
Review

The post-glacial history of the Finnish mammalian fauna

Pirkko Ukkonen

Ukkonen, P., Department of Zoology, P.O. Box 17 (P. Rautatiekatu 13), FIN-00014 University of Helsinki, Finland

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Mammalian fossils and subfossil stray finds are extremely scarce in Finland, the latter consisting mainly of marine mammals. Animal bones from cultural sites, the so-called refuse fauna, are far more abundant, offering more precise information especially of the faunal history of terrestrial mammals. The Holocene subfossil fauna is rather monotonous and no distinct faunal periods can be detected. The earliest postglacial finds are from the Boreal chronozone and contain species connected with young forest habitats. Mammal remains from the Atlantic chronozone are more complex, including species associated with both coniferous and mixed oak forests. Reindeer remains from Atlantic dwelling sites in southeast Finland indicate an early invasion of the wild forest reindeer (*Rangifer tarandus fennicus* Lönnberg) in the area. Seal remains are found not only in coastal areas but also at dwelling sites located on the shores of inland lakes. Their proportion increases in the Late Atlantic refuse fauna, but the cause of this phenomenon is not yet fully understood.

1. Introduction

The early history of the Finnish mammalian fauna is little known. Bones are poorly preserved in the acid soil typical of most of the Finnish peninsula. Pre-Holocene mammalian remains are extremely scarce and so are the subfossil stray finds consisting mainly of marine mammals like seals and harbour porpoise. Except for a few studies concerning the genetics and morphology of small mammals (Halkka et al. 1987, Jalkanen 1989), our conceptions of the early history of Finnish mammals are mainly assumptions based on what

is known about the environmental changes in the Holocene and the ecological requirements of different species.

A review of the early history of the Scandinavian fauna is given by Ekman (1922), a more recent one by Lepiksaar (1986), who also includes the Baltic countries. Comments on the history of the Finnish mammals are found in Siivonen (1972), and Kurtén (1988) has summarized the Finnish fossil and subfossil mammalian finds. The subfossil seals were studied by Forstén & Alhonen (1975, 1977), the postglacial occurrence of the beaver by Forstén & Lahti (1976) as well as Lappalainen & Lahti (1972),

and the history of the reindeer by Siivonen (1975) and Montonen (1972).

Subfossil bone material from archeological sites, the so called refuse fauna, has mainly been used for studies concerning the economy of pre-historic man (Ailio 1909, Forstén 1972, Forstén & Blomqvist 1977, Kokkonen 1978, Lindqvist 1988, Matiskainen 1989, Rauhala 1977, Siiriäinen 1981, 1982, Taavitsainen 1980, Vikkula 1981). Extensive studies on faunal history and biogeography based on refuse faunas have not been published in Finland.

In this paper I will introduce both the subfossil stray finds and the available data on the refuse fauna, and discuss their significance in connection with the history of deglaciation and the development of climate and vegetation in Finland.

My emphasis is on the qualitative analysis of the data. However, since bone fragment numbers have been used in speculations about the distribution and abundance of certain species, especially the elk (Forstén 1972, Siiriäinen 1981, 1982), some remarks are made concerning limitations and possibilities of quantitative methods in faunal history studies based on refuse faunas.

2. Material and methods

2.1. Pre-Holocene and Holocene stray finds

The pre-Holocene and Holocene stray find data is based on the literature. The finds are often dated by correlation with pollen zones or Baltic stages, only seldom with chronozones. My interpretation of the temporal distribution of the finds may, therefore, in some cases be contested.

2.2. Subfossil refuse fauna

The data on the refuse fauna is based on osteological analyses of subfossil mammalian remains from Stone Age cultural sites in Finland and, to some extent, in Russian Karelia (Appendix). The bones were analysed morphologically by comparing the fragments with modern mammalian skeletons, using — in most cases — the collections of the Zoological Museum in Helsinki as reference material. Animal bones from cultural sites have been analysed by myself and by several other Finnish and foreign osteologists (Appendix). Animal remains from cultural sites in Finland have never been analysed systematically — rather the samples have been chosen due to different archeological interests, or simply depending on financial resources.

Some of the osteological analyses used in my study have been published (Ailio 1909, Forstén 1972, Forstén & Blomqvist 1977, Kokkonen 1978, Lindqvist 1988, Matiskainen 1989, Rauhala 1977, Siiriäinen 1981, 1982, Taavitsainen 1980, Vikkula 1981), part of the data is unpublished. When possible, original analysis lists were used in order to make the different samples comparable.

I restricted my study to Stone Age dwelling sites because of the change in the structure and composition of the bone material at the beginning of the Bronze Age (ca. 3200 BP). From that time the proportion of the unburned bones increases and domestic animals appear in the material. Sites lacking reliable dating (radiocarbon, shore displacement, pollen stratigraphy or artefacts) were excluded. The remaining sites were arranged in six groups according to their age (Table 1).

Table 1. Periods used in the study (I–VI) and their correlation with the Flandrian chronozones and subchronozone (following Mangerud et al. 1974) and the Stone Age chronology in Finland (modified after Siiriäinen 1981).

Period	Age BP	Chronozone/ Subchronozone	Cultural stages
VI	4000–3000	Middle Subboreal	Kiukainen
V	5000–4000	Early Subboreal	Comb ceramic III, Pyheensilta, Corded Ware Culture, Kierikki, Jettböle
IV	6000–5000	Late Atlantic	Comb ceramic I–II, Säräisniemi 1, Jäkärälä
III	7000–6000	Middle Atlantic	late Mesolithic
II	8000–7000	Early Atlantic	middle Mesolithic
I	9000–8000	Boreal	early Mesolithic

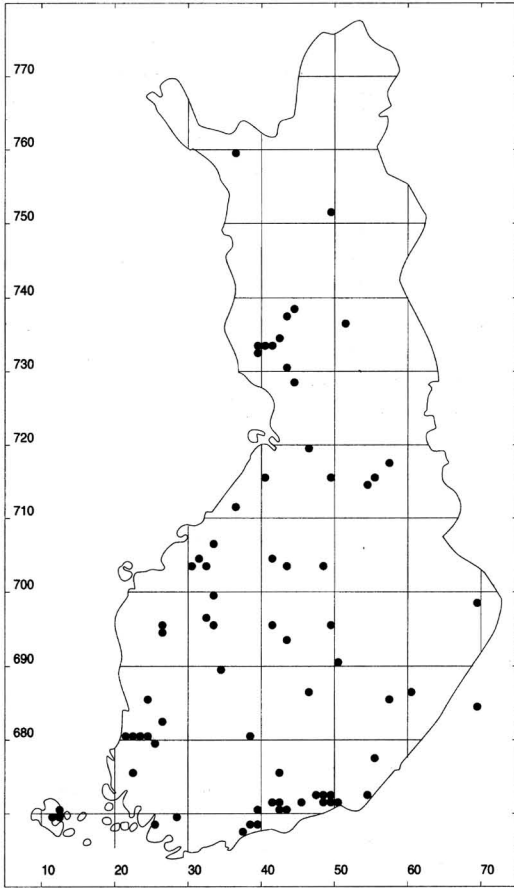


Fig. 1. Stone Age dwelling sites included in the study. Location in 10-km squares of the Finnish uniform 27°E grid.

The refuse fauna studied consists of 150 samples from 109 cultural sites and includes 8776 analysed bone fragments. The sites cover Finland fairly well, except eastern Finland and Lapland (Fig. 1), but their distribution in time is uneven (Fig. 2).

Domestic animals, except the dog, were excluded from the analysis as well as all uncertain identifications. Taxa higher than the species were included only in the case of the seals, the canids and the mustelids. Identification of seals to species level is extremely difficult in the fragmented burned bone material. Among the canids, the wolf and the dog, and the dog and the red fox, are often difficult to distinguish from each other. In the case of the small mustelids, the problem is the sexual size dimorphism of the species.

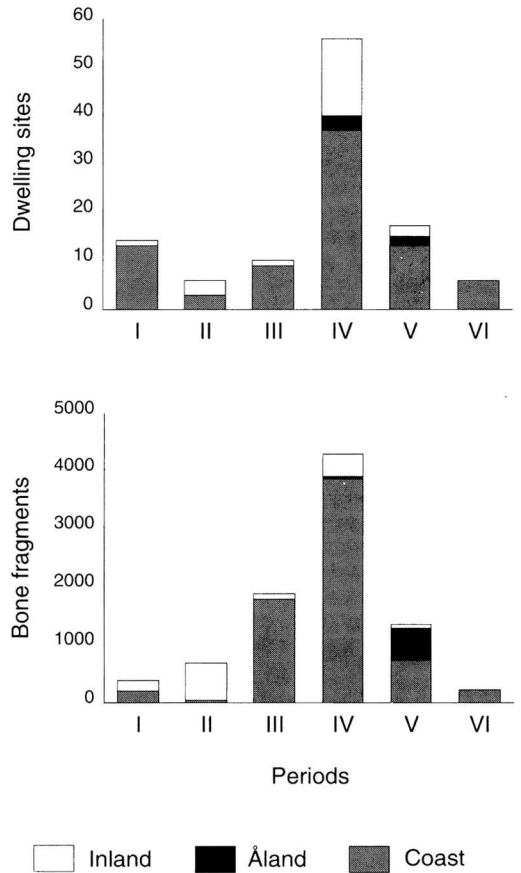


Fig. 2. Distribution of Stone Age dwelling sites and bone fragments during different periods. I = 9000–8000 BP, II = 8000–7000 BP, III = 7000–6000 BP, IV = 6000–5000 BP, V = 5000–4000 BP, VI = 4000–3000 BP.

2.3. Limitations of the archeological material

Problems of interpreting archeological bone material are discussed by Fortelius (1981) and others. The main problem from a zoological point of view is the fact that the bones do not represent the whole local fauna but merely species hunted by man. Hunting and butchering methods, tool making, etc. further change the anatomical and species composition.

Bones are poorly preserved in acid soil, but heating seems to improve their preservation considerably. Thus, the Finnish refuse fauna consists almost exclusively of so called burned bones. Heating causes shrinking and deformation of the

bones, which can make the identification of the fragments problematic. A further difficulty in analysing burned bone material arises from its fragmentation — the pieces only seldom exceed 1×1 cm. The processes involved in the shaping and preservation of burned bone are not yet fully understood and studies concerning their taphonomy are scarce (Matskainen 1989, Okkonen 1991).

The dislocating of bones by scavengers, the differentiated preservation of bones of different species and of different parts of the skeleton, and the varying accuracy of the excavation methods further influence the composition of the final refuse fauna.

One of the major problems in analysing refuse faunas is the dating of the cultural sites. Shore line sites can be dated more easily and more reliably than inland sites with help of the shore displacement curves. Inland dwelling sites were used for longer periods and many of them — located on lake shores — were later destroyed by the decline and transgression of the lakes due to the land uplift.

2.4. Qualitative and quantitative analysis of the refuse faunas

The problems listed above complicate and restrict the use of archeological bone material in zoological studies. In qualitative analyses the problems can be controlled. My conclusions concerning the geographic and taxonomic distribution of the species are based on the principle that the refuse fauna of a dwelling site represents a biased sample of the fauna at or near the site during its occupation.

Quantitative methods are difficult to apply to archeological bone material. The calculation of minimum individual numbers, a method broadly used in other countries, cannot be applied to the burned, highly fragmented Finnish material, where the absolute numbers of different skeletal parts cannot be counted (Fortelius 1981). Fragment numbers do not directly represent the abundance of a species, but they can to some extent be used in comparing refuse faunas from different periods or from different locations.

I have used bone fragment numbers and numbers of discovery sites to examine changes

in the proportions of different species in the refuse fauna and to discuss their possible causes. The analysis based on bone fragment numbers is sensitive to all errors related to taphonomy, excavations methods, and identification. In addition, the uneven temporal distribution of the finds and the high variance in the sample sizes decrease the reliability of a quantitative analysis and make a statistical analysis of the data problematic. An analysis based on the number of discovery sites is more robust, but the problem with the uneven temporal distribution of the sites and their low number still remains. This phenomenon may be spurious, however, reflecting the probability of preservation and discovery of the dwelling sites or it may be related to changes in the population numbers and hunting strategies of prehistoric man. Because of these problems, no statistical methods were used in the analysis.

3. Results

3.1. Composition of the pre-Holocene and Holocene subfossil fauna

The few Finnish pre-Holocene finds are listed in Table 2 with datings and references to papers in which they were described. The dam deposit of

Table 2. Published pre-Holocene stray finds (species, source, site and age) of arctic fox, mammoth, reindeer, and beaver in Finland. Datings of the mammoth finds from Donner et al. 1979.

<i>Alopex lagopus</i> (from Kurtén 1966)
Tenhola, younger Dryas
<i>Mammuthus primigenius</i> (from Donner 1965)
Pohja
Espoo, >43 000 BP
Helsinki, 15 500 BP
Helsinki
Tuulos
Nilsia
Lohtaja, 25 200 BP
Iijoki
Haapajärvi
<i>Rangifer tarandus</i> (from Siivonen 1975)
Tornio, 34 000 BP
<i>Castor fiber</i> (from Aalto et al. 1989)
Vimpeli, dam deposit, 107 000 y (thermoluminescence dating)

beaver (*Castor fiber* L.) (Aalto et al. 1989), dated to the Eemian interglacial, constitutes the oldest known evidence of mammals in Finland. All mammoth (*Mammuthus primigenius* Blum.) remains are in secondary position. Three of the finds have been dated using radiocarbon (Donner et al. 1979), as has the fossil reindeer (*Rangifer tarandus* L.) antler, found in Tornio (Siivonen 1975). The late glacial find of an arctic fox (*Alopex lagopus* L.) (Kurtén 1966) is dated on the basis of pollen analysis to the Younger Dryas.

The Holocene subfossil stray finds are listed in Table 3. They consist mainly of marine mammals like seals and harbour porpoise (*Phocoena phocoena* L.), the only terrestrial mammals being the beaver, the arctic hare (*Lepus timidus* L.) and the badger (*Meles meles* L.). The composition of the mammal remains from Stone Age cultural sites (Table 4) is more complex, especially for terrestrial mammals.

Table 3. Published subfossil stray finds (period, species, sites) in Finland.

Preboreal period	
<i>Phoca hispida</i> :	Kovjoki ¹
Boreal period	
<i>Phoca hispida</i> :	Ähtävä, Ylistaro, Nurmo, Ilmajoki ¹ ; Lapua ² ; Ruukki ³
<i>Phocoena phocoena</i> :	Petsamo ⁴
Atlantic period and Litorina stage in general	
<i>Meles meles</i> :	Hyvinkää ⁵
<i>Castor fiber</i> :	cranium, Vihanti ^{6,7} ; gnawed wood, Isojoki ⁸
<i>Lepus timidus</i> :	Kannus ⁹
<i>Halichoerus grypus</i> :	Teuva ¹⁰
<i>Phoca groenlandica</i> :	Närpiö ^{11,12}
<i>Phoca hispida</i> :	Ylistaro ¹⁴ ; Muhos ¹ ; Oulainen ²
<i>Phocoena phocoena</i> :	Tenhola ¹³ ; Närpiö ¹⁴
Subboreal period	
<i>Castor fiber</i> :	gnawed wood, Liperi ¹⁵
<i>Phoca groenlandica</i> :	Pietarsaari, Närpiö, Laihia ¹⁶ ; Laihia, Vaasa, Pori ¹ ; Alatornio, Kirkkonummi ²
<i>Phoca hispida</i> :	Oulujoki ^{11,12} ; Vähäkyrö ⁹ ; Ulvila ¹
<i>Phocoena phocoena</i> :	Pori ¹⁷

¹ Forstén & Alhonen 1975; ² Forstén & Alhonen 1977; ³ Salmi 1944; ⁴ Aario 1939; ⁵ Alhonen et al. 1987; ⁶ Metsävainio 1950; ⁷ Anonymous 1951; ⁸ Forstén & Lahti 1976; ⁹ Salmi 1948; ¹⁰ Forstén 1979; ¹¹ Korvenkontio 1936; ¹² Sauramo 1936; ¹³ Metzger 1921; ¹⁴ Salmi 1949; ¹⁵ Lappalainen & Lahti 1972; ¹⁶ Salmi 1963; ¹⁷ Forstén 1975.

3.2. Geographic distribution of the finds

Species present in the refuse fauna, the number of dwelling sites containing bones of different species, and the number of identified bone fragments are listed in Table 5. For most of the species the number of discovery sites is rather low, the most common species being seals, the beaver, the elk (*Alces alces* L.), and the arctic hare. The geographic distribution of the finds for most species is scattered, and no clear distribution patterns can be detected. The geographic distribution of the seals and the reindeer is shown in Fig. 3. Seal bones are found not only in coastal areas but also on dwelling sites situated on the shores of inland lakes. Reindeer remains are scarce and appear in the refuse fauna for the first time in the Atlantic chronozone. Four of the discovery sites are situated in northern Finland, four in south-eastern Finland.

Table 4. Mammal finds from Stone Age cultural sites in Finland. I = 9000–8000 BP, II = 8000–7000 BP, III = 7000–6000 BP, IV = 6000–5000 BP, V = 5000–4000 BP, VI = 4000–3000 BP. Period I = Boreal chronozone, periods II–IV = Atlantic chronozone, periods V–VI = Subboreal chronozone.

	I	II	III	IV	V	VI
Terrestrial mammals						
<i>Canis familiaris</i>	x		x	x	x	
<i>Vulpes vulpes</i>	x		x	x		
Canidae sp.			x	x	x	
<i>Ursus arctos</i>			x	x	x	
<i>Lutra lutra</i>			x			
<i>Martes martes</i>			x	x		x
Mustelidae sp.			x	x	x	
<i>Sus scrofa</i>			x		?	
<i>Alces alces</i>	x	x	x	x	x	
<i>Capreolus capreolus</i>	x					
<i>Rangifer tarandus</i>			x	x	x	x
<i>Sciurus vulgaris</i>			x	x	x	
<i>Castor fiber</i>	x	x	x	x	x	x
<i>Lepus timidus</i>	x		x	x	x	x
Marine mammals						
<i>Halichoerus grypus</i>						x
<i>Phoca groenlandica</i>						x
<i>Phoca hispida</i>	x	x		x	x	x
Phocidae sp.	x	x	x	x	x	x
<i>Phocoena phocoena</i>						x

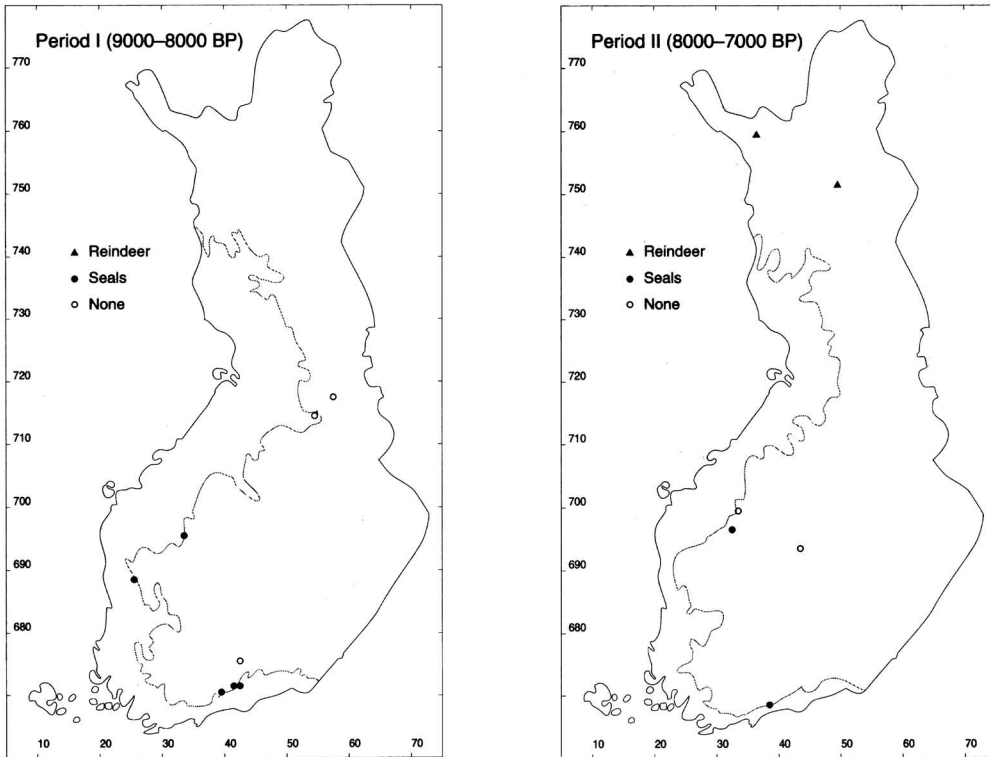


Fig. 3. Geographical distribution of seal and reindeer finds in Stone Age dwelling sites. Coast lines for periods I, III, IV and V (after Birks & Saarnisto 1975), and for period II (after Eronen 1983) indicated in grey. Periods as in Fig. 2.

3.3. Taxonomic distribution of the finds

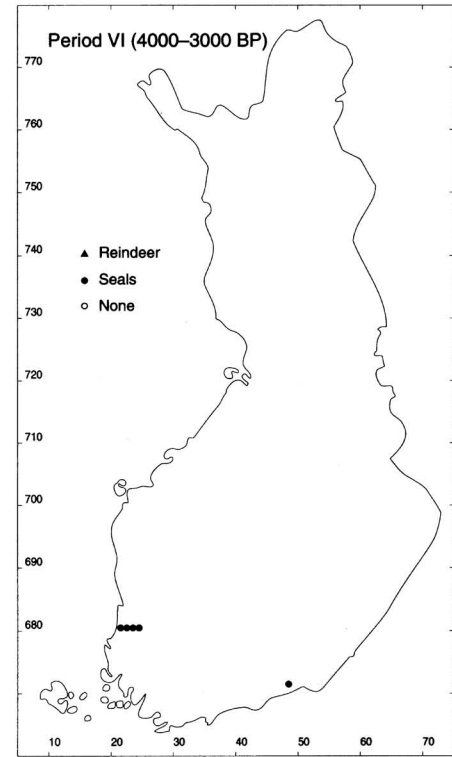
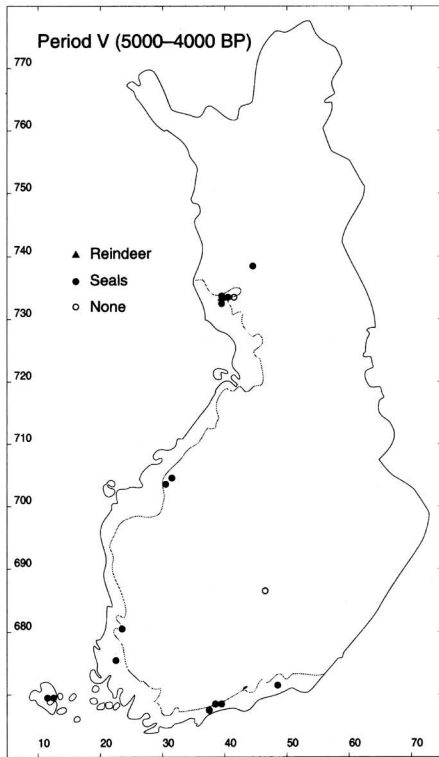
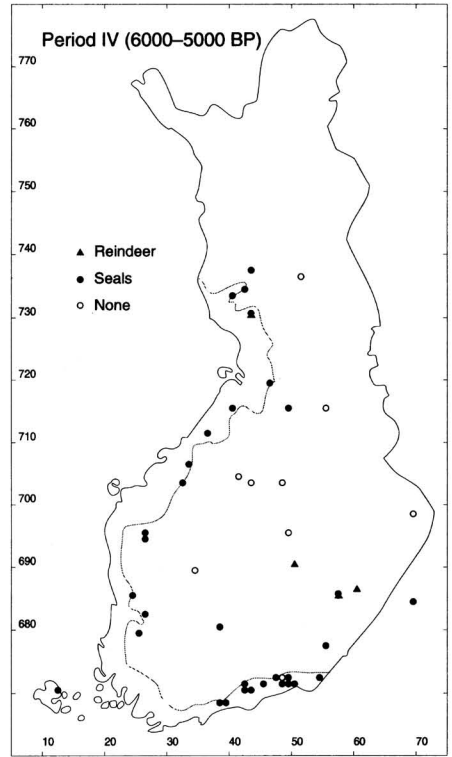
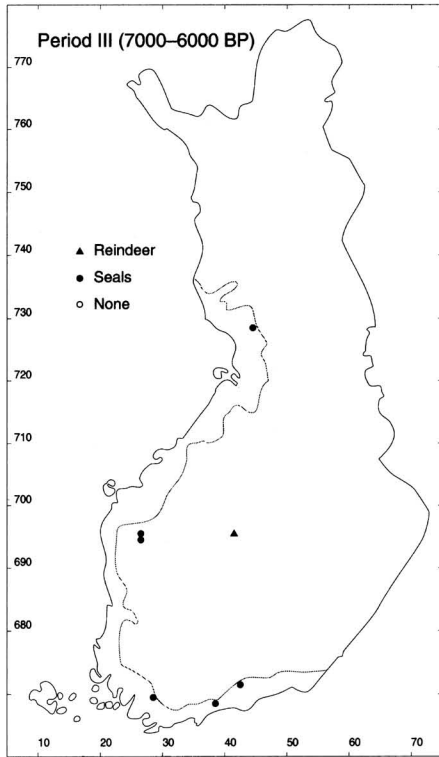
The frequency of discovery sites for different species is given in Fig. 4. In the first two periods the species number is low, but it increases dramatically in the third period, i.e., in the middle of the Atlantic chronozone, even though the total number of dwelling sites remains low. In the Middle Subboreal the number of species drops again, along with the decreasing number of dwelling sites.

Remains of terrestrial carnivores are rare in the Finnish refuse fauna. Domestic dog (*Canis familiaris* L.) is already present among the oldest finds, along with the red fox (*Vulpes vulpes* L.). Wolf (*Canis lupus* L.) has not been identified in the refuse fauna, but the species may be included in the category Canidae. The few brown bear (*Ursus arctos* L.) remains are mainly fragments of claws and other phalanges, indicating that the

finds originate from furs. Mustelids are represented by otter (*Lutra lutra* L.) and pine marten (*Martes martes* L.), the latter appearing in the refuse fauna in the Middle Atlantic. It is possible, however, that the category Mustelidae contains also other small mustelids. Lynx (*Lynx lynx* L.) has been identified at one location, but this site was not included in the study because it could not be dated.

Seal remains have been found at most of the coastal dwelling sites and at several inland sites, too. Harbour porpoise has been identified only in the refuse fauna of Åland, and only from the Early Subboreal.

Of the Artiodactyla, the elk is the most common species in the refuse fauna. It is present at both the coastal and the inland dwelling sites, at all periods except for the last one, i.e., the Middle Subboreal chronozone. Reindeer has been identified from eight sites only, most of them situated



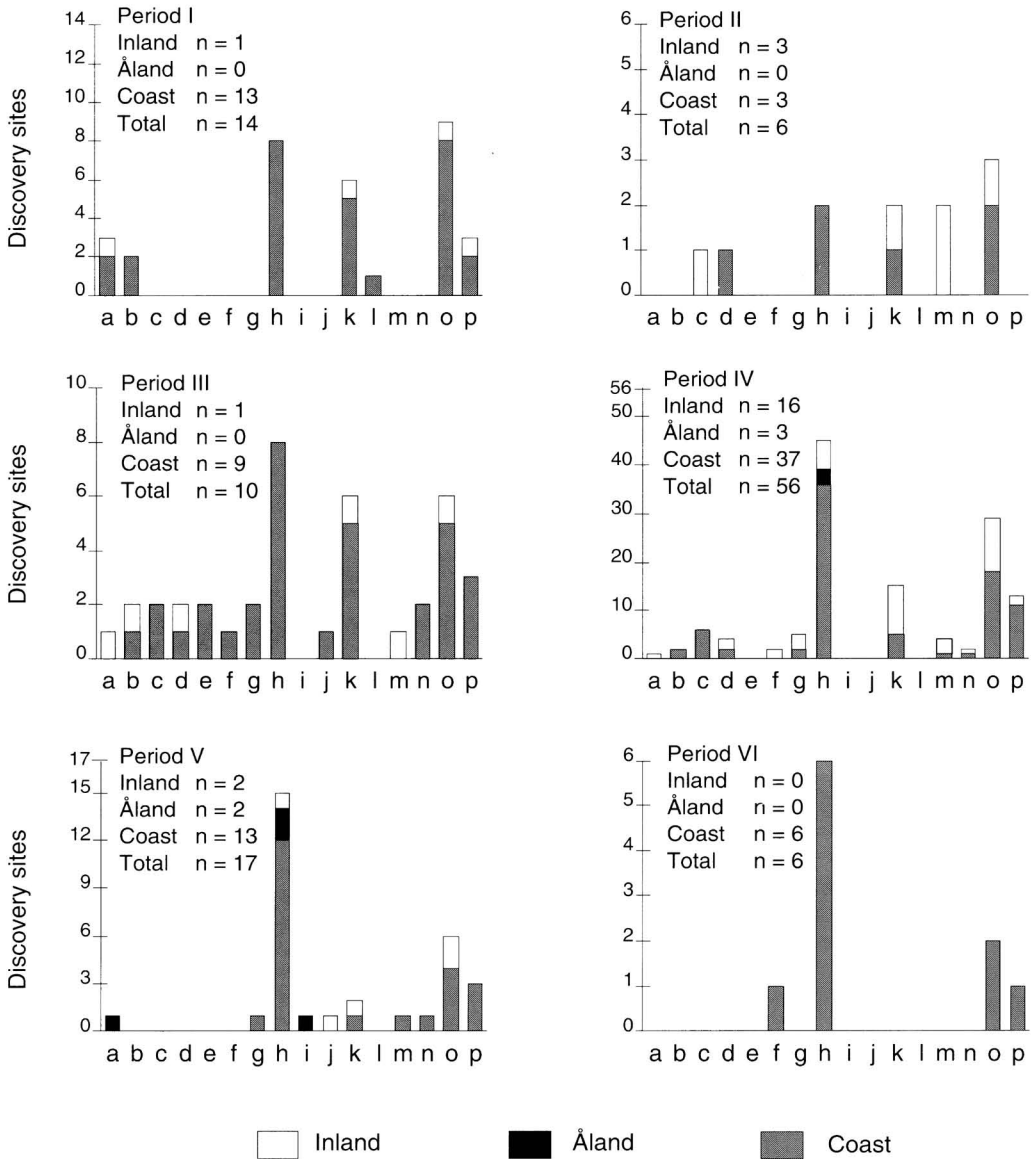


Fig. 4. Taxonomic distribution of the finds. a = *Canis familiaris*, b = *Vulpes vulpes*, c = Canidae, d = *Ursus arctos*, e = *Lutra lutra*, f = *Martes martes*, g = Mustelidae, h = Phocidae, i = *Phocoena phocoena*, j = *Sus scrofa*, k = *Alces alces*, l = *Capreolus capreolus*, m = *Rangifer tarandus*, n = *Sciurus vulgaris*, o = *Castor fiber*, p = *Lepus timidus*. Periods as in Fig. 2. Note the different scales.

inland. Roe deer (*Capreolus capreolus* L.) was identified from one site, dated to the Boreal chronozone. Wild boar (*Sus scrofa* L.) bones were found at two dwelling sites dated to the Middle Atlantic and the Early Subboreal. In the latter case the bones were situated in pits, and may have been in secondary position.

Red squirrel (*Sciurus vulgaris* L.) appears in the refuse fauna in the Middle Atlantic, but its frequency remains low. Beaver, on the other hand, is common throughout the whole study period, although its frequency drops slightly at the beginning of the Subboreal. Bones of arctic hare are found at dwelling sites from nearly all periods.

3.4. Abundance of the species in the refuse fauna

The changes in the abundance of the remains of different species in the refuse fauna of coastal dwelling sites were analysed using both the number of discovery sites and bone fragments (Fig. 5). The

frequency and abundance of the seals seem to increase in the Middle or Late Atlantic at the cost of other species, especially the elk. The number of inland dwelling sites is too low for reliable analyses. It should, however, be noted that elk is present at 10 of 16 inland dwelling sites dated to the Late Atlantic chronozone (Table 5).

Table 5. Quantitative data for analysed bone fragments from Stone Age dwelling sites. Number of dwelling sites (first row) and number of analysed fragments (second row). C = Coastal sites, Å = Åland, I = Inland sites. Periods I–VI as in Table 4 (periods without finds omitted).

	C I	II	C II	III	C III	I III	C IV	Å IV	I IV	C V	Å V	IV	C VI	Total
<i>Canis familiaris</i>	2 5	1 4	– –	– –	– –	1 4	– –	– –	1 1	– –	1 34	– –	– –	6 48
<i>Vulpes vulpes</i>	2 12	– –	– –	– –	1 6	1 4	2 2	– –	– –	– –	– –	– –	– –	6 24
Canidae sp.	– –	– –	– –	1 22	2 6	– –	6 12	– –	– –	– –	– –	– –	– –	9 40
<i>Ursus arctos</i>	– –	– –	1 9	– –	1 1	1 8	2 3	– –	2 4	– –	– –	– –	– –	7 25
<i>Lutra lutra</i>	– –	– –	– –	– –	2 11	– –	– –	– –	– –	– –	– –	– –	– –	2 11
<i>Martes martes</i>	– –	– –	– –	– –	1 10	– –	– –	– –	2 5	– –	– –	– –	1 2	4 17
Mustelidae sp.	– –	– –	– –	– –	2 3	– –	2 3	– –	3 4	1 8	– –	– –	– –	8 18
Phocidae sp.	8 79	– –	2 4	– –	8 1327	– –	36 3545	3 51	6 114	12 641	2 497	1 7	6 218	84 6483
<i>Phocoena phocoeana</i>	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	1 38	– –	– –	1 38
<i>Sus scrofa</i>	– –	– –	– –	– –	1 1	– –	– –	– –	– –	– –	– –	1 4	– –	2 5
<i>Alces alces</i>	5 34	1 24	1 6	1 1	5 38	1 35	5 15	– –	10 71	1 4	– –	1 1	– –	31 229
<i>Capreolus capreolus</i>	1 1	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	1
<i>Rangifer tarandus</i>	– –	– –	– –	2 613	– –	1 5	1 2	– –	3 6	1 3	– –	– –	– –	8 629
<i>Sciurus vulgaris</i>	– –	– –	– –	– –	2 3	– –	1 1	– –	1 2	1 7	– –	– –	– –	5 13
<i>Castor fiber</i>	8 79	1 134	2 23	1 8	5 340	1 41	18 223	– –	11 162	4 32	– –	2 32	2 4	55 1074
<i>Lepus timidus</i>	2 2	1 2	– –	– –	3 24	– –	11 37	– –	2 22	3 22	– –	– –	1 8	23 117
Dwelling sites total	13	1	3	3	9	1	37	3	16	13	2	2	6	109
Fragments total	212	164	42	644	1770	97	3843	51	391	717	569	44	232	8776

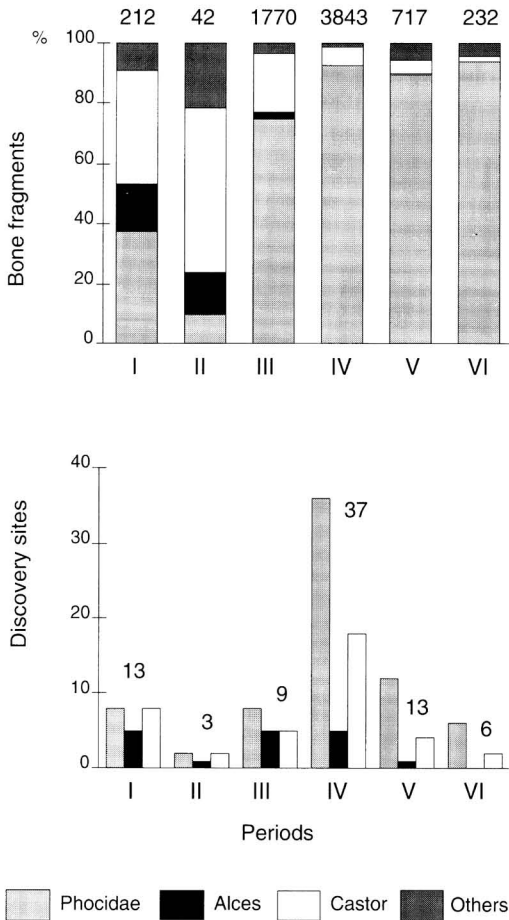


Fig. 5. Proportions of main game species in the refuse fauna of coastal Stone Age dwelling sites based on numbers of bone fragments and discovery sites. Numbers above bars are total fragment and dwelling site numbers, respectively. Periods as in Fig. 2.

4. Discussion

The Finnish subfossil fauna is rather monotonous and no distinct faunal periods — like for instance in Denmark (Aaris-Sørensen 1989) — can be detected. This phenomenon may indicate a gradual completion of the fauna with no great shifts in its composition, but it may also be artificial and reflect hunting traditions of prehistoric man rather than the development of the fauna.

4.1. The early terrestrial fauna

The southernmost areas of the Finnish peninsula were deglaciated during the Late Weichselian and then submerged by waters of the Baltic (Eronen 1983). The pollen composition of the Younger Dryas (11 000–10 000 BP), with high percentages of non-arboreal pollen, indicates a tundra vegetation (Donner 1965). The colonisation of the Finnish peninsula by mammals became possible during this period by two routes: from the south through the Karelian isthmus, and directly from the east. These immigration routes probably remained the most important ones during the entire colonisation of the area.

The datings of the youngest mammoth find from Herttoniemi in Helsinki — 9030 ± 165 BP (Pearson et al. 1976) and $15\,500 \pm 200$ BP (Donner et al. 1979) — are difficult to interpret in accordance with the present views of the deglaciation process and the history of the mammoths. According to Lepiksaar (1992) the Herttoniemi find — along with the ca. 9800 years old find from Kunda, Estonia — could, however, represent a late mammoth population living during the Weichselian deglaciation. Vartanyan et al. (1993) recently reported a discovery of a population of dwarfed mammoths living on Wrangel Island in the Arctic Ocean as late as 7000–4000 years ago.

The late Glacial find of arctic fox (Kurtén 1966) is in good accordance with the climatic and vegetational image of the Younger Dryas. It is not possible to reconstruct the early fauna on the basis of one single find, but in my opinion the find clearly indicates that also the arctic fauna colonised Finland from the south and not from the north as proposed by Siivonen (1972). During the Younger Dryas southern Finland was still isolated from the supposed refuge areas on the Norwegian coast by an extensive glacier (Eronen 1983).

The terrestrial fauna of the Preboreal chronozone (10 000–9000 BP) remains unknown; there are no remains from this period from Finland or adjacent areas in Russian Karelia (Marvin 1977). By the end of the period the whole area of Finland was deglaciated (Ignatius et al. 1980) and the southern parts of the country were covered with open birch forests (Donner 1972).

The oldest postglacial finds are from the Boreal chronozone (9000–8000 BP). The amel-

ioration of the climate and the increase in the area of dry land promoted the spread of the vegetation and the fauna to the Finnish peninsula. Pine displaced birch as the dominant tree and the forests became more closed (Donner 1972). Young deciduous and pine forests offered favourable habitats for red fox, elk, beaver, and arctic hare, the remains of which have been found in the earliest Stone Age dwelling sites.

The presence of roe deer in the refuse fauna of Ruoksmäki, Askola, in southern Finland — although based on a single bone fragment — can indicate an early southern impact on the Finnish fauna. Roe deer remains have been found also at contemporaneous dwelling sites in Kunda and Narva in Estonia (Paaver 1965). In Russian Karelia roe deer bones have been identified from dwelling sites dated to the Atlantic and Subboreal chronozones (Marvin 1977, Savvateev & Vereshchagin 1978, Vereshchagin 1979).

The subfossil fauna of the Atlantic chronozone (8000–5000 BP) is much more complex than that of the earlier periods. The appearance of bear, squirrel, and pine marten in the refuse fauna reflects the advance of pine forests earlier in the Boreal (Donner 1972, Hyvärinen 1972). Beaver, elk, and arctic hare bones still dominate in the material, however. According to Lepiksaar (1986) the increasing humidity in this period must have favoured the beaver and other amphibious species, such as the otter and the European mink (*Mustela lutreola* L.). The former is represented in the Finnish refuse fauna, but of the latter there is no concrete evidence. The species may, however, be included in the category Mustelidae.

Reindeer appears in the refuse fauna for the first time in the Atlantic chronozone. Altogether the reindeer finds are rare and hardly justify the previous conception of early Finland as a “land of the reindeer hunters”.

The appearance in the subfossil fauna of southern species like badger and wild boar reflect the amelioration of the climate and the changes in the vegetation. The dominance of pine decreases and the proportion of oak, elm, linden, and hazel pollen increases in the pollen diagrams of southern Finland (Donner 1971).

The decrease in the species number of the subfossil fauna in the Subboreal chronozone (5000–2500 BP) is in my opinion artificial. It is

due to the drop in the number of dwelling sites rather than to an impoverishment of the fauna itself, possibly with the exception of southern species like the wild boar. The spruce forests, spreading from the east, reached southern Finland in this period, displacing deciduous and mixed oak forests (Donner 1972). It can be assumed that the composition of the mammalian fauna was already quite modern in this period, resembling the present boreal fauna.

4.2. The special case of the reindeer

The subfossil remains of terrestrial mammals are still too scarce to give any clear picture of the distribution of different species in different periods. The climatical changes have certainly caused fluctuations in the distribution of the species, especially the southern elements of the fauna. Such fluctuations are known from historical times, too, for instance in the case of the polecat (*Mustela putorius* L.) (Kalela 1948a), and possibly the roe deer (Kalela 1948b).

The geographical distribution of the reindeer finds is interesting. Four dwelling sites with reindeer remains (Saarijärvi, Pieksämäki, Sulkava and Sääminki) are located in south-eastern Finland and dated to the Middle and Late Atlantic. Deciduous forests dominated by birch and including trees of the mixed oak forest hardly represent a habitat one associates with the mountain reindeer (*Rangifer tarandus tarandus* L.) of the arctic tundra. The forest reindeer (*Rangifer tarandus fennicus* Lönnberg), common almost throughout Finland in the 18th century (Montonen 1972), is a much more plausible candidate. This contradicts the earlier conceptions of the history of this subspecies (or ecotype) in the Finnish peninsula. According to Montonen (1972), forest reindeer was absent from southern Finland in the Atlantic, and Lepiksaar (1986) assumes that it first immigrated to Finland and further to northern Scandinavia in the Subboreal together with the spread of the spruce forests.

It should be emphasized that mountain and forest reindeer bones are morphologically indistinguishable in the highly fragmented burned bone material. Even elk and reindeer bones are mostly distinguished by their size. The red deer

(*Cervus elaphus* L.), found in Sweden, Norway, Estonia and Latvia since the Boreal (Lepiksaar 1986), would be well suited to the Finnish Atlantic fauna. Because of the problems in identifying different cervid species in the refuse fauna, verification of the possible existence of red deer in Finland, discussed earlier by Forstén (1972), is extremely problematic.

4.3. Marine mammals

The deglaciation of the Baltic basin led to the formation of the Baltic Ice Lake (Eronen 1983). The basin was isolated from the North Sea until about 10 200 years ago, when a connection to the ocean was opened through Central Sweden with a drop in the sea level marking the beginning of the Yoldia stage (Eronen 1983). Lake Ladoga was already isolated from the Baltic before the Yoldia stage (Saarnisto 1970) and the Karelian isthmus was formed. The connection between the Baltic basin and the ocean was broken again because of the glacio-isostatic land uplift about 9500 years ago and the Baltic entered the Ancylus-lake stage (Eronen 1983). The sea level rose again and part of the Karelian isthmus was temporarily submerged. Owing to the continuous land uplift lake basins were isolated from the Baltic around 9000–8000 BP (Saarnisto 1970). Around 8500–8000 BP, the eustatic rise of ocean levels led to the opening of a new outflow channel at the Straits of Denmark (Eronen 1983). After this so called Mastogloia stage the Baltic basin entered its Litorina stage around 7500 BP (Eronen 1983).

Seal remains are by far the most common category in the Finnish subfossil fauna, both as stray finds and in the dwelling site material. In the refuse faunas their identification to species is in most cases impossible. The archeological finds include some harp seal (*Phoca groenlandica* Erxl.) and grey seal (*Halichoerus grypus* Fabr.) finds, but most of the fragments probably belong to the ringed seal (*Phoca hispida* Schreb.).

Ringed seal is already common in the stray finds belonging to the Ancylus-lake stage of the Baltic sea (Preboreal and Boreal), which shows that the species immigrated to the Baltic sea at its Yoldia-sea stage. When the great inland lakes

were isolated from the Baltic sea, seals were trapped in them. The recent ringed seal population of Lake Saimaa is a relict from this time.

Seal remains are found in the coastal area and in the refuse fauna of seven inland dwelling sites. Two of them (Sulkava, Lappee) are located on the shore of the ancient Lake Saimaa and one (Sortavala) on a former island in Lake Ladoga. Other inland dwelling sites with seal remains are Säräisniemi, Luopioinen and Rovaniemi at the Lakes Oulunjärvi, Kukkia and Kolpene, respectively. The remaining site, Vihanti, was located very near the coast.

When interpreting the inland seal finds one should consider the possibility that the seals were hunted at the coast and then transported to the dwelling site (Ailio 1909). This uncertainty is inherent in the interpretation of the whole refuse fauna. If the other finds are regarded as a sample of the local fauna, I do not see any reason to discard this principle in the case of the seals. The fact that isolated seal populations exist today only in Lakes Saimaa and Ladoga does not exclude their former existence in other inland lakes, too. The extinction of these populations can be explained by intensive hunting by man, but may as well be caused by demographic factors acting in small, isolated populations (Järvinen & Varvio 1986).

The harp seal appears in the refuse fauna for the first time in the Subboreal (dwelling sites in Espoo, Jomala and Sund, and possibly Eurajoki, Evijärvi, Harjavalta, and Purmo). The major part of the stray finds is also from this period. According to Lepiksaar (1986) there are three hypotheses concerning the Baltic history of the harp seal: the species may be a relict from the Yoldia-sea stage, it may have established breeding populations in the Baltic, or the finds may come from periodical migrations of harp seals. All Finnish finds are connected with the Litorina stage of the Baltic sea, which indicates a relatively late immigration of the species to the area. The question whether the seals established a breeding population or not may be difficult to solve, the specific identification of juvenile seal bones being even more difficult than that of adult individuals. The harp seal disappeared later from the Baltic fauna.

Grey seal is rare in the Finnish subfossil fauna. The stray find from Teuva is dated to the Litorina

stage, i.e., to the Early Atlantic, the two refuse fauna finds to the Early Subboreal. Grey seal is common only in the refuse fauna of the Bronze Age dwelling site at Kökar in Åland (Forstén & Alhonen 1975).

Remains of the harbour porpoise are rare in the subfossil material. The Baltic stray finds are dated to the Atlantic and Subboreal chronozones, the refuse fauna finds from Jomala, Åland, to the Early Subboreal (Winge, archive notes).

4.4. Abundance of different species in the refuse fauna

The proportion of bone fragments of a species in the refuse fauna does not reflect its abundance in the natural fauna itself. The changes in the proportions can be artificial, being caused by the difference in the sample sizes. An analysis based on the number of discovery sites is in my opinion more reliable and shows that prehistoric man for one reason or another changed his preference from elk to seals in the Late Atlantic. The phenomenon may be connected with hunting culture only, or it may reflect the changes in the availability, i.e., the abundance, of the species. In the latter case the reason could be looked for in the increase of the seal populations or decrease of the elk populations.

Forstén (1972) has discussed the possibility of a shift northward of the range of the elk during the Atlantic. Siiriäinen (1982) proposes that the species became depleted due to over-exploitation and/or changing environment. In my material elk is present also in southern Finland until the Middle Subboreal. At inland sites, not included in the quantitative analysis, elk is present at ten out of a total of sixteen Late Atlantic dwelling sites. These facts do not support the assumption of a decreasing elk population. The proportional decrease in the number of elk finds seems to be a phenomenon connected with the coastal area and may, therefore, be caused by the increasing availability or desirability of seals. The absence of elk in the Middle Subboreal may be explained by the fact that the material does not include any inland sites dated to this period.

The changes in the abundance of different species is apparent in the refuse fauna of adja-

cent countries, too. Verešchagin (1979) reports an abrupt decrease in the proportion of elk bone fragments after the Atlantic in the refuse fauna of the Baltic countries. According to Lepiksaar (1986) the shift in man's prey preferences from leaner game (cervids and aurochs) to fat meat (seals and pigs) may reflect the deterioration of the climate at the end of the Subboreal.

5. Conclusions

The colonisation of the Finnish peninsula by mammals began during the Late Weichselian with the invasion of arctic species from the south. The development of the postglacial fauna was gradual with no great shifts in its composition. The first colonisers were species associated with young deciduous forests. These were followed by species associated with pine and mixed oak forests, the latter indicating a southern impact on the fauna. The geographic distribution of the finds reveals some new aspects concerning the faunal history of certain species. Forest reindeer seems to have invaded southeastern Finland earlier than previously assumed, i.e. in the Atlantic. Seal remains from inland dwelling sites indicate strongly that Lakes Ladoga and Saimaa were not the only inland lakes inhabited by seals soon after their isolation from the Baltic basin.

Refuse faunas are practically the only concrete evidence of the early mammalian fauna in Finland. The results of the refuse fauna analysis do not radically alter the previous conceptions concerning the development of the fauna, but they show that the history of Finnish mammals — at least that of species hunted by man — can be studied in spite of the lacking or scarce stray finds. Faunal studies based on concrete evidence, i.e. mammalian remains, can form a more reliable basis for discussions about the early fauna and the economy of man in Finland.

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Appendix. List of Stone Age dwelling sites, catalogue numbers (KM = National Museum, SatM = Satakunnan Museo, Åm = Ålands Museum), analysing osteologists (LB = Leif Blomqvist, PE = Per Ericson, TF = Tarja Formisto, AF = Ann Forstén, MF = Mikael Fortelius, SF = Stella From, JJ = Jukka Jernvall, SN = Sirpa Nummela, PU = Pirkko Ukkonen, HW = Herluf Winge) of the samples, classification of the sites (A = Åland, C = Coast, I = Inland), and period (I–VI, see Fig. 2).

Alajärvi Kurejoki Rasi	KM 11771	MF	C	II
Alajärvi Kurejoki Rasi	KM 12583	AF	C	II
Alavus Rantatöysä Rantalainvainio	KM 12583	AF	C	I
Alavus Rantatöysä Vasikkahaka	KM 10171	AF	C	I
Askola Naikkila Haiti Myllypelto	KM 12935	JJ	C	I
Askola Naikkila Rahkaissuo	KM 13302	AF	C	I
Askola Naikkila Ruoksmäa	KM 12599	JJ	C	I
Askola Naikkila Ruoksmäa	KM 13067	JJ	C	I
Askola Naikkila Ruoksmäa	KM 13303	JJ	C	I
Askola Naikkila Takalan Hopeapelto	KM 13064	JJ	C	I
Askola Nietoo Mattila Tallikäärö	KM 12934	JJ	C	III
Askola Pappila Saunapelto Perunamaa	KM 12603	JJ	C	III
Askola Pappila Saunapelto Perunamaa	KM 13068	JJ	C	III
Askola Pappila Siitapellonhaka	KM 12933	JJ	C	III
Askola Pappila Siitapellonhaka I	KM 12600	JJ	C	IV
Askola Vahijärvi Siitela Kotopelto	KM 9213	JJ	C	I
Askola Vakkola Ahlstedt'in pelto	KM 12647	JJ	C	I
Askola Vakkola Suursuo	KM 12605	JJ	C	III
Askola Vakkola Toppinen	KM 12264	JJ	C	I
Askola Vakkola Toppinen	KM 12266	JJ	C	I

Elimäki Hämeenkylä	KM 13649	MF	C	IV	Miehikkälä Heikkilä	KM 4564	MF	C	IV
Enontekiö 89 Hetta Museotontti	KM 23877	SF	I	II	Muhos Pyhänsivu Honkala	KM 3871	HW	C	IV
Enontekiö 89 Hetta Museotontti	KM 24464	SFSN	I	II	Paltamo Kiehimänsuu Kaarre	KM 15225	MF	C	I
Enontekiö 89 Hetta Museotontti	KM 25256	PU	I	II	Pieksämäki Naarajärvi	KM 21519	MF	I	IV
Espoo Bosmalm	KM 23045	TF	C	V	Pieksämäki Naarajärvi	KM 22019	MF	I	IV
Espoo Bosmalm	KM 22026	TF	C	V	Pielavesi Kivimäki	KM 24465	SF	I	IV
Espoo Bosmalm	KM 22396	TF	C	V	Pihtipudas Rönnny	KM 3938	HW	I	IV
Espoo Bosmalm	KM 23809	TF	C	V	Pihtipudas Rönnny	KM 4146	HW	I	IV
Eurajoki Etukämpä	KM 17274	MF	C	VI	Pihtipudas Vuohtojärvi	KM 3938	HW	I	IV
Evijärvi Jokela Koskimäki	KM 11904	MF	C	IV	Pomarkku Honkakoski Myllytörmä	KM 9560	MF	C	IV
Evijärvi Lahdenkylä Isokangas	KM 20603	MF	C	V	Porvoo Henttala	KM 11617	AF	C	IV
Harjavalta Hiittenharju Laurila	SatM 16.445	MF	C	V	Porvoo Munkby Böle	KM 17387	MF	C	IV
Harjavalta Hiittenharju Motocross	KM 20493	MF	C	V	Porvoo Munkby Böle	KM 19799	MF	C	IV
Harjavalta Kaunismäki	KM 12816	MF	C	VI	Porvoo Munkby Böle	KM 17074	MF	C	IV
Harjavalta Lyytikänharju	KM 13554	MF	C	VI	Purmo Hundbacka Myllykangas	KM 20723	MF	C	V
Harjavalta Lyytikänharju	KM 13842	MF	C	VI	Pyhtää Siltakylä Brunamossen I	KM 20613	MF	C	V
Harjavalta Nakkila Kaunismäki	KM 11594	MF	C	VI	Pyhtää Siltakylä Brunamossen II	KM 20614	MF	C	V
Helsingin mk. Kaarela Etelä-Vantaa 2	KM 18470	MF	C	IV	Rautio Kivimaa	KM 23381	SF	C	IV
Helsingin mk. Hakkilan tienhaara	KM 18502	MF	C	IV	Ristijärvi Karhulan kylä Likoniemi	KM 15713	MF	I	IV
Helsinki Etelä-Kaarela Malminkartano	KM 19902	MF	C	IV	Rovaniemi 236 Jaatila Ojala	KM 25585	PU	C	IV
Helsinki Haaga Kaupintie	KM 19319	MF	C	V	Rovaniemi 236 Jaatila Ojala	KM 24065	PU	C	IV
Helsinki Pitäjänmäki Leikkikenttä I	KM 15485	MF	C	IV	Rovaniemi 277 Saarenk. Piirittävaara	KM 25334	PU	I	V
Honkajoki Lauhala Hietaranta	KM 12257	AF	C	I	Rovaniemi Ala-Korkalo Siikan. III 1	KM 14338	MF	C	IV
Hyrnsalmi Koppeloniemi	KM 20634	MF	I	I	Rovaniemi Ala-Korkalo Siikan. III 1	KM 14410	MF	C	IV
Ilomantsi Piilovaara Syväys	KM 18200	MF	I	IV	Rovaniemi Rautiosaari Turpeenniemi	KM 14709	MF	C	IV
Jomala Jättböle	KM 4630	HW	A	V	Rovaniemi Rautiosaari Turpeenniemi	KM 14278	MF	C	IV
Jomala Jättböle	KM 5907	HW	A	V	Ruovesi Ylistalo	KM 9272	MF	I	IV
Joutsa Kälä Mieskonmäki	KM 25355	PU	I	V	Saarjärvi Tarvaala Summassaari	KM 11865	AF	I	III
Kemijärvi Haveri	KM 15043	MF	I	V	Saarjärvi Tarvaala Summassaari	KM 12234	AF	I	III
Kerava Yli-Kerava Pisinmäki	KM 15432	AF	C	I	Saarjärvi Tarvaala Summassaari	KM 14537	AF	I	III
Kerava Yli-Kerava Pisinmäki	KM 15832	AF	C	I	Salo Villillä Pukkila	KM 20620	MF	C	III
Kiikoinen Uusi Jaara	KM 9409	MF	C	IV	Saltvik Vargstenslätten	ÅM 472	MF	A	IV
Kiikoinen Uusi Jaara	KM 8826	MF	C	IV	Saltvik Västra Jansmyra	ÅM 482	MF	A	IV
Kiikoinen Uusi Jaara	KM 9269	MF	C	IV	Saltvik Östra Jansmyra	ÅM 483	MF	A	IV
Kiukainen Uotinmäki	KM 3574	HW	C	VI	Simo Tainiari	KM 25797	PU	C	IV
Kiukainen Uotinmäki	KM 4275	HW	C	VI	Simo Tainiari	KM 24925	PU	C	IV
Kokemäki Kraviojankangas	KM 20584	MF	C	IV	Simo Tainiari	KM 22398	PU	C	IV
Kokkola Kallis Bläckis II	KM 22821	TF	C	IV	Sodankylä Autiokenttä II	KM 20592	MF	I	II
Kokkola Kallis Bläckis II	KM 22629	TF	C	IV	Sortavala Otsoniemi	KM 7898	MF	I	IV
Kuivaniemi 3 Veskan kangas	KM 24423	PU	C	III	Sulkava Kapakkamäki	KM 20787	MF	I	IV
Kuivaniemi 3 Veskan kangas	KM 24928	PU	C	III	Sulkava Kapakkamäki	KM 8823	MF	I	IV
Kuivaniemi 3 Veskan kangas	KM 25800	PU	C	III	Sund Kolsvidja	KM 13383	PE	A	V
Kuortane Ylijoki Lahdenkangas	KM 16856	AF	C	II	Sund Kolsvidja	ÅM ?	PE	A	V
Kurikka Jäniskallio	KM 16946	MF	C	IV	Suonenjoki Saunaniemi	KM 14821	MF	I	IV
Kurikka Kaistila II	KM 16555	MF	C	IV	Suonenjoki Saunaniemi	KM 14448	MF	I	IV
Kurikka Kuivamäki	KM 17078	MF	C	IV	Säräisniemi Nimisjärvi Niemelänmäki	KM 2378	HW	I	IV
Kurikka Mieto Rajala	KM 18134	MF	C	IV	Säräisniemi Nimisjärvi Niemelänmäki	KM 3147	HW	I	IV
Kurikka Myllykylä Topee	KM 17486	MF	C	III	Säräisniemi Nimisjärvi Niemelänmäki	KM 4080	HW	I	IV
Kurikka Palomäki	KM 16880	MF	C	III	Sääminki Pääskylähti	KM 9085	MF	I	IV
Kurikka Puska	KM 16738	MF	C	IV	Tervola 107 Lapinniemi Kuokkamaa	KM 25565	PU	C	IV
Kymi Huruksela Töyrylä	KM 17509	MF	C	IV	Tervola 110 Lapinniemi Veittonen	KM 25566	PU	C	V
Kymi Juurikorpi I	KM 12750	MF	C	IV	Tervola 116 Lapinniemi Myllyaho	KM 24587	PU	C	V
Kymi Laajakoski Porkka	KM 17689	MF	C	IV	Tervola 117 Koivu Tynnyripari	KM 25567	PU	C	IV
Kymi Laajakoski Porkka	KM 18116	MF	C	IV	Tervola 118 Koivu Alakangas	KM 24589	PU	C	V
Kymi Mäyräsmäki	?	MF	C	IV	Tervola 30 Törmävaara	KM 23399	SF	C	V
Kymi Niskasuo	KM 17075	MF	C	IV	Tervola 30 Törmävaara	KM 22481	SF	C	V
Kymi Tavastila Tuuli	?	MF	C	IV	Tervola 30 Törmävaara	KM 22070	SF	C	V
Lahti Renkomäki Ristola	KM 18501	MF	C	I	Vantaa Etelä-Vantaa	KM 18450	MF	C	IV
Lahti Renkomäki Ristola	KM 18320	MF	C	I	Vantaa Etelä-Vantaa 2 (Mätäoja)	KM ?	AF	C	IV
Laitila Kotjala Nästinristi	KM 20606	MF	C	V	Vantaa Etelä-Vantaa 3 (Mätäoja3)	KM 18978	MF	C	IV
Lappee Rutola Saksanniemi	KM 12169	MF	I	V	Vantaa Hakkila Stenkulla	KM 20660	MF	C	V
Liljendal Andersby Kvarnbacken	KM 9273	MF	C	IV	Vantaa Kaarela Jönsas (länsi)	KM 19274	MF	C	II
Liljendal Andersby Kvarnbacken	KM 18900	MF	C	IV	Vantaa Myyrmäki Kilteri	KM 19231	MF	C	III
Liljendal Andersby Kvarnbacken	KM 19152	MF	C	IV	Vihanti Pitkäsaari	KM 3759	HW	I	IV
Luopioinen Padankoski Hietaniemi	?	LB	I	IV	Äänekoski Kapeenkoski	KM 25301	PU	I	II