigraphy of the locality, as well as radiocarbon analyses made prior to this study. *Project dating* refers to radiocarbon analyses carried out in connection with this study.

Species	Anat. part	Locality	Reference	Stored at	Previous dating	Lab.nr.	Project dating	Lab.nr.
Alopex lagopus	skull	Tenhola	Kurtén 1966	GM	Younger Dryas			
Meles meles	vertebrae	Hyvinkää	Alhonen <i>et al.</i> 1987	ZM				
Alces alces	mt	Lapua	Jungner & Sonninen 1983	ZM	2,760+/-170	Hel-811		
Alces alces	atlas	Säkylä		ZM				
Rangifer tarandus	antler	Tornio	Siivonen 1975	ZM Oulu	34,300+2,000/-1,450	Hel-254		
Rangifer tarandus	antler	Parkano, Vatajajärvi	Schulman 1910	ZM 6545			470+/-70	Hel-3940
Rangifer tarandus	mt fr.	Karijoki Susiluola		NM			1030+/-65	Hela-229
Rangifer tarandus	antler	Helsingin mlk., Vestersundom		ZM 6548			220+/-80	Hel-4013
Rangifer tarandus	antler	E. Karelia, Kemjärvi		ZM 6547			180+/-70	Hel-4011
Rangifer tarandus	antler	Kuru, Rasinmäki		ZM 3696			160+/-90	Hel-4012
Rangifer tarandus	antler	Leivonmäki		ZM 6546			150+/-70	Hel-4010
Rangifer tarandus	antler	Ätsäri	Schulman 1910	ZM				
Rangifer tarandus	antler	Vaasa		ZM				
Equus caballus	skull	Föglö		ZM				
Equus caballus	mandible	Pitajämäki		ZM				
Equus caballus	humerus	Alahärmä		ZM				
Equus caballus	?	Tuusula		ZM				
Mammuthus primigenius	molar	lijoki	Holm 1904; Korvenkontio 1915	RM			31,970+/-950	Ua-14190
Mammuthus primigenius	femur	Lohtaja	Okko 1949; Donner <i>et al.</i> 1979	ZM	25,200+/-500	Hel-1075	24,450+/-385	Hela-295
Mammuthus primigenius	tusk	Haapajärvi	Okko 1953	ZM			28,740+/-670	Hela-294
Mammuthus primigenius	molar	Nilsjä	Malmgren 1874-75; Ramsay 1900; Korvenkontio 1915	GM			22,420+/-315	Hela-281
Mammuthus primigenius	2xhumerus fr.	Tuulos	Rosberg 1924	UC?				
Mammuthus primigenius	humerus	Helsinki, Herttoniemi	Pearson <i>et al.</i> , 1965; Donner <i>et al.</i> 1979	ZM	15,500+/-200	Hel-1074	15,910+/-155	Hela-321
Mammuthus primigenius	premolars	Helsinki, Tööliö	Korvenkontio 1915	GM			23,340+/-350	Hela-281
Mammuthus primigenius	molar	Espoo	Metzger 1921; Donner <i>et al.</i> 1979	ZM	>43,000 BP	Hel-1076		
Mammuthus primigenius	costa	Pohja, Brödorp	Ramsay 1897; Rosberg 1901	St. P.?				
Castor fiber	skull	Vihanti	Metsävainio 1950; Anonymous 1951; Ukkonen 1997	ZM Oulu	2,670+/-75	Hela-108		
Castor fiber		Ranua	Forstén & Lahti 1976					
Lepus timidus	skeleton	Kannus, Välikannus	Salmi 1948	ZM				
Phoca groenlandica	skeleton	Närpiö	Korvenkontio 1936; Sauramo 1936	NM 10087:2	Litorina		5890+/-70	Hela-441
Phoca groenlandica	skeleton	Pietarsaari, Sundby	Salmi 1963	ZM 6970	Subboreal		2800+/-65	Hela-437
Phoca groenlandica	bones	Närpiö, Pjelaax	Salmi 1963	ZM 6966	Subboreal			
Phoca groenlandica	skeleton	Laihia, Potila	Salmi 1963		Subboreal			
Phoca groenlandica	skeleton	Laihia, Ruto	Forstén & Alhonen 1975	ZM 6973	Subboreal			
Phoca groenlandica	skeleton	Vaasa, Roparnäs	Forstén & Alhonen 1975	ZM 6971	Litorina		2995+/-70	Hela-438
Phoca groenlandica	bones	Pori	Forstén & Alhonen 1975		Litorina			
Phoca groenlandica	bones	Alatornio, Liekanjoki	Forstén & Alhonen 1977	ZM 6951	Litorina		4810+/-70	Hela-432
Phoca groenlandica	skeleton	Espoo or Kirkkonummi	Forstén & Alhonen 1977	ZM 6952	Litorina		5290+/-175	Hela-433
Phoca hispida	skeleton	Kuivaniemi, Vakkurinkangas	Forstén & Alhonen 1975	NOM				
Phoca hispida	bones	Kovjoki, Ävist (Uusikaarlepyy)	Forstén & Alhonen 1975	ZM 6974	Yoldia/Ancylus		8270+/-80	Hela-434
Phoca hispida	bones	Ähtävä, Yliähtävä	Forstén & Alhonen 1975	ZM 6945	Ancylus		8195+/-135	Hela-435
Phoca hispida	skeleton	Ylistaro, Rintamattila	Forstén & Alhonen 1975	ZM 6972	Ancylus		8495+/-80	Hela-439
Phoca hispida	skeleton	Nurmo, It. Kimpimäki	Forstén & Alhonen 1975	ZM 6978	Ancylus		9505+/-85	Hela-440
Phoca hispida	bones	Ilmajoki	Forstén & Alhonen 1975	ZM 6968	Ancylus			
Phoca hispida	bones	Lapua, Tiistejoki	Forstén & Alhonen 1977	ZM 6953	Ancylus			
Phoca hispida	bones	Ruukki	Salmi 1944	ZM 6977	Ancylus			
Phoca hispida	bones	Ylistaro, Kaukolankylä	Salmi 1949	ZM 6976	Litorina			
Phoca hispida	skull+bones	Muhos, Honkalankylä	Forstén & Alhonen 1975	ZM 6965	Litorina		5115+/-75	Hela-436
Phoca hispida	skeleton	Oulainen, Tiitjärvi	Forstén & Alhonen 1977	ZM 6957	Litorina			
Phoca hispida	bones	Oulujoki	Korvenkontio 1936; Sauramo 1936	ZM 6980	Litorina			
Phoca hispida	skull+bones	Vähäkylä, Rekilänkylä	Salmi 1948	ZM 6963	Litorina			
Phoca hispida	bones	Ulvila, Harjunpää	Forstén & Alhonen 1975	SM 16.400	Litorina			
Phoca sp.	mt l	Karijoki, Susiluola	Ukkonen, unpubl.	NM	2505+/-75	Hela-230		
Halichoerus grypus	skull fr.	Teuva	Forstén 1979	ZM 6942	Litorina			
Phocoena phocoena	skeleton	Tenhola	Metzger 1921	GM	Litorina			
Phocoena phocoena	skeleton	Närpiö	Salmi 1949	ZM	Litorina			
Phocoena phocoena	bones	Pori, Tuorsniemi	Forstén 1975; Alhonen 1974	NM	Litorina			