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Quaternary ostracods from Estonia and their application in palaeoenvironmental reconstruction



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CONTENTS

LIST OF PUBLICATIONS	6
ABBREVIATIONS	7
ABSTRACT	8
1. INTRODUCTION	10
2. THEORETICAL BACKGROUND	13
2.1. Use of ostracods in palaeoecological research	13
2.2. Late-glacial and Holocene freshwater ostracod faunas in Europe	15
2.3. Recent and subfossil freshwater ostracod fauna in Estonia	16
2.4. Ostracod species as Quaternary environmental indicators	17
3. GEOLOGICAL AND PALAEOECOLOGICAL CONDITIONS	21
Weichselian glaciation	21
3.2. Biotic response to environmental changes in lacustrine systems	23
3.3. Climatic conditions and post-glacial history of lake basins in	
Estonia	25
4. MATERIAL AND METHODS	27
4.1. Overview of the lakes and sections studied	27
4.2. Methods	30
4.3. Characteristic features of ostracod assemblage as environmental	
indicators	33
4.3.1. Environmental indication from taphonomic features	33
4.3.2. Water depth indication from ostracod data	34
4.3.3. Indicators for change in temperature and oxygen regime	35
4.3.4. Indicators of trophic conditions	33
4.4.5. Oxygen isotope composition of ostracou carapaces as an	36
	20
5. KESULIS	38
of the studied sequences	41
5.1.1 History of small lakes in Estonia inferred on ostracod data	42
5.1.2 Late-glacial and Holocene ostracod faunas in Estonia	47
6 DISCUSSION	50
6.1 Evolution of lacustrine ostracod faunas during the late-glacaial	50
and the Holocene in Ousternary sediments in Estonia	50
6.2 Ostracods and palaeoenvironmental changes in Estonia	53
7 CONCLUSIONS	57
 9 ELITUDE DESEADCH DEDSDECTIVES 	50
6. FUTURE RESEARCH FERSFECTIVES	50
ACKNOWLEDGEMENIS	59 60
	00
SUMMAKY IN ESIUNIAN	12
PUBLICATIONS	75

LIST OF PUBLICATIONS

- Paper I Sohar K. & Kalm V. 2008. 12.8 ka long palaeoenvironmental record revealed by subfossil ostracod data from lacustrine freshwater tufa in Lake Sinijärv, northern Estonia. *Journal of Paleolimnology*, 40, 809–821.
- Paper II Sohar K. & Meidla T. 2009. The late glacial and early Holocene environmental history of shallow lakes in Estonia revealed from subfossil ostracod data. *Geological Quarterly*, 53, 209–218.
- Paper III Kalm V. & Sohar K. 2010. Oxygen isotope fractionation in three freshwater subfossil ostracod species from early Holocene lacustrine tufa in northern Estonia. *Journal of Paleolimnology*, 43, 815–828.
- Paper IV Sohar K. & Meidla T. 2010. Changes in Early Holocene lacustrine environment inferred from subfossil ostracod record in Varangu section, northern Estonia. *Estonian Journal of Earth Sciences*, 59, 195–206.

Author's contribution

- Paper I the author is responsible for field and laboratory studies, ostracod analyses (identification, photography, distribution and diversity statistics, and environmental interpretation), sedimentology, and preparation of samples for ¹⁴C AMS analyses and for preparing the manuscript.
- Paper II the author is responsible for field and laboratory studies, ostracod analyses (identification, photography, distribution and diversity statistics, and environmental interpretation), sedimentology, preparation of samples for ¹⁴C AMS analyses and for preparing the manuscript.
- Paper III the author is responsible for field and laboratory studies, ostracod analyses (photographing, identification, environmental interpretation), and preparation of ostracods for stable isotope analyses, sedimentology, preparing the samples for ¹⁴C AMS analyses, and for complementing the manuscript.
- Paper IV the author is responsible for field and laboratory studies, ostracod analyses (identification, photography, distribution and diversity statistics, and environmental interpretation), sedimentology, preparation of samples for ¹⁴C AMS analyses, and for preparing the manuscript.

ABBREVIATIONS

- LG late-glacial LGM the Last Glacial Maximum
- the Scandinavian Ice Sheet SIS
- HTM the Holocene Thermal Maximum
- LOI – loss-on-ignition

ABSTRACT

The thesis focuses on analysis of Quaternary freshwater ostracod subfossils, ostracod species distribution and autecology of indicator species in order to reconstruct lacustrine palaeoenvironments for the post-late Weichselian glaciation in Estonia. Five lake sediment cores (covering the late-glacial and Holocene) were studied, representing the development of lacustrine environments in northern (Sinijärv, Varangu), eastern (Elistvere, Pedja) and western (Ermistu) Estonia. Available information on ostracods in the Holocene sediments in Lake Peipsi (eastern Estonia) and in late-glacial silts in the Haljala section (northern Estonia) and Pikkjärv section (eastern Estonia) was incorporated into the study. Well preserved calcareous subfossils of ostracods occurred as carapaces and disarticulated valves of juvenile and adult specimens, indicating minor post-mortem transportation and their rapid deposition. Altogether 30 freshwater ostracod species were identified in subfossil assemblages. All these species are known from the modern and subfossil record in Estonia and in central and northern Europe.

Ostracods colonized large lakes very early after the ice retreat from current Estonian territory and the ostracod fauna responded to climatic changes during the late-glacial time. Pioneer species in the late-glacial Haljala lake (*Eucypris* cf. virens, Limnocythere inopinata, Cyclocypris ovum, Pseudocandona compressa, Candona candida) colonized the lake margin area already at *ca*. 13.8–13.6 ¹⁴C cal kyr BP following a temperature increase after ice decay. Temperature decrease at *ca*. 13.6–13.1 ¹⁴C cal kyr BP favoured species which inhabit cold, oligotrophic, well-ventilated bottom waters in profundal areas of large lakes (*Limnocytherina sanctipatricii, Cytherissa lacustris*).

Compared to early late-glacial minerogenic sediments the ostracod fauna is more variable and heterogeneous in late-glacial and Holocene freshwater tufa sequences. The composition of the ostracod fauna reflects changes in the water level, temperature, trophic status and vegetation cover of the lake. The succession of ostracod assemblages show a general evolution of lake environments in Estonia: the "candida-fauna" represents phase of large oligotrophic lakes; the succeeding "stevensoni-fauna" indicates shallower mesotrophic open lakes; and the "cordata-fauna" refers to a shallow, aged, eutrophic water body with dense, emerged vegetation. Finally, appearance of *Scottia pseudobrowniana* suggests paludification of lake margins.

Water level in isolated water bodies began to decrease already at the end of late-glacial and at the beginning of the Holocene, as indicated by the dominance of warm and eutrophic conditions favouring *Metacypris cordata* in tufa sequences. Also, the predominance of *Metacypris cordata* suggests an increasing temperature toward the Holocene Thermal Maximum and higher productivity in lakes during the first part of the Holocene.

In the lakes studied changes in ostracod assemblages reveal like palaeoecological signals. However, the environmental shifts were not contemporaneous, suggesting that the influence of local catchment features, such as water level, groundwater inflow, vegetation cover and nutrient input, was stronger than that of regional climatic conditions.

Keywords: ostracods, lacustrine sediments, tufa, late-glacial, Holocene, palaeoenvironmnent, Estonia

I. INTRODUCTION

It is acknowledged that the modelling of future possible climate fluctuations of temperate areas is largely based on studies of fluctuations in the climate and environment for the time period following the last deglaciation. Sediments of freshwater lakes formed through the accumulation of biological, chemical and physical components and terrigenous, cosmogenic and volcanogenic particles from within and outside of the lake are good archives for this purpose (Douglas, 2007; Cohen, 2003).

Numerous proxy indicators can be teased out of the sediment matrix and analyzed to infer past environmental conditions; for example, biological indicators include algae, plants, zooplankton and benthic organisms that have been used for palaeolimnological studies (De Deckker & Forester, 1988). Aquatic organisms are the best recorders of climatic changes available in the fossil record (Birks *et al.*, 2000). A good proxy indicator is one that reproduces often, is abundant, easily identified, readily preserved in sediments and reflects specific environmental conditions (Douglas, 2007). Variations in lake temperature, water level and chemical composition can be determined in the subfossil record (Cohen, 2003). Lake surface water temperature during the summer months appears to react more sensitively to interannual variability in meteorological forcing than does air temperature, supporting the use of temperature-sensitive lacustrine biota as indicators of climate change (Livingstone & Lotter, 1998).

Palaeoecological studies that focus on the late-glacial (hereinafter "LG", the period between the decay of glaciers of the Late-Weichselian glaciation and the beginning of the Holocene) and the Holocene (last 10 000 ¹⁴C years or *ca*. 11.7 ¹⁴C cal kyr in Earth's history; Walker *et al.*, 2009) often use pollen, diatoms, macroplant remains, chrinomids and molluscs for (palaeo-) environmental reconstructions (*e.g.* Itkonen *et al.*, 1999; Heiri & Lotter, 2003; Seppä & Poska, 2004; Davies & Griffiths, 2005; Antonsson *et al.*, 2006; Brooks, 2006; Gedda, 2006; Amon & Saarse, 2010; Amon *et al.*, 2010).

Ostracods are microscopic crustaceans with a bivalved calcareous carapace that totally encloses the body and the appendages. Adults are typically 0.5–2.0 mm long. Ostracods, as benthic crawlers and swimmers, are found in both the littoral or profundal areas of a lake (Griffiths & Holmes, 2000; Cohen, 2003). Ostracods are an important group of animals for palaeolimnology, because of their excellent preservability, abundance, their long fossil and subfossil record and relative ease of identification. Thus, in Quaternary science ostracods are an excellent source of information on past environments. Ostracod carapaces are particularly well preserved in calcareous sediments – tufas or travertines. Herein the term "tufa" indicates calcareous sediments in temperate cool freshwater lakes. Thus, the palaeoecological interest in freshwater ostracods focuses on calcareous sediment sequences that often have the potential to yield subfossil sequences in fine resolution that cover periods of thousands of years (Griffiths, 1995a). Ostracod subfossils and their assemblage structure in lake sediments potentially reflect the evolution of the water body, in terms of changes in trophic conditions and variations in water and air temperatures, lake level and aquatic vegetation. Freshwater ostracods have potential to provide information on past ratios of precipitation to evaporation (Carbonel *et al.*, 1988; Griffiths & Holmes, 2000; De Deckker, 2002). Knowledge of the habitat preferences of recent ostracod species facilitates an estimation of past environmental conditions. For example, the presence of *Cytherissa lacustris* implies oligo- to mesotrophic oxygen-rich cool freshwaters, *Metacypris cordata* in turn indicates eutrophic warmer freshwaters, and the phytophilic species *Cypridopsis vidua* infers emerged vegetation.

Information derived from ostracod subfossils is widely used in the reconstruction of late-glacial and Holocene environmental conditions in southern and central Europe (*e.g.* Absolon, 1973; Günther, 1986; Löffler, 1986, 1997; Griffiths, 1995b, 1999; Griffiths *et al.*, 1994, 1996; Roca & Juliá, 1997; Krzymińska & Przezdziecki, 2001; Viehberg, 2004; Wilkinson *et al.*, 2005; Belis *et al.*, 2008). Pioneering palaeoecological studies based on ostracods from LG and Holocene calcareous tufas focus on material from Belgium (Van Frausum & Wouters, 1990), from Holocene chalk streams and tufas in the British Isles (Ham, 1982; Taylor *et al.*, 1994; Griffiths *et al.*, 1996; Griffiths, 1999; Davies & Griffiths, 2005), and from interglacial tufas from France (Preece *et al.*, 1986). In recent decades stable isotope studies have increasingly focused on ostracod carapace material in order to reconstruct past climates (*e.g.* von Grafenstein *et al.*, 1994, 1999; Hammarlund, 1999; Schwalb, 2003; Garnett *et al.*, 2004).

The records of many types of fossils, for example, pollen, diatoms, and macro plant remains are available for palaeoecological research on lacustrine deposits. Many researchers studying Estonian sequences (e.g. Veski, 1998; Saarse & Veski, 2001; Seppä & Poska, 2004; Poska & Saarse, 1999; Poska et al., 2004, 2008; Veski et al., 2005; Niinemets & Saarse, 2006, 2007; Hang et al., 2008; Niinemets, 2008; Sillasoo et al., 2007, 2009) have interpreted aspects of palaeoecology and Holocene forest dynamics from pollen and plant remains analyses of freshwater sediments. However, pollen in lake sediments is often not in situ but carried into lakes by wind and water from surrounding areas (Cohen, 2003). Reconstruction of Baltic Sea history and the associated development of coastal areas as well as record of changes in recent trophic conditions are heavily based on proxy data from diatom analyses (Heinsalu & Veski, 2007; Heinsalu et al., 2007; Punning & Puusepp, 2007; Heinsalu & Alliksaar, 2009). Abundant proxy data serves as a good background for palaeoenvironmental research into the largely unstudied freshwater ostracod fauna of Estonia.

Recent freshwater ostracod faunas of Estonia have been described by Järvekülg (1959, 1960, 1961, 1995, 2001) and Timm & Järvekülg (1975). Previous studies of Quaternary ostracod faunas from Estonia were on material

from the Late-Saalian lacustrine silt (Rattas *et al.*, 2010) and in the Early Holocene bottom deposits of Lake Peipsi (Niinemets & Hang, 2009).

The aim of the present PhD research was to determine the distribution of freshwater ostracods in the late-glacial and Holocene lacustrine sediments in Estonia, and to utilize the knowledge on habitat preferences of ostracod species in order to reconstruct changes in lacustrine palaeoenvironments after the Late-Weichselian glaciation in northern Baltic area. Specific objectives of the project were:

- To reveal the occurrence and distribution pattern of ostracod assemblages in the late-glacial and Holocene sediments in Estonia;
- To reconstruct the dynamics of the development of ostracod assemblages in freshwater bodies of water formed after the retreat of the last Scandinavian Ice Sheet (SIS) from its south-eastern sector;
- To apply the ostracod subfossil record and biostratigraphy in palaeoenvironmental reconstructions (*e.g.* changes in temperature, trophic level, water level) for the post-glacial period in Estonia. This information supports the consecutive stable isotope analyses produced from ostracod calcite to reconstruct the palaeotemperature throughout the late-glacial and Holocene;
- To interpret the ostracod-derived palaeoenvironmental information in the context of the post-glacial environmental changes and climate history of temperate areas of northern Europe.

2. THEORETICAL BACKGROUND

Ostracod subfossils in Quaternary sediments are extremely useful in reconstructing past environments. Ostracods occur in all types of freshwater environments. They are common components in lacustrine faunas, especially in non-acidic environments (Griffiths & Holmes, 2000). Good preservation in sediments, especially in freshwater tufas, is an additional advantage in studying ostracod subfossils. The palaeoenvironmental information that they provide will depend on the setting of the regional environmental system (Griffiths & Holmes, 2000). From a practical viewpoint ostracods are relatively easily employed for use in Quaternary palaeoecology as their study does not require complex preparation techniques. Ostracod carapaces are also useful for geochemical analyses: autochthonous low-magnesium calcite of the carapace is produced in a short time (hours) under ambient conditions and thus is a good target for stable isotope analysis that gives information on past temperatures.

2.1. Use of ostracods in palaeoecological research

Ostracods are common as microfossils, since the two calcified valves are easily preserved in sediments after death (Martens & Horne, 2009). The earliest occurrence of marine ostracods is during the Early Ordovician (Tinn & Meidla, 2004; Williams *et al.*, 2008) and the first freshwater faunas are of Carboniferous age (Holmes & Horne, 1999).

The Class Ostracoda is subdivided into five orders that were present in the Ordovician; some of them are now extinct. The Myodocopida and Platycopida are extant and exclusively marine, and the ubiquitous Podocopida is the most diverse group at the present day, found in marine, brackish and fresh waters (Martens & Horne, 2009). Ostracod species are environmentally and geographically diverse and are known from aquatic environments from the Arctic to the tropics, from deserts to high-mountains, and from very dilute to highly saline waters, including lakes, ponds, springs, streams, rivers, estuaries and oceans; some species even occur in semi-terrestrial environments and within groundwater (De Deckker & Forester, 1988).

There are about 200 genera of recent freshwater ostracods and *ca*. 2000 species worldwide (Martens *et al.*, 2008). Palaearctic, which includes most of Europe, Asia and northern Africa, is the zoogeographical region that has the highest specific diversity of freshwater ostracods with more than 700 species (Martens *et al.*, 2008).

Freshwater ostracods disperse over distances through passive transport by invertebrate and vertebrate animals, and even via humans. However, migratory movement assisted by birds is most probably a major means of ostracod dispersal. The eggs of many ostracod species are resistant to desiccation and excellent candidates for dispersal by the wind. Some ostracods may have been

widely distributed through the circumglobal transport of eggs by high altitude winds (Meisch, 2000). Ostracods reproduce by sexual and asexual (parthenogenesis) modes. In the case of parthenogenetic or gravid brooding females, one specimen is theoretically sufficient to initiate a new population (Martens *et al.*, 2008). Like others crustaceans, ostracods grow by moulting their carapaces: up to eight times prior to reaching adulthood (Griffiths & Holmes, 2000). Ontogenetic studies suggest that this number could have been higher in Paleozoic ostracods (Hinz-Schallreuter & Schallreuter, 1999).

Most lacustrine ostracods are benthic crawlers and swimmers, found in both littoral and profundal regions of lakes. Ostracods living in continental aquatic environments are quite selective with respect to the environments in which they live (De Deckker & Forester, 1988). They are sensitive to the temperature, salinity, anion composition and nutrient status of their host waters, together with a range of other habitat variables such as the depth, size and permanence of the water body, substrate type, aquatic macrophyte cover and energy level, turbidity and dissolved oxygen content. Thus, ostracods have excellent potential as palaeoenvironmental indicators (Holmes & Horne, 1999; Griffiths & Holmes, 2000).

Recent ostracod species are identified especially based on their soft-part characteristics. However, genetic studies suggest that even morphological uniform populations may contain several cryptic taxa (*e.g.* Bode *et al.*, 2010). Subfossil ostracod material used in Quaternary studies comprises calcitic carapaces and valves. Their soft parts are not preserved and the diagnostic features for identification of species are valve size, shape and sculpture and muscle scar patterns. Most of the relevant palaeoecological information is derived by identification of specimens to specific or generic level, together with data on presence or absence and absolute number or percentage of species. The approach to palaeoecological reconstruction using ostracods involves qualitative methods based on the perceived autecology of individual species in order to estimate habitat conditions (Griffiths & Holmes, 2000). The level of palaeoenvironmental information that can be derived from subfossil ostracods depends largely on the extent to which the ecological preferences of individual recent species are known.

Ostracod population structure can be obtained through a direct examination of subfossil ostracod valves: a life assemblage can be recognized if all growth stages are recovered from the same sample (Holmes, 1992). Assuming that juveniles and adults cohabit, the recovery of valves representing all stages from the same sample will indicate that the material has not been reworked. Conversely, species in the same population represented by only part of their complete ontogeny are likely to be allochthonous (Whatley, 1988).

2.2. Late-glacial and Holocene freshwater ostracod faunas in Europe

Freshwater ostracod species are recorded from Pleistocene and Holocene sequences across Europe (Griffiths, 1995a; Meisch, 2000). Many species (*e.g. Candona candida, Candona neglecta, Ilyocypris bradyi, Cypridopsis vidua, Cypria ophtalmica, Herpetocypris reptans, Pseudocandona compressa*) have a broad geographic distribution, suggesting high tolerance levels to different environmental variables. These species are found from high latitudes to the Mediterranean region in Europe (Külköylüoğlu *et al.*, 2007). Ostracod species have "preferred" climatic and environmental optima, and they track these back and forth over landscapes as conditions fluctuate through time (Griffiths, 2001). For example, the decrease in abundance of *Limnocytherina sanctipatricii* and *Cytherissa lacustris* in lakes of central Europe is likely a result of northward retreat of the polar front during the Early Holocene (Schwalb *et al.*, 1998).

In Europe the colonization of deep modern lakes by ostracods started very early after the deglaciation. C. lacustris, L. sanctipatricii, Leucocythere mirabilis, C. candida were the pioneer species and the LG ostracod fauna is typical of the profundal zone of great lakes with minerogenic sediments. This type of ostracod fauna is widely distributed in well-oxygenated, oligotrophic, cold and deep lacustrine environments in Europe (Löffler, 1975, 1986; Danielopol et al., 1993; Griffiths et al., 1994; Krzymińska & Przezdziecki, 2001; Schwalb et al., 1998; Belis et al., 1999, 2008; Meisch, 2000). However, the LG ostracod fauna may also contain shallow lake (maximum depth a few meters) representatives (Scharf et al., 2005). Metacypris cordata, Darwinula stevensoni, Fabaeformiscandona protzi, C. vidua, Cvclocvpris ovum, Limnocythere inopinata and Notodromas monacha are common species in the Holocene of central Europe and the British Isles (Löffler, 1986; Griffiths et al., 1994; Griffiths & Evans, 1995; Griffiths, 1999; Viehberg et al., 2008). M. cordata is clearly the dominant species in the Lower Holocene sediments of central Europe (Absolon, 1973; Viehberg, 2004; Griffiths & Evans, 1995; Viehberg 2004).

In central Europe Absolon (1973) divided the LG and Holocene ostracod faunas into two separate groups, the *"candida-"and "cordata-fauna"*. The first group contains *C. candida, P. compressa, H. reptans, Potamocyypris villosa* and *C. ovum* whilst the *"cordata-fauna"* consists of *M. cordata, D. stevensoni, N. monacha* and *F. protzi*. The transitional fauna between these successions contain *L. sanctipatricii, F. protzi, C. vidua, Pseudocandona marchica, L. inopinata, C. ophtalmica* and *Cypria exsculpta*. Later a similar division of ostracod assemblages was recognised in central Europe (Günther, 1986; Löffler, 1986) and the British Isles (Griffiths & Evans, 1995).

Ostracod species present in the LG "*candida*-fauna" possess desiccationresistant life-history stages and could have been dispersed by a variety of means; most are ecologically polyvalent (Griffiths & Evans, 1995). However, the "*candida*-fauna" is essentially cold, oligotrophic and benthic (Griffiths, 2001). In the dispersal of the fauna, next to wind, carriage in melt water and migratory movements of water birds provided considerable assistance. The LG fauna elements are usually species habiting cool and oligotrophic environs in large lakes (*e.g. C. lacustris, C. candida, L. mirabilis* and *L. sanctipatricii*).

Unlike the "candida-fauna", the "cordata-fauna" consists of more eurythermal, free-swimming and phytophilic species (Griffiths & Evans, 1995; Griffiths, 2001). Decrease in abundance of *L. mirabilis* and *C. lacustris* in Holocene lakes is probably related to rising trophic conditions (Scharf, 1993). Typical Holocene ostracod species (*D. stevensoni, M. cordata*) prefer small and shallow, vegetation-rich and seasonally permanent water bodies with higher nutrient status. Their dispersal takes place by hydrological means (Griffiths & Evans, 1995; Griffiths, 2001). The advent of the "cordata-fauna" tends to signify broad-scale environmental changes: increased ambient temperatures, increase in ecosystem productivity and associated change in trophic degree (from oligotrophy to some higher state).

In shallow lake basins, increasing autochthonous and allochthonous bioproductivity is enforced by progressive anionic leaching from the surrounding catchment. This culminates with encroachment of littoral and basin closure, and thus the "*cordata*-fauna" records an extinction of the lake, before the ostracod record itself is obliterated by the change to humic deposition. Then the water body moves through meso-/eutrophy into dystrophy, and phytic species increase until wetland forms (*e.g. Scottia*) appear (Griffiths & Evans, 1995; Griffiths, 2001).

2.3. Recent and subfossil freshwater ostracod fauna in Estonia

The modern Estonian ostracod fauna is similar to the fauna of the temperate zone as recorded in continental Europe and the British Isles and distributed over the western Palaearctic Zoogeographical Region (Meisch, 2000; Henderson, 2002; Jurmalietis, 2003; Nagorskaya & Keyser, 2005). In Estonia over seventy ostracod species are found from recent freshwater basins – lakes, rivers, springs, temporal and permanent pools and ditches (Järvekülg, 1959, 1960, 1961, 1995). In addition ostracods described from the Baltic Sea are represented in coastal water bodies of Estonia, both brackish and freshwater species (Järvekülg, 1973; Timm *et al.*, 2007).

Freshwater species that are common in Estonia are C. lacustris, L. sanctipatricii, Fabaeformiscandona levanderi, Candonopsis kingselii, Physocypria kliei, Ilyocypris decipens, Cypridopsis parva and M. cordata. Species such as Dolerocypris fasciata, C. vidua, Cyclocypris laevis, C. ovum, N. monacha, C. ophtalmica, Candona weltneri, Pseudocandona parallela, D. stevensoni and L. inopinata occur predominantly in littoral areas of lakes. In

ponds, there are species such as *Pseudocandona rostrata* and *P. compressa* (Järvekülg, 1995). Cyclocypris serena, Cypria curvifurcata and Potamocypris wolfi occur only in rivers and frequently together with C. ovum, C. laevis and C. vidua (Järvekülg, 1995, 2001). Ostracods found in springs include Tonnacvpris estonica (characteristic, in large numbers, of springs in the Pandivere area, northern Estonia), Psychodromus olivaceus (abundant in springs on Saaremaa Island and in north-western Estonia), Potamocypris fulva and Potamocypris pallida (Timm & Järvekülg, 1975). Ostracod diversity is high in littoral zones, and a particularly high number of species and individuals occur in temporal water bodies and seasonal pools, where Eucypris crassa, Eucypris virens, Eucypris elliptica, Koencypris ornata, Tonnacypris lutaria, Bradleystrandesia fuscata, Bradlevstrandesia reticulate, Cyclocypris globosa, Cyprois marginata, Pseudocandona stagnalis, Pseudocandona pratensis, Pseudocandona sucki, Pseudocandona parallela, Cypris pubera, Heterocypris incongruens and C. ovum dominate (Järvekülg, 1961, 1995). Ostracod diversity increases with increase of vegetation (Kiss, 2007).

In general, the deep lake habitat is characterized by low diversity assemblages with stable species composition. In Estonian lakes, the profundal zone is considered to be poor in numbers of ostracod species, with the most dominant species being *C. lacustris* and *L. sanctipatricii* (Järvekülg, 1961).

The oldest Quaternary ostracod remains in Estonia are recorded from the Arumetsa quarry in south-western Estonia where the Late-Saalian massive clay yields *C. lacustris* and *I. bradyi*. The presence of these species is interpreted as an indication of a cold-water environment (Rattas *et al.*, 2010).

Earlier or in parallel to the current PhD project, some other data were published on the Weichselian late-glacial ostracod fauna in Estonia. The present author recorded LG ostracods (*C. lacustris, C. candida* and *L. mirabilis*) from silty bottom sediments of Lake Pikkjärv in the Saadjärve Drumlin Field, eastern Estonia (Sohar, 2004). The Weichselian LG fauna was also documented by the author from sediments of the Haljala palaeolake (Saarse *et al.*, 2009) where *C. candida, C. lacustris, P. compressa* and *L. sanctipatricii* dominate. *C. ovum, C. laevis* and *E. virens* were also identified in this ostracod fauna. Niinemets and Hang (2009) identified ostracods in Early Holocene tufa from Lake Peipsi where the fauna composed primarily of *C. lacustris, C. candida, L. sanctipatricii, F. protzi, F. levanderi* and *I. bradyi,* accompanied by *H. reptans* and *D. stevensoni.*

2.4. Ostracod species as Quaternary environmental indicators

Ostracod species found from Quaternary sediments in Estonia are also known from other regions, both in southern and central Europe. However, several species tolerate certain ambient conditions and this enables the use of ostracods

in Quaternary studies. In the following are presented ecological characteristics of some common ostracod species in freshwater basins.

M. cordata is a species indicator of eutrophic and mesotrophic conditions of ageing lakes. It is a warm-stenothermal summer form and pure freshwater species, commonly associated with littoral vegetation, peat or macrophyte rootmasses (Hiller, 1972; Meisch, 2000; Nagorskaya & Keyser, 2005). The species evades groundwater habitats (Danielopol et al., 1996). In Estonia it is common in littoral areas of small lakes, together with D. fasciata, C. exsculpta and C. ophtalmica (Järvekülg, 1959). Some specimens are recorded in recent faunas from Matsalu Bay in western Estonia, among dense reed beds (at water depth 0.5-1.2 m and salinity < 0.5%), where it occurs together with other freshwater species such as Stenocypria fishceri, Ilvocypris gibba, C. ophtalmica, C. exsculpta, C. candida, P. compressa, C. vidua and with the marine and brackish water species Cyprideis torosa and Heterocypris salina. The preferred bottom sediments for the species are organic muds and it can survive in conditions with a high H₂S content (Järvekülg, 1985). *M. cordata* appears, presumably, when the lake level is decreasing and water temperature is rising. M. cordata refers to an ageing eutrophic lake with emerged water plants in littoral zone, or marks dystrophy, shallowing and basin encroachment and closure (Walker *et al.*, 1993; Griffiths, 1999).

D. stevensoni is considered as a rare species in the lakes and rivers in Estonia; it preferably occupies profundal areas of lakes (Järvekülg, 1959). It is also found in shallow open lagoons and coastal freshwater shallow lakes in western Estonia and its islands, where it occurs together with *C. torosa*, *F. protzi* and *C. exsculpta* (Timm *et al.*, 2007). In Finland it is recorded from oligotrophic shallow lake with muddy bottom (Ranta, 1979).

C. candida is a cosmopolitan species, associated with lakes, rivers, ponds and temporal pools; it may occupy depths down to 300 m. It is both ecologically and temporally ubiquitous. The absence of *C. candida* is more remarkable than its presence. Co-occurrence with other eurytopic species (*e.g. C. ophtalmica, C. ovum*) may be used to indicate a colonisation phase or a stressful or unsuitable environment that precludes colonisation by more specialised species (Griffiths, 1995b). In Estonia *C. candida* is numerous and abundant among vegetation in permanent water bodies. However, it is considered to prefer cold water conditions (Järvekülg, 1959). It is also recorded from springs (Timm & Järvekülg, 1975), shallow coastal lagoons and lakes (Timm *et al.*, 2007). In Estonia it is also found in temporal water bodies, where it prefers vegetationrich biotopes. In plant-poor waters, it occurs in muddy bottoms. In permanent waters (including brackish waters), it is found in alkaline waters (pH 7.4–8.3). Seasonally, adult specimens have been found from June to October (water temperature up to 9.4 °C) (Järvekülg, 1961).

L. inopinata is an open-water benthic species that prefers calm shallow waters with enhanced detritus content such as macrophyte debris. Populations of L. inopinata are confined to the littoral zone and to open lake areas (Yin et

al., 1999). It tolerates a wide range of environmental conditions and occurs in both small and large lakes, ponds, ditches, brooks on sandy or muddy bottoms and may occupy coastal areas with slight salinity (Meisch, 2000). It is common in Estonian lakes and rivers (Järvekülg, 1959).

C. lacustris exclusively inhabits the benthic area of cold, well-oxygenated lakes of low productivity, where it lives on fine, silty sediments (Griffiths, 1995b). In laboratory experiments its temperature adaptation plateau is in the 10–15°C range (Newrkla, 1985). *C. lacustris* is typical of lakes over 100 m deep. The highest densities occur in oligo-mesotrophic lakes at depths between 12 and 40 m (Meisch, 2000). In Estonian lakes it is rare, occupying only sublittoral and profundal zones of large lakes (Järvekülg, 1959).

L. sanctipatricii is clearly a cold stenothermal form, occurring sublittorally in lakes and other still water bodies and may be sensitive to eutrophic conditions (Griffiths, 1995b; Meisch, 2000). In Estonia it is recorded from large lakes in profundal zones, together with *C. lacustris* and at around depths of > 6 m (Järvekülg, 1959; Mäemets, 1977).

L. mirabilis prefers sublittoral and profundal zones of cold oligotrophic lakes (minimum depth 12 m). It is considered as LG lacustrine species, which disappeared in the Holocene as a consequence of natural eutrophication (Meisch, 2000).

I. bradyi is predominantly stream dwelling, or lives on vegetation. It is strongly associated with springs and undoubtedly considered crenophilous. Occurrence in other habitats is explained through drift (Griffiths, 1995b). In Estonia *I. bradyi* is recorded from cold springs (Timm & Järvekülg, 1975).

T. estonica occurs in cold springs of the Pandivere Upland region. It is associated with cold waters and sandy bottom conditions (Järvekülg, 1960, Timm & Järvekülg, 1975). Van der Meeren *et al.* (2009) documented the species from cold oligotrophic springs with sandy bottom sediments from Mongolia.

F. protzi tends to be found in larger water bodies and generally can be collected in winter. It is a cold-water stenotherm form that has never been reported from running waters. It is generally found on sandy or muddy sediments with plants detritus (Griffiths, 1995b). In Estonia it is found in lakes fed by springs and in profundal and littoral zones of lakes (Järvekülg, 1959; Timm & Järvekülg, 1975). It does not tolerate high trophic conditions (Hiller, 1972; Meisch, 2000). *F. levanderi* is a cold water preferring species found in spring-fed lakes in Estonia (Timm & Järvekülg, 1975). It may occur in both littoral and profundal areas of lakes (Meisch, 2000).

C. vidua, C. ovum, C. exsculpta, C. ohptalmica are ubiquitous. In Estonia they are common species occupying temporal and permanent waters. They are especially common and numerous in littoral zones of lakes, occupying several biotopes, including areas with sparse vegetation and sandy lake bottoms (Järvekülg, 1959, Timm & Järvekülg, 1975). The phytophilic summer form and active swimmer *C. vidua* prefers stagnant plant-rich water bodies. It is known

from poorly oxygenated to oxygen-saturated waters (De Deckker, 1988). In Estonia it is recorded from temporal springs, Fe-rich and saline waters, and even from waters influenced by high fertilisation in agriculture. Also C. vidua occupies temporal waters with pH values of 6.4–7.7. It survives the autumn and winter seasons in the littoral zone (found in January temperature +0.6 °C) (Järvekülg, 1961). C. ovum prefers plant-rich stagnant waters. In a water body with sparse vegetation C. ovum is observed on sandy, muddy gravely and clayey bottoms. It tolerates acidic and alkaline environs (pH 6-8.6), but is more frequent in acidic waters. In temporal waters its adult specimens are found from May to November, at a water temperature of +5.7 - +27.2°C. In permanent waters adult specimens occur also in the winter months of December, January, and March (Järvekülg, 1961). C. ophtalmica is recorded from lakes, ponds, rivers and springs in Estonia. In temporal waters it is common in both plant-rich and plant-poor biotopes. It may occupy the profundal areas of lakes and may survive in anoxic conditions and in niches that are unfavourable to other species (Griffiths & Martin, 1993; Martín-Rubio et al., 2005). C. exsculpta occurs mostly in lakes, in both the littoral and profundal zones. Rare occurrences are also known from permanent pools and rivers (Järvekülg, 1959). Griffiths & Evans (1991) described C. ophtalmica and C. ovum from small ponds, where algae or other lower plants are present.

P. rostrata occurs in permanent and temporal small lakes and in springs and interstitial groundwater and is considered to be a cold stenothermal species (Meisch, 2000; Keatings *et al.*, 2002). In Wales, UK, *P. rostrata* dominates together with associates *C. ovum*, *C. vidua* and *M. cordata* in Early Holocene calcareous sediments indicative of a littoral environment with increasing eutrophication and a progressive shallowing of lake waters (Walker *et al.*, 1993; Griffiths, 1999).

In Estonia *P. villosa* is found in springs, spring-fed ponds and littoral zones of lakes with sparse vegetation, where the bottom deposits are sand, mud, clay, or tufa, and the waters are alkaline (pH 7.5–8.0). Adult and juvenile specimens are present from June to August, at water temperatures up to 22 °C (Järvekülg, 1959; Järvekülg, 1961; Timm & Järvekülg, 1975).

Scottia pseudobrowniana, together with *M. cordata*, is documented as a semi-terrestrial species that occurs on floating fen soil (Meisch, 2000; Danielopol & Vespremeanu, 1964). *S. pseudobrowniana* prefers alkaline warm waters (Külköylüoĝlu & Vinyard, 2000). In northern Europe the species apparently prefers colder waters (Henderson, 2002). The species is unknown in recent Estonian lakes.

C. kingsleii occurs, but rarely, in recent lakes in Estonia. It is found in littoral zones with sandy, muddy bottoms and in vegetation-rich lakes (Järvekülg, 1959). It is associated with *M. cordata* and *S. pseudobrowniana* in freshwater habitats (Meisch, 2000; Danielopol & Vespremeanu, 1964).

3. GEOLOGICAL AND PALAEOECOLOGICAL CONDITIONS

The territory of Estonia is located in the north-western part of the East European platform. Structurally it lies on southern slope of the Fennoscandian Shield. The crystalline basement is covered by sedimentary bedrock of Ediacaran and Cambrian sandstones and siltstones, Ordovician and Silurian limestones and dolomites and Devonian sandstones and carbonates. Estonia was subjected to the last Scandinavian (Weichselian) Glaciation, being influenced both by glacial erosion and deposition. The relief of the bedrock has been significantly shaped by Quaternary ice sheets. The bedrock is covered with glacial sediments and the modern glacial topography was formed mostly in course of the Late-Weichselian glaciation. The thickness of the Quaternary cover, predominantly of tills, glaciofluvial and glaciolacustrine deposits, varies from less than 5 m in northern Estonia to more than 100 m in southern Estonia (Raukas & Kajak, 1997).

3.1. Environmental and climate change after termination of the Late-Weichselian glaciation

During the Late-Weicshelian glaciation the Scandinavian Ice Sheet (SIS) reached the maximum extent (the last Glacial Maximum – LGM) in its southeastern sector (Valdai Heights in the Russian Plain) at ca. 20.0-18.0 cal kyr BP (OSL and calibrated ¹⁴C datings: Lunkka et al., 2001; OSL and calibrated ¹⁴C datings: Svendsen *et al.*, 2004; ¹⁰Be ages: Rinterknecht *et al.*, 2007, 2008). The territory of Estonia became deglaciated between ca. 14.7-12.7 ¹⁴C cal kyr BP (Kalm, 2006). Following the ice decay, extensive ice-dammed lakes spread over the area. The Baltic Ice Lake was the biggest that developed in front of the receding ice sheet. Already at ca. 13.3 ¹⁴C cal kyr BP the Baltic Ice Lake extended to the ice-free areas in current Latvia, Estonia and north-western Russia (Rosentau et al., 2009). Approximately at the same time (ca. 13.3–12.8 ¹⁴C cal kyr BP) there was dry land in the Pandivere area (northern Estonia) and in southern Estonia according to palaeogeographical reconstructions of the Baltic Ice Lake (Rosentau et al., 2009). Saarse et al. (2009) and Amon & Saarse (2010) claim that the ice margin receded from northern Estonia even much earlier, at ca. 13.8 ¹⁴C cal kyr BP. Over the low topography western Estonia the Baltic Ice Lake extended much longer, until between 12.3–11.6 ¹⁴C cal kyr BP. Because of the mutual connections via a system of straits in central Estonia the Baltic Ice Lake had initially the same water level as the Glacial Lake Peipsi and Võrtsjärv. These strait systems were closed at *ca.* 12.8–11.7 ¹⁴C cal kyr BP, prior to the final drainage of the Baltic Ice Lake due to the isostatic uplift (Rosentau et al., 2009). Glacial Lake Peipsi

became isolated from the Baltic Ice Lake at *ca*. 12.4–11.7 ¹⁴C cal kyr BP and Glacial Lake Võrtsjärv at *ca*. 12.4–12.0 ¹⁴C cal kyr BP (Rosentau *et al.*, 2009). In general, the topographically higher the lake basin, the earlier it got isolated from the local ice lakes or from waters of the Baltic Ice Lake.

At the time of LGM the climate was extremely dry and cold, the mean annual temperature along the eastern margin of the SIS was below -6° C, but a sharp climatic turnover to warmer summers started around 15.0 ¹⁴C cal kyr BP (Hubberten et al., 2004). The climate, however, remained very dry, with cold winters. At the LG/Holocene transition the mean annual temperature increased rapidly (ca. 5° C) and summer lake-water temperature increased to ca. 12° C in northern Europe (Hammarlund et al., 1999). At ca. 12.5 ¹⁴C cal kyr BP climate become more humid and general degradation of permafrost started, accompanied by a change from tundra-steppe into wet tundra and forest tundra (Hubberten et al., 2004). During the LG climate fluctuated toward colder and warmer episodes, as registered in the oxygen isotope records of ice-cores from Greenland (Lowe et al., 2008). Transitions from cold to warm periods are considered as rapid events (von Grafenstein et al., 1999). In multi-millennial time-scales the main factors that affect the Holocene climate change are related to orbital forcing (changes in obliquity, precession and eccentricity), which involves re-distribution of solar energy, both seasonally and latitudinally. Climatic oscillations are reflected in changes in the Holocene lake levels, in the oceanic thermohaline circulation, and in freshwater flows from proglacial lakes during the final stage of deglaciation (Bradley, 2005).

Climate reconstructions from northern Europe (Heikkilä & Seppä, 2003) show cold climate at the beginning of the Early Holocene (annual mean temperature $-3-0^{\circ}$ C). However, the reconstruction of mean annual temperature suggests a very rapid but steady warming from *ca*. 10.7–9.0 ¹⁴C cal kyr BP onwards, to the Holocene Thermal Maximum (HTM) at 8.0–4.5 ¹⁴C cal kyr BP (Heikkilä & Seppä, 2003; Seppä & Poska, 2004; Antonsson *et al.*, 2008; Seppä *et al.*, 2009). The Early Holocene has been suggested as the most oceanic climate period, but probably with a high variability in temperature in northern Europe (Giesecke *et al.*, 2008). In northern Europe at the earlier part of the HTM the mean annual temperature was 2.0–2.5° C higher than at present and July temperature values were 1.5° C higher than today (Seppä *et al.*, 2009). The climate trend from the moist Early Holocene towards a dry and warm Middle Holocene was caused by a changing atmospheric circulation together with summer anticyclonic circulation that dominated during the Middle Holocene (Antonsson *et al.*, 2008).

The Early Holocene warming was interrupted by short-term coolings at *ca*. 10.3–9.3 and *ca*. 8.6–8.2 ¹⁴C cal kyr BP (the so-called 8.2 kyr event) (*e.g.* von Grafenstein *et al.*, 1998; Barber *et al.*, 1999; Björk *et al.*, 2001; Seppä & Poska, 2004; Rohling & Pälike, 2005; Hammarlund *et al.*, 2005; Lowe *et al.*, 2008). In annually laminated lake sediments in southern Estonia pollen and vegetation response to the short cool period was recognized at 8.4–8.08 cal ¹⁴C kyr BP

(Veski *et al.*, 2004). The "8.2 kyr event" appears to have been generally cool over much of the Northern Hemisphere, where large ice sheets were still present, as evidenced by major ice rafting, strengthened atmospheric circulation over the North Atlantic and Siberia. At least one large pulse of glacier melt water into the North Atlantic probably enhanced production of sea ice, providing an additional positive feedback on climate cooling (Mayewski *et al.*, 2004). The melt water flooding events could have induced decrease in the oceanic thermohaline circulation (Magny, 2007).

After the HTM, at about 4.5 ¹⁴C cal kyr BP the mean annual temperature clearly drops in northern Europe (Heikkilä & Seppä, 2003; Seppä & Poska, 2004). The cooler anomalies occurred at 3.8–3.0 and 0.5–0.1 ¹⁴C cal kyr BP and were associated with increasing humidity over northern European mainland, consistent with the correlation between cold and humid/warm and dry modes of summer weather in the region as a result of variations in the oceanic and atmospheric circulation in the North-Atlantic–North-European region (Seppä *et al.*, 2009). Thus, the Late Holocene experienced a humid and variable climate (Hammarlund *et al.*, 2003).

3.2. Biotic response to environmental changes in lacustrine systems

Lakes have fluctuated in size in response to climatically induced changes in the hydrological regime, including precipitation/evaporation balance over the catchment system of the lake. Water-level fluctuations affect space and habitat availability, water chemistry, stratification, and mixing regimes (Jones & Jordan, 2007). A transect running down-slope and offshore from the shoreline reveal a change in habitat and lake organisms. In the photic, shallow littoral zone, high rates of photosynthesis can normally be supported and a high diversity of organisms is encountered. Near the shoreline emergent macrophytes are often present, either attached to the substrate or floating nearshore, forming a substrate for attached or crawling organisms (Cohen, 2003). Changes in lake level will have an effect on the spatial distribution of littoral macrophytes, which is primarily a function of light intensity and water depth. In the sublittoral zone, light penetration is reduced, and large macrophytic plants are absent, but lower levels of benthic primary production may persist from algal or bacterial growth (Cohen, 2003). As one begins to move away from the littoral zone with the increasing water depth, the submerged/floating macrophytes increase in importance; they are replaced in the deeper sublittoral zone by lowlight taxa (e.g. Chara). With increase in lake level the marginal taxa will steadily be replaced by deep-water taxa (Jones & Jordan, 2007). In the aphotic, profundal zone the food resources are provided through secondary productivity, by settling detritus and microbial food resources. In this environment, variation in species abundance and diversity is driven by currents and nutrient availability (Cohen, 2003).

Lacustrine ecosystems are controlled by the quantity and periodicity of the water resource, lake size, depth, basin origin and climate. Water levels in shallow lakes fluctuate intra- and interannually depending on regional climatic conditions (Coops et al., 2003). Phases of higher lake level coincide with an increase in annual precipitation, a decrease in summer temperature and a shortening of the growing season. Periods of low lake level correspond to a decrease in annual precipitation, an increase in summer temperature and a longer growing season (Magny, 2007). The period with higher temperatures characterizes low water levels and dry climate. Low temperatures at the beginning of the Early Holocene were associated with high water levels, whereas low water levels and dry conditions prevailed during the following period of high temperatures due to high summer evapotranspiration and lower precipitation in northern Europe (Hammarlund et al., 2003; Antonsson et al., 2006; Antonsson & Seppä, 2007). The response to increasing temperatures at the end of the LG and the beginning of the Holocene was immediate in the lakes and their catchments. Many organisms that were present expanded their populations within a year or two and cold-preferring species became extinct (Birks et al., 2000). The aquatic ecosystem development during the LG and Early Holocene showed that the large LG biotic changes were synchronous, and were driven by the overriding forcing factor of temperature. Later, in the Early Holocene the changes were more gradual and more independent of each other, showing that other factors become important, such as the dissolved and particulate material from the catchment, base and nutrient status of the lake water, and internal process of ecosystem succession and sediment accumulation. The lake biota does not depend only on regional climatic conditions, but also on changes in the lake catchment and on internal processes within the lake (Birks et al., 2000).

As the lake basin in-fills with sediments, its volume is decreased and, with a constant total loading of nutrients, it becomes increasingly eutrophic. The increase in trophic condition of a lake is a slow and natural process in geological history of a lake. Eutrophication likewise increases the rate of sedimentation in the basin. Lakes also become overgrown from the shoreline and in shallow shore regions emergent macrophytes (reeds, rushes) accumulate nutrients that contribute to natural eutrophication (Lampert & Sommer, 2007). The rise in trophic status often coincides with elevated temperatures that are known from the period of HTM (Andersson, 2010 and references therein).

In general, also sediment structure and composition refers to water level changes in the lake; coarser minerogenic deposits correspond to shallower water and higher hydrodynamics. Organic sediments such as gyttja and peat characterize shallow water or late stages of lake infilling. Low lake water levels often correspond to an escalation of peat and organic detritus deposition in the near-shore areas. Water high-stand periods are characterized by inwash and accumulation of predominantly minerogenic sediments. Sediments deposited during the Early Holocene or earlier often have a more offshore and deeper stratigraphic position in a lake than the younger ones (Magny, 2007).

The coarser fractions of tufa consist mainly of various carbonate concretion morphotypes of biochemical origin (from bacterial activity) associated with the photosynthetic activity of aquatic plants (Pedley, 1990; Viles & Goudie, 1990; Magny, 2007). Over much of Europe the tufa started to form during the LG or at the beginning of Holocene and deposition was widespread roughly between 11.0-4.0 ¹⁴C cal kyr BP (Goudie *et al.*, 1993; Griffiths & Pedley, 1995; Baker & Simms, 1998; Dramis *et al.*, 1999; Garnett *et al.*, 2006; Pentecost, 2005). Tufas accumulated during the Holocene within the geographical area of the last glaciation (Hammarlund *et al.*, 2003; Gedda, 2006; Diefendorf *et al.*, 2006), as well as outside of it (Kele *et al.*, 2003; Dramis *et al.*, 1999; Andrews *et al.*, 2000).

3.3. Climatic conditions and post-glacial history of lake basins in Estonia

Estonia is located in the northern Europe on the eastern coast of the Baltic Sea between 57–60° N. It represents a transition zone from the maritime climate type on islands to the continental one in East Estonia. In spite of its comparatively small area, climatic differences in the territory of Estonia are large, especially during the winter (Jaagus, 1997). The annual air temperature oscillations are affected by the Atlantic Ocean, the North-Atlantic stream, and the dominant westerly winds that bring moist air masses to continent. In western Estonia the climate is maritime type and the mean January air temperature is -3.5° C and in July it is $+16.5 - +17^{\circ}$ C. In eastern Estonia in January the mean air temperature is $-6 - -6.5^{\circ}$ C and in July $+16.5^{\circ}$ C. The annual mean precipitation in western Estonia is 550–350 mm and in eastern region 650–700 mm (Saarse *et al.*, 1996; Jaagus, 2002).

In Estonia modern lake basins started to form after the last deglaciation. At present there are about 1500 small lakes (surface area less than 10 km²) in Estonia and most of them are shallow, less than 10 m deep. Many small lakes are lost completely or partially as a result of intensive sedimentation and the lowering of lake levels. The water level normally fluctuates 1–2 m annually. The catchment areas of lakes are small and therefore the resistance time is long (water changes 2–4 times annually). Estonian lakes are dimictic, in April and in October the water masses mix and the water temperature over the water column is +4° C. In very shallow lakes (< 5 m) the temperature of water column is almost uniform during ice-free seasons: the difference between surface and bottom temperatures is only a few degrees. Thermal stratification occurs in deep lakes and difference reach *ca*. 20° C. Mid-summer surface water temperatures

are between $+19^{\circ}$ C and $+29^{\circ}$ C, but the near basin floor the temperature is only *ca.* $+4^{\circ}$ C. Water transparency is *ca.* 1.5-3.0 m in small lakes, but some "hard-water" lakes are transparent to the basin floor (*e.g. ca.* 8 m in Lake Äntu Sinijärv). Higher concentrations of chloride ions occur in coastal lakes (Mäemets & Saarse, 1995). Modern small lakes in Estonia have high biological productivity (Mäemets, 1977).

Most basins of small lakes are of glacial origin and glacigenic bottoms sediments (predominantly glaciolacustrine silt and clay) are covered with postglacial lacustrine sediments. In sediment sequences the transition from glaciolacustrine to lacustrine deposition is marked by the end of varved clays layers and the onset of lake silts and clays with low values of organic matter and with plant remains (Pirrus & Saarse, 1978). LG silts, sands and clays, and Holocene gyttja, tufa and peat hold information on vegetation history and climate change. Pollen data from the oldest LG lake sediments indicate dry periglacial climate and peaky flora. The LG climate warming and permafrost decline resulted in trees with wide ecological preferences and aquatic plants started to spread in lakes. Climatic cooling at the end of LG caused a reappearance of tundra floral assemblages (Mäemets & Saarse, 1995). Lakes were oligotrophic during the LG in Estonia (Mäemets & Saarse, 1995).

Infilling and overgrowing processes have gradually reduced the number and volume of lakes, although new isolated water bodies formed from former lagoons and bays of the Baltic Sea due to the land uplift in north-western and western Estonia (Kessel, 1968; Saarse, 1997). Lakes in the Saadjärve Drumlin Field are glacial in origin, resulting from a combination of glacial depression and erosion. These lakes were submerged by a proglacial lake, but when the threshold of the proglacial lake was freed of ice, the water level dropped and independent development of the inter-drumlin lakes started. These lakes are elongated in direction of ice movement and contain LG sediments (varved clays, silts, silty clays, fine sand) and Holocene deposits (gyttja, tufa) (Saarse, 1997).

Intensive tufa formation took place in the Pandivere Upland, and surroundings of the Saadjärv Drumlin Field (Mäemets & Saarse, 1995). The tufa is variable in its properties; mostly it comprises a light beige calcareous mud, laminated or massive and unstratified. It contains macro remains of plants or invertebrate subfossils, such as molluscs and gastropods. The tufa formation was extensive during the Early and Middle Holocene (Männil, 1967) and was later replaced by accumulation of organics in Estonia (Mäemets & Saarse, 1995).

In Estonia the most pronounced lowering in lake level occurred *ca*. 10.2-8.9 ¹⁴C cal kyr BP and *ca*. 4.5-3.5 ¹⁴C cal kyr BP. Lakes were at the highest levels about 10.7, 7.8 and 3.2 ¹⁴C cal kyr BP (Saarse *et al.*, 1995). Low water level periods were characterized by dryer climatic conditions. Wetter conditions occurred at the beginning of Early and Middle Holocene (Saarse, 1997).

4. MATERIAL AND METHODS

The sedimentary material that served as the source of palaeoenvironmental information for this PhD project originates from five lacustrine sections. Sediment cores were taken from sites using a Belorussian-type corer in ice (winter) or from lake margins (summer). The ostracod fauna recovered reflects the development of lacustrine environments in northern (Sinijärv, Varangu), eastern (Elistvere, Pedja) and western (Ermistu) Estonia (Fig. 1) through the LG and the Holocene. In the interpretations and discussions herein all available data on the ostracod distribution in the Quaternary sediments of Estonia (Niinemets & Hang, 2009; Saarse *et al.*, 2009; Rattas *et al.*, 2010) has also been taken into account.



Fig. 1. Location of studied Quaternary sections in Estonia comprising ostracod data: 1 – Lake Sinijärv (Paper I), 2 – Varangu (Papers III, IV), 3 – Lake Elistvere (Paper II), 4 – Pedja (Early Holocene Lake Võrtsjärv) (Paper II), 5 – Lake Ermistu (Paper II), 6 – Lake Pikkjärv (Sohar, 2004), 7-9 – Lake Peipsi (Niinemets & Hang, 2009), 10 – Haljala (Saarse *et al.*, 2009), 11 – Arumetsa (Rattas *et al.*, 2010).

4.1. Overview of the lakes and sections studied

Lake Sinijärv is located on the southern slope of the Pandivere Upland in northern Estonia (59°03′45′′ N, 26°14′24′′ E), where Ordovician and Silurian limestones are covered with tills and glaciofluvial gravels of various thickness (3–15 m). Zones of tectonic dislocations and the frequent occurrence of fractures in the limestone bedrock have facilitated the occurrence of karst

processes in this region. Many groundwater-fed springs therefore flow out of the upland slopes and result in paludification. These springs have good water yield (100–1000 l/s), and normally the amount of total dissolved matter is 0.3-0.4 g/l. The annual average precipitation in the region is *ca*. 700 mm/yr (Arold, 2005).

The basal part of the 480 cm long sediment core from Lake Sinijärv (Fig. 2) comprises grey, clayey silt, overlain by (at depth 475–434 cm) a layer of massive gyttja. The remainder of the sequence (434–0 cm) is composed of freshwater tufa, in some levels rich in fragments of aquatic mosses (intervals 219–164 cm and 70–0 cm). The tufa interval at 379–340 cm depth is Fe-rich and the fresh light tufa turns to a reddish-brown colour upon oxidation in air.

Lake Elistvere is located in eastern Estonia, in the Saadjärve Drumlin Field. Lake basins developed in the Saadjärve Drumlin Field as a result of the drumlinization of glacial and glaciofluvial deposits distal to the Pandivere (bedrock) Upland. The retreat of proglacial lakes from the Saadjärve Drumlin Field has left only small isolated lakes in the inter-drumlin depressions (Rosentau *et al.*, 2007). Deposition of LG varved clays, silts, silty clays, fine sand was followed by deposition of Holocene sediments (gyttja, tufa) in variable thickness (Saarse, 1997). According to pollen data (Pirrus, 1983), accumulation of the tufa started in the lake basin in the Early Holocene.

Lake Elistvere was cored from the near-shore paludal area $(58^{\circ}35'12'' \text{ N}, 26^{\circ}40'54'' \text{ E})$. The 350 cm long sediment section starts with silt and fine sand (350-325 cm) which is covered by a thin layer of gyttja (325-321 cm). The latter is overlain by an 82 cm thick (321-239 cm) tufa layer and the uppermost 239 cm of the sediment column consists of peat (Fig. 2).

The Pedja drill core, taken from the Laeva bog in east-central Estonia (58°30'22'' N, 26° 16'2'' E), contains lacustrine sediments that reflect the early history of Lake Võrtsjärv. Lacustrine development at the site lasted until the water level lowered and shallow marginal areas (including the Pedja site) were overgrown and turned into a peat bog. Three sedimentary units are present in the core from the Pedja site (Fig. 2): homogenous LG sand and silt (750–730 cm), a layer of tufa (730–583 cm) and a thick peat complex (583–0 cm). The area of Lake Võrtsjärv was larger at the beginning of Holocene than that of the contemporary lake (Moora & Raukas, 2004). The Pedja core was not dated, however, according to palynological data, the calcareous deposits formed during the Early Holocene age continue into the Middle Holocene (Moora & Raukas, 2004). Pronounced water level decrease took place *ca*. 7.7 ¹⁴C cal kyr BP (Moora *et al.*, 2002).



Fig. 2. Lithostratigraphy of studied sequences with positions and ages of radiocarbon dated samples.

Lake Ermistu in western Estonia represents the type of lake which formed from former lagoons and bays of the Baltic Sea, due to land uplift in the north-western and western parts of Estonia (Kessel, 1968; Saarse, 1997; Veski, 1998). Sediment core $(58^{\circ}21'18'' \text{ N}, 23^{\circ}58'45'' \text{ E})$ was taken from the shore of Lake Ermistu. The sediment sequence consists of six distinct layers (Fig. 2): sand (615–598 cm), peat (598–588 cm), silty calcareous gyttja (588–546 cm), sand (546–523 cm), tufa (523–384 cm), dark greenish-brown gyttja (384–80 cm) and peat (80–0 cm). The pollen record in Lake Ermistu has been carefully analysed (Veski, 1998); the lower peat layer accumulated at *ca*. 10.5 ¹⁴C cal kyr BP when the lake basin was isolated due to isostatic uplift.

The Varangu core section (59°02'17'' N, 26°07'10'' E) represents an old, desiccated groundwater-fed lake, located on southern slope of the Pandivere Upland in northern Estonia. The core was taken from the eastern edge of a tufa pit that covers a large part of the tufa area in the former lake. The lowermost part of the core has dark grey silty clay (333–293 cm) which is overlain by a thick bed of tufa (293–28 cm). The topmost part (28–0 cm) of the sequence comprises a soil layer (Fig. 2).

4.2. Methods

The general stratigraphy and sedimentary characteristics of the cores were documented on site. The core sections were then wrapped in plastic film, for making analyses in the laboratory. The 5 cm diameter core was divided into 1 to 5 cm thick sediment slices (*ca*. $5-50 \text{ cm}^3$) for ostracod analyses, while parallel cores were used for radiocarbon dating and for loss-on-ignition (LOI) estimation. Sediment slices for ostracod analyses were wet-sieved (using 50 µm or 63 µm sieves) and dried at a room temperature. From the dry sediments ostracod subfossil valves and carapaces were picked with a wet paintbrush under an Olympus stereomicroscope. Adult and juvenile ostracod valves and carapaces were stored in micro-slides.

Generally, the preservation of the ostracod subfossils was sufficient for identification, which was based on valve morphology such as shape, size, morphology of the adductor muscle field and the hinge and free margin, and also dimorphic features and sculpture (Fig. 3). Ostracod species identification, species nomenclature and basic ecological interpretation are mainly based on Meisch's monograph (2000). Subfossil material from Estonia was compared to and verified against British Quaternary ostracod collections in Natural History Museum in London, UK.



Fig. 3. Morphology of ostracod carapace used in identification of subfossil taxa. A – lateral view of carapace, B – dorsal view of carapace, C – internal view of carapace.

Juvenile material was not identifiable in every case and was classified as Candonidae spp., although it may actually belong to several ostracod species. Absolute numbers of ostracod species in the samples is given in the distribution diagrams. Carapaces and valves of juveniles as well as the adults were counted as specimens. The ratio of adult/juvenile specimens was also estimated.

To calculate the biodiversity of an ostracod community, the Shannon-Wiener index (H') was used:

$$H' = -\Sigma p_i \ln p_i$$
,

where p_i represents the proportion of each species in the sample. The Shannon-Wiener index is dependent not only on the relative abundances of specimens, but also on the number of taxa (Hammer & Harper, 2006).

All identified ostracod species were imaged by scanning electron microscopy (SEM). Specimens were mounted on SEM plates, cleaned with a paintbrush, and covered with thin layer of cold or platinum in vacuum. SEM was undertaken at the Centre of Material Research at Tallinn University of Technology, at the Department of Geology, University of Tartu, Estonia, and at the Natural History Museum, London, UK. For isotope analysis of ostracod calcite, the specimens were rinsed with distilled water to remove the sediment matrix. Whole carapaces were opened to clean the inside surface of valves. Stable isotopic analyses from ostracod and tufa carbonate were performed at the Iso Analytical Ltd. Laboratory, UK with precision better than 0.3‰ for ¹⁸O and better than 0.2‰ for ¹³C.

The loss-on-ignition (LOI) analyses were performed at the Department of Geology, University of Tartu, Estonia. The organic content of the sediment was estimated by LOI at 500° C and carbonate content from LOI between 500° and 1000° C multiplied by 2.27, after Gedda (2001).

The AMS¹⁴C dates were obtained at the Poznań Radicarbon Laboratory, Poland and conventional ¹⁴C datings in the Radiocarbon Laboratory of the Department of Geology, University of Tartu, Estonia. The OxCal v3.10 and v.4.0 programmes (Bronk Ramsey, 1995, 2001) were used for calibration of radiocarbon ages. The dates in this thesis are expressed as ¹⁴C cal kyr BP.

In this thesis the LG and Holocene stratigraphy of Estonia follows the stratigraphic scheme of Kukk *et al.* (2000), while the ages of major stratigraphic boundaries were calibrated and expressed as mean values of calibration ranges (Early to Middle Holocene, 11.7–8.8 ¹⁴C cal kyr BP; Middle to Late Holocene, between 8.8 and 2.6 ¹⁴C cal kyr BP).

If not directly dated, the age-boundaries of sedimentary units or ostracod assemblages were derived from age-depth models that were derived separately for each dated section (Fig 4; Papers I, III, IV).



Fig. 4. Age-depth models of sedimentation in lakes Elistvere, Varangu, Sinijärv and Ermistu (Papers I–III).

4.3. Characteristic features of ostracod assemblage as environmental indicators

Reconstruction of past environmental conditions based on the composition of ostracod subfossil assemblages requires knowledge of the ecological preferences of recent ostracod species. Ostracods are capable of rapidly invading newly available habitats with suitable environmental conditions. Environmental factors control the distribution of ostracod species and, accordingly, certain indicator species can infer particular environmental conditions.

4.3.1. Environmental indication from taphonomic features

The validity of any palaeoenvironmental reconstruction based on subfossil assemblages depends on knowledge of the relevant taphonomy. If the subfossils have been transported from elsewhere, the reconstruction may be invalid unless that fact is taken into account (Holmes, 1992). Ostracod subfossils behave sedimentologically like sand grains. Because of their relatively large size and mass their down-slope transport can result in considerable mixing of littoral and profundal species in lakes wherever there are relatively steeply sloping lake floors. Ostracods are preserved in sediments as carapaces, isolated valves or fragments. The presence of ostracod carapaces infer rapid burial processes beneath sediments, avoiding excess scavenger or bacterial activity and oxygen levels that might decompose the weak hinges of the carapace (De Deckker, 1988). Predominantly disarticulated valves in sediments perhaps infer a slow sedimentation rate and thus slow burial and isolation of the ostracod subfossils. After death of an ostracod, the carapace opens eventually and decomposes due to microbial activity (Danielopol *et al.*, 1986).

If only adult specimens are present in a subfossil assemblage, it suggests possible post-mortem reworking of sediments, and sorting of the ostracod subfossils in a higher energy environment. Occurrence of both adult and juvenile specimens infers lower energy conditions and thus is likely to be an autochthonous ostracod assemblage (Whatley, 1988; Holmes, 1992; Griffiths & Holmes, 2000; De Deckker, 2002). Subfossil fragments in sediments refer to post-mortem redeposition or even destruction due to coring procedure.

Ostracods are taxonomically complex and sensitive environmental indicators and they are found in most alkaline sediments that are usually deposited under oxic conditions. Because of their calcitic exoskeleton ostracod subfossils are poorly preserved in even mildly acidic bodies of water. Dissolution of ostracod valves also occurs in organic-rich sediments (gyttja, peat) due to reduced pore water pH, resulting from oxidisation of organic matter (De Deckker & Forester, 1988; Holmes *et al.*, 1998).

Subfossil ostracod valves may become dark brown or black if anoxic conditions prevail in sediments after the death of the ostracods (De Deckker, 1988). Ostracod valves that have been buried to great depth and undergone pressure and temperature changes appear grainy and normally transparent valves may become coloured. Evidence of biological corrosion, micro-borings and holes of microborers (bacteria or fungi) may be present on the surface of subfossil ostracod carapaces and valves (Danielopol *et al.*, 1986).

4.3.2. Water depth indication from ostracod data

Water level variation in a lake can affect the littoral fauna, which has to adapt to the changes and migrate to suitable depths. This applies to ostracods, and it is possible to reconstruct changes in water depths from ostracod assemblages in lake sediment sequences. Ostracods can be grouped into species that occur in shallow lacustrine waters and vegetated littoral zones of lakes and ponds, and in those of deeper water (Löffler, 1997; Griffiths & Holmes, 2000). The distribution of ostracod species is closely dependent on the distribution of macrophytes, especially charophytes (which may be related to water depth), on the chemical composition of the bottom waters, and on the types of sediment present (Griffiths & Holmes, 2000). Mourguiart *et al.* (1986) showed that the deepest parts of lakes with organic-rich sediments may lack ostracods, but areas less than 10 m deep with carbonate rich sediments and charophytes are very rich in ostracods (*e.g. C. vidua, Darwinula* sp., *H. reptans*).

In Europe, the most typical deep-water fresh-water ostracod species are *C. lacustris*, *C. candida*, *C. neglecta*, *L. sanctipatricii*, *L. mirabilis* (inhabiting waters >12 m deep) and *F. protzi*, that dominates in profundal zones, often together with *C. ophtalmica* (Griffiths *et al.*, 1993; Griffiths & Holmes, 2000; Namiotko *et al.*, 2006; Namiotko & Martins, 2008; Mischke *et al.*, 2010).

Analysis of the relationship between water depth and subfossil ostracod assemblages showed that *L. inopinata* occurs only in shallow water less than 10 m deep (Mischke *et al.*, 2010). The occurrence of *C. ovum, H. reptans and P. villosa* indicate very shallow waters only a few meters deep (Scharf *et al.*, 2005). The distribution of *P. rostrata* is often associated with submerged vegetation in the littoral zone of lakes and *C. vidua* is usually associated with *Chara* mats. Margins of meso-eutrophic lakes also harbour strongly phytophilic species, notably *M. cordata*. The shallower parts of oligo-mesotrophic lakes are often inhabited by *D. stevensoni*, which infers water depth less than 8 m (more often even less than 3 m) deep (Meisch, 2000; Griffiths & Holmes, 2000).

4.3.3. Indicators for change in temperature and oxygen regime

The knowledge of the temperature and oxygen requirements of particular ostracod species and its application in climate and lake level studies has become increasingly important. Most ostracod species have upper and lower limits of temperature tolerance and the presence and abundance of particular species reflects the temperature regime of a locality. In shallow lakes, which are thermally coupled to the atmosphere, ostracod subfossil records may also provide information on past air temperatures (Griffiths & Holmes, 2000).

A number of ostracod species prefer cool conditions for their life cycles and reproduction. *C. lacustris* is restricted to cool environments, as is *L. sanctipatricii*, *L. mirabilis*, *I. bradyi*, *C. candida*, *F. levanderi* and *F. protzi*. *C. candida*, *F. protzi*, *L. sanctipatricii* and *C. ophtalmica* are even found in Arctic freshwaters (Löffler, 1997; Wetterich *et al.*, 2008; van der Meeren, 2009). *C. lacustris* is a cold water species whose presence can infer a Pleistocene age for the host sediments, and the presence of *L. sanctipatricii* most likely refers to the early stage in lake development during the LG when the summer temperatures were mostly below 10–15° C (Löffler, 1997).

The abundance of M. cordata is related to temperate conditions and its appearance refers to the transition from the LG to the Holocene, and an associated remarkable temperature rise (Meisch, 2000, Griffiths & Evans, 1995).

Some ostracod species have well defined requirements for dissolved oxygen content in the waters they live in. A few species need well oxygenated water for their life cycle (*e.g. C. lacustris*; Newrkla, 1985; Geiger, 1993) but others, like for example *M. cordata*, can survive at very low dissolved oxygen concentrations brought along by eutrophication (Danielopol *et al.*, 1996; Meisch, 2000; Griffiths & Holmes, 2000). *C. ophtalmica* may survive in hypoxic waters with high CO₂ concentrations and it may occupy greater depths in a lake (Martín-Rubio *et al.*, 2005).

4.3.4. Indicators of trophic conditions

Ostracod assemblages may be sensitive to variations in the trophic status in lacustrine systems, as reflected in changes of assemblage structure. Onset of natural eutrophication is normally caused by warm and humid climate periods. Eutrophication may also result from increased input of allochthonous organic material and nutrients (Löffler, 1997).

L. mirabilis, which often co-exists with *C. lacustris,* clearly prefers oligotrophic environments and its abundance decreases as the lake turns eutrophic (Meisch, 2000). Nowadays, also, intensive human impact may cause the disappearance of these species (Löffler, 1997; Meisch, 2000; Belis *et al.*, 2008). The presence of *D. stevensoni* may infer shallow oligo-mesotrophic lakes with no vegetation in marginal zones (Ranta, 1979; Belis *et al.*, 2008). The presence of *M. cordata* infers some higher degree of trophic conditions in the areas where macrophyte masses and organogenic sediments dominate in shallow lake margins, and indicates dystrophy or ageing of a water body (Griffiths & Evans, 1995; Meisch, 2000; Belis *et al.*, 2008).

The faunas described by Absolon (1973) typify ecological conditions in newly-formed water bodies: the "*candida*-fauna" refers to a oligotrophic and benthic environment; the "*cordata*-fauna", on the contrary, typically characterizes waters with higher nutrient load. Normally a water body develops through mesotrophy and eutrophy into dystrophy, and phytophilic ostracod species appear when wetlands are present (Griffiths, 2001).

Scharf (1998) documented changes in the trophic status of the Lake Arendsee, Germany, where the oligotrophic lake turned to eutrophic because of sewage loading. This led to the disappearance of the oligotrophic ostracod fauna (*e.g. C. lacustris, F. protzi*), which was replaced by species (*e.g. M. cordata, H. reptans, L. inopinata*) more tolerant to higher trophic condition.

4.4.5. Oxygen isotope composition of ostracod carapaces as an environmental indicator

Water of the lakes that are predominantly fed on precipitation reflects the mean oxygen isotopic composition of the precipitation of the catchment area, which depends on air temperature. Therefore, the isotopic composition of ostracods from a lake provides a link to air temperature variation (von Grafenstein *et al.*, 1999). During evaporation, water vapour becomes enriched in the lighter isotope ¹⁶O and the residual water becomes enriched in the heavier isotope ¹⁸O (Leng & Marshall, 2004). During precipitation, the heavier isotope condenses first and is enriched in rain and snow, and the cloud moisture is subsequently depleted in ¹⁸O as rain out continues. The factors that affect the isotopic composition of water in the lake are evaporation, which changes with relative humidity, temperature, wind stress, lake surface area and water residence time (Schwalb, 2003). Decreasing lake volume in a relatively dry climate leads to enrichment in ¹⁸O due to increased evaporation/inflow ratio and atmospheric equilibrium. Intervals of humid climatic conditions increased lake volume and rise, and cause depleted isotopic ratios (Hammarlund *et al.*, 2003).

Ostracod carapaces provide a source of calcite for oxygen isotopic analyses and are composed primarily of low-Mg calcite, which reflects the geochemistry of the host water body of the ostracod. Carapaces are formed using Ca^{2+} and HCO_3^{-} ions taken directly from ambient water at the time of carapace secretion, which is a rapid process as it lasts only a few hours (Turpen & Angell, 1971). As the ostracod carapace is secreted over a very short time and not built up incrementally then its composition is a time- and space-specific "snapshot" of
water composition. When information about the depth preferences and seasonal cycles of growth is known, the use of material of only one ostracod species allows very close constraints to be placed on timing and location of calcite formation (Griffiths & Holmes, 2000). Because of that the chemistry of ostracod carapaces is increasingly used to reconstruct the chemistry and the temperature of water in which they lived, with the ultimate aim of reconstructing past environmental conditions including effective precipitation, air temperature, changes in evapotranspiration ratio, lake water level or depth, atmospheric circulation and the carbon cycle of the lake and its catchment area (Holmes & Chivas, 2000; Ito et al., 2003). Heaton et al. (1995) emphasized the need for caution when using isotopic data from single ostracod valves in palaeoclimatic studies. They found large ranges of ${}^{18}O/{}^{16}O$ ratios among modern valves of the same species at the same time. Also, there is a systematic offset between ¹⁸O of valve carbonate compared to ¹⁸O expected for a theoretical calcite formed in isotopic equilibrium (von Grafenstein et al., 1999; Ito et al., 2003). Stable isotope record from lacustrine ostracods can be used to estimate temperature oscillations throughout the LG and Holocene in Europe as shown by Von Grafenstein et al. (1994), Anadon et al. (2006), Hammarlund (1999), Schwalb et al. (1994), Garnett et al. (2004) and many other researchers.

5. RESULTS

Altogether 30 freshwater ostracod species (10 genera), represented by some 28 000 specimens, were identified in the Quaternary deposits in Estonia (Table 1). Most of them are also known from the recent freshwater ostracod record in Estonia. Only two species, *S. pseudobrowniana* and *L. mirabilis* have not been documented from recent local faunas. These species are as follows (taxonomic scheme after Meisch, 2000):

Phylum Arthropoda Subphylum Crustacea Pennant, 1777 Class Ostracoda Latreille, 1806 Order Podocopida Sars, 1866 Suborder Podocopina Sars, 1866 Infraorder Darwinulocopina Sohn, 1988 Superfamily Darwinuloidea Brady & Norman, 1889 Family Darwinulidae Brady & Norman, 1889 Genus Darwinula Brady & Robertson, 1885 Species Darwinula stevensoni (Brady & Robertson, 1870) Superfamily Cypridoidea s. str. Baird, 1845 Family Candonidae Kaufmann, 1900 Subfamily Candoninae Kaufmann, 1900 Genus Candona s. str. Baird, 1845 Species Candona candida (O.F. Müller, 1776) Species Candona neglecta Sars, 1887 Genus Fabaeformiscandona Kristić, 1972 Species Fabaeformiscandona holzkampfi (Hartwig, 1900) Species Fabaeformiscandona levanderi (Hirschmann, 1912) Species Fabaeformiscandona protzi (Hartwig, 1898) Genus Pseudocandona Kaufmann, 1900 Species Pseudocandona albicans (Brady, 1864) Species Pseudocandona compressa (Koch, 1838) Species Pseudocandona rostrata (Brady & Norman, 1889) Species Pseudocandona sucki (Hartwig, 1901) Genus Candonopsis Vávra, 1891 Species Candonopsis kingsleii (Brady & Robertson, 1870) Subfamily Cyclocypridinae Kaufmann, 1900 Genus Cypria Zenker, 1854 Species Cypria exsculpta (Fisher, 1855) Species *Cypria ophtalmica* (Jurine, 1820) Genus Cyclocypris Brady & Norman, 1889 Species Cyclocypris laevis (O.F. Müller, 1776) Species Cyclocypris ovum (Jurine, 1820)

Family Ilyocyprididae Kaufmann, 1900 Subfamily Ilyocypridinae Kaufmann, 1900 Genus Ilvocypris Brady & Norman, 1889 Species Ilvocypris bradvi Sars, 1890 Family Cyprididae Baird, 1845 Subfamily Cypridinae Baird, 1845 Genus Cypris O.F. Müller, 1776 Species Cypris pubera O.F. Müller, 1776 Subfamily Eucypridinae Bronshtein, 1947 Genus Eucypris Vávra, 1891 Species *Eucypris virens* (Jurine, 1820) Genus Tonnacvpris Diebel & Pietrzeniuk, 1975 Species Tonnacypris estonica (Järvekülg, 1960) Species Tonnacypris lutaria (Koch, 1838) Subfamily Herpetocypridinae Kaufmann, 1900 Genus Herpetocypris Brady & Norman, 1889 Species Herpetocypris reptans (Baird, 1835) Subfamily Scottiinae Bronshtein, 1947 Genus Scottia Brady & Norman, 1889 Species Scottia pseudobrowniana Kempf, 1971 Subfamily Cypridopsinae Kaufmann, 1900 Genus Cypridopsis Brady, 1867 Species Cypridopsis vidua (O.F. Müller, 1776) Genus Potamocypris Brady, 1870 Species Potamocypris similis, G.W. Müller, 1912 Species Potamocypris villosa (Jurine, 1820) Superfamily Cytheroidea Baird, 1850 Family Limnocytheridae Klie, 1938 Subfamily Limnocytherinae Klie, 1938 Genus Limnocythere s. str. Brady, 1867 Species *Limnocythere inopinata* (Baird, 1843) Genus Limnocytherina Negadaev-Nikonov, 1967 Species Limnocytherina sanctipatricii (Brady & Robertson, 1869) Genus Leucocythere Kaufmann, 1892 Species Leucocythere mirabilis Kaufmann, 1892 Subfamily Timiriaseviinae Mandelstam, 1960 Genus Metacypris Brady & Robertson, 1870 Species Metacypris cordata Brady & Robertson, 1870 Family Cytherideidae Sars, 1925 Genus Cytherissa Sars, 1925 Species Cytherissa lacustris (Sars, 1863)

Species	Arumetsa (Rattas et al., 2010	Haljala (Saarse <i>et al.</i> , 2009)	Pikkjärv (Sohar, 2004)	Peipsi (Niinemets & Hang, 2009)	Võrtsjärv (Pedja) (Paper II)	Varangu (Paper IV)	Ermistu (Paper II)	Elistvere (Paper II)	Sinijärv (Paper I)	Recent (Järvekülg, 1959, 1961, 1995)
Candona candida			O	0	0	•0	0	0	0	х
Candona neglecta							0			х
Candonopsis kingsleii						0				х
Cyclocypris cf. laevis										х
Cyclocypris ovum			0		0	0		0	0	х
Cypria exsculpta					0	0		0	0	х
Cypria ophtalmica			_						0	х
Cypriaopsis viaua		•	•0		0	0	0	0	0	X
Cypris ci. pubera	•	_	_	0			0	0		X
Cymerissa lacustris	Ŷ	-	-	0	0		0			X
Eucopris of virans		_		0	0		0			X
Eucypris Ci. virens Fabaeformiscandona		-			0		0	0		×
holzkampfi					0		0	0		^
Fabaeformiscandona levanderi				0		•0			0	х
Fabaeformiscandona protzi			0		0	0	0	0	0	х
Herpetocypris reptans				0	0					х
Ilyocypris bradyi	\diamond			0			0			х
Leucocythere mirabilis						•				
Limnocythere inopinata					0	0	0	0	0	х
Limnocytherina sanctipatricii				0		•	0			х
Metacypris cordata					0	0	0	0	0	х
Potamocypris similis					0					х
Potamocypris villosa						0				х
Pseudocandona albicans									0	х
Pseudocandona compressa									0	х
Pseudocandona rostrata						0			0	х
Pseudocandona sucki					_		0			x
Scottia pseudobrowniana					0	-				
Tonnacypris estonica						•				X
1 onnacypris cl. lutaria						•				Х

Table 1. Quaternary and recent freshwater ostracod species in Estonia (Late-
Saalian/minerogenic sediments – \diamond ; late-glacial/minerogenic sediments – \blacksquare ; late-
glacial/tufa – \Box ; Holocene/minerogenic sediments – \bullet ; Holocene/tufa – \circ ; recent – x).

Quaternary ostracod remains were found in two types of sediments: lacustrine sandy silts and clay, and in freshwater calcareous mud (tufa). LG and/or Lower Holocene fine sand and silty clay are rich in ostracod subfossils while in coarse sand layers of the same age ostracods are absent. The richest and most abundant ostracod fauna was identified from the freshwater tufa layers. Ostracods were not found in organogenic deposits (gyttja), probably due to the dissolution of calcareous material.

Ostracod subfossils occur as carapaces, valves, and valve fragments; dissolution marks were observed on some carapaces. In cases the ostracod remains were autochthonous, and therefore, enabled subsequent environmental interpretation. In the Early Holocene silty clay layer at Varangu only valves and a mixed assemblage occurred (Paper IV). Scavengers or transportation possibly disarticulated the ostracod shells post-mortem.

In the tufa beds the abundance of whole carapaces was high, suggesting rapid sedimentation and burial. Juveniles were also well represented (adult/juvenile ratio *ca*. 70:30). In the Varangu tufa bed instars (A-8 or A-7) occur in subfossil carapaces of females of *Metacypris cordata* (Paper III).

Within the ostracod material there is no evidence of recrystallization or deformation. Ostracod valves are mostly white or transparent. In an Fe_{-total} rich sediment layer in Lake Sinijärv some ostracod specimens were brownish-red in colour. With regard to isotope studies ostracods from tufa were white or transparent and, thus, in a pristine condition and ideal for analysis (Paper III).

5.1. Ostracod assemblages and environmental interpretations of the studied sequences

The studied LG and Holocene sequences of Estonia represent sediments of small lakes of temperate area and ostracods preserved in these sediments reflect the past lacustrine environment (Papers I–IV). The ostracod fauna recorded is indicative of cool and temperate limnic freshwaters, no riverine (*e.g. Cyclocypris serena, Cypria curvifurcata*) or marine elements were recorded. Taxa which colonize temporary water bodes, like species of the genus *Eucypris*, where not recorded in the tufa layers, although it was found from LG minerogenic sediments. The LG and Holocene ostracod assemblage is typical of permanent still water bodies. However, presence of *T. estonica* and *P. villosa* suggests some influence of spring systems in Lake Varangu (Paper IV).

11

5.1.1. History of small lakes in Estonia inferred on ostracod data

Lake Sinijärv (Paper I)

Complete faunal history of ostracods throughout the Holocene is obtainable only from the Lake Sinijärv section (a 434 cm long tufa sequence). Continuous freshwater tufa precipitation in Lake Sinijärv, northern Estonia, started at *ca*. 12.8 ¹⁴C cal kyr BP and has continued up to nowadays. In total, 12 ostracod species were identified in the tufa. Silt and gyttja in the lowermost portion of the core section are barren of ostracod subfossils. In the Sinijärv tufa sequence (Fig. 5A) the LG and Early Holocene (ca. 12.8–10.6 ¹⁴C cal kyr BP), in the depth of 434–383 cm the assemblage composed mainly of *M. cordata*. Very few remains of C. candida and P. compressa are present. Evaporation likely exceeded precipitation, and groundwater level was low. The trophic level was high. The most significant change in the ostracod succession occurred at ca. 10.6 ¹⁴C cal kyr BP (at 383 cm), when a typical littoral, polythermophilic fauna (dominated by *M. cordata*) was replaced by a sublittoral, meso- to stenothermophilic ostracod fauna, suggesting water level rise and a shift toward meso- to oligotrophic conditions (F. protzi, C ophtalmica, P. compressa, P. albicans, C. exsculpta and C. ovum in the depth interval of 383–348 cm). This environmental shift suggests reduction of bottom spring feeding of the lake before *ca*. 10.6 ¹⁴C cal kyr BP.

Ca. 8.0–7.4 ¹⁴C cal kyr BP new species in the ostracod assemblage was *F. levanderi* (in the interval of 348–225 cm). The number of species from previous assemblage decreased sharply which may colonize profundal areas (*e.g. C. ophtalmica, C. exsculpta*). Few remains of littoral species *L. inopinata* occurred in the interval also. The composition of the assemblage suggests lowered water level during this period. Middle and Late Holocene periods (6.6–0 ¹⁴C cal kyr BP) were characterized by dominant species cold water preferring *P. rostrata* and *F. protzi* in the interval of 225–0 cm (*F. levanderi* disappeared at *ca.* 6.6 ¹⁴C cal kyr BP in the interval of 225 cm). *P. rostrata* is related groundwater fed lakes, thus appearance of the taxa suggests increased water level as a result of intensive groundwater inflow to the lake.

The ostracod fauna showed quite cold bottom conditions in the lake throughout the Holocene (*F. levanderi, F. protzi, P. rostrata, C. candida*). The highest diversity of ostracod fauna was between 10.6 and 8.0^{-14} C cal kyr BP.



Fig. 5. Age, lithology, ostracod distribution and diversity index (H') in the fossiliferous part of Sinijärv (A), Elistevere (B), Pedja (C) sequences (Papers I, II). Legend see in Fig. 2.

Lake Elistvere (Paper II)

In the Elistvere section, ostracod subfossil remains were recorded only in the tufa sequence (321-239 cm) (Fig. 5B). The dating shows the LG age of the basal beds of tufa (*ca.* 12.8 ¹⁴C cal kyr BP). Altogether nine ostracod species were identified. With the tufa accumulation littoral ostracods populated the basin and *M. cordata* occurs together with *C. vidua, C. ovum, L. inopinata* in the tufa interval, suggesting the sampling area to represent a shallow lake margin with vegetation. Less common were *L. inopinata, C. candida, Fabaeformiscandona holzkampfi, C.* cf. *pubera, F. protzi, C. exsculpta.* The gradual increase of abundance of *M. cordata* suggests the lake level lowering, increase in ambient temperature and in trophic level. Datings suggest that the water level lowered and marginal zone of the lake paludified at *ca.* 10.2 ¹⁴C cal kyr BP. The diversity index increases also upward in the section.

Early Holocene Lake Võrtsjärv (Pedja section; Paper II)

Ostracod remains were found in the tufa sequence only, and in total 12 ostracod species were recognised. The oldest ostracod assemblage in the fossiliferous part of the Pedia tufa section (from marginal zone of the Early Holocene Lake Võrtsjärv) in the interval of 735-721 cm is characterized by abundant C. candida, L. inopinata, C. vidua, C. ovum, F. holzkampfi, H. reptans, C. exsculpta, D. stevensoni, P. similis (Fig. 5C). Presence of this assemblage is indicative of a shallow mesotrophic lake with less vegetation in shore area of the lake. A shift in assemblage structure followed, and disappearance of L. inopinata, H. reptans, and D. stevensoni occurred. Changes in the ostracod assemblage may be related to rising water level (at 721-690 cm of tufa sequence). A new water level lowering occurred when M. cordata made its appearance (690–583 cm of sequence) co-occurring with C. candida, C. vidua, C. ovum, F. holzkampfi, C. exsculpta, F. protzi. The number of M. cordata increases gradually in the upper part of the sequence, but rest other species are rare. A gradual increase of abundance of M. cordata is likely due to a progressive eutrophication of the water body, the ancient Lake Võrtsjäry. In the tufa-peat transition zone M. cordata co-occurs only with S. pseudobrowniana and C. ovum and has a very high population density. As the peat accumulation started just above this level, the appearance of S. pseudobrowniana is apparently related to the transition of the marginal parts of the lake from the lacustrine to the wetland (peat-bog) stage.

Lake Ermistu (Paper II)

In the Ermistu core (Fig. 6A) ostracod remains occur only in (588–546 cm) the Early Holocene sediments and 12 ostracod species were found. In silty calcareous gyttja, remains of *D. stevensoni, L. inopinata, C. candida, C. vidua*



Fig. 6. Age, lithology, ostracod distribution, diversity index (H') in the fossiliferous part of Ermistu (A) and Varangu (B) sequences (Papers II, IV). Legends see in Fig. 2.

F. holzkampfi occur. The occurrence of this assemblage suggests cool oligo to mesotrophic (sub) littoral waters with the lack of vegetation *ca.* at 10.5-10.3 ¹⁴C cal kyr BP. In the transition between calcareous gyttja and sand layer (546–523 cm) very few carapaces and valves of *L. inopinata, I.* cf. *bradyi, C. lacustris,* and *F. protzi* occurred. In the sand interval *D. stevensoni* did not occur. It is noteworthy that *L. sanctipatricii* and *C. lacustris,* two species typical of oligotrophic cold-stenothermal environments, occur in this transgressive silty calcareous gyttja/sand interval. The sand layer is overlain by tufa (interval 523–418 cm). In this layer *M. cordata* is dominating, occurring together with *P. sucki, C. neglecta, I. bradyi, C. candida, F. protzi, L. inopinata.* The highest

diversity in this section was recorded. This ostracod assemblage refers to the shallowest water level and a high productivity, lasting from ca. 10.1 ¹⁴C cal kyr BP up to ca. 9.5 ¹⁴C cal kyr BP. The ostracod fauna contains no indication of overgrowing of the area, which is present in the contemporaneous sediments of the Elistvere and Pedja sections. Although Lake Ermistu has a specific history, representing a former bay or lagoon of the Baltic Sea, it was exclusively characterized by freshwater ostracod fauna as documented from the Early Holocene, similarly to the shallow water bodies in eastern Estonia.

Lake Varangu (Paper III, IV)

From Varangu sequence (Fig. 6B) 15 ostracod species were identified. The Early Holocene silty clay contains $(11.2-9.3)^{14}$ C cal kyr BP; 330–293 cm) subfossils of *C. candida, T. estonica, L. mirabilis, L. sanctipatricii, F. levanderi,* and *T.* cf. *lutaria.* Occurrence of *T. estonica, L. mirabilis, L. sanctipatricii* suggest the formation of the silty clay layer took place in an oxygen-rich cool and oligotrophic profundal area of the lake, with a spring inflow to lake basin. Material of *T. estonica* is likely the first fossil record of this species worldwide (Paper IV). Appearance of only adult valves of ostracods and species from different habitats (*e.g.* crenophilous *T. estonica* and lacustrine *L. sanctipatricii, L. mirabilis*) suggest allochthonous and mixed assemblages in this sediment layer. The highest diversity occurred in this oldest ostracod assemblage in the sequence.

In the tufa layer above silty clay layer ostracod carapaces and valves were autochthonous. The interval with a mixed assemblage is overlain by a tufa bed (293–262 cm) being dated approximately as 9.3–9.1 ¹⁴C cal kyr BP. This bed contains plant remains and its ostracod assemblage is dominated by C. candida. Few remains of littoral species of C. cf. ovum, C. exsculpta, P. cf. villosa, P. compressa, L. inopinata occurred in this interval suggesting lowered water level and increased temperature. During 9.1-8.6 ¹⁴C cal kyr BP (262-180 cm) occurred species cold water and oligotrophic conditions preferring F. protzi together C. cf. ovum, C. exsculpta, C. vidua. In this interval P. rostrata made its appearance also. A slight cooling and productivity decrease during ca. 9.1-8.6 ¹⁴C cal kyr BP preceded further temperature rise and water level lowering ca. 8.6–7.4 ¹⁴C cal kyr BP (180–28 cm), leading to the development of an eutrophic lake and ceasing of the tufa precipitation. In this interval M. cordata and P. rostrata remains occur together C. kingsleii in sediments suggesting shallowing warm nutrient- and vegetation rich water body toward the end of tufa formation (*ca*. 7.4 14 C cal kyr BP; Papers III, IV).

Co-occurrence of warm stenothermal *M. cordata* and cold stenothermal *P. rostrata* is rather peculiar and may suggest presence of a thermocline in the water body, as benthic species preferring groundwater inflow and exobenthic ostracod avoiding groundwater both occur in the subfossil assemblage (Paper IV). The ostracod stable oxygen isotopic analyses (*ca.* 8.5 ¹⁴C cal kyr BP) show

low δ^{18} O values, -10.05 ‰ (SD=0.64) for exobenthic *M. cordata*, -9.34 ‰ (SD=0.27) for *C. kingsleii* and -8.75 ‰ (SD=0.34) for benthic *P. rostrata*, (Paper III). Such a dispersive oxygen isotopic composition of ostracods may suggest that the upper water masses were more affected by variations in air temperature and precipitation during the summer period; the valves of benthic *P. rostrata* had also more uniform isotopic composition suggesting more stable temperature condition in the near bottom waters. The period was probably characterized by the higer effective humidity, as upper water masses were depleted by heavier isotope ¹⁸O (Fig. 7).



Fig. 7. Formation of isotope composition of ostracod subfossils according to ecological preferences of species suggests lower evapotranspiration ratio in freshwater basin in summer seasons before the HTM when the surface water became depleted in the heavier isotope ¹⁸O.

5.1.2. Late-glacial and Holocene ostracod faunas in Estonia

Distribution of ostracod species in the sediments is recorded throughout the post-glacial period. The main colonization of the area by ostracods took place roughly at the transition of LG and Holocene (Fig. 8). The LG and Early Holocene silts and clays are characterized by the cosmopolitan species *C. candida*, occurring together with the cold stenothermal *L. mirabilis*, *L. sanctipatricii*, *C. lacustris* (Haljala, Pikkjärv, Varangu sites). Such

assemblage structure (the "*candida*-fauna" *sensu* Absolon, 1973) is typical of large cold oligotrophic lakes. In the LG and Early Holocene the tufa sequences contain abundant *M. cordata*, and the corresponding assemblage may be interpreted as the "*cordata*-fauna" *sensu* Absolon (1973) (Papers I–IV). The latter assemblage is more species-rich than the "*candida*-fauna". Ostracod species in the *cordata*-assemblage are sensitive to environmental changes, like lowering water level, temperature fluctuation, changes of trophic status of a lake (Papers I–IV).



Fig. 8. Development of ostracod fauna in Estonia during the LG and Holocene (Papers I–IV; Sohar, 2004; Niinemets & Hang, 2009; Saarse *et al.*, 2009). Solid line – time interval of the species distribution according to age-depth models; dotted line – time ineterval of species distribution derived from correlation of sediment layers/palaeoenvironmental events.

M. cordata and *D. stevensoni* did not co-occur in Estonian lakes at the beginning of the Holocene (Paper II). *D. stevensoni* made its appearance before the invasion of *M. cordata*, being accompanied by *L. inopinata, C. candida, C. vidua, H. reptans* and *I. bradyi*. The "stevensoni-fauna" was a transitional ostracod fauna between the oligotrophic "candida-fauna"and eutrophic

"*cordata*-fauna" in Estonia. Occurrence of *D. stevensoni* likely refers to oligo-/mesotrophic conditions in shallow water bodies with open waters, *i.e.* without or with only minimal aquatic vegetation (Pedja and Ermistu sections) (Paper II).

Development of a lake from an oligotrophic water body towards meso-to eutrophic state and formation of a paludal area bring along distinct changes in the composition of ostracod assemblages (Fig. 9). Oligotrophic lakes of Estonia are characterized by the "candida-fauna" (Sohar, 2004; Saarse et al., 2009; Paper IV). Rise of temperature and nutrient level brings a lake into the oligo- to mesotrophic state, supporting higher ostracod diversity and the appearance of the "stevensoni-fauna" (Paper II). Progressive eutrophication and ageing of a water body create favourable conditions for *M. cordata*. Appearance of this species, together with other typical littoral taxa, is indicative of lowering water level and shrinking lake basin. These changes cause a gradual increase of population density of *M. cordata* (Papers I, II, IV). Eutrophication and development of dense vegetation in marginal areas of a lake is a characteristic feature of the Early Holocene. Transition of the overgrown water body into a paludal area may result in the appearance of *S. pseudobrowniana* in the low-diversity "cordata-fauna" (Paper II).

Trophic status		Indicator species	Sediments
overgrowing/ terrestrialisation	Î	Scottia pseudobrowniana	
meso-/eutrophic	vard ageing el decrease	Metacypris cordata	Tufa
oligo-/mesotrophic	volution tow ral lake lev	Darwinula stevensoni	
oligotrophic	lake e [.] a gene	Candona candida	Silt/caly/ fine sand

Fig. 9. Succession of freshwater ostracod assemblages in Estonia from the LG to the HTM according to changes (water level, trophic status) in ambient waters (Papers I, II, IV).

Appearance of *P. rostrata* in the Middle and Late Holocene does not fit the above model. *P. rostrata* is recorded from the tufa beds of Lake Sinijärv and Varangu tufa pit, but not recorded from the eastern or western parts of Estonia. It has the same distribution areas as the spring-related *T. estonica*. This may be interpreted as evidence of groundwater preference in *P. rostrata*.

6. DISCUSSION

6.1. Evolution of lacustrine ostracod faunas during the late-glacaial and the Holocene in Quaternary sediments in Estonia

In the last late-glacial ostracods populated very early large water bodies in central and northern Europe. Pioneer species were normally *L. mirabilis, C. lacustris, L. sanctipatricii, C. candida, C. neglecta,* subfossils of which occur in LG clays and silts (Scharf, 1993; Schwalb *et al.*, 1994; Löffler, 1986, 1997; Schwalb *et al.*, 1998; Krzymińska & Przezdziecki, 2001; Namiotko *et al.*, 2006; Viehberg *et al.*, 2008; Hammarlund, 1999; Hammarlund *et al.*, 1999). This conclusion is supported with the Estonia data as well. *C. lacustris,* accompanied with *I. bradyi,* is documented also in the Late-Saalian clay deposit in western Estonia (Table 1) (Rattas *et al.,* 2010), suggesting that these two were the pioneer species, following the termination of glacial environments.

The last Scandinavian Ice Sheet (Late-Weichselian) grew large enough to divert melt water from the margin of the ice sheet in northern Europe across the Baltic Basin to eastern Europe. At *ca.* 15.0 ¹⁴C cal kyr BP it formed large ice dammed lakes (the Baltic Ice Lake, Pri-Valdai Ice Lake), due to temperature increase (Hubberten *et al.*, 2004; Mangerud *et al.*, 2004). Large freshwater bodies were suitable for primal aquatic habitants.

Lakes with minerogenic (sand, clay) sedimentation have a low organic content and are considered oligotrophic (Håkanson & Jansson, 1983). The assemblages associated with minerogenic sediments contain benthic species which require high oxygen concentrations in the cold bottom waters and inhabit profundal areas of large lakes (*C. lacustris, C. candida, L. mirabilis, L. sanctipatricii* – Danielopol *et al.*, 1988; Meisch, 2000; Mischke *et al.*, 2010). Few of the species, *e.g. C. lacustris* and *Leucocythere* sp., have water depth optima deeper than 30 m.

In Estonia ostracods colonised freshwater basins after the decay of the last ice cap. The earliest post-glacial ostracod subfossils are found in lacustrine silty clays and clayey silts or in fine sand (Table 1; Fig. 8). The LG species were distributed mainly with melt water flows and in course of water level changes caused by melting glaciers and permafrost. Similar possibilities of ostracod distribution were suggested by Griffiths & Evans (1995) in northern Europe. Judging from the presence of arctic ichtyofauna in the LG Baltic Ice Lake (Paaver & Lõugas, 2003; Kukk *et al.*, 2000), a passive way of distribution may also have played some role in migration of ostracod species.

Ice retreated from the current Estonian territory between *ca*. 14.7–12.7 ¹⁴C cal kyr BP (Kalm, 2006). As described by Davydova *et al.* (2001), Birks *et al.* (2000), Heikkilä *et al.* (2009), LG terrestrial and aquatic ecosystems readily

responded to climatic changes. Changes in the composition of LG ostracod assemblages reflect temperature and water level fluctuations in lakes.

The oldest subfossil ostracod record of post-glacial Estonia comes from the Haljala palaeolake in northern Estonia, where the pioneer species were temperate, shallow water ostracods *E*. cf. virens, *C*. candida, *C*. ovum, *P*. compressa and *L*. inopinata. Appearance of these species marks a temperature increase at ca. 13.8–13.6 ¹⁴C cal kyr BP (Saarse et al., 2009). The earliest records of *L*. sanctipatricii and *C*. lacustris are younger, between ca. 13.6 and 13.1 ¹⁴C cal kyr BP. This may refer to the incompleteness of the data set, as the early colonization history of the lacustrine environments was most likely similar to the respective developments in the other parts of Europe. For example Scharf et al. (2005) recorded the appearance of *C*. candida, *C*. ovum, *H*. reptans, *C*. vidua, *P*. villosa, *L*. inopinata and *I*. decipiens in sediments of the former lake of Miesenheim, northern-western Germany ca. 13.4–12.0 ¹⁴C cal kyr BP.

Ostracod fauna in minerogenic sediments of Lake Pikkjärv (eastern Estonia) is also of LG age (after R. Pirrus, 1983; not directly dated). The dominant species in the LG sediments of this lake were *C. lacustris, C. candida, L. mirabilis* suggesting cool conditions in a large water body (Sohar, 2004). According to many studies in Europe (Schwalb *et al.*, 1998; Krzymińska & Przezdziecki, 2001; Belis *et al.*, 2008; Viehberg *et al.*, 2008) co-occurrence of *C. lacustris, C. candida, L. mirabilis* and *L. sanctipatricii* refers to profundal zones of large deep well ventilated lakes with silty or clayey bottom sediments. A similar assemblage was recorded in silty clays at the Varangu site, where it persisted until the middle Early Holocene (11.2 to 9.3 ¹⁴C cal kyr BP) (Table 1; Paper IV).

In modern ostracod fauna, the species typical of oligotrophic lakes (like *C. lacustris* and *L. sanctipatricii*), are not very common in smaller lakes but are still found together in profundal areas of large lakes in Estonia (Järvekülg, 1959). *L. mirabilis* invaded large cool lakes with minerogenic sedimentation during the LG and Early Holocene, until rising temperatures and rising trophic status turned unfavourable to this species. *L. mirabilis* does not tolerate higher trophic status, warmer ambient temperatures and anoxic conditions. It disappears in course of enrichment of the lake sediments with organic material and decreasing oxygenation of the water-sediment interface (Meisch, 2000).

Already at the end of LG, isolated water bodies started to replace proglacial large lakes in Estonia. Precipitation of freshwater tufa began in many lakes at ca. 12.8 ¹⁴C cal kyr (Papers I, II). The water level lowering in lakes was due to Billingen drainage and land uplift (Rosentau *et al.*, 2009). At the beginning of the Holocene, the sedimentary environment turned humic or alkaline in the lake basins. Ostracod distribution occurred by hydrological means or as a passive transport by mammals or avifauna. In addition, ichtyofauna may have contributed to passive dispersal of the latest LG and Holocene ostracod species in Estonia (Paaver & Lõugas, 2003).

The above described developments introduced more eurythermal ostracod species in littoral areas of lakes. The ostracod fauna is heterogeneous and of variable species composition in the Holocene tufas of Estonia (Figs. 5–6; Papers I–IV). The dominant species were *M. cordata, C. vidua, C. candida, P. rostrata* and *C. ovum.* Griffiths & Evans (1995) suggested calcareous conditions to be unsuitable for *M. cordata* and refer the species mainly to humic deposits. However, the occurrence of this species in the LG and Holocene calcareous deposits of Estonia, but also in calcareous deposits in other parts of northern Europe (Griffiths, 1999; Walker et al., 1999), suggests that calcareous habitats were still favourable to this species.

Although *M. cordata* is very common, it is not present in every studied sequence. Subfossils of *M. cordata* are recorded from several lakes:

- Lake Sinijärv between *ca*. 12.8–10.6 ¹⁴C cal kyr BP (Paper I);
- Lake Elistvere, the subfossil record *ca*. 12.8–10.2 ¹⁴C cal kyr BP (Paper II);
- Lake Ermistu in western Estonia, where *M. cordata* occurred in sediments deposited between *ca*. 10.2 and 9.5 ¹⁴C cal kyr BP (Paper II);
- at Varangu site where the species occurred in much younger sediments, dated as *ca*. 8.6–7.4 ¹⁴C cal kyr BP (Paper IV);
- in the Pedja core (Lake Võrtsjärv deposits), the occurrence of *M. cordata* was not directly dated but indirect evidence suggests it to occur in the Early Holocene or early Middle Holocene (Paper II). The strait system between Lake Peipsi and Lake Võrtsjärv closed *ca.* 12.8–11.7 ¹⁴C cal kyr BP (due to isostatic uplift: Rosentau *et al.*, 2009) and this event marked the beginning of decrease of volume of the Lake Võrtsjärv. Moora *et al.* (2002) have supposed that the lake retreated from the study area nearly 7.7 ¹⁴C cal kyr BP.

The data listed above demonstrate that *M. cordata* can be recorded in the sediments of different age but its presence is referring to similar changes in palaeoenvironments. At the same time, it still did not colonize lakes with minerogenic sedimentation.

The "candida-fauna" sensu Absolon (1973) contains C. candida, P. compressa, P. villosa, C. ovum, and some other taxa not common in Estonia. Typical representative species of his "cordata-fauna are M. cordata and D. stevensoni, together with some other typical central European taxa. The "candida-fauna" can also be recognized in Estonia, being composed of C. candida, L. sanctipatricii, L. mirabilis, C. lacustris, and T. estonica. Judging from palaeoenvironmental reconstructions of the area, this was a cold stenothermal fauna (Sohar, 2004; Saarse et al., 2009; Paper IV). Similar candida-assemblages are also recognised in the Holocene sediments on the British Isles (Griffiths & Evans, 1995) and in central Europe (Günther, 1986; Löffler, 1986, 1997; Viehberg, 2004). Günther (1986) and Viehberg et al. (2008) also suggest this fauna to be characteristic of the minerogenic sediments.

Ostracod species belonging to the "*cordata*-fauna" in Estonia are eurythermal, colonising favourably lakes with tufa precipitation, and this new assemblage is more species-rich than the "*candida*-fauna". These taxa were still sensitive to changing water level, temperature fluctuations and changing trophic status (Papers I–IV).

An intermediate assemblage of *D. stevensoni* can be recognized before invasion of *M. cordata* in several localities of Estonia (Pedja, Ermistu). In central and southern Europe, *M. cordata* and *D. stevensoni* are found in the same ostracod assemblages at the beginning of the Holocene (Belis *et al.*, 2008; Viehberg *et al.*, 2008). In Estonia, *M. cordata* and *D. stevensoni* were not found together. *D. stevensoni* co-occurs with *L. inopinata, C. candida, C. vidua, H. reptans* and *I. bradyi*, in the Holocene sediments of the Lake Peipsi also together with *C. lacustris, C. candida, F. levanderi, F. protzi, L. sanctipatricii* (Niinemets & Hang, 2009). The record from Lake Peipsi shows that the *stevensoni* assemblage has some overlap with the "candida-fauna" and likely comprises a transition between the oligotrophic "candida-"and eutrophic "cordata-fauna" (Paper II).

The Holocene ostracod fauna is generally similar to the modern freshwater ostracod fauna in permanent shallow lakes in Estonia. The species recognized in the calcareous sediments (tufa) are known in modern small lakes in Estonia, however, only half of the recent species have a subfossil record. This may partly be due to the fact that recent depositional environments are too different of the Holocene alkaline lakes. Alkaline lakes are nowadays rare in Estonia.

6.2. Ostracods and palaeoenvironmental changes in Estonia

Changes in ostracod assemblages in freshwater systems serve as a proxy of environmental changes. Autecology of ostracod species allows to reconstruct environmental history, *e.g.* changes in relative water level, temperature and trophic status of small lakes in Estonia through the Late-Pleistocene and the Holocene (Papers I–IV).

With the exception of *L. mirabilis* and *S. pseudobrowniana*, the rest of the LG and the Holocene taxa are present in the recent ostracod fauna of Estonia as well. All the freshwater ostracod species identified in the studied Quaternary sequences in Estonia (Papers I–IV; Rattas *et al.*, 2010; Saarse *et al.*, 2009) are also common in modern, the LG and the Holocene faunas throughout northern and central Europe (summaries in Griffiths, 1995a and Meisch, 2000).

M. cordata has wide geographical distribution. It is found in most regions of Estonia, both in LG and Early Holocene tufa sequences (Papers I–IV), with the exception of the Early Holocene sediments of Lake Peipsi (Niinemets & Hang, 2009). Disappearance of *M. cordata* from the tufa sequences is a result of intensifying groundwater inflow during the Early Holocene, as documented

14

from the Pandivere area (Paper I). There is an evidence from the other areas (observations from Austrian, Romanian, English lakes) that *M. cordata* avoids groundwater inflows (Danielopol *et al.*, 1996). The groundwater in the Pandivere Upland area, northern Estonia, has been Fe-rich during the Early Holocene (Paper I) and high Fe concentrations were lately measured in the recent spring waters too (Syrovetnik *et al.*, 2007). This may suggest that the changes in the population density of *M. cordata* may partly be related to the changes in water chemistry.

P. rostrata, if compared to *M. cordata* had more restricted distribution. It occurs in the Middle- to Late-Holocene tufa sequences in the Pandivere area which is rich in springs (Papers I, III, IV). In modern European ostracod fauna *P. rostrata* is found in ponds of calcareous wetlands, fed by springs that flow out from the Cretaceous chalk (Keatings *et al.*, 2002). This available information suggests that the occurrence of *P. rostrata* may be indicative of an increased groundwater discharge into the water body.

Although the subfossil record of *T. estonica* is unknown outside Estonia (Paper IV) and the species is also rare in modern ostracod fauna in Europe (van der Meeren *et al.*, 2009), its recent distribution in Estonia and co-occurrence with other modern species (Timm & Järvekülg, 1975) suggests a controlling mechanism on its distribution which is similar to that in *P. rostrata*.

S. pseudobrowniana is often documented as being related to springs, but semi-terrestrial way of life has been observed as well (Meisch, 2000). It inhabits floating fens of shallow lakes, in association with *C. kingsleii* and *M. cordata* (Danielopol & Vespremeanu, 1964). In Estonia *S. pseudobrowniana* points to aged water-bodies, rather than to the spring-water systems, appearing in composition of the "*cordata*-fauna" in course of paludification of lake shores (Paper II).

Comparative analysis of data from studied freshwater tufa sequences revealed similar ostracod distribution patterns. This is best reflected in dynamics of *M. cordata*. However, the fact that *M. cordata* is recorded in sediments of different ages (see above) suggests that similarity in ostracod distribution patterns between the studied sections is most likely due to similar environmental trends that were non-contemporaneous.

Figure 10 is summarizing local changes in composition of ostracod assemblages, changes of water level and temperature in the studied lakes. It visualizes the similar but non-contemporaneous trends in environmental history of different water bodies. This proves that regional climatic changes are not the only factor influencing lake biota and evolution of lakes. Other factors, like dissolved and particulate material from the catchment, the base and nutrient status of the lake water and the internal process of ecosystem succession and sediment accumulation (Birks *et al.*, 2000; Väliranta *et al.*, 2007) have likely been equally important during the Holocene.



Fig. 10. Distribution of indicator ostracod species in studied sequences showing local environmental changes during the LG and the Holocene (Papers I, II, IV and Niinemets & Hang, 2009).

Development of water bodies is well reflected in the succession of ostracod assemblages. The "*candida*-fauna" reflects an early, oligotrophic stage in lake evolution, being also related to high water level in a lake. Studies of pollen and sediments suggest high lake levels for the beginning of Holocene in Estonia (Punning *et al.*, 2003; Koff *et al.*, 2005). This may be due to increasing humidity over the northern mainland, maritime climate (Seppä *et al.*, 2005; Giesecke *et al.*, 2008; Seppä *et al.*, 2009) and relatively low temperatures (Hammarlund *et al.*, 2003; Seppä *et al.*, 2005). Appearance of the "*stevensoni*-fauna" is characteristic of the mesotrophic phase in the development of a lake while the "*cordata*-fauna" is indicative of the eutrophic/dystrophic phase. The early appearance of *M. cordata* (12.8 ¹⁴C cal kyr BP) supports the idea that lowering of water levels and a temperature rise in lakes started already during

the LG in Estonia. Saarse *et al.* (1995) concluded that this happened in the Early Holocene but the dated ostracod records from Lake Sinijärv and Lake Elistvere clearly refer to the LG ages (Papers I, II). The periods of the highest temperatures during the HTM were characterised by progressively lowering lake levels and dry climate, culminating in the middle of the Holocene in northern Europe (Heikkilä & Seppä, 2003; Hammarlund *et al.*, 2003; Seppä & Poska, 2004; Antonsson *et al.*, 2006; Gedda, 2006; Antonsson *et al.* 2008; Seppä *et al.*, 2009; Heikkilä *et al.*, 2010). The prevalence of *M. cordata* and a gradual increase of its abundance in the Early Holocene sediments are due to this water level lowering and increase of both, temperature and trophic status of the particular lake (Papers II, IV; Fig. 10).

Differences in O-isotopic composition of valve calcite of ostracod species with different habitat preferences (exobenthic *M. cordata* has lower ¹⁸O values (-10.05 ‰) than benthic *P. rostrata* (-8.75 ‰) – Paper III) suggest low evapotranspiration rates, high water levels and increased groundwater discharge before the Holocene Thermal Maximum. Intervals of more humid climate conditions are characterized by increased lake volume and relatively depleted isotopic ratios (Hammarlund *et al.*, 2003).

A gradual decrease in temperature is recorded since *ca*. 4.5–4.0 ¹⁴C cal kyr BP in northern Europe, being visible both in the pollen and stable isotopic records (Hammarlund *et al.*, 2003; Heikkilä & Seppä, 2003; Seppä & Poska, 2004; Seppä *et al.*, 2005; Antonsson & Seppä, 2007). Changes in the Late Holocene ostracod assemblage structure in northern Estonia, the appearance of *P. rostrata* in particular, are in agreement with these data, suggesting increasing water level and high groundwater discharge (Paper I).

7. CONCLUSIONS

- The Quaternary ostracod subfossils record in Estonia comprises 30 freshwater species recorded from minerogenic sediments (predominantly cold-preferring species) and freshwater lacustrine tufa deposits (more thermophilous species). Organic lacustrine sediments are barren of ostracod remains. Ostracod shells, if present, are well preserved and mostly *in situ* conditions.
- Late-glacial and Holocene ostracods occur in the modern freshwater fauna of Estonia, except for *Scottia pseudobrowniana* and *Leucocythere mirabilis*, and are known in the western and northern European subfossil and recent faunas as well. The subfossil record of *Tonnacypris estonica* in northern Estonia is the first documentation of subfossil occurrence of this species worldwide.
- The late-glacial ostracod fauna was temperature-dependent. The late-glacial pioneer species were thermophilous *Limnocythere inopinata, Cyclocypris ovum, Pseudocandona compressa,* and cold water preferring *Candona candida, Leucocythere mirabilis, Limnocytherina sanctipatricii, Cytherissa lacustris,* both faunas appearing soon after the Late-Weichselian ice decay in Estonia.
- Changes in the composition of the ostracod assemblages in tufa sequences reflect changes in ambient temperature, lake level and trophic conditions. *Metacypris cordata, Darwinula stevensoni, Pseudocandona rostrata,* and *Candona candida* are the most important taxa for interpreting palaeo-environmental changes in Estonian lakes
- The dated ostracod record refers to first clear evidence of lake water level lowering and a temperature increase in Estonia already during the lateglacial (*ca.* 12.8^{14} C cal kyr BP).
- The "candida-fauna" and the "cordata-fauna" by Absolon (1973) were recognized in Estonian lacustrine sediments but they refer to non-contemporaneous environmental changes in the studied lakes. Appearance of the "cordata-fauna" refers to an ageing eutrophic freshwater body with emerged aquatic vegetation. Specific feature for Estonia is that between the "candida-" and "cordata-faunas" a transitional "stevensoni-fauna" occurs, implying to mesotrophic lake with cooler and open water.
- Oxygen isotopic composition of valve calcite of exobenthic *Metacypris* cordata (average $\delta^{18}O = -10.05 \%$) has lower ¹⁸O values than that of benthic *Pseudocandona rostrata* ($\delta^{18}O = -8.75 \%$), suggesting that there was low evapotranspiration rate, increased lake volume and high groundwater discharge before the Holocene Thermal Maximum.
- Similar ostracod successions in the tufa sequences are mostly noncontemporaneous. This suggests that, since the end of late-glacial and beginning of the Holocene, development of the lakes was more affected by local changes in the catchments (water level, productivity, temperature, vegetation, groundwater inflow) than by regional climatic changes.

8. FUTURE RESEARCH PERSPECTIVES

Advanced research using ostracod subfossils will contribute to high-resolution reconstructions of air/water temperature histories since the late-glacial. Calcite of ostracod carapaces is among the best materials for stable isotopic analyses that can produce quantitative temperature data for the Quaternary (*e.g.* Anadon *et al.*, 2006; Schwalb, 2003; Schwalb *et al.*, 1994; von Grafenstein *et al.*, 1994; 1998; Holmes *et al.*, 2010). The present study demonstrates that freshwater tufa deposits are the best sediment archives where subfossil ostracods are preserved in large quantities and in good preservation. One of the best study objects in this respect is Lake Sinijärv in northern Estonia which reveals ostracod subfossil record since the late-glacial up to now. In addition, ostracod-containing tufa sequences of the Eemian age are also known to cover lengthy periods of time and thus provide an opportunity for comparative palaeoecological research of two different interglacials.

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18

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SUMMARY IN ESTONIAN

Mageveelised karpvähid pärastjääaegsetes setetes ja nende kasutamine paleokeskkonna rekonstrueerimisel Eestis

Paleokeskkonna uuringud on muutunud oluliseks kogu maailmas. Selleks, et näha ette võimalikke tuleviku arengusuundi, püütakse mõista minevikus toimunud kliimamuutusi. Järvede elustik, sh põhjaloomastik, on tundlik keskkonnas toimuvate muutuste suhtes, reageerides veetaseme, temperatuuri, toitelisuse, soolsuse kõikumistele. Õietolmu, ränivetikate ja taimejäänuste uurimine järvesetetest on laialt levinud. Antud töös kasutatakse esmakordselt Eestis karpvähkide ehk ostrakoodide subfossiile, interpreteerimaks keskkonnamuutusi peale viimast jääaega. Karpvähid (u 0,5–2 mm) on veelised organismid, kelle pehmet keha ümbritseb kahepoolmeline lubiainest koda, mis säilib setetes pärast looma surma. Teades tänapäevaste karpvähkide keskkonnaeelistusi on võimalik interpreteerida mineviku veelist keskkonda.

Mandriliustik taandus Eesti aladelt ligikaudu 14 700–12 800 aastat tagasi ning jääpaisjärvede sulavetest kujunesid veetaseme alanemisel järved. Peale liustiku taandumist asustasid karpvähid kiiresti suured pärastjääaegsed mageveekogud. Karpvähkide koosluste struktuur sõltus esialgu enamasti temperatuurist ning esimesed soojenemisele viitavad liigid olid *Limnocythere inopinata, Candona candida* (13 800–13 600 aastat tagasi). Järgnes kliima jahenemine u 13 600–13 000 aastat tagasi ning karpvähiliste seas levisid külmalembesed liigid, näiteks *Cytherissa lacustris* ja *Limnocytherina sanctipatricii*, mida on leitud nii Haljala piirkonnast, kinnikasvanud Varangu järve setetest kui ka Saadjärve voorestiku Pikkjärve aleuriidist.

Isoleerunud järvenõgudes hakkas ligikaudu 12 800 aastat tagasi (Äntu Sinijärv, Elistvere) või kohati ka viimase jäävaheaja, Holotseeni (viimased 11 700 aastat) algul (Varangu, Ermistu, Võrtsjärv) kuhjuma valkjasbeež järvelubi. Erinevates uuritud läbilõigetes võib täheldada karpvähkide koosluste muutusi, mis viitavad veekogude vananemisele. Ilmneb teatud indikaatorliikide reeglipärane levik, nt madala toitelisusega hapnikurikkas jahedas ning sügavas järves oli levinud C. candida, kuid avaveelisele madaldunud veekogule oli iseloomulik Darwinula stevensoni ning rohketoitelises soojas taimestikurikkas kaldavööndis domineeris Metacypris cordata. Poolmaismaalise eluviisiga Scottia pseudobrowniana esinemine järvesetete noorimates kihtides viitab kinnikasvamisjärgus järvenõole. Veekogude vananemine oli seotud veetaseme langusega, temperatuuri tõusuga ning toitelisuse kasvuga Holotseeni esimesel poolel, mis ajaliselt langeb kokku kliimaoptimumiga. Ehkki selline arengumudel on järvedele tüüpiline, ei ole muutused järvedes ega ostrakoodikooslustes leidnud aset samaaegselt. Järvede arengut mõjutasid mitte ainult temperatuurimuutused, vaid ka sademete ja aurumise vahekorra ning toitelisuse muutused Holotseeni esimesel poolel. Holotseeni teisel poolel viitab karpvähkide kooslus (Sinijärv) jahedamale keskkonnale ning tõusnud veetasemele, mis langeb kokku
Põhja-Euroopas viimaste aastatuhandete jooksul valitsenud külmema ning niiskema kliimaga.

Karpvähkide kasutamine paleoklimaatilistes rekonstruktsioonides väärib edaspidi süvendatud tähelepanu, kuna nende kodade geokeemiline analüüsimine (isotoopkoostis) annab ainulaadset informatsiooni temperatuurikõikumiste kohta pärast jääaega.

PUBLICATIONS

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Publications

- Tinn O., Meidla T., Sohar K. 2010. Intraspecific variation and polymorphism in the ostracode *Conchoprimitia socialis* (Brøgger, 1882) from the early Middle Ordovician Baltoscandian Palaeobasin. *Bulletin of Geosciences*, 85, DOI 10.3140/bull.geosci.1183.
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Kvaternaari paleokeskkonna rekonstrueerimine, karpvähid, järvelubi, stabiilsed isotoobid

Erialane enesetäiendus

- 2007 erialane enesetäiendus Londoni Loodusmuuseumis
- 2008 kursus "Ostrakoodiuuringud", University College London
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Publikatsioonid

- Tinn O., Meidla T., Sohar K. 2010. Intraspecific variation and polymorphism in the ostracode *Conchoprimitia socialis* (Brøgger, 1882) from the early Middle Ordovician Baltoscandian Palaeobasin. *Bulletin of Geosciences*, 85, DOI 10.3140/bull.geosci.1183.
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