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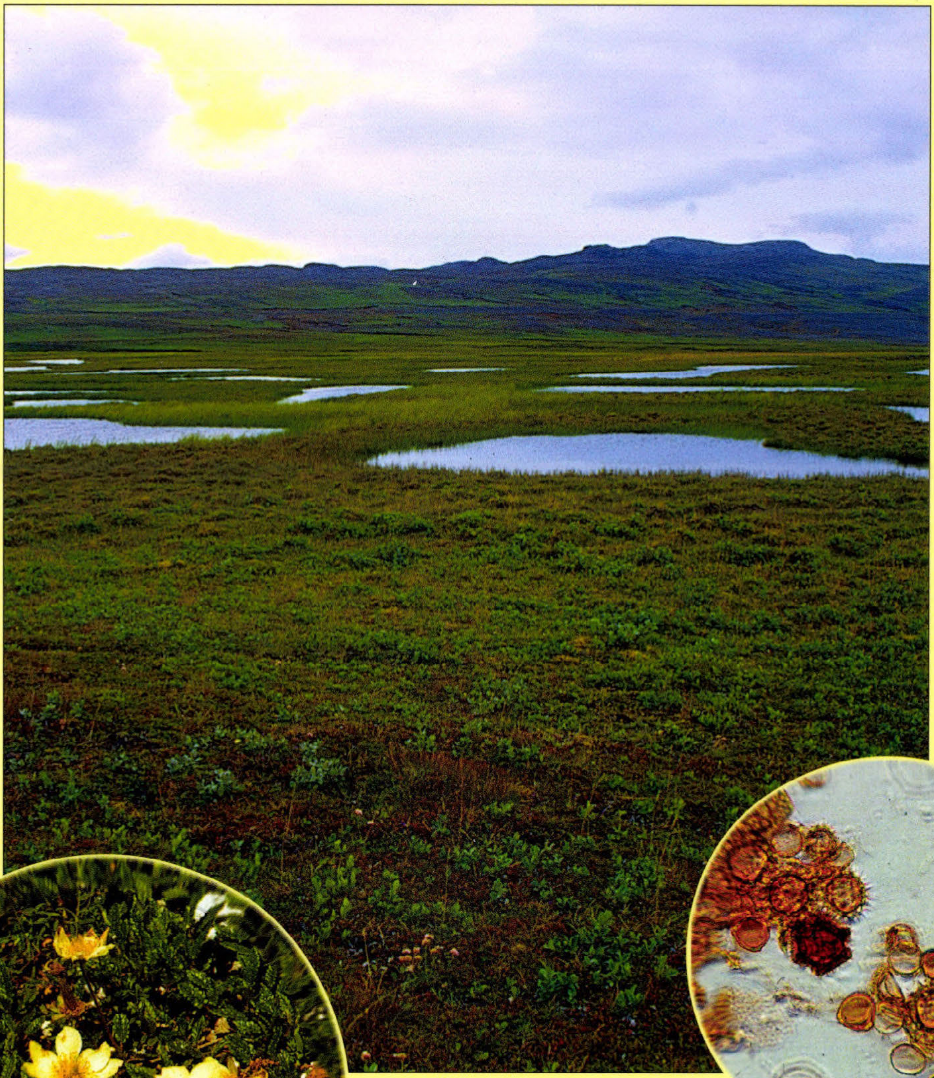

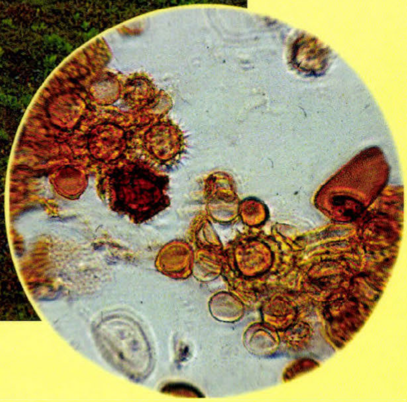

Geographical Research Institute
Hungarian Academy of Sciences

QUATERNARY VEGETATION HISTORY IN HUNGARY

Theory–Methods–Practice

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GEOGRAPHICAL RESEARCH INSTITUTE
Research Centre for Earth Sciences
Hungarian Academy of Sciences

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MAGDA JÁRAI-KOMLÓDI

Dedicated to the memory of Professor Bálint Zólyomi (1908–1997), an eminent botanist and geographer, surveyor of flora and vegetation of the Carpathian Basin, initiator of palynological research in Hungary

Geographical Research Institute
Research Centre for Earth Sciences
Hungarian Academy of Sciences

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1. INTRODUCTION

Present-day large-scale vegetation types of Hungary had developed during Tertiary when the ultimate major changes in forest characteristics took place. According to the paleobotanical evidence both temperate deciduous and tropical-subtropical evergreen forests of Central Europe had consisted of mixed deciduous and coniferous species until Miocene. The main elements of the forests were *Picea*, *Quercus* and *Alnus*, together with many other several characteristic arboreal species of Late Tertiary as the gymnospermous *Sequoia*, *Taxodium*, *Sciadopitys* and *Tsuga*, and the angiospermous *Carya*, *Pterocarya*, *Eucommia*, *Nyssa*, *Liquidambar*, *Aesculus*, *Magnolia*, *Styrax*, *Meliosma* and *Phellodendron*. Vegetation types differed from their present-day analogues to a great extent. Nowadays many taxa and forest elements among afore mentioned genera can be found only in South-East Asia or North America. The specialization of the communities by tree genera started ca 20 million years ago. First forests were formed which contained angiosperm trees exclusively, then large areas became covered also by gymnosperm stands, finally these communities were further specialized by dominant tree species: first *Picea abies*, then *Abies alba* and *Pinus sylvestris* forests emerged.

Although in Late Tertiary (Miocene, Pliocene) gradual cooling and increasing continentality of Earth had become reflected in biosphere, the latest Tertiary (Pliocene, Reuver) climate was still warmer and more humid all over North Eurasia than nowadays. July mean temperature was higher by 2–3 °C in Central and Western Europe and by 4–5 °C in Eastern Europe than nowadays. January and annual mean temperatures were also at least 5–7 °C higher in Central and Eastern Europe and Siberia. Annual mean precipitation is estimated to have been 300 mm higher compared to the present-day values. In general climate was more oceanic.

Thus at the beginning of Tertiary, for example during Eocene, in the present-day temperate areas including the Carpathian Basin vegetation was predominantly tropical with evergreen trees and palms. At that time the *Nipa* palm encountered nowadays only in tropical mangrove vegetation of the Old World was found in Hungary. Significant evolutionary steps such as the appearance of *Poaceae* took also place at that time (Palaeocene).

From the Late Tertiary, however, the vegetation of the modern Northern temperate zone had already changed significantly mainly due to the spread of the so-called arctotertiary species and to the consequent formation of new plant associations. Although there is no proof of phylogenesis and with a few exceptions nearly all of the present-day genera had evolved by that time, several new species had arisen and all those having lived before became extinct. Exceptions included some species of certain monotypic genera like the Chinese *Eucommia ulmoides* or the North American *Liriodendron tulipifera*.

The most intense climatic deterioration took place during the Quaternary, which started ca 2.5 million years ago. From these times we know at most about the formation of new species. Since then floristic composition of vegetation, position of vegetation zones and area of taxa have changed predominantly. Flora have impoverished gradually. Practically, all of the tropical genera became extinct in Europe owing to the major environmental changes, mainly in relation with the gradually expanding glaciation in the temperate zone (Andreánszky 1954; Járai-Komlódi 1982; Járai-Komlódi & Vida 1983).

Late Tertiary and the whole Quaternary chronostratigraphy of geological formations of the Carpathian Basin was prepared on the basis of correlation of geomorphological and biostratigraphical data (Kretzoi & Pécsi 1980; Hertelendi , 1992).

1.1. General remarks on Pleistocene

During glacials the prevailing vegetation types of the Carpathian Basin were the open and dispersed subarctic coniferous taiga forests, the bushy forest-tundra and the treeless cold steppe. During warmings (under a climate similar to that of nowadays, or at most 2–3°C warmer, Wright 1977) the vegetation was like today, especially in the last, Eemian interglacial which already lacked tropical Tertiary species.

Climate, however, was not uniform even during the four major European glaciations in the classical sense, namely the Günz (=Cromer), Mindel (=Elster), Riss (=Saale), Würm (=Weichsel), as the rate of cooling, the extent of glaciations and ice sheets differed in time and space (*Fig. 1*).

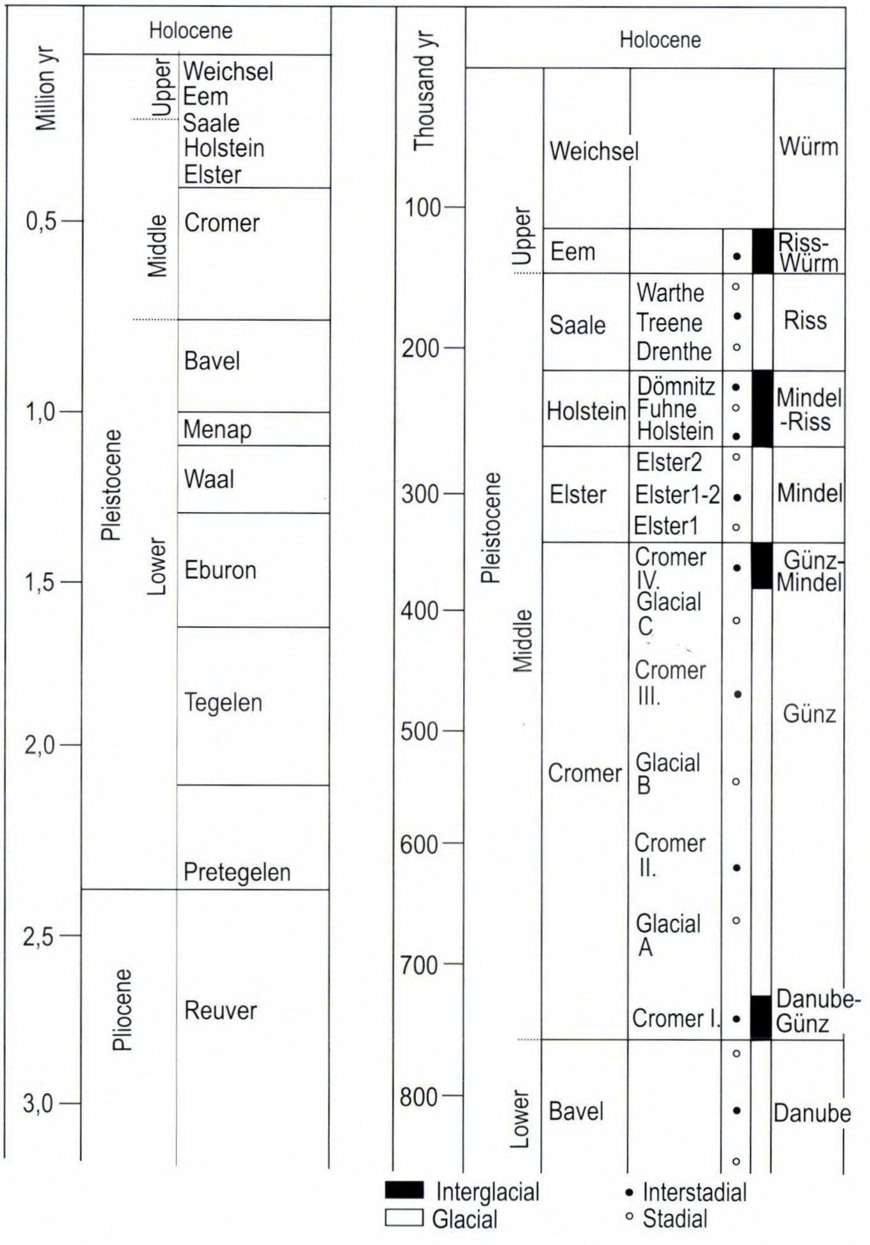

Fig. 1. Chronological subdivision of the Pleistocene according to the north European and Alpine nomenclatures (after Frenzel 1992/b; Lang 1994)

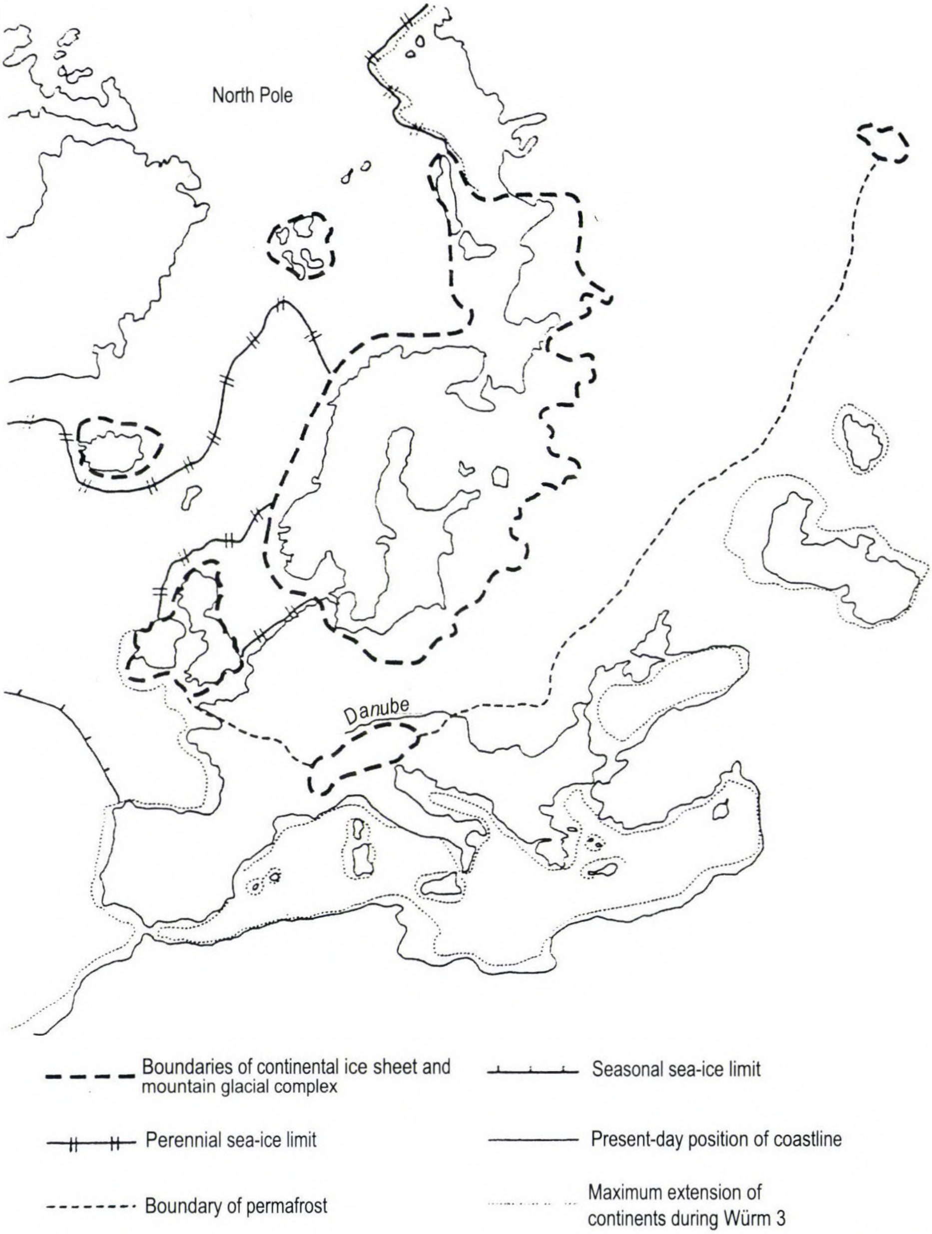

Fig. 2. Extension of the inland ice sheet and the southern boundary of permafrost in Europe, during the maximum cooling of the last glaciation (after Frenzel *et al.* 1992/b)

During Weichselian glacial, for example, the 2–3 km thick continuous arctic ice cap reached down to the latitude of 40° in North America and to the 50–55° in Europe, approximately to the Moscow-Cracow line. Unlike North America (except for Alaska Plain) and North Europe where the ice sheet had reached considerable extension, in Asia no traces of continental ice sheet could be observed only mountain glaciation was recorded.

Northern Siberian Plain as a whole remained devoid of ice cover even during the maximum glaciation. At the same time, in mountainous areas not only in Europe (in the Alps) and North America, but in Southern Europe and Asia (including some tropical mountains) the glaciers had expanded, and new temporary glaciers were formed in several areas (Frenzel , 1992/a). Snowline descended even by 1–2 thousand meters depending on height and extension of the mountains.

It follows from the above that the territory what is now Hungary was not covered with contiguous ice. Its total area situated within the periglacial environment of Europe was protected by the Carpathians, only the highest ranges of the latter were glaciated (*Fig. 2*). In spite of this, cooling was so dramatic that during actual glaciations the annual mean temperature even in the periglacial Carpathian Basin is assumed to have dropped 10–12°C below the present-day values, sometimes and in some places it could even fall below zero (Frenzel , 1992/a). The massive glacial loess cover in the Carpathian Basin, spreading over large areas in Hungary, especially in the Great Hungarian Plain, along its margins and in West Transdanubia (Pécsi 1997) is also an evidence of periglacial climate. The most valuable climatic indicators in loess are fossil snail shells, but sometimes important plant fossils such as charcoal and pollen have also been preserved.

Periglacial effect of inland glaciations was more uniform in flatlands than in the mountains, that is why arboreal vegetation became more restricted over the Great Hungarian Plain during maximum glaciations. Beside fossils this is evidenced by the occurrence of steppe and forest-steppe like paleosols in Quaternary layers. Extinction might also have been more extensive in the Great Hungarian Plain, as it can be observed in present-day flora (Fekete 2000).

In the Carpathian Basin more favourable conditions seem to have prevailed in the mountains, even at higher altitudes. In mountain ranges of medium height the partly unglaciated southern steep slopes of lofty peaks, and of sharp ridges (the so-called nunataks) with favourable microclimate provided shelter for some temperate deciduous tree species against the dramatic climatic deterioration. These small patches of climatic oases are called refugia (Andreánszky 1941; Ives 1974).

Providing explanation for the causes of glacials is the most intriguing task of astronomy, climatology and earth sciences; this question has not yet been answered completely. The major triggers have proven to be cosmic in origin and concerned oscillations of the Earth's axis of rotation and its orbit around the Sun (Milankovitch 1930).

The theory elaborated by Milankovitch was first applied in Hungary by György Bacsák who proved to be most active in its verification in the first half of the 20th century (Bacsák 1940a, 1940b, 1942). Their concept and calculations regarding the origin of glacials, the trends and characteristics of climatic changes also responsible for the interglacials are still accepted with certain modifications (Bariss 1989, 1991; Broecker & Denton 1990; Idnurm & Cook 1980).

It is difficult to differentiate between layers of Late Pliocene and Quaternary sediments. Thus, our knowledge about the Pliocene/Pleistocene boundary (Rónai 1968; Járai-Komlódi 1971; Miháltzné Faragó 1973, 1982; Lőrincz 1987; Krolopp 1995) and that about Early Pleistocene in the Carpathian Basin is rather limited. This is not only owing to the unavailability of precisely dated findings, but mainly because of the high complexity of Ice Age events including changes in climate and environment in periglacial zones.

The Carpathian Basin, due to its geographical position and geomorphic evolution shows a high variability of climatic features even nowadays. It has been affected by several different climate types such as submediterranean, oceanic and continental (Zólyomi 1939; Borhidi 1961).

Considering its relatively small area it is notable that two major European climatic borderlines (according to Köppen's classification) are crossing here: the boundary between the warm-temperate and cold-temperate zones and the one between the humid and semiarid zones (Borhidi 1981).

It is highly probable that various climatic effects manifested themselves also during the Pleistocene. Astronomers and climatologists in the early 20th century (Milankovitch 1930; Bacsák 1940a, b, 1942) already drew attention to the fact that climates identical to those derived from the astronomical calculations can be conceived only in ice-free Europe or, during the ice-ages, in areas lying south of the periglacial zone.

In areas covered with ice sheet it is the albedo (radiation reflectance), while in periglacial zones dry and cold torrent winds blowing from the glaciated highlands that could modify the astronomically predicted climate. This is a natural explanation for the observation that sometimes astronomically calculated climatic changes during the Pleistocene involve the appearance of flora and fauna with opposite climatic demands.

That is the reason also for the finds that even the considerable interglacials like Eemian and Holstein had not been continuous long and warm periods with exclusive thermophilous plants and animals, as the glacials had also variations in the flora and fauna. Even during the glacial maximum (Weichsel, Pleniglacial B) there were slight climatic oscillations and non-glacial plant and animal species survived as it has been evidenced recently in the Carpathian Basin (Bariss 1989; Sümegi & Krolopp 1995) as well. To conclude, highly heterogeneous climatic conditions prevailed during the Pleistocene, caused by several shorter or longer, colder or warmer climatic spells or by regional and local differences.

Often the responses of biosphere to these changes could seem unexpected or erratic, therefore, in most of the cases the former vegetation and animal populations can only be reconstructed in general. This is because vegetation responses depend not only on climate and physiological features, but also on the highly complex and interrelated impacts of environmental factors. These environmental factors as a rule have been recovered faintly as the fossils from that ecologically unstable and highly variable geological period indicate mostly the local conditions, sometimes the regional ones but they hardly testify to global ecological trends.

2. VEGETATION OF THE CARPATHIAN BASIN IN THE LOWER AND MIDDLE PLEISTOCENE

The major part of the Quaternary comprising ca 1.6 million years is called Lower (Early) Pleistocene while a much shorter period of about 700 thousand years is called Middle Pleistocene (*Fig. 1*). As the Pliocene/Pleistocene boundary is uncertain, no uniform agreement has been reached about the upper border of Lower Pleistocene. Some place it to the beginning of Duna–Günz (Cromer I) interglacial, others to that of Günz–Mindel

(Cromer IV), while a third group of experts hold that it started with the Mindel (Elster) glaciation. The chronology framework used below has been published in a recent complex work about the evolution history of the European Quaternary (Lang 1994) *(Fig. 1)*. According to this, the Plio/Pleistocene boundary is drawn at about ”2.3–2.4 million years ago.

2.1. Lower Pleistocene

The main feature of Lower Pleistocene during over its one and a half million years' (2.4 million yr – 760 thousand yr BP) history had been a lack of a severe cooling to create conditions for the development of inland ice sheet. Several shorter or longer spells of cooling and warming of lower amplitudes, however, are assumed to have taken place.

The Pleistocene started with a cooling period (Pretegelen) following the Reuver at the end of Pliocene when the Tertiary forests retreated slightly and during the following warming (Tegelen) they expanded again. They were rich in *Pinus*, and poorer in Tertiary elements. So, the dramatic transition from the Early Tertiary forests extremely abundant in species to the relatively poor forests during the Late Pleistocene interglacial could already been observed in the first interglacial of Pleistocene (Lang 1994).

The considerable and relatively rapid decrease in vegetation diversity concerned not only the trees but also the terrestrial non-arboreal flora including the aquatic vegetation.

Decrease in the number of species varied in different parts of Europe, from southeast to northwest. It is probably due to the fact that some species occupying refugia during glacials could move less and less farer to the north and northwest from one interglacial to another one. That is why Lower and Middle Pleistocene flora had been impoverishing at a slower rate and the process took place later in Central and Southeastern Europe, like in Hungary, than in Northern and Northwestern Europe.

Zelkova or *Celtis* stand as good examples, for they had been missing already since the Tegelen in Northern Europe, however, they still had been found during Eemian interglacial in Hungary (Járai-Komlódi 1964).

The East Asian *Pterocarya* from the family *Juglandaceae* persisted for the most. It was widespread in Europe during the Lower and Middle Pleistocene interglacials. It was still found in Southern Europe in the first half of the last glacial (Weichsel), while north of the Alps it has not existed since the Holstein interglacial. Finally, also the same is suggested by the data about Hungarian Cromer interglacial forests (except for the Győrújfalu assemblage thought to have the same age). They are more abundant in subtropical and Mediterranean broad-leaved species than the flora found north of Hungary (in England, Germany and in the Netherlands). During the Lower Pleistocene the spread of the representatives of thermophilous vegetation in the beginning of the interglacials, and its retreat at the end of interglacials happened simultaneously.

Vegetation dynamics and the order of species appearance during the interglacials of that time can only be hardly recognized, evidently because of the possibility of rapid and more or less simultaneous retreat of their spread from the nearby refugia.

Our knowledge of the Hungarian Lower Pleistocene biostratigraphy is rather restricted. Molluscan biostratigraphy is tackled in details for the Middle and Upper Pleistocene primarily (Füköh 1995). Pollen analysis provides description of only few but rather rich Lower Pleistocene flora with the distinction of several climatic events.

Most information was recovered with the palynological examination of the borehole cores in the Trans Tisza Region covering the whole Pleistocene (Miháltzné Faragó 1982) and of the Jászladány profiles. The latter is the richest Lower Pleistocene assemblage in Hungary so far (Lőrincz 1987). On the basis of the preceding finds, three main vegetation types could be reconstructed in Hungary depending on the climatic changes during the Lower Pleistocene:

During the unfavourably cooler and more humid phases coniferous forests prevailed, mainly with *Pinus sylvestris* and *Picea,* mixed with deciduous trees like *Alnus*, *Betula* and *Salix*, constituting mixed boreal forests, fenwood and gallery forests, with *Ericaceae* as characteristic species.

During warmer and more humid climatic spells mixed-oak forests expanded with *Ulmus*, *Tilia* and *Acer*, and rich aquatic and riparian vegetation flourished including *Cyperaceae* and *Typha*.

The dry and warm phases were characterized by a high diversity of Mediterranean deciduous forests. Finally, a very typical feature of the Hungarian Lower Pleistocene flora was the survival of several Tertiary species. Pollen of such exotic species missing from the present-day flora have been recorded as *Pterocarya*, *Cedrus*, *Zelkova*, *Keteleeria*, *Nyssa*, *Engelhardtia* and palms.

2.2. Middle Pleistocene

Forest evolution and differentiation among certain forest types during interglacials can be recorded only from Middle Pleistocene in Europe. In the beginning (Cromer) it can be recognized vaguely, from the Holstein more distinctively, unfolding regional differences as well. Main tendencies in forest development had been similar all over Europe and in all interglacials: at the beginning of interglacials *Betula* and *Pinus sylvestris* prevailed, later mixed-oak deciduous forests expanded, often including *Alnus*. *Picea* had been present in all interglacials. Regional differences manifested themselves mostly in the order of appearance of mixed-oak deciduous forest species and in the composition of forests, for example in their diversity and in the presence of Tertiary arboreal species. Tendency of forest development during interglacials is quite similar to their Holocene counterpart. Not accidentally, for Holocene is the last interglacial still in progress.

The richest and most important Middle Pleistocene macrofossil assemblage in Hungary came to light at the Vértesszőlős excavation. At the same time, this was the first stratigraphic-palaeontologic-palaeoecological excavation and until present it remains the most complex one.

At this almost half million years old (based on Th-U isotope datings) early hominid (*Homo erectus seu sapiens palaeohungaricus*) campsite spanning from Cromer IV to Holstein interglacial, famous paleontological assemblages, namely vertebrate and invertebrate animal fossils and plant remains (pollen and macrofossils) have been recovered. Climatic and vegetation history can be traced back to the Cromer IV interglacial (*Fig. 1*). The richest fossil assemblage of the site is of Elster age.

From more than 20 profiles 6600 plant fossils had been determined during 13 years of investigations, during which approximately 200 species became identified. Apart from some mosses (fossil Bryophytes of the sites had already been described earlier by Boros in 1952) and Pterydophytes, macrofossils were all arboreal remains (most of them angiospermous broadleaved trees with numerous exotic thermophilous Tertiary and ten different coniferous taxa): leaf imprints, seeds and fruits. Plant macrofossil examinations were completed with palynological analyses. The paleobotanical investigations suggested uniform conclusions regarding both paleoenvironment and paleovegetation. Further these results had been confirmed by paleontological data on Ostracods, Molluscs and small and big mammals. The site itself and its paleoenvironment were described as a result of interdisciplinary research efforts (Skoflek & Budo 1967; Skoflek 1968, 1990; Járai-Komlódi 1973/b, 1990; Kretzoi & Dobosi 1990).

2.2.1. Cromer interglacial complex

Middle Pleistocene starts with the Cromer interglacial complex which is characterized by a high frequency of climatic fluctuations. The Cromer, according to our latest knowledge, consisted of at least 4 warming and 3 cooling spells (*Fig. 1*), that corresponds to the formerly known Danube–Günz and Günz–Mindel interglacials and the Günz glacial in between. Middle Pleistocene ends in the Saale glaciation.

Identification of Lower and Middle Pleistocene interglacials before the Holstein is uncertain all over Europe, but out of all the reconstructions that of Cromer interglacial complex is the most ambiguous, both from geochronological and paleontological aspects.

The reconstruction of the 300 thousand years long Cromer complex of Middle Pleistocene is very rare all over Europe. Its most significant excavation reaches back to the 19th century in England, where the first rich paleontological assemblages came to light at different sites, close to the town of Cromer as a result of the activities by Reid, Geikie, Wilson, Thomson, Dnigan and West (in Lang 1994). Further Cromer sites were recovered in Germany (Lüttig, Rhein, Müller: in Lang 1994), Italy (Lona & Follieri 1957) and in the Netherlands (Zagwijn 1957, 1985). Summarized evaluation of the Cromer interglacial profiles had been carried out on the basis of the major trends in vegetation history and forest development (Grüger 1968; Lang 1994).

Hungarian Middle Pleistocene pollen and macrofossil findings can be related to these investigations. They do not concern the excavation of Cromer profiles exclusively, but in the course of the palynological examination and description of profiles spanning the whole Pleistocene Cromer data came to light as well (Miháltzné Faragó 1982; Lőrincz 1987). Other sources were the reconstruction of Older Cromer (Süttő, Dunaalmás, Leshegy, Mogyorós-bánya) and the first study of Cromer IV interglacial flora jointly with macrofossils (Skoflek 1990) at the rich Vértesszőlős site from Middle Pleistocene. Leaf imprints, fruits and seeds, with Tertiary exotic remains among them, revealed a diverse aquatic and arboreal vegetation reflecting warm humid climate at the end of Cromer IV: *Picea, Fraxinus, Alnus, Ulmus, Celtis, Pterocarya stenoptera, Carya, Laurus nobilis, Ficus tiliaefolia, Syringa.* Although Skoflek separated this phase from the first interstadial of Elster ambiguously, the flora rich in Tertiary elements confirm the correlation of the assemblage with the Cromer IV interglacial (Skoflek & Budo 1967; Skoflek 1968, 1990).

The recently published Győrújfalu findings considered to belong to the Cromer interglacial have not been identified stratigraphically within the Cromer complex, and no absolute dating has been carried out yet. Stratigraphical position of the assemblages was mainly based on Mollusc fauna.

The flora found, however, is really the richest in Hungary so far with regard to the abundance of aquatic and riparian taxa as local climatic indicators. According to the author (Bajzáth 1998), it does not contain species of the so-called "Brasenia-complex" characteristic to Cromer flora, although these are considered highly important in the differentiation between interglacials (Velichkevich 1992).

The Győrújfalu assemblage is poor in arboreal remains as well. In the published list only five coniferous and five deciduous taxa appear, and it completely lacks Tertiary exotic tree fossils. So this assemblage does not seem to contribute to our knowledge about the Cromer vegetation history and forest development (Bajzáth 1998).

The findings were recovered not *in situ*, but from a secondary site i.e. in blocks of clay drift and mud from fluvial sediment. This means that the statement of the author might be erroneous about the site containing the first Cromer flora from Hungary.

Moreover, it puts under question a further statement about a Cromer flora being unique even in an international comparison, and that only three Cromer sites are encountered in Europe (Bajzáth 1998).

As it has already become clear from the foregoing, for over 30 years macofossils and for more than 20 years pollen have been investigated from this interglacial complex in Hungary, and for more than 100 years about 50 Cromer profiles has been examined throughout Europe (Lang 1994).

Anyhow, placing the Győrújfalu assemblage to the Lower Pleistocene is not correct.

2.2.2. *Outline of the vegetation of Middle Pleistocene*

According to the pollen and macrofossil assemblages recovered up to now, varied and diverse vegetation lived during the Middle Pleistocene. In the cold periods (although real inland glaciation had not occurred) taiga and forest-tundra prevailed. In these subarctic coniferous forests, in the Carpathian Basin (including the Great Hungarian Plain), beside *Pinus sylvestris* and *Picea abies*, *Pinus cembra, Larix* were also characteristic, with *Selaginella*. During the Elster and Saale glaciations these forests retreated, part of the Great Hungarian Plain probably became treeless and on this almost treeless cold steppe, *Artemisia, Chenopodiaceae* and *Saxifraga* together with other pioneer and steppe elements, had made the landscape variegated (Mihàltzné Faragó 1982). However, the warming periods were characterized with intense formation of woodland and the expansion of thermophilous broad-leaved trees and mixed oak forests, and with the presence of subtropical Mediterranean species. During the dry and mild interstadial or warm interglacial spells of Middle Pleistocene, Mediterranean species missing from our present-day endemic flora lived in the Carpathian Basin, because they gradually became extinct in the subsequent glacials.

At Vértesszőlős, in the rich Elster interstadial flora *Celtis, Catalpa, Olea, Laurus, Cercis, Syringa, Buxus* and *Cercidiphyllum crenatum* appear, which latter together with *Ficus tiliaefolia* and *Parrotia fagifolia* (Tertiary species) were first detected from Quaternary sediment in Hungary (Skoflek & Budo 1967). Among the Vértesszőlős finds five species newly introduced in science were discovered. These are *Syringa pleistocaenica* and *Syringa pannonica*; *Catalpa Miklósi* bearing the name of professor Miklós Kretzoi, *Rubus samueli* named after the Vértesszőlős prehistoric early man, Sámuel, and *Sorbus vértesi* cherishing the memory of László Vértes, an archaeologist of international renown, discoverer of the site (Skoflek 1990).

The Holstein interglacial flora in Europe differs from both the previous Cromer interglacial complex and the subsequent Eemian interglacial flora since coniferous forests (*Picea, Abies*) were spread almost all over Europe except for Southern Europe. This could mean that either the climate was severer or coniferous forests consisted of other ecotypes differing from the present-day species, and area of their occurrence was not controlled by climate but by other factors.

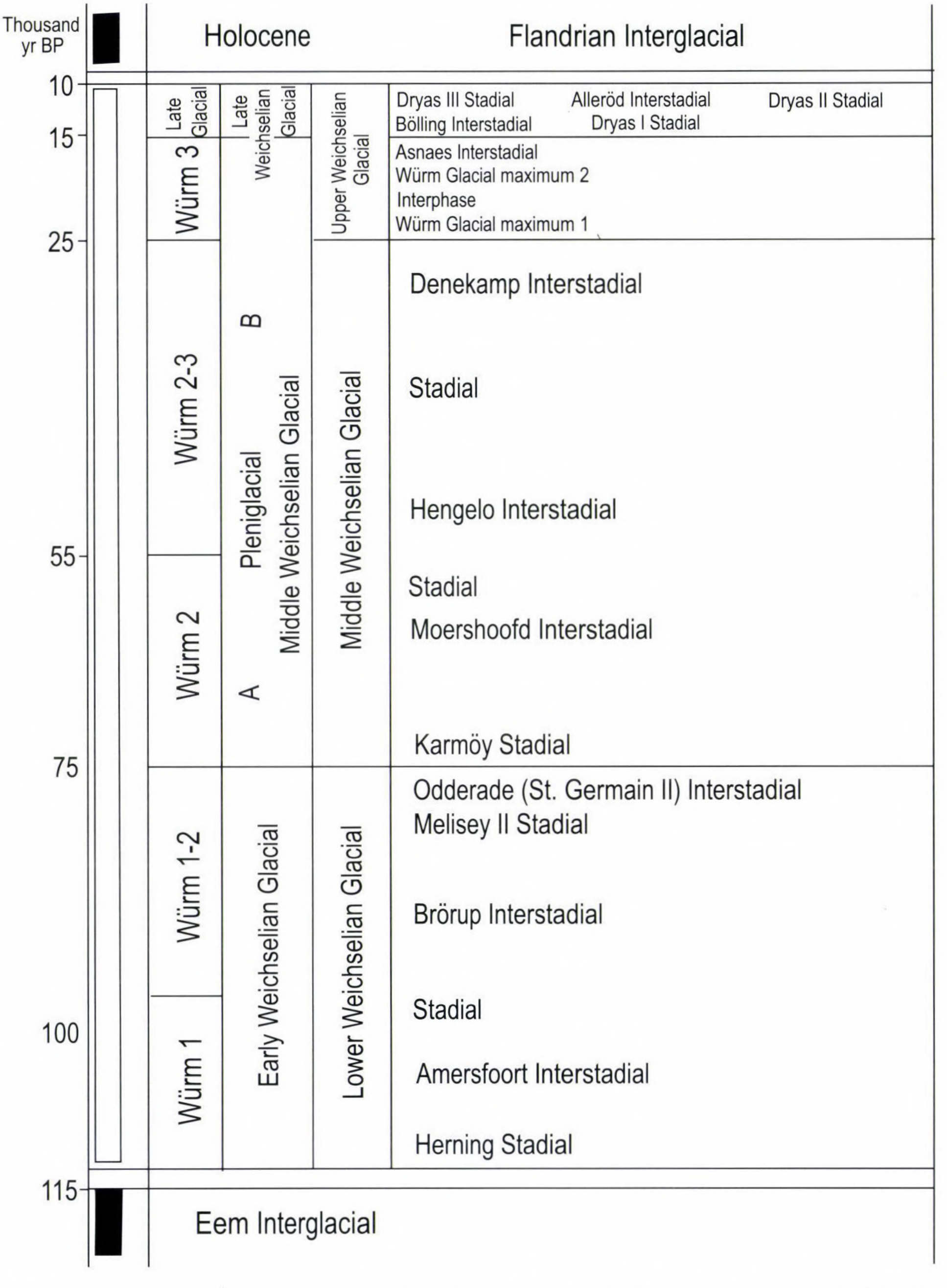

Fig. 3. Subdivision of the Würm (Weischselian) glacial (after Frenzel *et al.* 1992/b; Lang 1994)

The Holstein flora, according to the macrofossils from Vértesszőlős and pollen data from other parts of Hungary (Miháltz & Miháltzné Faragó 1965; Miháltzné Faragó 1982) was similar to the European ones (Lang 1994), with much Picea and mixed broad-leaved trees (*Quercus*, *Ulmus*, *Tilia*, *Carpinus*), still containing a lot of Tertiary species.

When climate turned to warm but remained humid enough, beside species of mixed oak forests and Tertiary species with temperate climate demands (*Carya*, *Pterocarya*), diverse aquatic and riparian vegetation is suggested by the fossils (Skoflek & Budo 1967; Skoflek 1968, Bajzáth 1998).

Algae, mosses, tangle and mud-species were found. During the Middle Pleistocene, in the Cromer complex the appearance of small aquatic ferns like *Salvinia* and *Azolla* (Lang 1994) was peculiar. Three species of *Azolla* were recovered firstly in Hungary from the Middle Pleistocene layers of the Vésztő borehole (Simoncsics & Széles 1979; Miháltzné Faragó 1982).

3. VEGETATION OF THE UPPER PLEISTOCENE

Hungarian Upper Pleistocene (Eem, Weichsel) vegetation is fairly known partly due to the detailed pollen examinations and partly to the rich macrofossil assemblages.

The latest anthracological examinations (Rudner & Sümegi 1998/a, Rudner 2001), following charcoal analyses in the cave sites of the Hungarian Middle Mountains and those from the 1930's onward (Stieber 1967), as well as fossil flora of Tata Mousterien site (Budo & Skoflek 1964), charcoal findings (Stieber 1964) and pollen flora (Járai-Komlódi 1964; Járai-Komlódi 1964) from the same site are valuable.

However, their thorough comparison with the forest development during the European Upper Pleistocene is rather restricted as we can hardly find long continuous profiles comprising the whole interglacial and glacial.

3.1. The Eemian interglacial flora

During the last interglacial, unlikely the Holstein, coniferous and deciduous forests were spreading all over Europe not simultaneously. The first to expand was mainly *Picea* (not *Picea abies*, but *Picea obovata*); then perhaps as a result of the melioration of climate the regression of the latter started. Later *Pinus sylvestris*, *Betula*, followed by *Quercus* and *Ulmus* and the shade loving *Tilia* began to immigrate and spread. These temperate forests covered nearly the whole of Europe whereas *Picea abies* and *Abies alba* had returned to Europe just by the end of this interglacial.

The richest Hungarian Eemian interglacial paleobotanical assemblage (macrofossils and pollen) became known during the Tata complex excavations (Vértes 1964). Unfortunately this profile does not comprise the whole interglacial either.

On the basis of the examinations in the earlier phase of this interglacial, under mild and humid climate, temperate mixed oak forest persisted in the Hungarian Middle Mountains with *Tilia*, *Ulmus* and several species of oak (*Quercus cerris, Q. pubescens, Q. robur, Q. petraea*). In the more favourable phases some Mediterranean species reappeared, like *Celtis*, the evergreen *Cupressaceae* and *Biota*, with *Corylus*, *Cornus* and *Rhamnus* in the shrub level. In the Great Hungarian Plain coniferous forests and (to a lesser extent) mixed oak forests with *Carpinus* were detected, without any Tertiary species (Miháltz & Miháltzné Faragó 1965; Miháltzné Faragó 1982; Lőrincz 1987).

In lakes mild climate preferring diverse aquatic flora like *Nymphaea*, *Nymphoides* and *Myriophyllum* survived. Towards the end of the interglacial, the approach of a new glaciation bringing colder climate thermophilous species became less and coniferous forests mixed with broad-leaved trees expanded.

The Hungarian paleobotanical finds of the Eemian interglacial either do not contain at all elements of Tertiary flora hitherto not indicated (Lőrincz 1987) or just the latest ones (*Celtis, Zelkova*) if any. Possibly, during the Saale glacial the Tertiary flora disappeared indeed, and the latest elements remained just because at the site the contemporary thermal springs created favourable microclimate. An example of this is the *Celtis in situ* leaf imprint (Járai-Komlódi 1964).

3.2. Palaeoecological and palaeobotanical aspects of the last (Weichselian) glaciation

This glacial phase was the last trial for the present-day biota and a factor of its formation. This is especially valid for the last glacial maximum during the Weichselian, being at the same time the coldest, driest and most extreme climatic phase during the whole Pleistocene, mainly in North America and Northern Europe where the most extensive continental ice sheets of the time had developed on Earth.

The continental ice sheet had exerted a rather massive impact upon the ice-free territories, as far as 1100 km south of its margin in North America, 600 km south of it in Europe, or even 700 km south of it e.g. in the East European Plain. This is clearly shown by the extremely cold winters, which means 10–14°C lower temperatures than nowadays, even in the Carpathian Basin (Frenzel 1992/a).

The two continents had been affected differently. In Europe the mountain ranges of east to west orientation (the Alps, the Carpathians and the Pyrenees) had moderated the influence of ice sheet and the icy, stormy and devastating winds blowing from the north, while the North-American north to south oriented mountains gave way to them.

Thus the deterioration of the winter climate compared to that of nowadays in both continents can be explained by the development of inland ice sheets.

According to the calculations, this cooling does not seem to have been expressed so markedly in summers, when the temperature was 8–10°C lower than today, and there was not such a striking difference between North America and Europe as during winters.

The other characteristic of summer climate was that due to the combined effect of the relatively high evaporation and at the same time because of the decreased precipitation (by 250–500 mm in the Carpathian Basin) insufficient moisture had been supplied for the periglacial ecosystems. In other words, the scattered vegetation in the Northern Hemisphere (and similarly in the Carpathian Basin) can be explained by aridity and not only by the fall of temperatures. Of course the proximity of the southern border of permafrost zone also could affect the formation of vegetation.

Geological evidence such as periglacial forms shows this border to have stretched somewhere across the Northern Carpathians, thus in the Carpathian Basin no continuous permafrost zone existed.

However, subject to the local geomorphological conditions sporadic permafrost could occur frequently, especially over the extensive muddy-clayey floodplains (Frenzel 1992/b; Pécsi 1997) (*Fig. 2*).

3.2.1. Chronological problems

The fact that during the Wechselian glacial there were several climatic fluctuations, became proven by astronomers, meteorologists already in the first half of the 20th century, altogether detecting three cooling intervals (Würm 1, 2, 3) and two warmings (Würm 1–2 and Würm 2–3) (Bacsák 1940/a). The effects of these climatic fluctuations, however, could not be demonstrated everywhere and always by the changes in biota. This is partly because the astronomically governed changes had not been uniform in amplitude. For instance, during the warming interval W2–3 after the „second" cooling event during the Weichselian (W2) did not have such a melting effect as the previous interstadial had, so the inland ice during this period did not shrunk significantly. This is suggested also by the fact that there was no reforestation in Western Europe during this interstadial (Lang 1994). On the other hand, geographical position had also influenced the manifestation and detection of these climatic spells of short duration in the biosphere.

Finally, various groups of flora and fauna tend to response to climatic events and to the generated palaeoecological changes in a different way. That is why the fossils of climate-sensitive, rapidly reacting living organisms, for example the widespread aquatic Ostracodes and the aquatic and terrestrial Molluscs have a great importance in reconstruction of past climates of any age.

These animal fossils refer to climatic oscillations (cooling, warming, aridification, humidification, hardly detectable using other methods of investigations) through the appearance or disappearance, mass growing or retreat of species with different ecological demands. The sparse appearance of plant and animal fossils with different ecological demands indicate mostly the changes in the local ecological conditions and in the microclimate, while mass propagation or extinction of characteristic, indicator taxa probably reflect changes in regional or global climate.

In the last decade in Western Europe, three times more climatic changes were shown for the Weichselian Glacial (instead of the earlier observed five, except for the late glacial) (*Fig. 3*). Thus it can be stated that the available data do not fit into a previous classical framework of Würm any more. No uniform scheme can be used for the Würm 3 glacial either. It is also hard to maintain e.g. the Alpine Lower-, Middle and Upper-Würm categories, not only because the borders are not defined sufficiently, but also because the criteria to be met are verifiable not always and at all sites, or the changes did occur not necessarily along the presumed boundaries. According to this nowadays a plenty and different kinds of ideas exist about the boundaries, and it seems that the Northern European chronology can be more applicable to the events of the last glacial epoch than the Alpine chronology, even within Central Europe. That is why this chronology was basically accepted also taking account the data by Frenzel (Frenzel 1992/b; Lang 1994) *(Fig. 3)*.

The Early Weichselian Glacial (115,000–75,000 BP) according to the latest data can be subdivided into three stadial and three interstadial phases. During the former Würm 1 earlier thought to have been a uniform stadial a warming has been detected called Amersfoort, so the Würm 1 hitherto known as a uniform glacial became divided into the Herning stadial following the Eemian interglacial, then the Amersfoort interstadial and another stadial phase. During Würm 1–2, however, a cooling can also be observable which separated the climatic phase that was considered to be a uniform interstadial into two warming periods. The first is the Brörup interstadial already found in Hungary (Járai-Komlódi 1966/b) and the second is the Odderade interstadial which had closed Würm 1–2. The Middle Weichselian Glacial or Pleniglacial A and B (75.000–15.000 BP) corresponds to the former Würm 2 and 3 stadials and the Würm 2–3 interstadial in between.

Pleniglacial A (= W2 and W2–3) contrary to a former concept to have been uniform now is suggested to have contained three stadials and three interstadials. Among these probably the Denekamp interstadial was pointed out in Hungary (Hertelendi 1992) but it has not been named yet.

The maximum glaciation (Pleniglacial B = W3) which started 25,000 years ago is not a uniform cooling either, as according to the recent investigations it shows two cold maxima with a milder „interphase" in between (Velichko 1992). Probably this „microinterstadial" could be reconstructed by pollen analyses (Borsy 1991) and by fossil malacofauna (Hertelendi 1992; Sümegi & Krolopp 1995) also in Hungary, but it has not yet been named properly.

Middle Weichselian Glacial or the so-called Würm 3 ends in the Asnaes interstadial (Velichko 1992). According to the absolute chronological datings this warming may correspond to the Lascaux interstadial already identified in Hungary (Borsy 1991; Sümegi & Krolopp 2000).

The Late Weichselian Glacial (15,000–10,000 BP) contains three stadials and two interstadials. In this transitory phase lasting from the last glacial to the beginning of Holocene reforestation no new major climatic fluctuations have been shown lately.

3.2.2. A historical sketch of research of the Weichselian Glacial in Hungary

Our knowledge of climatostratigraphy and biochronology of the Weichselian Glacial has been extending due to its multifold research and a growing number of publications.

Studies on Quaternary vegetation in Hungary started from the 1920's but the first paleobotanical results from Pleistocene sequences became known in the 1940's. All of the initial data were related to the last glacial: the thermophilous flora of Mezőberény peat considered of Würm interstadial age, the Tiszafüred pollen (Zólyomi 1940, 1946) and the pollen spectrum of a flora of Magdalenian age (Greguss 1940). Most of the data were sporadic ones concerning just the final phase of the Weichselian Glacial (Zólyomi 1937; Csinády 1960).

The first Upper Pleistocene chronology with a summary of vegetation history (Soó 1940) was evaluated on the basis of scanty palynological and extremely rich macrofossil (i.e. macrocharcoal) examinations accomplished in the 1940's. Later the accumulating research data enabled the compilation of further summary works on vegetation history (Zólyomi 1952, 1958; Soó 1959/a, b) although they have dealt mainly with the Holocene reforestation and contained less information about the flora during the Weichselian and Late Glacials.

The basis for the studies were provided by the chronostratigraphy of the Pleistocene sequences, first of all by the geological investigations of loess, an especially characteristic glacial sediment in the Carpathian Basin (Scherf 1935, 1936; Kriván 1957; Kriván & Nagy 1963; Kretzoi & Pécsi 1971; Pécsi & Schweitzer 1991; Pécsi 1997).

There was advancement in the knowledge about paleoecology of the studied time period. Using the earlier achievements (Kordos & Járai-Komlódi 1988) a global climatostratigraphical scheme has been established (Kordos & Ringer 1991) on the basis of vole fauna. Moreover, based on

Mollusca, *Gastropoda* faunas and pollen findings the Weichselian and Late Glacial paleoecological conditions were described in detail (Hertelendi 1992, Sümegi & Krolopp 1995) and the relationship between Mesolithic/ Neolithic cultures and the contemporary climate has been tackled (Sümegi & Kertész 1998).

The first detailed botanical subdivision of the Weichselian Glacial in Hungary was set out by pollen analysis (Járai-Komlódi 1966/a, b) with a description of the Brörup interstadial flora in Hungary including forest development, terrestrial and aquatic non-arboreal vegetation. For the identification of geological age stratigraphical data were used (Emil Scherf), and apart from pollen findings, charcoal remains (József Stieber), plant macrofossils (Andrzej Srodron) and snail fossil (Endre Krolopp) were also involved. Beside further complete or partial paleobotanic evaluation of the Weichselian Glacial (Miháltz Miháltz-Faragó 1965; Miháltz-Faragó 1982; Borsy 1991, 1992; Járai-Komlódi 1991; Zólyomi 1995; Willis 1997, 2000; Magyari 1999; Jakab & Magyari 2000, 2002; Rudner & Sümegi 1998/b) important, mainly climate-oriented paleoecological achievements (Zólyomi 1958; Járai-Komlódi 1969, 1973/a; Kordos 1981; Sümegi 1998, 1999/b; Rudner & Sümegi 1998/a; Magyari 2002) were published as well *(Fig. 3)*. The most detailed and up-to-date climato-stratigraphic subdivision of the Upper Pleistocene in the Carpathian Basin is based on biostratigraphy, notably on the analyses of fossil snails (Sümegi & Krolopp 1995). Five main climatic intervals (stadials, interstadials) and nine shorter oscillations have been identified during the Weichselian Glacial.

3.2.3. Forest development and vegetation during the cold intervals of the Weichselian Glacial

During the last glaciation as a whole, open taiga forests dominated by coniferous trees and treeless steppes prevailed with a mosaic pattern of the two. Variation in the woodland/steppe ratio indicates past ecological changes.

Thus, under extremely cold and dry climate, treeless steppe (with tundra elements of sporadic appearance) expanded primarily over the Great (Hungarian) Plain, but it could not be considered genuine tundra vegetation either climatically or floristically. In the mountains, e.g. in the higher altitudes of the Carpathian Mountains the frost resistant cold demanding pines could survive as the main forest components. Moreover, in refugia with milder climate some deciduous trees had survived, as had some conifers in the Great Plain.

Of the arboreal species this severe climate was best tolerated by *Pinus sylvestris*. During the cold stadials the similarly frost tolerant *Larix decidua* mixed only locally owing to its high humidity demand. *Pinus sylvestris* was however the most frequent and widest spread arboreal species throughout the Pleistocene and not only in the cold intervals but also during the milder spells as well. This was due to its three basic characteristic features:

It is a common species with a broad spectrum of ecological tolerance virtually with no preference of habitat or climate. It is frost and drought resistant and tolerates warm climate and high atmospheric precipitation. It survives on any kind of soil. Basically a light demanding species it also tolerates shade.

It grows rapidly, renews well, therefore it is able to colonise hitherto treeless areas and expand over them, being a pioneer species. That is why reforestation phase as a rule starts with the spread of *Pinus sylvestris.* Later pine forests are gradually transformed into mixed ones.

Besides, it is a genetically flexible species that adapts well and has 14 micromorphologically distinguishable ecotypes in Europe only (Staszkiewicz 1961).

During the extremely cold but more humid stadials the alpine, subnival *Larix decidua* with frost resistance and high moisture demand might expand among *Pinus sylvestris*.

The third most frequent Pleistocene arboreal species is the northerly, alpine, subnival *Picea abies* which tends to expand when the climate turns humid but it is still cold as this species is less frost tolerant. Its optimum ecological circumstance is cool and humid climate. Nowadays it forms forests in areas with annual mean precipitation over 700 mm.

The composition of Pleistocene coniferous woodland might be affected considerably by the light demand of the arboreal species. Of the latter *Pinus sylvestris* and *Larix* are species with rather high light demand. *Larix* does not bear even its own shading and always constitutes scattered stands. Thus, under improving (even for *Picea*) climatic conditions it was *Larix* that tended to mix with *Pinus sylvestris* and not *Picea* (or the latter did it to a lesser extent). After clearing and forest fires or due to climatic deterioration light conditions might become a more important ecological factor than the decrease of temperature or precipitation, so *Larix* became more competitive compared to shade-tolerant *Picea*. This is what could happen in the open pine forests and had led to the formation of the so-called pine forest steppe.

Finally, the different spatial distribution of the two heliophilous species, *Pinus sylvestris* and *Larix* over the Carpathian Basin could be controlled by further ecological circumstances such as soil properties. Whilst *Pinus sylvestris* could grow on any kind of soil, *Larix* prefers deep and fresh carbonate soils.

The above referred basic environmental factors and ecological demands of the arboreal plants interacted in a very complex manner as in the past and do so at present. We often are unable to comprehend these conditions because in most of the cases we are not able to reconstruct the cause–effect relations of past ecological events e.g. owing to the lack of knowledge of the contemporary ecotypes.

In the beginning of the stadials the interstadial pine-birch forests still existed. *Picea abies* and *Picea omorica* could be encountered (pollen findings) and *Pinus peuce* is known (macrofossils). However, *Pinus cembra* and *Larix* have a growing importance and later forest dwarfing and the development of a subarctic–subnival scrub landscape (*Salix reticulata*, *Alnus incana*, *Pinus montana*, *Betula nana*) is confirmed by macro- and microfossils (Tuzson 1929, Szepesfalvi 1930, Scherf 1935, Járai-Komlódi 1966/b, 2000). Following the Brörup interstadial, i.e. during the Pleniglacial A cooling (more or less coinciding with the Würm 2 stadial) fossil findings testify to a rather humid environment. It is indicated by the appearance of some tundra elements such as *Koenigia islandica*. This typical arctic-alpine chionophilous tundra plant (preferring cold and humid conditions) nowadays is an inhabitant of the northern latitudes and its fossil findings are very rare. This is the first occurrence on the territory of Hungary (Járai-Komlódi 1966/b); other Pleniglacial fossil pollen data are known from the Western Carpathians where plant remains of spongy (grassy and sedgy) tundras and those of aquatic species were found such as *Myriophyllum*, *Botrychium*, *Koenigia*, *Hippuris*, *Potamogeton*, *Chara* (Koperowa & Srodon 1965).

Humid climate is suggested by a mosaic appearance of species within certain hygrophilous plant communities (arctic sedgy meadows, tundra elements, subalpine tall grass vegetation) of the Hungarian assemblages such as *Cyperaceae*, *Selaginella selaginoides*, *Botrychium*, *Huperzia selago*, *Polygonum bistorta*, *Sanguisorba officinalis*, *Polemonium*. Several cold tolerant mosses such as *Scorpidium scorpioides*, *Drepanocladus exannulatus*, *D. vernicosus*, *D. fluitans* (Boros 1952) at present missing from the Great Plain and encountered only in the nival regions of the Carpathians and on the northern humid and boggy tundras could live in habitats similar to *Koenigia* as suggested by fossil findings. The prevalence of cold and humid climate is also supported by the fossil snails found in the area like the cold tolerant species with high humidity demand like *Succinea oblonga*, *Cochlicopa lubrica* and some molluscs typical of loess like *Vallonia costata*, *Pupilla muscorum* (Krolopp 1966).

Finally, during the latest deposition of loess material during the maximum of the Weichselian glaciation, under an extremely dry climate, the arboreal vegetation must have been very scanty in the Carpathian Basin. Woodland had virtually vanished in the very centre of the Great Plain, the scattered coniferous forest stands mixed with deciduous trees remained in spots or they could survive in isolated refugia; this is suggested by pollen and macrofossil findings of *Larix*, *Pinus sylvestris*, *P. cembra*, *P uncinata*. Radiocarbon dated "*in situ*" charcoal findings have a special importance. Aquatic plants and hygrophilous elements had disappeared and continental cold loess steppe plants dominated instead (Járai-Komlódi 1966/b; Stieber 1967; Sümegi 1999/b; Willis 2000; Rudner 2001). It is well known that with regard to the global climate and vegetation zones during the coldest phases of the Weichselian stadials (W3, Pleniglacial B) the Carpathian Basin belonged to the extensive Eurasian steppe zone. Accordingly, the dominant vegetation of the time was treeless loess steppe, mosaic-like steppe and tundra vegetation (Frenzel 1992/b) also supported by numerous (mainly pollen and mollusc) findings. However this rather general picture could be modified and made more complicated by the geomorphological position of the studied area (e.g. plains, middle mountains, surface waters) and the refugia for survival, and also by the adaptation abilities of biosphere through the regional and local conditions as reflected by the fossil findings. This is suggested by the earlier detailed pollen analytical examinations over the Great Plain (Járai-Komlódi 1966/a) confirmed by more recent investigations based mainly on charcoal analyses (Willis 2000). Disregarding the sporadic "*in situ*" survival of coniferous trees in certain refugia, paleoecological and paleontological data obtained up to now suggest that under the severe climates of the last glacial the typical vegetation in the Carpathian Basin was the treeless xerothermic steppe, especially in the plains.

Comparing the xerothermic steppe on the territory of present-day Hungary during the last glacial with the contemporary open vegetation of Eurasia, a conclusion can be drawn that the loess steppe in the Great Plain during the pleniglacial showed certain characteristic features different from the Pleistocene xerothermic open vegetation types of areas situated both east and west of the region in concern.

Thus the open vegetation of both stadials (Pleniglacial A and B) in the central part of the Great Plain (environs of Kiskunfélegyháza) displayed similarities with the contemporary types of the southern parts of the Eurasian continent, mainly due to a frequent occurrence of *Chenopodiaceae*. Still it differed from the latter with an almost complete absence of *Artemisia* whilst it did not bear any kinship with the East Austrian spectra. However the stadial open vegetation along the margin of the Great Plain (Trans Tisza Region: Timár) forms a transition between the similar vegetation reconstructed for the areas located east and west of the Carpathian Basin. Of the eastern types it had related to the so called northern type rich in *Artemisia* and other dicotyledons, at the same time differing from it with an almost complete absence of *Chenopodiaceae*.

On the other hand, the Hungarian stadial loess steppes stood out with their richness in *Poaceae* and differed from the type characteristic of the eastern hilly foreland of the Alps lacking *Chenopodiceae* but rich in *Artemisia* and dicotyledons (Frenzel 1964; Járai-Komlódi 1966/b).

The Pleniglacial B flora reconstructed for the central part of the Great Plain is very poor both in arboreal and non-arboreal vegetation elements. The once dominant rich heliophilous vegetation of steppes had decimated by this time and the species typical of the arctic boggy meadows and tall grass vegetation disappeared. The dominant vegetation could be a cold loess steppe poor in species where the dominant dicotyledons were *Chenopodiceae* (constituting 83% of non-arboreal pollen in the diagram). It could be similar to the present-day Mongolian Upland covered by Artemisia steppes with *Chenopodiceae*, *Kochia* and *Ceratoides latens*. The remains of the latter have been recovered in a single location in Hungary perhaps as a relic species of the past having become extinct since then.

Refugia were suggested for some areas along the eastern margin of the Alps, in the Carpathians and their foreland for the Weichselian stadials (Firbas 1949; Frenzel 1960, 1964). Moreover, earlier investigations regarded the Great Plain as a refugium for coniferous trees at least to some extent (Zólyomi 1953, 1958, Soó 1959/a, b) or wholly (Firbas 1949), a hypothesis that only partly became confirmed subsequently.

According to our investigations during a previous stadial (cca Würm2) of the Weichselian and especially in its earlier phase arboreal vegetation really could exist in the marginal zone of the Great Plain. In the last (cca Würm3) stadial of the Weichselian Glacial, at least in the central part of the Great Plain, no refugia could be reconstructed because the percentage of fossil arboreal pollen had dropped dramatically. Its appearance compared to that of non-arboreal pollen was very probably the result of a long distance transport to the treeless areas than of an "*in situ*" occurrence. The more recent, mainly "*in situ*" macrocharcoal findings (Willis 2000) have tended to confirm the previous concept about the existence of refugia in the Carpathian Basin for some tree species even during the cold stadials of the Weichselian Glacial. The latest data have made us reconsider the earlier concept (Járai-Komlódi 1966/b) and the reconstructed (although based on scattered findings) arboreal plants i.e. pines and also some deciduous species can be regarded "*in situ*", an evidence of refugia in the Great Plain.

3.2.4. Forest development and vegetation in the phases of warming during the Weichselian Glacial

Reforestation in the interstadials generally begins with the formation of subarctic taiga and – in favourable conditions and in warmer interstadials – with that of mixed taiga forests. The most typical, almost constant species of pine taiga are *Pinus sylvestris*, *Picea* and *Larix*. During warming phases of different duration and various temperature amplitudes their dominance was alternating or they mixed with other coniferous or deciduous species.

Thus, under mild and humid climate *Picea* took over and if temperature rose even higher and climate became more balanced the appearance of *Abies alba* was probable. Among the four dominant coniferous species *Abies* is the one with the most restricted tolerance with regard to its ecological demand.

It is a subalpine species and its requirements include balanced climate with abundant precipitation and air humidity. Its temperature demand is average but it tolerates frost and cold poorly. It is also specific in its habitat demands, preferring mesophilous, fresh soils rich in nutrients with neutral pH. Comparing to other pine species *Abies* is always of scattered appearance. Similar to its present-day behaviour being mixed with other species it never constituted pure stands in Pleistocene. Recently it has mixed both to *Picea* and *Fagus* along the border zone between them due to its high shade tolerance.

Beside *Betula* and *Larix* the following species also appeared: *Quercus*, *Ulmus*, *Tilia*, *Carpinus* and *Fraxinus* and a rich aquatic flora can be reconstructed both for the Brörup interstadial (Járai-Komlódi 1966/b) and the "Lascaux" climatic amelioration (Borsy 1991). *Alnus* forests grew along the floodplains of rivers, on the aluvial soils with high moisture content. In the lowermost spots tall grass of subnival character existed with dicotyledons and flowering meadows and, on the flood-free higher surfaces treeless, grassy loess steppe rich in *Artemisia* could be found with heliophilous plants.

Major changes in arboreal vegetation took place only by the end of interstadials with the advent of climatic deterioration. With the decrease of *Pinus* and *Betula* and forest composition had been modified. P. *cembra* had become increasingly frequent and beside arboreal *Betula*, a characteristic alpine species, *Betula nana* appeared in the pollen spectra. This was the first indication of *Betula nana* fossil pollen in the Hungarian Pleistocene flora (Járai-Komlódi 1966/b). In the Great Plain scattered *P. cembra* and *Larix* forests could exist simultaneously.

The most detailed interstadial flora during Weichselian Glacial has been recovered from the Brörup layers with pollen analysis. Completing them with previous macrofossil data (Szepesfalvi 1928, 1930; Tuzson 1929; Scherf 1936; Boros 1952; Srodon 1966) concerning forest development and the composition of non-arboreal vegetation a more differentiated picture could be presented (Járai-Komlódi 1966/b, 2000).

3.2.4.1. Early Weichselian warming. The vegetation during the Brörup interstadial

According to pollen data, there could be subarctic *Betula* groves mixed with *Pinus* in the central part of the Great Plain, on the Danube–Tisza

Interfluve. They could be composed by *Pinus sylvestris*, *Betula pendula*, and *B. pubescens*, mixed with *Salix* and *Alnus* locally. Other coniferous species such as *Pinus cembra*, *Picea abies*, *P. omorica*, *Abies alba*, *Larix decidua* and deciduous trees could occur only sporadically. This was the first evidence of *P. omorica* fossil pollen for the Hungarian Pleistocene. Today this arctotertiary species lives only in a single refugium in the Balkans as a late glacial relic (Fischer & Járai-Komlódi 1970, Járai-Komlódi 1966/a, b, 1970).

In contrast to the situation outlined above, along the north-eastern border of the Great Plain (Trans Tisza Region) pine stands – mainly *Picea abies*, *P. omorica* and *Pinus sylvestris* – prevailed. Fossil pollen findings evidence to the expansion of *Alnus* along the watercourses and to the occurrence of *Hippophaë rhamnoides* drift-bank scrubs on point-bars. By the end of interstadials *Pinus cembra* and *Larix* pollen also appeared. They probably formed either scattered pine forest steppe or taiga (Járai-Komlódi 1966/a, b, 1970). This has been corroborated by recent macrocharcoal find-

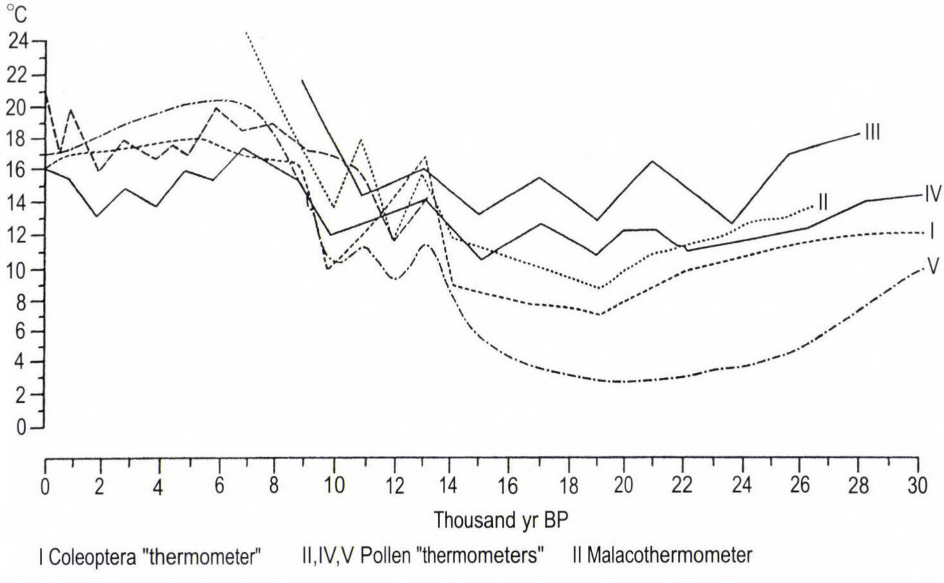

Fig. 4. Reconstruction of July mean temperatures for the past 30,000 years using various paleontological methods (Hertelendi *et al.* 1992)

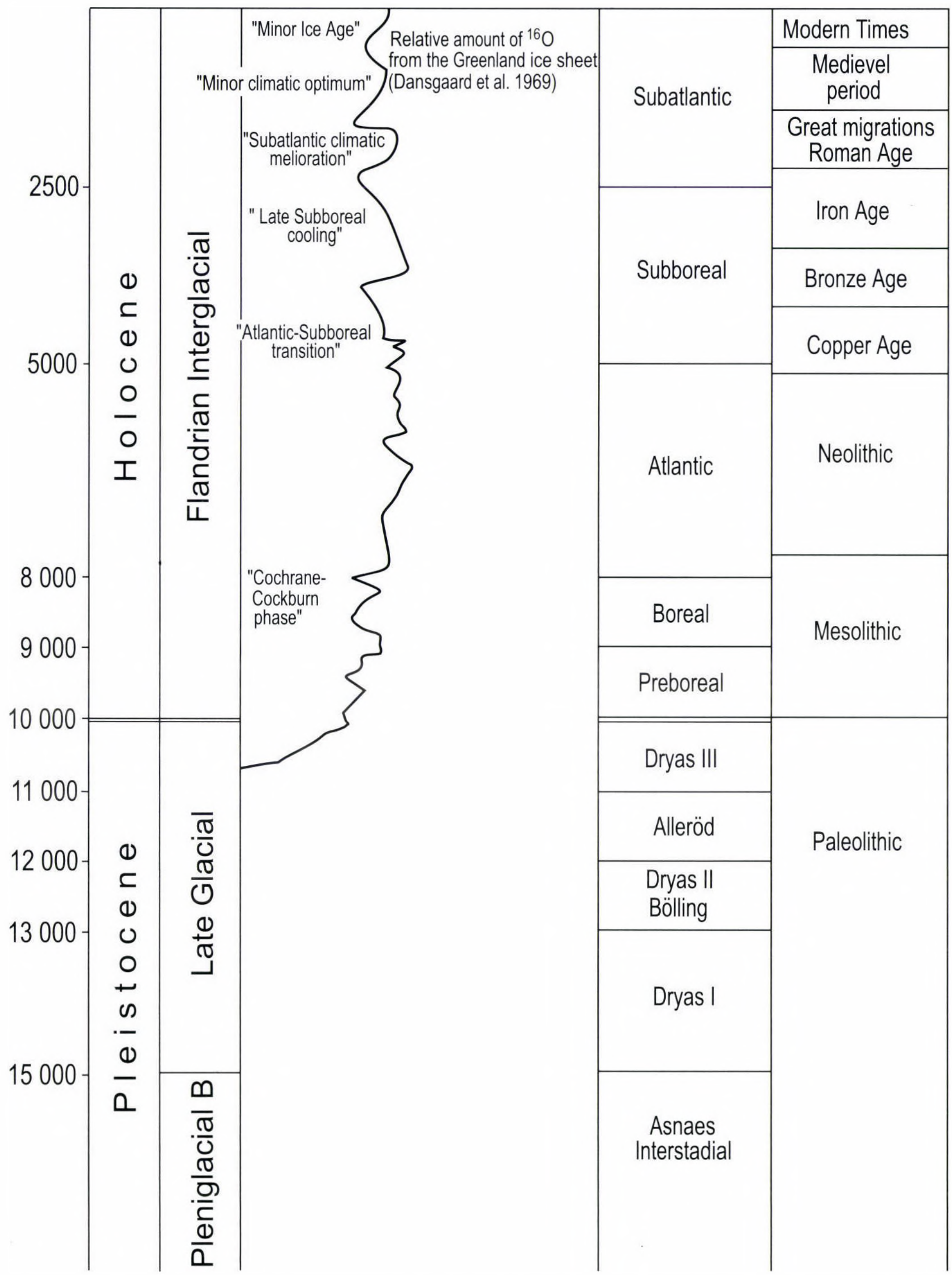

Fig. 5. Chronological subdivision of the Late Glacial and Holocene and climatic fluctuations during the Holocene (after Dansgaard *et al.*1969; Lang 1994)

ings (Sümegi 1996, 1999/a) as well. At that time *Alnus* and other deciduous species showed expansion.

In pine-birch open forests *Betula pubescens* dominated in boggy environments and *B. pendula* did in drier areas over the two macroregions of the Great Plain (those situated west and east of the Tisza).

Thermophilous deciduous trees (*Quercus*, *Ulmus*, *Tilia*, *Carpinus*, *Fraxinus*, *Fagus*) generally occurred sporadically. Probably the climate during Brörup interstadial was adequate for their survival even in the Great Plain but it was not favourable for their expansion. (It should be noted that the estimated July mean temperature was 17–18°C.) According to the charcoal findings (Stieber 1967) this arboreal vegetation was typical of the surrounding middle mountains.

However it could not spread over the plain because the "*in situ*" *Betula* as a pioneer species had colonised the habitats immediately when the climate turned milder and it presented a barrier to the invasion of the area by other deciduous trees.

The non-arboreal vegetation i.e. the flora on meadows and peat deposits and the aquatic vegetation was also different in the two areas of the Great Plain. On the Danube–Tisza Interfluve humid subarctic meadows had formed among the patches of woodland (with *Selaginella*, *Pleurospermum*). By the end of the interstadial some species of subarctic tall grass vegetation (*Polygonum bistorta*, *Sanguisorba officinalis*) appeared. Over the floodplains, reed, rush and aquatic species grew in the water of bogs as it is suggested by an enrichment of *Batrachium*, *Myriophyllum*, *Spargarium* and *Potamogeton* in the pollen spectra.

Along the north-eastern margin of the Great Plain (Trans Tisza Region) a tall grass vegetation existed that was much richer in species than that on the Danube–Tisza Interfluve. Beside *Polygonum bistorta* and *Sanguisorba officinalis* typical of both regions on the peripheries of the plain, *Filipendula cf. ulmaria*, *Geranium*, *Thalictrum*, *Symphytum*, *Epilobium*, *Rumex*, *Urtica* and *Apiaceae* pollen are added in the spectra. It confirms a flora rich in flowers. The alpine and subarctic *Pleurospermum* and some other elements of the recent tundra and subalpine vegetation such as *Huperzia selago*, *Selaginella* and *Ericaceae* also appeared.

In the higher and drier areas grassy meadows were to be found with dicotyledonous flowers. Many types of *Asteraceae* could be reconstructed; of them *Artemisia* was the most important, and some Pleniglacial and

Late Glacial heliophyton elements also appeared, like *Sanguisorba minor*, *Helianthemum*, *Ephedra* and *Armeria*.

Tall grass vegetation was predominant in the Trans Tisza Region, whilst the xerothermic grassland with a higher biodiversity was typical on the Danube–Tisza Interfluve.

Palynological examinations and macrofossil data of the sites in both regions suggest a generally cool and humid climate. Beside the remains of a rich coniferous flora, *Alnus* and the aquatic species it is confirmed by the fossil malacofauna where aquatic snails (*Bithynia tentaculata*, *B. leachi*) were the widest spread species (Krolopp 1966).

3.2.5. Flora of the Late Glacial

The Late Glacial was a phase of continuous climatic amelioration (disregarding some minor oscillations in temperature) lasting for ca 5000 years after the maximum of the last glaciation (15,000–10,000 BP).

The northern European division of the Late Glacial i.e. the three cold Dryas stadials and the warmer interstadials between them (Bölling, Alleröd) could only partly and in some places be detected in Hungary (Zólyomi 1965, 1978, 1995; Járai-Komlódi 1968, 1991; Stieber 1969; Miháltzné Faragó & Mucsi 1971; Kordos 1981, Miháltzné Faragó 1983; Csongor & Félegyházi 1987; Borsy 1991; 1992; Hertelendi 1992; Sümegi & Krolopp 1995; Willis *et al.* 1995; Nagyné Bodor & Járai-Komlódi 1999; Magyari 2002).

Probably these intervals of climatic oscillations with hardly more than 1,000, in some cases only some hundreds years duration are not reflected markedly in the vegetation changes in Hungary and they cannot be separated from each other, even if their boundaries are determined precisely by radiocarbon dating. Starting from the maximum of Weichselian Glacial during the early cold stadials in Hungary (just like in the major part of Europe) the climate was relatively dry and harsh, similar to the Weichselian stadials. Subarctic shrubs and dealpine vegetation prevailed with *Betula nana* and *Selaginella* and in the lower and more humid surfaces with marshy patches. The dominant vegetation was, however, a cold and dry continental steppe with *Artemisia*, rich in grass species such as *Chenopodiceae*, *Ephedra*, *Helianthemum*. This flora was similar to that generally characteristic for the periglacial areas during the interstadials but a slow reforestation had already started with coniferous species intermixing then with deciduous trees towards the Holocene. First the pioneer species *Betula* and *Hippophaë*, later in the milder interstadials the thermophilous broad-leaved *Ulmus*, *Quercus* and *Tilia* appeared. The prevalence of a milder and more humid climate (Alleröd interstadial) is also indicated by the fossil findings of abundant aquatic vegetation of bog and gallery forests rich in ferns (Járai-Komlódi 1966/a, 1968).

Dryas I. stadial. Pollen data in the Danube–Tisza Interfluve suggest subarctic and predominantly treeless vegetation with *Betula nana*, arctic-alpine *Selaginella*, has become extinct in Hungary since then and with heliophilous continental steppe elements like *Artemisia*, *Chenopodium*, *Ephedra* (Mihâltzné Faragó & Mucsi 1971).

Bölling interstadial. On the Danube–Tisza Interfluve *Pinus*, *Picea* and *Betula* forests expanded and *Hippophaë* appeared. Of non-arboreal taxa pollen of *Poaceae*, *Artemisia* and *Chenopodium*, of the aquatic and wetland plants, pollen of *Myriophyllum*, *Cyperaceae* and glacial moss (*Scorpidium*) were recorded (Mihâltzné Faragó & Mucsi 1971; Csongor & Félegyházi 1987; Zólyomi 1995).

Dryas II stadial. According to pollen analysis (Járai-Komlódi 1968; Mihâltzné Faragó & Mucsi 1971) a conclusion could be drawn that during Dryas II the hitherto treeless loess steppe had enriched in heliophilous continental steppe elements, like *Artemisia* species, *Chenopodiceae*, *Armeria*, *Gypsophila*, *Helianthemum*, *Ephedra*. In other places mossy, licheny subarctic meadows and patches of *Pinus*, *Picea* and *Betula* taiga forests appeared (Nagyné Bodor & Járai-Komlódi 1999), the latter with tall grass vegetation. *Selaginella selaginoides* was also reconstructed. Tall grass vegetation was characterised by species *Epilobium*, *Rumex*, *Sanguisorba*, the alpine-boreal *Pleurospermum* and *Thalictrum*. Along the rivers and on point-bars *Salix* and *Alnus* and *Hyppophaë* might form shrubs. Palynological analyses on the Danube–Tisza Interfluve hardly produced fern pollen and aquatic species never occurred in pollen profiles from this stadial. Scattered *Larix* and *Pinus cembra* woodland of the middle mountains had become enriched in *Betula* and *Pinus sylvestris*.

Alleröd interstadial. During this short and rapid warming (lasting for ca 1200 years) *Pinus sylvestris* and *Betula* woodland was expanding in the Carpathian Basin like all over Europe. In these forests other deciduous trees also appeared, e.g. *Populus tremula* and *Corylus* in the south of Germany, whereas *Ulmus, Quercus, Tilia* in Hungary (Járai-Komlódi 1966/a, Miháltzné Faragó & Mucsi 1971; Csongor & Félegyházi 1987). Contemporary forest could resemble the present-day European taiga (pine–beech forests of southern type mixed with deciduous trees) encountered in the western part of Russia and Ukraine. On the river banks *Salix–Populus–Alnus* groves existed whilst in bog depressions peat-fern–alder forests could develop. Massive reforestation is suggested on the Danube–Tisza Interfluve by the pollen diagrams (with non-arboreal pollen that had dropped from 45 to 8 per cent).

The milder and more humid climate is indicated by the expansion of ferns and aquatic species such as *Miriophyllum, Potamogeton, Typha, Sparganium* and *Nymphaeceae* in the pollen spectra. At the same time in the elevated and drier areas the treeless steppe partly survived under the continental climate.

According to the palynological analyses the climate of the Alleröd phase in the Carpathian Basin probably was more continental than that in northern and north-western Europe.

Dryas III stadial. During the following (and last) short cold spell of the Late Glacial lasting 600–800 years there were areal changes in woodland extension rather than in the composition of forest. The area covered by woodland had shrunk and the cold-dry loess steppe rich in *Artemisia* species and *Chenopodiaceae* advanced. At this time *Ephedra* and *Selaginella* still lived in the Great Plain. Aquatic species had become restricted in number, gallery and bog forests decreased in area and *Hippophaë* formed groves with *Salix* and *Alnus*.

The Late Glacial fossil flora shows remarkable similarities with that of the Brörup interstadial reconstructed for the Great Plain (Járai-Komlódi 1966/b) when also *Pinus, Betula* and *Alnus* were the dominant arboreal species with only few thermophilous deciduous trees. Of the herbaceous vegetation there were also many species in common: *Ephedra distachya* and *E. fragilis, Helianthemum, Gypsophila, Centaurea montana, C. scabiosa, Sanguisorba officinalis, S. minor, Hippophaë, Filipendula, Thalictrum, Pleurospermum, Epilobium, Artemisia, Poaceae* and *Selaginella*.

The most relevant difference between the Late Glacial and the Weichselian interstadial flora was the increased importance of *Picea abies* and *P. omorica* during the Brörup interstadial. It has been made evident both by fossil pollen findings and macrofossils that *Picea* was a characteristic component of forests in the Great Plain, too. Moreover their presence during stadials was also confirmed (Járai-Komlódi 1966/b, 1970) even though in a much lower percentage compared to Brörup floras reconstructed in the western and northwestern Carpathians. Their importance has been corroborated recently by "*in situ*" macrocharcoal findings (Willis 2000).

3.2.6. Have a genuine tundra and "Dryas-flora" ever existed in the Carpathian Basin?

On the basis of paleobotanical evidence achieved during the last decades a conclusion can be drawn that in Central Europe including the Carpathian Basin a treeless vegetation had been predominant during the stadials of Pleniglacials, and this is especially valid for the Great Plain. Arboreal vegetation occurred only sporadically, forest could be encountered in patches or in islet-like refugia. As it was mentioned above from these phases dominated by cold and dry climate pollen findings of several plants were recovered first in Hungary (Járai-Komlódi 1966/b; Miháltzné Faragó & Mucsi 1971) which nowadays are encountered in nival, arctic or subarctic tundra regions. Of them the most important were *Selaginella* and *Koenigia islandica* or *Betula nana*; the latter is an alpine species but as a relic has survived in some middle mountain areas of Europe. After more than 40 years these pollen findings became supported by macrofossil data. Moreover, a communication reported about *Dryas octopetala* to have been detected as well (Bajzáth 1999). Hopefully an detailed description of these findings could be read soon as a scientific contribution.

The sporadic appearance of some of tundra plants is convincing evidence to the climatic changes and contemporary flora. By no means it would testify, however, to the existence of extensive tundra vegetation in the Carpathian Basin. Similarly the sporadic appearance of *Dryas* would not mean the presence of a genuine "Dryas flora". The definition of floras, beyond the floristic data comprises several decisive floristic and paleoecological factors (such as climate, soils), among others a massive appearance of the index fossil, which has not yet been recovered in Hungary. The biostratigraphic assemblage can hardly be considered even as a scattered one and the characteristic species of the European "Dryas flora" such as the arctic–alpine *Loiseleuria procumbens* or the nival *Oxyria digina*, many typical *Silene*, *Saxifraga*, *Potentilla* and several other taxa have not been found so far in the glacial and late glacial floras in Hungary. The absence of contiguous tundra phenomena (Frenzel 1992/a; Pécsi 1997) and macrocharcoal finds stand against the presence of genuine tundra (Rudner & Sümegi 1998/a, b). In the light of the above arguments, a statement by B. Zólyomi from 1952 still sounds valid scientifically: "Real tundra never existed in Hungary, the traces of "Dryas flora" so characteristic for glacials, is completely missing here". Nevertheless, a remark should be added that even though the presence of "Dryas flora" has not yet been proven but findings of some tundra plants have become recovered since the 1960's and some has already been identified by macrofossils as well.

3.2.7. Survival, refugia

As a result of the dramatically changing climate during the Pleistocene lasting for several hundreds of thousand years the formerly Tertiary tropical and subtropical vegetation had undergone a fundamental change.

Arboreal species had a much less chance to survive than the non-arboreal ones although to trace the latter is more problematic for methodological reasons. Thus, herbaceous macrofossils are significantly less frequent and their identification is more ambiguous.

Plants having survived in refugia returned and spread during the phases of interglacial warming but they had been mixed and decimated. In the meantime some species survived as relics forever cut from their original areas of distribution. These are protected rarities of Hungarian flora. Further interpretation of a notion 'relic' and important remarks on the opportunities of survival of relic species are contained in a recent detailed publication (Kun 1998).

Part of temperate flora spread again in the Carpathian Basin reappearing from refugia. Arboreal plants, not only pines but deciduous trees as well, survived the severest stadials of the last (Weichselian) glacial mainly in the western, southern and south-eastern margins and in the submontane areas of ice-free Europe. These were the mixed deciduous forests near to the Atlantic seaside, the evergreen subtropical and Mediterranean vegetation in North Africa and south-western Asia. Undoubtedly, on the territory of Europe survival had been restricted for two reasons: from the north it was the coldness and from the south the continental tree barrier (Sahara) inhibiting the southward migration of several arboreal species thus causing their extinction (Andreánszky 1954). Over the huge zone of periglacial tundra and steppe they could survive the periods of severe climate in small populations scattered far from each other.

Some deciduous species could survive the last glacial in several refugia, whilst others found shelter in one or two refugia. For example those taxa having expanded rapidly during the Late Glacial and in the beginning of the Holocene, like species of mixed oak forests, must have come from several refugia. In certain refugia only one single or two species, in others several taxa might be inherited from the past. If the environs of a refugium indicated by macrofossils show an abundance of pollen taxa it suggests a site rich in species. Such refugia could be found both in the Alps and Carpathians.

Conclusions on the place of some Weichselian refugia are sometimes based on the direction of migration of some trees during the Late Glacial and Holocene (Glimeroth 1995). The main trends in the change of distribution areas were already dealt with by Scandinavian researchers (Post 1929) in the early 20th century. Nowadays the past migration trends of several important species can be traced well on the basis of the several Quaternary pollen spectra.

As a result of their isolated areas refugia could be localised by pollen analysis just vaguely. It is even less probable that in the area delimited in this way macrofossil remains could be found. There have hardly been any references to the whereabouts of such localities (Lang 1992, 1994). Macrofossils found "*in situ*" i.e. in their habitats, such as cave findings (Stieber 1967) or the more recent charcoal remains (Rudner & Sümegi 1998/b) completed with radiocarbon data and pollen analyses can be instrumental in the reconstruction of the glacial refugia in the Carpathian Basin (Willis 2000).

However one should be cautious in generalisations and with setting up rigid hypotheses, especially for such a critical geological time as the Pleistocene. For instance, on the basis of botanical and paleoecological evidence it is improbable that the eastern Mediterranean *Carpinus orientalis* could find a refugium in the Great Plain with an extremely cold continental climate during the maximum glaciation of the Weichselian Glacial

(Willis 2000). This is not supported either by "*in situ*" macrofossils or by findings analysed lately. At the same time the survival of *Carpinus betulus* in a refugia sounds conceivable and its is also supported by macrocharcoal analyses (Rudner 2001). Due to the geographical setting and geomorphic evolution of the Carpathian Basin the paysages of Hungary showed diversity in the past and they remained variable for the present both from ecological and landscape aspects.

There is a rather superficial generalisation that during the Upper Weichselian maximum cooling the whole area of the present-day Hungary was an "open parkland landscape" (Willis 2000) as several data are in contradiction with this concept.

Not only paleobotanical examination suggests the expansion of treeless cold continental steppes during the maximum cooling of the Weichsel, especially in the central parts of the Great Plain (Járai-Komlódi 1966/b; Borsy 1992; Rudner 1997; Sümegi & Kertész 1998) but faunistic findings as well. On the basis of micromammal (vole) fossils at 20,000–19,000 yr BP (W_3) distinctly cold continental steppe fauna became dominant in the Carpathian Basin.

All these conclusion are corroborated by archeological findings as the earlier cultures became extinct in this climatic zone and were replaced by Upper Paleolithic steppe cultures (Kordos & Ringer 1991).

Even in the different landscape regions, e.g. in the Great Plain or within specific zones, such as the forest steppe vegetation shows diversity at present (Zólyomi & Fekete 1994) and this must have been the case in the past as well.

It also must be taken into account that during the maximum cooling the local ecological conditions, the so-called micro-environmental factors might differ from the regional climatic features. In these small "climatic oases" the local temperature and moisture supply could be sufficient for the survival of plant and animal species in smaller spots of habitats.

Beside the available refugia provided by geographical factors (niches on the slopes of southern exposition, riverbank zones, littoral environment, proximity of thermal springs etc.) the appearance of some arboreal species (like Scots pine and larch) during glacials was facilitated by their ecological tolerance mentioned above.

It is possible that exactly the sporadic appearance of these groves had made the local climate under the tree canopies more tolerable compared to the regional one.

This had helped some plant and animal species with higher ecological demand survive the glacial epochs (Kordos 1977, 1987/a, b; Willis 2000). The importance of microclimate can be proven by the example of desert flora living on loess bluffs in the Carpathian Basin (Pócs 1999).

3.2.8. Specific features of flora and vegetation at the end of the glacial

It has already been known for long that Late Glacial vegetation both in Hungary (Járai-Komlódi 1966/a; Willis 1995, 1997) and Europe (Iversen 1954; Godwin 1956; West 1964; Wasilikowa 1964; Lang 1994) had a special floristic composition, which cannot be identified with the present-day formations or associations either on the basis of pollen examinations or by macrofossil findings.

There are rather complex causes behind these phenomena. On the one hand they could be found in the paleoecological factors following the glaciation and in mixing of floras during the glacials. During the Late Glacial (as a result of the continuously changing climate during the glacials and fairly unstable paleoecological conditions) the flora consisted of both polar and nival species mixed with continental steppe elements of the plains in unglaciated areas of Europe, including the Carpathian Basin.

This multifold mixing with different amplitudes of several floras was the reason why the distribution area of numerous species had undergone changes in a complex way or survived in various forms causing a completely different present-day pattern in comparison with that of the original one (Andreánszky 1954).

On the other hand the major global environmental changes had been shaped further by the frequent, intense and rapid modifications of the edaphic and local climatic factors. In the beginning of the Holocene the environmental conditions were rather unstable that could result in formation of mosaics composed by communities also enhanced by the mosaic-like pattern of climates and soils in the Carpathian Basin during the past 30,000 years (Sümegi & Kertész 1998).

Besides, amongst the ecological factors e.g. light conditions could be favourable for the expansion of the heliophilous steppe elements or of the arctic-alpine elements such as *Ephedra* as it happens at present as well.

The area of the latter is associated presently with the very warm and sunny conditions but it can also be found beyond the north polar circle in Siberia and in the nival regions of Tibet with adequate light conditions.

This is obvious because light is one of the most decisive ecological factors. On several occasions macrofossils, the present-day area of distribution or coenological behaviour of which are very different and today they never occur together, were found in each other's neighbourhood.

Thus e.g. in glacial layers in the southeast of Poland the fruits of Pontian halophite *Crambe aspera* and remains of leaves of *Dryas octopetala* were recorded together (Ku³czyñski 1932; Lang 1994).

The plant communities of the former periglacial areas could not have a very long history as the recurring climatic changes must have made effects upon their development, evolution and composition.

Thus when comparing the fossils with the recent flora or vegetation they are found far from being identical; rather they might be a similarity between them with regard to some individual features (Iversen 1954; West 1964; Járai-Komlódi 1966/a; Moor 1990). Recent investigations into vegetation history seem to have supported this concept. All species have a history of their own. The present similarity and identical appearance do not necessarily mean similar or identical history of evolution.

Under the climate of the past two and a half million years which was not stable at all, the response of the species to the Quaternary climatic oscillations had been strictly individual: migration of each and every species was controlled by its physiological demand and range of tolerance.

All these could hardly facilitate the joint evolution of some species, thus the long-term development of the communities. Due to the individual behaviour of the species along their history the floristic composition of plant communities was changing more or less gradually , thus the recent vegetation systems relying on the floristic base cannot be applied for the past (Lang 1992; Glimeroth 1995).

4. POSTGLACIAL VEGETATION HISTORY IN HUNGARY

The Pleistocene terminated with the cooling phases of Dryas toward the end of the Weichselian Glacial, and at that time, ca 10,000 years ago the Holocene began which showed climatic changes of smaller amplitudes than the Late Glacial. It could be characterised by an intense warming and reforestation and might indicate the advent of a new (Flandrian) interglacial (*Fig. 4, 5*).

With regard to its main trends the Holocene vegetation history in Hungary was similar to that in Central Europe. The basic differences concerned the behaviour of pines, the composition of non-arboreal flora and the formation and development of the natural and cultural steppe (Járai-Komlódi 1987). Paleoecological reconstruction based on the latest pollen-analytical results (Magyari 2002) and on micromammal fossils (Kordos 1981) was very fruitful.
The Holocene vegetation differs fundamentally from the vegetation of the Late Pleistocene. Under the gradually improving climate deciduous trees had returned from their refugia in Southern Europe and in the Carpathian Basin thus colonising the European temperate zone. An almost exclusive dominance of steppes and pines in the Carpathian Basin through many thousand years had come to an end. Pine forests occupied mainly the northern cold temperate boreal taiga zone and the pine-forest altitude zone in the mountains, whilst the other parts of the temperate zone had become populated with deciduous trees.

4.1. Preboreal

Due to its dominant vegetation type in literature Preboreal is frequently referred to as the pine-birch phase. In the beginning the fragmentation and regression of the contemporary Scandinavian ice sheet and the expansion of mixed *Pinus–Betula* forests were the main trend in the wake of the global warming. In the very beginning of the Holocene the climate was still very harsh, cold and dry, but solar radiation had been intensifying and the Carpathian Basin soon became inhabited not only by pines, birches and treeless steppes. As throughout Central Europe, broad-leaved trees also appeared and gradually expanded in the area what now is Hungary. At first *Betula* and *Alnus*, then *Ulmus*, *Corylus*, *Quercus*, *Tilia*, *Fraxinus*, *Acer*, *Carpinus* and *Fagus* species. The succession of the appearance of tree genera and also the spread of the latter however were affected by several ecological factors. These were mainly the climatic oscillations and soil formation processes plus internal genetic and physiological features like pioneer character, competitiveness, rate of reproduction, seed production and spreading ability, ecological tolerance and, most decisively, the distance from refugia. In the mountains mixed taiga forests, in the Great Plain forest steppe and steppe existed but *Pinus sylvestris* and *Betula* dominated everywhere.

During the Preboreal with a relatively short duration reforestation took place at a surprisingly rapid pace with considerable changes occurring in the composition of vegetation, primarily in that of the forests. The main reason was a significant climatic amelioration. During the 2000 to 2500 years that had passed between the maximum cooling of the Late Glacial and the climatic optimum of the Holocene the July mean temperature rose by at least 8°C in Central Europe.

According to the latest studies (Willis 1997) the Holocene reforestation with deciduous trees, the relatively rapid retreat of gymnosperms and the development of brown forest soils instead of podzolic ones all were caused by different factors, primarily by the extensive and frequent fires in pine forests. The rapid change of the Preboreal pine–birch forests into deciduous forests is an inevitably local feature but the idea of the authors that soil properties might have exerted a decisive impact on the post-glacial forest development can be of general validity.

4.2. Boreal

After the Preboreal there was a rise in temperature and a fall in precipitation throughout Europe. In the mountains of the Carpathian Basin and in the Great Plain with favourable conditions, e.g. on the peripheries and along the rivers thermophilous deciduous forests (*Ulmus*, *Quercus*) lived with *Corylus* shrubs, in the beginning with abundant and later vanishing *Pinus sylvestris*.

The climate which was much warmer and drier than during the Preboreal, did not facilitate forest development, among others due to the decrease of the groundwater table, especially in the central part of the Great Plain (Zólyomi 1953, Járai-Komlódi 1968). According to the pollen analytical examinations the Great Plain had partly become treeless, the rate of herbaceous species in the pollen spectra generally was 30%. The loess and sand landscapes in many places were natural steppes, warm and dry continental steppe meadows while in other areas, like along the margin of the Great Plain or on the Danube–Tisza Interfluve, on the sandy promontories near the rivers forest steppe survived. In the early Boreal this mosaic-like vegetation could be *Pinus sylvestris* forest steppe with an abundance of pine (42%) with gradually expanding *Quercus*, *Tilia* and *Corylus* and with a considerable share of steppe elements. Nowadays similar vegetation is to be found in Ukraine. Later, in the second half of the Boreal, deciduous trees outcompeted *Pinus sylvestris* and mixed-oak forest steppe developed. The first *Corylus* peak also occurred at that time. During the Boreal *Corylus* had not such a great extension in the Great Plain as in Western Europe. In the beginning of the Boreal the vegetation was rich in *Pinus sylvestris* and poor in *Corylus*, while by the end of the phase *Corylus* enriched and *Pinus sylvestris* retreated (Járai-Komlódi 1968). Recent pollen examinations showed mixed oak deciduous forests in the northeastern part of the Great Plain for the Boreal (Willis 1995).

In the *Pinus sylvestris* forests of the middle mountains deciduous trees expanded from the beginning of the Boreal, and by the end of the phase pine forests became completely outcompeted by mixed oak forests with *Ulmus*, *Tilia*, *Fraxinus*, *Acer*, and *Corylus* shrubs. Forests mixed with climatic xerothermic steppe meadows also in the mountains extending along the valleys of the Carpathians as high as the spruce zone.

This might be the time of migration and spread of Pontian– Central Asian species although the increasingly cold resistant Eurasian continental elements like *Ceratoides latens and Bassia prostrata* or *Artemisia* could migrate to the former (glacial and late glacial) steppes in Hungary. The karst grassland having developed from the subnival rock-grassland – especially the continental steppe-meadows on the slopes – could be widespread. Steppe elements having descended from limestone and dolomite slopes mixed with the submediterranean karstic shrub forests and grassland elements expanding from the south.

Smaller lakes had turned into swamps. Aquatic vegetation became poorer but in larger lakes under the impact of warming thermophilous aquatic plants appeared, e.g. pollen of *Nymphaceae* could be detected. The expansion of *Alnus* forests started in the second half of the Boreal, with underwood rich in ferns (*Thelypteris palustris*). This is to confirm the hypothesis that lakes and peat bogs had not dried completely on the Danube–Tisza Interfluve and it is also corroborated by archeological data (Kertész & Sümegi 1999).

During the Holocene probably the Boreal was the most critical phase with respect to the survival of glacial relic vegetation living in peat bogs and lakes. Evidently it was a phase of extinction of numerous species as refugia, protected microclimatic niches, humid and cool peat bogs (e.g. Bátorliget) had shrunk considerably thus restricting the area where the glacial plants could survive the dry and warm Boreal.

4.2.1. Steppe and cultural steppe

From the vegetation historical viewpoint in the issue of steppe and cultural steppe it is probably the events having taken place during the Boreal and Atlantic phases are the most intriguing in Hungary. In particular parts of the Great Plain, namely on the inner loess plateaus, sand spots and on sodic soils the last patches of the treeless climatic steppe could exist in the Boreal. At that time and during the Atlantic the forest steppe formed which was the last natural landscape in the Great Plain,. Nevertheless, Hungary's image has closely been related to the genuine climatic "puszta" (also supported by an incorrect tourist information). In spite of this, R. Soó in his works written in the early 20th century disclosed the origin of the Hungarian steppe. It was also him to reconstruct the whole Great Plain and the south–southeastern slopes of the middle mountains belonging to the climatic forest steppe zone and to claim that the presently treeless areas of Hungary are not climatic steppes. They have emerged as a result of the clearance of the original forest steppe i.e. they are cultural steppe (Soó 1931, 1940; Járai-Komlódi 1993). The relic landscapes and plants recovered later, macrofossils and results of pollen analyses have supported this. The present-day "puszta" has a completely different origin from the Boreal steppe as the former was shaped and it has been maintained up to now by the human activities. Thus, disregarding the spots of relic landscapes, whole of the Great Plain is a cultural landscape today, where the formation of steppe has been associated with human life.

However its vegetation (at least partly) is inherited from the former climatic steppes, steppe patches of the forest steppes, and from the karstic slopes of the North Hungarian Mountains. This relic flora was preserved within the relic landscapes and edaphic steppe-spots through the steppe patches of the climatic forest steppe and cultural steppe of today as well. In the northeastern part of the Great Plain (Trans Tisza Region) a larger area of closed forests has been suggested than on the Danube–Tisza Interfluve where steppe and forest-steppe seem to have dominated (Willis 1995, 1997).

4.3. Atlantic

The phase Atlantic is considered the climatic optimum of the Holocene, as the climate had turned more humid but it was still warm. This balanced submediterranean climate had given an impetus to forest development and promoted immigration of mediterranean and submediterranean species into the area that now is Hungary. Forests shifted northward and toward higher altitudes in the mountains all over Europe.

Deciduous forests, composed primarily by *Quercus*, *Ulmus* and *Tilia*, expanded in the plains. The overwhelming part of the middle mountains had become covered by continuous *Quercus* forests, where *Carpinus* and *Fagus* could mix sporadically. In the higher mountains *Fagus*, *Carpinus* and mainly *Picea* dominated, in the Tatras *Abies alba* expanded. In some places like on the Balaton Highland dense *Fagus* forests existed in the first part of Atlantic phase.

Fagus probably spread from the western Balkans (Illyric flora province) along the eastern foreland of the Alps to Transdanubia, then further to the North Hungarian Mountains (Zólyomi 1980, 1987).

The Carpathian Basin had been reforested. In the steppe spots of the Great Plain trees (mainly *Quercus*) expanded. At these times the last natural landscape of the Great Plain, the mixed-oak forest steppe formed. According to the palynological examinations *Corylus* had the same dominant role over the Great Plain, especially in the second half of the Atlantic phase, like during the Boreal.

The more humid and warm climate of the Atlantic obviously was very favourable for its growth. Its greater areal extension was inhibited probably by the deciduous forests. In some places dense *Quercus* forests had formed. In these woodlands *Carpinus* and *Fagus* appeared, *Hedera* crept upon the trees, and *Ilex* lived in the shrub level. *Pinus sylvestris–Betula* mixed forests virtually had disappeared.

Bog groves and gallery forests of Alder became widespread with an abundance of *Vitis sylvestris*. In oxbow lakes, abandoned watercourses and in interdune depressions rich paludal and bog vegetation could be found.

The relic *Ophrys* and *Orchis* protected nowadays probably emigrated from the south to the bogs in Hungary at these times. It is detectable palynologically that the lake vegetation became denser in comparison with the Boreal, namely with the appearance of *Nymphoides*, *Saggitaria* and *Alisma*.

In the emerging forest steppes grasses and Boreal steppe elements were replaced by dicotyledonous forest species and shrubs (*Viburnum*, *Ligustrum*). It is since then that the Neolithic cultures have left permanent imprint on natural landscapes.

4.4. Subboreal

Approximately 5,000 years ago the climate turned colder again but it still remained humid. This had stimulated closing of the forests, expansion of montainous tree species (*Fagus*, *Carpinus*, *Picea*) and spread of swamp and bog vegetation. Oak forest retreated, *Corylus* had lost its former significance. *Carpinus–Quercus* forests expanded in the Hungarian Middle Mountains and a zone of *Fagus* forests had formed. According to the investigations by Zólyomi (1936) *Abies alba* presently missing from the Middle Mountains, also expanded rapidly. On the basis of pollen data the forest had been closing in the peripheries of the Great Plain as well. In the central part of this macroregion oak forest steppe existed, the composition of which had changed however as mixed forests with *Carpinus* and *Fagus* existed with their accompanying species.

The postglacial forest expansion probably reached its maximum in the Great Plain during these times; peat bogs and *Fagus* were most frequent. The total reforestation must have inhibited only by the waterlogged and peaty areas and by forest clearance activities of the pastoral and farming people of the time. Irreversible changes in the Great Plain started to turn this region into a cultural landscape.

4.5. Subatlantic

In the Subatlantic following the Subboreal, the climate underwent some deterioration as it had become more continental. Mean annual precipitation decreased whilst temperature showed a slightly rising trend. In the mountain regions *Quercus*, *Carpinus–Quercus* and *Fagus* forests were found whereas in the Great Plain as the westernmost section of the extensive eastern European forest steppe zone, the oak forest-steppe formed the natural vegetation. *Fagus* retreated from the Great Plain except for its northern areas and the area under *Carpinus* shrank, whilst in the mountains the retreat of *Fagus* and expansion of *Carpinus* could be reconstructed. The endemic mixed pine forest patches found in western Transdanubia, an area close to the Alps represented the Central European pine forests.

Human impact upon the environment had accelerated. Pastoral and farming activities and the stormy events of history sweeping over the territory of present-day Hungary increasingly affected the formation of primeval vegetation. This is proven by a considerable increase of the ratio of grass species in pollen spectra, and by the appearance of cereals and weeds like *Centaurea*, *Plantago*, *Portulaca*, *Polygonum* and *Rumex* (Járai-Komlódi 1968).

5. HUMAN IMPACT UPON NATURAL ENVIRONMENT

Humans conquered more and more land from the nature during the past thousands of years. In the 18th century intensive water regulation started, followed then by the cultivation of arable land, later involving chemical fertilisers and, subsequently, pesticides. Forestry and water management underwent mechanisation, animal husbandry expanded, quicksands had been fixed and alkali soils ameliorated, landscape-alien species were planted and simultaneously adventive weeds became imported, thus shaping the present-day landscapes of Hungary.

Nowadays, except for some relic landscapes and species conserving the ancient vegetation ensembles, most of the mountains are characterised by intensive forest management, whereas in the Great Plain the former natural forest steppe has been turned into a cultural steppe. By now the original vegetation has decreased down to the tenth of the country.

According to the climatic and soil conditions an overwhelming portion of Hungary forms part of the European deciduous forest zone. Most of the Great Plain is to be regarded a westernmost continuation of the East European forest steppe zone. The mixed pine forests in west Transdanubia belong to the Central European pine forests.

Prior to the advent of the human activities that have changed environmental conditions fundamentally, at least 85% of the area of Hungary was covered by ancient deciduous woodland, mainly by oak forests. Today 17% of the country's territory is covered with forests but only 9% can be regarded remain of the ancient vegetation. The rest (with an area of ca 160,000 hectares) is repeatedly planted, strongly modified, degraded forest. Nevertheless "our forests represent approximately 45% of our flora and a considerable amount of protected species" (Bartha 1999).

In Hungary the number of nature conservation areas of national importance amounts to 139, comprising ca 500 hectares. Indigenous vegetation and wild flora has been endangered increasingly over the past fifty and even more in the last twenty years, owing to the global environmental crisis. Over the past fifty years 44 native species became extinct or disappeared. This comprises 2% of the total flora (2148 species). More than 600 species are more or less imperiled or need protection, among them 35 species figure on the International Red List of Endangered Species compiled by IUCN. At present 516 species are protected in the whole area of the country; 52 of them are strictly protected. Indicative of the efficiency of landscape protection measures 9 national parks have been founded till recently (Farkas 1999).

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Pollen sampling

Some grams of peaty soil might contain several thousand pollen grains

Treeless tundra with a peat house (Iceland)

Tundra landscape, with dwarfed birch stand (*Betula pubescens*) in the foreground (Iceland)

Birch stand on tundra in Lapland

Flowery tundra vegetation: willow, avens, crowberry, thrift (*Salix lanata, Dryas octopetala, Empetrum nigrum, Armeria alpina*) (Iceland)

Dwarf scrub of birch, willow and heather (*Betula nana, Salix herbacea, Calluna vulgaris*)
in Lapland

Preboreal forests on the territory what is now Hungary could be rich in flowers and tall grass vegetation similar to present-day Siberian taiga forest

Fleabane (*Erigeron arcticus*) is a lovely plant of polar tundra

Primrose (*Primula auricula*) is a Pleistocene relic species in Hungary

Cold stadials of the Late Glacial were named after mountain avens (*Dryas octopetala*)

Tundra formed on lava field (Iceland)

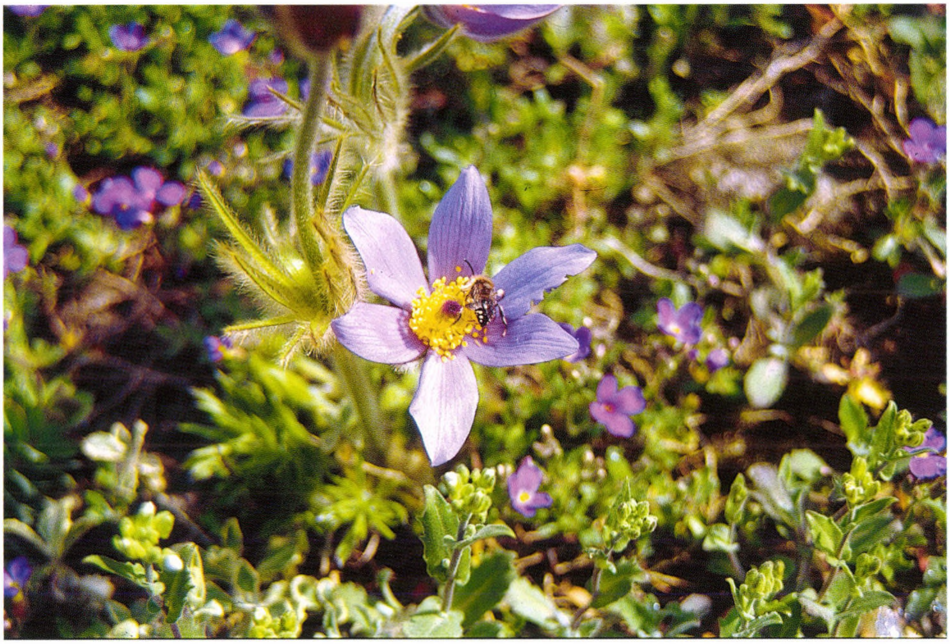
Flowery field in tundra environment (Iceland)

Ligularia sibirica a Pleistocene relic of taiga has recently extinct from Hungarian flora

Iris sibirica a fragile flower of taiga is a rare and endangered species of Hungarian flora

Patches of oak forest steppe still occur in the Great Hungarian Plain (Bélmegyer)

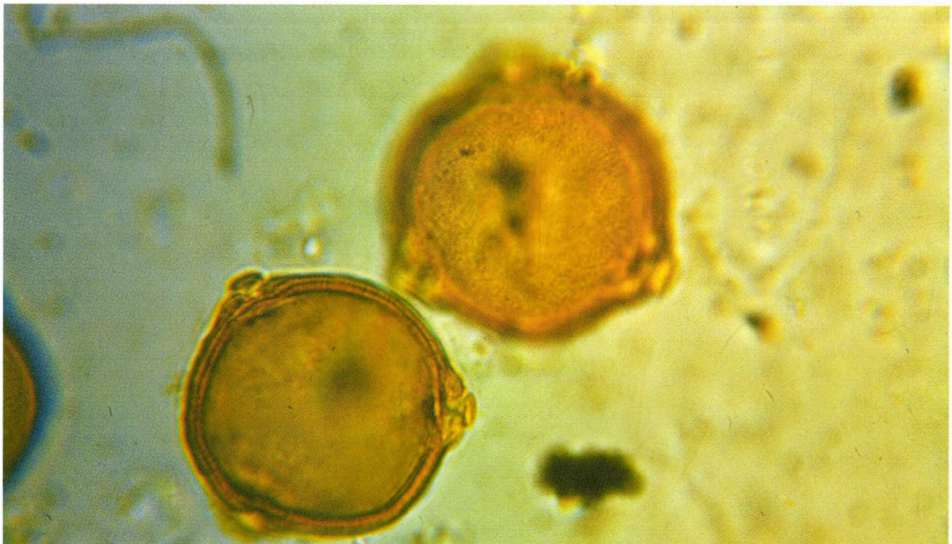
Climatic zonal relic oak forest on loess (*Aceri tatarici Quercetum roboris Zólyomi* 1957) at Kerecsend, Hungary



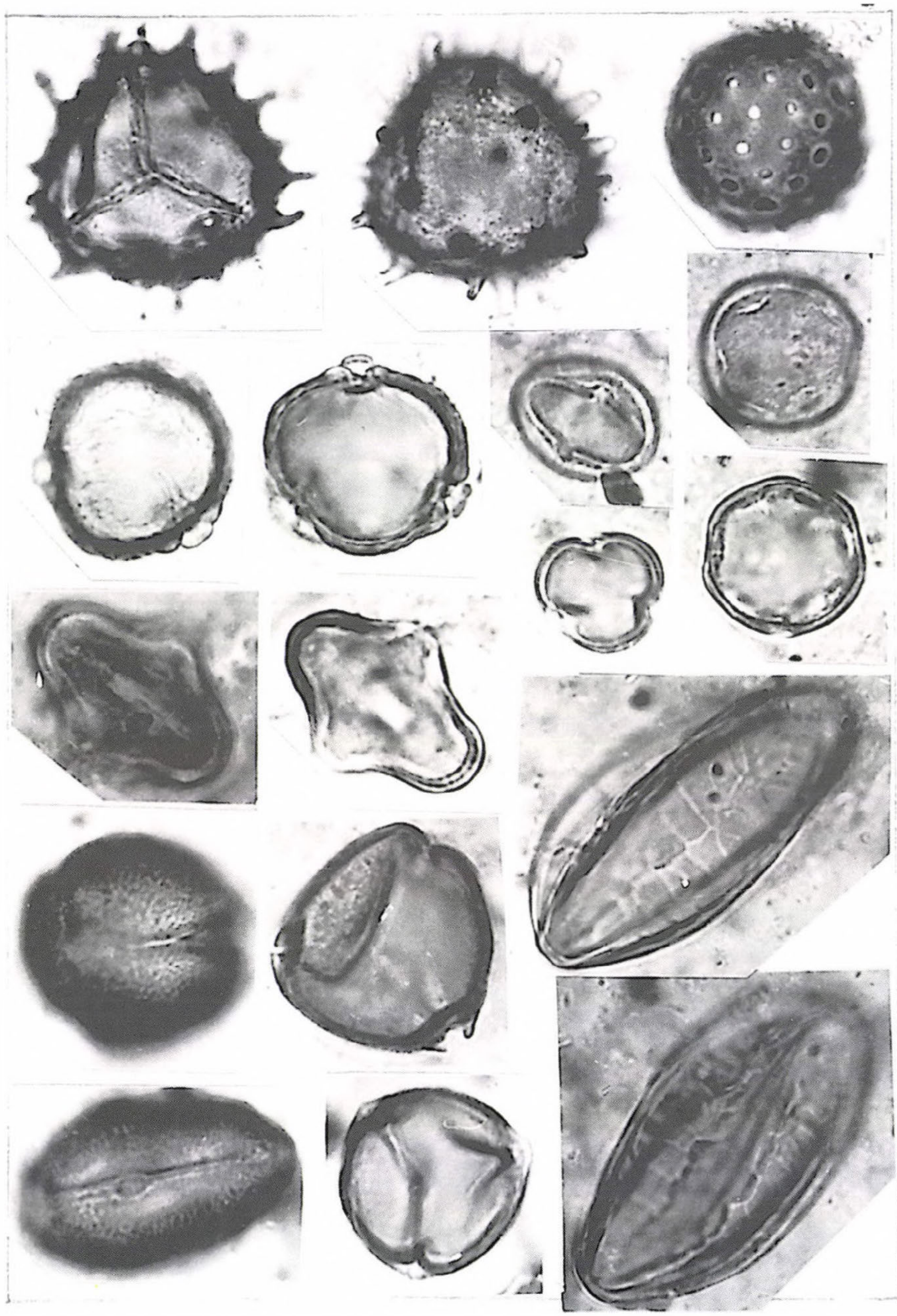
Pasque flower (*Pulsatilla patens*), a flower in Hungarian steppes, is on the verge of extinction

Holly (*Ilex aquifolium),* was native during Holocene climatic optimum

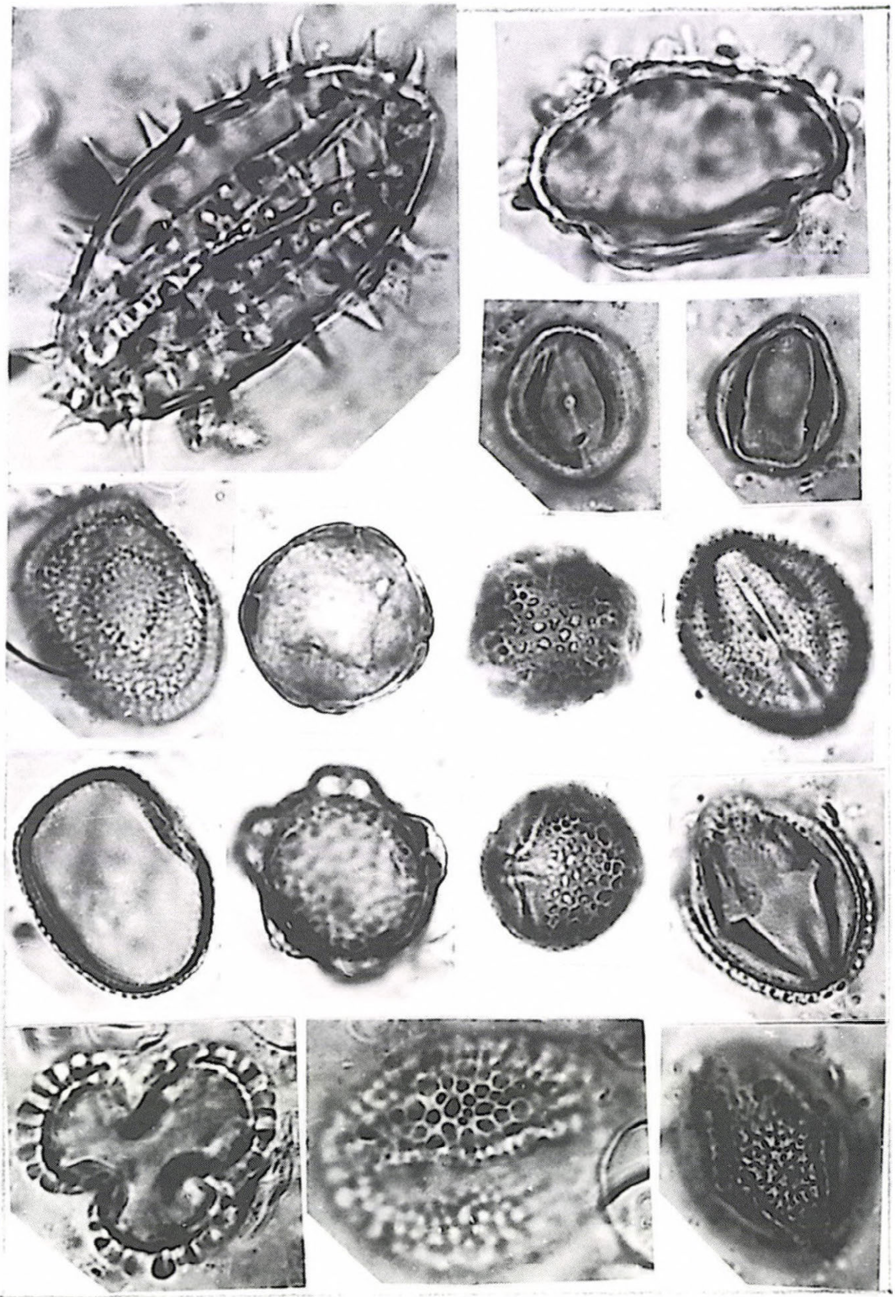
Microscopic photograph of pollen



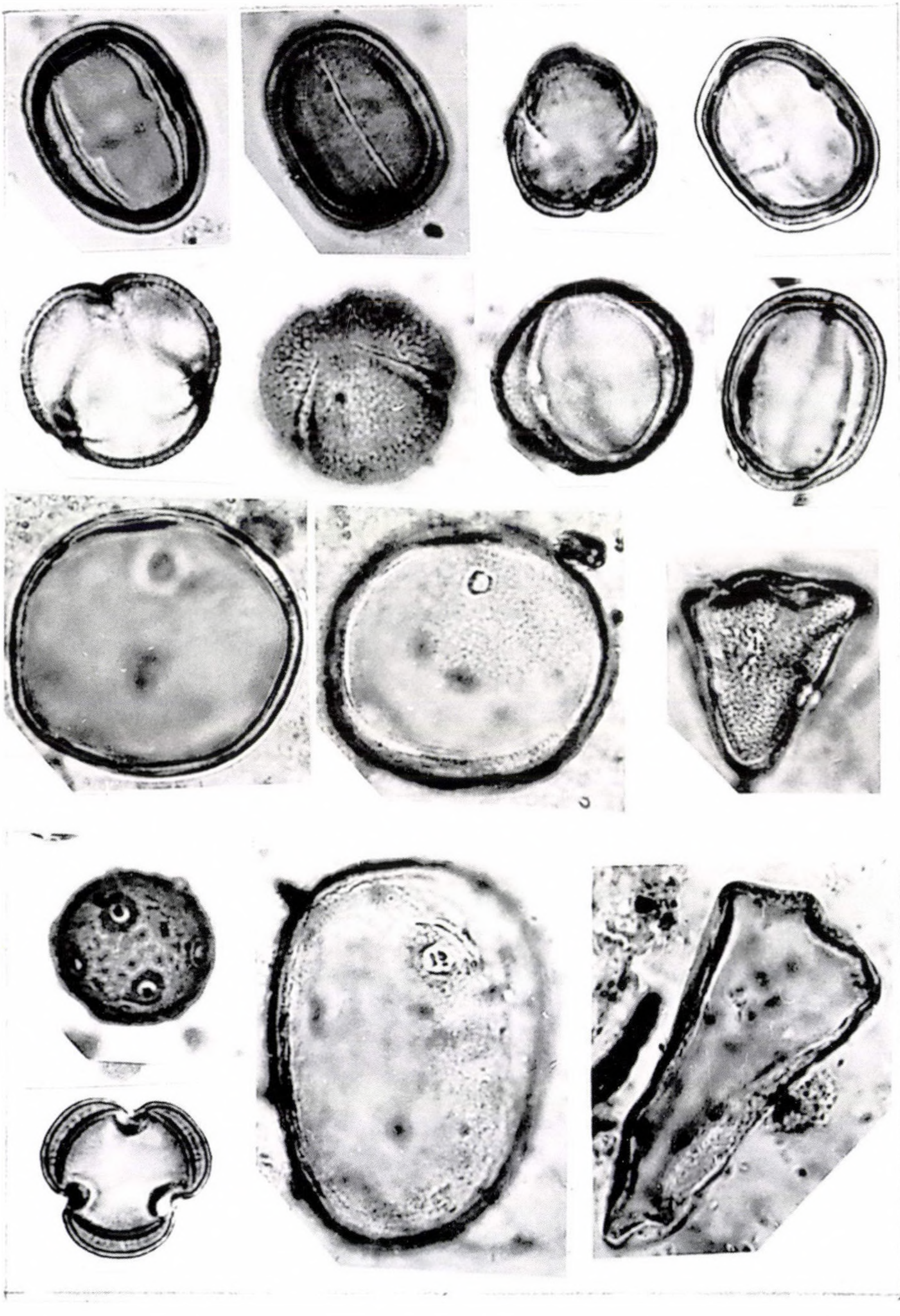
Sanguisorba minor pollen



Fossil pollen grains of the Late Glacial from the Great Hungarian Plain



Fossil pollen grains typical of the Holocene climatic optimum



Fossil pollen grains of some crop plants and weeds typical of the Late Holocene

The accumulation of knowledge of Quaternary vegetation history in Hungary started in the mid-20th century, primarily with palynological studies on Holocene forest development by Bálint Zólyomi.
Based on these initial results, using sophisticated methods and in co-operation with the related scientific disciplines, the vegetation history of Hungary could be extended back to the Lower Pleistocene, with a special reference to reconstructions for the Late Pleistocene (Weichsel). With the involvement of archeological investigations several aspects of human impacts during the last thousands of years have become identified as well.
The present publication is aimed at a summary of results achieved over the past fifty years.