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## LATE GLACIAL AND HOLOCENE ENVIRONMENTAL CHANGES AT OSŁONKI, CENTRAL POLAND

## SCULPTURE OF ELYTRA IN SPECIES FROM FAMILY DYTISCIDAE (INSECTA: COLEOPTERA)

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## FOREWORD

Dorota Nalepka

The Kujawy region (Central Poland) has been excavated and investigated by archaeologists since the early 1930s. The south region of Kujawy, near Brześć Kujawski, has been intensively archaeologically explored since the same time (Jażdżewski 1938, Grygiel 2004). As this region has been intensively used for agriculture due to its fertile soils since the early Neolithic time, it is of great interest (Jażdżewski 1938, Grygiel 1986, 2004, Grygiel and Bogucki 1997).

The nature researchers, biologists (palaeobotanists) and geomorphologists were invited to this region in the 1980s. The palaeobotanists searched biogenic sediments containing micro- and macrofossil plant macroremains, which bring adequate information of vegetation cover in the past. The main interest was the influence of Neolithic farmers on the changes of vegetation and the question of its scale – local or regional, and the question how deep changes they provoked. Moreover, it is important how they used plants in their economy: which plants they cultivated, which ones they used from the wild vegetation and how they managed to keep animals. The geologists and geomorphologists looked for the evidences of environmental abiotic changes in the past. Finally, the positive results were found not far west from Brześć Kujawski, in the Osłonki region by the nature researchers. The multi-proxy studies included several disciplines. Only chosen results of four investigated environmental disciplines are presented in this volume (geomorphology by B. Nowaczyk, palynology by D. Nalepka, cladocerans by M. Gąsiorowski, and molluscs by S. W. Alexandrowicz).

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# CHANGES IN NATURAL ENVIRONMENT IN THE VICINITY OF OSŁONKI (KUJAWY, CENTRAL POLAND) IN THE LIGHT OF GEOLOGICAL AND GEOMORPHOLOGICAL INVESTIGATIONS

Bolesław Nowaczyk

Abstract. Geomorphological and geological studies in the vicinity of a Neolithic stronghold at Osłonki in Kujawy region revealed such landforms as ground moraine, glacial trough, and biogenic plains. They were formed under the impact of direct accumulation of an ice-sheet, its meltwater, and biogenic accumulation. Detailed analyses of the relief and deposits using palaeobiological studies made it possible to reconstruct relief development and environmental changes in the Pleni-Vistulian, Late Vistulian and Holocene. The landscape from the times when prehistoric man occupied this area is presented.

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## INTRODUCTION

Very intensive archaeological investigations in the vicinity of Brześć Kujawski have been carried out for many decades. The history of these investigations has recently been discussed in detail by Grygiel (2004) in a very extensive monograph. From the beginning of the 1970s, Grygiel has been investigating the relics found in Brześć Kujawski (Grygiel 1976). When in the 1990s he expanded the area of his investigations, he found a defensive Neolithic settlement at Osłonki, about 7 km north-west of Brześć Kujawski (Grygiel and Bogucki 1994). As a result of further penetration of the areas adjacent to Osłonki new sites were discovered, namely at Miechowice and Konary. The settlement was then the object of detailed modern excavation work, carried out on a very extensive area.

In addition to excavation work, analyses of selected elements of the natural environment in the area very close to the archaeological sites were made at the initiative of Ryszard Grygiel by an interdisciplinary team of research workers. The analyses were aimed, first of all, at the reconstruction of the living conditions of a pre-historic man. Reconstruction work included attempts at explaining what happened earlier and what happened later, until historical times.

The interdisciplinary investigations comprised lithology and palaeobiological geomorphology, and plant macrofossil study, as well as malacological and cladoceran analysis and radiocarbon datings of organic remains found in Neolithic settlements and biogenic deposits in water bodies in their vicinity. Most of the results of these investigations have been published and reported; some remain to be published (Alexandrowicz 2005, Bieniek 1999, 2005, Gąsiorowski 2005, Gąsiorowski and Nalepka 2002–2003, Leszczyńska 2000, Nalepka 1999, 2002–2003, 2005a, b, Nalepka *et al.* 1998, Nowaczyk 1996, 2005, Nowaczyk *et al.* 2002).

Detailed geological and geomorphological investigations of the area of Osłonki started in 1993 and were carried out for a few seasons, in the settlements (when the latter were left by the archaeologists) and on the plains of biogenic accumulation and ground moraine in their direct vicinity.

## LOCATION OF THE SITE AND MORPHOLOGY OF THE AREA AROUND OSŁONKI

The area of detailed investigations is located within the Kujawy Upland in the Inowrocław Plain (Krygowski 1961). It was fully covered by the Baltic (Vistulian, Weichselian) ice-sheet, the last of the glaciations (Fig 1A). It is bordered by the Bachorza River Valley in the north and in the south by a series of terminal moraines, which belong to the Radziejów oscillation. In the east, it is bordered by the Zgłowiączka River Valley and a transformed glacial trough, which links these two valleys, and in the west by the glacial trough of Gopło Lake. On Galon's map (1953), these extensive areas are nothing else but flat and wavy moraine plains (Fig. 1B), which include depressions, usually oval, extending from north-west to south-east, arranged perpendicularly to the face of the Vistulian continental glacier of the Leszno or Poznań phase. In the southern part of the area there occur ridges and hillocks of the terminal moraine, which Murawski (1957) called the Radziejów oscillation.

Archaeological sites are located on the flat terminal moraine, situated some 2.5 km south-west of the Bachorza River Valley and some 2 km west of the Zgłowiączka River Valley, and the transformed glacial trough, which joins these two valleys near Brześć Kujawski (Fig. 2). The ground moraine plain is at an altitude of some 90 m above sea level and the denivelations within its area range 86–94 m above sea level. The ground moraine plain features fairly steep slopes, which end at the bottoms of the valleys and the transformed glacial trough. The difference in height is about 15 m.

In the ground moraine plain a few depressions occur, usually oval in shape, with areas up to a few hectares large. They are arranged in a sequence marked on Galon's map (1953) (Fig. 1B) and Nowaczyk's map (1996) (Fig. 2), extending from north-west to south-east, over a distance of some 21 km, from Żakowo, via Osłonki, to Kuczyna. Within this sequence low elevations, which separate individual depressions, can be seen. In the past there was no surface outflow from the entire area; today the area is covered by channel system deposits. Genetically, it can be treated as a glacial trough, with rather obscure shapes. This classification of the form has been corroborated by Niewiarowski (1983). Wiśniewski and Molewski (1994), on the other hand, claim that this form came into being when the ice under the moraine cover, separated from the edge of the receding continental glacier, melted. In the western part of Miechowice-Parcele, a short erosion-denudation parallel valley, ending in the transformed glacial trough joining the

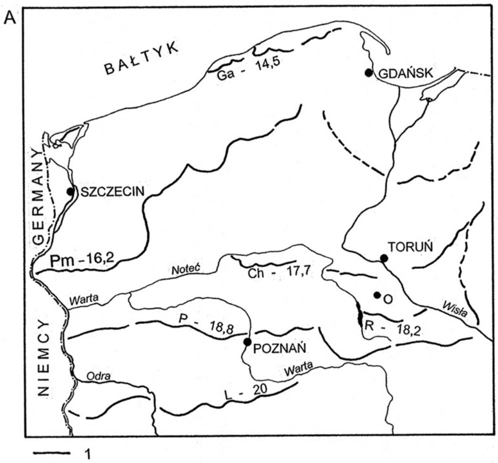

Fig. 1A. Phases of Vistulian glaciation after Kozarski (1995), modified:

1 – ranges of individual phases, subphases and oscillations, L – Leszno phase, P – Poznań phase, Pm – Pomeranian phase, Ga – Gardno phase, Ch – Chodzież (Kujawy) subphase, R – Radziejów oscillation, O – Osłonki

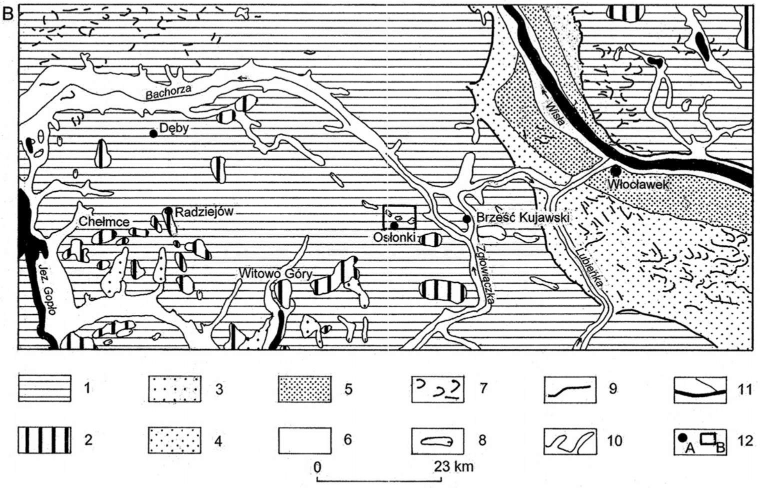

Fig. 1B. Geomorphological map of the Inowrocław Plain and the Vistula River Valley near Włocławek (after Galon and Roszkówna, in: Galon 1953): 1 – flat ground moraine, 2 – hills and moraine ridges, 3 – outwash plain, 4 – higher terrace, 5 – lower terrace, 6 – valley bottoms, 7 – dunes, 8 – depressions without outflow, 9 – edges of the Vistula River Valley, 10 – erosion-denudation valleys, 11 – hydrographic network, 12 – A – towns, B – area of investigation

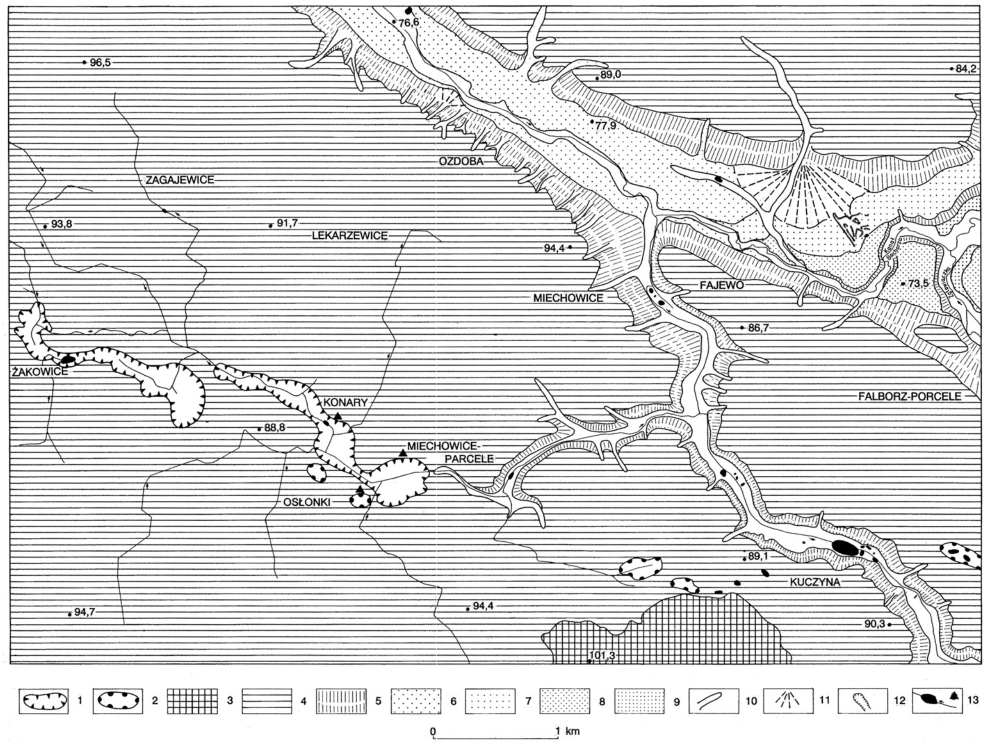

Fig. 2. Geomorphological map of the Osłonki area (Nowaczyk 1996):

1 – glacial troughs, 2 – melt-out depression after blocks of buried ice, 3 – terminal moraines of the Radziejów Oscillation, 4 – flat ground moraine, 5 – slopes of valleys and transformed glacial troughs, 6 – river terrace 79–80 m above sea level, 7 – terrace 75–77 m above sea level, 8 – terrace 72–74 m above sea level, 9 – erosion terrace 66–70 m above sea level, 10 – floors of river valleys and erosion-denudation, small valleys and rivers, 11 – alluvial fans, 12 – anthropogenic landforms, 13 – hydrographic network

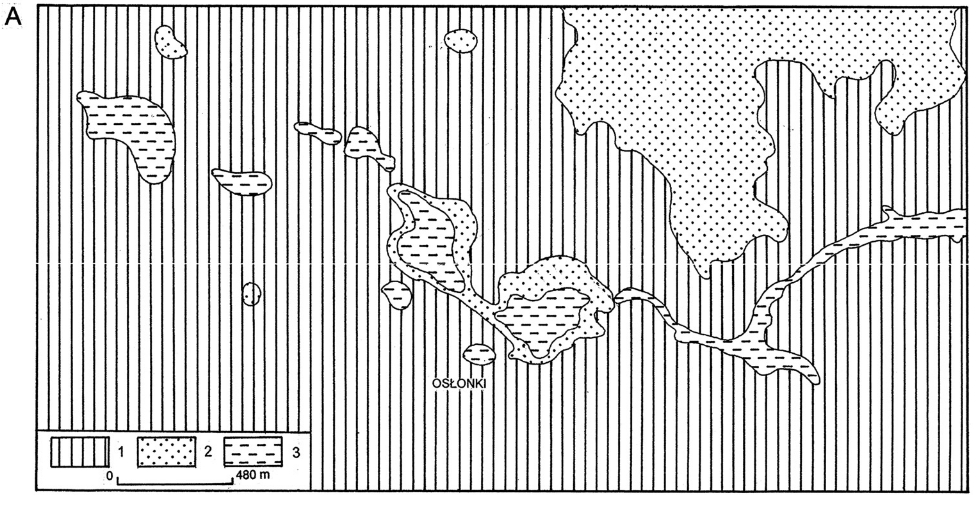

Fig. 3A. Geological map of the area near Osłonki after Leszczyńska (2000); modified by the author: 1 – moraine till, 2 – ablation sands on moraine till, 3 – biogenic deposits (peats, loams, gyttja, organic silts)

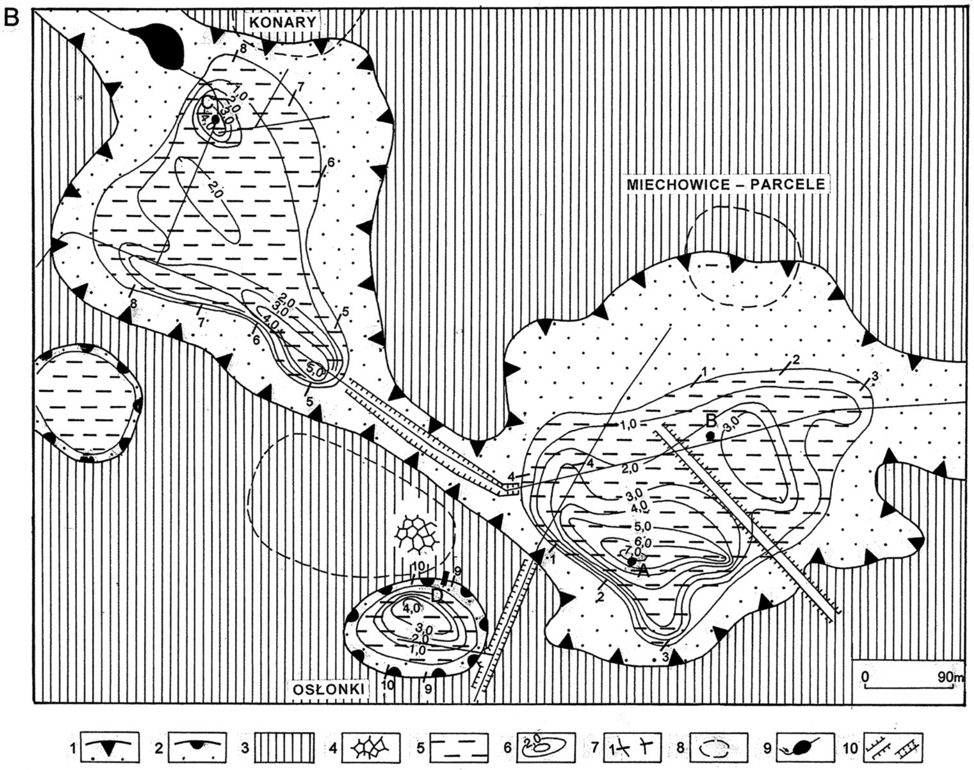

Fig. 3B. Geomorphological-lithological map and thicknesses of biogenic deposits of the area neighbouring the archaeological sites at Osłonki, Miechowice and Konary: 1 – glacial trough – ablation sands on the trough, 2 – melt-out depressions after blocks of buried ice, 3 – flat ground moraine – moraine till, 4 – polygons of frost fissures, 5 – plains of biogenic accumulation – peats, gyttja, organic silts, 6 – lines joining places with the same thickness of biogenic deposits, 7 – lines of geological sections, 8 – approximate range of Neolithic settlements, 9 – hydrographic network, 10 – contemporary anthropogenic landforms (embankments and cuttings). Circles indicate the places where profiles for palaeobiological investigations and physical-chemical analyses were taken: A-Os 94-9, B-Os 16, C-Os 57, D-Os 94-5

valleys of Bachorza and Zgłowiączka, is found. We can assume that this valley developed on the glacial trough.

Three of the depressions mentioned above are found in the direct neighbourhood of the sloping troughs of the Neolithic settlement at Osłonki and the archaeological remains at Miechowice and Konary (Fig. 3B). They are clearly visible in the relief. They are sloping and their flat bottoms are from 1.5 to 3.5 m below the surface of the ground moraine, where the archaeological sites were located (Figs. 4 and 5). The smallest depression is located south of the defensive settlement in Osłonki. The morphological axis of this form is from west to east, and the length of the bottom is some 130 m. North-west of the settlement there is another, irregularly shaped, depression. Its bottom in the western part is some 300 m wide, while in the eastern part it is only 80 m wide. The longer axis is 380 m long. The last of the forms under analysis is located north-east of the defensive settlement. It is oval in shape, and its longer axis extends from south-west to

Fig. 4. Osłonki. In the foreground large-area archaeological cuttings, in the background a biogenic accumulation plain in a depression situated north-east of the stronghold (locality 1 after Grygiel 2004; photo by B. Nowaczyk)

Fig. 5. Konary: a view of large-area archaeological cuttings and the biogenic accumulation plain in a depression situated north-east of locality 1 at Osłonki. Readily discernible is the southern scarp of the glacial trough (photo by B. Nowaczyk)

north-east over a distance of some 380 m. Its maximum width is 250 m. Both the latter depressions are separated by an elevation. Today, it is crossed by a drainage ditch.

## AIM AND METHODS

There were a few aims of the geological and geomorphological investigations in the vicinity of Osłonki, which were part of interdisciplinary investigations: 1 – identification of the lithology under the Neolithic relics and in the adjacent areas; 2 – determination of the sequence and thickness of biogenic deposits which fill the depressions near the archaeological sites; 3 – identification of the forms of the relief and the processes that made them against the background of the relief of a larger area; 4 – determination of grain size and abrasion grade of quartz grains of clastic deposits, which were part of the area forms and frost structures; 5 – determination of physical and chemical features of biogenic deposits, and 6 – reconstruction of palaeogeographic events.

These aims were accomplished by the geological and geomorphological mapping methods. During the work, archaeological diggings and borings made in the biogenic accumulation plains (74) and ground moraine (19) were analysed in detail.*

In the first case, borings by the Instorf probe (cup ø – 5 cm) were made alongside the profile lines (Fig. 3B) (see also Fig. 1 in Nalepka in this volume), located perpendicularly to the morphological axis of the glacial trough and melt-out depression. The distances between the borings in the profile lines were 30 m on average. They were smaller only in the border zone. In the ground moraine the borings were made as recommended in the Instruction to the Detailed Geological Map of Poland (1996), i.e. 3 borings per kilometre in case of areas with a simple geological structure. Having probed the biogenic accumulation reservoirs, points were selected from which cores were sampled by means of the Instorf probe (cup ø – 8 cm) for palaeobiological, physical and chemical analyses (Fig. 3B). Two cores were taken from the deepest part of the eastern reservoir (Os 94-9), each 9 metres long. One of them was used to carry out the palynological analysis and the analysis of cladocerans. The other was divided into 10 cm sections (in a few cases the dimensions were different). These were used to carry out malacological analyses, analyses of $CaCO_3$ and organic substance content. Core Os 16 was taken from the same reservoir, located about 190 metres north of the one mentioned earlier (Fig. 3B). Apart from taking 1 $cm^3$ of material for palynological research, it was divided into 10 cm sections and used to carry out physical and chemical analyses. Analyses of $CaCO_3$ were made by the Scheibler method and organic content was determined by the sample calcination method at the temperature of 550°C.

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* Borings in the biogenic accumulation plains were made by the present author together with Dr. Dorota Nalepka. Borings in the ground moraine were made by I. Leszczyńska (M.Sc. Thesis, 2000), Institute of Geology, Adam Mickiewicz University, Poznań.

In the biogenic accumulation reservoir directly adjacent to the Neolithic defensive settlement in the south, in addition to the borings necessary to identify the type and thickness of the deposits, Nalepka (2002–2003, 2005b) made a 25 m long digging to the maximum depth of 4 metres. This helped to give a better insight into the sequence of deposits. Among the peats and gyttja, lenses and layers of clastic deposits were found. Samples were taken (19) to analyse the grain size and physical and chemical properties.

Samples of deposits were taken from the ice wedge, which contained primary mineral material, and from moraine till, in which they were found. These samples were taken from the diggings near cabin 14 and hollow 194 (Grygiel 2004). Till samples were also taken from the boring made in Konary (Fig. 3B). All these samples (60+19) were analysed with respect to grain size by the sieve and aerometric methods, and with respect to the abrasion grade of the quartz grains (fraction 1.0-0.8 mm) by the mechanical graniformametry method, using Krygowski's graniformameter (1964).

## DESCRIPTION OF DEPOSITS AND LITHOSTRATIGRAPHY

Analyses of sections in large area of archaeological diggings (Fig. 4 and 5) and many borings, as well as geological and geomorphological mapping prove that the area of ground moraine, where the archaeological relics in the vicinity of Osłonki, Miechowice and Konary are found and a considerable part of the adjacent area, is built of moraine till (Fig. 3A). Patches of ablation sands, about 1 m thick, resting on the moraine till are found in a few places only. The largest patch of these sands is found north of the site at Miechowice. The depressions found in the till are filled with biogenic deposits (Fig. 3B).

In the profiles of archaeological diggings sandy ablation till was identified, up to a few dozen centimetres thick, at the top. The soil humus layer was developed on this till. That layer extends all over the areas taken by the Neolithic settlements. Alongside the border of biogenic accumulation plains, under the humus layer, there are clayey ablation sands of different thickness. Under these deposits, in turn, there is dense, basal moraine till, brown in colour, with a thickness greater than 5 metres. Many pieces of Scandinavian rocks, each different in size, are found in the basal moraine till and the sandy ablation till. The rocks include granites, sandstones, limestones, quartzite, porphyry, gneiss, gabbro and others (Leszczyńska 2000). Some of these rocks are erratics with a very precisely defined place of origin in Scandinavia. These rocks were used by the Neolithic man to make tools.

In the moraine till, in a few places (Fig. 3B), near cabin 14 and hollow 194 (Grygiel 2004), polygons of frost fissures with primary mineral material occur (Fig. 6). They can be seen in aerial photographs in Grygiel's monograph (2004) – Fig. 38-1, 41, 42-1, 66-1,2. In the vertical cross-section they look like an ice wedge, and have a width of a few centimetres (Fig. 7). Analyses of the grain size of the deposits sampled from two

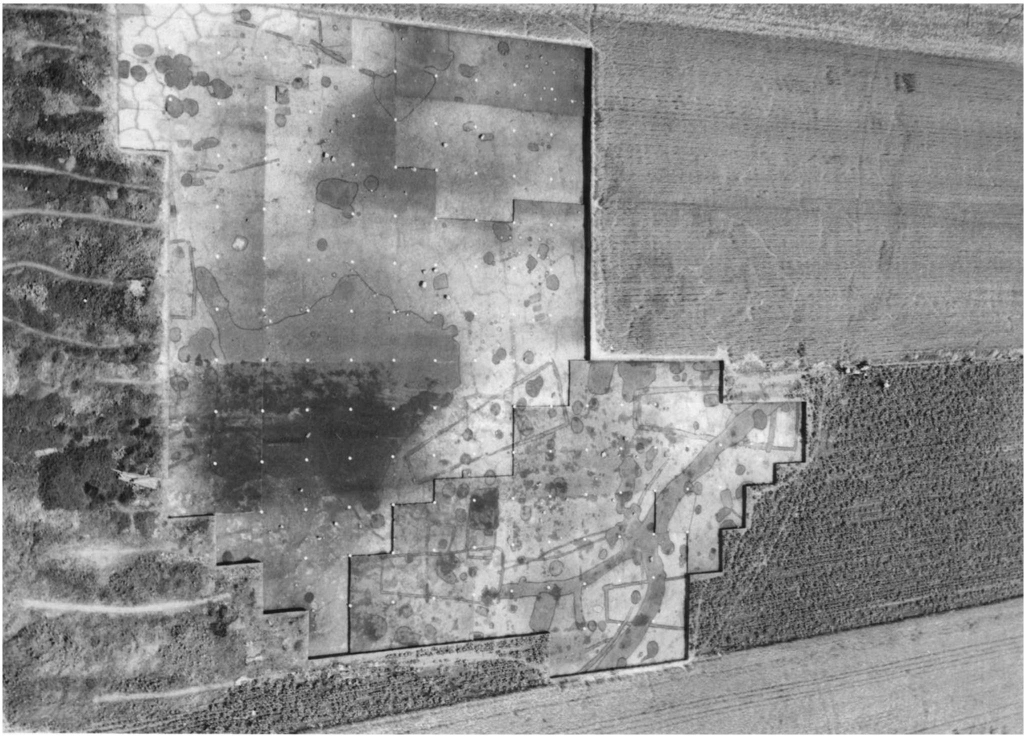

Fig. 6. Osłonki – locality 1. A cutting with clearly visible archaeological objects and frost wedge polygons (photo by R. Grygiel)

ice wedges have revealed that they are filled with medium-size sand and fine sand, with 0.25-0.16 and 0.16-0.1 mm fractions being dominant. The average diameter of Mz grain for these deposits (average of 10 samples) is 0.15 mm (0.08-0.20 mm) and the standard deviation (σ) is 1.80 (1.16-2.65). These deposits are poorly sorted. The ratios were calculated according to the equations suggested by Folk and Ward (1957). It is sand with those features, which Goździk (1970), Kozarski (1972), Nowaczyk (1972), Kasprzak (1996) and others ascribe to aeolian sands. This genesis is also corroborated by a percentage of well-rounded grains, type γ, which is higher than that in the moraine till. The moraine till adjacent to these forms features a smaller percentage of medium-grained and fine sands and a relatively large percentage (usually higher than 50%) of silt, clayey and colloidal fractions (Fig. 7). The till contains only a small amount of coarse-grained material. The average diameter of the grains for the 7 analysed samples of moraine till is 0.04 mm and that of the standard deviation – 2.95 (2.77-3.15). The moraine till is poorly sorted. Similar grain sizes and statistical ratios of grain size are found in the moraine till sampled at the Konary site (Leszczyńska 2000). The moraine till in all the samples under analysis contains some 10% of calcium carbonate. Its percentage is not different in the vertical section.

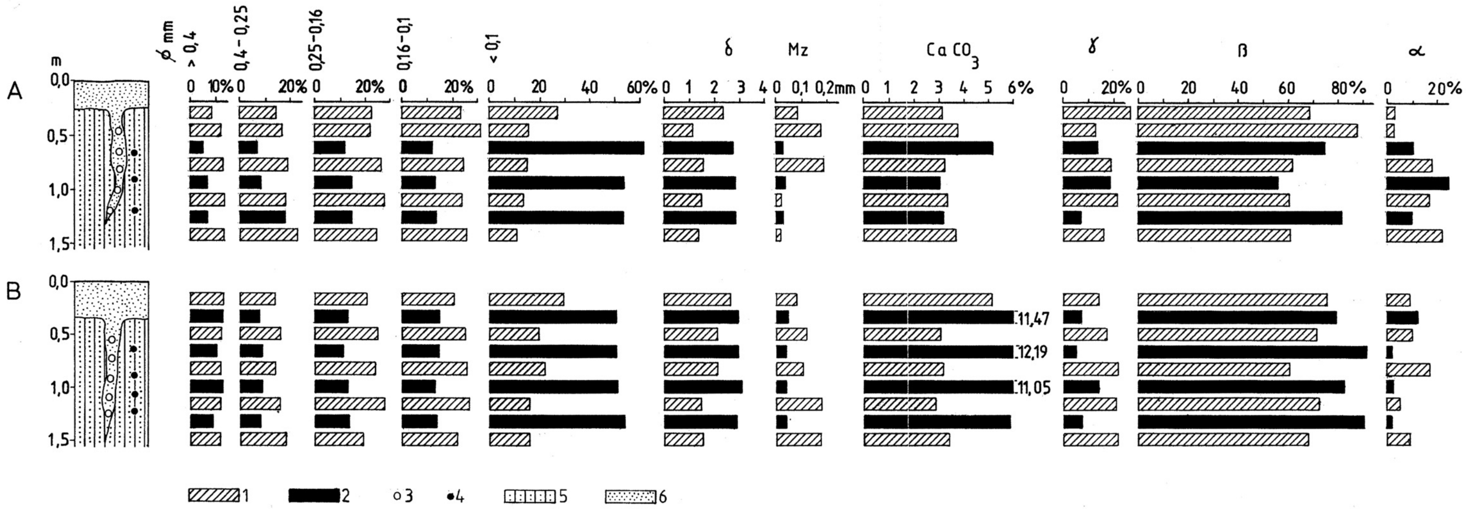

Fig. 7. Structures of frost wedges near cabin 14 (A) and hollow 194 (B) in Osłonki, histograms of grain size and statistical indices of grain size, content of $CaCO_3$ and the types of quartz grain dressing of sands filling the ice wedges and hollows and moraine till: 1 – sands filling the frost wedges, 2 – moraine till, 3 – places where samples from sands filling frost wedges were taken, 4 – places where samples from moraine till were taken, 5 – moraine till, 6 – ablation sands and sands filling frost wedges

The depressions in the ground moraine are filled with biogenic deposits – peat earth, peats, loams and organic clays, calcareous gyttja, detritus gyttja and bog lime. The analysis of borehole logs and geological sections (Fig. 8) showed that there is a thin layer (one centimetre or a few centimetres thick) of peat on a layer of the sands, loams, clays or moraine till of unknown thickness. It is fairly common in Polish (but not only Polish) reservoirs of biogenic sedimentation of glacial origin (Więckowski 1966, 1993, Nowaczyk 1976, 1994, Błaszkiewicz 1998, 2003, Molewski 1999, Wojciechowski 2000 and others). This layer is covered with calcareous gyttja or bog lime bearing malacofauna. Its thickness is from a few centimetres to a few metres. In many places, calcareous gyttja or bog lime is not underlain by a peat layer, but lies directly on the clastic deposits mentioned above. Detritus gyttja was found in a few boreholes. However, because of its small thickness and insular occurrence, it has not been marked on the geological sections. A layer of gyttja with a small percentage of calcium carbonate and a very small amount of malacofauna, having a very intense black-olive colour and being very much compressed, was found in some boreholes made in the reservoir north-east of the Neolithic settlement (Fig. 9A). It occurs in the bottom part of the sedimentation reservoir, under the light-coloured calcareous gyttja. In a few places, in the border littoral zones, in the top part of the calcareous gyttja or bog lime, the latter two are interspersed with sand. This suggests that there was some ablation on the slopes of the glacial trough. In the middle part of the depressions lenticular sandy interbeddings, 1–3 cm thick, are found. They are records of the aeolian processes taking place in winter in the vicinity of reservoirs of biogenic accumulation. Calcareous gyttja or bog lime in many places in the top part interfaces (Fig. 8) with one or two layers of peat, a few centimetres thick. Its presence suggests some change of hydrological conditions during its deposition. Most probably, the water level decreased then. On the calcareous gyttia occurs a layer of peat, which changes into peat earth, or a layer of peat earth only (Fig. 8). In these deposits, abundant malacofauna was found. The thickness of these deposits is not uniform – from a few centimetres to nearly two metres.

The sequence of the deposits presented above proves that the depressions were places of changeable sedimentation conditions in the past. Initially, there were marshes, later lakes and finally, in the terminal phase of the development of biogenic accumulation reservoirs, marshes again.

It follows from the analysis of many boreholes made within the studied landforms that the thickness of the deposits that filled them was different. Consequently, the morphology of the bottom of these depressions is also different.

The reservoir north-east of the Neolithic settlement is the deepest one. In its southern part there is a longitudinal, narrow gully, extending from the east to the west. The maximum thickness of infilling deposits is 8.6 m (Os 94-9). In the north-eastern part of the landform in question, another overdeepening is seen (Fig. 3B) and the thickness of the biogenic deposits is 3.5 metres.

The reservoir of biogenic sedimentation located north-west of the defensive Neolithic settlements (site 1 – Grygiel 2004) is shallower. Two small hollows occur within this

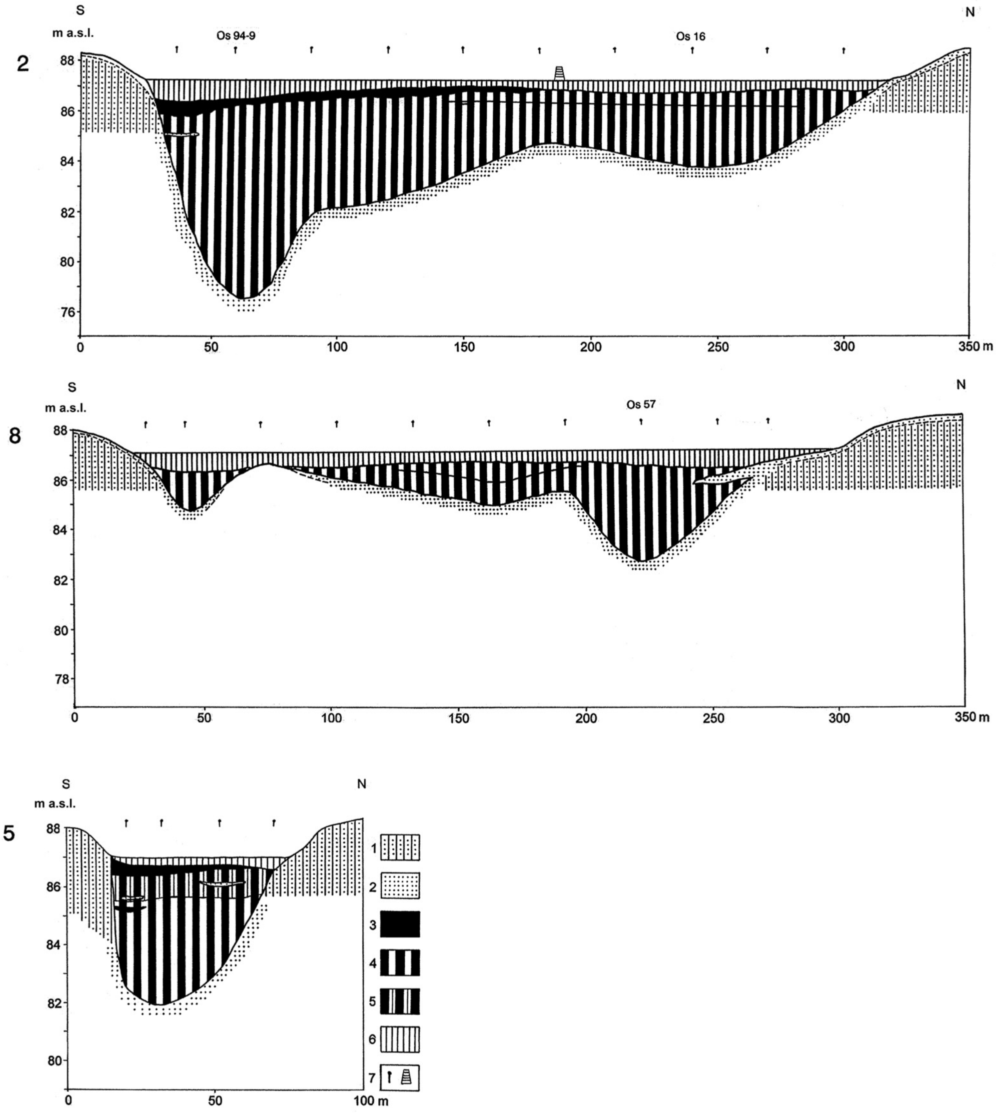

Fig. 8. Geological sections across reservoirs of biogenic accumulation and moraine upland:

1 – moraine till, 2 – ablation sands, 3 – peat, 4 – calcareous gyttja, lake chalk and detritus gyttja with malacofauna, 5 – organic silt, 6 – loams, 7 – borings, anthropogenic landforms (railway embankment)

landform. One of them (Fig. 3B and 8), with an elongated trough-like shape, is found in the southern part and is deeper. The thickness of infilling biogenic deposits is 5.3 metres. The other hollow, oval in shape, has a maximum depth of 4.5 metres and is found in the north-western part of the landform. The remaining part of the reservoir is shallower. The thickness of biogenic deposits is up to 2 metres.

The last of the reservoirs, which was investigated in detail, is located south-west of site 1 in Osłonki. The maximum thickness (Fig. 3B) of the biogenic deposits that fill it is 4.1 metres.

In the trough in question, west of Konary, there are other reservoirs of biogenic accumulation, which were not investigated in detail. Single boreholes made in this area (Leszczyńska 2000) suggest (Fig. 3A) that they are filled with 1.5 m thick peat or with peat and gyttja (of maximum thickness – 2.1 m).

Two sections of deposits from the depression located north-west of the defensive settlement in Osłonki (Fig. 3B) were sampled for physical and chemical investigations. The first one, which served as the basis for all investigations of the natural environment in Osłonki, was 9 m long (Os 94-9) and the other, taken from another overdeepening, was 4 m long (Os-16). Detailed descriptions of the deposits from these profiles are given in Tables 3 and 4 by Nalepka (in this volume). Consequently, it is not necessary to quote these descriptions for the second time.

The analysis of the diagram (Fig. 9A) reveals a varying content of $CaCO_3$ and organic substance in the deposits of profile Os 94-9.

Trace quantities of organic substance are found in sands with grains of gravel and an admixture of clay, at the depth of 861-900 cm, which is the base of biogenic deposits. The amount of $CaCO_3$ is from 5.5 to 8.3%. The percentage of this compound is higher, i.e. 27.7%, in the peat covering the sand (at the depth of 850-861 cm) and that of organic substance is increased to 5.4%. Peat sedimentation started in the Bølling (Nalepka 2005b and in this volume). Clearly lower percentages of organic substance (1.2-1.8%) and $CaCO_3$ (7.2-10.4%) are found in the sands, which cover the peat. The sands are most probably the result of washing out or aeolian processes, which occurred in the direct vicinity of the depression, then a fairly shallow one. As a result of these processes, the sand was deposited on the peat. A layer of gyttja with clay, dark-grey-olive and black-olive in colour, above the sand (822–545 cm), contains different quantities of organic substance and $CaCO_3$. Directly over the sand, in a layer situated at the depth of 809–822 cm, and in the section at a depth of 610 cm, the amount of $CaCO_3$ is decreased; only in some fragments of the section it is over 10%, whereas in other fragments it is lower than 10%. On the other hand, the percentage of organic substance in the layer in question is clearly higher, i.e. 24 to 40%. Sedimentation of this black-olive and dark-grey-olive layer of gyttja took place in the Allerød and Younger Dryas (Nalepka 2005b and in this volume). From a depth of 610 cm one can observe a clear growth of $CaCO_3$, which, in some segments, is higher than 80%. Such considerable quantities of this compound occur in the top layer of black-olive gyttja and light-coloured calcareous gyttja with thin layers of detritus gyttja (Tab. 3, Nalepka in this volume), deposited at a depth

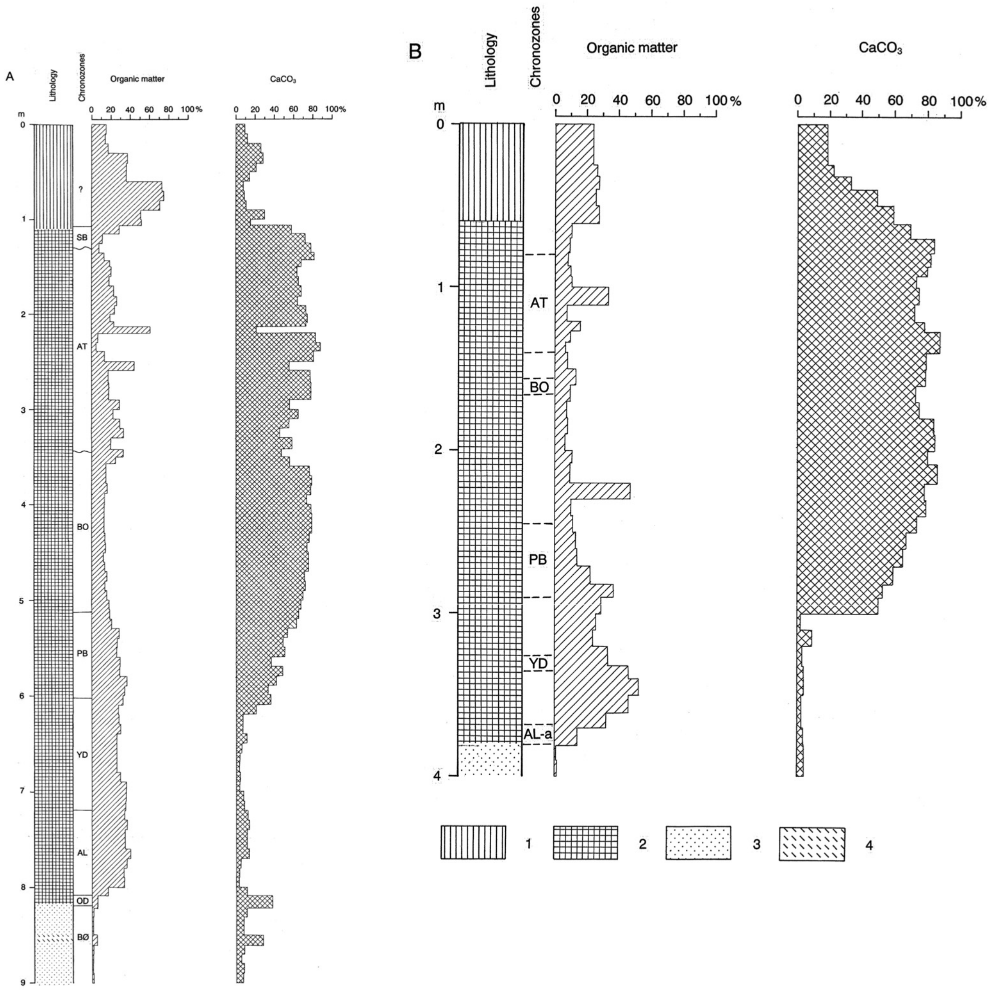

Fig. 9. Diagrams of organic substance and calcium carbonate contents in the deposits from boreholes Os 94-9 (A) and Os-16 (B): 1 – peat, 2 – gyttja, 3 – sand, 4 – humus

of 110 cm. The organic substance in the deposits of the bottom part of the section in question is around 30%, in the middle part it drops down to some 12%, and in the top part it rises again to some 25%. Sedimentation of calcareous gyttja started at the end of the Younger Dryas and ended in the Subboreal period. Peat and peat earth lying over the calcareous gyttja with thin layers of detritus gyttja (from 110-0 cm), have a smaller content of $CaCO_3$ (7.5-2.8%) compared to the layer underneath. There is more organic substance, which is contained between 13.8 and 74.8%.

Malacofauna shells are present in the deposits of the entire Os 94-9 section. Their concentration differs. In some segments only trace quantities are found, in others many shells are present. The malacofauna shells are discussed in detail by Alexandrowicz (2005 and in this volume).

It follows from the diagram showing the quantity of $CaCO_3$ and organic substance (Fig. 9B) in the deposits of the second analysed section (Os-16) (Tab. 4 in Nalepka, this volume) that there are significant differences. In the sand with grains of gravel underlying the biogenic deposits, at the depth of 381–400 cm, there occur trace quantities of organic substance and the quantity of $CaCO_3$ is 4.6%. A clear increase of organic substance (14.4%) can be observed in the layer of gyttja or peat, at the depth of 370–381 cm. The percentage of $CaCO_3$ is similar to that discussed before. The layer at the depth of 300–370 cm contains some lime carbonate – 2.9–9.2%. This layer is marked by a rather considerable quantity of organic substance, ranging from 24.7% to 52.8%. At a depth of 300 cm, a gradual increase of $CaCO_3$ is observed – from 2.5 to 50.4%, and then up to 86%. More than 50% of $CaCO_3$ is found up to a depth of 40 cm. It comprises a layer of calcareous gyttja with clay and thin layers of detritus gyttja (Tab. 4 in Nalepka, this volume) and the bottom part of peat earth. The percentage of organic substance at a depth of 300 cm is rather considerable (about 30%), but then it falls to some 7%, although it occasionally grows. This is characteristic of the layer of lacustrine deposits. At the boundary between gyttja and peat earth, i.e. at a depth of 59 cm, the percentage of organic substance grows (27.7-24%).

The analysis of both diagrams depicting the content of $CaCO_3$ and organic substance (Figs. 9A and B) reveals some regularity – there is little $CaCO_3$ in the bottom of the deposits that fill the depression. The palynological analysis made for the deposits from section Os 94-9 (Nalepka 2005b and in this volume) proves that sedimentation of some of the deposits with little $CaCO_3$ took place in the Bølling, Older Dryas, Allerød and Younger Dryas. In the area of Wielkopolska, this period was characterized by very severe climatic conditions (Kozarski 1995). It follows from the analysis of malacofauna (Alexandrowicz 2005 and in this volume) that the reservoir in which the sedimentation of biogenic deposits took place was shallow. Based on this, I think that blocks of buried ice did exist in the depression and in the adjacent areas there was permafrost, and, consequently, lime carbonate could not have been washed from the moraine tills. When the blocks of the buried ice and the permafrost disappeared in the final part of Younger Dryas, the process of chemical denudation started, as a result of which greater quantities of $CaCO_3$ dissolved in water were supplied in to area of the moraine till. It was then absorbed by fauna and flora, and when the latter decayed, it was deposited at the bottom of the lakes.

For the picture of the events in the area in question to be complete, a notion must be made of a depression located north-west of the defensive settlement. A section of deposits (Os 57) was taken from that depression (Fig. 3B); a detailed description of the section is given in Table 5 in an article by Nalepka (2005b and in this volume). An expert palynological analysis, which she made, proves that the sedimentation of biogenic deposits in this reservoir started in pre-Allerød time.

In conclusion of this chapter some remarks must be made about the depression directly adjacent in the south to the Neolithic defensive settlement (Fig. 3B). In the deepest part of the digging, as follows from the precise description of the deposits in Table 2 of Nalepka's paper (2005b and in this volume), peat silt is deposited on sandy clay. The beginning of its sedimentation goes back to the younger phase of the Allerød (Nalepka 2002–2003, 2005b and in this volume). Subsequently, these sediments became covered with biogenic deposits, which contained an admixture of silty and clayey fraction. Gyttja and peat were identified in these sediments. Biogenic sediments contain lenses and layers of silts, clays and sands. They are found at different depths and their sequence is shown in Fig. 3 in Nalepka's paper (2002–2003 and in this volume). These deposits are poorly sorted, which suggests that they originated when the adjacent bottom moraine was washed. I think that the development of these processes was triggered by human activities. However, because of considerable destruction of the biogenic deposits, it is difficult to present a complete stratigraphy for the section analysed palynologically (Nalepka 2002–2003).

## RECONSTRUCTION OF CHANGES IN THE NATURAL ENVIRONMENT

The reconstruction of changes in the natural environment in the vicinity of Osłonki is based on the study of the development of relief and lithology. Palaeobiological investigations carried out by Nalepka (2005a, b and in this volume) and Alexandrowicz (2005 and in this volume) contributed significantly to the findings. The relief of the Kujawy Upland, on which we find archaeological artefacts, was shaped by the last continental glacier, the Vistulian ice sheet, its melt waters and the climatic conditions, which first led to the formation of perennial permafrost, followed by its disappearance and melting of the blocks of dead ice. Later, a certain role was played by the deposition of biogenic deposits and denudation processes and, to a limited extent, aeolian processes. The two latter ones are attributed to man.

The Vistulian ice-sheet covered the upland in question and, using the depression existing from the time of earlier glaciations, entered the Płock Basin. Galon (1953), Galon and Roszko (1967), Mojski (1984) and others express an opinion that the terminal moraines in the vicinity of Płock belong to the Leszno phase. Mojski (1960, 1969), Skompski (1969) and Kozarski (1995), on the other hand, include them in the Poznań phase (Fig. 1A). According to the chronostratigraphic estimates made by Kozarski (1995), the continental ice sheet remained from about 20,000 to 18,800 years BP on the line of terminal moraines of the Leszno and Poznań phases. At that time, the melt waters of the ice sheet in the area comprising the terrain as far away from its head as tens of kilometres, flowed down the crevasses and wells (Fig. 10A) to the bottom of the ice-sheet. Subsequently, using a tunnel or clefts or tunnels and crevasses, under the hydrostatic pressure, they flowed in the direction of the glacier gate, in the process eroding troughs of different depth. For some time now many scholars (Kozarski 1966-1967, Pasierbski 1979, Galon 1983, Niewiarowski 1993 and others) have believed that this activity of subglacial waters was responsible for the formation of a glacial trough.

Subsequently to the subglacial erosion a trough was formed with vertical dimensions, which are difficult to define (Fig. 10B), extending from Żukowo through Osłonki to the vicinity of Kuczyna and farther in the south-eastern direction. At a certain moment, small movements of the continental glacier caused the breaking of the ceiling of the glacier tunnel and/or repositioning of ice blocks lying next to the crevasse, which filled up the trough (Fig. 10C). Melt waters continued to flow, using the depression, and deposited the sediments they transported between and on the ice blocks. They were subsequently covered (Fig. 10D) with a layer of clastic deposits (gravels, sands, silts, clays and flow tills); it is impossible to reconstruct their thickness. For a long time these deposits protected the buried ice from melting. According to Galon (1953) and Niewiarowski (1989), this time was dependent on the thickness of the mineral cover lying on the ice block. On the other hand, Nowaczyk (1994) and Błaszkiewicz (2003) link it also to the kind of the cover. Improvement of the climatic conditions or reduced transport of ice resulted in the recession of the continental glacier from the line of terminal moraines of the Leszno or Poznań phases (cf. above different views) and the younger moraines of the Radziejów oscillation (Fig. 1A and 1B) to the line of the terminal moraines of the Chodzież subphase (Kozarski 1995) or Kujawy subphase (Niewiarowski 1983). As a result of the disappearance of the continental glacier, a basal layer of moraine till and ablation sediments were deposited (Fig. 10E) and an extensive area of flat ground moraine with small denivelations was formed. A shallow depression in the place of the present-day trough at that time (~18,000-17,700 years BP) cannot be excluded.

The uncovered surface of the bottom moraine was exposed to severe climatic conditions, which, according to Kozarski (1995), were characterized in north-western Poland by negative mean annual air temperature (Leszno phase –12 up to –20°C, Pomeranian phase –1 to –2°C), high gradients between the temperatures of the air and the ground and air dryness, as well as the presence of arctic desert. These conditions favoured the existence or formation of perennial permafrost and, at the same time, preservation of the blocks of buried ice. The traces of presence of perennial permafrost in Osłonki was found in the diggings, in which Grygiel (2004) uncovered traces of the Neolithic defensive settlement. These are (Figs. 6 and 10E) polygons of frost fissures with the primary mineral filling. In the Neolithic period the polygons of these fissures were crossed by the foundations of buildings erected by man. According to Czeppe (1966), Dylik

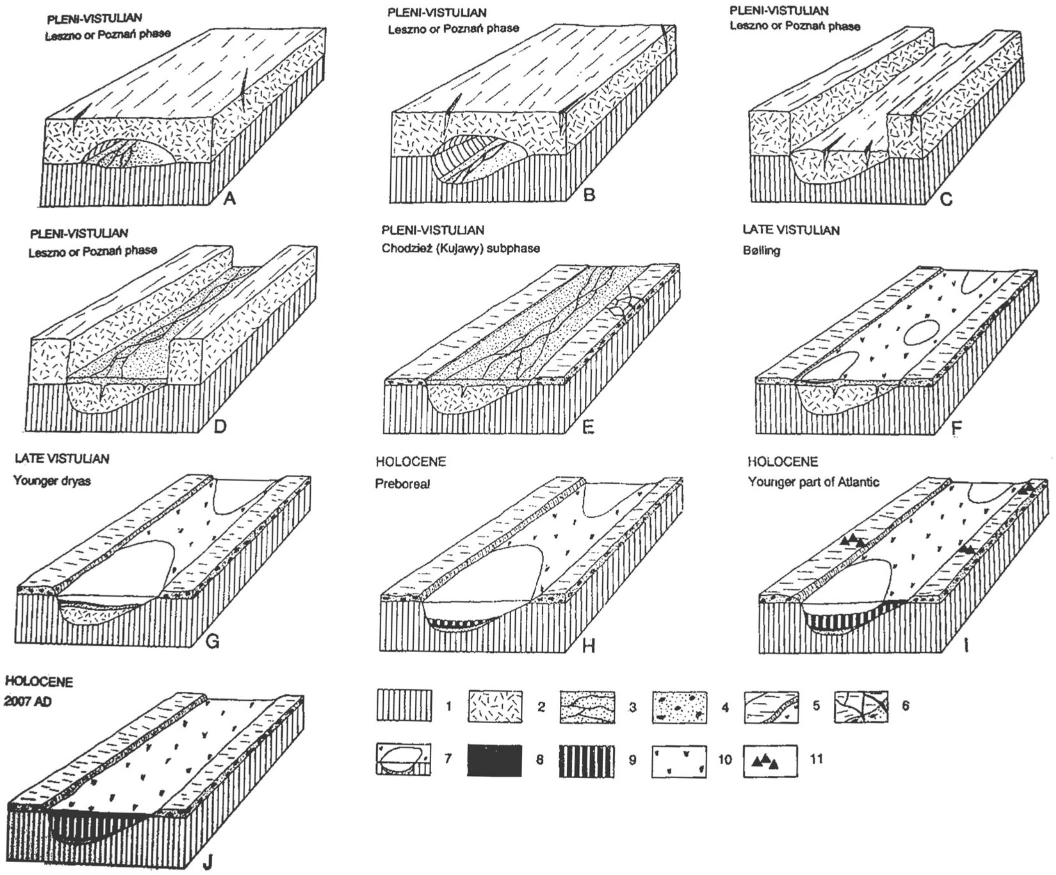

Fig. 10. Stages in the development of the glacial drainage channel in the Osłonki area:

1 – substratum: glacial and fluvioglacial deposits, 2 – glacial ice, 3 – subglacial streams and subaerial braided streams, 4 – till, 5 – flat ground moraine, 6 – frost wedge polygons and sand-wedge, 7 – lakes, 8 – peat, 9 – gyttja, 10 – biogenic accumulation plains, 11 – settlements and burial grounds of the Lengyel Culture

and Maarleveld (1967), Black (1969), Washburn (1973), Jahn (1975), Romanowski (1977), Kozarski (1995), Nowaczyk (2001) and others, such polygons were formed during rapid drops in air temperature in the low temperature range. They were formed as open wedge-like fissures in the vertical plane, with a width of 10–15 cm in the top and about 1–2 cm in the bottom (Fig. 7). Sand grains blown by the wind or moved saltationally on the surface of the vegetation-free bottom moraine fell into the open fissures. This process, as has been observed by Nowaczyk (2001), occurs even on surfaces poor in material susceptible to aeolian transport (which was the case of the area near Osłonki). Erosion, resulting in wind-polished stones, was also present then. The classical form of the stones is that of wind-faceted pebble, found among the ground stones deposited on the ground moraine. The formation process of ice continued probably until a considerable improvement of the climatic conditions and disappearance of perennial permafrost. The aeolian activity stopped or was restricted to a considerable extent when flora appeared.

When the climatic conditions improved at the beginning of the late Vistulian, heat reached the blocks of buried ice, which started to melt. Consequently, on the surface above them shallow depressions appeared, the size of which does not necessarily correspond to the present-day forms (Fig. 3B). A few such shallow depressions could have existed in the area under analysis. They turned into marshes and were covered by vegetation, the composition of which was described in detail by Nalepka (2005b and in this volume). When the vegetation died (Fig. 10F), a thin layer of peat was formed (Os 94-9 layer 850–861 cm, Tab. 3 in Nalepka, this volume). According to Nalepka (*op. cit.*), its accumulation started in the Bølling. However, after some time, it was interrupted by the rinsing or aeolian processes, which were responsible for the deposition of an over 20 cm thick layer of sand (822–850). It should be pointed out that traces of aeolian activity at that time were found to a limited extent in Poland (Węglewice) by Rotnicki and Tobolski (1969). The processes described above were stopped by the sedimentation of another biogenic layer, namely clay-rich gyttja, which took place in the younger part of Bølling and Older Dryas. Deposition of this layer continued throughout the Allerød and the older part of Younger Dryas (Fig. 2 in Nalepka, this volume). The climatic conditions of this part of Late Vistulian (Bølling-Younger Dryas) time were variable. The type of vegetation and vegetation density are closely related to that part of the Late Vistulian. The vegetation is discussed in detail in a paper by Nalepka (2005b). Throughout this period the depth of the lake reservoir was increasing and, at the same time, the thickness of typically lake biogenic deposits was also increasing. The thickness of this layer reaches approximately 200 cm. Its sedimentation, as follows from palaeobiological analyses (Alexandrowicz 2005 and in this volume, Nalepka 2005b and in this volume) occurred in a shallow reservoir. Therefore, we can assume that there were blocks of buried ice under the mineral and biogenic deposits in the older part of the Younger Dryas. They disappeared completely in the younger part of the Younger Dryas (Fig. 10G), what is substantiated by the malacofauna characteristics of deeper parts of reservoirs in the deposits from that period. A similar situation was observed by Alexandrowicz and Nowaczyk (1982) in Pomorsko near Zielona Góra. It should be emphasized that the analyses of malacofauna helped to determine the time of complete melting of the blocks of buried ice, which is difficult to determine otherwise. When the blocks of buried ice melted completely in the younger part of the Younger Dryas, the depth of the lake reservoir north-east of the defensive settlement, at the place in which core Os 94-9 was taken, was approximately 6.5 m from the present-day surface of the biogenic accumulation plain. The depth of the reservoir probably changed over time, sometimes the changes being more persistent and sometimes less persistent, but today it is impossible to determine these changes precisely, because of considerable anthropogenic transformation of the bank zones extending around the biogenic accumulation plains. These plains bear records of different water levels in the lakes. This is true of the different level in the history of the reservoirs discussed so far, and the history that took place in the Holocene.

In the reservoir north-west of the Neolithic defensive settlement, accumulation of biogenic deposits started, according to Nalepka (2005b and in this volume), in pre-Allerød time. We can assume that at the same time the blocks of buried ice in the gully under analysis started to melt.

Melting of the blocks of dead ice buried in the depression south of the settlement started later, in the younger phase of the Allerød interstadial. Such different times of the melting of the blocks of buried ice in locations close to each other was earlier found in the Brda outwash (Nowaczyk 1994, Błaszkiewicz 2003). The reasons for this have been given above.

The development of water and rush flora, connected with the improvement of the climatic conditions that started at the beginning of the Holocene, resulted in the deposition of organic substance on the bottom of the studied reservoirs, which made them shallower. At the beginning of the Preboreal period, the depth of the lake located north--east of the Neolithic defensive settlement was about 6 m. Because of further sedimentation of the deposits, its depth and the depth of the lake decreased. At the beginning of the Atlantic period it was 3.4 m (Fig. 10H) and at the end of the period – only 1.4 m. On the basis of the deposit thickness map (Fig. 3B) we can assume that throughout the existence of the lake greater depths occurred only in its southern part, close to the defensive settlement.

In the younger part of the Atlantic period, as follows from pollen analysis and radiocarbon datings (Nalepka 2005a, b and in this volume), an Early-Neolithic man appeared, as it is substantiated by the findings of artefacts and objects of the Linear Pottery culture (LPC) and the Lengyel culture (KL) (Grygiel 2004). Hence, near his settlements (Fig. 10I), man found lakes of a small area and depth, surrounded with peat bogs with the flora described by Nalepka (2005a, b and in this volume). Man's presence and his agricultural activity, mainly in the area of bottom moraine, usually involved thinning out and destruction of the flora. On the areas which were permanently or periodically deprived of flora (human settlements and arable areas) conditions prevailed, which favoured the processes of washing and blowing of loose ablation sands, humus and silt aggregates and carbon dust (Nowaczyk *et al.* 2002). Washed off the slopes of the gully by the waters of torrential rains or rapid melts, they were transported to the banks of the reservoirs. Small deltas appeared, overlying the gyttja. Soon they covered the gyttja and peats. It seems likely that abrasion along the banks played a small role in the deposition of sands in the bank area on organic deposits. The presence of sandy lenses and greater admixture of sand in the biogenic deposits in the central parts of the reservoirs can be attributed to aeolian processes, which occurred only during winter. Winds of considerable speeds blew sand off the land onto the ice surface of frozen lakes, which was deposited there in the form of non-continuous layer with different thickness. When the ice melted, it settled on the lake bottom, on the gyttja. When the sand layer on the ice was thicker, a sand lens settled on the bottom of the lake. Thin layers resulted only in a greater admixture of sand in the biogenic sands.

The growth of biogenic deposits in the depressions under analysis led to the disappearance of lake reservoirs. Unfortunately, as pollen in the biogenic deposits have been poorly preserved, their age cannot be precisely determined. The lake transformed into a peat bog with characteristic fauna and flora (Nalepka 2005b and in this volume, Alexandrowicz 2005 and in this volume).

In historical times water was reclaimed in this area – the excavations led to the change of hydrological conditions. In the depression north-east of the defensive settlement, an embankment was built for the railway delivering sugar beetroots to the sugar factory in Brześć Kujawski.

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# LATE GLACIAL AND HOLOCENE HISTORY OF VEGETATION AT OSŁONKI (KUJAWY, CENTRAL POLAND)

DOROTA NALEPKA

Abstract. Changes from unforested area during Bølling (Late Glacial) up to forested one during Atlantic (Holocene) time in south Kujawy region was done by pollen analysis. The influence of early Neolithic farmers (Linear Pottery culture, Lengyel culture and Globular Amphorae culture) on the vegetation cover was characterized, as well as the agriculture near the archaeological site at Osłonki was interpreted on the basis of pollen analysis.

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## INTRODUCTION

The southern Kujawy region has been intensively used for agriculture due to its fertile soils (JAŻDŻEWSKI 1938, GRYGIEL 2004, GRYGIEL and BOGUCKI 1997) since the early Neolithic time. Studies on the Late Glacial and the Holocene vegetation history of this area were done by pollen analysis (NALEPKA 2005). Special attention was paid to the vegetation development under natural and anthropogenic circumstances.

## RESEARCH AREA, MATERIAL AND METHODS

The Osłonki region is situated in the south-eastern part of the Kujawy Lake District (KONDRACKI 1994) in Central Poland. The archaeologically explored sites are located in the Osłonki (52°37'N, 18°48'E), Miechowice and Konary villages (Fig. 1). At present, the majority of the area is used for agricultural purposes, but among them three flat-bottom basins filled with biogenic sediments are present (NOWACZYK *et al.* 2002, and in this volume). All of them were drained in the twentieth century, and in the late 1990s one of them was turned into a fish-pond, as the organic sediments were dug up for gardening purposes. A detailed description of the geomorphological investigations and results is presented in a separate paper (NOWACZYK, this volume).

Palynological analyses done from three cores obtained from two of these basins filled with biogenic sediments were the basis for description of environmental changes;

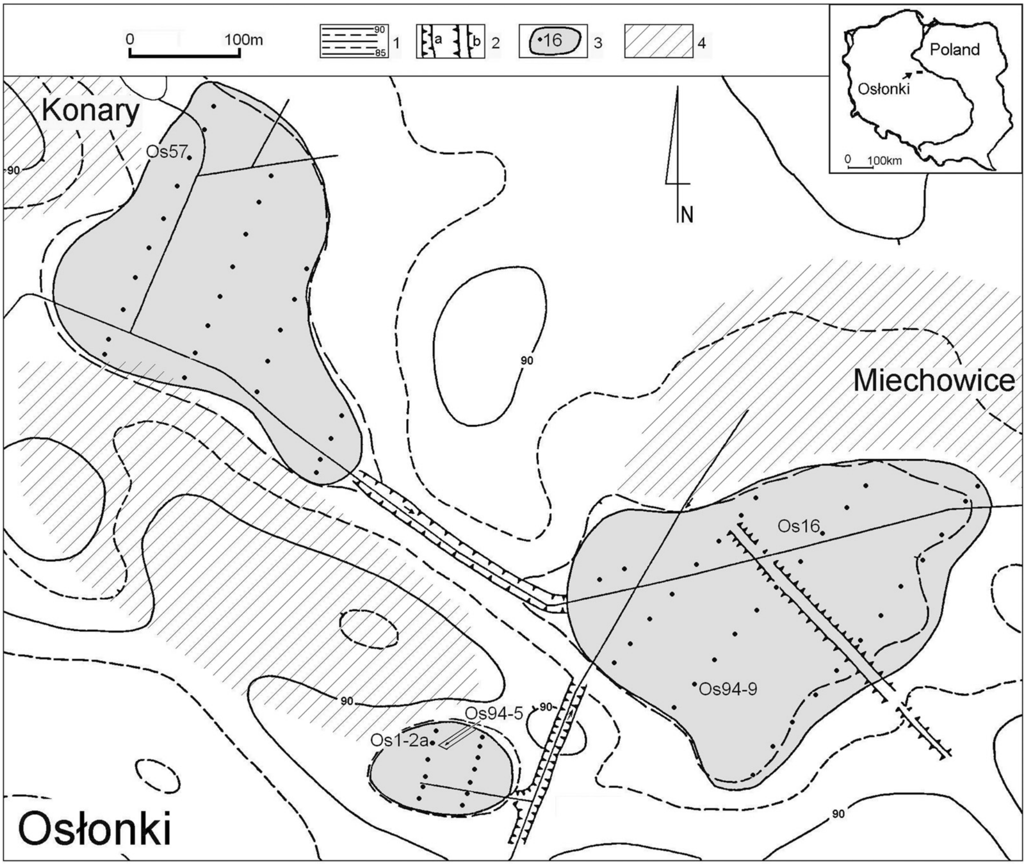

Fig 1. Location of the investigated profiles in the basins in the Osłonki area: 1 – contour lines in 1.25 m intervals, 2 – contemporary anthropogenic forms: cuttings (2a – ditches) and embankments (2b banks), 3 – plains of biogenic accumulation (peats, gyttia, organic silts) and numbers of investigated profiles in the basins, 4 – approximate range of Neolithic settlements

the remaining cores from all the basins provided supplementary data (Nalepka 2005). Tables 1–5 contain detailed description of the studied sediments.

Two profiles (Os 1-2a – core, taken using a Więckowski-type corer and Os 94-5 – trench) were collected from the southern basin (Fig. 1). The third one (Os 94-9 – core taken using Russian cores) was collected from the eastern basin (Fig. 1). This profile, showing the most complete sediment record (almost undisturbed), was analysed by macrofauna remains: Cladocera (Gąsiorowski 2008, Gąsiorowski and Nalepka 2004, and in this volume) and molluscs (Alexandrowicz, this volume).

The samples taken for pollen analysis were prepared by standard Erdtman acetolysis technique (Faegri *et al.* 1989), together with a known number of indicator spores of *Lycopodium* (Stockmarr 1971). For counting sporomorphs, drawing the diagrams and maps, and implementing numerical analysis, the POLPAL computer programs were

Table 1

Lithological description of the Osłonki Os 1-2a profile. The depths are measured from the field point at 0.15 m below the present surface level (after Nalepka 2005, simplified)

| Obtained segments [cm] | Description of sediment |
|---|---|
| 0–32 | Clay with recent plant roots, sand and shells of molluscs |
| 100–108 | Clay with recent plant roots and shells of molluscs |
| 108–118 | Peaty mud with recent plant roots and shells of molluscs (transitory level) |
| 118–151 | Sandy clay with fragments of plant roots and shells of molluscs |
| 151–153 | Clay |
| 200–221 | Clay (217–221 m destroyed) |
| 221–260 | Peaty mud |
| 270–300 | Silty gyttja with small admixture of sand, small fragments of herb tissues and shells of molluscs |
| 300–437 | Peat |
| 437–446 | Silty peaty mud |
| 446–486 | Sandy clay |

Table 2

Lithological description of the Osłonki Os 94-5 profile. The depths are measured from the field point at 0.38 m below the present surface level (after Nalepka 2005, simplified)

| [cm] | Description of sediment |
|---|---|
| 0–13 | Clay with recent plant roots, sand and shells of molluscs |
| 13–28 | Clay with recent plant roots, sand and shells of molluscs and pieces of clay, sand and small pebbles |
| 28–37 | Clay with black humus |
| 37–52 | Humus with plant roots and shells of molluscs. Clay is present as small lenses |
| 52–100 | Clay with humus with plant roots and shells of molluscs |
| 100–130 | Sandy clay with plant roots and shells of molluscs |
| 130–138 | Sand with clay |
| 138–238 | Peaty mud with sand, plant roots and shells of molluscs |
| 238–242 | Peaty mud with sand, plant roots and shells of molluscs and anthrax |
| 242–283 | Gyttja slightly sandy with plant roots and shells of molluscs |
| 283–291 | Clay with small amount of sand, and shells of molluscs |
| 291–298 | Peat (mostly *Sphagnum*) |
| 298–325 | Peaty mud slightly clayey |
| from 325 | Sandy clay |

Table 3

Lithological description of the Osłonki Os 94-9 profile. 0.00 m level of described sediments = the surface (after Nalepka 2005, simplified)

| cm | Description of sediment |
|---|---|
| 0–41 | Recent soil with fragments of herb tissues and shells of molluscs |
| 41–67 | Clay with recent plant roots, tissues of herbs and shells of molluscs |
| 67–110 | Peat with plant roots, tissues of herbs and shells of molluscs |
| 110–138 | Detritus gyttja with tissues of herbs. Transitory level between peat and gyttja |
| 138–150<br>150–158<br>158–167<br>167–177<br>177–185<br>185–195<br>195–200<br>200–212 | Gyttja slightly laminated, with plant roots, and shells of molluscs |
| 212–223 | Detritus gyttja with plant roots, tissues of herbs and shells of molluscs |
| 223–231 | Peat with plant roots, tissues of herbs and shells of molluscs |
| 231–244 | Clay/gyttja |
| 244–255 | Detritus gyttja with plant roots, tissues of herbs and shells of molluscs |
| 255–260 | Gyttja with shells of molluscs |
| 260–274 | Gyttja with plant roots and shells of molluscs |
| 274–292 | Gyttja with shells of molluscs |
| 292–307 | Gyttja with plant roots, tissues of herbs and shells of molluscs |
| 307–311<br>311–318<br>318–332<br>332–335<br>335–343<br>343–345<br>345–350<br>350–351 | Gyttja |
| 351–545 | Gytia with shells of molluscs |
| 545–809 | Silty gyttja with shells of molluscs |
| 809–822 | Gyttja with shells of molluscs |
| 822–850 | Sand |
| 850–861 | Silty peat strongly decomposed |
| 861–900 | Silty sand with pebbles up to 0.5 cm in diameter |

Table 4
Lithological description of the Osłonki Os 16 profile. 0.00 m level of described sediments = the surface (after Nalepka 2005, simplified)

| cm | Description of sediment |
|---|---|
| 0–25 | Recent soil with fragments of herb tissues, roots and shells of molluscs |
| 25–59 | Clay with recent plant roots, tissues of herbs and shells of molluscs |
| 59–70 | Gyttja |
| 70–127 | Silty detritus gyttja with recent plant tissues of herbs |
| 127–150 | Silty gyttja with tissues of herbs and shells of molluscs |
| 150–152 | Reworked |
| 152–170 | Silty gyttja with tissues of herbs and shells of molluscs |
| 170–283 | Silty gyttja with tissues of herbs and shells of molluscs |
| 283–370 | Silty peat strongly decomposed or silty detritus gyttja |
| 370–381 | Gyttja? |
| 381–400 | Sand with pebbles up to 2 cm of diameter |

Table 5
Lithological description of the Osłonki Os 57 profile. 0.00 m level of described sediments = 0.15 m below the surface (after Nalepka 2005, simplified)

| cm | Description of sediment |
|---|---|
| 0–60 | Clay with sand, recent plant roots, tissues of herbs and shells of molluscs |
| 60–143 | Clay with small amount of plant tissues |
| 143–263 | Gyttja with small amount of shells of molluscs |
| 263–395 | Detritus gyttja with small amount of shells of molluscs |
| 395–400 | Transition from gyttja to peaty mud |
| 400–411 | Silt |
| 411–450 | Sand, slightly silty |

used (Walanus and Nalepka 1999, 2004, Nalepka and Walanus 2003). LPAZ description of the Os 94-9 pollen diagram is shown in Table 6.

The chronology was done based on correlation among relative palynological dating, absolute radiocarbon determinations from biogenic sediments, and archaeological artefacts collected from Osłonki and Miechowice sites. Radiocarbon determinations are presented as conventional $^{14}$C dates BP and the 68% and 95% ranges of calibrated age are denoted, as BC1 and as BC2 (Fig. 2), respectively (Grygiel 2004, Nalepka 2005).

Table 6

Osłonki Os 94-9. Description of local pollen assemblage zones (LPAZ) (Fig. 2) (after Nalepka 2005, simplified)

| Name of LPAZ | Depth [cm] | Description of pollen spectra |
|---|---|---|
| Os$_{94\text{-}9}$ 1<br>NAP-*Betula nana* | 851–860 | The high frequency of NAP, increases of *Betula nana*-t. and *Betula*, decrease of *Pinus sylvestris*. The appearance of *Hippophaë rhamnoides*, presence of *Juniperus communis*, *Pinus cembra*-t., *Salix*, as well as *Alnus*, *Corylus avellana*, *Quercus*, recognized here as re-bedded.<br>The upper limit: not known due to the presence of hiatus. |
| Os$_{94\text{-}9}$ 2<br>*Pinus* | 820–823 | The high frequency of *Betula nana*-t. Increase of *Pinus sylvestris*. Presence of *Hippophaë rhamnoides*, *Juniperus communis*, *Salix* and *Salix polaris*-t. as well as rebedded *Alnus*, *Corylus avellana*, *Quercus*. Decrease of corroded sporomorphs.<br>The upper limit: rise of *Salix*, *Hippophaë rhamnoides*, *Juniperus communis*, and considerable decrease of *Pinus sylvestris* curve. |
| Os$_{94\text{-}9}$ 3<br>*Betula nana-*<br>*-Hippophaë-*<br>*-Juniperus* | 810 | Only one spectrum included. The maximum value of *Hippophaë rhamnoides*, *Salix*, the first maximum of *Juniperus communis*. The high frequency of *Betula nana*-t. is continuously present. The presence of *Larix* and rebedded *Alnus*, *Quercus*, *Fraxinus excelsior.*<br>The upper limit: drop of *Hippophaë rhamnoides*, *Juniperus communis*, *Salix*, Poaceae. |
| Os$_{94\text{-}9}$ 4<br>*Betula nana-*<br>*-Pinus cembra* | 763–801 | *Pinus sylvestris* and *Betula* on similar level. *Betula* curve fluctuates. High frequency of *Betula nana*-t., presence of *Juniperus communis* although discontinuous curve. Continuous and relatively high curves of *Pinus cembra*-t. and *Populus*. Re-bedded pollen grains: *Alnus*, *Quercus*, *Corylus avellana*, *Ulmus* are present. Slight increase of *Artemisia*. Presence of corroded sporomorphs. High frequency of charcoal in some spectra.<br>The upper limit: drop of *Betula nana*-t. |
| Os$_{94\text{-}9}$ 5<br>*Pinus-Betula nana* | 720–748 | Temporary increase of *Pinus sylvestris*, the opposite of *Betula*. Slight decrease of *Betula nana*-t. *Juniperus communis* and *Artemisia* curves low but continuous. Presence of *Salix polaris*-t., *Pinus cembra*-t., *Populus*, *Larix*. Disappearance of re-bedded sporomorphs. Discontinuous presence of charcoal.<br>The upper limit: drop of *Pinus sylvestris*, *Betula nana*-t. curves, rise of *Betula*. |
| Os$_{94\text{-}9}$ 6<br>*Betula nana-*<br>*-Juniperus-*<br>*-Artemisia* | 603–710 | The rise up to maximum of *Juniperus communis*, the maximum frequency of *Artemisia*, high frequency of *Betula nana*-t., and Cyperaceae, relatively high Chenopodiaceae. *Salix polaris*-t. curves low, but almost continuous. Presence of *Pinus cembra*-t., *Larix*, *Populus*. Single pollen grains of *Hippophaë rhamnoides* and rebedded sporomorphs. Gradually decrease of *Pinus sylvestris*, low value of *Betula*. The high frequency of NAP.<br>The upper limit: drop of *Betula nana*-t., *Juniperus communis*, *Artemisia*, Chenopodiaceae and NAP curves. |

| | | |
|---|---|---|
| $\mathrm{Os}_{94\text{-}9}$ 7<br>*Betula-*<br>*-Filipendula* | 572–597 | The rise up to maximum of *Betula*, decrease of *Pinus sylvestris*. Disappearance of *Hippophaë rhamnoides* and *Salix polaris*-t. Decrease of Chenopodiaceae and *Artemisia*.<br>The upper limit: drop of *Betula*, *Betula nana*-t. and *Juniperus communis*. |
| $\mathrm{Os}_{94\text{-}9}$ 8<br>*Ulmus-*<br>*-Filipendula* | 513–567 | Relatively high frequency of *Filipendula*. Low and continuous *Ulmus* curve. Increase of *Pinus sylvestris*. Disappearance of *Betula nana*-t., significant drop of *Juniperus communis* and Cyperaceae. In the upper part appearance of *Corylus avellana*, *Quercus* and *Fraxinus excelsior* pollen grains. Appearance of charcoal.<br>The upper limit: increase of *Quercus*. |
| $\mathrm{Os}_{94\text{-}9}$ 9<br>*Ulmus-Corylus* | 348–508 | Gradually increase of *Corylus avellana*. Low and continuous curve of *Ulmus*. *Filipendula* curve still on relatively high level. In the upper part rise of *Quercus*, *Alnus* and *Fraxinus excelsior* as well as charcoal.<br>The upper limit: significant decrease of AP curve. |
| $\mathrm{Os}_{94\text{-}9}$ 10<br>*Alnus-Corylus-*<br>*Quercus* | 245–344 | High frequency of *Alnus*, *Corylus avellana*, *Quercus*, *Ulmus*, *Fraxinus excelsior* and *Tilia cordata*-t. Higher frequency of *Artemisia*. Low frequency of *Betula*, gradual decrease of *Pinus sylvestris*. Appearance of Cerealia undiff., *Triticum*-t., *Hordeum*-t. single pollen grains. The rise of *Urtica dioica*-t., particulary in the lower part. Presence of charcoal.<br>The upper limit: not known due to the presence of hiatus. |
| $\mathrm{Os}_{94\text{-}9}$ 11<br>*Alnus-Ulmus-*<br>*-Corylus-Quercus* | 140–221 | The maximum of *Quercus*, *Alnus*, *Corylus avellana*, *Ulmus*, *Fraxinus excelsior* and *Tilia cordata*-t.. Slight rise of *Artemisia*. Low and discontinuous curves of Cerealia undiff. (0.0-0.9%), *Triticum*-t., *Hordeum*-t. Continuous presence of *Pteridium aquilinum*. Appearance of first pollen grains of *Carpinus betulus*. Relatively high frequency of charcoal.<br>The upper limit: drop of *Alnus*, *Ulmus*, *Corylus avellana*, *Quercus* and significant rise of corroded sporomorphs. |
| $\mathrm{Os}_{94\text{-}9}$ 12<br>*Carpinus*-NAP | 112–136 | Gradually increase of *Carpinus betulus* and Poaceae. *Plantago lanceolata* as single pollen grains, but almost continuous. In the lower part significant rise of Chenopodiaceae and corroded sporomorphs and increase of Cyperaceae. Low and continuous curve of Cerealia undiff. *Artemisia* at constant level. The very high frequency of charcoal.<br>The upper limit: drop of AP excluding *Pinus sylvestris*, increase of Poaceae and corroded sporomorphs. |
| $\mathrm{Os}_{94\text{-}9}$ 13<br>Poaceae? | 108 | Only one spectrum included. Spectrum not interpreated due to the rapid rise of corroded sporomorphs, Poaceae, and low value of AP. The relatively high requency of *Plantago lanceolata*. Presence of charcoal. |

## DEVELOPMENT OF VEGETATION IN THE AREA OF OSŁONKI

Development of vegetation in the Osłonki area has been characterized after correlation of the local pollen assemblage zones that are fully described in a monograph by NALEPKA (2005). The oldest organic deposits have been palynologically dated to the Bølling interstadial, the youngest ones to the Subboreal.

### Late Glacial

Bølling. Low mats of *Salix polaris and Betula nana* were growing in the developing patches of tundra. Scattered specimens of the light-demanding and cold-resistant *Larix*, *Pinus cembra* and some instances of an arborescent *Betula* and *Pinus sylvestris* have been noted together with shrubs of *Juniperus communis* and *Hippophaë rhamnoides* in dry sites. Light-demanding herbs like *Gypsophila, Helianthemum, Peplis*, and *Selaginella selaginoides* were present.

In the still flowing waters, which were developing further into a small and shallow lake (NOWACZYK, this volume), *Nymphaea alba* and *Ceratophyllum* grew. During the discussed period vegetation did not form a complete cover.

Older Dryas. This climate deterioration was reflected by changes in the vegetation. In the landscape there was a decrease in the participation of pine and birch. Cold-resistant larch trees were growing as scattered specimens. More favourable conditions were becoming prevalent for the development of light-demanding plants, both herbaceous ones and shrubs. They resulted in good development of juniper stands in the study area. *Hippophaë rhamnoides* was growing in great abundance. Wet habitats were very favourable for the development of willow thickets. Stands of *Betula nana* were still well developing.

Allerød. Open birch and pine forests occurred in this area. However, a part of the study area was still occupied by light-demanding and herbaceous plants, shrubs, and cold-resistant trees of *Pinus cembra*, *Populus*, and *Larix*. In the younger part of this period, open pine forest with an admixture of birch predominated in dry areas but did not cover the entire terrain, allowing for the development of heliophilous plants. The stands of tundra communities with *Betula nana* and *Salix polaris*, as well as other *Salix* shrubs occupied moist sites.

Younger Dryas. Heliophilous herbs and shrubs dominated the landscape that was more open than in the previous period. Thickets of *Juniperus communis* and *Hippophaë rhamnoides* expanded, and different communities of herbaceous plants, which have been already present in the Allerød, invaded new areas. In this period, tundra communities with *Betula nana*, *Salix polaris*, and *Selaginella selaginoides* attained optimal conditions in mesic habitats. Scattered trees of *Pinus cembra*, *Larix*, and *Populus* continued to grow, while *Pinus sylvestris* and *Betula* appeared as scattered trees only and did not form forest stands.

## Holocene

Preboreal. During the older part of this period climate warming resulted in the final disappearance of the arctic tundra communities and in the development of forests. At first, there were birch and birch-pine forests, as the mesophilous trees had not yet reached the study area due to their slower dispersal rates. Not far from the study site the first *Ulmus* could have been growing. During the younger part of this chronozone, the final disappearance of the tundra communities with *Betula nana* took place. Pine-birch and birch-pine forests dominated the landscape. *Ulmus*, which had already reached the study area, could have formed a small admixture within these forests.

Boreal. During the Boreal chronozone, the birch and birch-pine forests were still developing in the study area. In the forests with birch dominance, elm was slowly spreading in small amounts. In the lower layer of the forest shrubs of *Corylus avellana* gradually obtained better conditions, indicating some amelioration of climate. Hazel developed plentifully and was probably overgrowing open patches of pinewood and dry edges of the forests. Since the middle part of this period, wet communities may have comprised *Quercus* and slightly later also *Fraxinus excelsior*. At the end of this period, in the landscape with the fertile habitats there were already deciduous forests in which oak, lime, elm, and ash trees were growing, with hazel in the understory, as well as birch copses.

Atlantic. Mixed deciduous forests, composed of *Quercus*, *Tilia*, *Ulmus*, *Fraxinus excelsior*, and *Corylus avellana* in various combinations, were dominant in the landscape. In the forest undergrowth – in burnt areas – the fern *Pteridium aquilinum* grew abundantly. On the permanently deforested areas various herbaceous communities developed, such as wet and fresh meadows and dry grasslands. Good conditions existed for the spread of herbaceous plants that demanded a higher amount of nitrogen in the soil, such as *Urtica* and *Plantago major*, resulting in ruderal communities. The presence of arable fields at that time is confirmed in the Osłonki profiles by the occurrence of single pollen grains of Cerealia undiff., *Triticum*-type, and *Hordeum*-type pollen grains, accompanied by pollen of segetal weeds such as *Ranunculus arvensis* and *Spergula arvensis*. The presence of arable fields was connected with the time when people of the Linear Pottery culture (LPC) and Lengyel culture (LC) inhabited the vicinity of Osłonki.

Atlantic or Subboreal. Mesophilous deciduous mixed forests continued to be the predominant vegetation type, but human impact on vegetation caused reduction of the forested areas.

Subboreal. Forested areas diminished, but their composition did not change. Grasses dominated the herbaceous communities in open areas. In the close neighbourhood of villages, open areas were covered with ruderal plants, by crops on the arable fields, and by *Rumex* and *Plantago* in the pastures and fallow lands. The higher amounts of *Artemisia* and Poaceae pollen together with the decrease of deciduous tree pollen are in agreement with the archaeologically documented presence of the Globular Amphorae culture (GAC) settlement.

Younger chronozones of the Holocene. In an open landscape, forests covered only a small area and their composition was changed, as *Pinus sylvestris* replaced deciduous trees. Juniper shrubs and various herbaceous communities occupied vast open areas. The high degree of deforestation and the presence of synanthropic plants indicated the use of large areas for economic purposes by farmers. The spread of *Juniperus communis* and *Rumex acetosella*, which grew on poor soils, may be evidence of impoverishment of various habitats. Open sites were used for agriculture (cultivation of fields and cattle breeding). The high increase of pollen of ruderal community indicators (e.g. *Artemisia*, *Urtica dioica*-type, *Plantago major*) suggests the existence of permanent settlements in the neighbourhood of the studied sites. The uppermost spectra indicate an open, almost tree-less landscape. Herbaceous plants are dominant, mainly grasses and ruderals. The agricultural activity increased, including both crop cultivation (Cerealia) and pasturage (*Plantago lanceolata*). Waste areas on poorer soils were present, where *Juniperus communis* shrubs had spread. Oak, poplar, alder and willow grew as scattered trees only. Temporary pine regeneration occurred.

## PALYNOLOGICALLY DOCUMENTED EARLY NEOLITHIC FARMING IN THE OSŁONKI REGION

Palynologically identified agricultural activities of Neolithic farmers and their impact on changes in the plant cover are referred to individual cultures on the basis of detailed correlations with the results of archaeological studies in the Osłonki region and are supported by radiocarbon dating and numerical methods.

Before the development of the early Neolithic occupation, primeval mixed deciduous forests with oak, lime, elm, ash, and hazel covered the landscape of the vicinity of Osłonki. Only small open areas with heliophilous herbs were present. The first farmers appeared in a forested environment. Cereals along with segetal weeds and ruderals reflected the spread of agriculture. Wheat and barley were cultivated. The inhabitants of Osłonki exploited wild resources, which were available in the neighbourhood. They used wood, first of all oak and pine, but also other trees and shrubs like birch, poplar, and hazel, although probably in smaller quantity. The landscape around the Lengyel settlement should be exploited quite heavily in the immediate vicinity of the houses and, furthermore, the timber requirements of long-house construction would have resulted in the cutting of substantial timber, to which the constant requirements for fuel, tool use, and house repair should be added. Generally, there is a picture of a very intensive local landscape use. After the end of the Lengyel settlement at Osłonki, the traces of the late Neolithic (Globular Amphorae and Funnel Beaker culture) sites in this area are found. In the upper part of the analyzed profiles, palynological records of human presence are scattered and discontinuous. They cannot be correlated with precisely dated archaeological artefacts collected from excavations.

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# RESPONSE OF CLADOCERA (CRUSTACEA) TO NEOLITHIC SETTLEMENT AT OSŁONKI (KUJAWY REGION, CENTRAL POLAND)

Michał Gąsiorowski

Abstract: Analysis of cladoceran remains was done on two cores from fossil lakes located near the Neolithic settlement site at Osłonki (Kujawy region, Poland). The cores provide records started from the Alleröd and the Younger Dryas, respectively. The cladoceran remains were used to reconstruct natural and anthropogenic eutrophication and changes in water ecosystems. Both water bodies were shallow and clear-water lakes during the Late Glacial period. Since the beginning of the Holocene, climatic and biotic changes induced natural, slow and gradual eutrophication. The evidence of intensive eutrophication started with the first occurrences the pollen and spores of crops and weeds. Human settlement caused significant changes in cladoceran species composition. The first occurrence of crop pollen was coincident with decline of plant-associated species and increase of euplanktonic taxa tolerant to high nutrient concentration.

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## INTRODUCTION

Excavations at Osłonki have discovered one of the largest settlements of early farmers in Polish Lowlands (Grygiel and Bogucki 1997). 30 trapezoidal houses and 80 graves constituted this Lengyel village. The intensive archaeological investigation combined with radiocarbon datings showed that this village was well prospered between 4,500 and 4,300 years BC (Nalepka 2005). Intensive palaeobiological investigations have been conducted in the nearby Osłonki village since 1994 (Nalepka 1999, 2004, 2005, Gąsiorowski and Nalepka 2004, Gąsiorowski, submitted).

Cladocera analysis has been used to track human impact on the water environment for many years (e.g. Szeroczyńska 1985, 1998, Schmidt *et al.* 2000). Even Mesolithic and Neolithic settlement changed a trophic state in small lakes and ponds. This activity was also reflected by changes in the presence and frequency of some Cladocera species remains, especially sensitive to shortages or overloads of nutrients.

## MATERIALS AND METHODS

Cladocera analysis was performed on two cores collected in small basins located close to the Lengyel village at Osłonki, Kujawy Lake District, Central Poland (52°37'N, 18°48'E) (Nalepka, this volume). The first core (Os 94-9) was taken about 150 m to the north-east from the village using a Russian peat-corer. The second core (Os 94-5) was collected from a smaller basin located directly to the south of the excavation area. Each subsample consisted of 1 $cm^3$ of wet sediments. Detailed lithological descriptions of both sequences were given in Nalepka (2005).

The samples were prepared for Cladocera analysis according to standard procedure (Frey 1986). The sediments were treated with 10% hydrochloric acid, then heated with 8% potassium hydroxide for 20 minutes in order to deflocculate the material, washed in distilled water, and finally sieved onto a 33 µm mesh. The sieved material was stored in 10 ml of distilled water. Temporary slides were used for identification and to count Cladocera remains. Each slide was prepared from a 0.1 ml portion of a sample. Two to five slides were scanned from each sample. Identification of Cladocera remains based on Flössner (2000) and Szeroczyńska and Sarmaja-Korjonen (2007). The basic sum for counting in most samples was 350-400 cladoceran remains (headshields, shells, ephippia, postabdomens). The most abundant body part was chosen for each species to represent the number of individuals, and the percentages were calculated from the sum of the individuals. The cladoceran zones were distinguished based on results of Conslink analysis (Gordon and Birks 1972). Ecological preferences of cladoceran species were taken from Müller (1964), Whiteside (1970) and Duigan (1992).

## RESULTS AND DISCUSSION

38 samples from core Os 94-9 and 18 samples from core Os 94-5 were analyzed for frequency of Cladocera remains. 38 and 31 taxa were identified in the cores, respectively. The most numerous were remains of Chydoridae, and species belonging to Sididae, Macrothicidae, Bosminidae and Daphnidae were also presented. The results of Cladocera analysis and zonation are summarized in Fig. 1.

In both palaeolakes, the Late Glacial was a time of the highest diversity of the cladoceran community (Gąsiorowski and Nalepka 2004, Gąsiorowski, submitted). Cladoceran record starts with the occurrence of several taxa, representing different ecological groups, i.e. planktonic genus *Bosmina*, plant-associated *Oxyurella tenuicaudis*, *Camptocercus rectirostris*, *Acroperus harpae* and *Pleuroxus spp.*, and dwelling on open-bottom *Leydigia acanthocercoides* and *Alona quadrangularis*. This suggests that relatively low temperature during the Late Glacial was not a limiting factor for Cladocera. The amount of nutrients in the water was sufficient for the development of dense vegetation and cladocerans. The water bodies were small and shallow lakes with cool and clear water, probably in a state of mesotrophy.

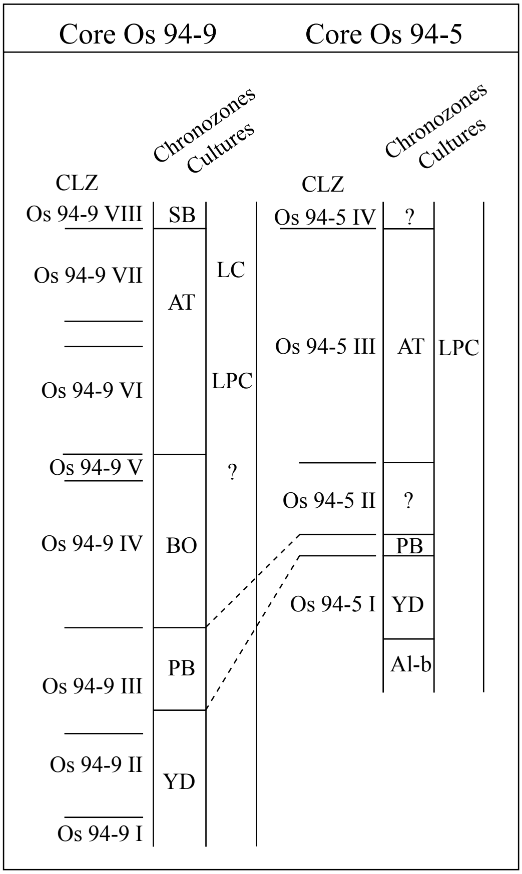

Fig. 1. Cladocera zonation (CLZ) of two cores (Os 94-9 and Os 94-5) from Osłonki site. Chronozones and cultures according to NALEPKA (2005). LPC – Linear Pottery culture, LC – Lengyel culture

The beginning of the Holocene was a period with stable, good living conditions for Cladocera. The climate changes, which strongly influenced terrestrial plant association, were not so clearly mirrored by zooplankton. The older and middle part of the Holocene, probably younger Preboreal and older Atlantic, is characterized mainly by an increase of pelagic species *Chydorus sphaericus sensu lato* (GĄSIOROWSKI and NALEPKA 2004). However, plant-associated *Acroperus harpae*, *Alonella nana* and *Alona rectangula* are also still abundant. The cladoceran community composition suggests a gradual transition between a macrophyte-dominated ecosystem to a planktonic-dominated one. It could be induced by changes of water alkalinity and turbidity and consequently increasing trophic state (VADEBONCOEUR *et al.* 2003).

The first occurrence of cultural indicators during Atlantic period is coincident with a strong increasing of pelagic *Chydorus sphaericus* and a decline of plant-associated species (GĄSIOROWSKI, submitted). It suggests an increase in the nutrient load (JEPPESEN et al. 2001) and partial damage to benthic communities (VADEBONCOEUR et al. 2003).

The Osłonki Neolithic settlement site was not occupied continuously (Grygiel and Bogucki 1997, Nalepka 2005). There were a few villages, which existed more or less in the same place. The earliest human activity is correlated with the Linear Pottery culture and has been very poorly recorded in the palaeobiological material (beginning of zone VI in core Os 94-9 and zone III in core Os 94-5, Fig. 1). That suggests the small scale of settlement which occurred during this period. The next colonizers belonged to the Lengyel culture. They more significantly impacted the water environment of studied water bodies and the highest increase of trophy was recorded during this period (zone VI and VII in core Os 94-9 and zone III in core Os 94-5). The last village was founded by people of the Globular Amphorae culture. In cladoceran diagrams, this period is represented by zone VIII in core Os 94-9 and possibly by zone IV in core Os 94-5. The cladoceran assemblages of these zones are slightly richer than in the previously studied period and suggest a partial recovery of trophic state and the plant-associated community. Moreover, they are better correlated with pollen indicators of pastures, while one of the characterized features of Globular Amphorae culture was higher importance of animal breeding (Nalepka 2004, 2005). The record from both lakes indicated the strong impact of Neolithic settlement on water biota. Even relatively low activity (extensive agriculture and animal breeding) completely changed the ecosystem dynamics.

The final periods of both fossil water bodies in existence were different. In the southern basin (core Os 94-5), termination of the lake followed period with specific cladoceran community. It was composed only of a few cladoceran taxa, i.e. *Alona rectangula*, *Chydorus sphaericus*, *Bosmina longirostris* and *Daphnia* spp. Such a species composition suggests the gradual disappearance of the lake (Szeroczyńska and Gąsiorowski 2002). Conversely, in the northeastern basin (core Os 94-9), the species diversity was relatively high until the end of the cladoceran record. Such a pattern of Cladocera decline might be related to the sudden disappearance of the water body without an intermediate stage. Both natural (e.g. climate changes) and anthropogenic (e.g. irrigation, land use changes) factors could control such an abrupt decay of a lake.

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# MALACOFAUNA OF LATE QUATERNARY LACUSTRINE DEPOSITS AT OSŁONKI (KUJAWY, CENTRAL POLAND)

Stefan Witold Alexandrowicz

Abstract. Successions of mollusc assemblages were described from two borehole cores drilled in the archaeological site at Osłonki. They indicate changes of sedimentary conditions and the environment in particular parts of the ancient melt-basin during Late Glacial and Holocene time. The section of lake sediments of pre-Allerød – Subboreal age, passing upwards into younger ones and deposited within swamps and marches, represents the south-western part of the basin. In the north-western part the deposition began some time later, but not before Allerød. Initially it took place on swampy and flooded meadows, which were transformed into a lake existing during the Early and Middle Holocene and drying up in the Late Holocene. The human impact had a substantial influence on the temporary impoverishment of the mollusc fauna.

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## INTRODUCTION

Rich and differentiated assemblages of molluscs occur in Late Vistulian and Holocene sediments filling the ancient melt-lake in Osłonki, about 20 km westward of Włocławek. They were found during excavations carried out within the framework of interdisciplinary investigations of the Early Neolithic settlement of the Linear Pottery Culture and the Lengyel Culture, an important and particularly interesting archaeological site known in this region (Nalepka 1999, 2004a,b, 2005a,b, and in this volume; Gąsiorowski, in this volume, Gąsiorowski and Nalepka 2004, Grygiel 2004, Nowaczyk and Nalepka 2005, Nowaczyk *et al.* 2002, Nowaczyk, in this volume).

Malacological study is based on 84 samples delivered to the author by Prof. B. Nowaczyk and Dr. D. Nalepka. Two sections of lacustrine deposits were taken into consideration. One of them – the borehole core "94–9", situated in the SW part of the basin is represented by 76 samples from the deepest zone of the lake (see also Tab. 3 in Nalepka, this volume). Another core ("16") characterises the SE part of the basin and includes only 8 samples (see also Tab. 4 in Nalepka, this volume). Both indicate the evolution of the lake and changes of the environment controlled by climate and human impact.

The described subfossil fauna of molluscs comprises 41 taxa (more than 11 thousand specimens). These are 14 species of land snails, 19 species of water snails and 6 species of bivalves, as well as shells of slugs identified conventionally as *Limacidae* and opercula of the water snail *Bithynia*. The following ecological groups of molluscs have been distinguished:

O – land snails typical of open environments,
M – mesophile land snails living in both shaded and open habitats,
H – higrophile snails characterising swamps and marches,
T – water molluscs connected with temporary drying up water bodies,
G – species of water basins growing with rich vegetation,
S – euryecological (indifferent) water molluscs living mainly on more or less muddy bottom.

Standard methods of malacological analysis described by Ložek (1964), Evans (1972) and the author (Alexandrowicz 1987, 1999) have been used in the present study. These are:

spectra of species (MSS) and specimens (MSI), based on the mentioned ecological groups,

indices of species constancy and domination (C-D) supplemented by their arithmetic mean (the Q index) and by normalized values ($C_i$-$D_i$),

number of taxa ($N_t$) and of specimens ($N_s$),

the Shannon-Weaver species diversity index (SWI),

malacological diagrams prepared with the special computer programme POLPAL (Walanus and Nalepka 1999, Nalepka and Walanus 2003).

Preliminary results of investigations were presented on 23 April 2004 during the scientific meeting organized by the Commission for Quaternary Palaeogeography of the Polish Academy of Arts and Sciences. Problems connected with archaeology, geomorphology, pollen analysis as well as fauna of Cladocera and molluscs have been discussed during this meeting (Alexandrowicz 2005, Gąsiorowski 2005, Grygiel 2005, Nowaczyk 2005, Nowaczyk and Nalepka 2005). The biostratigraphy and age of mollusc-bearing lacustrine sediments are based on results of pollen analysis and radiocarbon dating described by Nalepka (1999, 2004a,b, 2005a,b).

## DOMINATING AND INDICATIVE SPECIES

Few species of water molluscs are represented by more than 500 specimens reaching the highest values of C-D indices (constancy – domination) and their arithmetic mean (index Q > 20). The following ones may be quoted as most numerous components of assemblages.

*Armiger crista* (Linnaeus, 1758) [*n* = 4,318] – species living in small permanent basins within rich vegetation, both in stagnant or slow flowing water, in near-shore zones of lakes, oxbows, ponds and bays of rivers grown with water plants.

*Gyraulus laevis* (Alder, 1838) [*n* = 2,554] – snail known in Central Europe mainly from numerous localities of Late Glacial and Holocene deposits, noted recently in different types of permanent water basins.

*Valvata cristata* (Müller, 1774) [*n* = 1,236] – species inhabiting small permanent or temporary water bodies with muddy bottom or intensively grown with water plants, such as ponds, ditches, bays of lakes and slow flowing rivers, even marches.

*Hippeutis complanatus* (Linnaeus, 1758) [*n* = 657] – snail preferring hard water, living within rich vegetation in permanent basins, such as lakes, oxbows, ponds as well as bays of rivers.

*Valvata piscinalis* (Müller, 1774) [*n* = 509] – soft-water species living mainly on muddy or sandy bottom in different types of water basins.

Few other species of land and water snails, as connected with specific live conditions are particularly useful for the interpretation of environmental changes. The following ones are represented by more than 100 specimens.

*Planorbis planorbis* (Linnaeus, 1758) [*n* = 242] – hard-water species typical of shallow basins with muddy bottom, more or less overgrown with water plants, temporary drying up even for a year. These are ponds, near-shore zones of lakes and river bays, small water bodies within swamps, marshes and wet meadows episodically flooded. The species tolerates the salinity up to few promille.

*Radix peregra* (Müller, 1774) [*n* = 221] – species connected with all types of permanent or temporary water bodies with muddy bottom, living also in ditches, pools and even in swamps and flooded meadows.

*Segmentina nitida* (Müller, 1774) [*n* = 199] – snail typical of temporary water bodies found in small and shallow, episodically existing basins within wet meadows, swamps, marshes, pet-bogs and near-shore zones of lakes with changing water level.

*Anisus leucostomus* (Millet, 1813) [*n* = 136] – species inhabiting small and shallow temporary water bodies, such as ditches, paddles and pools as well as on flooded meadows in shores of lakes and bays of rivers or streams, resisting drying conditions.

*Galba truncatula* (Müller, 1774) [*n* = 128] – amphibiotic species living in small temporary water bodies, in swamps, marshes and ditches, also in flooded pastures, wet meadows and bushes.

*Vallonia pulchella* (Müller, 1774) [*n* = 202] – land snail connected with open environments, mainly with meadows on slopes and valley bottoms, also with temporary flooded wet meadows and bushes spread along sides of rivers and lakes.

*Punctum pygmaeum* (Draparnaud, 1801) [*n* = 150] – mesophile land snail inhabiting both shaded and open habitats like bushes, light deciduous forests and even meadows.

*Carychium minimum* Müller, 1774 [*n* = 128] – higrophile snail typical of wet meadows, bushes, brushwood and forests.

*Succinea putris* (Linnaeus, 1758) [*n* = 119] – species living in wet and swampy habitats in marshes, temporary flooded meadows and bushes mainly along riversides, banks of lakes or other water bodies, even within reed and bulrush.

*Vertigo antivertigo* (Draparnaud, 1801) [*n* = 105] – higrophile snail connected with wet meadows, swamps and marshes, living within mosses and grasses.

## SUCCESSIONS OF MOLLUSC ASSEMBLAGES

### South-western part of the lake

The mollusc fauna has been studied in the borehole Osłonki-9A, situated only few centimetres away of the core Osłonki 94-9 described by Nalepka (2004a, b, 2005a, b) and Gąsiorowski and Nalepka (2004). The sequence of sediments in both sections is nearly identical. The analysed material represents the interval 0.1 – 8.2 m (75 samples). A succession of 15 communities (M-1 – M-15) joined in 5 types of the fauna (F-I – F-V) has been distinguished (Table 1).

Table 1

Malacofauna of Late Quaternary sediments of the borehole core 9A from the south-western part of the melt-lake. F-I-F-V – types of the fauna, M-1–M-15 – assemblages of molluscs, m(b) – depth, Ek – ecological groups of molluscs (explanation as in Fig. 2), number of specimens: I – 1-3, II – 4-9, III – 10-31, IV – 32-99, V – 100-316

| Ek | F – | – I | | – II | | | | | – III | | | | – IV | | | – V |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | M – | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| | m (b) – | 8,25 | 6,85 | 6,25 | 5,95 | 5,05 | 4,35 | 3,74 | 3,46 | 3,36 | 2,45 | 2,17 | 1,65 | 1,39 | 1,03 | 0,55 |
| O | *Pupilla muscorum* (L.) | | | | | | | | | | | | | | | II |
| O | *Vallonia pulchella* (Müller) | | | | | I | | | | | I | | | II | I | IV |
| M | *Succinea oblonga* (Drap.) | | | | | | | | | | | | | I | | I |
| M | *Cochlicopa lubrica* (Müller) | | | | | | | | | | | | | | | II |
| M | *Vertigo alpestris* *Alder* | | | | | | | | | | | | | | | I |
| M | *Vertigo angustior* *Jeffreys* | | | | | | | | | | | | | | | II |
| M | *Punctum pygmaeum* (Drap.) | | | | | | | | | | | | | | | IV |
| M | *Limacidae* | | | | | | | | | | I | | | | | II |
| M | *Euconulus fulvus* (Müller) | | | | | | | | | | | | | | I | |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| M | *Trichia hispida* (L.) | | | | | | | | | | | | | | I | II |
| H | *Carychium minimum Müller* | | | | | | I | I | | | | | | | II | III |
| H | *Succinea putris* (L.) | | | | | I | | | | | I | | | II | II | III |
| H | *Vertigo antivertigo* (Drap.) | | | | | | | | | | | | | II | I | III |
| H | *Vallonia enniensis* (Gredler) | | | | | | | | | | | | | I | I | I |
| H | *Zonitioides nitidus* (Müller) | | | | | | | | | I | I | I | I | I | | I |
| T | *Galba truncatula* (Müller) | | | | I | | | | | | I | | I | III | II | III |
| T | *Galba occulta* (Jackiewicz) | | | | | | | I | | | | | II | | | I |
| T | *Planorbis planorbis* (L.) | | | | | | | | | I | I | | III | III | III | III |
| T | *Anisus leucostomus* (Millet) | | | | | | | | | | | | II | I | II | III |
| T | *Segmentina nitida* (Müller) | | | | | | | | | | | I | II | III | II | II |
| T | *Pisidium obtusale* (Lam.) | I | | I | | I | | | | | | | | II | I | III |
| G | *Valvata cristata* Müller | | | IV | II | IV | IV | | | | | I | II | V | IV | IV |
| G | *Acroloxus lacustris* (L.) | | | | | | | I | | | I | | I | II | I | |
| G | *Radix peregra* (Müller) | I | | I | II | III | III | III | I | I | I | II | | I | I | |

Table 1

Malacofauna of Late Quaternary... cd.

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| G | *Anisus vorticulus* (Troschel) | | | I | I | I | | | | | | | | II | | |
| G | *Armiger crista* (L.) | II | III | IV | IV | V | V | V | | IV | V | V | V | V | III | I |
| G | *Hippeutis complanatus* (L.) | | | III | III | IV | IV | III | | I | I | I | I | III | II | |
| G | *Pisidium milium* Held | | | | | I | I | I | | | | | | II | I | I |
| S | *Valvata piscinalis* (Müller) | I | I | IV | III | IV | IV | | | | | | | III | | |
| S | *Bithynia tentaculata* (L.) | | | | I | I | | I | | | I | | I | | I | II |
| S | *Bithynia – operculum* | | | | I | II | | II | | | | | I | II | II | III |
| S | *Radix ovata* (Drap.) | | | | | III | III | I | | II | II | III | III | | | |
| S | *Lymnaea stagnalis* (L.) | | | | | | I | II | I | I | I | I | I | I | I | |
| S | *Anisus contortus* (L.) | | | | I | | | | | | | | | I | II | I |
| S | *Gyraulus albus* (Müller) | | | | | | | | | | | | | II | | |
| S | *Gyraulus laevis* (Alder) | I | I | III | III | V | V | IV | | III | V | III | III | III | I | |
| S | *Planorbarius corneus* (L.) | | | | | I | I | | | | | | | I | I | I |
| S | *Unionidae* | | | | | | | | II | | | | | | | |
| S | *Sphaerium corneum* (L.) | II | II | III | II | | | | | | | | | I | I | I |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S | *Pisidium lillieborgi* Clessin | | | I | | | | | | | | | | | | |
| S | *Pisidium subtruncatum* Mal. | | | | | | | | | | | | | I | | I |
| S | *Pisidium nitidum* Jenyns | | | I | I | I | I | I | | | | | | II | | I |

**M-1** (7.0–8.2 m; samples 1–4) – a poor community of water molluscs composed of 6 species with *Sphaerium corneum* (L.) and *Armiger crista* (L.). The occurrence of *Pisidium obtusale* (Lam.), small shells similar to *P. obtusale lapponicum* Clessin – a species typical of the cold climate is noteworthy.

**M-2** (6.4–6.9 m; samples 5–10) – a quite similar very poor assemblage with *Sphaerium corneum* (L.) and *Armiger crista* (L.) and *Pisidium milium* Held.

**M-3** (6.1–6.3 m; samples 11–13) – a relatively rich community (11 taxa) characterized by numerous specimens of *Armiger crista* (L.), *Valvata cristata* Müller, *V. piscinalis* (Müller), *Hippeutis complanatus* (L.), *Gyraulus laevis* (Alder) and *Sphaerium corneum* (L.).

**M-4** (5.2–6.0 m; samples 14–22) – a similar assemblage (12 taxa) with the decreasing number of *Valvata cristata* Müller and *Sphaerium corneum* (L.).

**M-5** (4.5–5.1 m; samples 23–30) – the fauna composed of 16 species, dominated by *Armiger crista* (L.) and *Gyraulus laevis* (Alder), with few specimens of land snails.

**M-6** (3.8–4.4 m; samples 31–35) – a quite similar assemblage (12 taxa) with the increased number of *Armiger crista* (L.), *Valvata cristata* Müller and *Hippeutis complanatus* (L.).

**M-7** (3.5–3.7 m; samples 36–38) – a similar community (13 taxa) with numerous specimens of *Armiger crista* (L.) and *Gyraulus laevis* (Alder), devoid of *Valvata cristata* Müller and *V. piscinalis* (Müller).

**M-8** (3.4–3.5 m; sample 39) – fragments of shells of *Unionidae* accompanied by few specimens of water snails.

**M-9** (2.6–3.4 m; samples 40–48) – poor fauna (8 taxa) with *Armiger crista* (L.) and *Gyraulus laevis* (Alder).

**M-10** (2.3–2.5 m: samples 49–51) – a similar fauna (14 taxa) with distinctly increased number of the two last mentioned species, enriched in few specimens of land snails.

**M-11** (1.8–2.2 m; samples 52–57) – a quite similar assemblage (9 taxa) distinctly dominated by *Armiger crista* (L.).

**M-12** (1.4–1.7 m; samples 58–60) – the fauna with *Armiger crista* (L.), *Gyraulus laevis* (Alder) and *Radix ovata* (Drap.), enriched in species characterising temporary water bodies, such as *Planorbis planorbis* (L.) (15 species).

**M-13** (1.1–1.4 m; samples 61–64) – a rich and differentiated assemblage (28 taxa) dominated by *Armiger crista* (L.) and *Valvata cristata* Müller, with the significant content of snails living in temporary water bodies: *Planorbis planorbis* (L.), *Segmentina nitida* (Müller), *Galba truncatula* (Müller), and with the admixture of higrophile land snails.

**M-14** (0.7–1.0 m; samples 65–69) – the fauna enclosing 25 species, with most numerous specimens of *Valvata cristata* Müller and *Planorbis planorbis* (L.).

**M-15** (0.1–0.6 m; samples 71–75) – a differentiated mollusc community (30 taxa) dominated by species of temporary water bodies, higrophile and mesophile snails, as well as land snails typical of open habitats, with numerous specimens of *Valvata cristata* Müller, *Planorbis planorbis* (L.), *Galba truncatula* (Müller), *Vertigo antivertigo* (Drap.), *Punctum pygmaeum* (Drap.), and *Vallonia pulchella* (Müller).

In the described sequence of mollusc assemblages, the number of taxa (Nt) and of specimens (Ns) in particular samples change distinctly (Fig. 1). The two first communities (M-1, M-2) are poorest ones. In samples 1-10, values Nt are 3 or 4 and Ns do not exceed 20. In two next communities (M-3, M-4; samples 11–22) both indices increase up to 10 and 100, respectively, while in assemblages M-5 – M-7 (samples 23–38) the number of species remains the same but the number of specimens reaches the highest values (about 200–500). The sample 39 (M-8) is the poorest one and in the next 9 samples (M-9) both indices stay still in low position (4 – 5 and 20 – 50). They increase in communities M-10 and M-11 (samples 49–57), but the main enrichment of the mollusc fauna falls in the uppermost part of the sequence (M-12 – M-15, samples 57–75). In this interval, the number of specimens oscillates between 20 and 250. Four intervals can be distinguished according to the Shannon-Weaver species diversity index (Din). The first one is characterized by low values (1.3–2.0) and corresponds with assemblages M-1 and M-2, the second one (of somewhat higher values: 1.6–2.6) with assemblages M-3 – M-7, the next one (1.0–1.8) with communities M-8 – M–11, while the last interval – with the youngest communities (M-12 – M-15), which are most differentiated (1.7–3.8). The three mentioned indices are related one to another to a large degree (Fig. 1).

The distribution of particular taxa within the described succession is clearly visible on malacological diagram (Fig. 2). Two species of water snails (*Armiger crista* and *Gyraulus laevis*) dominate in the whole sequence except its upper part. In the lowermost segment the occurrence of *Sphaerium corneum* is noteworthy. Few species are numerous in two intervals (*Valvata piscinalis*, *V. cristata*, *Hippeutis complanatus*), while the uppermost part of the succession is characterized by land snails and species of temporary water bodies.

Malacological spectra of species (MSS) and of specimens (MSI) reflect the content of particular ecological groups of molluscs in the described assemblages (Fig. 3). The most distinct limit falls between communities M-11 and M-12. Molluscs of two groups: S – molluscs living in stagnant water basins and G – typical of water bodies grown with plants, constitute the fauna of the lower and middle parts of the sequence (M-1 – M-11). The admixture of land snails marked on MSS spectra (M-5 – M-7 and M-9 – M-11) is

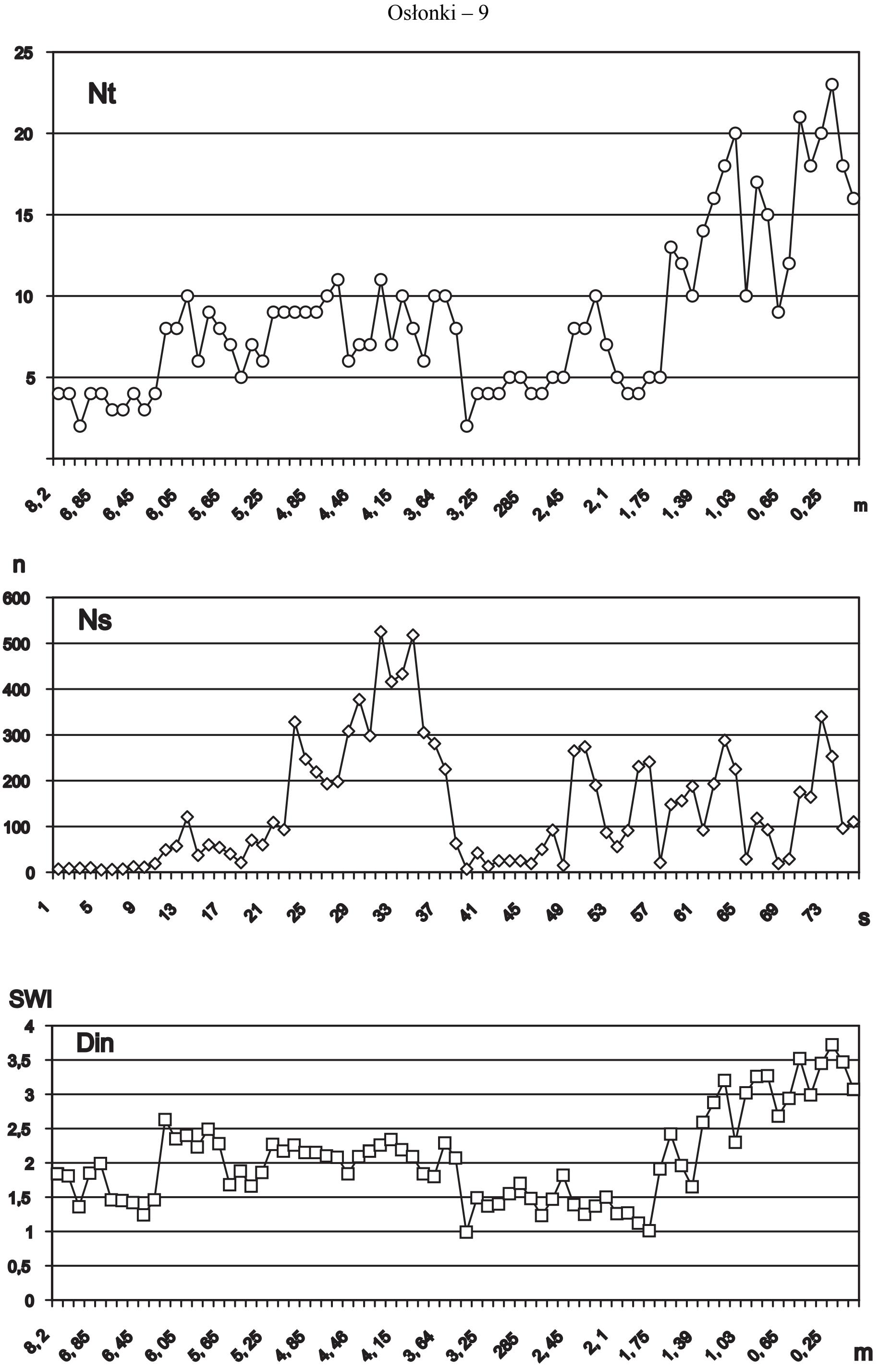

Fig. 1. Main indices of mollusc assemblages from the borehole core 9 (south-western part of the melt-lake). Nt – number of taxa, Ns – number of specimens, Din – species diversity index (after Shannon and Weaver). m – depth in metres, s – number of sample

Osłonki – 9A

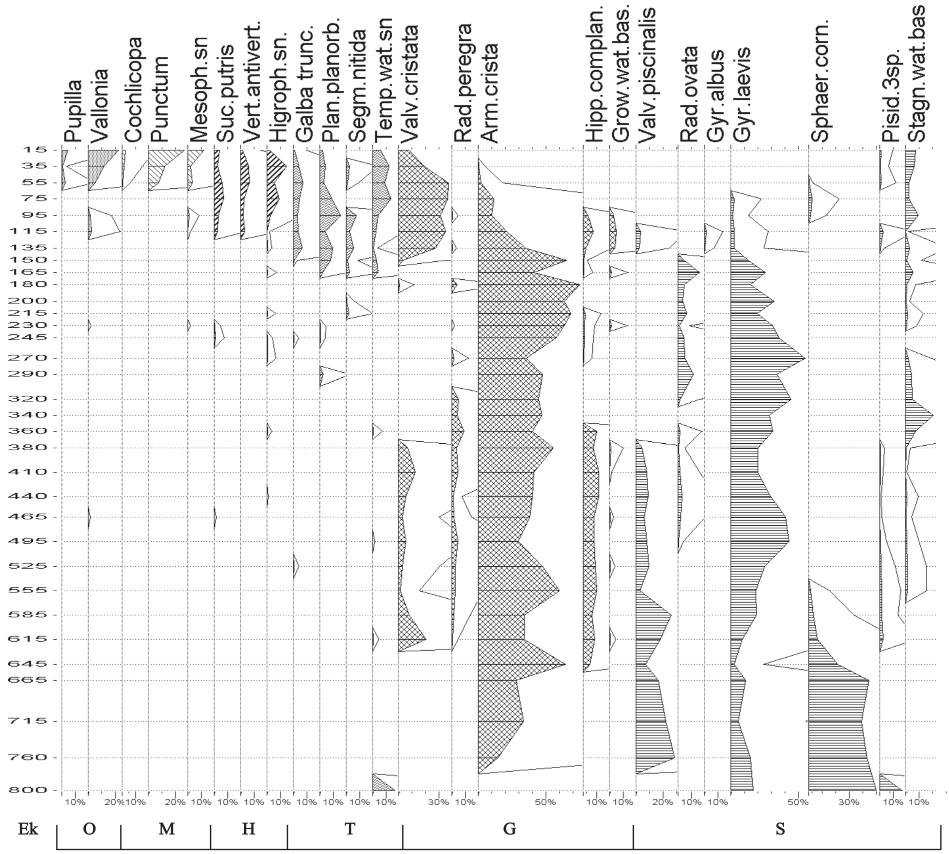

Fig. 2. Malacological diagram of the borehole core 9A (south-western part of the melt-lake). Ek – ecological groups of molluscs: O – open-country snails, M – mesophile species, H – higrophile molluscs, T – species of temporary water bodies, G – molluscs preferring water basins with rich vegetation, S – indifferent water molluscs

derived from the waterside surrounding the lake. The increasing content of molluscs (species and specimens) of temporary water bodies and later also land snails in the upper and the uppermost part of the section (M-12 – M-15) corresponds with the final stage of the lake. It became gradually filled with sediments, grown and alternated into a swamp, pet-bog and wet meadow with small episodic water bodies.

The mentioned assemblages of molluscs can by grouped in five types of fauna, which reflect the main phases of transformation of sedimentary and ecological environment. Indices of constancy and domination (C-D) as well as the Q-index were used to indicate much important and characteristic species (Table 2).

**F-I** (M-1, M-2) – the initial phase of the shallow water basin unfavourable for molluscs developed in the cold climate of the Late Vistulian – indicative species: *Armiger crista*, *Sphaerium corneum*, *Valvata piscinalis.*

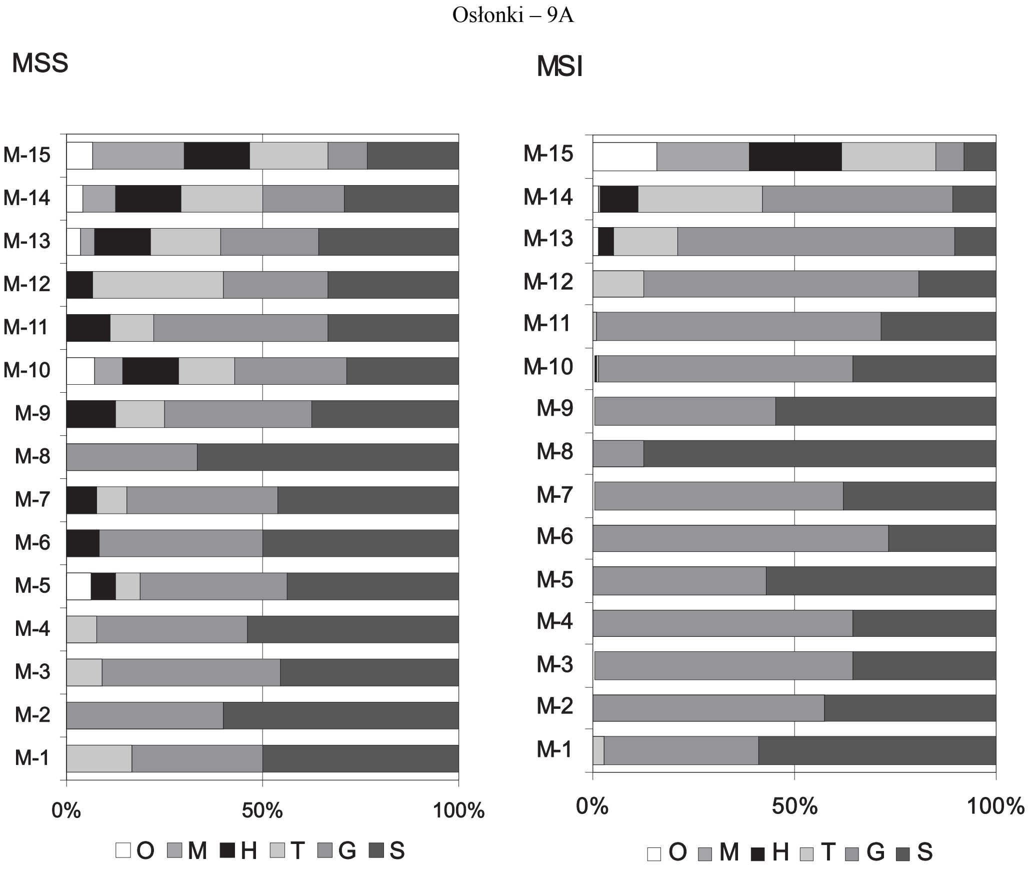

Fig. 3. Malacospectra of mollusc communities from the south-western part of the melt-lake. MSS – spectra of species, MSI – spectra of specimens, M-1–M-15 – assemblages of molluscs, O-M-H-T-G-S – ecological groups of molluscs (explanation as in Fig. 2)

**F-II** (M-3 – M-7) – the amelioration of ecological conditions subsequently to the warming of the climate during the Early Holocene – indicative species: *Armiger crista*, *Gyraulus laevis*, *Hippeutis complanatus*, *Valvata piscinalis*, *V. cristata.*

**F-III** (M-8 – M-11) – the substantial impoverishment of the fauna caused by human impact followed by the improvement of live conditions, which became more favourable for water snails in the mild climate of the Middle Holocene – indicative taxa: *Armiger crista*, *Gyraulus laevis*, *Radix peregra.*

**F-IV** (M-12-M-14) – at the termination of the Middle Holocene and during the Subboreal Phase, the lake become more and more shallow with the enlarged near-shore zone controlled by fluctuations of the water level – indicative species: *Armiger crista*, *Valvata cristata*, *Planorbis planorbis*, *Gyraulus laevis.*

**F-V** (M-15) – the final phase of the lake transformed gradually into swamps, marches and meadows – indicative species: *Valvata cristata*, *Punctum pygmaeum*, *Vallonia pulchella*, *Carychium minimum*, *Vertigo antivertigo.*

Table 2

Indices of constancy (C-1–C-5) and domination (D-1–D-5) of species. F-1–F-V – types of the fauna, Q – arithmetic mean of C-D

| F-I | D-1 | D-2 | D-3 | D-4 | D-5 |
|---|---|---|---|---|---|
| C-5 | | | | | 2 |
| C-4 | | | | 1 | |
| C-3 | | 1 | | | |
| C-2 | 3 | | | | |
| C-1 | | | | | |

| | |
|---|---|
| 5-5 – *Armiger crista* | Q = 68,4 |
| 5-5 – *Sphaerium corneum* | Q = 56,5 |

| F-II | D-1 | D-2 | D-3 | D-4 | D-5 |
|---|---|---|---|---|---|
| C-5 | | | 3 | | 2 |
| C-4 | 1 | 1 | | | |
| C-3 | | | | | |
| C-2 | 3 | 1 | | | |
| C-1 | 13 | | | | |

| | |
|---|---|
| 5-5 – *Armiger crista* | Q = 64,8 |
| 5-3 – *Hippeutis complanatus* | Q = 29,8 |
| 5-3 – *Valvata piscinalis* | Q = 26,4 |
| 5-3 – *Valvata cristata* | Q = 23,6 |

| F-III | D-1 | D-2 | D-3 | D-4 | D-5 |
|---|---|---|---|---|---|
| C-5 | | | | | 2 |
| C-4 | | 2 | | | |
| C-3 | | 1 | | | |
| C-2 | 1 | | | | |
| C-1 | 11 | | | | |

| | |
|---|---|
| 5-5 – *Armiger crista* | Q = 75,9 |
| 5-5 – *Gyraulus laevis* | Q = 54,2 |
| 4-2 – *Radix peregra* | Q = 21,7 |

| F-IV | D-1 | D-2 | D-3 | D-4 | D-5 |
|---|---|---|---|---|---|
| C-5 | | 1 | 2 | | 2 |
| C-4 | | 2 | | | |
| C-3 | 3 | 5 | | | |
| C-2 | 9 | 3 | | | |
| C-1 | 7 | | | | |

| | |
|---|---|
| 5-5 – *Armiger crista* | Q = 55,1 |
| 5-5 – *Valvata cristata* | Q = 45,9 |
| 5-3 – *Planorbis planorbis* | Q= 27,4 |
| 5-3 – *Gyraulus laevis* | Q = 23,8 |

| F-V | D-1 | D-2 | D-3 | D-4 | D-5 |
|---|---|---|---|---|---|
| C-5 | | 7 | 2 | 2 | 1 |
| C-4 | 3 | 3 | | | |
| C-3 | 1 | 2 | | | |
| C-2 | 5 | | | | |
| C-1 | 4 | | | | |

| | |
|---|---|
| 5-5 – *Valvata cristata* | Q = 47,2 |
| 5-4 – *Punctum pygmaeum* | Q = 36,3 |
| 5-4 – *Vallonia pulchella* | Q = 33,9 |
| 5-3 – *Carychium minimum* | Q = 27,5 |
| 5-3 – *Vertigo antivertigo* | Q = 23,2 |

Normalized values of constancy (Ci) and domination (Di)

| | | Ci | Di |
|---|---|---|---|
| | F-I | 57,3 | 43,0 |
| | F-II | 31,2 | 16,6 |
| | F-III | 25,1 | 16,2 |
| | F-IV | 39,7 | 16,9 |
| | F-V | 64,2 | 21,7 |

Different normalized values of constancy and domination ($C_i$ and $D_i$) characterize the distinguished types of the fauna. Low values of these indices correspond with assemblages of differentiated fauna with numerous species, while high values – with communities dominated by a limited number of species (Table 2).

The described succession of mollusc assemblages reflects changes of the environment in the western part of the ancient melt-lake since the Pre-Allerød up to the Late Holocene (Nalepka 2005b), both of ecological and sedimentary conditions. In the initial stage it was a shallow water basin with muddy bottom, inhabited by a poor community composed of few species of snails and bivalves, represented by a small number of specimens (F-I). During the Early Holocene it was just a lake grown by water plants. Ecological conditions ameliorated gradually and the mollusc fauna became more and more rich and differentiated (F-II). The human impact connected with the Neolithic settlement disturbed the ecological balance of the lake and caused a considerable impoverishment of the mollusc fauna (F-III). Assemblages with species typical of temporary water bodies and with numerous land snails (F-IV, F-V) correspond with the final stages of the evolution of the mentioned water basin falling to the Late Holocene.

## North-eastern part of the lake

The section Osłonki-16, documented by 8 samples, encloses mollusc-bearing lake sediments 4 m thick. The succession of 5 communities (M-1 – M-5) has been distinguished in these sediments (Table 3).

Table 3

Malacofauna of Late Quaternary sediments of the borehole core 16 from the north-eastern part of the melt-lake (explanation as in Table 1)

| Ek | M – | – I | – II | – III | | | – IV | | – V |
|---|---|---|---|---|---|---|---|---|---|
| | S – | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| | m – | 3,5-4,0 | 3,0-3,5 | 2,5-3,0 | 2,0-2,5 | 1,5-2,0 | 1,0-1,5 | 0,5-1,0 | 0,2-0,5 |
| O | *Pupilla muscorum* (L.) | II | | | | | | | |
| O | *Vallonia pulchella* (Müller) | | | | | | III | III | IV |
| M | *Cochlicopa lubrica* (Müller) | | | | | | | | II |
| M | *Euconulus fulvus* (Müller) | | | | | | I | I | |
| M | *Trichia hispida* (L.) | | | | | | I | I | II |
| H | *Carychium minimum Müller* | | | | | | | II | III |
| H | *Succinea putris* (L.) | I | | | | II | III | II | III |
| H | *Vertigo genesii* (Gredler) | III | | | | | | | |
| H | *Vertigo antivertigo* (Drap.) | | | | | | | I | III |
| H | *Vallonia enniensis* (Gredler) | | | | | | II | | |
| H | *Zonitioides nitidus* (Müller) | | | | | | II | I | |
| T | *Aplexa hypnorum* (L.) | | | | | | I | | |

Table 3

Malacofauna of Late Quaternary... cd.

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| T | *Galba truncatula* (Müller) | | | | | | III | II | II |
| T | *Galba occulta* (Jackiewicz) | | | | I | II | I | II | II |
| T | *Planorbis planorbis* (L.) | | | | II | II | III | III | IV |
| T | *Anisus leucostomus* (Millet) | | | | | | | | IV |
| T | *Segmentina nitida* (Müller) | | | II | III | III | III | III | IV |
| T | *Pisidium obtusale* (Lam.) | | | | | | | II | III |
| G | *Valvata cristata Müller* | | III | IV | III | II | III | IV | IV |
| G | *Acroloxus lacustris* (L.) | | | | | I | II | | |
| G | *Radix peregra* (Müller) | | II | I | III | II | | | |
| G | *Anisus vorticulus* (Troschel) | | | | | III | | | |
| G | *Armiger crista* (L.) | | III | IV | IV | IV | IV | IV | III |
| G | *Hippeutis complanatus* (L.) | | | I | III | II | | | |
| G | *Pisidium milium Held* | II | | | | I | I | II | |
| S | *Valvata piscinalis* (Müller) | | | III | II | | | II | |
| S | Bithynia tentaculata (L.) | | | I | | | | I | I |
| S | *Bithynia – operculum* | | | II | I | | | III | III |
| S | *Radix ovata* (Drap.) | | | I | II | III | III | II | |
| S | *Lymnaea stagnalis* (L.) | | | | | II | I | I | I |
| S | *Anisus contortus* (L.) | | | | | | | III | III |
| S | *Gyraulus albus* (Müller) | | | | I | I | II | | |
| S | *Gyraulus laevis* (Alder) | | I | III | III | III | V | IV | |
| S | *Planorbarius corneus* (L.) | | | | | II | II | | |
| S | *Unionidae* | | | | I | | | | |
| S | *Sphaerium corneum* (L.) | | II | | | | | | I |
| S | *Pisidium subtruncatum* Mal. | II | | | | | | II | I |
| S | *Pisidium nitidum Jenyns* | | | I | III | I | | | |

**M-I** (3.5–4.0 m; sample S-1) – a poor assemblage composed of land snails (3 species) and bivalves (2 species), with a considerable content of *Vertigo genesii* (Gredler), the species typical of Late Glacial living in moist habitats.

**M-2-II** (3.0–3.5 m; sample S-2) – the fauna of snails living in temporary water bodies with the admixture of *Sphaerium corneum* (L.).

**M-III** (1.5–3.0 m; samples S-3 – S-5) – a community of molluscs dominated by *Armiger crista* (L.) with a considerable content of species living in temporary water basins.

**M-IV** (0.5–1.5; samples S6 – S-7) – differentiated fauna with numerous specimens of *Armiger crista* (L.), *Gyraulus laevis* (Müller) and species of temporary water bodies with an admixture of land snails.

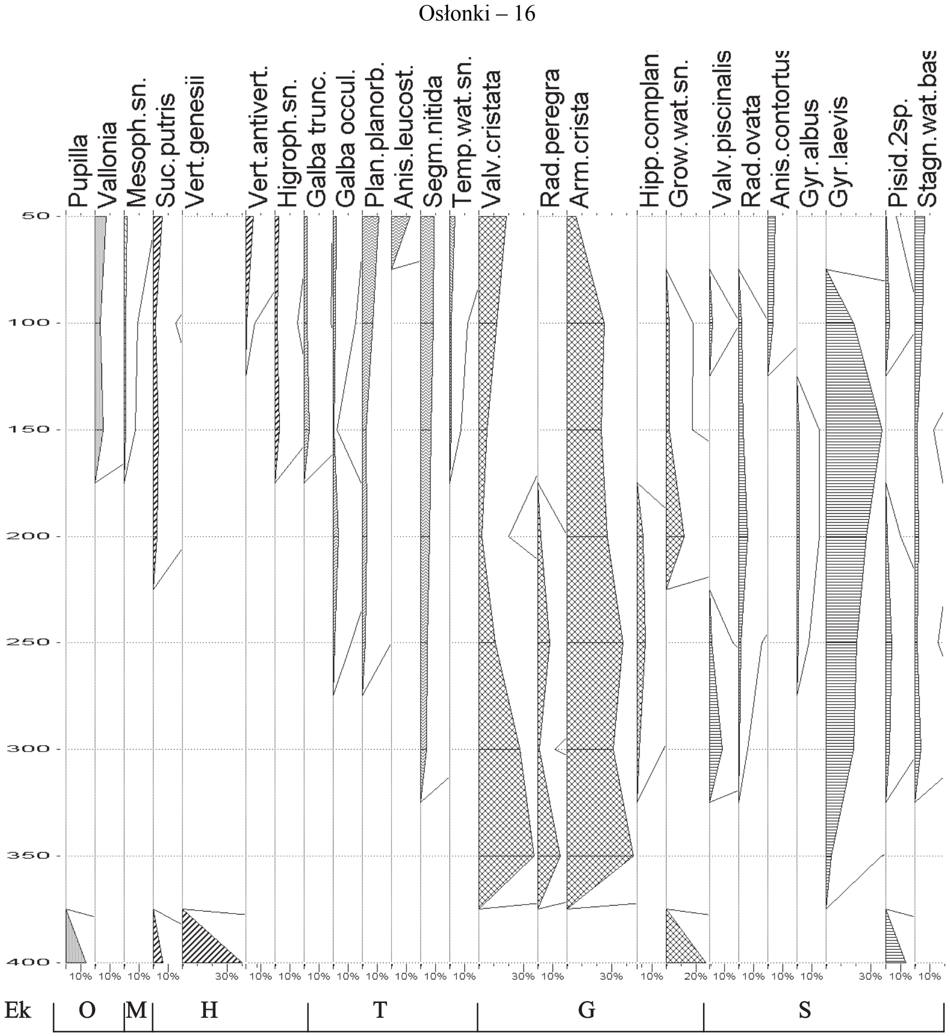

Fig. 4. Malacological diagram of the borehole core 16 (north-eastern part of the melt-lake). Explanation as in Fig. 2

**M-V (**0.2 – 0. 5m; sample S-8) – an assemblage of water and land snails dominated by *Planorbis planorbis* (L.), *Anisus leucostomus* (Millet), *Valvata cristata* Mülller, *Segmentina nitida* (Mülller), and *Vallonia pulchella* (Mülller).

The number of species and specimens in the lower part of this sequence does not exceed 5 (Nt) and 35 (Ns), in the middle part – 17 and 250, while in the upper part it attains 20–23 and 330–430, respectively. Similarly, the species diversity index (SWI) increases upward from 2.0 up to 2.8, and finally to 8.3.

Malacological diagram reflects the distribution of particular taxa in the mentioned succession (Fig. 4). Higrophile snails: *Vertigo genesii* and *Succinea putris* are most

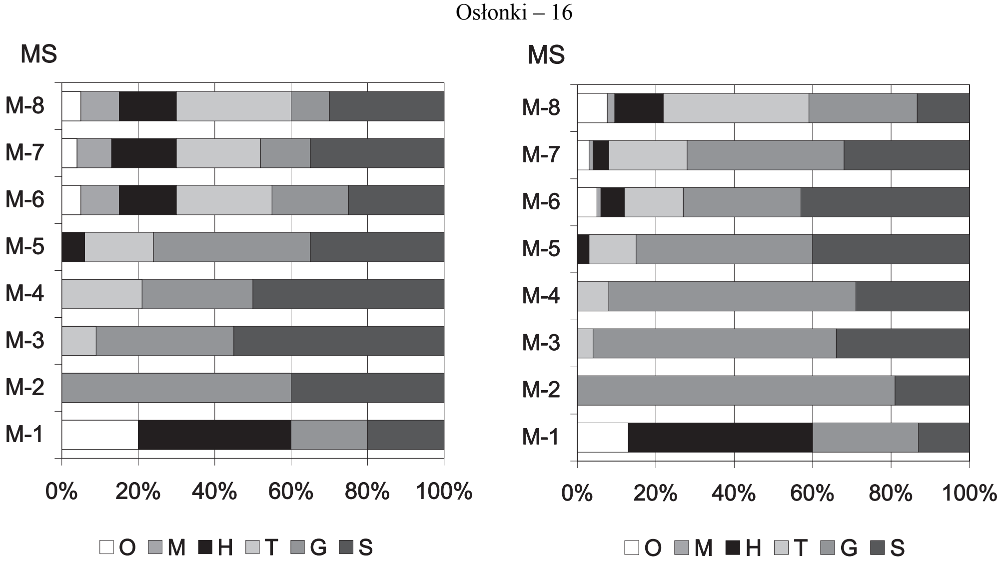

Fig. 5. Malacospectra of mollusc communities from the north-eastern part of the melt-lake. Explanation as in Fig. 2

typical in the lowermost part of the sequence, while three species of water snails: *Armiger crista*, *Gyraulus laevis* and *Valvata cristata* dominate in its middle part. The last mentioned species reaches a considerable content two times and snails connected with temporary water bodies as well as land snails close the succession.

Malacological spectra of species (MSS) and specimens (MSI) characterise main changes of mollusc assemblages and subsequently the phases of development and transformation of the water basin (Fig. 5). During the initial phase in the Allerød, the environment was particularly suitable for land sails connected with moist habitats (M-I). In the next one the fauna had been dominated by water molluscs (M-II – M-III) and later the content of snails living in temporary water bodies as well as of land snails increased gradually (M-IV – M-V). Changes reflecting the human impact are not clearly expressed in this sequence of mollusc assemblages.

## INTERPRETATION

The shaping and evolution of the melt-lake in Osłonki are reflected by successions of differentiated mollusc assemblages found in two borehole cores of Late Quaternary lacustrine sediments. During the Late Vistulian, subsequently to the advanced deglaciation in the south-western part of the area, a depression with a water body developed gradually above the buried blocks of dead ice. It was soon transformed into a shallow permanent water basin with muddy bottom and ecological conditions unfavourable for molluscs, which stayed without considerable changes up to the termination of the

Younger Dryas. The poor mollusc fauna F-I from the core "9A" characterises this first stage of the lake. Warming of climate in the Allerød led to a gradual spreading of the mentioned melt-depression. In its north-eastern part, temporary flooded swamps and marches had been developing at that time to be transformed into a water body grown with rich vegetation. Poor communities of molluscs with land snails and later with species living within water plants, found in the lower part of the borehole "16", correspond with this episode (M-I, M-II).

During the Early Holocene, the lake was just stabilised and reached a depth exceeding 5 m, being overgrown by macrophytes and inhabited by relatively rich and differentiated assemblages of molluscs. In its south-western part the fauna was dominated by species typical of permanent water basins. Live conditions, which were initially less favourable, improved with time and the number of specimens increased three- up to five-times (F-II, M-3 – M-4 → M-5 – M-7). In the north-western part of the lake, a considerable admixture of snails living in temporary water bodies indicates fluctuations of the water level in the near-shore zone of the basin (M-III).

Ecological crisis marked distinctly in mollusc communities found in borehole "16" is assigned to the Atlantic Phase of the Holocene, and was connected with the activity of man, namely with Neolithic settlement situated close to the shore of the lake. It is possible that some species of bivalves (*Unionidae*) have been episodically utilised as food and their shells were found in one sample (M-8). The number of species and specimens decreased considerably up to the lowest level, subsequently with values of the differentiation index, which do not exceed 1.6 (F-III). Shells of *Unionidae*, which were found only in one sample (M-8), may be connected with utilisation of these relatively big bivalves as food. Fluctuations in the number of specimens reflect a temporary diminishing of the human impact (M-10). Species typical of permanent water basins dominate in the south-western part of the depression, while in its north-western part the content of molluscs typical of temporary water bodies and higrophile snails or even other land snails increase markedly (F-III, M-IV). These differences indicate this part of the lake, which at that time became gradually shallower, temporary drying up and even passing into swamps and marches.

During the Late Holocene, the same changes spread just over the whole lake and simultaneously ecological conditions ameliorated. In the south-eastern part of the depression, the communities of molluscs became more rich and differentiated and the number of both species and specimens as well as values of the differentiated index increased considerably. The relatively high content of snails connected with temporary water bodies and higrophile land snails reflect the terminal phase of the lake evolution, which had been transforming first into swamps with temporary water bodies, and finally into marches and wet meadows (F-IV, F-V). The described differences between successions of mollusc assemblages in two analysed boreholes ("9A" and "16") correspond with the course of evolution and transformation of this ancient melt-lake, as indicated by lithology of sediments as well as by pollen and cladoceran analyses (Gąsiorowski 2005, Nalepka 2005a, b, Nalepka and Nowaczyk 2005, Nowaczyk 2005).

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# THE SCULPTURE OF ELYTRA IN SPECIES FROM THE FAMILY DYTISCIDAE (INSECTA: COLEOPTERA) AS A DIAGNOSTIC FEATURE FOR THE IDENTIFICATION OF SUBFOSSIL MATERIAL

Mieczysław Mazur and Daniel Kubisz

Abstract. Three categories of the elytral sculpture in the dorsal area of 138 central European Dytiscidae species have been distinguished, i.e.: macrosculpture, first-degree microsculpture, and second-degree microsculpture. On the basis of a kind, arrangement, and quantitative proportions of eight sculpture elements (punctures, sulci, clefts, granules, areas, stripes, carinae and folds), 14 types and 39 varieties of the sculpture have been described. Additionally, sexual dimorphism of and seven other types of the sculpture, not related to the sex have been distinguished. Importance of the discussed sculpture features for the identification of the subfossil Dytiscidae remains was stressed. Using the diagnostic features, a key for identification of subfossil Dytiscidae was compiled.

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## INTRODUCTION

The numerous and widely distributed family Dytiscidae is also numerously represented in the fossil material. The oldest remnants of contemporary species originate from the Upper Miocene (Galewski and Głazek 1973, 1978) and in the Quaternary deposits (and particularly Holocene ones) they are regularly found (Coope, 1969; Elias, 1983; Lemdahl, 1988; Nazarov, 1984; Pawłowski *et al.*, 1987; Pearson, 1963). The remnants of Dytiscidae have been preserved in large amounts because these beetles lived in the environments (i.e. different water reservoirs), which provided particularly favourable conditions for fossilisation.

The aim of this study is to describe the diverse and variable sculpture of the dorsal area of elytra in Dytiscidae (Fig. 1.1). Difficulties in identifying the subfossil remnants of these beetles inclined us to deal with this problem. The existing descriptions are based mainly on features that have not been preserved in fossils, such as the structure of legs and ventral part of the body. Specimens found in the Quaternary deposits are usually much damaged and incomplete, and single elytra constitute large part of the material (Nazarov 1984). Keys for the identification of the contemporary members of this family (e.g. Franciscolo 1979, Schaeflein 1971, Zaitsev 1953) treat the body sculpture as one of many diagnostic features, particularly useful on a species level. In addition, the interpretation of different structures is unsatisfactory, as shown by a poor nomenclature used for the description of strongly differentiated elements and types of the sculpture.

For the identification of the subfossil Dytiscidae one may use also other features which do not change during the process of fossilisation (e.g. colour of the cuticle) or which can be reconstructed on the basis of the preserved fragments (size, shape), but their significance is smaller than that of the body sculpture.

The results of the present paper are to make the identification of the subfossil remnants of Dytiscidae easier. In some cases it is possible to identify the remnants to the species level, in others only to the group of species of the same genus or different genera. Some elements of the body sculpture were already used for the identification of subfossil material by some authors (e.g. Lemdahl and Nilsson 1982). Also Nakane (1999), describing the diversity of microsculpture in 24 of the 100 Japanese species, stressed its diagnostic significance. However, researchers dealing with this problem have not introduced any uniform system for the classification of microsculpture, which could simplify its characterisation.

The authors hope that the presented method of describing and grouping the sculpture elements of elytra allows one to add to the key other, not included species of Dytiscidae in this study, which may occur in the fossil material. In the future the described system should also be applied for the identification of species from other groups of beetles, which have the sufficiently diverse microsculpture. To this aim, it is possible to use other study techniques, in addition to simple observation under the microscope (Khalaf 1980).

## MATERIAL AND METHODS

The results obtained are based on more than 3,000 specimens examined; they represent 138 central European species of Dytiscidae (Table 1). The binocular magnifying glass (100 ×) was used for describing the elements, types and varieties of the sculpture. The magnification used is optimal for an analysis of the first-degree microsculpture. In some cases of the second-degree microsculpture it appeared too small, but this element is rarely used for the identification. Macrostructures occurring only in few species are usually well visible with the naked eye (e.g. carinae in females of the genus *Dytiscus*) or at least noticeable in the bright light (carinae and stripes in the species of the genus *Colymbetes*); the 25 × magnification is sufficient to describe them.

The material used in this work originated from the collection housed in the Museum of Natural History, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland.

## RESULTS

### Elements of sculpture

In the family Dytiscidae, among the 139 examined species, the eight principal components of sculpture, named the elements, were distinguished. Differences between these elements are, generally, rather well marked and only in case of some species it may be difficult to assign them to the categories distinguished. These are:

– Punctures – isodiametric or slightly elongated depressions with more or less sharp edges (this last feature make them different from hollows). In terms of the shape there are rotund, oval, inversely oval, elliptical, spindle-shaped, lanceolate, kidney-shaped and irregular punctures distinguished (Fig. 1.2). Also, the hollows differ in shape, which allows one to distinguish flat-bottomed, conical, alveolate and bowl-shaped punctures (Fig. 1.3). The flat-bottomed punctures have, contrary to the remaining three categories, a relatively large area of the bottom, usually only slightly smaller than the diameter of the puncture. It should be stressed, however, that the 100 × magnification not always allows one to describe univocally the type of a hollow; that is why this feature has been neglected in the characteristics of some varieties of the puncture sculpture. To estimate the depth of punctures, a comparison with a three-grade scale is needed. This scale is formed by three selected species: shallow punctures – *Suphrodytes dorsalis*; punctures

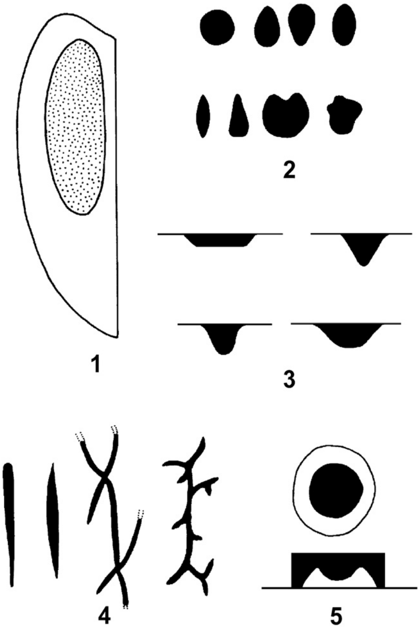

Fig. 1. 1 – localization of the dorsal area on the elytron; 2 – shape of the punctures, in dorsal view; 3 – shape of the punctures depression; 4 – shape of the sulci; 5 – crater-like granule, in dorsal view and in vertical section

of medium depth – *Hydroporus tristis*; deep punctures – *Hygrotus impressopunctatus*. The punctures are one of the most frequent elements of the sculpture of the elytra.

– Sulci (grooves) – trough-like or cleft-like depressions of different length and width. Their depth is much variable within the family. On account of the outline they may be divided into two groups: simple and branched (fork-like branched) grooves (Fig. 1.4). The branches of the sulci are in some types of the sculpture connected with each other, forming sinuous channels or the irregular reticulum. The sulci are elements of the micro- and macrosculpture in many species of Dytiscidae.

– Clefts – delicate, shallow incisions in the form of short and straight lines or long and sinuous lines. In many cases they turn continuously into sulci, and like these they enter into the composition of a few types of the sculpture.

– Granules – arcuate convexities with a more or less rotund base. They occur only in spaces between carinae in females of the species from the genus *Acilius*. They are provided with a relatively large central point, that is why they are named crater-like granules (Fig. 1.5). They have a typical form only in the central part of the space between carinae, whereas closer to the carinae they become flat and turn into large flat-bottomed punctures, often with rod-like margins. All the crater-like granules, seen from above, look like emarginate punctures.

– Areas – vari-form fragments of the surface of elytra, delimited by clefts and sulci. There were isodiametric (length = width), elongate (length < width) and transverse (length > width) areas distinguished. If it is impossible to determine the front and back

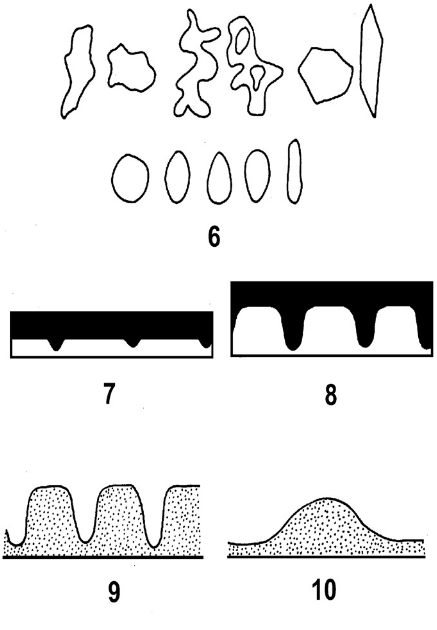

Fig. 2. 6 – shape of the areas; 7 – stripe cross section; 8 – carina, cross section; 9-10 – shape of the dorsal curvature of the carina

in the examined remain of a elytron, these last two groups are given a common name of the elongate areas. These areas are most often irregular in shape (fork-like branched or not branched); they are rarely polygonal, rotund, elliptical, oval, inversely oval and longitudinally rectangular (Fig. 2.6). Clefts and sulci separating the areas may be of equal or unequal width.

– Stripes – linear, strongly elongate areas on the body surface, separated from each other by relatively shallow and narrow sulci. Their width is at least several times bigger than the width of sulci (Fig. 2.7). They occur only in the genus *Colymbetes*. They are placed transverse on the elytra, and in some places their pattern is disturbed by more or less numerous ramifications of these elements (Fig. 3.13). On account of the considerable length of stripes, amounting to several millimetres, they are reckoned among the elements of the macrosculpture.

– Carinae – longitudinal or transverse, clearly convex listels separated from each other by deeply hollowed, narrow or wide, folds (Fig. 2.8). They differ from stripes in, above all, length. Taking into account the shape of carinae on the cross-section, one may distinguish: flattened carinae on the top and arcuately convex carinae (Fig. 2.9-10). The length of carinae, amounting to at least 10 mm, qualifies them among the elements of macrosculpture.

– Folds – narrow and low, elongate rodlike swellings, often branched (Fig. 8.44); in places they may turn into clefts or even sulci. These elements of sculpture were found only in male *Cybister lateralimarginalis*.

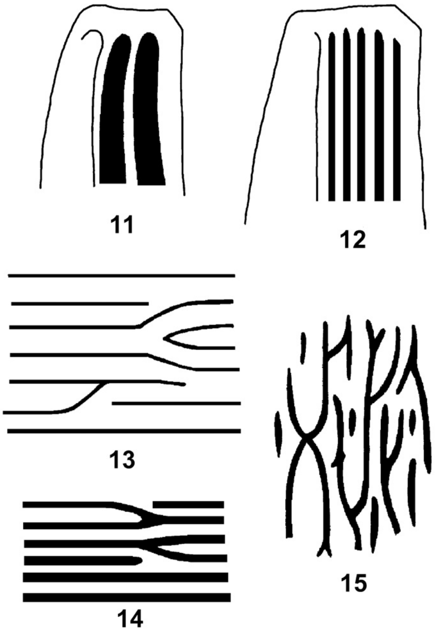

Fig. 3. 11 – longitudinal carinae in the macrosculpture Cr3; 12 – longitudinal carinae in the macrosculpture Cr1; 13 – stripe-like sculpture; 14 – transverse carinae in the macrosculpture Cr2; 15 – sulcate macrosculpture

The differentiation in size of the described elements allows one to distinguish three levels of the sculpture: macrosculpture (Ma), first-degree microsculpture (Mi1) and second-degree microsculpture (Mi2). The macrosculpture is formed by elements more than 1 mm long (carinae, stripes, sulci), which are not contained as a whole in the dorsal area. The first-degree microsculpture is composed of elements, the size of which is within a range of 0.06-0.01 mm; they usually occupy only small part of the dorsal area. All elements which are below 0.01 mm in size represent the second-degree microsculpture. They occur on the surface of Mi1 elements or fill spaces between them.

## Types and varieties of sculpture

The classification of sculpture among types and varieties is based on the kind and arrangement of its elements. In addition to the basic sculpture (background sculpture) covering the entire surface, in most of the examined species, in the dorsal area there is also the supplementary sculpture, formed by longitudinal rows of punctures or grooves. The size of punctures in the rows, their shape and arrangement, as well as the length of grooves are varied, which may be used for the identification of subfossil remains. This question needs, however, a further study; that is why it is treated in this work only marginally (Table 1). Generally, 14 (for the most part distinctly marked) types of the basic sculpture have been distinguished:

1. Carinate sculpture (Cr, Ma) – composed of parallel carinae, separated by cleft-like or trough-like, very wide sulci. It occurs in three varieties:

Cr1 (Fig. 3.12). Carinae longitudinal, wide, high, flattened, usually with distinct edges, not branched, sometimes connected with each other at a short distance. In the dorsal area five-six carinae are visible. Sulci, separating the carinae, narrow and deep, cleft-like.

Table 1

The sculpture of the dorsal area in species from the family Dytiscidae (nomenclature after Löbl and Smetana 2003). C – channel sculpture; Cr – carinate sculpture; G – granulate sculpture; Ma - macrosculpture; Mi1 – first-degree microsculpture; Mi2 – second-degree microsculpture; P – punctate sculpture, Pd – row punctures in the supplementary sculpture; [Pd] – row punctures barely visible; Pg – polygonal sculpture; Pl – fold sculpture; PR – punctate-reticulate sculpture; PS – punctate-sulcate sculpture; PSq – punctate-squamous sculpture; R – reticulate sculpture; S – sulcate sculpture; SC – sulcate-channel sculpture; Sd – sulci in the supplementary sculpture; Sq – squamous sculpture; SP – sulcate-punctate sculpture; St – stripe-like sculpture; 1–16 – sculpture varieties; + – sculpture weakly differentiated; – sculpture lacking; → - transition between types and varieties of the sculpture

| Species | Basic sculpture | | | Supplementary sculpture |
|---|---|---|---|---|
| | Ma | Mi1 | Mi2 | |
| *Noterus clavicornis* (De Geer) | – | – | + | Pd |
| *Noterus crassicornis* (Müller) | – | – | + | Pd |

| Species | Basic sculpture | | | Supplementary sculpture |
|---|---|---|---|---|
| | Ma | Mi1 | Mi2 | |
| *Hydroporus angustatus* Sturm | – | P-6 | Sq | – |
| *Hydroporus brevis* Sahlberg | – | P-3,12 | – | – |
| *Hydroporus discretus* Fairmaire & Brisout | – | P-3 | – | Pd |
| *Hydroporus elongatulus* Sturm | – | P-6,12 | Sq | – |
| *Hydroporus erythrocephalus* (L.) | – | P-1 | Sq→Pg | – |
| *Hydroporus ferrugineus* Stephens | – | P-6,12 | Sq | [Pd] |
| *Hydroporus foveolatus* Heer | – | P-3 | – | Pd |
| *Hydroporus fuscipennis* Schaum | – | P-3 | – | [Pd] |
| *Hydroporus glabriusculus* Aube | – | P-6 | Sq | – |
| *Hydroporus gyllenhalii* Schiodte | – | P-12 | Sq | – |
| *Hydroporus kraatzii* Schaum | – | P-6 | Sq | [Pd] |
| *Hydroporus longicornis* Sharp | – | – | Sq | – |
| *Hydroporus marginatus* (Duftschmid) | – | P-4 | – | Pd |
| *Hydroporus melanarius* Sturm | – | P-12,13 | Sq | [Pd] |
| *Hydroporus memnonius* Nicolai | – | P-13 | Sq | Pd |
| *Hydroporus morio* Aube | – | P-6 | Sq→Pg | – |
| *Hydroporus neglectus* Schaum | – | P-6 | Sq | – |
| *Hydroporus nigellus* Mannerheim | – | P-6 | Sq→Pg | [Pd] |
| *Hydroporus nigrita* (F.) | – | P-6 | Sq | – |
| *Hydroporus nivalis* Heer | – | P-1 | Sq | – |
| *Hydroporus obscurus* Sturm | – | P-6,12 | Sq | – |
| *Hydroporus palustris* (L.) | – | P-1,6 | Sq→Pg | [Pd] |
| *Hydroporus planus* (F.) | – | P-3 | – | [Pd] |

| Species | Basic sculpture | | | Supplementary sculpture |
|---|---|---|---|---|
| | Ma | Mi1 | Mi2 | |
| *Hydroporus pubescens* (Gyllenhal) | – | P-1 | – | – |
| *Hydroporus rufifrons* (Duftschmid) | – | P-12 | Sq→Pg | – |
| *Hydroporus scalesianus* Stephens | – | P-6 | Sq→Pg | – |
| *Hydroporus striola* (Gyllenhal) | – | P-6 | Sq | [Pd] |
| *Hydroporus tristis* (Paykull) | – | P-6 | Sq | – |
| *Hydroporus umbrosus* (Gyllenhal) | – | P-6 | Sq | – |
| *Suphrodytes dorsalis* (F.) | – | P-1,6 | Pg | – |
| *Laccornis oblongus* (Stephens) | – | P-13 | – | – |
| *Graptodytes bilineatus* (Sturm) | – | P-6 | Sq | – |
| *Graptodytes granularis* (L.) | – | P-6 | Sq | – |
| *Graptodytes pictus* (F.) | – | P-6 | Sq | – |
| *Porhydrus lineatus* (F.) | – | P-6 | Pg, + | – |
| *Hygrotus* (*Coelambus*) *confluens* (F.) | – | P-5,10 | – | [Pd] |
| *Hygrotus* (*Coelambus*) *enneagrammus* (Ahrens) | – | P-5 | – | Pd, Sd |
| *Hygrotus* (*Coelambus*) *flaviventris* (Motschulsky) | – | P-5 | – | Pd |
| *Hygrotus* (*Coelambus*) *impressopunctatus* (Schaller), male | – | P-11 | – | – |
| *Hygrotus* (*Coelambus*) *impressopunctatus* (Schaller), female | – | P-11, P-4 | Sq→Pg | Pd |
| *Hygrotus* (*Coelambus*) *parallellogrammus* (Ahrens), male | – | P-14 | – | – |
| *Hygrotus* (*Coelambus*) *parallellogrammus* (Ahrens), female | – | P-14, P-4 | Sq→Pg | [Pd] |
| *Hygrotus* (*Coelambus*) *polonicus* (Aube) | – | P-4 | Sq→Pg | – |
| *Hygrotus* (s.str.) *decoratus* (Gyllenhal) | – | P-10,12 | – | – |

| Species | Basic sculpture | | | Supplementary sculpture |
|---|---|---|---|---|
| | Ma | Mi1 | Mi2 | |
| *Hygrotus* (s.str.) *inaequalis* (F.) | – | P-7,14 | – | – |
| *Hygrotus* (s.str.) *quinquelineatus* (Zetterstedt) | – | P-10 | –, + | – |
| *Hygrotus* (s.str.) *versicolor* (Schaller) | – | P-10 | – | – |
| *Deronectes aubei* (Mulsant) | – | P-2 | P→Sq | Cr |
| *Deronectes latus* (Stephens) | – | P-2 | Sq→Pg | [Pd] |
| *Deronectes platynotus* (Germar) | – | P-2 | Sq→Pg | Cr |
| *Stictotarsus griseostriatus* (De Geer) | – | P-5 | – | Pd |
| *Nebrioporus airumlus* (Kolenati) | – | P-5 | + | Pd |
| *Nebrioporus assimilis* (Paykull) | – | P-5 | + | Pd |
| *Nebrioporus canaliculatus* (Lacordaire) | – | P-5 | + | Cr |
| *Nebrioporus depressus* (F.) | – | P-5 | – | Pd |
| *Scarodytes halensis* (F.) | – | P-4 | – | Pd |
| *Oreodytes alpinus* (Paykull) | – | P-6 | Sq→Pg | Sd |
| *Oreodytes sanmarkii* (Sahlberg) | – | P-6 | Sq | Pd→Sd |
| *Oreodytes septentrionalis* (Gyllenhal) | – | P-6 | Sq→Pg | [Pd] |
| *Bidessus delicatulus* (Schaum) | – | P-5 | – | Sd |
| *Bidessus minutissimus* (Germar) | – | P-5 | – | Sd |
| *Bidessus unistriatus* (Schrank) | – | P-3 | – | Sd |
| *Hydroglyphus geminus* (F.) | – | P-6 | Sq→R | Sd |
| *Hydroglyphus hamulatus* (Gyllenhal) | – | P-5 | + | – |
| *Hydrovatus cuspidatus* (Kunze) | – | P-6,12 | Sq | – |
| *Hyphydrus ovatus* (L.) | – | P-14 | –, + | – |
| *Hyphydrus ovatus* (L.) | – | P-13 | Pg | – |

| Species | Basic sculpture | | | Supplementary sculpture |
|---|---|---|---|---|
| | Ma | Mi1 | Mi2 | |
| *Laccophilus hyalinus* (De Geer) | – | R-3 | Sq | Pd |
| *Laccophilus minutus* (L.) | – | Pg-2, Sq | | [Pd] |
| *Laccophilus poecilus* Klug | – | Pg-2, Sq | | Pd |
| *Copelatus haemorrhoidalis* (F.) | – | P-8 | Sq | Pd |
| *Platambus maculatus* (L.) | – | PR-2 | – | Pd |
| *Agabus affinis* (Paykull) | – | Pg-4 | – | Pd |
| *Agabus biguttatus* (Olivier) | – | R-3 | – | Pd |
| *Agabus biguttulus* (Thomson) | – | Pg-1 | – | Pd |
| *Agabus bipustulatus* (L.) | – | R-1 | Sq | Pd |
| *Agabus clypealis* (Thomson) | – | PSq-4 | – | 2Pd |
| *Agabus congener* (Thunberg) | – | Pg-1 | – | – |
| *Agabus conspersus* (Marsham) | – | R-3 | – | Pd |
| *Agabus didymus* (Olivier) | – | PSq-3 | | Pd |
| *Agabus fuscipennis* (Paykull) | – | Pg-1 | – | Pd |
| *Agabus guttatus* (Paykull) | – | PR-3 | – | Pd |
| *Agabus labiatus* (Brahm) | – | PR-4 | – | 2P |
| *Agabus melanarius* Aube | – | R-2 | Sq,+ | Pd |
| *Agabus nebulosus* (Forster) | – | R-3 | – | 2P |
| *Agabus paludosus* (F.) | – | R-3, PR-2 | – | Pd |
| *Agabus striolatus* (Gyllenhal) | – | R-1 | Sq | Pd |
| *Agabus sturmii* (Gyllenhal) | – | R-4 | Sq | [Pd] |
| *Agabus uliginosus* (L.) | – | PR-1 | – | 2P |
| *Agabus undulatus* (Schrank) | – | PSq-2 | – | Pd |
| *Agabus unguicularis* (Thomson) | – | PR-1 | – | Pd |
| *Ilybius aenescens* Thomson | – | Pg-1 | –,+ | [Pd] |
| *Ilybius angustior* (Gyllenhal) | – | Pg-1 | Sq | [Pd] |
| *Ilybius ater* (De Geer) | – | Pg-1 | – | [Pd] |
| *Ilybius chalconatus* (Panzer) | – | Pg-4 | –,+ | Pd |

| Species | Basic sculpture | | | Supplementary sculpture |
|---|---|---|---|---|
| | Ma | Mi1 | Mi2 | |
| *Ilybius crassus* Thomson | – | Pg-1 | –,+ | [Pd] |
| *Ilybius erichsoni* (Gemminger & Harold) | – | Pg-3 | Sq→P | Pd |
| *Ilybius fenestratus* (F.) | – | Pg-1 | – | [Pd] |
| *Ilybius fuliginosus* (F.) | – | Pg-1 | – | [Pd] |
| *Ilybius guttiger* (Gyllenhal) | – | Pg-1 | – | [Pd] |
| *Ilybius neglectus* Erichson | – | Pg-4 | Sq→P | Pd |
| *Ilybius quadriguttatus* (Lacordaire) | – | Pg-1 | – | [Pd] |
| *Ilybius similis* Thomson | – | Pg-1 | – | [Pd] |
| *Ilybius subaeneus* Erichson | – | Pg-1 | – | [Pd] |
| *Ilybius subtilis* (Erichson) | – | Pg-1 | + | Pd |
| *Ilybius wasastjernae* (Sahlberg) | – | PR-3 | + | Pd |
| *Rhantus bistriatus* (Bergstrasser) | – | C-2 | – | Pd |
| *Rhantus consputus* (Sturm) | – | C-1 | – | Pd |
| *Rhantus exsoletus* (Forster) | | C-1 | – | Pd |
| *Rhantus frontalis* (Marsham), male | – | C-2 | Sq→P | Pd |
| *Rhantus frontalis* (Marsham), female | – | C-2, SC | Sq→P | – |
| *Rhantus grapii* (Gyllenhal) | – | Sq, Pg-2 | | Pd |
| *Rhantus latitans* Sharp | – | C-1, Pg-1 | – | Pd |
| *Rhantus notaticollis* (Aube) | – | C-1, Pg-1 | Sq→P | Pd |
| *Rhantus suturalis* (Mac Leay) | – | Pg-4 | Sq→P | Pd |
| *Rhantus suturellus* (Harris) | – | C-1, Pg-1 | | Pd |
| *Colymbetes fuscus* (L.) | St | P-16 | | Pd |
| *Colymbetes paykulli* Erichson | St | P-16 | Sq→P | Pd |
| *Colymbetes striatus* (L.), male | St | – | Sq | [Pd] |
| *Colymbetes striatus* (L.), female | Cr-2 | – | Sq | [Pd] |
| *Hydaticus aruspex* Clark | S | Sp-1 | +, Sq | Pd |
| *Hydaticus continentalis* Balfour-browne | – | Sp-1 | + | Pd |

| Species | Basic sculpture | | | Supplementary sculpture |
|---|---|---|---|---|
| | Ma | Mi1 | Mi2 | |
| *Hydaticus grammicus* (Germar) | – | P-10 | + | Pd |
| *Hydaticus seminiger* (De Geer) | – | PSq-1 | | Pd |
| *Hydaticus transversalis* (Pontoppidan) | – | SP-2 | Sq, + | Pd |
| *Dytiscus circumcinctus* (Ahrens), male | – | SP-1 | Sq→P | 2 Pd |
| *Dytiscus circumcinctus* (Ahrens), female | Cr-1 | P-15 | Pg→P | Pd, Pd4 |
| *Dytiscus circumflexus* F., male | – | SP-1 | Sq→P | 2 Pd |
| *Dytiscus circumflexus* F., female | –, Cr-1 | SP-1 | Pg→P | 2Pd |
| *Dytiscus dimidiatus* Bergstrasser, male | – | SP-1 | P | 2Pd |
| *Dytiscus dimidiatus* Bergstrasser, female | Cr-1 | P-15 | Pg→P | Pd4 |
| *Dytiscus lapponicus* Gyllenhal, male | – | SP-1 | Sq→P | 2Pd |
| *Dytiscus lapponicus* Gyllenhal, female | Cr-1 | P-15 | Pg→P | Pd4 |
| *Dytiscus latissimus* L., male | – | SP-1 | P | 2Pd |
| *Dytiscus latissimus* L., female | Cr-1 | P-6 | Pg→P | Pd4 |
| *Dytiscus marginalis* L., male | – | SP-1 | Sq→P | 2Pd |
| *Dytiscus marginalis* L., female | Cr-1 | P-15 | Pg→P | Pd4 |
| *Dytiscus semisulcatus* (Müller), male | – | SP-1 | P | Pd |
| *Dytiscus semisulcatus* (Müller), female | Cr-1 | P-6 | Pg→P | Pd3 |
| *Acilius canaliculatus* (Nicolai), male | – | P-9 | Pg→P, + | Cr |
| *Acilius canaliculatus* (Nicolai), female | Cr-3 | G | Pg→P, + | Pd |
| *Acilius sulcatus* (L.), male | – | P-9 | Pg→P, + | Pd |
| *Acilius sulcatus* (L.), female | Cr-3 | G | Pg→P, + | Pd |
| *Graphoderus austriacus* (Sturm) | – | SP-1 | Sq, + | Pd |

| Species | Basic sculpture | | | Supplementary sculpture |
|---|---|---|---|---|
| | Ma | Mi1 | Mi2 | |
| *Graphoderus bilineatus* (De Geer) | – | SP-1 | Sq, + | Pd |
| *Graphoderus cinereus* (L.) | – | SP-1 | + | Pd |
| *Graphoderus zonatus* (Hoppe) | – | SP-1 | + | Pd |
| *Cybister lateralimarginalis* (De Geer), male | – | Pl | P | Pd |
| *Cybister lateralimarginalis* (De Geer), female | S | – | P | – |

Cr2 (Fig. 3.14). Carinae transverse, narrow, medium in height, flattened to arcuately convex, often fork-like branched; their edges developed to a various degree (depending on the type of convexity). Sulci separating the carinae narrow, rather deep, cleft-like.

Cr3 (Fig. 3.11). Carinae longitudinal, rather low, arcuately convex. Only two carinae visible in the dorsal area. Sulci (spaces between carinae) wide and shallow, trough-like.

2. Stripe-like sculpture (St, Ma) – composed of longitudinal, in many places fork-like branched stripes (Fig. 3.13).

3. Sulcate sculpture (S, Ma) – composed of branched, longitudinal and oblique sulci, connected with each other in many places (Fig. 3.15). The majority of sulci are more than 1 mm long, only in places there are much shorter sulci and large, spindle-like punctures, which represent the first-degree microsculpture.

4. Punctate sculpture (P, Mi1) – composed of equal or unequal punctures in size, regularly to irregularly arranged. On the basis of the size of punctures, the three types of puncturation were distinguished: a) simple (punctures equal or almost equal in size); b) double (two kinds of punctures, differing markedly in size); c) multiple (small, medium-sized and large punctures). In the case of double or multiple puncturation, larger punctures are named large and smaller – small, irrespective of their absolute size. The punctate sculpture occurs in 16 varieties in many species representing different genera:

P1 (Fig. 4.16). Puncturation simple. Punctures medium-sized, rotund, shallow, flat-bottomed, dense, almost regularly arranged. Interspaces as wide as the diameter of punctures or narrower.

P2 (Fig. 4.17). Puncturation simple. Punctures medium-sized, rotund, shallow, mostly flat-bottomed, irregularly arranged. Interspaces differing in width, markedly narrower to much wider than the diameter of punctures.

P3 (Fig. 4.18). Puncturation simple. Punctures medium-sized, mostly rotund, rarely elliptical or oval, of medium depth, dense, almost regularly arranged. Interspaces as wide as the diameter of punctures or narrower, with distinct longitudinal clefts or grooves.

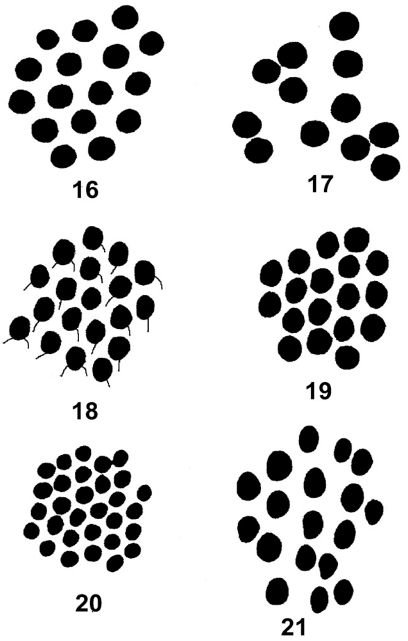

Fig. 4. Varieties of the punctate sculpture: 16 – sculpture P1; 17 – P2; 18 – P3; 19 – P4; 20 – P5; 21 – P6

P4 (Fig. 4.19). Puncturation simple. Punctures medium-sized, rotund or elliptical, of medium depth, dense, evenly arranged. Interspaces almost half as narrow as the diameter of punctures.

P5 (Fig. 4.20). Puncturation simple. Punctures small, mostly rotund, dense, almost regularly arranged. Interspaces narrower than the diameter of punctures.

P6 (Fig. 4.21). Puncturation simple. Punctures medium-sized, mostly elliptical, rarely oval to inversely oval, of medium depth or shallow, usually irregularly arranged. Interspaces narrower or wider than the diameter (length) of punctures.

P7 (Fig. 5.22). Puncturation simple. Punctures rather large, rotund or oval, deep, alveolate or conical, dense, regularly arranged. Interspaces always narrower than the diameter of punctures.

P8 (Fig. 5.23). Puncturation simple; punctures medium-sized, lanceolate and spindle-shaped, dense, regularly arranged. Interspaces generally narrower then the length of punctures.

P9 (Fig. 5.24). Puncturation double. Large punctures kidney-shaped (with few rotund punctures), rather deep, conical, irregularly arranged; spaces between them differing in width, very narrow (punctures subcontiguous) to wide (punctures distant from each other; their diameter smaller than the width of interspaces). Small punctures several times smaller and more numerous than large punctures, irregularly arranged, in places poorly visible (due to well-developed Mi2); interspaces narrower or wider than the diameter of small punctures.

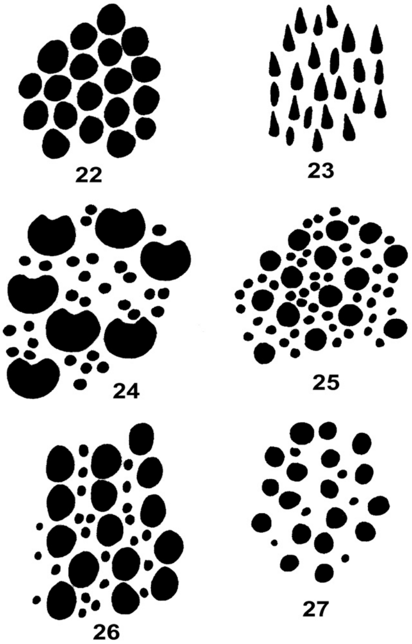

Fig. 5. Varieties of the punctate sculpture: 22 – sculpture P7; 23 – P8; 24 – P9; 25 – P10; 26 – P11; 27 – P12

P10 (Fig. 5.25). Puncturation double. Large punctures rotund, bowl-shaped or alveolate, sparse, unevenly arranged; interspaces narrower to wider than the diameter of these punctures; small punctures ca. 2–3 times smaller and more numerous than the large ones, dense to sparse, of medium depth, almost regularly or irregularly arranged, depending on a species.

P11 (Fig. 5.26). Puncturation double. Large punctures usually elliptical and oval, deep, bowl-shaped and/or alveolate, arranged in less or more regular longitudinal rows; spaces between punctures in rows often very narrow and deep; spaces between rows narrower or wider than the diameter of punctures. Small punctures more numerous than the large ones, mostly elliptical and oval, irregularly arranged; interspaces narrower or wider than the diameter of small punctures.

P12 (Fig. 5.27). Puncturation double. Large punctures rotund or oval (just as the small ones), of medium depth, almost regularly arranged; interspaces as wide as the diameter of punctures or narrower. Small punctures sparse, sometimes difficult to find, ca. two times smaller than the large ones.

P13 (Fig. 6.28). Puncturation double. Large punctures mostly elliptical or oval, of medium depth , almost regularly arranged; interspaces narrower or wider than their diameter (length). Small punctures almost as numerous as large ones; scattered, with interspaces usually wider than their diameter.

P14 (Fig. 6.29). Puncturation multiple. Punctures rotund and/or elliptical, deep, alveolate or conical, very dense; interspaces much narrower than the diameter (length) of punctures.

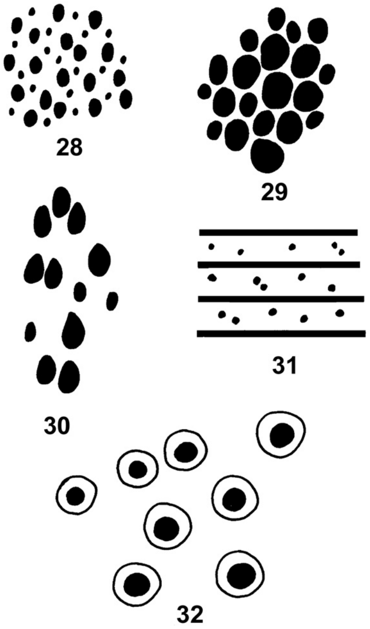

Fig. 6. Varieties of the punctate granulate sculpture: 28 – punctate sculpture P13; 29 – P14; 30 – P15; 31 – P16; 32 – granulate sculpture with the crater-like granules

P15 (Fig. 6.30). Puncturation multiple. Large and medium-sized punctures more numerous than small ones, elliptical or oval, deep, conical and alveolate, irregularly arranged, contiguous or separated from each other by a distance equal or greater than their length.

P16 (Fig. 6.31). Puncturation simple. Punctures rotund, generally small, shallow, sparse, irregularly arranged. Interspaces often many times wider than the diameter of punctures. Sculpture on the stripes.

5. Granulate sculpture (G, Mi1) – composed of crater-like, regularly to irregularly arranged granules. Interspaces narrower or wider than the diameter of these granules (Fig. 6.32).

6. Reticulate sculpture (R, Mi1) composed of areas whose length and/or width is at least several times bigger than the width of clefts and sulci. In this type of sculpture, the areas are named meshes and the line intersections – knots. Some species show a transition from the reticulate sculpture to the polygonal sculpture. In this paper, four varieties of the reticulate sculpture have been distinguished:

R1 (Fig. 7.33). Meshes large (0.1–0.4 mm), strongly elongate, mostly 5–10 times longer than wide, straight, linear or sinuous, with constrictions. Extensions of the reticulum lines are scarce, sulcus-like.

R2 (Fig. 7.34). Meshes predominantly large (0.1–0.3 mm), elongate, usually two-four times as long as wide, polygonal. Extensions of the lines of reticulum sulcus-like, rarer puncture-like.

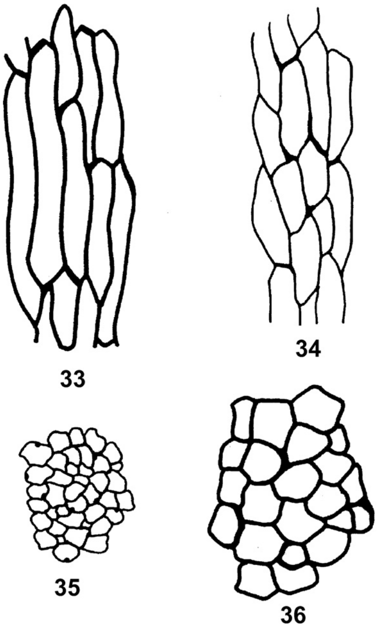

Fig. 7. Varieties of the reticulate sculpture: 33 – sculpture R1; 34 – R2; 35 – R3; 36 – R4

R3 (Fig. 7.35). Meshes small (0.02–0.03 mm), vari-form, isodiametric, longitudinal and transverse (in different proportions); meshes elongate, at the utmost two-three times as long as wide. Lines of the reticulum often with fine, puncture-like extensions. Tiny punctures sometimes occur also within meshes.

R4 (Fig. 7.36). Meshes medium-sized (0.05–0.06 mm), of different shapes, isodiametric and slightly elongate (the latter are less numerous). Lines of the reticulum rather wide, in places sulcus-like. This sculpture is transitory to the polygonal type.

7. Channel sculpture (C, Mi1) – composed of the branched and curved areas, separated from each other by sulci (so-called channels). Sulci with numerous bends and blindly ending arms. This type of sculpture often (even within the dorsal area) turns into the polygonal sculpture. The two varieties of the channel sculpture were distinguished:

C1 (Fig. 8.41). Arms of the areas are usually not connected with each other.

C2 (Fig. 8.42). Arms of the areas often join, “cutting off” sulci (channels) of various length.

8. Polygonal sculpture (Pg, Mi1) is composed of areas of various shapes; their size is often slightly bigger than the width of grooves separating them. The polygonal sculpture sometimes shows transitions to the reticulate and channel types. In the examined species, four varieties of the polygonal sculpture were identified:

Pg1 (Fig. 8.37). Areas medium-sized, isodiametric and longitudinal (in some cases also transverse), mixed in different proportions, regularly arranged. Sulci without conspicuous extensions.

Pg2 (Fig. 8.38). Areas small, only isodiametric, agglomerated.

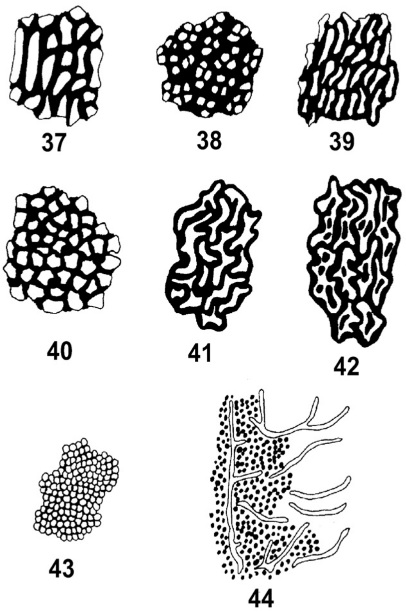

Fig. 8. Varieties of the polygonal, channel, squamous, and fold sculpture: 37 – polygonal sculpture Pg1; 38 – Pg2; 39 – Pg3; 40 – Pg4; 41 – channel sculpture C1; 42 – C2; 43 – squamous sculpture; 44 – fold sculpture

Pg3 (Fig. 8.39). Areas medium-sized, mostly longitudinal (on average five-eight times longer than their maximum width), often with distinct constrictions, regularly arranged. Sulci in places widened.

Pg4 (Fig. 8.40). Areas isodiametric and slightly elongated, irregular in shape, often with ragged edges. Sulci in places with puncture-like extensions (this last feature is better or poorer visible, depending on a sight angle).

9. Squamous sculpture (Sq, Mi1–Mi2) – composed of dense, subequal in shape, rotund, oval or elliptical areas. The body surface gives the impression of being covered with fine scales (Fig. 8.43). It occurs most often as the first-degree microsculpture, and only in few species its elements are as small as in Mi2.

10. Fold sulculpture (Pl, Mi1) is composed of longitudinal, oblique or transverse, low and, in places, flattened, irregularly arranged, mostly branched folds. The best-shaped folds are in the anterior part of the dorsal area, whereas towards the elytral apex and sides they gradually fade, turning into fine clefts (Fig. 8.44). The puncturation between the folds is characteristic of Mi2.

11. Punctate-reticulate sculpture (PR, Mi1) formed by the reticulum with distinct puntures in the knots or within the meshes, representing the first-degree microsculpture. In this paper, four varieties of this sculpture have been described:

PR1 (Fig. 9.45). Puncturation simple. Punctures mostly smaller than the meshes of the reticulum, rotund or irregular in shape, rather sparse, irregularly arranged in the knots of the reticulum. Interspaces as wide as the diameter of punctures or several times

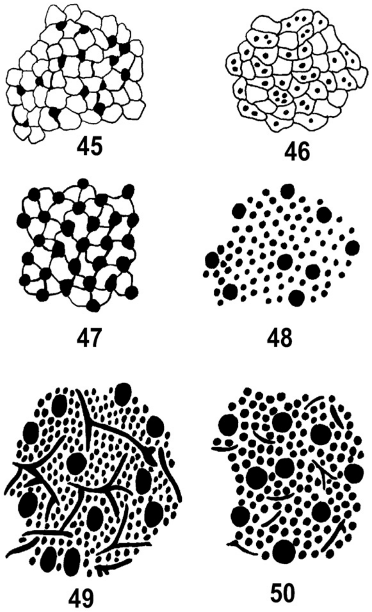

Fig. 9. Varieties of the punctate-reticulate and sulcate-punctate sculpture: 45 – punctate-reticulate sculpture PR1; 46 – PR2; 47 – PR3; 48 – PR4; 49 – sulcate-punctate sculpture SP1; 50 – SP2

wider; meshes of the reticulum of various shapes, usually isodiametric with scarce longitudinal and transversal meshes, differing in size.

PR2 (Fig. 9.46). Puncturation simple; punctures several times smaller than the meshes of the reticulum, predominantly rotund, arranged in one-four within the meshes. The meshes of various shapes, isodiametric or transverse. The lines of the reticulum in places sulcus-like widened, without puncturation in the knots.

PR3 (Fig. 9.47). Puncturation simple. Punctures mostly smaller than the meshes of the reticulum, usually rotund, dense, almost regularly arranged in the knots of the reticulum; interspaces mostly narrower than the diameter of punctures. Meshes vari-form, isodiametric to slightly elongate. The reticulum turns in places in the polygonal sculpture.

PR4 (Fig. 9.48). Puncturation double. Punctures rotund, placed in the knots of the reticulum. Large punctures sparse, irregularly arranged; interspaces wider than or equal to their diameter; small punctures dense, almost regularly arranged, interspaces usually narrower than or equal to their diameter. The meshes of the reticulum differing in size, usually smaller than the diameter of small punctures, some of them even smaller than the diameter of the small punctures. Just as in variety 3, the reticulum turns into the polygonal sculpture.

12. Sulcate-punctate sculpture (SP, Mi1) is characterized by the occurrence between punctures of irregular simple and/or branched sulci and clefts. In this work, two varieties of this sculpture have been distinguished:

SP1 (Fig. 9.49). Puncturation double. Large punctures rotund, oval or elliptical, sparse, irregularly arranged; interspaces narrower or wider than the diameter of these punctures. Small punctures rotund or oval, dense, regularly arranged. Sulci and clefts differing in length, branched, forming in places closed areas.

SP2 (Fig. 9.50). Puncturation double. Both kinds of punctures rotund. Large punctures sparse, irregularly arranged, with interspaces narrower or wider than their diameter. Small punctures ca. twice as small as large punctures, dense, regularly arranged; interspaces narrower than the diameter of these punctures. Sulci short, mostly not branched.

13. Sulcate-channel sculpture (SC, Mi1) – composed of the elements of the channel sculpture (second variety), forming a background for considerably larger, longitudinal and oblique, simple and branched sulci (Fig. 10.51). The channel sculpture turns in places into the punctate sculpture.

14. Punctate-squamous sculpture (PSq, Mi1–Mi2) – composed of the elements of the punctate and squamous sculptures, mixed in various proportions. The size of scale-like areas and punctures indicates the transition between Mi1 and Mi2 or univocally Mi2 (in the majority of the species). Four varieties of this sculpture have been distinguished:

PSq1 (Fig. 10.54). Puncturation double. Punctures arranged between scale-like areas. Large punctures rotund, ca. twice as large as small punctures, sparse, irregularly arranged, with interspaces usually much wider than their diameter. Small punctures

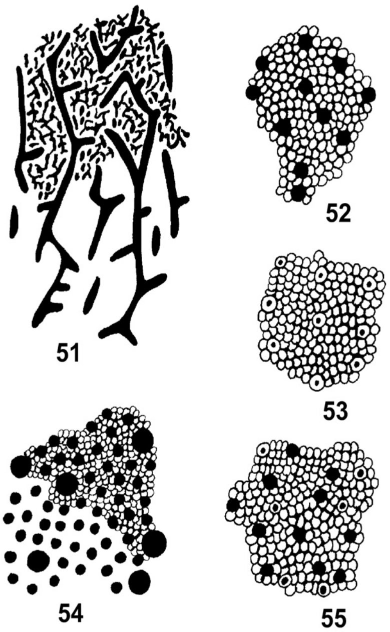

Fig. 10. 51 – sulcate-channel sculpture; 52 – punctate-squamous sculpture PSq2; 53 – PSq3; 54 – PSq1; 55 – PSq4

also rotund, dense, with interspaces narrower than or equal to their diameter. Scale-like areas predominantly oval or elliptical, slightly smaller than the diameter of the small punctures.

PSq2 (Fig. 10.52). Puncturation simple (sometimes punctures differ slightly in size). Punctures mostly rotund, rather sparse, usually irregularly arranged between scale-like areas. Areas identical or slightly differing in shape and size (transition to the punctate-polygonal sculpture), smaller than the diameter of the punctures.

PSq3 (Fig. 10.53). Puncturation simple. Punctures round, shallow, rather sparse, irregularly arranged amidst scale-like areas. Scales with punctures mostly larger than the remaining ones.

PSq4 (Fig. 10.55). Puncturation simple. Punctures round, rather sparse, irregularly arranged: between scale-like areas (larger) and on them (smaller). Scale-like areas rounded, but often irregular in shape, showing a transition to the polygonal type of sculpture.

The used magnification makes the full characteristics of the second-degree microsculpture impossible. In many species Mi2 does not occur or is composed of poorly distinguishable, more or less indistinct and scattered elements; however, in many cases it is sharp enough to be classified among one of the described types of sculpture. The most frequent type is the squamous sculpture (Sq) and its transitional forms to the polygonal (Sq→Pg), punctate (Sq→P) and reticulate (Sq→R) sculptures, while the "pure" polygonal (Pg) and punctate sculptures (P) and transitional structures (i.e. P→Pg, P→Sq) are much rarer.

## Variation of sculpture

The sculpture of the dorsal area shows certain intraspecific variation, concerning the development and frequency of occurrence of particular elements and their arrangement on the surface of elytra (Table 2). The intraspecific variability of this feature often has a character of sexual dimorphism. The different sculpture in males and females and dimorphism in females are frequent phenomena in the family Dytiscidae. The sexual dimorphism, marked on the levels of types and varieties, was noted in the genera *Hygrotus* (subg. *Coelambus*), *Hyphydrus*, *Rhantus*, *Colymbetes*, *Dytiscus*, *Acilius*, and *Cybister*. The female dimorphism, consisting in that some females have the sculpture of elytra identical to that of males, whereas others – often markedly different, occurs in *Hygrotus impressopunctatus* (Mi1, Mi2), *H. parallelogrammus* (Mi1, Mi2), *Rhantus frontalis* (Mi1), *Dytiscus circumcinctus* (Ma, Mi1, Mi2), and *D. circumflexus* (Ma, Mi1, Mi2). Variability not related to sex is more or less marked in particular species (Table 1), but usually is within a given type of the sculpture. Below, there are the main directions of intraspecific variability described, as indicated by more or less continuous transitions between the distinguished types of the sculpture.

Table 2
Diversification of the elytral sculpture in the dorsal area in the family Dytiscidae.
N – number of species, other abbreviations in Table 1

| Genus | N | Mi1 | Mi2 | Ma |
|---|---|---|---|---|
| *Noterus* Clairville | 2 | – | + | – |
| *Hydroporus* Clairville | 29 | P-1, 3, 4, 6, 12, 13 | Sq, Sq→Pg, - | – |
| *Suphrodytes* Gozis | 1 | P-1,6 | Pg | – |
| *Laccornis* Gozis | 1 | P-13 | – | – |
| *Graptodytes* Seidlitz | 3 | P-6 | Sq | – |
| *Porhydrus* Guignot | 1 | P-6 | Pg, + | – |
| *Hygrotus* subg. *Coelambus* Thomson | 6 | P-4, 5, 10, 11, 14 | Sq→Pg, - | – |
| *Hygrotus* s.str. Stephens | 5 | P-7, 10, 12, 14 | +, – | – |
| *Deronectes* Sharp | 3 | P-2 | P, P→Pg, P→Sq | – |
| *Stictotarsus* Zimmermann | 1 | P-5 | – | – |
| *Nebrioporus* Regimbart | 4 | P-5 | +, – | – |
| *Scarodytes* Gozis | 1 | P-4 | – | – |
| *Oreodytes* Seidlitz | 3 | P-6 | Sq, Sq→Pg | – |
| *Bidessus* Sharp | 3 | P-3, 5 | – | – |
| *Hydroglyphus* Motschulsky | 2 | P-5, 6 | Sq→R, + | – |
| *Hydrovatus* Motschulsky | 1 | P-6, 12 | Sq | – |
| *Hyphydrus* Illiger | 1 | P-13, 14 | Pg, +, – | – |
| *Laccophilus* Leach | 3 | Sq, Pg-2, R-3 | Sq | – |
| *Copelatus* Erichson | 1 | P-8 | Sq | – |
| *Platambus* Thomson | 1 | PR-2 | – | – |
| *Agabus* Leach | 19 | R-1, 2, 3, 4, Pg-1, 4, PR-1, 3, 4, Psq-2, 3, 4 | Sq, +, – | – |
| *Ilybius* Erichson | 15 | Pg-1, 3, 4, PR-3 | Sq, Sq→P, +, – | – |
| *Rhantus* Dejean | 10 | C-1, 2, Pg-1, 2, 4, SC | Sq→P, – | – |
| *Colymbetes* Clairville | 3 | P-16, – | Sq, Sq→Pg | St, Cr-2 |
| *Hydaticus* Leach | 5 | P-10, SP-1, 2 | Sq, Psq-1, + | – |
| *Dytiscus* L. | 7 | P-6, 15, SP-1 | Sq→P, Pg→P | Cr-1, – |
| *Acilius* Leach | 2 | P-9, G | Pg→P, + | Cr-3, – |
| *Graphoderus* Dejean | 4 | SP-1 | Sq, + | – |
| *Cybister* Curtis | 1 | Pl, – | P | S, – |

1. Sq→Pg2. This type of transition is observed in *Rhantus grapii, Laccophilus minutus* and *L. poecilus*. Assuming that the starting point is a uniform squamous pattern, the phenomenon manifests itself in separation of the groups of areas, often accompanied by

changes in their shape. In species from the genus *Laccophilus* one may also distinguish one, poorly marked transitional stage – the reticulate sculpture where particular meshes are filled with scales.

2. Pg1→C1. A transition of the polygonal sculpture (first variety) into the channel sculpture (first variety) is almost continuous; it comprises several stages differing from each other in the proportions of simple to branched areas (the latter originate probably as a result of the connection of simple areas). The described transition is noticeable in the series of specimens representing *Rhantus notaticollis, Rh. suturellus* and *Rh. latitans*, as well as within the dorsal area in a single specimen (branched areas predominate in the inner part of the dorsal area).

3. R3→PR2. Distinction between third variety of the reticulate sculpture and second variety of the punctate-reticulate sculpture is often subjective. In the first case punctual widenings occur mainly on the lines of a reticulum, whereas punctures within meshes are mostly very small and represent Mi2. This structure turns in a continuous way into the pattern where punctures on the lines of the reticulum disappear and punctures within meshes increase in size, becoming elements Mi1. The described variability occurs in *Agabus paludosus*.

4. P1→P6. In this case the variability concerns the shape of punctures and pattern of their arrangement (Figs. 3.14 and 4.19) and is found in *Hydroporus palustris and Suphrodytes dorsalis*.

5. P3→P12, P6→P12. The variability described using these symbols manifests itself in the occurrence within a species of the two types of puncturation: simple and double, the number of small punctures being in P-12 insignificant as compared with large punctures. In addition, the transition of P-6 into P-12 may be accompanied by a small change in the shape of punctures. This type of variability is exemplified by *Hydroporus brevis, H. elongatulus, H. obscurus, H. ferrugineus*, and *Hydrovatus cuspidatus*.

6. P10→P12, P12→P13. In the double puncturation a ratio of the number of large punctures to the number of small punctures is not stable and shows certain variability, allowing one to distinguish the three types of puncturation (the number of small punctures is equal to, smaller than or bigger than the number of large punctures). In the majority of species this variability is within the limits of the described types of puncturation, except for *Hygrotus decoratus* (P-10→P-12) and *Hydroporus melanarius* (P-12→P-13).

7. P7→P14. Transition of the simple puncturation into the multiple puncturation (or inversely) was observed in *Hygrotus inaequalis*. The examination of a larger series of specimens from this species allows one to find that the presented variability has a continuous character.

In the majority of the species examined the sculpture of the dorsal area is uniform or shows small, gradual changes from its central part to the sides. Some of the above mentioned species from the genera *Rhantus* and *Hygrotus confluens* are exceptions. In these species the inner part of the dorsal area is doubly punctured (P10), and the outer part – simply punctured (P5).

The differentiation of the sculpture within genera is illustrated in Table 2. It shows that particular taxa of this rank differ in the range of variability of the discussed feature. Taking into account the five most numerous genera (comprising from 10 to 29 species), one may find that the most heterogeneous is the genus *Agabus* (four types and 12 varieties of the sculpture), whereas the genus *Hydroporus* (one type, 6 varieties) should be placed on the opposite end of the scale. The groups of species which were distinguished on the basis of the sculpture of the dorsal area correspond to a small degree to the accepted division of the family Dytiscidae into genera. More than half of the types and varieties of the sculpture occur in two or more systematical genera and only four taxa in the rank of genus (*Deronectes*, *Copelatus*, *Platambus* and *Cybister*) have the specific sculptures (Ma or Mi1).

A key for the identification of the subfossil Dytiscidae using the macrosculpture and the first-degree microsculpture in the dorsal area of elytra is as follows.

Each identification of subfossil remains needs their comparison to the contemporary specimens of particular species. This procedure is, particularly in the case of larger taxa, very time-consuming and troublesome because one should have a complete comparative collection. The aforementioned key makes the task easier, as it enables the preliminary selection of species, allowing their assignment to the groups with a similar sculpture of elytra (Table 3). Numbers placed in square brackets at theses or antitheses refer to appropriate items in Table 3.

Table 3
Division of the species into groups on the basis of the macro- and first-degree microsculpture

| Sculpture | Species | Item |
|---|---|---|
| Cr1 | females: *Dytiscus circumcinctus*, *D. circumflexus*, *D. dimidiatus*, *D. lapponicus*, *D. latissimus*, *D. marginalis*, *D. semisulcatus* | 1 |
| Cr2 | *Colymbetes striatus* (female) | 2 |
| Cr3 | females: *Acilius canaliculatus*, *A. sulcatus* | 3 |
| St | *Colymbetes fuscus*, *C. paykulli*, *C. striatus* (male) | 4 |
| S | *Cybister lateralimarginalis* (female) | 5 |
| P1 | *Hydroporus erythrocephalus*, *H. nivalis*, *H. palustris*, *H. pubescens*, *Suphrodytes dorsalis* | 6 |
| P2 | *Deronectes aubei*, *D. latus*, *D. platynotus* | 7 |
| P3 | *Hydroporus brevis*, *H. discretus*, *H. foveolatus*, *H. fuscipennis*, *H. planus*, *Bidessus unistriatus* | 8 |
| P4 | *Hydroporus marginatus*, *Hygrotus impressopunctatus*, *H. parallellogrammus*, *H. polonicus*, *Nebrioporus depressus*, *Scarodytes halensis* | 9 |
| P5 | *Hygrotus confluens, H. enneagrammus, H. flaviventris, Nebrioporus canaliculatus, N. airumlus, N. assimilis, Stictotarsus griseostriatus, Bidessus delicatulus, B. minutissimus, Hydroglyphus hamulatus* | 10 |

| Sculpture | Species | Item |
|---|---|---|
| P6 | *Hydroporus angustatus, H. elongatulus, H. ferrugineus, H. glabriusculus, H. kraatzii, H. morio, H. neglectus, H. nigrita, H. obscurus, H. palustris, H. scalesianus, H. striola, H. nigellus, H. tristis, H. umbrosus, Suphrodytes dorsalis, Graptodytes bilineatus, G. granularis, G. pictus, Porhydrus lineatus, Oreodytes alpinus, O. sanmarkii, O. septentrionalis, Hydroglyphus geminus, Hydrovatus cuspidatus, Dytiscus latissimus* (female), *D. semisulcatus* (female) | 11 |
| P7 | *Hygrotus inaequalis* | 12 |
| P8 | *Copelatus haemorrhoidalis* | 13 |
| P9 | males: *Acilius canaliculatus*, *A. sulcatus* | 14 |
| P10 | *Hygrotus confluens*, *H. decoratus*, *H. quinquelineatus*, *H. versicolor*, *Hydaticus grammicus* | 15 |
| P11 | *Hygrotus impressopunctatus* | 16 |
| P12 | *Hydroporus brevis*, *H. elongatulus*, *H. ferrugineus*, *H. melanarius*, *H. obscurus*, *H. gyllenhalii*, *H. rufifrons*, *Hygrotus decoratus*, *Hydrovatus cuspidatus* | 17 |
| P13 | *Hydroporus melanarius*, *H. memnonius*, *Laccornis oblongus*, *Hyphydrus ovatus* | 18 |
| P14 | *Hygrotus parallellogrammus*, *Hygrotus inaequalis*, *Hyphydrus ovatus* | 19 |
| P15 | females: *Dytiscus circumcinctus*, *D. dimidiatus*, *D. lapponicus*, *D. marginalis* | 20 |
| P16 | *Colymbetes fuscus*, *C. paykulli* | 21 |
| G | females: *Acilius canaliculatus*, *A. sulcatus* | 22 |
| R1 | *Agabus bipustulatus*, *A. striolatus* | 23 |
| R2 | *Agabus melanarius* | 24 |
| R3 | *Laccophilus hyalinus*, *Agabus biguttatus*, *A. conspersus*, *A. nebulosus*, *A. paludosus* | 25 |
| R4 | *Agabus sturmii*, *Ilybius neglectus* | 26 |
| C1 | *Rhantus consputus*, *Rh. exsoletus*, *Rh. latitans*, *Rh. notaticollis*, *Rh. suturellus* | 27 |
| C2 | *Rhantus bistriatus*, *Rh. frontalis* | 28 |
| Pg1 | *Agabus biguttulus*, *A. congener*, *A. fuscipennis*, *Ilybius subtilis*, *I. aenescens*, *I. angustior*, *I. ater*, *I. crassus*, *I. fenestratus*, *I. fuliginosus*, *I. guttiger*, *I. quadriguttatus*, *I. similis*, *I. subaeneus*, *Rhantus latitans*, *Rh. notaticollis*, *Rh. suturellus* | 29 |
| Pg2 | *Laccophilus minutus*, *L. poecilus*, *Rhantus grapii* | 30 |
| Pg3 | *Ilybius erichsoni* | 31 |
| Pg4 | *Agabus affinis*, *Ilybius chalconatus*, *Rhantus suturalis* | 32 |
| Sq | *Laccophilus minutus*, *L. poecilus*, *Rhantus grapii* | 33 |
| Pl | *Cybister lateralimarginalis* (male) | 34 |

| Sculpture | Species | Item |
|---|---|---|
| PR1 | *Agabus uliginosus*, *A. unguicularis* | 35 |
| PR2 | *Platambus maculatus*, *Agabus paludosus* | 36 |
| PR3 | *Agabus guttatus*, *Ilybius wasastjernae* | 37 |
| PR4 | *Agabus labiatus* | 38 |
| SP1 | *Hydaticus continentalis, H. aruspex, D. circumflexus*, males: *Dytiscus circumcinctus, D. circumflexus, D. dimidiatus, D. lapponicus, D. latissimus, D. marginalis, D. semisulcatus; Graphoderus austriacus, G. bilineatus, G. cinereus, G. zonatus* | 39 |
| SP2 | *Hydaticus transversalis* | 40 |
| SC | *Rhantus frontalis* (female) | 41 |
| PSq1 | *Hydaticus seminiger* | 42 |
| PSq2 | *Agabus undulatus* | 43 |
| PSq3 | *Agabus didymus* | 44 |
| PSq4 | *Agabus clypealis* | 45 |

1. Elytra with macrosculpture 2.
   – Elytra without macrosculpture 6.
2. Macrosculpture of carinate type 3.
   – Macrosculpture of other type 5.
3. Carinae longitudinal 4.
   – Carinae transverse; sculpture Cr2 (Fig. 3.14) [2].
4. Dorsal area with five-six carinae; sculpture Cr1 (Fig. 3.12) [1].
   – Dorsal area only with two carinae; sculpture Cr-3 (Fig. 3.11) [3].
5. Macrosculpture composed of stripes; sculpture St (Fig. 3.13) [4].
   – Macrosculpture composed of sulci; sculpture S (Fig. 3.15) [5].
6. Microsculpture with crater-like sulci; sculpture G (Fig. 6.32) [22].
   – Microsculpture without crater-like sulci 7.
7. Microsculpture composed of two element kinds 8.
   – Microsculpture composed of one element kind 15.
8. One of microsculpture elements are sulci 9.
   – Microsculpture without sulci 10.
9. Microsculpture of sulcate-channel type; sculpture SC (Fig. 10.51) [41].
   – Microsculpture of sulcate-punctate type; sculpture SP1-2 (Fig. 9.49–50) [39, 40].
10. Microsculpture of punctate-reticulate type 11.
    – Microsculpture of punctate-squamous type 12.
11. Punctures arranged in meshes of the reticulum; sculpture PR2 (Fig. 9.46) [36].

– Punctures arranged in knotes of the reticulum; sculpture PR1, 3 (Fig. 9.45, 9.47) [35, 37].

12. Puncturation double; sculpture PSq1 (Fig. 10.54) [42].

– Puncturation simple 13.

13. Punctures arranged exclusively between the scale-like areas; sculpture PSq2 (Fig. 10.52) [43].

– Punctures variously arranged 14.

14. Punctures arranged in the middle of scale-like areas; sculpture PSq3 (Fig. 10.53) [44].

– Punctures arranged on and between the scale-like areas; sculpture PSq4 (Fig. 10.55) [45].

15. Microsculpture composed of punctures 16.

– Microsculpture composed of other elements 18.

16. Punctures of the microsculpture subequal in size; sculpture P1-8, 16 (Figs. 4.16-5.23, 6.31) [6–13, 21].

– Punctures of the microsculpture unequal in size 7.

17. Puncturation multiple; sculpture P14, 15 (Figs. 6.29-30) [19, 20].

– Puncturation double; sculpture P9-13 (Figs. 5.24–6.28) [14–18].

18. Microsculpture composed of folds; sculpture Pl (Fig. 8.44) [34].

– Microsculpture composed of variously shaped areas 19.

19. Areas subequal in form, scale-like; sculpture Sq (Fig. 8.43) [33].

– Areas different, often irregular shaped 20.

20. Sulci several times smaller than the areas width; microsculpture of reticulate type 21.

– Sulci slightly smaller than the areas width 22.

21. All the reticulum meshes elongate; sculpture R1, 2 (Figs. 7.33–34) [23, 24].

– Reticulum meshes isodiametric and elongate; sculpture R3, 4 (Figs. 7.35–36) [25, 26].

22. Sulci strongly sinuous, with wavy margins; sculpture C1, 2 (Figs. 8.41–42) [27, 28].

– Sulci not sinuous, mostly with straight margins 23.

23. In microsculpture prevail isodiametric areas; sculpture Pg2, 4 (Figs. 8.38, 8.40) [30, 32].

– In microsculpture prevail elongate areas; sculpture Pg1, 3 (Figs. 7.35, 8.37) [29, 31].

## CONCLUSIONS

In summing up the presented results of our studies, two most important conclusions may be drawn:

1. Due to its high diversity and a relatively small intraspecific variability, the sculpture of the dorsal area fulfils two principal conditions of the usefulness in the taxonomy.
2. Because of its durability, this sculpture may be used as one of the main features for the identification of the subfossil remains of Dytiscidae.

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