PLANT MACROFOSSILS AND MALACOCOENOSES OF QUATERNARY MINERAL-ORGANIC SEDIMENTS AT STARUNIA PALAEONTOLOGICAL SITE AND VICINITY (CARPATHIAN REGION, UKRAINE)

Renata STACHOWICZ-RYBKA¹, Mariusz GAŁKA², Witold P. ALEXANDROWICZ³ & Stefan W. ALEXANDROWICZ⁴

¹ W. Szafer Institute of Botany, Polish Academy of Sciences, Department of Palaeobotany, ul. Lubicz 46, 31–512 Kraków, Poland, e-mail: r.stachowicz@botany.pl

² Department of Biogeography and Palaeoecology, Faculty of Geosciences, Adam Mickiewicz University ul. Dzięgielowa 27, 61-680 Poznań, Poland, e-mail: gamarga@wp.pl

³ Faculty of Geology, Geophysics and Environmental Protection, AGH University of Science and Technology, Al. Mickiewicza 30, 30-059 Kraków, Poland, e-mail: wpalex@geol.agh.edu.pl

⁴ Polish Academy of Arts and Sciences, ul. Sławkowska 16, 31-016 Kraków, Poland, e-mail: sz.alex@wp.pl

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Abstract: The unique nature of the Starunia palaeontological site, where near-perfectly preserved large mammals were discovered at the beginning of the 20th century, and incomplete knowledge on the development of palaeoenvironment in the Velyky Lukavets River valley in the Late Pleistocene and Holocene were the reasons for undertaking new comprehensive palaeobotanical and malacological studies. Starunia is also one of the sites bearing Pleistocene fossil flora, rare in this part of Europe. The results of plant macrofossil analysis show that in the Weichselian Middle Pleniglacial the landscape was dominated by steppe and tundra plant communities, being represented mostly by various grass and sedge species. Areas of higher humidity were covered with shrub tundra with *Betula nana*. The temperature requirements of taxa which are cool climate indicators show that the minimum July temperature amounted to at least 10°C. The record of Late Weichselian malacofauna confirms the dominance of an open landscape, mostly with steppe and steppe-tundra communities, as well as the presence of a dry, continental climate. At the beginning of the Holocene, an improvement of climatic and humidity conditions led to a fast local expansion of plant communities of the low and transition peat bog type, in the surroundings of shallow, periodically drying-up water pools. From the Middle Pleniglacial up to the present day, the area has been characterized by the presence of species tolerating an increased amount of salt in the environment. Their presence should be associated with natural brine effluences derived from Miocene strata in the bedrock.

Key words: Upper Pleistocene, Holocene, palaeoenvironment, plant macroremains, malacology, Starunia, Ukrainian Carpathians.

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INTRODUCTION

In 1907, in an ozokerite (earth wax) mine at Starunia (Ukraine) remains of a woolly mammoth and rhinoceros preserved in an unusually good condition were discovered (Łomnicki, 1914). Thanks to saturation with petroleum and brine, both soft tissues and bones were preserved. Apart from the woolly rhinoceros and mammoth, numerous plant remains, like fruits, leaves and wood fragments were found (Raciborski, 1914a, b; Szafer, 1914). In 1929, during excavations conducted by the Polish Academy of Arts and Sciences, a nearly intact carcass of woolly rhinoceros was

found, being so far the only such specimen in the world. Flora from the rhinoceros direct surroundings and from the animal interior was partially studied by Szafer (1930). Moreover, several species of molluscs – snails and bivalves – were determined (Łomnicki, 1908, 1914).

The unique character of the Starunia site, as well as incomplete knowledge on the Pleistocene vegetation history of this area, were the reasons for undertaking new comprehensive palaeobotanical research with the application of modern methods. The study of plant macroremains as well as malacological research were carried out as part of a project conducted by the AGH University of Science and Technology in Kraków (Kotarba, 2009). Material for palaeobotanical and malacological studies was taken from fullycored boreholes made in autumn 2007 and spring 2008. A detailed analysis of plant macroremains was applied to samples taken from boreholes Nos 4', 22 and 28, and two outcrops in the Velyky Lukavets River valley (denoted as VL-1 and VL-3), whereas malacological analysis was carried out on the material sampled from boreholes Nos 4, 5, 14, 22 and 43.

The study of flora and fauna accompanying the mammoth and woolly rhinoceros remains from Starunia play a significant part in detailed reconstructions of the palaeoenvironment, including succession of local vegetation, and the estimation of climate and ecological conditions in the water basin, in which bodies of the large mammals were found.

LOCATION AND GEOLOGICAL STRUCTURE OF THE STUDY AREA

The site, known for the discovery of unique specimens of the extinct woolly rhinoceros and mammoth, is situated in the area of a closed mineral wax mine at Starunia, about 130 km to the SE of Lviv. The study area, covering the surface of about 10.5 ha, is located in the vicinity of Starunia village, in the valley of the Velyky Lukavets River and the Rinne Stream, in the foreland of the Border Beskid Mts., within the Gorgany Fore-Carpathians (Kravchuk, 1999).

The Quaternary sediments filling the Velyky Lukavets River valley rest on the Lower Miocene molasse strata of the Vorotyshcha salt-bearing beds, developed as mudstones and clayey shales with sandstone intercalations, in which beds of marls, as well as strata, lenses and veins of gypsum, pyrite, sulphur, anhydrite, rock-salt, potassium salt and ozokerite can be found (Mitura, 1944; Korin, 2005). These strata are occasionally replaced by the Sloboda Conglomerates and sandstone-shale Dobrotiv beds.

The above-mentioned strata, together with underlying flysch rocks, build the Boryslav-Pokuttya Unit, forming several slices thrust one over another to the NE (Koltun *et al.*, 2005). In the top part of the flysch series there occur clayey shales, mudstones and sandstones (so-called Kliwa Sandstones) of the Menilite beds. The Lower Miocene complex terminates with the Stebnik beds.

Pleistocene sediments, particularly of the clayey facies, in which the large vertebrates were found, were saturated with brine and petroleum derived from the underlying Miocene strata. Close to Starunia, effluences of brine and oil, small lakes, and even mud volcanoes occur on the ground surface (Kotarba, 2005).

HISTORY OF PALAEOBOTANICAL RESEARCH

In 1907, in the clays of mineshaft IV, apart from the woolly rhinoceros, mammoth and other animal remains, numerous plant remains in the form of fruits, leaves, and wood

fragments were found. The leaves and fruits were studied by Raciborski (1914a, b), who determined several species of trees, shrubs, and herbaceous plants. The most frequently represented were leaves of two oak species: *Quercus sessiflora* and *Q. robur*, and two willow species: *Salix amygdalina* and *S. sabuly*. Analysis of wood fragments was carried out by Szafer (1914). An abundant material was formed by large parts of trunks, boughs and small twigs. Like in case of leaves, the wood composition was dominated by oak and willow. There also occurred numerous wood pieces of elm, ash and birch.

On the basis of analysis of plant macroremains, the researchers obtained the picture of vegetation corresponding to the present-day flora found in the surroundings of mineshaft IV. Later excavations revealed that both mammals remains and plant remains were placed in a secondary deposit (Nowak & Panow, 1930; Szafer, 1930). The carcass of the second rhinoceros, found in 1929, was surrounded by grey clays with a large admixture of organic material. Flora from the clavs of the direct surroundings of the rhinoceros and from the animal interior was partially studied by Szafer (1930). The remaining material is housed at the Palaeobotanical Museum of the W. Szafer Institute of Botany of the Polish Academy of Sciences in Kraków. On the basis of the flora composition, Szafer (1930) stated that it corresponds to the environment of present-day arctic tundra, and he related the age of the examined deposits to the "maximum diluvial glaciation", Cracovien. Radiocarbon dating, carried out in 1971 (Kubiak, 1971), changed the suggested stratigraphic position of the rhinoceros to an interstadial of Middle Weichselian age, the Hengelo interstadial (Granoszewski, 2002). However, the precision of this radiocarbon determination is not reliable (Kuc et al., 2005). In the Carpathian Mountains two sites of cool floras exist, which are, at the moment, associated with this interstadial - Brzeźnica (Mamakowa & Starkel, 1974) and Jasło-Bryły (Mamakowa & Wójcik, 1987), both situated in the Wisłoka River valley. In the grey clays of Starunia there also occurred twigs of mosses, which were studied by Szafran (1934) and Gams (1934). A detailed study on the willow leaves was undertaken by Kucowa (1954), who distinguished several species on the basis of leaf morphology.

In the outcrops of the Velyky Lukavets River, numerous fragments of coniferous and deciduous tree trunks were found. Their age was determined as the Middle Ages (12th to 14th centuries) by Krapiec (*cf.* S. W. Alexandrowicz *et al.*, 2005), on the basis of dendrochronological analysis.

HISTORY OF MALACOLOGICAL RESEARCH

Data concerning the malacofauna of Quaternary deposits from the Starunia area are insufficient and were collected only in the first stage of excavations, in 1907 (S. W. Alexandrowicz, 2003, 2004). A list of fauna with a commentary was published by Łomnicki (1908), and later these data, in a slightly expanded version, were included in a monograph published by the Academy of Arts and Science (Bayger *et al.*, 1914). In publications dealing with later excavations conducted between 1929 and 1933, the malacofauna was not mentioned. However, the remaining notes show that during the rinsing of deposits a few mollusc shells were found, but they were not studied and were probably lost (S. W. Alexandrowicz, 2003, 2004). The mollusc fauna was also recorded in fen soils of the Lukavets Maly River near the Gvizd village, located in Starunia's close surroundings (Rogala, 1907; S. W. Alexandrowicz *et al.*, 2005). So far, papers by Rogala (1907) and Łomnicki (1908) are the only studies of malacofauna in Quaternary deposits of Starunia and its closest area (S. W. Alexandrowicz, 2003, 2004). Even poorer is the knowledge on the present-day malacofauna in Starunia, being limited only to superficial observations carried out during fieldwork in the years of 2007 and 2008.

MATERIAL AND METHODS

Plant macroremains

There were over 40 fully-cored boreholes made in the study area, with a drill core diameter of 6–12 cm and reaching the base of Quaternary sediments. Analysis of plant macroremains was carried out for material obtained from five study sites in the Velyky Lukavets River valley (Fig. 1).

Sampling for analysis of macroscopic plant remains was conducted in a close association with sampling for pollen analysis. Each sample for pollen analysis was taken in the middle of a 10 cm segment meant for macroscopic plant remains analysis (Stachowicz-Rybka *et al.*, 2009).

The samples, 150 ml in volume, were macerated using a 10% KOH solution and detergents (in case of silts supersaturated with bitumens). After boiling the deposits to a pulp, the samples were wet-sieved on a sieve with the mesh diameter of 0.2 mm. Material remaining on the sieve was sorted out under a binocular low-power microscope. All the plant remains qualifying for identification were segregated and placed in a mixture of glycerine, water and ethanol in a ratio of 1:1:1, with an addition of thymol.

The found plant remains: seeds, fruits, needles, and other vegetative parts were identified using keys, atlases and other publications (Velichkevich & Zastawniak, 2006, 2008; Beijerinck, 1947; Berggren, 1969; Kats *et al.*, 1965; Nilsson & Hjelmquist, 1967), as well as the reference collection of present-day seeds and fruits and the fossil flora collections from the Palaeobotanical Museum of the W. Szafer Institute of Botany of the Polish Academy of Sciences in Kraków.

Well preserved remains were determined to the rank of species. Names of vascular plants follow Mirek *et al.* (2002).

The radiocarbon datings were performed by the Poznań Radiocarbon Laboratory (for details see Kuc *et al.*, 2009).

Qualitative and quantitative results are presented in diagrams plotted with the POLPAL software for Windows (Nalepka & Walanus, 2003; Walanus & Nalepka, 1999). The distinction of zones was carried out according to the presence of one or several most numerous or characteristic taxa. The names of the zones given in Table 1 originate from these taxa. Boundaries between the zones were indicated on the basis of the appearance, disappearance, increase or decrease in the number of taxa of quantitative or indicative significance.

Malacofauna

The studied material included samples from drill cores. The samples, about 0.5–0.7 kg each, represented thickness intervals of 0.25 m. Although they were taken from several drill cores, mollusc shells preserved well enough to enable species determination were found only in a few. Laboratory processing of the material included maceration and wet-sieving of sediment, followed by a selection of all intact mollusk shells and their fragments qualifying for identification. The determination was carried out with use of publications and comparative collections. The determined species were classified to ecological groups defined by Ložek (1964) and S. W. Alexandrowicz (1987). In the analysed material, the following groups are represented: species of open environments (group 5 - O), euryecological (mesophile) snails typical for habitats of medium humidity (group 7 - M), euryecological (mesophile) snails typical for humid habitats (group 8 – M), hygrophile taxa inhabiting fens and swamps (group 9 - H), and aquatic molluscs (group 10 - W). The results are compiled in the Malacological Spectrum of Individuals - MSI (Ložek, 1964; S. W. Alexandrowicz, 1987). The basis of the palaeoclimatic interpretation was the distinction of mollusc species groups, reflecting their present-day northern range (Sparks, 1969; Kerney et al., 1983; S. W. Alexandrowicz, 1987). Zoogeographic composition of the groups was described on the basis of a pattern presented by Ložek (1964) and S. W. Alexandrowicz (1987). Ternary diagrams illustrate the environmental changes in the area of Starunia at the time when the discussed sediments were accumulated. Malacological analysis was carried out for mollusc shells and shell fragments obtained from cores of six boreholes Nos 4, 5, 14, 22, 28 and 43 (Fig. 1). Unfortunately, lithological properties of the sediments, particularly a very low content or lack of calcium carbonate, created conditions strongly unsuitable for the preservation of specimens that could be indisputably determined to species or even genera. Among several dozen of obtained samples, only 7 did contain specimens qualified for determination. In a few other samples there occurred a heavily crushed shell material, the determination of which was impossible. The whole analysed fauna includes 20 mollusc species: 14 land snails, 3 aquatic snails and 3 bivalves. Additionally, there also appeared calcium plates produced by unshelled snails arbitrarily named Limacidae. In all analysed samples, a total of almost 250 specimens was determined. The number of taxa in particular samples fluctuated from 3 to 13, and the number of specimens from 8 to 121, respectively.

DESCRIPTION OF SEDIMENTS AND ZONES OF PLANT MACROREMAINS

A detailed description of sediment from sections selected for analysis of plants macroremains, as well as the

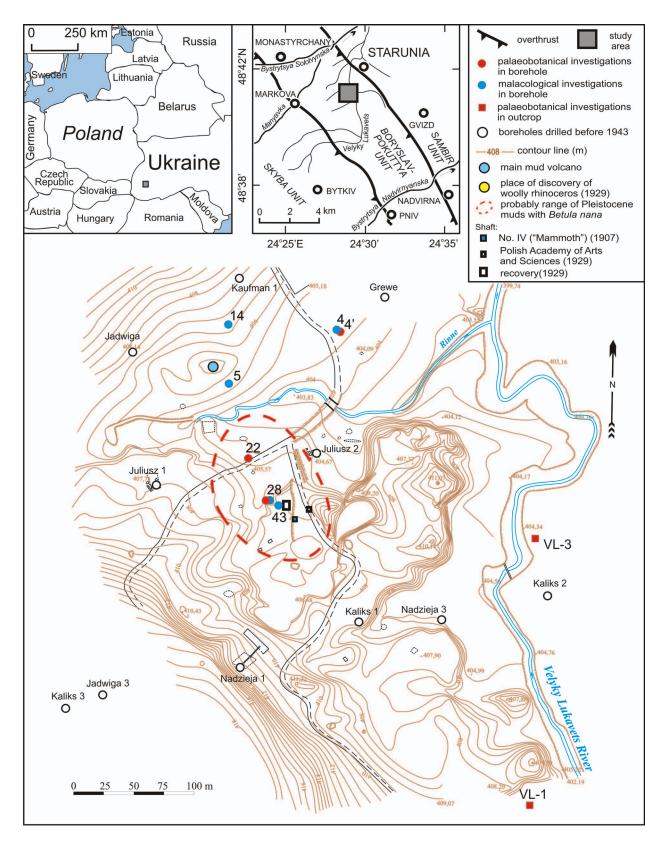


Fig. 1. Sketch map of the Starunia palaeontological site and surrounding area (Carpathian region, Ukraine) with the location of palaeobotanical and malacological studies

Table 1

Description of Local Macrofossil Assemblage Zones L MAZ

Local Macrofossil Assemblage Zones L MAZ	Depth (m)	Zone description
Borehole 4'		
Star 4'/I Batrachium	5.10-4.35	Single fruits of <i>Batrachium</i> sp., Poaceae and <i>Typha</i> sp. seeds are recorded
Star 4'/II Betula nana	4.35-3.60	The only zone with fruits and scales of <i>Betula nana</i> and single fruits of <i>Betula</i> sp. present. From the bottom to the top the participation of Poaceae sp. seeds increases. Mire plants: <i>Eleocharis palustris</i> and <i>Schoenoplectus tabernaemontani</i> appear
Star 4'/III Schoenoplectus- Eleocharis	3.60-3.45	Aquatic plants are represented by <i>Potamogeton filiformis</i> and <i>Zannichellia palustris</i> . Among mire plants, <i>Eleocharis palustris</i> and <i>Schoenoplectus tabernaemontani</i> reach their highest values. Poaceae reach their maximum values in the whole section. At the top, the Caryophyllaceae are recorded for the first time and <i>Typha</i> sp. appears again
Star 4'/VI Eleocharis-Poaceae	3.45-2.55	The frequency of mire plant remains decreases, aquatic plants disappear. Values for Poaceae sp., <i>Eleocharis</i> sp. and <i>Typha</i> sp. are considerably lower than in the preceding zone
Star 4'/V Schoenoplectus-Typha	2.55-2.15	At the bottom, aquatic plants: <i>Potamogeton filiformis</i> and <i>Zannichellia palustris</i> , appear again. <i>Typha</i> sp. reaches its highest values in the whole section. The participation of Poaceae and <i>Eleocharis</i> sp. increases again
Star 4'/VI <i>Typha-Juncus</i>	2.15-1.15	The number of diaspores decreases significantly. Single seeds of <i>Typha</i> sp., <i>Plantago lanceolata</i> and <i>Potentilla</i> sp. are found
Star 4'/VII Juncus	1.15-0.7	Dominance of Juncus cf. glaucus/effusus, Juncus sp. and Typha sp. seeds. Single fruits of Mentha sp. and Carex sp. are also present
Borehole 22		
Star 22/I Betula nana-Eleocharis	5.90-4.80	The zone is characterized by the presence of very numerous <i>Eleocharis palustris</i> fruits, with a culmination in the middle part. The diaspores of Poaceae, <i>Triglochin maritimum</i> , <i>Juncus</i> sp. and <i>Bidens tripartita</i> also reach their highest values in this zone. Moreover, several aquatic and mire plants: <i>Zannichellia palustris</i> , <i>Potamogeton filiformis</i> , <i>Batrachium</i> sp. and <i>Schoenoplectus lacustris</i> were determined
Star 22/II Triglochin-Betula nana- Poaceae	4.80-4.20	<i>Betula nana</i> reaches its maximum values. Seeds of <i>Poaceae</i> sp. and, <i>Juncus</i> sp., as well as seeds and fruits of <i>Triglochin maritimum</i> , are still very numerous. Only single remains of aquatic plants: <i>Zannichellia palustris</i> and <i>Batrachium</i> sp. were determined in the bottom section of the zone
Star 22/III Juncus -Betula nana	4.20-3.40	The number of diaspores decreases significantly in all ecological groups. <i>Juncus</i> sp. still retains high values. Plants of humid areas: <i>Eleocharis palustris, Comarum palustre</i> and <i>Triglochin maritimum</i> are still represented relatively well
Star 22/VI Juncus	3.40-2.80	The upper boundary of the zone is indicated by the last occurrence of <i>Betula nana</i> remains. Plant remains frequency is very low. Only <i>Juncus</i> sp. seeds are quite numerous
Star 22/V Phragmites-Cenococcum	2.80-0.20	A zone with the lowest plant remains frequency in all ecological groups. The remains of <i>Betula</i> sect. <i>Albae</i> , <i>Abies alba</i> and plants of humid habitats like <i>Schoenoplectus lacustris</i> , <i>Stachys palustris</i> and <i>Eriophorum vaginatum</i> were determined
Star 22/VI Poaceae-Juncus	0.20-0.00	The number of remains increases, particularly belonging to plant of humid habitats. Seeds of Poaceae sp., <i>Juncus</i> sp. and <i>Chenopodium album</i> as well as fruits of <i>Taraxacum officinale</i> reach high values
Borehole 28		
		ples from the depth between 640 and 50 cm. Only several samples from the top of the section contained plant <i>psa</i> , <i>C. elata, Potentilla erecta, Plantago major</i> and <i>Phragmites australis</i> that could be determined
Outcrop VL1		
Star VL1\I Cenococcum geophilum	3.15-2.35	The zone is characterized by the presence of numerous <i>Cenococcum geophilum</i> sclerotia at the top of the section and a small number of plant macroremains. Remains of trees and shrubs: <i>Betula nana</i> , <i>B. humilis</i> , <i>Juniperus communis</i> and <i>Rubus idaeus</i> are present. Single seeds of <i>Viola palustris</i> and fruits of <i>Urtica dioica</i> are also found
Star VL1/II Betula nana	2.35-2.05	The lower boundary of the zone is indicated by an increase in the number of <i>Betula nana</i> fruits, and the upper boundary - by their last occurrence. <i>Carex</i> sp. div. 2-sided reach their maximum number. Fruits of <i>Betula</i> sect. <i>Albae</i> and <i>Scirpus sylvaticus</i> were also determined. No remains of mire and aquatic plants were found
Star VL1/III <i>Typha</i> sp.	2.05-1.65	The zone of highest values for <i>Typha</i> sp. and <i>Carex</i> sp. div. 3-sided. Fruits of <i>Betula</i> sect. <i>Albae</i> represent trees
Star VL1/ IV	1.65-0.95	Zone of the lowest frequency of remains. Single seeds of <i>Juncus</i> sp. and sclerotia of <i>Cenococcum geophilum</i> are present
Star VL1/V Juncus-Lychnis flos-cuculi	0.93-0.00	Zone characterized by an increase in the participation of remains of plants from humid and peat bog habi- tats. Maximum values are reached by <i>Juncus</i> sp. and Poaceae sp. The only zone, in which <i>Potentilla erecta</i> , <i>Lychnis flos-cuculi</i> as well as <i>Ranunculus lingua</i> (which represents an aquatic environment) are found

Local Macrofossil Assemblage Zones L MAZ	Depth (m)	Zone description
Outcrop VL3		
Star VL3/I Alnus incana-Alisma plantago-aquatica/ lanceoloata	2.10-1.75	The only zone, in which tree macrofossils occur. The presence of <i>Alnus incana</i> , <i>A. glutinosa</i> and <i>Picea abies</i> was recorded. As an aquatic plant, <i>Alisma plantago-aquatica/lanceolata</i> was determined. There also occurred <i>Polygonum hydropiper</i> , <i>Sparganium neglectum</i> and <i>Carex pseudocyperus</i>
Star VL3/ II Alisma plantago- aquatica/lanceoloata	1.75-1.30	<i>Alisma plantago-aquatica/lanceoloata</i> is still highly numerous. Aquatic plants are also represented by <i>Sparganium neglectum</i> and <i>Polygonum hydropiper</i> . At the top of the zone, the participation of <i>Scirpus sylvaticus</i> increases
Star VL3/III Scirpus silvaticus- Poaceae	1.30-0.50	The seeds of <i>Alisma plantago-aquatica/lanceolata</i> almost disappear. The participation of <i>Scirpus sylvaticus</i> , <i>Carex</i> cf. divulsa and <i>Ranunculus</i> cf. <i>repens</i> increases. After a decrease of <i>Carex</i> cf. <i>divulsa</i> there is an increase of <i>Juncus</i> sp. The participation of Poaceae seeds is the highest in this zone
Star VL3/IV Poaceae-Plantago media	0.50-0.00	Increase of the content of remains of plants with lower humidity requirements. Diaspores of <i>Sambucus</i> sp., <i>Plantago media</i> and <i>Taraxacum officinale</i> , not recorded so far, were found. Oospores of <i>Chara</i> sp. appear as representation of plants from aquatic habitats

spatial distribution of Quarternary sediments in the Velyky Lukavets River valley, were presented by Sokołowski *et al..*, (2009). The analysis of plant macroremains was carried out for material obtained from boreholes Nos 4', 22 and 28 and outcrops VL-1 and VL-3 (Fig. 1).

Borehole No. 4'

Borehole No. 4' is located in the NE part of the study area (Fig. 1) and includes 4.35 m of organic sediments, from which 87 samples were taken. The examined sediments rest on Miocene strata and are covered by a mine dump, 0.7 m thick. The section is represented mainly by clayey mud with plant detritus, peat, biogenic mud, and mud saturated by bitumen (Fig. 2). The conducted analysis of botanical composition allows for a distinction of 7 phases in the development of vegetation – Star 4' I–VII (Table 1).

Borehole No. 22

Borehole No. 22 is located about 160 m to the SE from the place of the rhinoceros and mammoth finding (Fig. 1) and includes 5.80 m of organic sediments, from which 59 samples were taken. The examined sediments are underlain by Miocene strata and are covered by a mine dump, 30 cm thick. The examined sediments include: clayey mud with plant detritus, peat mud, coarse-clastics saturated by bitumen and peat in the top section (Fig. 3A). The conducted analysis of botanical composition allows for a distinction of 6 phases in the development of vegetation – Star 22 I–VI (Table 1).

Borehole No. 28

Borehole No. 28 is located closest to the place of finding of large mammals (Fig. 1, Table 1) and includes 6.1 m of organic sediments, from which 34 samples were analysed. The examined sediments are placed on Miocene strata and are covered by a mine dump, 30 cm thick. They are composed mostly of clayey mud and a peat (0.5 m thick) at the top of the section. A gravel bed occurs at the base of the clayey deposits. The analysis of botanical composition shows that there are almost no plant remains, which could be qualified for determination. A poor content of plant remains made plotting the diagram and detailed analysis of the vegetation development phases impossible.

Outcrop VL-1

Outcrop VL-1 (Fig. 1), located on the Velyky Lukavets River left bank, is 3.0 m thick. From the segment of organic sediments, 49 samples were taken for analysis. The base of the sampled outcrop is marked by the river bed level, whereas at the top a mine dump bed, about 2 m thick, occurs. The conducted analysis of botanical composition allows for a distinction of 6 phases in the development of vegetation – Star VL-1 I-VI (Fig. 3B, Table 1).

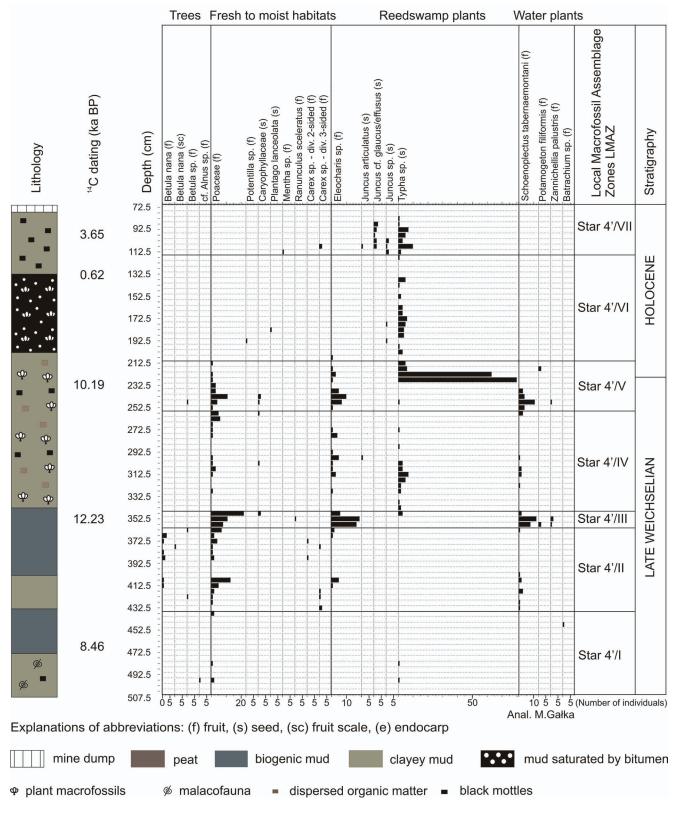
Outcrop VL-3

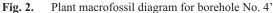
From outcrop VL-3 (Fig. 1), located on the Velyky Lukavets River right bank, 21 samples were taken from the segment of mineral-organic sediments, 2.1 m thick. The base of the core is marked by the river bed level, whereas the top is marked by a gravel bed, several centimetres thick. Up the section, a *ca*. 1.2 m thick bed of fen soil occurs, with soil developed at the top (Sokołowski *et al.*., 2009). The conducted analysis of botanical composition allows for a distinction of 4 phases in the development of vegetation – Star VL-3 I-IV (Fig. 4, Table 1).

DESCRIPTION OF MALACOFAUNA

Samples for malacological analysis were taken from five boreholes Nos 4, 5, 14, 22 and 43 (Fig. 1).

From borehole No. 4 one sample was taken from a depth of 4 m, containing a very poor fauna (with 3 species and 8 specimens). The group found here is composed of two aquatic mollusc species: *Galba truncatula* (Müll.) and *Pisi-dium obtusale laponicum* (Cless.), and a hygrophile land snail taxon – *Vertigo genesii* (Gred.). There also occurred quite numerous, small fragments of *Vertigo* or *Columella* shells, not qualifying for determination. The group presented above is typical for a very cold climate and strongly





boggy habitats. It characterizes an arctic tundra environment.

In borehole No. 5, in one sample taken from a depth of 2.3 m, a poor mollusc group (with 4 species and 27 specimens) was found. It was characterized by dominance of

aquatic species typical for shallow and periodically disappearing pools: *Galba truncatula* (Müll.) and *Anisus leucostomus* (Mill.). It is completed by land snail species associated with open habitats of a diversified humidity: *Pupilla muscorum* (L.) and *Vertigo angustior* Jeffr. From borehole No. 14 two samples were taken, including a quite abundant mollusc group. In the lower sample, taken from a depth of 2.3 m, the mollusc fauna is poor (7 species, 25 specimens). It is characterized by numerous occurrence of aquatic species, *Galba truncatula* (Müll.) and *Radix peregra peregra* (Müll.), which are accompanied by land, mainly hygrophile snails: *Vertigo antivertigo* (Drap.) and *Succinea putris* (L.). The upper sample (from a depth of 2.0 m) abounds in mollusc shells (13 species and 121 specimens). The four most important taxa found here are: *Galba truncatula* (Müll.), *Radix peregra peregra* (Müll.) and *Anisus leucostomus* (Mill.), as forms typical for periodical water pools, and *Pisidium casertanum* (Poli.), as an euryecological bivalve species. The group is completed by land snails.

Boreholes Nos 5 and 14 are located close to each other and they were sampled at a similar depth (Fig. 1). The malacofauna groups identified in the three samples described above have a similar species composition and represent a similar type of habitat. This indicates the existence, at least in the northern part of the study area, of a shallow and periodically disappearing water pool, surrounded by open land habitats with a quite high humidity. A fact worth noticing is also the total lack of cold-adapted species.

In borehole No. 22, two samples taken from the top of the section (at the depths of 0.1–0.2 m and 0.2–0.3 m) contained similar mollusc groups covering a total of 8 taxa and 33 specimens. Malacofauna is dominated by land species typical for open and relatively dry habitats: *Vallonia pulchella* (Müll.), *Pupilla muscorum* (L.), and *Vertigo pygmaea* (Drap.). It is completed by mesophile species of habitats showing medium humidity. Aquatic forms are of accessory importance. All species included in the presented group occur in the present-day area of Starunia. The group's ecological description corresponds to the present-day environment.

In borehole No. 43, a sample taken from a depth of 7.7 m contained a poor fauna (with 6 species and 15 specimens). The mollusc group was represented virtually by only two ecological groups: hygrophile species, *Vertigo genesii* (Gred.) and *Vertigo geyeri* Lindh., and aquatic forms typical for episodic pools, *Galba truncatula* (Müll.) and *Pisidium obtusale laponicum* (Cless.). All the taxa identified in the sample are characterized by a very high thermal tolerance and are typical for boggy environments of polar tundra. The mollusc shells were accompanied by small, unfortunately not qualifying for determination, fragments of bones, most probably belonging to a large mammal.

OLDER MALACOLOGICAL DATA

The mollusc group found by Rogala (1907) in the Maly Lukavets River terrace in Gvizd village contained mainly species typical for a cold climate, such as *Succinea oblonga* Drap. or *Columella columella* (G.Mart.). The composition of malacofauna indicates a humid tundra habitat (S. W. Alexandrowicz *et al.*, 2005). A considerably more abounding group was described by Łomnicki (1908), who studied mollusc shells collected from the mineshaft, in which the remains of mammoth and first rhinoceros were found. The de-

termined fauna included as many as 28 species (Łomnicki, 1908; Bayger et al., 1914) represented by numerous specimens. Unfortunately, during later studies it came out that the malacological material came from an old mine dump, which was, at the end of the 19th century, used to fill the mineshaft. The material included species occurring at that time in the area of Starunia (Nowak & Panow, 1930; S. W. Alexandrowicz, 2003, 2004). The correctness of such an interpretation is indicated by an excellent condition of the shells (with colour and organic parts preserved), as was emphasized by Łomnicki (1908), as well as by the composition of the group, in which an important part was played by species with very high thermal requirements, like Helix pomatia (L.), Helix lutescens Rossm., and others (S. W. Alexandrowicz, 2003, 2004). For these reasons, this fauna can be used only to estimate the composition of those fauna groups, which occurred in the area of Starunia more than 100 years ago.

DESCRIPTION OF CHOSEN MOLLUSC SPECIES

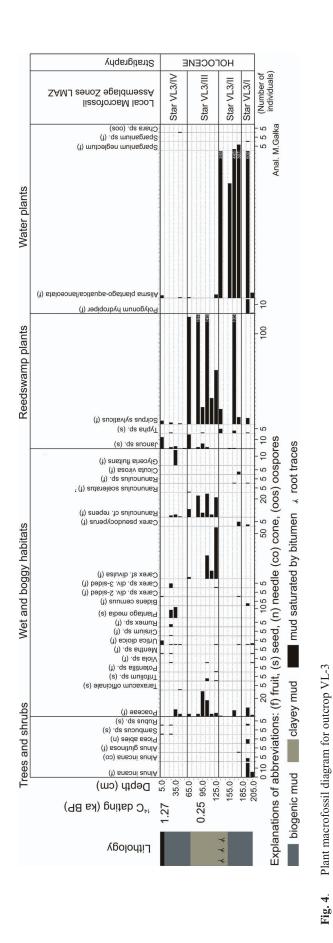
Only several out of 21 mollusc taxa identified in the analysed samples are of significant importance for palaeoenvironmental reconstruction and stratigraphical interpretations.

Pisidium obtusale laponicum Cless. – a taxon of the subspecies rank, considered a species by some authors. At present, this bivalve is found only in northern Europe, in arctic and subarctic areas. It is very common in the Late Glacial carbonate lacustrine sediments and is virtually absent from Holocene deposits (W. P. Alexandrowicz, 1999). At present, it inhabits small, shallow pools with standing water and luxuriant plant vegetation. It also may, for a short period, survive in boggy land environments.

Galba truncatula (Müll.) (Fig. 5H-1) – a widely spread holarctic species. It is a snail with a broad ecological tolerance found in various kinds of pools with standing waters. Most of its typical habitats are small, periodically disappearing and drying overflow areas. In spite of being an aquatic species, it can survive in humid land biotopes, even for a period of several months. *Galba truncatula* (Müll.) is one of snails found most commonly in the Late Glacial and Holocene deposits. It is very often accompanied by *Anisus leucostomus* (Mill.) and *Pisidium obtusale* (Lam.), as well as by hygrophile land species such as *Succinea putris* (L.) and *Zonitioides nitidus* (Müll.), and in deposits associated with cold periods also by *Vertigo genesii* (Gred.) and *Vertigo geyeri* (Lindh.).

Anisus leucostomus (Mill) (Fig. 5H-2) – a palaeoarctic species with a broad climatic tolerance. It is a form typical for small, heavily overgrown aquatic pools, which can be also found in boggy land biotopes. Together with *Galba truncatula* (Müll.) it forms a faunal group characteristic for episodic water pools. Anisus leucostomus (Mill.) is commonly found in Late Glacial and Holocene sediments.

Vertigo genesii (Gred.) (Fig. 5LG-2) – a North European species, characteristic for boggy and open biotopes of a swamp type. Most frequently, its presence is associated



with the Late Glacial. It is particularly common in the Younger Dryas, where it is usually accompanied by *Vertigo geyeri* Lindh. and *Columella columella* (G. Mart.). In Holocene sediments, it is a relict form occurring very rarely. In Scandinavia and locally in Western Europe, a significant participation of *Vertigo genesii* (Gredl.) is recorded in sediments of the Lower and even Middle Holocene (Ložek, 1964; Limondin-Lozouet, 1992; Krolopp & Sümegi, 1993; S. W. Alexandrowicz & W. P. Alexandrowicz, 1995a, b; W. P. Alexandrowicz, 1997, 1999, 2004).

Vertigo geyeri Lindh. (Fig. 5LG-1) – a boreal-alpine species found in biotopes very similar to the ones inhabited by Vertigo genesii (Gredl.). Most frequently, the two taxa are found together and form a group, very characteristic for the close of the Latest Glacial, recorded for numerous sites in the whole of Europe (Ložek, 1964; S. W. Alexandrowicz, 1987; Limondin-Lozouet, 1992; Krolopp & Sümegi, 1993; S. W. Alexandrowicz & W. P. Alexandrowicz, 1995a, b; W. P. Alexandrowicz, 1997, 1999, 2004).

Pupilla muscorum (L.) (Fig. 5LH-2) – a widely spread holarctic taxon with a high thermal tolerance. It is found in deposits associated with the coldest glacial phases (loesses) as well as in sediments deposited in the climatic optima of interglacials. At present, it is one of snails most commonly found in the whole of Middle Europe. *Pupilla muscorum* (L.) is found at completely open sites, dry or of medium humidity.

Vallonia pulchella (Müll.) (Fig. 5LH-1) – taxon of similar ecological valence to described above. It is found mainly in Late Glacial and Holocene deposits in different types of land sediments. The species in question is typical for open and relatively dry environment. Malacocenoses with large amount of *Vallonia pulchella* (Müll.) usually accompanied by Vallonia costata (Müll.) and other cold-tolerant land snails are regarded as characteristic for Late Glacial and Early Holocene sediments deposited in land, dry and open environments (Ložek & Thoste 1972; S. W. Alexandrowicz & W. P. Alexandrowicz, 1995a).

DEVELOPMENT OF PALAEOENVIRONMENT

Palaeobotanical and malacological studies, radiocarbon dates ($40,000 \pm 700$ yrs BP, $43,000 \pm 1100$ yrs BP), and a detailed analysis of sediments of the Velyky Lukavets River valley indicate that the development of the valley began in the Early Weichselian or even in the Eemian Interglacial, whereas the sedimentation of clayey sediments occurred in the Middle Pleniglacial (Moershoofd interstadial) and was continued in the Hengelo/Denekamp interstadial, as well as in the Late Glacial and Holocene (Stachowicz-Rybka *et al.*, 2009; Sokołowski & Stachowicz-Rybka, 2009; Kuc *et al.*, 2009).

Middle Pleniglacial

In the plant macroremains diagrams (Figs 2, 3 A, B, 4), local zones were distinguished and, on the basis of the local vegetation development phases, an attempt was made to

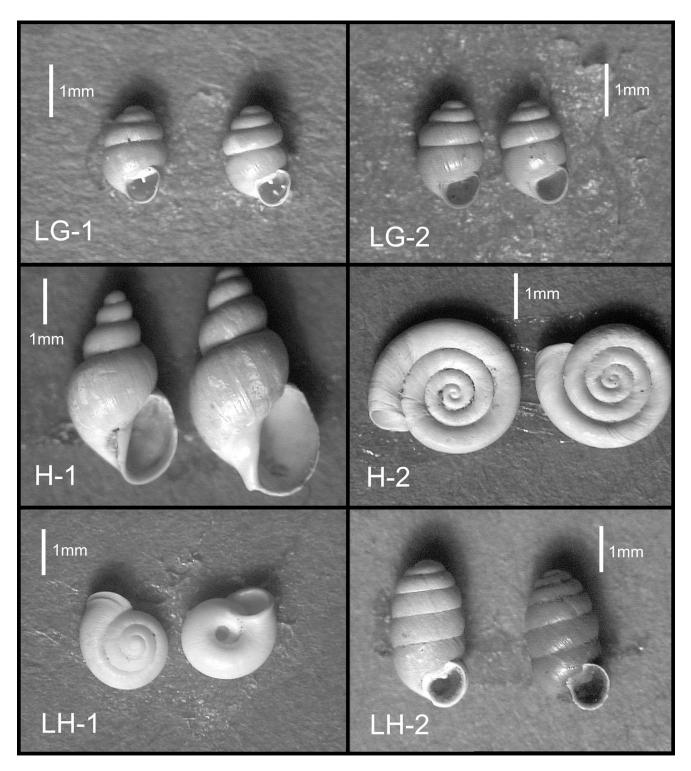


Fig. 5. Shells of typical snails from the Late Glacial and Holocene deposits from Starunia. Species typical for Late Glacial deposits: **LG-1** – *Vertigo geyeri* Lindholm, **LG-2** – *Vertigo genesii* (Gredler). Species typical for Holocene deposits: **H-1** – *Galba truncatula* (Müller), **H-2** – *Anisus leucostomus* (Millet). Species typical for Late Holocene deposits: **LH-1** – *Vallonia pulchella* (Müller), **LH-2** *Pupilla muscorum* (Linnaeus). Photos by W. P. Alexandrowicz

correlate them with each other, as well as to assess the stratigraphical correlation.

In the Velyky Lukavets River valley the oldest sediments were documented for drillings Nos 22 and 28. Unfortunately, since hardly any macroscopic plant remains were found in drilling No. 28, the only drilling material remaining for analysis was from No. 22 (Table 1, Fig. 3A). Both the quantity and variability of plant macroremains, determined for the basal deposits of section 22 in the Star 22/I-III zones, indicate that the plant communities of that time, in all land habitats surrounding the lake and in the lake itself, were varied and abundant.

The lacustrine pool was surrounded in that period mostly by *Betula nana* (Fig. 6A, B, C, D), *Salix* sp., *Betula*

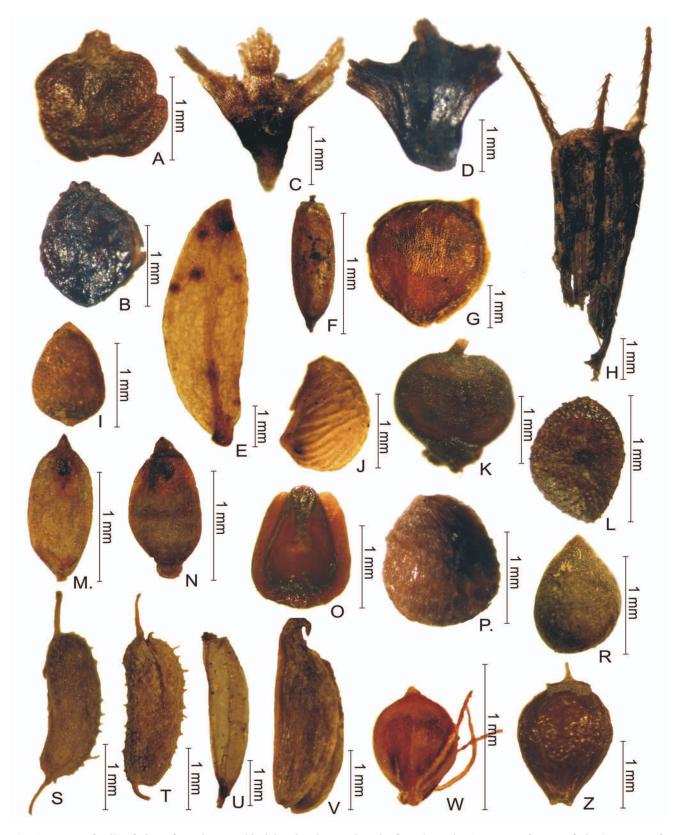


Fig. 6. Macrofossils of plants from the Late Glacial and Holocene deposits from Starunia. **A, B** – *Betula nana*, fruit; **C, D** – *Betula nana*, fruit scale; **E** – *Salix* sp. leaf; **F** – *Typha* sp., seed; **G** – *Ranunculus acris*, fruit; **H** – *Bidens tripatrita*, fruit; **I** – *Urtica dioica* fruit; **J** – *Potentilla erecta* fruit; **K** – *Carex elata*, fruit; **L** – *Plantago major*, seed; **M**, **N** – *Poaceae* sp., fruit; **O** – *Lycopus europaeus*, fruit; **P** – *Batrachium* sp., fruit; **R** – *Viola palustris*, seed; **S**, **T** – *Zannichellia palustris* fruit; **U** – *Triglochin maritimum*, seed; **V** – *Triglochin maritimum*, fruit; **W** – *Scirpus sylvaticus*, fruit; **Z** – *Eleocharis palustris*, fruit. Photos by R. Stachowicz-Rybka and M. Gałka

humilis and, occasionally, tree birches (*Betula* sect. Albae). Therefore, the patches of tundra vegetation must have played a significant part in the landscape around the lake.

In the sediments surrounding the rhinoceros's carcass, Szafer (1930) determined 14 plant species, among which *Betula nana* is worth particular consideration, as a species occurring very plentifully in the forms of fruits, scales, and leaves. The species gave name to deposits ("clays with *Betula nana*") associated with beds, in which the discoveries of large mammals are located. Moreover, Szafer (1930) determined a number of species confirming the glacial type of the Starunia flora, such as *Dryas octopetala*, *Salix reticulata*, and *Thalictrum alpinum*. Out of the species listed by Szafer (1930), the only ones found in the currently examined sediments were: *Betula nana*, *B. humilis*, and numerous *Carex* species.

The remains of *Betula nana* were recorded in sediments of all examined sections apart from section VL-3. Both the radiocarbon dates and succession of vegetation suggest that the presence of the above-mentioned remains in sections VL-1 and 4' should be associated with the cooling of climate during the Late Weichselian, being the time of occurrence of last the woolly rhinoceroses and mammoths. The oldest sediments including the remains of *Betula nana* were dated to the Middle Pleniglacial and were found in sections 22 and 28. Geologic survey and radiocarbon datings (Sokołowski & Stachowicz-Rybka, 2009; Kuc *et al.*, 2009) conducted for adjacent sections are likely to indicate a broader range of the sediments of that age (Fig. 1).

In both the older and the currently examined flora no tree remains were found, what indicates a dominance of open and woodless plant communities. This is confirmed by palynological data (Stachowicz-Rybka et al., 2009). Undoubtedly, the dominant plant communities in the landscape were tundra and steppe communities, the presence of which was marked mostly by the occurrence of various grass and sedge species. The Star 22/I and Star 22/II zones are characterized by the occurrence of exceptionally numerous grass fruits. Among the latter, the presence of Puccinellia distans (Fig. 6M, N) is worth emphasizing. It is a species with an exceptionally high resistance for soil salinity. It is assumed that 5-10 g of salt per 1 kg of soil is optimum for this halophyte's requirements. However, as it is stated by Kozłowski et al.. (2004), even with 73 g of sodium chloride per 1 kg of soil the growth of the plant is still possible. Puccinellia distans is found in Starunia at present, similarly as Lepigonium salinum (currently Spergularia salina) mentioned among the meadow flora by Łomnicki (1914). Together, they form patches in areas of the highest salinity (Mościcki et al., 2009).

In wet and eutrophic habitats, as well as in drying-up waterside habitats, the therophyte phytocoenoses appeared. They are represented by species characteristic for various present-day Bidentetea tripartiti units, like *Bidens tripartita* (Fig. 6H) or *Ranunculus sceleratus*.

From the Middle Pleniglacial up to the present day, the area has been characterized by the presence of *Triglochin maritimum*, which is not frequently found in Quaternary sediments (Stachowicz-Rybka, 2005) and is currently in danger of with extinction. It grows in Europe, mainly on sea

shores, but also in halophylic, boggy meadows and transition bogs. Outside Europe, it has essentially a circumboreal distribution (Davy & Bishop, 1991; Looman, 1976).

It is worth emphasizing that currently in Starunia the species is found in large numbers, forming quite dense stands in boggy areas (Mościcki *et al.*, 2009).

The reedswamp area was undoubtedly dominated by *Eleocharis palustris* (Fig. 6Z) and *Typha* sp. (Fig. 6F), which are found together in Phragmition communities. However, considering the fact that the remains of *Eleocharis palustris* appear in very large quantities in the bottom section of the zone and suddenly disappear, it can be assumed that they formed monospecies transitory communities. Currently, plant communities of that type occur as the outer belt of reedswamp vegetation. Highly numerous fruits of this species show that the bedrock must have contained a lot of calcium carbonate.

Because of salinity, aquatic communities were dominated by Zannichellia palustris (Fig. 6S, T), which prefers extremely eutrophic or slightly saline, standing or slow-flowing waters. It grows at various depths in littoral shallows of lakes and rivers. Its participation in younger parts of the zone gradually decreases. Zannichellia palustris, together with Potamogeton filiformis, which is also a halophylous species, could have formed plant communities of a type similar to the present-day Parvopotamo-Zannichellietum (Matuszkiewicz, 2001).

In the group of species characteristic for Weichselian sites (Velichkewich & Zastawniak, 2006), Eleocharis palustris and Potamogeton filiformis are distinguished as species appearing in the close or in the beginning of interglacials, most often in the tundra or woody tundra landscape. These species, as well as other taxa indicating cool climate, were recorded in zones Star 22 I-III. The minimum July temperature for both Eleocharis palustris and Potamogeton filiformis is 10°C (Kolstrup, 1980; Mamakowa, 1997). The minimum July temperature for Betula nana is 7°C (Brinkkemper et al., 1987), and for Triglochin maritimum - 8°C (Lambracht et al., 2007). The tolerance range of these taxa indicates that the Middle Pleniglacial minimum temperature in July amounted to at least 10°C and was comparable with temperatures dominating in Western Europe (Huijzer & Vandenberghe, 1998). Therefore, the seasonally frozen ground at Starunia was likely to be controlled by cold climatic conditions.

Late Weichselian

The Late Weichselian (Alleröd and Younger Dryas) sediments were documented in several zones of the analysed sections: Star 4'/I-V, Star 22/IV-V, and Star VL-1/I-III (Figs 2, 3A, B).

The basin, the presence of which was confirmed by the occurrence of aquatic flora, was at that time still surrounded mainly by: *Betula nana* (Fig. 6A, B, C, D), *Salix* sp., *Betula humilis*, and *Juniperus communis*, and occasionally by: *Betula* sect. *Albae* and *Picea abies*, and in more humid habitats also by *Alnus incana* and *Alnus* sp. Therefore, in the landscape surrounding the lake, an important part must have been played by patches of tundra vegetation, which were

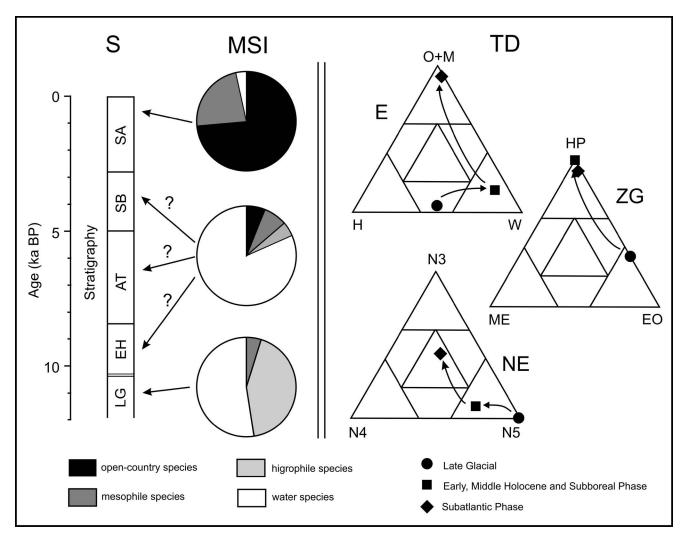


Fig. 7. Tri-component diagrams of the Late Glacial and Holocene malacofauna of Starunia. S – stratigraphy: KA BP – age in thousands of years, LG – Late Glacial, EH – Early Holocene, AT – Atlantic Phase, SB – Subboreal Phase, SA – Subatlantic Phase, MSI – malacological spectrum of individuals (based on Ložek, 1964 and S. W. Alexandrowicz, 1987); TD – ternary diagrams, E – ecological, O – opencountry species, M – mesophile species, H – higrophile species, W – water species, NE – northern extent of taxa, N₃ – species reaching 62° northern latitude, N₄ – species reaching the North Polar Circle, N₅ – species crossing the North Polar Circle, ZG – zoogeographical, HP – widespread species, ME – Middle-European species, EO – European species of limited extent

gradually entered by loose boreal forest communities. Simultaneous occurrence of *Cenococcum geophilum* sclerotia indicates an open character of the vegetation surrounding the lake and an increase in solifluction processes (Ławrynowicz, 1983).

Herbaceous communities of land plants are characterized by the presence of exceptionally numerous grass seeds, as well as occasional macrofossils of various heliophilous plant species, such as: Caryophyllacae, *Plantago lanceolata, Viola palustris* (Fig. 6R), and *Potentilla erecta* (Fig. 6J). This indicates the maintenance of steppe-tundra communities in the landscape.

Star 4'/III and Star 4'/V zones are a period of improvement in climatic conditions of the basin. The basin was colonized by aquatic plants, like *Potamogeton filiformis, Zannichellia palustris*, and *Batrachium* sp. In shallow basins, up to several dozen centimetres deep, there occurred *Schoenoplectus tabernaemontani*, preferring slightly salty waters. Swamp communities were dominated by *Eleocharis* sp., *Typha* sp., and *Juncus* sp. A characteristic feature of the Starunia flora is a very poor frequency of aquatic plant taxa, including climatic indicators. The reason for such a condition could be the constant and quite high water salinity, as well as contamination with petroleum, penetrating from Miocene strata in the bedrock.

The environmental chemistry could be also adverse for the development of molluscs. Malacofauna determined for the sections of drillings in the area of the Starunia mine are poor, but evidently diversified. The mollusc group considered to be the oldest one was identified in samples taken from boreholes Nos 4 and 43 (Fig. 1). It is typical for boggy habitats with periodically retained small water pools (Fig. 7MSI). The discussed fauna corresponds to an association described by Rogala (1907) in Gvizd village. The malacocoenoses, similar when considering their structure and species composition, were described from numerous sites in the whole of Middle and Northern Europe, including sediments dated with the ¹⁴C method (Ložek, 1964; S. W. Alexandrowicz, 1987; Limondin-Lozouet, 1992; Krolopp & Sümegi, 1993; S. W. Alexandrowicz & W. P. Alexandrowicz, 1995a, b; W. P. Alexandrowicz, 1997, 1999, 2004, and many others). They are considered to be indicative groups, typical for the Late Glacial. The coexistence of *Vertigo genesii* (Gred.) and *Vertigo geyeri* Lindh. is characteristic for the Younger Dryas (S. W. Alexandrowicz, 1987; Limondin-Lozouet, 1992; W. P. Alexandrowicz, 1997, 2004). Therefore, the discussed fauna is probably associated with this cold phase of the Late Glacial.

Holocene

The Holocene sediments were documented in several zones in all analysed sections: upper part of Star 4'/V, Star 4'/VI-VII, upper part of Star 22/V, Star 22/VI, upper part of Star VL-1/III, Star VL-1/IV-V, and Star VL-3/I-IV (Figs 2, 3A, 3B, 4).

In the VL-3 section, of Late Holocene age (as indicated by the date of 1,275±30 years BP as well as by the lack of cool climate indicators), the plants growing in the shore area of the water pool are very well represented, particularly in the Star VL-3/I and VL-3/II zones (Fig. 4). Apart from Alisma plantago-aquatica/lanceolata, there also grew Polygonum hydropiper, Sparganium neglectum, and Carex pseudocyperus. The presence of these taxa indicates a constant inundation of the area or the existence of a shallow water pool, which was gradually shallowing and eventually disappeared, as confirmed by the appearance of Scirpus sylvaticus, Carex cf. divulsa, Ranunculus cf. repens, and Juncus sp. Towards the top of the VL-3 section, the content of diaspores of plants with lower humidity requirements increases. In the sediments of that period the diaspores of Sambucus sp., Plantago media (Fig. 6L), and Taraxacum officinale, not recorded so far, were found.

The Holocene sediments of sections 4' and 22 contained a few plant macrofossils, also indicating the existence of a shallow, periodically drying up water basin, with a developed belt of swamp communities and peat bogs. The youngest malacocoenosis comes from the top of the section of borehole No. 22. The fauna found here contains mainly species preferring open land habitats, similar to those observed at present (Fig. 7MSI). This group can be associated with the Late Holocene. Such an age interpretation is confirmed by the group structure, composition and location in the section. This youngest phase, corresponding to the historical period, is probably associated with the fauna described by Łomnicki (1908).

The molluse group identified in sections of boreholes Nos 5 and 14 does not contain cold-adapted components and is characterized by a very high participation of species occurring in shallow and episodic water pools (Fig. 7MSI). It represents a climatic phase falling in the Holocene. However, because of the lack of indicator species, radiocarbon datings and palynological data, determination of a more precise stratigraphical range of the discussed group is impossible.

An analysis of tri-component diagrams allows for a description of the changes in mollusc fauna and natural environment in the area of the Starunia mine in the Late Glacial and Holocene. Diagram E (Fig. 7TD-E) presents changes in the character of habitats. In the Late Glacial, open and boggy biotopes of a tundra type dominated. This period is associated with the findings of large mammal fauna (S. W. Alexandrowicz, 2004). In the Holocene, in the area of Starunia mine, a shallow, periodically drying and disappearing water pool developed. Because of poor malacological material, the reconstruction of its range, development and time of occurrence was impossible. The disappearance of the above mentioned pool and the development of relatively dry, open land habitats is associated with the Late Holocene. Diagram NE (Fig. 7TD-NE) illustrates the groups' thermal tolerance. Faunas of the Late Glacial contain only those species, which at present occur to the north of the polar circle. With the climate warming, the more important were forms with higher temperature requirements. The presence of thermophylous species, such as Helix pomatia (L.) and Helix lutescens Rossm., was recorded only by Łomnicki (1908) in a fauna occurring here probably in the 19th century. Diagram ZG presents changes in the groups' zoogeographic structure. Groups associated with the Late Glacial are characterized by a considerable participation of North-European taxa and cold-adapted boreal-alpine forms. The Holocene faunas are composed only of species with broad geographic ranges (Fig. 7TD-ZG).

CONCLUSIONS

The results of palaeobotanical and malacological studies in the Starunia area indicate that:

1. the lack of tree remains in the Middle Pleniglacial flora indicates dominance of open woodless communities. Undoubtedly, the landscape was dominated by tundra communities with *Betula nana* and steppe communities, marking their presence with the occurrence of various grass and sedge species;

2. the zone of sediments containing *Betula nana* remains is widely spread throughout the study area. It was found in three sections (4', 22 and VL-1) located far from each other. However, only in borehole No. 22 the zone with *Betula nana* can be classified to the Middle Pleniglacial. In both borehole No. 4' and outcrop VL-1, the zone belongs to the Late Weichselian;

3. the tolerance range of species being cool climate indicators shows that the minimum July temperature in the Velyky Lukavets River valley in the Middle Pleniglacial fluctuated between 7 and 10°C;

4. a characteristic feature of the Starunia flora is very poor frequency of aquatic plant taxa. The reason for such a condition could be the constant and quite high water salinity, as well as contamination by petroleum penetrating from the Miocene strata in the bedrock, or an adverse climate, particularly in the Pleistocene;

5. from the Middle Pleniglacial up to the present day, the area has been characterized by the presence of species tolerating an increased amount of NaCl in the environment, such as: *Zannichellia palustris, Triglochin maritimum, Schoenoplectus tabernaemontani, Puccinellia distans*, and *Eleocharis palustris.* Their occurrence should be associated with natural effluences of brines, deriving from Miocene strata in the bedrock;

6. the malacofauna identified in borehole logs drilled in the area of Starunia mine is poor, but evidently diversified. Three significantly different types of groups can be distinguished here. Particular types are characterized by both different habitats and climatic conditions, what indicates that they are of different ages;

7. the sequence of mollusc groups is quite typical for the entire Middle Europe. Evolution of habitats, beginning with the Late Glacial humid tundra, through the Holocene lacustrine phase, ends with the Late Holocene open and dry biotopes.

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REFERENCES

- Alexandrowicz, S. W., 1987. Malacological analysis in Quaternary research. (In Polish, English summary). *Kwartalnik AGH, Geologia*, 12 (1-2): 3–240.
- Alexandrowicz, S. W., 2003. Krytyczny przegląd malakofauny z wykopalisk w Staruni. (In Polish). Prace Komisji Paleogeografii Czwartorzędu Polskiej Akademii Umiejętności, 1: 159–162.
- Alexandrowicz, S. W., 2004. Starunia and the Quaternary research in the tradition and initiatives of the Polish Academy of Arts and Science. (In Polish, English summary). *Studia i materiały do dziejów Polskiej Akademii Umiejętności*, 3: 5–261.
- Alexandrowicz, S. W. & Alexandrowicz, W. P., 1995a. Molluscan fauna of the Upper Vistulian and Early Holocene sediments of South Poland. *Biuletyn Peryglacjalny*, 34: 5–19.
- Alexandrowicz, S. W. & Alexandrowicz, W. P., 1995b. Quaternary molluscan assemblages of the Polish Carpathians. *Studia Geomorphologica Carpatho-Balcanica*, 29: 41–54.
- Alexandrowicz, S. W., Alexandrowicz, W. P. & Krapiec, M., 2005. Holocene terrace of the Velyky Lukavets River in Starunia: sediments and dendrochronology. In: Kotarba, M. J. (ed.), *Polish and Ukrainian geological studies (2004–2005) at Starunia the area of discoveries of woolly rhinoceroses.* Polish Geological Institute and Society of Research on Environmental Changes "Geosphere", Warszawa–Kraków: 95–102.
- Alexandrowicz, W. P., 1997. Malacofauna of Quaternary deposits and environmental changes of the Podhale Basin during the Late Vistulian and Holocene. (In Polish, English summary). *Folia Quaternaria*, 68: 7–132.

Alexandrowicz, W. P., 1999. Evolution of the malacological as-

semblages in North Poland during the Late Glacial and Early Holocene. *Folia Quaternaria*, 70: 39–69.

- Alexandrowicz, W. P., 2004. Molluscan assemblages of Late Glacial and Holocene calcareous tufa in Southern Poland. *Folia Quaternaria*, 75: 3–309.
- Bayger, J. A., Hoyer, H., Kiernik, E., Kulczyński, W., Łomnicki, A. M., Łomnicki, J., Mierzejewski, W., Niezabitowski, W., Raciborski, M., Szafer, W. & Schille, F., 1914. *Wykopaliska Staruńskie*. (In Polish). Muzeum im. Dzieduszyckich, Lwów, 15, 386 pp.
- Beijerinck, W., 1947. Zadenatlas der Nederlandische flora. H. Veenman & Zonen, Wageningen, 316 pp.
- Berggren, G., 1969. Atlas of seeds and small fruits of Northwest-European plant species with morphological descriptions. Part 2. Cyperaceae. Swedish Natural Science Research Council, Stockholm, 66 pp.
- Brinkkemper, O., Van Geel, B. & Wiegers, J., 1987. Palaeoecological study of a Middle Pleniglacial deposits from Tilligte, The Netherlands. *Review of Palaeobotany and Palynology*, 51: 235–269.
- Davy, A.J. & Bishop, G.F., 1991. Biological Flora of the British Isles. *Triglochin maritima* L. (*Triglochin maritimum* L.). *Journal of Ecology*, 79: 531–555.
- Gams, H., 1934. Die Moose von Starunia als Vegetations und Klimazeugen. *Starunia*, 2: 1–6.
- Granoszewski, W., 2002. Macroscopic plant remains associated with excavations of mammoth and wooly rhinoceros at Starunia (Ukraine) in 1907 and 1929. (In Polish, English summary). *Wiadomości Botaniczne*, 46 (3/4): 29–34.
- Huijzer, B. & Vandenberghe, J., 1998. Climatic reconstruction of the Weischelian Pleniglacial in northwestern and central Europe. *Journal of Quaternary Science*, 13: 391–417.
- Kats, N. Ya., Kats, S. V. & Kipiani, M. G., 1965. Atlas i opredelitel' plodov i semyan vstrechayushchikhsya v chetviertichnykh otlozheniyach SSSR. (In Russian). Izdat. Nauka, Moskva, 367 pp.
- Kerney, M. P., Cameron, R.A. & Jungbluth, J., 1983. Die Landschnecken Nord - und Mitteleuropas. Paul Parey, Hamburg, Germany, 384 pp.
- Kolstrup, E., 1980. Climate and stratigraphy in northwestern Europe between 30,000 BP and 13,000 BP, with special reference to the Netherlands. *Mededelingen Rijks Geologische Dienst*, 32/15: 181–253.
- Koltun, Y. V., Dudok, I. V., Kotarba, M. J., Adamenko, O. M., Pavluk, M. I., Burzewski, W. & Stelmakh, O. R., 2005. Geological setting and petroleum occurrence of the Starunia area, fore-Carpathian region, Ukraine. In: Kotarba, M. J. (ed.), Polish and Ukrainian geological studies (2004–2005) at Starunia – the area of discoveries of woolly rhinoceroses. Polish Geological Institute and Society of Research on Environmental Changes "Geosphere", Warszawa–Kraków: 61–77.
- Korin, S. S., 2005. Miocene salt-bearing Vorotyshcha Beds in the Starunia area, fore-Carpathian region, Ukraine. In: Kotarba, M. J. (ed.), *Polish and Ukrainian geological studies (2004– 2005) at Starunia – the area of discoveries of woolly rhinoceroses*. Polish Geological Institute and Society of Research on Environmental Changes "Geosphere", Warszawa– Kraków: 79–86.
- Kotarba, M. J., 2005. Interdisciplinary Polish and Ukrainian studies on the Starunia extinct fauna site in the years 2004–2005. In: Kotarba, M. J. (ed.), Polish and Ukrainian geological studies (2004–2005) at Starunia – the area of discoveries of woolly rhinoceroses. Polish Geological Institute and Society of Research on Environmental Changes "Geosphere", Warszawa–Kraków, pp. 9–20.

- Kotarba, M. J., 2009. Interdisciplinary studies at Starunia palaeontological site and vicinity (Carpathian region, Ukraine) in the years 2006–2009: previous discoveries and research, purposes, results and perspectives. *Annales Societatis Geologorum Poloniae*, 79: 219–241.
- Kozłowski, S., Goliński, P., Zielewicz, W., Lembicz, M. & Rogowski, A., 2004. Changes in the chemical composition of spreading meadow-grass (*Puccinellia distans* L. Parl.) against the influence of salinity as anthropogenical factor. (In Polish, English summary). *Annales Universitatis Mariae Curie-Skłodowska, Lublin – Polonia*, 59, 4E: 1965–1976.
- Kravchuk, Y. S., 1999. Geomorfologija Peredkarpattia. (In Ukrainian). Merkator, Lviv, 188 pp.
- Krolopp, E. & Sümegi, P., 1993. Vertigo modesta (Say), Vertigo geyeri Lindholm 1925 and Vertigo genesii (Gredler 1856) species in Pleistocene formations of Hungary. Malacological Newsletter, 12: 9–14.
- Kubiak, H., 1971. Datowanie radiowęglem ¹⁴C szczątków nosorożca włochatego ze Staruni. (In Polish). Wszechświat, 10: 267–268.
- Kuc, T., Różański, K., Goslar, T., Kubiak, H. & Kotarba, M. J., 2005. Radiocarbon dating of remnants of woolly rhinoceroses and mammoth from Starunia, fore-Carpathian region, Ukraine. In: Kotarba, M. J. (ed.), *Polish and Ukrainian geological studies (2004–2005) at Starunia – the area of discoveries of woolly rhinoceroses.* Polish Geological Institute and Society of Research on Environmental Changes "Geosphere", Warszawa–Kraków: 195–203.
- Kuc, T., Różański, K., Goslar, T. & Stachowicz-Rybka, R., 2009. Radiocarbon dating of plant remnants in Quaternary sediments at Starunia palaeontological site and vicinity (Carpathian region, Ukraine). *Annales Societatis Geologorum Poloniae*, 79: 289–296.
- Kucowa, I., 1954. Krytyczny przegląd gatunków wierzb (Salix L.) z osadów glacjalnych Polski. (In Polish). Acta Societatis Botanicorum Poloniae, 23 (4): 807–837.
- Lambracht, E., Westberg, E. & Kadereit, J. W., 2007. Phylogeographic evidence for the postglacial colonization of the North and Baltic Sea coasts from inland glacial refugia by *Triglochin maritima* L. *Flora*, 202: 79–88.
- Limondin-Lozouet, N., 1992. Biogéographie Holocène de Vertiginidae (Mollusca – Gastropoda) Européens: relations la dernière deglaciation. Compte Rendus de Academie des Science de Paris, 315, 2: 1281–1287.
- Looman, J., 1976. Biological flora of the Canadian Prairie Provinces IV. *Triglochin* L., the genus. *Canadian Journal of Plant Science*, 56: 725–732.
- Ložek, V., 1964. Quartärmollusken der Tschechoslovakei. *Rozpravy Ústředniho Ústavu Geologického*, 31: 3–374.
- Ložek, V. & Thoste, V., 1972. Eine Spätglaziale Molluskenfauna aus dem Bereich der Niederterasse südlich von Köln. *Decheniana*, 125: 55–61.
- Ławrynowicz, M., 1983. Cenococcum graniformae in Poland. (In Polish, English summary). Acta Mycologica, 19 (1): 31–40.
- Łomnicki, A. M., 1908. Die Mollusken im pleistozänen Thon des Mammuthschachtes in Starunia. (In Polish, German summary). Kosmos, 33: 73–76.
- Łomnicki, M., 1914. Wykrycie mamuta i nosorożca dyluwialnego. (In Polish). Wykopaliska Staruńskie. Muzeum im. Dzieduszyckich we Lwowie, 15: 1–8.
- Mamakowa, K., 1997. Compiling, entering and processing of Polish data relating to the last interglacial. Scientific report no 2. Unpublished report, Archive of the W. Szafer Institute of Botany Polish Academy of Sciences, Kraków, 15 ms. pp.

Mamakowa, K. & Starkel, L., 1974. New data about the profile of

Young Quaternary deposits at Brzeźnica on the Wisłoka river, the Carpathian Foreland. *Studia Geomorphologica Carpatho-Balcanica*, 8: 47–53.

- Mamakowa, K. & Wójcik, A., 1987. Osady organiczne środkowego Vistulianu w Jaśle-Bryłach (dolina Wisłoki). (In Polish). Kwartalnik Geologiczny, 31: 213–214.
- Matuszkiewicz, W., 2001. Przewodnik do oznaczania zbiorowisk roślinnych Polski. (In Polish). Wydawnictwo Naukowe PWN, Warszawa, 537 pp.
- Mirek, Z., Piękoś-Mirkowa, H., Zając, A. & Zając, M., 2002. Flowering plants and Pteridophytes of Poland. A checklist. (In Polish, English summary). W. Szafer Institute of Botany Polish Academy of Sciences, Kraków, 442 pp.
- Mitura, F., 1944. *Geologia złoża wosku w Staruni*. (In Polish). Unpublished report, Archive of the Jagiellonian University, Kraków, 18 ms. pp.
- Mościcki, W. J., Toboła, T. & Zarzyka-Ryszka, M., 2009. Salinity of Quaternary sediments and halophytes at Starunia palaeontological site and vicinity (Carpathian region, Ukraine). *Annales Societatis Geologorum Poloniae*, 79: 391–402.
- Nalepka, D. & Walanus, A., 2003. Data processing in pollen analysis. Acta Palaeobotanica, 43(1): 125–134.
- Nilsson, O. & Hjelmquist, H., 1967. Studies on the nutlet structure of South Scandinavian Species of *Carex. Botaniska Notiser*, 120: 460–485.
- Nowak, J. & Panow, E., 1930. The geological conditions of the Starunia excavations. In: Nowak, J., Panow, E., Tokarski, J., Szfer, W. & Stach, J. (eds), The second wolly rhinoceros (Coelodonta antiquitatis Blum.) from Starunia, Poland. Bulletin Internationale de l' Académie Polonaise des Sciences et des Lettres de Cracovie, Ser. B, Cracovie: 1–7.
- Raciborski, M., 1914a. Roślinność szybu mamutowego w Staruni. (In Polish). In: Bayger, J.A., Hoyer, H., Kiernik, E., Kulczyński, W, Łomnicki, A. M., Łomnicki, J., Mierzejewski, W., Niezabitowski, W., Raciborski, M., Szafer, W. & Schille, F. (eds), Wykopaliska Staruńskie. Muzeum im. Dzieduszyckich, Lwów, 15: 27–29.
- Raciborski, M., 1914b. Liście i owoce mamutowego szybu w Staruni. (In Polish). In: Bayger, J.A., Hoyer, H., Kiernik, E., Kulczyński, W, Łomnicki, A. M., Łomnicki, J., Mierzejewski, W., Niezabitowski, W., Raciborski, M., Szafer, W. & Schille, F. (eds), *Wykopaliska Staruńskie*. Muzeum im. Dzieduszyckich, Lwów, 15: 30–33.
- Rogala, W., 1907. Przyczynek do znajomości dyluwialnych utworów Galicyi. (In Polish). Kosmos, 32: 350–363.
- Sokołowski, T. & Stachowicz-Rybka, R., 2009. Chronostratigraphy and changes of environment of Late Pleistocene and Holocene at Starunia palaeontological site and vicinity (Carpathian region, Ukraine). *Annales Societatis Geologorum Poloniae*, 79: 315–331.
- Sokołowski, T., Stachowicz-Rybka, R. & Woronko, B., 2009. Upper Pleistocene and Holocene deposits at Starunia palaeontological site and vicinity (Carpathian region, Ukraine). *Annales Societatis Geologorum Poloniae*, 79: 255–278.
- Sparks, B. W., 1969. Nominarie molluscan in archaeology. Science in Archaeology, 33: 395–406.
- Stachowicz-Rybka, R., 2005. Reconstruction of climate and environment in the Augustovian Interglacial on the basis of select plant macrofossil taxa. *Special Papers, Polish Geological Institute*, 16: 127–132.
- Stachowicz-Rybka, R., Granoszewski, W. & Hrynowiecka-Czmielewska, A., 2009. Quaternary environmental changes at Starunia palaeontological site and vicinity (Carpathian region, Ukraine) based on palaeobotanical studies. *Annales Societatis Geologorum Poloniae*, 79: 279–288.

- Szafer, W., 1914. Anatomiczny rozbiór drzew i krzewów mamutowego szybu w Staruni. (In Polish). In: Bayger, J. A., Hoyer, H., Kiernik, E., Kulczyński, W, Łomnicki, M., Łomnicki, J., Mierzejewski, W., Niezabitowski, W., Raciborski, M., Szafer, W. & Schille, F. (eds), Wykopaliska Staruńskie. Muzeum im. Dzieduszyckich, Lwów: 34–36.
- Szafer, W., 1930. Flora tundry staruńskiej. (In Polish). Rozprawy Wydziału Matematyczno-Przyrodniczego PAU, 70B: 20–28.
- Szafran, B., 1934. Mchy dyluwium w Staruni. (In Polish). *Starunia*, 1: 1–18.
- Velichkevich, F. Yu. & Zastawniak, E., 2006. Atlas of the Pleistocene vascular plant macrofossils of Central and Eastern Europe, Part 1 – Pteridophytes and monocotyledons. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 224 pp.
- Velichkevich, F. Yu. & Zastawniak, E., 2008. Atlas of the Pleistocene vascular plant macrofossils of Central and Eastern Europe, Part 2 – Herbaceous dicotyledons. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 379 pp.
- Walanus, A. & Nalepka, D., 1999. POLPAL Program for counting pollen grains, diagrams plotting and numerical analysis. *Acta Palaeobotanica, Suplement*, 2: 659–661.