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MATEUSZ ANTCZAK[*]

PALAEOECOLOGICAL SIGNIFICANCE OF LATE GLACIAL AND HOLOCENE MOLLUSCS

Abstract

The remains of molluscs preserved in the sediments allow reconstruction the paleoenvironment and climate of the Late Glacial/Holocene lakes. Based on bivalves and gastropods fossil it is possible to describe some aspects of environment chemistry, dynamics, vegetation and sediment character. Analysis based on comparison with modern animals can also help to describe the diversity of this type, speed of evolution and evolutionary strategies of different groups of Mollusca.

Keywords: palaeoecology, Bivalvia, Gastropoda, fossils, water chemistry, evolution

Introduction

Molluscs are one of the most diverse phyla of invertebrates, which includes many classes: Scaphoda, Polyplacophora, Monoplacophora, Aplacophora, Cephalopoda, Bivalvia, Gastropoda. Representatives of the last two groups are adaptated to fresh waters. Analysis on modern molluscs shows that particular taxa demonstrate distinct preferences relative to specific ecological and climatic factors. Conclusions from such analysis are used in stratigraphy and paleoecology of the Quaternary period (Alexandrowicz 1987) (Table 1).

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[*] Adam Mickiewicz University, Faculty of Geographical and Geological Sciences, Institute of Geology (Collegium Geologicum), Maków Polnych 16, 61-606 Poznań, e-mail: mateusz.antczak@amu.edu.pl.

Table 1. Stratigraphy and malacostratigraphy of the Late Glacial and Holocene (based on Alexandrowicz 2004)

	Climatic phase	Age (ka)	Molluscs	„Malacostratigraphy”
HOLOCENE	Last millenium	900 – rec	*Bithynella austriaca*	Bithynella austriaca
	Subatlantyk	2,800–900	*Bithynia tentaculata*	Bithynia tentaculata
	Subboreał	5,100–2,800		
	Atlantyk	8,400–5,100	*Bithynia tentaculata, Lymnaea truncatula, Armiger crista*	
	Boreal	9,300–8,400	*Gyraulus laevis, Bithynia tentaculata, Lymnaea truncatula*	
	Preboreal	10,250–9,300		Gyraulus laevis
LATE GLACIAL	Younger dryas	11,000–10,250	*Anisus leucostomus, Lymnaea truncatula, Gyraulus laevis*	
	Allerød	11,800–11,000	Gyraulus laevis, Pisidium stewartii, Lymnaea truncatula	
	Pre-allerød	14,000–11,800	*Pisidium obtusale laponicum, P. stewarti*	Pisidium obtusale laponicum

Such comparisons may also be possible with Late Neogene (Pliocene) assemblages, because in the Late Neogene most of extant fresh-water molluscs already existed, and because they are preserved in many sediment types, especially carbonates (Kelts and Talbot 1990). Twenty-eight species of bivalves and 50 species of gastropods are known from fresh waters in Poland. Most of them can be found in sediments of Late Glacial and Holocene. Other species can also be found, such as arctic species (i. e. *Pisidium obtusale laponicum*), which settles in polish lakes during cold climatic phases, like Pre-allerød phase (14,000–11,800 ka) (Dyduch-Falniowksa 1992; Alexandrowicz 2004; Hrynowiecka-Czmielewska 2009) (Table 1). Abundant fossils that are present in the sediments for some species provide data on the palaeoenvironment (by correlation with living representatives of a given species and their dependence on specific environmental factors). The basis of such interpretation is to group species inhabiting a similar range of tolerance to environmental conditions (Alexandrowicz 1995; Piechocki 1979). For example, if we find fossils of (i.e.) bivalves which nowadays lives in waters with high calcium content, like *Theodoxus fluviatilis*, we can assume that the fossil lake in which these organisms lived also had high calcium content.

Palaeecological significance of malacofauna

Preserved in the sediments, fossils of bivalves and gastropods help us to reconstruct palaeoenvironment and palaeoclimate. Analysis of the fossilized malacocenosis (a multispecies assemblage of molluscs at specified area; Żmudziński et al. 2002) allows to draw conclusions on:

- water hardness and calcium content,
- quantity of the oxygen,
- water chemistry (acidity, alkalinity),
- temperature,
- iron content,
- salinity,
- insolation,
- water fertility,
- water polution.

Some unique molluscs communities also allow reconstruction of water level fluctuations and climatic conditions, even suggesting specific climatic phases of the Late Glacial and Holocene (Ralska-Jasiewiczowa 1989; Alexandrowicz 1997) (convergent with palinological evidences (see: an exemplary analysis; Makohonienko et al. 1998). In addtition, analysis of shell isotop ratios can be helpful (Apolinarska 2009a, 2009b; Alexandrowicz 2004).

Some species are highly specialized to their habitats, while some others have wide tolerance to ecological conditions. Different species in the same genera sometimes inhabit clearly distinct environmental and climatic conditions, which suggests rapid evolution of the molluscs. On the other hand representatives of some groups settle in nearly the same biotopes (i. e. there is only little variety in Planorbidae, especially genus *Anisus*, which except the *Ancylus fluviatilis*, all prefer shallow, calm waters with muddy bottom and dense vegetation). The most diversified is the *Pisidium* clade (Piechocki 1979; Piechocki and Dyduch-Falniowksa 1993; Skompski 1983). According to fossilworks.org database, *Pisidium* clams are known for 28.4 Ma deposits. Modern representatives of this clad are known for Late Pliocene and early Pleistocene. Half of the *Pisidium* occurrences listed in the palaeobiology Database are from Pleistocene and Quartenary deposits, which supports the rapid evolution probability. Representatives of the *Anisus* genus have similiar stratigraphic range (Miocene – recent), but are not as diversified as *Pisidium* clams.

Different environmental factors affect the differentiation of malacocenosis. Below are explanations of this impact and examples of modern molluscs, which prefer divergent conditions.

Calcium

Water hardness and calcium content are very important in molluscs development. Because shells are built from calcium, it is assumed that hard waters (rich in calcium) are more preferred by bivalves and gastropods than soft waters. Molluscs, which are living in the waters with calcium deficiency have thinner, and easily crushable shells, consequently they are more vulnerable to predator attacks (Lamper and Somer 2007). However, it is possible that molluscs living in the soft waters can recompensate calcium deficiency with appropriate diet (Fromming 1956) (Table 2).

Table 2. Relationship between the water hardness and molluscs occurence (Piechocki 1979; Piechocki and Dyduch-Falniowska 1993; Skompski 1983; Alexandrowicz 2004)

Species	Water hardness
Margatifera margatifera	soft waters
Pisidium casertanum	soft waters
Pisidium conventus	soft waters
Acroloxus lacustris	hard waters
Theodoxus fluviatilis	hard waters
Pisidium subtruncatum	hard waters

Stream

Majority of the bivalves and gastropods prefer standing water. A smaller group of molluscs typically inhabit streams. Representatives of this group have special adaptation for such conditions, e.g. *Ancylus fluviatilis* with a strong suction cup foot and limpet-like shell (Bogdanowicz et al. 2008), using its foot to attach to the rocks. *Ancylus* is streamresistant no matter how it is situated relative to the flow direction (Lampert and Somer 2007) (Table 3).

Table 3. Relationship between the stream (flow) and molluscs occurence (Meier-Brook 1975; Kasprzak 1975; Piechocki 1991; Piechocki 1979)

Species	Stream (flow) attitude
Anodonta cygnea	standing waters
Pisidium lilljeborgii	standing waters
Valvata piscinalis	standing waters
Pisidium tenuilineatum	Reophile
Unio crassus	Reophile
Ancylus fluviatilis	Reophile

Bottom of the reservoir (sediments)

The character of the deposits influences the type of molluscs that occurs. Some can live in almost all kinds of the substrate, like *Anisus contornus*, which can settle on plants, rocks and logs of trees as well as on silty, sandy and peaty bottoms (Piechocki 1979). Other species have specific needs. The character of the lake (or river) deposits is especially important for bivalves that bury themselves in the bottom of the reservoir, like members of the Unionidea family. Due to their lifestyle, these bivalves prefer sandy and silty bottoms (Dyduch-Falniowska 1993) (Table 4).

Table 4. Relationship between the bottom of the reservoir (sediments) and molluscs occurrence (Piechocki 1979; Piechocki and Dyduch-Falniowska 1993; Skompski 1983; Alexandrowicz 2004)

Species	Sediment type at bottom of the reservoir
Planorbarius corneus	Plants
Theodoxus fluviatliis	Stony
Aplexa hypnorum	Sandy-clayey
Valvata Piscinalis	Silty
Pisidium lilljeborgii	Sandy
Pisidium pseudosphaerium	Peat

Oxygen

Occurrence of the Mollusca representatives in fresh waters can also depend on the amount of the oxygen. During oxygen deficiency periods some gastropods can crawl to the surface of the reservoir and remain in constant contact with the surface membrane (Piechocki 1979). Some species are more resistant to the periodical oxygen deficiency than others.

Microstructure of the shells found in the deposits can help in the interpretation of the quantity of oxygen in the past. Many species in the inner calcite layer of the shells possess canals perpendicular to the surface. On the inner surface of the shell they are visible as pores. The highest amount of such pores were described in *Pisidium personatum* shells. High number of the pores (canals) is characteristic for species, which lives in environment with periodical oxygen deficiency (Dyduch-Falniowska 1983; Adler and Fiechtner 1989) (Table 5). Thus, shells with many pores found in the fossil record suggests low oxygen content.

Table 5. Relationship between the quantity of oxygen in water and molluscs occurrence (Piechocki 1979, Piechocki and Dyduch-Falniowska 1993; Skompski 1983; Alexandrowicz 2004)

Species	Oxygen content preferences
Anadonta cygnea	high oxygen content
Sphaerium solidium	high oxygen content
Planorbis carinatus	high oxygen content
Sphaerium corneum	resistant to periodic oxygen deficiency
Pisidium conventus	resistant to periodic oxygen deficiency
Gyraulus laevis	resistant to periodic oxygen deficiency

pH

Water chemistry is also important environmental factor. Bivalves and gastropods avoid waters that are strongly acidic (pH < 4) and strongly alkaline (pH > 10). They prefer slightly acidic, neutral and slightly alkaline waters. Most molluscs settle in reservoirs with slightly alkaline waters (see: water hardness) (Piechocki Dyduch--Falniowksa 1993). In the most inhospitable, acidic waters lives two *Psisidium* representatives: *Pisidium casertanum* [pH ~ 4,4] (Mackie and Filippance 1983) and *Pisidium* obtusale [pH ~ 4–5] (Klimonowicz 1962) (Figure 1).

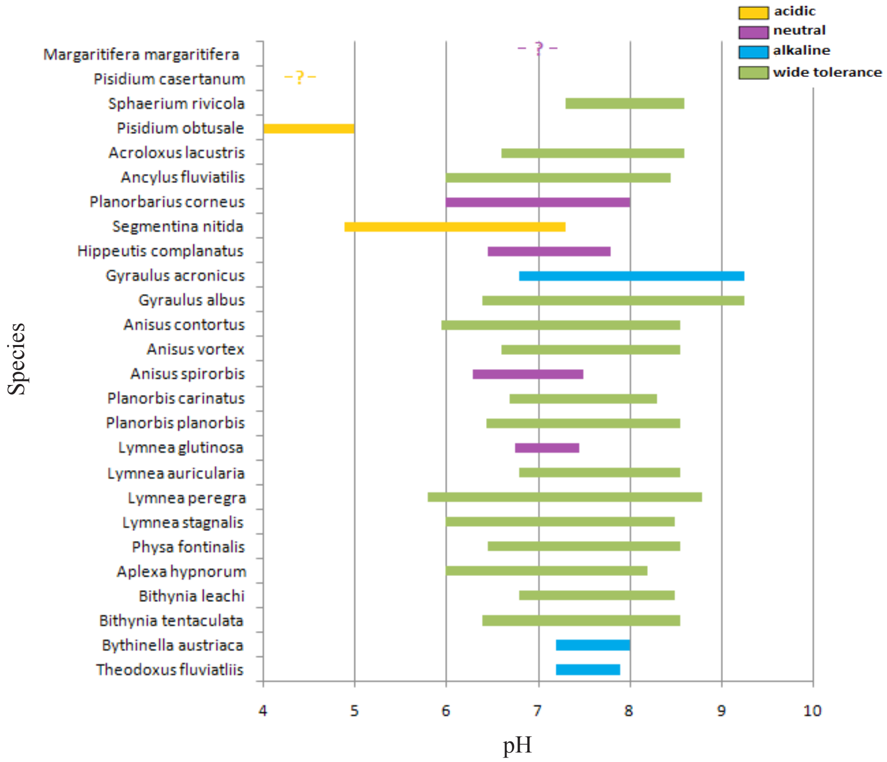

Figure 1. Relationship between water pH and molluscs occurrence (Piechocki 1979; Piechocki and Dyduch-Falniowska 1993; Skompski 1983; Alexandrowicz 2004)

Temperature

Molluscs occurrence in fresh waters highly depend on the water temperature. Appropriate temperature is necessary for correct growth, reproduction and nutrition. For most of the species known from Poland the most favorable temperature range is 20–25°C.

Some species are resistant to low temperatures and can survive winter at the bottom of the lake or, like *Planorbarius corneus* (Piechocki 1979) (Table 6).

Table 6. Relationship between water temperature and molluscs occurrence (Piechocki 1979; Piechocki and Dyduch-Falniowska 1993)

Species	Temperature preferences
Pisidium personatum	cold waters
Pisidium concentus	cold waters
Bithynella austriaca	cold waters
Physa acuta	warm waters
Anisus vortex	warm waters
Anisus contornus	warm waters

Vegetation

Lakes rich in plants are settled by higher number of molluscs. Vegetation is important mostly for gastropods. Some of them are connected with specific plant species (in some cases it can be a result of co-evolution), and the occurence of their fossils in the sediment may indicate the fossil lake's flora (Piechocki 1979) (Tables 7 and 8) because plants serve molluscs in several ways:

- as a main element of their diet,
- as a hide from predators,
- as a place of attachement of the egg coccons (Piechocki 1979).

Table 7. Cooccurrence of plants and algae with molluscs (Piechocki 1979; Piechocki and Dyduch-Falniowska 1993)

Species	Plants and algae
Gyralus albus	*Potagemon, Elodea Canadensis*
Gyralus rossmaessleri	*Potagemon, Cladophora,* Charophyta
Gyralus riparius	Cypraceae, peatland plants, Marchantiophyta
Pisidium casertanum	*Potagemon, Equisetum*
Sphaerium corneum	Green algae (Protococcaler)

Table 8. Relationships between reservoir vegetation and molluscs occurrence (Piechocki 1979; Piechocki and Dyduch-Falniowska 1993)

Species	Reservoir
Lymnaea stagnalis	high vegetation
Bithynella austriaca	high vegetation
Bithynia leachi	high vegetation
Pisidium lilljeborgii	very low vegetation

Other specific condition

There are species which have other special needs or species resistance to environmental conditions in biotopes, where other molluscs cannot survive. i. e. *Anisus leucostomus* settles reservoirs with bottom sediments that are high iron. In contrast, high fertility of the lake deposits representatives of *Planorbis corneus* can achieve smaller siezes (Piechocki 1979). *Musculium lacustre* bivalves are the most resistant to lack of water and can live in the reservoirs that periodically dry (McKee and Mackie 1983). Insolation difference in the shells of living animals and subfossil remains can be observed. *Viviparus* snails have more strongly marked colored stripes when they live in well-insolated waters. Bivalves and gastropods has also different resistant to salinity. Some can live in the waters of Baltic Sea – 5–6‰ near the surface and more than 10‰ near the bottom (Kautsky 1991) (Figure 2).

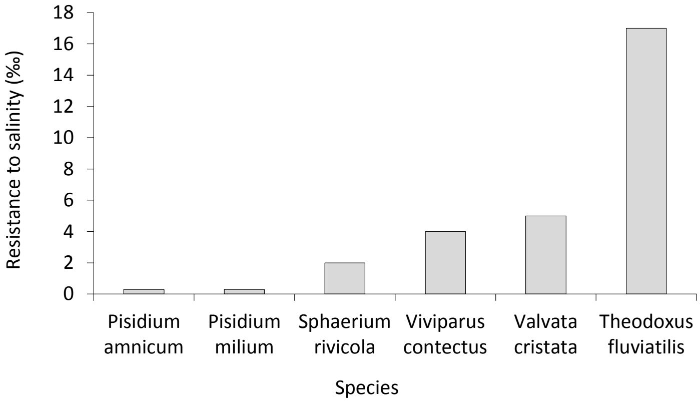

Figure 2. Molluscs resistant to saltinity (Piechocki 1979; Piechocki and Dyduch--Falniowska 1993)

Lake zonation

Sometimes molluscs are so strongly adapted to their environment, that they live only in specific zone of the lake. Even different species from the same genus are specialized to live in its different zones, which slightly differs from other zones. Differences between lake zones are: insolation, sediments, vegetation, food and oxygen availability. Palaeointerpretations are complicated by the fact, that many species migrate during ontogeny from depths of the lake to more shallow waters (Table 9).

Table 9. Relationship between lake zonation and molluscs occurrence (Piechocki 1979; Piechocki and Dyduch-Falniowska 1993)

Littoral zone	Sublittoral zone	Profundal zone	Shallow reservoirs
Pisidium crassum	*Pisidium henslowanum*	*Pisidium casertanum*	*Anodonta cygnea*
Unio crassus	*Pisidium subtruncatum*	*Pisidium nitidum*	*Valvata naticina*
Planorbis carinatus	*Gyraulus albus*	*Pisidium conventus*	*Valvata pulchella*
Anisus vortex	*Valvata Piscinalis*	*Valvata Piscinalis*	*Valvata cristata*

Water clarity

Some of the fresh-water animals can be used as water clarity indicators (Kolkwitz and Marsson saprobic system). Bivalves and gastropods can also be used as bioindicators of water clarity. Three types of waters can be distinguished using molluscs as indicators: polluted (α-mesosaprobic), fairly clean (β-mesosaprobic) and clean (oligosaprobic) (Piechocki 1979; Piechocki and Dyduch-Falniowska 1993) (Table 10). System using bivalves as bioindicators is used in many cities, like Swarzędz or Gdańsk (Wykosiński 2011).

Table 10. Water clearence indicators in saprobic system (Piechocki 1979)

α -mesosaprobic	β-mesosaprobic	Oligosaprobic
Physa acuta, Sphaerium corneum, Sphaerium rivicola	*Theodoxus fluviatilis, Viviparus contectus, Valvata piscinalis, Bithynia tentaculata, Aplexa hypnorum, Physa fontinalis, Lymnaea stagnalis, Lymnaea auricularia, Lymnaea peregra, Lymnaea corvus, Lymnaea trancatulata, Planorbis planorbis, Planorbarius corneus, Anisus vortex, Acroloxus lacustris, Anisus contortus, Gyraulus albus, Unio crassum, Unio pictorum, Unio tumidus, Anodonta cygnea*	*Bythinella austriaca, Ancylus fluviatilis, Margaritifera margaritifera, Pisidium tenuilineatum, Pisidium lilljeborgii, Pisidium moitessiearianum, Dreissenna polymorpha*

Exeplanary Analysis

Convergence of reconstructions based on molluscs, plants, algae and pollen, proves that fossils of the molluscs found in the lake sediments of the Late Glacial and Holocene can be used to reconstruct the palaeoenvironmental conditions, as an example to this statement lacustrine sediment sequence from Bożejewice (Kuyavia-Pomerania province) can be reffered (Figure 3). Herein analysis of the lower part of B1/97 core (by Makohonienko et al. 1998) is presented. Significance of fresh-water Mollusca representatives is specified.

Section 1 (Pre-allerød)

Thill of the lacustrine sequence represents over 1m thick carbonate silts with small amount of organic matter. Within the molluscs remains the most abundant are *Gyraulus laevis, G. acronicus, G. rossmaessleri, Pisidium lilljeborgi, P. obtusale lapponicum i P. stewarti*. These are species specific for cold waters. Occurrence of *Pisidium obtusale lapponicum* and *P. stewarti* with small amount of fossils indicates shallow lake of periglacial zone. The composition of the malacofauna suggests arctic (subarctic) climate and Pre-allerød period. Palynological foundings proves this hypotesis. Polar willow (*Salix polaris/herbacea*), white dryas (*Dryas octopetala*), ephedra (*Ephedra distachya*), juniper (*Juniperus*) and others. Microfossils other than pollens also indicates ecosystem specific for Late Glacial – poor phytoplankton with a predominance of a green algae *Pediastrum kawraiskyi*.

Section 2 (Pre-allerød/Allerød)

Second section of the core represents mainly *Valvata piscinalis*, *V. pulchella* and *Pisidum substruncatum*. Abundance of the species and specimens increases. Among the common findings are also *Lymnaea peregra*, *Armiger crista* and *Sphaerium corneum*, molluscs with higher thermic demandings. However shells of specific for cold waters *Gyraulu laevis and G. rossmaessleri* still occur, which suggests that section 2 corresponds to transition period (from arctic to warmer climate). Occurrence of mentioned species suggests also that reservoir became deeper – species characteristic for sublitoral zone appeared. In this part of the profile not only molluscs, but also micro and macrofossils of plants like sea-buckthorns (*Hippophae*), juniper and willow are more common. Acumulation of mineral matter decreased in opposite to detritus and calcium carbonate.

Section 3 (Allerød)

In the third part of the core many species of plants, gastopods and bivalves occur. With the transition section 2, it has almost 0.5 m of thickness. At first mainly *Armiger crista*, *Valvata Pulchella*, *V. piscinalis*, *Segmentina nitida*, *Pisidium pulchellum* and *P. millium* occur, which suggest strongly overgrown lake. Reservoir was probably permanent, because not resistant to drying out the lake *Armiger crista* is abundant (half of the specimens found in the thrid section of the core B1/97 beongs to this species. Occurrence of the reophilic *Pisidium henslowanum*, *Unio* and *Anodonta* suggests that high level of the water was caused by river supply. Later the lake became more shallow, which reflects changes in palynological record and decreasing number of *Armiger crista* in opposite to *Acroloxus lacustris*, dwelling in the area of rushes. Communities of submerged plants and algae (Charophyta, *Potamogeton*) have been replaced by club-rushes (i. e. *Schoenoplectus lacustris*). Pollens suggests development of birch (*Betula*) and pine (*Pinus*) woods (warmer climate).

Section 4 (Younger dryas)

In the lower and center part of this section there are no molluscs fossils besides fragments of *Valvata piscinalis* shells and some hard to recognize *Pisidium* and *Unio* representatives. The inhibition of the malacofauna developmnent probably is the result of disadvantageous environment conditions, i. e. higher acidity. Important factor was $CaCO_3$ deficiency – there was a change in deposition, in place of carbonate sediments, non-carbonate detritic gytjas (70 cm thick) appeared. However, the main reason of decreasing number of molluscs in the lake was low temperature. Palynological analysis confirms, that this section corresponds to the coldest phase of Late Glacial – Younger dryas. In place of pines and birches, appeared willows and juniper. Shallowing of the lake stopped. Submerged plants started to appear again.

In the upper part of the forth section warming and improvement of environmental condition can be observed. Juniper and willow pollens became more rare, and birch pollen begin to dominate (birch is the plant which quickly respond to warming).

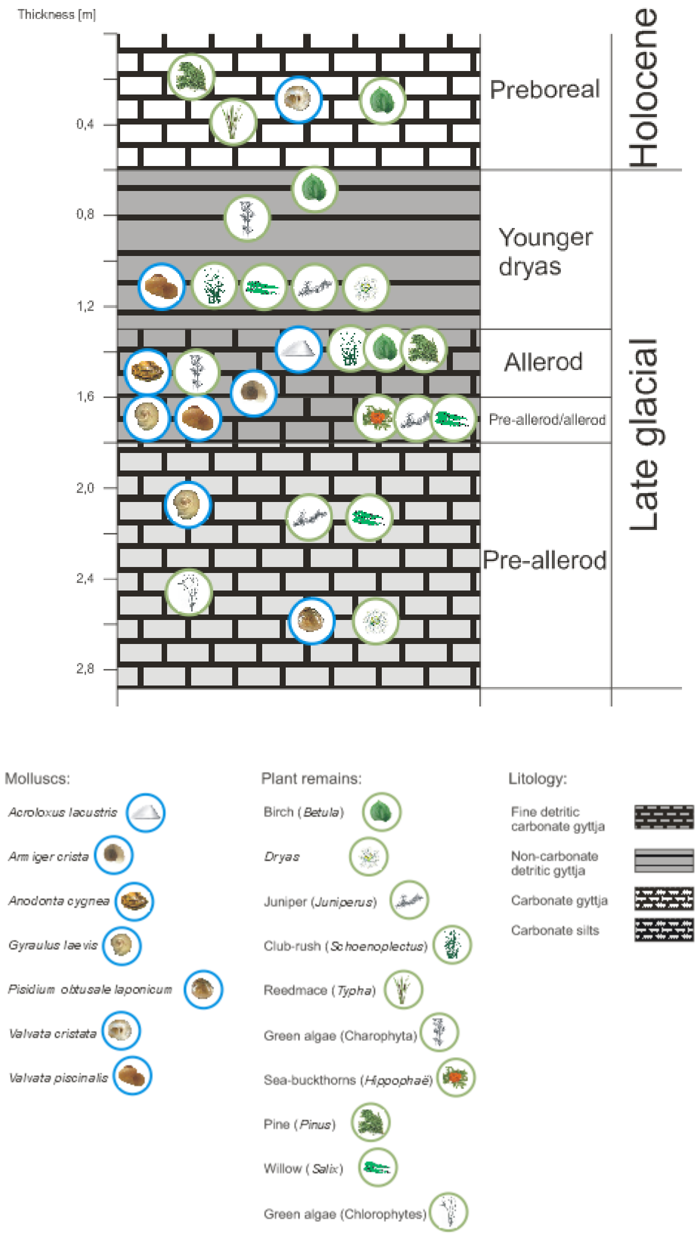

Figure 3. Late glacial-Holocene lacustrine deposits from Bożejewice (central Poland) (based on: Makohonienko et al. 1998).

Section 5 (Preboreal)

The last section of the profile is the assemblage of molluscs with *Valvata cristata*, *V. piscinalis*, *V. pulchella*, *Lymnaea peregra* and *Acroloxus lacustris*. A few remains of *Pisidium milium*, *P. nitidum* and *Unio* fragments occur. Foundings suggests rise of the temperature, water level and high calcium content. In the reservoir carbonate gytjas were deposited. Content of the $CaCO_3$ in this sediments is very high, which (with confirmed by palynological studies rise of the temperature) allows malacofauna to quickly develop. In this core section pollens of the birch, pine , aspen (*Populus*), hazel (*Corylus*) were found, which is typical for the preboreal forest. Within the plant macrofossill seeds of the reedmace (*Typha latifolia),* which indicates warm climate (Figure 3).

Summary

Analysis of environmental preferences of modern molluscs can be used to reconstruct Late Glacial and Holocene environmental conditions and palaeoclimate, based on fossilized shells of bivalves and gastropods. However, such interpretations should be based on a group of species, not one. Malacofauna analysis usually corresponds with palynological studies. Based on such comparisons it is possible to describe environmental changes and Late Glacial and Holocene stratigraphy.

Various species within the same genus often indicates distinctly different environmental conditions and climate, which suggests rapid molluscs evolution. The most diversified are bivalves *Pisidium*. Poorly diversified are gastropods Planorbidae, like *Anisus.*

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PALEOKOLOGICZNE ZNACZENIE PÓŹNOGLACJALNYCH I HOLOCEŃSKICH MIĘCZAKÓW

Streszczenie

Zachowane w osadzie szczątki ślimaków i małży pozwalają na zrekonstruowanie paleośrodowiska i klimatu jezior późnego glacjału i holocenu. Przeanalizowanie składu kopalnej malakocenozy pozwala wyciągać wnioski dotyczące temperatury i chemizmu wód jeziora (zwłaszcza obecności wapnia i żelaza), jego rozmiarów, żyzności, alkaliczności (kwasowości) i innych. Niektóre specyficzne zbiorowiska ślimaków i małży pozwalają opisać wahania poziomu wód i warunki klimatyczne, a nawet sugerują określone fazy klimatyczne późnego glacjału i holocenu (zgodne z fazami określonymi przez badania palinologiczne). Porównanie z żyjącymi przedstawicielami słodkowodnych Mollusca umożliwiają także opisanie zróżnicowania tej grupy bezkręgowców oraz tempa ewolucji poszczególnych taksonów.

Słowa kluczowe: paleoekologia, małże, ślimaki, skamieniałości, chemizm wód, ewolucja

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