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Remarks on the Weichselian megafauna (*Mammuthus, Coelodonta* and *Bison*) of the "intraglacial" area around the Baltic basin[1]

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The entire fossil material of *Mammuthus primigenius*, *Coelodonta antiquitatis* and *Bison priscus* from the "intraglacial" area in Fennoscandia, Estonia and Latvia is reviewed for the first time. The finds can be referred to three age groups, partly on the basis of radiocarbon dates: Eemian / Early Weichselian (very rare), Weichselian interstadials, and Late Weichselian. The sedimentology and taphonomy of the finds suggest that the interstadial material was preserved within blocks of frozen sediment or ice, and perhaps transported by the moving ice sheet over short distances. There is no evidence of specimens surviving long-distance transport by the ice sheet, which probably destroyed a large proportion of the material originally preserved. The late-glacial (Weichselian deglaciation) material is better preserved and includes relatively more non-dental material. These later finds are confined to Scania, Finland south of the Salpausselkä and the Baltic Republics.

1. Introduction

At its maximum extent, the Scandinavian Ice Sheet of the Weichselian glaciation extended over all of Fennoscandia, the entire basin of the Baltic Sea, and its borders to the East and South. Ecologically the vast ice-covered area must have been a sterile desert, offering no means of permanent existence to mammals. In spite of this, numerous remains of large mammals of latest Pleistocene age have been found within this intraglacial area, in Fennoscandia as well as in the northern Baltic Republics of Estonia and Latvia.

Although a number of reports on these finds have been published, a review of the finds from the whole area has hitherto been lacking. The aim of this paper is to present such a review and inventory, limited to the distribution of the three extinct megaherbivores *Mammuthus primigenius* (woolly mammoth), *Coelodonta antiquitatis* (woolly rhinoceros) and *Bison priscus* (steppe bison). The distribution and nature of the finds is presented and discussed in relation to palaeoecological and taphonomic factors and to faunal history.

[1] Dedicated to the memory of Professor Björn Kurtén.

2. Localities and literature

The localities are listed below according to species, country and geographical location (see Fig. 1).

Mammuthus primigenius (Blumenbach, 1803)

Norway

I. Gudbrandsdal Valley (continued to the basin of Lake Mjøsa): 10 localities with 16 finds
   a. Finds along the principal valley with River Lågen: 1. Islet of Krokstadøya near Vigerust Farm at Dovre (1929). — 2. Gravelpit at Kvam (1964, 1967, 1968, 1970). — 3. Gravelpit at Fåvang (1941, 1959).
   b. Finds in the minor valleys: 4. River Storebekken at Skarvang (1886). — 5. Vågåvann (1933, 1973). — 6. River Otta (1910). — 7. River Ula (1944).
   c. Mjøsa Lake basin: 8. Lillehammer (1954). — 9. Skreia at Toten (1955). — 10. Gravelpit at Jessheim (1930).
   Literature: Øyen (1931:1), Holtedahl (1931:10), Bergersen (1932:1,4,8,10), Heintz (1945:1,3,4,5,6, 7,10; 1955:1,3,4,5,6,7,8,10; 1956:9; 1962:2,3; 1965:2,9; 1969:2; 1971:1-10; 1974:2,5). See also Berglund et al. (1976).

Sweden

II. Southern Norrland (Prov. Ångermanland, Jämtland and Medelpad); 6 localities with 6 finds (incl. 1 skeleton)
   a. The Basin of Lake Storsjö: 1. Önet on Frösö Island (1915). — 2. Gravelpit at Pilgrimstad (1944).
   b. The valleys of Faxälv and Ångermanälv Rivers: 3. Ramsele (1949). — 4. Sollefteå (1949).
   c. The valley of River Indalälven: 5. Gravelpit at Kånkback (1975). — 6. Sattna (1935).
   "Big bones" are said to have been found in 1877 in a gravelpit at Önsta in Jämtland (Kulling 1945:80). A find of a humerus of *Ovibos*, found in the Rosenhill gravelpit on Frösö Island, originally reported as a "metapodial" of mammoth (Thorslund 1937; cf. Kulling 1945).
   Literature: Frödin (1916:1), Gavelin (1935:6), Geijer (in Kulling 1945:2), Kulling (1945,1946:2), Sandegren (1950:3,4), Magnusson et al. (1957:2:297-298), Lundqvist & Pleijel (1976:5).

III. Basin of Lake Siljan (Prov. Dalarna): 2 localities with 2 finds
   1. Lerdal at Back (1956). — 2. Rättvik at Lake Siljan (1956).
   Literature: Thorslund (1957).

IV. Stockholm (Prov. Uppland): 1 locality with 2 finds
   1. Stockholm, presumably a gravelpit at Brunkebergsåsen (1849).
   Literature: Werdelin & Ericson (1989).

V. Lower valley of River Götaälv (Bohuslän): 1 locality with 3 finds
   1. Gravelpit of Dösebacka, on the right side of Götaälv, opposite to the Nol Station (1931, 1961, 1964). In 1904 a tibia, presumably of *Ovibos*, was found here (cf.Munthe 1905). "Large limb bones" are said to have been found here in 1918 and 1921, but do not appear to have been preserved.
   Literature: Jägerskiöld (1932), Hillefors (1961, 1964, 1969), Lepiksaar (1968, fig. on p.20)

VI. West and south-west Scania (Prov. Skåne): 6 localities with 8–9 finds
   1. Bårslöv (1884; another find from here is said to have been destroyed during a fire around 1913, cf. Liljegren 1975).— 2. Djurslöv (1930). — 3. Gravelpit at Lockarp (1939). — 4. Risebjär in Arrie Parish (1934, 1951). — 5. Tittente Farm in Svedala Parish (1863). — 6. Gravelpit at Örsjö (around 1940, 1972).
   Literature: Erdmann (1868:5), Geijer (in Kulling 1945:4,5), Persson (1961), Liljegren (1975), Berglund et al. (1976).

In addition to the finds of geographic group VI, three finds of mammoth-remains are preserved from Scania (cf. Angelin 1867; Liljegren 1975; Berglund et al. 1976).

Finland

VII. Ostrobothnia (Pohjanmaa): 3 localities with 4 finds
   1. River Ijoki (about 1751). — 2. Lohtaja near the Gulf of Bothnia (about 1949). — 3. Haapajärvi (1952).
   Literature: Quensel (1804:1), Holm (1904:1), Korvenkontio (1914:1), Okko (1949:2), Donner (1961:3).

VIII. Central Finland: 2 localities with 2–3 finds
   1. Nilsiä at Lake Syväri (about 1874). — 2. Tuulos (about 1924).
   Literature: Malmgren (1875:1), Korvenkontio (1914:2), Rosberg (1924:1).

IXa. North-western shoreland of the Gulf of Finland: 4 localities with 4 finds
   1. Brödtorp at Pohja (Pojo) (about 1901). — 2. Espoo (about 1925). — 3. Helsinki (about 1914). — 4. Herttoniemi (1954).
   Literature: Rosberg (1901:1), Korvenkontio (1914:3), Metzger (1925:2), Donner (1961:4). Cf. Pearson & al. (1965), Berglund et al. (1976).

Estonia

IXb. Southern shoreland of the Gulf of Finland: 7 localities with 9 finds
   a. Finds around Tallinn (Prov. Harjumaa): l. Paljassaar (Carlos) (before 1870). — 2. Pirita (Brigitten) (before 1870). — 3. Between Lasnamägi and Lake Ülemiste (1915). — 4. At Lake Ülemiste (about 1930).
   b. Finds east of Tallinn in Prov. Harjumaa: 5. Ihasalu (1930).

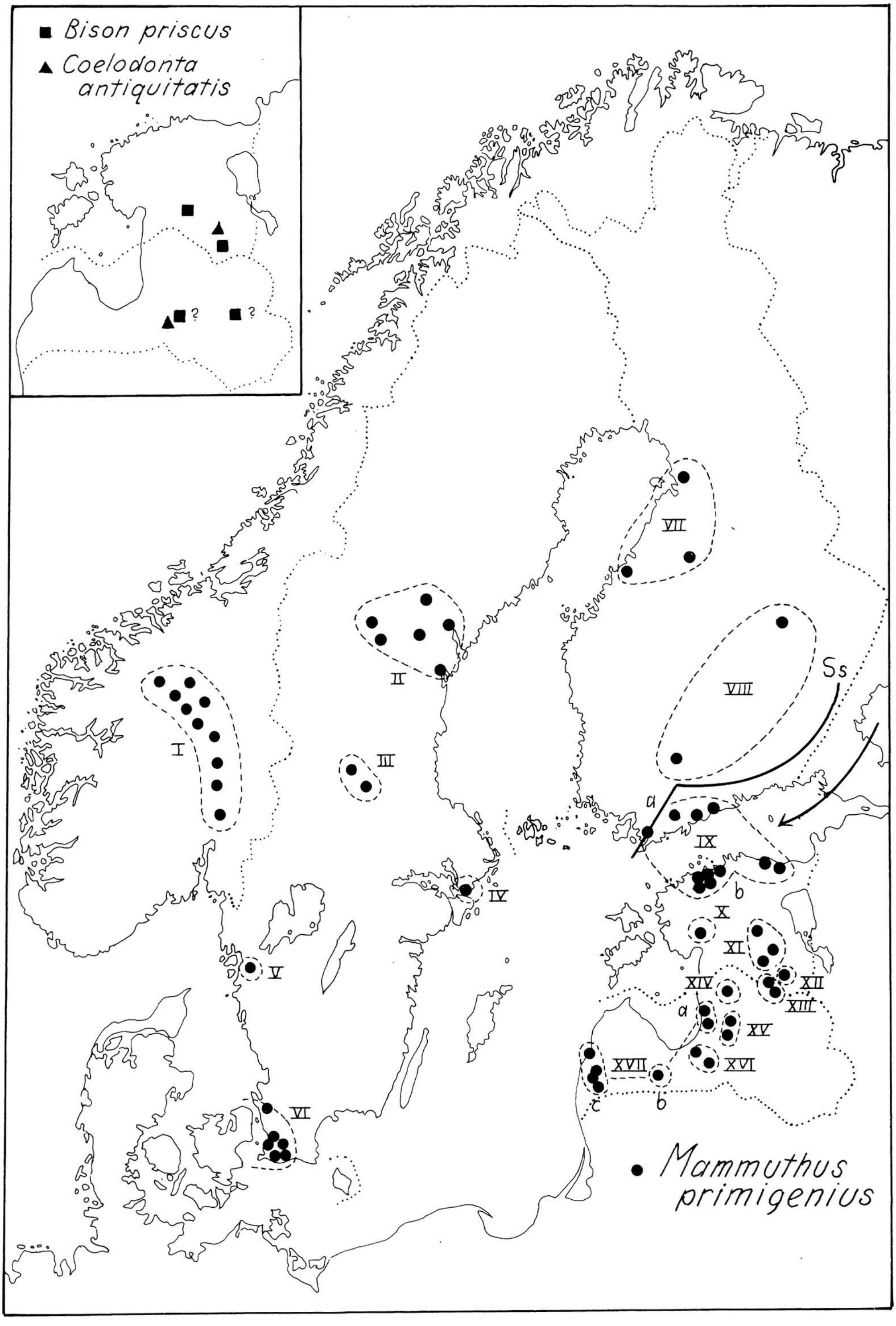

Fig. 1. Localities around the Baltic where remains of *Mammuthus primigenius*, *Coelodonta antiquitatis* and *Bison priscus* have been found. — Ss: the end-morain ridges of Salpausselkä.

c. Finds in Prov. Virumaa: 6. Kunda Lammasmägi (1935). — 7. Püssi (Neu Isenhof) in Lüganuse (Luggenhusen) Parish (before 1884).

Literature: Grewingk (1874:2; 1881:1,2 ; 1884:7), Grevé (1909), Thomson (1934:1,2,4,5), Eplik (1935:3), Indreko (1936:6), Lepiksaar (1937).

X. Valley of River Pärnujõgi (Prov. Pärnumaa): 1 locality with 1 find

1. Taali (Staëlenhof)(before 1861).

Literature: Grewingk (1861, 1874, 1881), Grevé (1909), Lepiksaar (1937).

A proximal fragment of a tibia, preserved in the collections of Museum of Zoology at Tartu University is said to have been found in Pärnumaa "a long time before 1930".

XI. Basin of River Emajõgi (Prov.Tartumaa): 3 localities with 4 finds

a. Finds north of Emajõgi: 1. Road between Puurmanni and Laeva (about 1895).

b. Finds south of Emajõgi: 2. Gravelpit at Kalmemägi near Elva (about 1874). — 3. Gravelpit at Oja in Hellenurme Parish (before 1884).

Literature: Grewingk (1884:3), H. Kauri (in litt.:2), Lepiksaar (1937:3), Paaver (1957:1).

XII. Lake Tamula (Prov. Võrumaa): 1 locality with 1 find

1. Sarvemägi (" Horn Hill" on the shore of Lake Tamula (1934).

Literature: Lepiksaar (1937).

XIII. Basin of River Mustjõgi (Prov. Võrumaa): 2 localities with 5 finds

1. Kallaste Gravelpit at Saru (1933, 1948). — 2. Tahkumägi ("Grindstone Hill") in the valley of the stream Peetrioja near Mõniste (Mentzen) (before 1874; about the end of the 19th Century; 1935).

Literature: Grewingk (1874:2, 1881:2), Greve(1909:2), Orviku (1933:1,2), Luha (1933:2), Lepiksaar (1937), Paaver (1957:1).

Latvia

XIV. Basin of Lake Burtnieku (Prov. Vidzeme): 1 locality with 1(2) finds

1. At Burtnieku ezeru (Burtnecksee) (before 1874). Literature: Grewingk (1874, 1881), Grevé (1909).

XV. Lower valley of River Gauja (Koiva, Livl.Aa) (Prov. Vidzeme): 2 localities with 2 finds

1. Gravelpit at Araiši (Arrasch) (before 1909). — 2. Ligatne (Ligat) (before 1861).

Literature: Grewingk (1874:2, 1881:2), Grevé (1909:1,2).

XVI. Lower valley of River Daugava (Düna): 2 localities with 2 finds

1. Meinhardts Muiža (Meinhardtshof) (about 1909). — 2. Ogre (Ogershof) (before 1874).

Literature: Grewingk (1874:2, 1881:2), Grevé (1909:1,2).

XVII. Coastal Lowland: 7 localities with at least 7 finds

a. Vidzeme Lowland near Limbaži: 1. Lades Muiža (Ladenhof) (before 1846). — 2. Gravelpit at Taurene (1932).

b. River Lielupe Basin : 3. Gala Muiža (Endenhof) at Sesava River (before 1881).

c. Baltic Coast of Kurzeme: 4. Labrags (Labraggen) (about 1909). — 5. Vecpils (after 1909). — 6. Between Durbe and Tadaiki (before 1881). — 7. Krute (Kruthen) (before 1874).

Literature: Grewingk (1874:4, 1881:3,4), Grevé (1909: 1,3,4). Dreimanis (in litt.:2).

Coelodonta antiquitatis (Blumenbach, 1803)

Estonia

1 locality with 1 find

Sulbi near Võru (Prov. Võrumaa) (1937).

Literature: Lepiksaar 1937.

Latvia

1 locality with 1 find

Lielvarde ("zwischen Lennewarden und Ringmundshof") in the lower valley of River Daugava (Prov.Vidzeme) (before 1861).

Literature: Grewingk (1861, 1881), Grevé (1909).

Sweden

The teeth of woolly rhinoceros mentioned by S. Nilsson in his lectures in 1847 cannot be verified, according to Möller (1923; cf. Liljegren 1975)

Bison priscus (H. v. Meyer, 1832)

Estonia

2 localities with 2 finds

1. Lake Võrtsjärv, dredged with a fishing-seine from the central part of the Lake (1936). — 2. Tahkumägi (Prov. Võrumaa) in the valley of Peetrioja, near the find of mammoth in XIII:2 (before 1874).

Literature: Grewingk (1874:2, 1878:2, 1881:2), Grevé (1909:2), Lepiksaar (1937:1,2).

Latvia

2 very dubious finds at 2 localities (?).

1. Lielvarde (Lennewarden) in the lower part of the valley of River Daugava valley (Prov. Vidzeme). — 2. Lake Lubanas ezeru (Lubahnsche See), Prov. Zemgale (before 1909).

Literature: Grevé (1909) reports these finds under *Bison priscus* together with finds of *B. bonasus*. According to Lamsters (1937), neither the specific identity nor the geological age of these finds is exactly known.

3. Historical remarks

The earliest known reports of mammoth finds from the area around the Baltic Sea date back to the second half of the 18th century. The first Fennoscandian find was a cheek tooth from Iijoki in present-day Finland. It was donated to the Royal Academy of Sciences in Stockholm in 1751 by a former apprentice to C. Linné, C. F. Mennander, at that time Professor physicus at Åbo (Turku) and later archbishop of Uppsala. A second early find is reported by Grewingk (1881), who mentions a report by J. B. Fischer in about 1769, concerning a mammoth cheek tooth from "Livonia" (either southern Estonia or northern Latvia of today). (J. B. Fischer was another student of Linné's, and the author of "Versuch einer Naturgeschichte Livlands", published in 1778 at Leipzig and 1791 at Königsberg.)

After somewhat more that two centuries of intentional collecting and scientific studies about 82 finds are known from the entire intraglacial area, distributed as follows: Norway 16, Sweden over 23, Finland 11, Estonia 20 and Latvia about 12. In addition, there are two finds of woolly rhinoceros (one from Estonia, one from Latvia) and two finds of steppe bison (both from Estonia). It must be said, however, that these megafaunal remains have been almost exclusively collected by the traditional passive method of simply waiting for new finds, and not by active prospecting at suitable localities.

4. Manner of discovery

The majority of finds so far have been discovered by workers in sand and gravel pits located in glaciofluvial formations (finds I:2,3,5,10; II:2, 5; III:1–2?; IV:1; V:1; VI:2–6; VIII:2; IXa:1; XI:2,3; XIII:1, XV:1; XVI:2; XVII a:2 XVII c:4). Remains have also been discovered when holes and ditches have been dug at construction sites and roadworks (finds I:3,9; II:1; IX b:4; XI:1). The digging of wells has also produced a few finds (I:8; II:6; the find of *Coelodonta* at Sulbi). Two finds have been dragged out of lakes or sea-beds by fishing seines (IX b:2; the *Bison* horncore from Lake Võrtsjärv (Estonia)).

A considerable proportion of the finds have simply been picked up as interesting objects, at the banks or beds of rivers, or by the shores of lakes or the sea. Such finds would seem to have been washed out of sediments by running water or waves (I:1,4,6,7; VII:1,3; VIII:1; IX b:1,3,5; XII:1; XIII:2 (cheek tooth found at the end of the 19th century).

The find IX b:6 has a curious history. This fragment of a mammoth tusk was found by the archaeologist R. Indreko during excavation of the type site of the mesolithic Kunda culture. Apparently the fossil had been discovered by mesolithic man, either on the shore of the former Lake Kunda or at the nearby coast of the Gulf of Finland. The peculiar shape and consistency of the tusk seem to have attracted enough curiousity for it to have been transported back to the dwelling site. This find may indeed be called a "bifossil" (cf. Pidoplitchko 1969).

That active prospecting may be successful has been demonstrated by O. Kulling, who discovered the complete and so far unique mammoth skeleton at Pilgrimstad (II:2), and by Å. Hillefors, who collected many important finds at a gravelpit at Dösebacka (V). One of the finds from Tahkumägi (XIII:2) was also collected by the archaeologist of the 1935 expedition. That "new" finds may come out of old museum drawers has recently been proven by Werdelin & Ericson (1989) (IV:1).

5. The material

Mammuthus primigenius

Tusks: 28 occurrences (number of specimens in brackets). I:2(2),3,5,9,10; II:1,2(2),5; III:2; V:I(2); VI:3–6; VII:3; IX b:5(2),6; X:1; XI:2,3; XIII:1,2, XVII a:1; XVII b:3; (II:2 has 256 small tusk fragments).

Cheek teeth: 36 occurrences. I:1,2,4,5,6,7; II:2(2),3,4,6; III:1; V:1; VI:1,2,6; VII:1: VIII:1,2; IXa:2,3; IXb:1-4,7; XI:1(2); XII:1; XIII:1,2; XV:1,2; XVI:1,2; XVIIa:2.

Postcranial remains: 32 identified bones. 1 vertebra I:3; 2 costae II:2; VIII:3; 4 scapulae I:8; II:2(2); XIII:2; 5 humeri II:2(2); VI:4; VIII:2; IXa:4; 3 ulnae I:2; IV:1 XVIIc:7; 3 carpalia

II:2(3); 1 metacarpale II:2; 3 pelves I:2; II:2 (ilium, pubis); 4 femora II:2(2); IV:1; IXb:5; 1 patella II:2; 4 tibiae II:2(2); IV:1; IXb:5; 1 fibula? II:2.

The material from Pilgrimstad (II:2) seems to comprise bones of an individual skeleton. Unfortunately, most of the elements have disintegrated into about 50 unidentifiable fragments (Kulling 1945, 1948; cited in Magnusson et al. 1957). Seven unidentified bones of mammoth have been reported from VII:2(2) and XVIIc:4–6. Most of the mammoth finds from the peri-Baltic area are too fragmentary to yield conventional measurements. A defective left femur from Pilgrimstad (II:2) has a maximum length of about 116cm (Kulling 1945).

Coelodonta antiquitatis

A single axis vertebra and a single femur are known. The axis (from Sulbi, southern Estonia) has a corpus length of +115 mm, a maximum height of 180 mm and a width at the praezygapophyses of 153 mm (Lepiksaar 1937).

Bison priscus

Only two horncores from Estonia are known (maximum length along curvature / circumference at basis):

Estonia: Võrtsjärv (Lepiksaar 1937) (500/348); Tahkumägi (Grewingk 1861) (450/380).

Denmark (Degerböl & Iversen 1945): Lysabil (Interglacial) (–/385); Egtved (Interglacial) (520/345).

The conformity of the Estonian finds with corresponding material from Denmark is evident. Horncores of the Late Glacial and Preboreal form of Bison from Denmark and southern Sweden, *Bison bonasus arbustotundrarum* Degerböl & Iversen, 1945, are markedly smaller. Recent *Bison bonasus* horncores are still smaller.

6. Evolutionary trends and ecological adaptations of mammoths

Three partly independent trends of progressive ecological specialisation may be distinguished in the evolution of the Eurasian Pleistocene mammoths:

1) increased specialisation of the cheek teeth for dealing with tough and abrasive grass,
2) a general adaptation to cold conditions, and
3) a possible increase in locomotor specialisations for moving in the broken terrain of highlands.

The dental evolution of mammoths is well known from the Lower Pleistocene *Mammuthus meridionalis* over the Middle Pleistocene *M. trogontherii* to the Late Pleistocene *M. primigenius*. The number of molar lamellae increased considerably during the evolution of the lineage, and this increase has been used to date isolated finds in terms of a "length/lamellae quotient" or LLQ (e.g. Soergel 1913, Guenther 1968). Such dating is problematical, however, and even at best only applicable to relatively large samples because of the considerable individual variation.

The anatomical cold adaptations of the woolly mammoth are well known from carcasses preserved in permafrost and from palaeolithic representations: the long woolly coat of hair, thick layer of subcutaneous fat, the wide anal flap formed by the base of the tail and the conspicuously small ears. The striae commonly present on the ventral aspect of the tusks could be added as evidence that the animals were able to cope with snow (a parallel in this and other features is the woolly rhinoceros; Fortelius 1983). Apart from these striations, however, these anatomical features are not reflected in the hard parts normally preserved.

Several authors have theorised about the whereabouts of the Eurasian woolly mammoths during interglacials, especially the Eemian. In this context the northern highlands have figured as potentially suitable refugia, offering open landscapes and cooler climates than the lowlands. Even the Scandinavian highlands have been suggested as mammoth refugia during the Eemian (Kurtén 1964).

The very conspicuously "humped" appearance of the woolly mammoth may be related to movement on the uneven substrates offered by these refugia. The study of the Tajmyr frozen mammoth by Garutt & Dubynin (1951) suggests that the hump is not solely formed by soft tissues and hair, but also by a kyphotic bend of the thoracic part of the vertebral column itself. Such an arrangement will shorten the body and bring the fore- and hindlegs closer together, a prerequisite for a balanced gait on an uneven surface.

7. Preservation and taphonomy

Three taphonomic categories may be distinguished among the peri-Baltic megafaunal localities:

1) single finds,
2) associated elements of single individuals and
3) thanatocoenoses of several individuals of one or several species.

The great majority of all finds consist of single elements, often fragmentary. Associated elements of a single individual are considerably less common. An example are the ulna and tibia of mammoth found together at Stockholm (IV:1).

Thanatocoenoses are local, but occur over the entire area. A monospecific death assemblage ("elephant graveyard") is known from a gravelpit at Kvam (I:2) (Heintz 1974). It comprises at least three mammoths of different size and age (including a "baby"). At Pilgrimstad (II:2) a mammoth skeleton occurs together with remains of reindeer (*Rangifer*) and elk (*Alces*). Mammoth and musk oxen (*Ovibos*) occur together at Dösebacka (V) and mammoth and *Bison priscus* at Tahkumägi (XIII:2).

It is very noticeable that most finds are of the most compact and durable dental and skeletal elements. This is hardly surprising, given the tremendous stress generated by the moving ice sheet and the limited and localised opportunities for preservation of animal remains.

Teeth and tooth fragments make up 73% of the material. The cheek teeth seem to be the most resistant against mechanical damage, perhaps because of their lamellar structure, with hard enamel-covered plates of dentine alternating with softer cement. In several areas (VIII, IX, XV, XVI) cheek teeth are more frequent than tusks, which consist of dentine only. At Dösebacka (V:1967) only a single enamel covering of a lamella was recovered, in the form of "chirite" (Lepiksaar 1968:20).

The dentine usually contains significant amounts of original collagen, which has been used for radiocarbon dating. In acidic and well-aerated sediments the calcium tends to dissolve out of the apatite of bones and teeth. However, especially when skeletal remains are present in great quantity, the escaping calcium may cement the sand into a hard concretion around the bones, and thus stop further decalcification. Examples are Taali (X) and especially Tahkumägi ("Grindstone Hill", XIII:2).

As preserved within the sediment, the finds usually retain their original anatomical shape quite well, but at sudden exposure and drying they tend to crack and disintegrate into small pieces. Numerous early finds of mammoth tusks must have been destroyed this way. Most specimens in museum collections have been treated with organic preservatives, which makes them unsuitable for radiocarbon dating. The best method of preserving mammoth tusks is by slow dessication, especially by freeze-drying, which simulates the natural method of preservation within the permafrost of subarctic Eurasia and North America.

During the Weichselian, permafrost conditions must have existed throughout the intraglacial area. The existence of permafrost is probably a major factor responsible for the preservation of interstadial faunal remains, despite the repeated advances of the ice sheet. The remains may have stayed within blocks of frozen sediment, and thus survived the destructive action of the advancing ice sheet. Such blocks must occasionally have been large enough to contain specimens of substantial size, as evidenced, for example, by a 112cm long tusk fragment from Kvam (I:2) or a 104cm long defective tusk from Kånkback (II:5). The brittle tibial diaphysis of the juvenile mammoth from Kvam (I:2) could only have survived if protected within frozen sediment or ice. Such frozen blocks are usually smaller, however, and leave broken ends of bones and tusks projecting from their surface. The projecting parts tend to be heavily worn, unlike the parts preserved within the block. Similarly, Donner (1988) has described striated clasts from Norinkylä in Finland, apparently fixed in frozen ground under the moving ice.

It must be emphasised that there is no evidence of long distance transport of megafaunal remains by moving ice. Transport over rocky substrates or within stony tills probably destroyed most of the interstadial faunal remains, except for a few that ended up in crevices or deep holes in the bedrock. All reports of megafaunal remains from "till" must be treated with much caution. Most likely such finds come from lacustrine clays or coarser glaciofluvial sediments. Even in the gravel of a river bed bones and teeth are soon destroyed by rolling, unless incorporated within ice-floes.

With few, if any, exceptions, the remains of Weichselian mammals from the intraglacial area seem to be derived from aquatic sediments. This is in good accordance with the general taphonomic rule that the carcasses of animals that die on land tend to be destroyed quickly by microbal decay and scavenging by large and small carrion feeders. Even bones tend to weather and disintegrate quite rapidly. Especially in calcium-poor environments rodents and other herbivores also destroy bones by gnawing or chewing. Only on isolated islands of the high arctic, without rodents and with a cold climate to slow down microbal activity may animal carcasses and bones remain virtually undamaged for centuries. Such extreme conditions, however, are unlikely to have prevailed in the intraglacial, even during interstadials.

Over considerable areas of Weichselian extraglacial Eurasia the rapid deposition of loess has contributed greatly to the preservation of bones. Remarkable accumulations of mammoth bones have thus been preserved, for example at various anthropogenic thanatocoenoses such as the traditional mammoth kill sites in Moravia or the huts constructed from mammoth tusks and bones from southern Poland and the Ukraine. In the intraglacial area, however, preservation by loess accumulation was not an available mechanism.

In contrast to carcasses on land, drowned animals or carcasses that end up in water may be transported far away from the site of death. Parts of single individuals may also become widely dispersed. During interstadial and late glacial time numerous temporary ice-dammed lakes and meltwater streams existed outside the ordinary drainage systems, and these may have served as transport channels for carcasses bloated by gas or enclosed within ice floes.

Thanatocoenoses have tended to form mainly in backwaters or deltas, or in deep parts of lakes or of the sea. During transport parts of the carcasses may, however, become detached and sink to the bottom elsewhere. The mandible, the skull and the legs (especially the anterior ones) tend to separate first. Local accumulations of teeth in bottom sediments may indicate the former presence of skulls or jaws, perhaps separated from such floating carcasses. Teeth may also easily become detached from the alveoli and end up as widely scattered single finds. Limb elements tend to be held together by the ligaments, and are often found in close association (e.g., IV, VII:2).

Finds of bony skeletal elements of interstadial age are much rarer than those of late glacial age, deposited beyond the range of the destructive ice sheet.

8. Preliminary remarks about faunal history and palaeozoogeography

South of the Baltic Sea a conspicuous concentration of mammoth finds corresponds to a zone at the margin of the Scandinavian ice sheet at its maximum extent. This "periglacial" zone runs through the eastern part of the Jutlandic Peninsula (Jylland), via northern Germany and Poland to south-eastern Lithuania, and further towards the north-east (cf. Aaris-Sørensen 1988, Berglund et al. 1976). In contrast, the finds in the intraglacial area are much more patchily and irregularly distributed. The pattern must reflect some interaction between the structure and size of the remains, local conditions for their preservation (or destruction), and the local lansdcape.

Three chronological categories of origin are conceivable for the intraglacial megafaunal remains:

1) Remains dating back to the early part of the Weichselian, before the Scandinavian glaciers reached the lowlands of the area.
2) Remains of mammoths from the Weichselian interstadials.
3) Remains of mammoths which lived in the area during the late Weichselian deglaciation.

A more precise reconstruction of the faunal history of the intraglacial area would require a great deal of work. In particular more dates of individual specimens are needed. Sadly, the usefulness of radiocarbon dating has so far been quite limited as far as isolated megafaunal remains are concerned, and the number of reliable finite dates is small (Heintz 1965, 1969, 1974, Berglund et al. 1976, Donner et al. 1979, Werdelin & Ericson 1989). This is partly because of problems with dating collagen from fossil bone, and partly because many finds apparently lie at or beyond the maximum age limit of the method. Dating based on vague "evolutionary trends" is of even less value, especially since demonstration of the trends themselves depends on independent dating of the fossils. For these reasons the ideas presented below must be considered very preliminary and due to amendment as more data becomes available.

8.1. Material from the Early Weichselian and the Weichselian interstadials

There are very few demonstrably Eemian/early Weichselian megafaunal remains known from the area. The most likely finds are those from "preglacial" buried valleys, cut deep into the Devonian sandstone bedrock in south-eastern Estonia and northern Latvia. The *Coelodonta* axis from Sulbi in Estonia, discovered at a depth of 4m, in red sands below two separate beds of alternating sand and clay, may belong to this oldest category. The identity of the proboscidean remains is uncertain (if, indeed, any specimens are of this age at all). The straight-tusked elephant (*Palaeoloxodon antiquus*) might well have been present in the Circum-Baltic area during the Eemian, as this species was common in Central Europe and England, and ranged as far north as Denmark (Aaris-Sørensen 1988). Postcranial material is largely indeterminate, and no Circum-Baltic dental remains seem to belong to this species. Kurtén (1964) suggested that *Mammuthus* may have used Scandinavia as an Eemian refugium.

Two Weichselian interstadial complexes may be recognised, one Early Weichselian, including the relatively warm Brorup Interstadial, and one cooler Middle Weichselian, preceding the maximum glaciation culminating at about 20 000 years B.P. (Mangerud 1976, Hillefors 1969, 1974, Lundqvist 1974, Lundqvist & Pleijel 1976, Berglund et al. 1976, Martinson et al. 1987).

During these interstadials species of the extraglacial theriofauna of Central Europe may have expanded their ranges towards the north. There is considerable evidence that the mammoths have done so. Whether *Coelodonta* and *Bison priscus* did so as well is less clear, as their remains have so far only been discovered to the south and south-east of the Baltic. Perhaps these animals of the plains avoided the rocky and uneven landscape of Fennoscandia (unlike the lateglacial/preboreal *Bison bonasus arbustotundrarum* Degerböl & Iversen 1945).

The advance of the ice appears to have destroyed most of the remains of interstadial faunas that may have been preserved. Only at localities with extremely suitable conditions for the preservation of old sediments and their fossils, especially in deep valleys and other depressions in the landscape, have interstadial sediments been preserved. At Pilgrimstad (II:2), for example, an entire mammoth skeleton was preserved in such a location. At Örsjö (VI:6), in the buried valley of Alnarp, remains of mammoth were preserved, while the remains of mammoth and *Bison* from Tahkumägi (XIII:2) also come from sediments filling a buried valley. All of these seem to have been deposited in basins connected with interstadial rivers. In a number of cases such as these, in locations less influenced by the ice sheet, skeletal parts have been preserved in addition to teeth.

A number of interstadial finds may have been washed out of of their sediments by recent waters (I:1,4,6,7; VII?; VIII?; XII:1). This also applies to the *Bison priscus* horncore from Lake V <rtsjärv. Others have been exposed by erosion at steep riverbanks (X; XIII:2). A considerable number of finds seem to have been displaced from their original positions by glaciofluvial waters before, below and behind the moving ice margin, transported within blocks of frozen sediment or ice, or in ice floes, and redeposited in holes or crevices of the bedrock, or in deltas, kames or sandurs. A large proportion of the finds of interstadial origin have been discovered during gravel and sand quarrying at such localities. Many specimens must have been lost during such operations, but they are also the most likely source of new material in the future.

All finds of mammoth north of Scania, as well as some of the Scanian finds, are presumed to be of interstadial origin (I–V). Finds from Finland north of the Salpausselkä (VII, VIII) are also likely to be of interstadial origin, as are finds from the "supra-aquatic" areas of Estonia

(X–XIII) and Latvia (XV, XVI, XVIIc:4), which were never reached by the Holocene transgressions of the Baltic.

In Scandinavia the majority of the interstadial finds (I–III, probably V) seem to derive from the earlier and more extensive of the Weichselian interstadials. Two radiocarbon dates support this contention: Lillehammer (I:8) with finite (?J.L.) ages of 45 000 +1500/–1200 and 46 000 +2000/-1500 B.P., and Kånkback (II:5) with an infinte age of >43 000 B.P. (cf. Heintz 1962, 1974, Lundqvist & Pleijel 1976).

The conspicuous restriction of Norwegian finds to the Gudbrandsdal Valley (I) and of the Swedish finds to the lowlands may indicate that the Scandinavian Highlands, with the exception of their southernmost part around Dovre, stayed glaciated throughout the earlier Weichselian interstadial. The age of the material from Dösebacka (V) is controversial. The latest date for the tusk fragment of 1931, which has been treated with organic preservative, is 36 000 +1550/-1300 (Lu-879), too young to be synchronous with the other material from the area, mentioned above. This age is also in disagreement with stratigraphic evidence (cf. Hillefors 1974, Berglund et al. 1976), and might profitably be tested by dating untreated fragments from 1961.

There are also other radiocarbon datings from Norway and Sweden, which, if reliable, may indicate ice-free areas in Scania and the Western coast of Sweden immediately prior to the glacial maximum at about 20 000 B.P.

Judging from the distribution of localities, mammoths were able to inhabit the Swedish lowland up to about 63°N during the older of the Weichselian interstadial complexes. In Finland it may have ranged to about 65°N.

8.2. Material from the Weichselian deglaciation

Deglaciation of the "intraglacial" area appears to have commenced at about 18 000 B.P., with a climatic amelioration and gradual reforestation of the area. Until this time the megafauna of the extraglacial area had existed in a cool and open grassland environment, and the rapid change in habitat must have brought about some degree of crisis for this specialized "mammoth fauna". In particular, biannual migrations between the periglacial heaths and moorlands of the north and the paraglacial grasslands of the loess-steppe zonobiome of the south became difficult or impossible, as a forest belt developed across the northern half of Eurasia. In central Eurasia, this meant starvation and eventual extinction for most megafaunal populations.

The northern populations of mammoth may have followed the periglacial strips of open grassland northwards with the retreating ice. Radiocarbon dates for finds from Lockarp (VI:3) of 13 090±120 and 13 360 ± 95 B.P. (Lu-796) indicate that mammoths had migrated into Scania at or shortly before that time, presumably *via* Denmark (cf. Berglund et al. 1976). There is no evidence that they spread further north, and this isolated population probably perished with the Low-Baltic readvance of the ice lobe.

Mammoths and other members of the Central European megafauna also moved north into the Baltic region, perhaps reaching Latvia by the Raunis interstadial at about 13 250 B.P. (Serebryanny & Raukas 1970), and Estonia around 12 000 B.P. (Kessel & Raukas 1980).

The late-glacial finds differ in state of preservation from the finds of interstadial age in consisting of relatively more skeletal elements besides teeth, presumably because they were never subjected to the action of the ice sheet. They are mainly found in coastal lowlands, formerly occupied by the Baltic Ice lake (XVII, IXb). The finds are not necessarily autochthonous, however, as transport from areas further away by meltwater in ice-dammed lakes and temporary streams is possible and even probable. There is a special need to stress this possibility for the finds on both sides of the Gulf of Finland (IXa,b). The old, "preglacial" basin of the Gulf appears to have formed the principal drainage for meltwaters at Dryas III time, in front of the Salpausselkä complex. It is conceivable that the mammoth finds of group IX may be derived from remains originally deposited in bottom sediments, later exposed by waves and carried west by ice-floes, like the erroctic boulders common on both shores of the present Gulf of Finland. If so, this would be a small scale example of the phenomenon responsible for the huge concentrations of mammoth remains at the deltas of the major Siberian rivers, or for that at the Doggerbank, corresponding to the deltas of the Weichselian Rhine and Elbe.

Only two finds of group IX have been radiocarbon dated, with somewhat conflicting results: Kunda Lammasmägi (IXb:6) at 9780 ± 260 B.P. (Ta-12; Liiva et al. 1966) and Herttoniemi (IXa:4). The latter was first dated by Pearson et al. (1976) at 9030 ± 165 B.P. (Tx-127), but a later date from a cleaned sample gave the age 15 500 ± 200 (Donner et al. 1979; Hel-1074). Nevertheless, the finds probably represent mammoths living during the Weichselian deglaciation, and might even conceivably represent the youngest population of mammoths of the intraglacial area. If so, this last relict population probably expired in isolation, unable to reach the open tundra or the steppe through the intervening forests.

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