

LATE GLACIAL AND HOLOCENE MOLLUSCAN ASSEMBLAGES IN DEPOSITS FILLING PALAEOLAGES IN NORTHERN POLAND

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Abstract

Late Glacial and Holocene carbonate lacustrine deposits developed as lacustrine chalk and calcareous gyttja are fairly widespread across northern Poland. They form fillings of palaeolakes which developed during the deglaciation. These formations are usually covered by peat. Rich and diversified malacofauna has been found in the aforementioned sediments. The profiles from 154 sites described and published by various authors were subjected to malacological analysis. In the whole material, 18 molluscan assemblages were distinguished, representing three types of habitats: terrestrial, of temporary water bodies, and of permanent water bodies. The composition and structure of these assemblages allows characterizing climate and differentiating habitats. The time-sequences of malacological assemblages provided possibility to define three types of malacological sequences. On the basis of these successions, a scheme of the lake water bodies evolution during Late Glacial and in northern Poland was elaborated.

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Key words: lacustrine chalk, calcareous gyttja, palaeolakes, molluscan assemblages, Late Glacial, Holocene, northern Poland

INTRODUCTION

The lacustrine chalk and calcareous gyttja form the fillings of palaeolakes which developed in high numbers during the deglaciation. These may also be found on the coasts of present-day lakes where they mark their previous wider extents. The accumulation of these lake sediments occurred chiefly during transitional periods between cold glacial phases and warm interglacials when dead ice blocks, trapped earlier in moraine or glaciofluvial sediments have melted. Drainage-less depressions of various sizes, depths and shapes were formed, and became stagnant bodies of freshwaters, subjected to complex evolution during the Late Glacial and Holocene. Some of them transformed into permanent lakes, others were filled with deposits and became peat bogs, and finally, terrestrial habitats with various moisture levels. The course of sediment-filling and disappearance of these depressions was reconstructed and described by numerous authors. The age of great majority of the sites with carbonate or mineral deposits filling palaeolakes is linked to declining phase of the last glaciation and with the Holocene. Also known are the occurrences of these sediments of the earlier interglacials, mainly Eemian and Mazovian (Holsteinian) (e.g. Skompski, 1996; S. W. Alexandrowicz and W. P. Alexandrowicz, 2010).

Palaeolakes are filled with various types of sediments. Common, and the most important from the viewpoint of malacological studies, are lacustrine chalk and calcareous gyttja.

Lacustrine chalk is a carbonate sediment occurring as a result of precipitation of CaCO_3 in water. This process is par-

ticularly intensive in the water bodies with abundant vegetation which can be associated with uptake of carbon dioxide by plants during photosynthesis. The calcium carbonate content exceeds 80%. The sediments are white, grey, sometimes yellowish or brownish. Some of them contain small lumps of calcium carbonate, and sometimes oolith or stromatolith-type structures (e.g. Rzepecki, 1983; Rutkowski *et al.*, 2002; Freytet and Verrecchia, 2002). Very often, the lacustrine chalk contain remnants of molluscs and ostracods.

The name of calcareous gyttja is given to these lake sediments that contain from 50 to 80% of calcium carbonate. Depending on the proportions of other components e.g.: mineral or organic substances, or organic detritus, a number of types are distinguished among calcareous gyttja. The classification of these sediments were taken up by many studies (e.g. Markowski, 1980; Rzepecki, 1983; Freytet and Verrecchia, 2002).

The carbonate deposits are accompanied by mineral deposits: sands and silts, and more rarely – gravels. Among the gravels, cobbles of Scandinavian rocks are represented most often by granites, gneisses or porphyries. In terms of their origin these are either moraine or glaciofluvial formations. In many sites these deposits occur at the bottom of palaeolake sequences.

Peats are of essential importance. They are associated with boggy environments and usually develop in the final stage of evolution of lake water bodies. They therefore occur at the top of depositional sequences and testify to overgrowing of lakes and their transformation into moist terrestrial environments. Thin interlayers or lenticles of peats are sometimes found also within the lake sediments. Their presence proves temporary shallowing of the lakes.

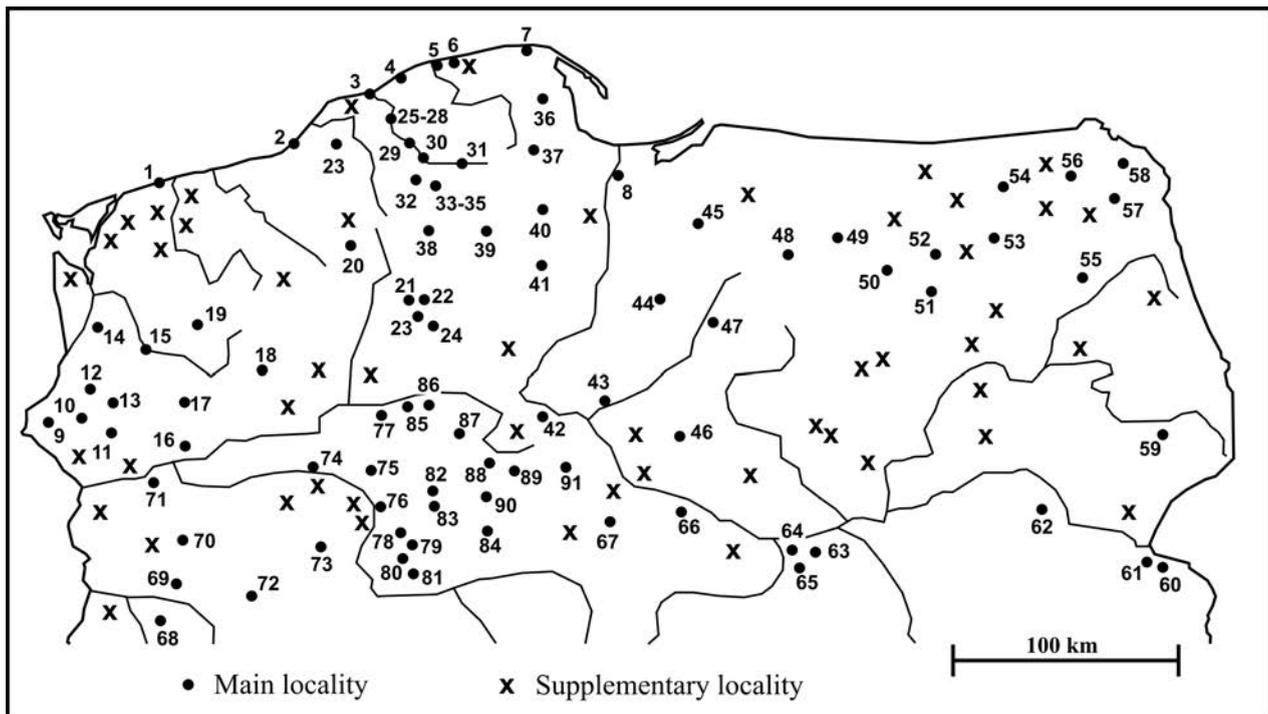


Fig. 1. Localization of mollusc-bearing calcareous lake sediments in Northern Poland. For explanations of numbers of localities (1–91) see Table 1.

The internal structures of the palaeolake fillings is often very complicated due to varying proportions and mutual relationships between the aforementioned principal genetic types of sediments. A total thickness of formations of the palaeolakes is from 0.5 to over 10 m.

Lacustrine chalk and calcareous gyttja often abound in shells of snails and bivalves. It is principally caused by high content of CaCO_3 in the sediments. Remnants of mollusk shells, usually less preserved and often bearing the traces of chemical dissolution may sometimes appear also within peats that accompany the carbonate sediments. Presence of molluscan shells in the lake sediments of Late Glacial and in northern Poland was recorded as early as in the 19th century and the early 20th by German geologists (e.g. Keilhack, 1888; Menzel, 1911). More detailed analyses of molluscan fauna in lacustrine chalk were undertaken by Dembińska (1924) during inter-war period. After WWII, a great progress was made in research of carbonate lake sediments. During the wide-range mapping and deposit documentation works, more than ten thousand sites with lacustrine chalk and calcareous gyttja were located and catalogued. Some of them became the topics of detailed and interdisciplinary studies, but huge majority still awaits a more elaborated research. Despite the fact that shells of snails and bivalves commonly occur in lacustrine chalk and calcareous gyttja, the state of recognition of malacocoenoses is far from being sufficient. In voluminous references there are many mentions on presence of malacofauna but without species identification. One can even assume that in many cases the shells of molluscs have been omitted or gone completely unnoticed. The studies listing faunas, sometimes with number of individuals of particular species are rare, and only exceptionally a full malacological analysis has been done, accompanied by palaeoecological

and palaeogeographical reconstruction based on such data. There are rather few more general studies nature, presenting changes and evolution of molluscan assemblages over larger areas (S. W. Alexandrowicz, 1989; W. P. Alexandrowicz, 1999, 2007).

MATERIAL AND METHOD

In order to describe the properties of changes in sequences of molluscan assemblages and to carry out reconstruction of the evolution of sedimentary in lake carbonate sediments, 91 sites were selected. Additionally, the data from 32 sites with fragmentary malacological data were used as well as those from 31 sites described in the early 20th century by German geologists. This last group of sites can be treated as a supplement only, as they contain very general data, and locations of most of these sites cannot be practically identified at present. Owing to this large number of sites, however, it was possible to characterise particular types of assemblages of the fauna as well as their compositions and structures. Results of these studies were published in a number of scientific articles (e.g. S. W. Alexandrowicz, 1989; W. P. Alexandrowicz, 1999, 2007). The study presented here represents an attempt to generalise results of studies completed at various sites and to present characteristics of main faunistic assemblages and their relationship with climate changes and evolution of water bodies during Late Glacial and Holocene. The most important sites which provided the basis for the presented analysis are compiled (Table 1, Fig. 1).

On the sites of lacustrine chalk and calcareous gyttja (Table 1), rich and diversified malacofauna was identified. The habitat and climatic requirements of particular species were discussed in detail in many publications. Several papers

Table 1

Main localities of mollusc-bearing calcareous lake sediments in Northern Poland.
For location of particular profiles see Fig. 1

No	Locality	References
1	Niechorze	Kopczyńska-Lamparska <i>et al.</i> (1984); S.W. Alexandrowicz (1989)
2	Dąbki	S.W. Alexandrowicz (1991)
3	Ustka	Brodniewicz (1979); S.W. Alexandrowicz <i>et al.</i> (1989, 1990); S.W. Alexandrowicz (1998); Wojciechowski (2012)
4	Poddąbie	Krzyszowski <i>et al.</i> (1998); S.W. Alexandrowicz (1999b)
5	Kluki	Wojciechowski (1995, 2011); S.W. Alexandrowicz (1999b)
6	Jeziro Łebsko	
7	Karwia	S.W. Alexandrowicz (1999b)
8	Skowarcz	W.P. Alexandrowicz (1999, 2002, 2005)
9	Chojna	Czepiec (1998)
10	Brzesko	Kowalkowski and Berger (1966)
11	Płoń	S.W. Alexandrowicz (1989)
12	Okrzeszyce	
13	Żabów	Kowalkowski and Berger (1971/72)
14	Zelewo	
15	Lubiatowo	S.W. Alexandrowicz (1989)
16	Osiek	S.W. Alexandrowicz (1980, 1989)
17	Prostynia	S.W. Alexandrowicz (1980); S.W. Alexandrowicz and Tchórzewska (1981)
18	Zdbice	S.W. Alexandrowicz and Tchórzewska (1981)
19	Zacisze	S.W. Alexandrowicz (1989)
20	Marcelin	S.W. Alexandrowicz and Tchórzewska (1981)
21	Jeziro Duże Głuche	
22	Jeziro Małe Głuche	Nowaczyk <i>et al.</i> (1999); Nowaczyk and S.W. Alexandrowicz (2008)
23	Jeziro Charzykowskie	
24	Jeziro Ostrowite	
25	Grabowo	S.W. Alexandrowicz and Tchórzewska (1981); Filonowicz and Krzyńska (1989); S.W. Alexandrowicz (1995b, 1999b)
26	Słupsk Słowiańska	
27	Słupsk Raclawicka	
28	Słupsk Południe	
29	Stożek Głazny	S.W. Alexandrowicz <i>et al.</i> (1989, 1990)
30	Dębica Kaszubska	
31	Gałężnia Mała	
32	Borzytuchom	S.W. Alexandrowicz and Tchórzewska (1981)
33	Jeziro Jasień	
34	Kozin	Florek <i>et al.</i> (1999)
35	Zawiaty	
36	Orle	S.W. Alexandrowicz (1988, 1999b)
37	Dolina Wierzycy	Błaszkiwicz and Krzyńska (1992)
38	Nowe Polaszki	S.W. Alexandrowicz (1989)
39	Sulęczyno	S.W. Alexandrowicz, Tchórzewska (1981)
40	Siwiałka	S.W. Alexandrowicz (1989)
41	Łubiana	S.W. Alexandrowicz, Tchórzewska (1981)
42	Fordon	Skompski (1961)
43	Lubicz	Urbański (1952)
44	Malinowo	
45	Florezaki	S.W. Alexandrowicz (1989)
46	Żuchowo	Urbański (1957)
47	Kurzętnik	Brodniewicz (1966)
48	Woryty	Dąbrowski ed. (1981); W.P. Alexandrowicz (1999)
49	Tłokowo	W.P. Alexandrowicz (1999)
50	Bezląwki	Świerczyński (1958)
51	Szestno	Skompski (1996)
52	Rudkowo	
53	Sołdany	S.W. Alexandrowicz (1989)
54	Kruklin	Stasiak (1963); Czepiec (1997)
55	Kulwasy	Żurek and Dzieczkowski (1971)
56	Jeziro Głębokie	W.P. Alexandrowicz (1999)
57	Jeziro Wigry	W.P. Alexandrowicz (2000, 2009)
58	Jeziro Gajlik	W.P. Alexandrowicz and Żurek (2010)
59	Kurowo	S.W. Alexandrowicz and Żurek (2005)
60	Zaczopki	W.P. Alexandrowicz and Kusznerczuk (2012)
61	Woroblin	
62	Radzików	Dobrowolski <i>et al.</i> (2012)
63	Olszewickie Błoto	S.W. Alexandrowicz (1983b)
64	Cisowe	
65	Zamość	S.W. Alexandrowicz and Żurek (1998)
66	Głowina	Brykczyński and Skompski (1979)
67	O słonki	
68	Zabór	S.W. Alexandrowicz (2005, 2008)
69	Pomorsko	S.W. Alexandrowicz (1980); S.W. Alexandrowicz and Nowaczyk (1982)
70	Szumiąca	
71	Zacisze	S.W. Alexandrowicz (1980)
72	Kielkowo	S.W. Alexandrowicz and Żurek (1991)
73	Niepruszewo-Cieśle	Apolinarska and Ciszewska (2006)
74	Bogdanowo	Skompski (1994)
75	Miętkowo	Kasprzak and Berger (1978)
76	Oz Budzyński	
77	Smuszewo	Dzieczkowski (1982)
78	Jeziro Bnin	
79	Jeziro Jeziory Wielkie	Wojciechowski (1999, 2000)
80	Jeziro Kurnickie	
81	Jeziro Raczyńskie	Wojciechowski (1999, 2000)
82	Imiołki	
83	Rybitwy	Apolinarska and Ciszewska (2006)
84	Józwin	Ciszewska (1996)
85	Krucz	
86	Chodzież	
87	Strzelce	
88	Byszkowice	Demińska (1924)
89	Szarlej	
90	Bytyń	
91	Bożejowice	Makohonienko <i>et al.</i> (1998)

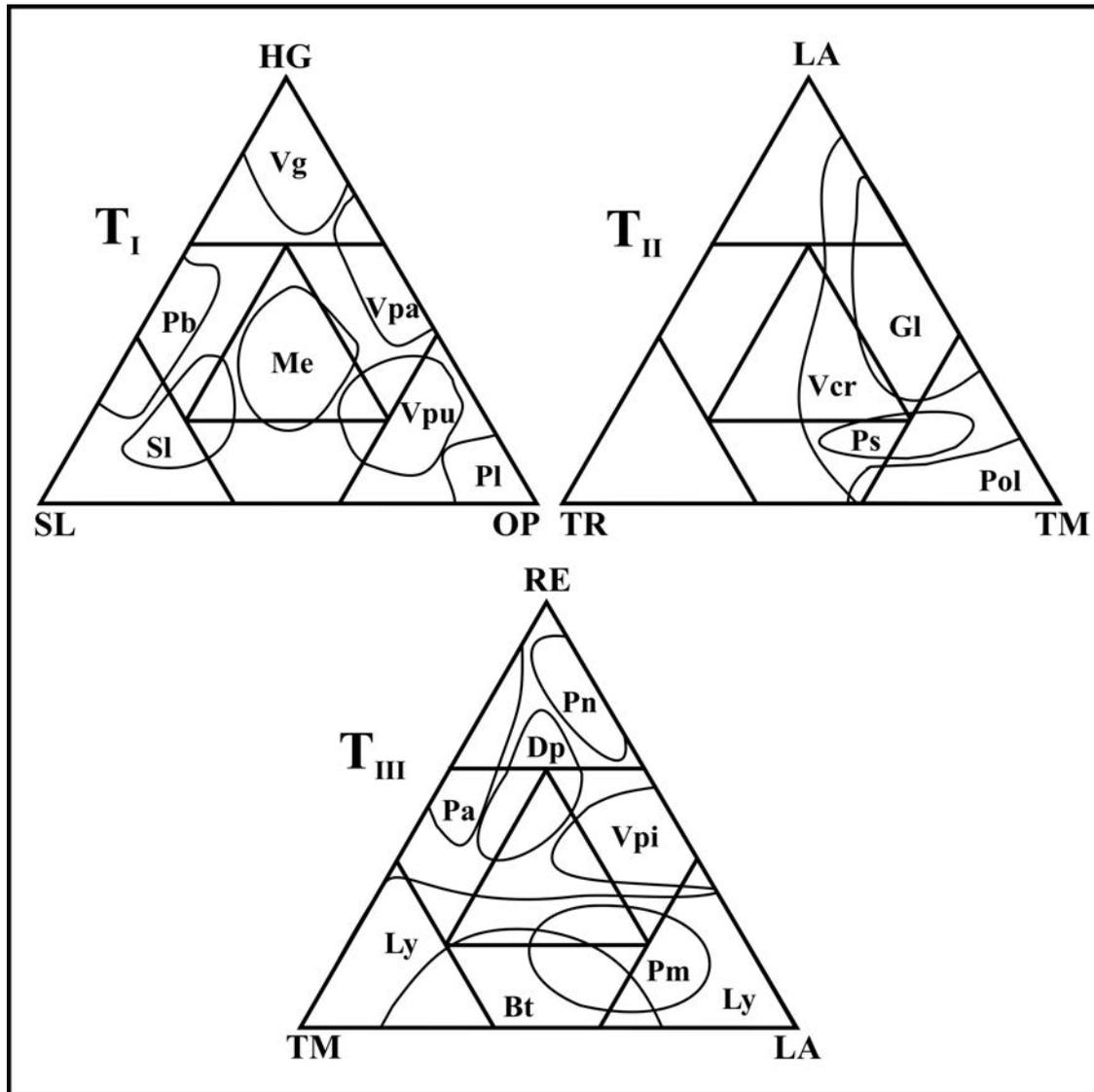


Fig. 2. Ecological structure of molluscan assemblages. T_I . Terrestrial habitats: SL – shady environments, OP – open environments, HG – moist environments; T_{II} . Temporary bodies of water: TR – terrestrial environments, TM – temporary bodies of water, LA – permanent bodies of water, T_{III} . Permanent bodies of water (lakes): TM – temporary bodies of water, LA – permanent bodies of water (lakes), RE – flowing water; explanations of symbols mollusc assemblages in text.

were used for this review of bivalves (Piechocki and Dyduch-Falniowska, 1993), aquatic (Piechocki, 1979) and terrestrial snails (Wiktor, 2004). The species were classified into ecological groups defined and described in detail by Lozek (1964), S. W. Alexandrowicz (1987), and S. W. Alexandrowicz and W. P. Alexandrowicz (2011). The last of the cited papers gave also the basic principles for grouping species and defining assemblages. Stratigraphic setting of particular assemblages was determined on the basis of their location in the sections, results of other published studies and analyses (palynological, diatomological, and radiocarbon dating) as well as stratigraphic characteristics of individual taxa of molluscs (Lozek, 1964; S. W. Alexandrowicz, 1987; W. P. Alexandrowicz, 2004). Index species for particular assemblages represent either the most typical forms (characteristic of certain types of habitats or certain climatic phases) or the taxa occurring in the highest numbers. This method for

distinguishing the assemblages was described by W. P. Alexandrowicz (2004) and S. W. Alexandrowicz and W. P. Alexandrowicz (2011).

RESULTS

Owing to the abundant material it has been possible to distinguish faunistic assemblages. Their structure and composition closely match the conditions under which the deposition of sediments filling the palaeolakes occurred. It should, nevertheless, be stressed that the malacological associations defined below can be much diversified. This diversification is caused by specific regional conditions as well as by various local factors. The assemblages of molluscs identified in Late Glacial and Holocene lake carbonate sediments can be allocated to one of three groups: assemblages with predominant terrestrial species, assemblages with predomi-

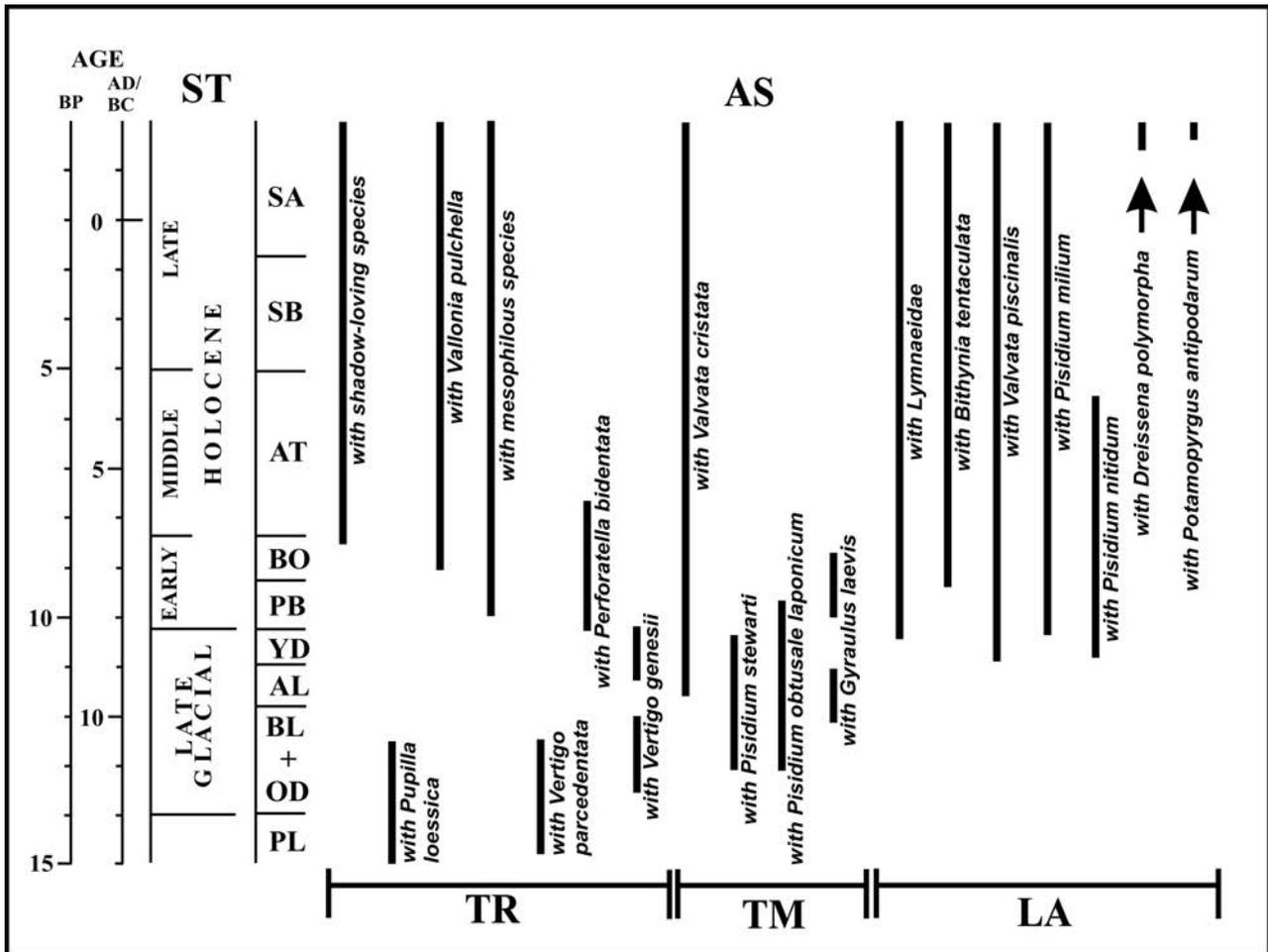


Fig. 3. Stratigraphic range of molluscan assemblages from calcareous lake sediments. ST. stratigraphy: PL – Pleniglacial, BL+OD – Older Dryas and Brlling AL – Alleröd, YD – Younger Dryas, PB – Preboreal Phase, BO – Boreal Phase, AT – Atlantic Phase, SB – Subboreal Phase, SA – Subatlantic Phase (subdivision of Holocene based on Starkel (1977)); AS. molluscan assemblages, TR – terrestrial habitats, TM – temporary bodies of water, LA – permanent bodies of water (lakes).

nant species typical of temporary or overgrowing water bodies, and assemblages with predominant species typical of permanent, open water bodies.

Assemblages with predominant terrestrial species (TR)

They are characterised by great diversity in both structure and composition. In the fillings of palaeolakes these assemblages are of little importance. They appear rarely and were recorded only in some sites. Usually, they occur in the bottom or at the top of sequences, indicating the preliminary or final phases of lake evolution.

The assemblage with shade-loving species (SI) is characterised by great species diversity. The dominant group is composed of shade-loving forms, among them both forest taxa: *Discus ruderatus* (Fér.), *Cochlodina laminata* (Mont.), and snails preferring slightly more open habitats (open forests, brush zones) – *Cepaea hortensis* (Müll.), *Bradybaena fruticum* (Müll.). A proportion of forms of shaded habitats usually reaches up to 50%. The supplementing elements include taxa with wide ecological tolerance: *Cochlicopa lub-*

rica (Müll.), *Eucomulus fulvus* (Müll.). Other ecological groups usually occur in minor proportions (Fig. 2T₁). The mentioned association has been found in few sites only and occurs within the sediments above the lake sequence, thus indicating a final phase of filling of lake basins. This association can be correlated with the period from a decline of Boreal Phase until the present (Fig. 3).

The assemblage with *Pupilla loessica* (PI) is a fauna of very poor species composition. The nominal taxon, *Pupilla muscorum* (L.) are accompanied by *Vallonia tenuilabris* (Brown) and occasionally, by the oligothermic bivalve species of *Pisidium hibernicum* (West.). Such faunas are typical for a very cold glacial climate and habitats of a polar steppe type with many small and shallow water bodies (Fig. 2T₁). Similar malacocenoses are commonly recorded in loess formations widespread throughout Central Europe (S. W. Alexandrowicz, 1995a; W. P. Alexandrowicz *et al.*, 2002). In northern Poland, this assemblage was found at Kurzętnik (Brodiewicz, 1966; W. P. Alexandrowicz, 1999, 2007), and in sediments underlying lake formations only. The association with *Pupilla loessica* represents a declining part of Pleniglacial and the earliest part of Late Glacial (Fig. 3).

The assemblage with *Vallonia pulchella* (Vpu) is marked by a predominant proportion of snails of open grassland habitats with variable moisture contents: *Vallonia pulchella* (Müll.), *Vallonia costata* (Müll.), and *Pupilla muscorum* (L.) (Fig. 2T_I). They are supplemented by mesophilous taxa: *Cochlicopa lubrica* (Müll.), *Euconulus fulvus* (Müll.), and hygrophilous taxa: *Succinea putris* (L.), *Carychium minimum* (Müll.). At some sites, an essential component of the aforementioned association is formed by aquatic molluscs living in small and temporarily disappearing water bodies: *Planorbis planorbis* (L.), *Galba truncatula* (Müll.). The shade-loving species are practically absent. At many sites, the fauna with *Vallonia pulchella* appears at the top of lake deposits, indicating the phases of disappearance of water bodies and their transformation into moist grasslands. This malacocoenosis is characteristic for mid-and late Holocene (Fig. 3).

The assemblage with mesophilous species (Me) is marked by presence of all ecological groups, although the forest and brush species, and aquatic forms are of secondary importance (Fig. 2T_I). The most important, however, are mesophilous forms: *Cochlicopa lubrica* (Müll.), *Euconulus fulvus* (Müll.), *Nesovitrea hammonis* (Ström), and *Vertigo angustior* (Jeffr.). These are supplemented by taxa of open: *Vallonia pulchella* (Müll.), *Vallonia costata* (Müll.), and of moist environments: *Succinea putris* (L.). The fauna hereby described represents the phases of disappearance of water bodies and is typical for the whole Holocene, and it occurs particularly often during Boreal and Atlantic Phases of the Holocene (Fig. 3).

The assemblage with *Vertigo parcedentata* (Vpa) is a very rare malacocoenosis, marked by presence of oligothermic hygrophilous species: nominal taxon, *Vertigo genesii* (Gredl.), and mesophilous species: *Columella columella* (G. Mart.). Also present are aquatic species with wide thermal tolerance – *Gyraulus laevis* (Ald.) (Fig. 2T_I). The taxa of open and shaded environments are absent. This fauna represents the tundra with moist substrate, very cold, polar climate and is correlated with the Pleniglacial and early Late Glacial (Fig. 3).

The assemblage with *Perforatella bidentata* (Pb) is a malacocoenosis poor in terms of species composition, marked by predominance of nominal species. *Perforatella bidentata* (Gmel.) is a shade-loving taxon, inhabiting forests of alder swamp type, growing on waterlogged sites (Fig. 2T_I). Besides the nominal species, hygrophilous forms: *Succinea putris* (L.), *Zonitoides nitidus* (Müll.), and aquatic molluscs living in temporary water bodies: *Galba truncatula* (Müll.), *Anisus leucostomus* (Mill.) are also important. Remaining ecological groups are represented sporadically only. The assemblage with *Perforatella bidentata* is typical for early Holocene, and particularly for Boreal Phase (Fig. 3). This association developed most often on shores of major lakes during low water level periods, in sediments that form inserts in gyttja and lacustrine chalk.

The assemblage with *Vertigo genesii* (Vg) is common and, at the same time, one of the most characteristic. The species preferring moist, sometimes waterlogged biotopes, developing under cold continental climate: *Vertigo genesii* (Gredl.), *Vertigo geyeri* (Lindh.), *Columella columella* (G. Mart.) and *Vertigo parcedentata* (Braun.) are of primary im-

portance (Fig. 2T_I). The second essential component includes euryecological mesophilous forms: *Euconulus fulvus* (Müll.) and *Nesovitrea hammonis* (Ström). The assemblage can be supplemented by oligothermic taxa characteristic for shaded habitats: *Semilimax kotulae* (West.) and *Arianta arbustorum* (L.). Occurrence of aquatic molluscs such as: *Gyraulus laevis* (Ald.), *Pisidium obtusale lapponicum* (Cless.) and *Galba truncatula* (Müll.) indicates presence of small, much overgrown or temporary water bodies. The malacocoenosis with *Vertigo genesii* is indicative of cold climate and domination of moist, usually open habitats of tundra type, and is characteristic for Late Glacial, and particularly the Younger Dryas. The upper limit of its occurrence is marked by the phase of rapid warming, manifested in the Preboreal Phase of the Holocene (Fig. 3).

The associations of similar compositions were described in many sections of genetically diverse sediments throughout Europe (e.g. Lozek, 1964; S. W. Alexandrowicz, 1987; Limondin-Lozouet, 1992; Krolopp and Sümegi, 1993; S. W. Alexandrowicz and W. P. Alexandrowicz, 1995; W. P. Alexandrowicz, 1997, 1999, 2004).

Assemblages with predominant species typical for temporary or overgrowing water bodies (TM)

The assemblage with *Valvata cristata* (Vcr) is a rich and diversified malacocoenosis in which two groups of aquatic molluscs predominate. The first, and usually more numerous group consists of species that are typical for shallow, small and much overgrown water bodies: *Valvata cristata* (Müll.), *Valvata macrostoma* (Mörch), *Acroloxus lacustris* (L.), and other species. The second group includes forms characteristic for temporarily disappearing water bodies: *Galba truncatula* (Müll.) and *Anisus leucostomus* (Mill.). There are often also euryecological aquatic molluscs: *Pisidium casertanum* (Poli.), *Radix baltica* (L.), and even rheophilous taxa as *Pisidium amnicum* (Müll.). The admixture of terrestrial species, chiefly hygrophilous, is usually fairly significant. More open biotopes are indicated by occurrence of *Succinea putris* (L.) and *Zonitoides nitidus* (Müll.) while in more shaded habitats, mesophilous species are common: *Vertigo angustior* (Jeffr.) and *Vertigo substriata* (Jeffr.) along with forms typical of waterlogged woods as *Perforatella bidentata* (Gmel.) (Fig. 2T_{II}). The presented malacocoenosis is typical for a biotope with a small, shallow water body, gradually filled with sediments. The characteristic feature of such small lake is an abundant development of vegetation, composed mostly of immersed plants. The composition of terrestrial fauna accompanying the aquatic species depends closely on features of the environment surrounding the water body. The malacocoenosis is composed of species with great thermal tolerance and can appear in various climatic stages of the Holocene, and even in the Late Glacial sediments (Fig. 3).

The assemblage with *Pisidium stewarti* (Pst) is indicated by dominance of bivalves. Along with the nominal species, there are also: *Pisidium lilljeborgii* (Cless.), *Pisidium obtusale lapponicum* (Cless.), and sometimes *Pisidium hibernicum* (West.). Snails are represented by oligothermic aquatic forms as *Gyraulus laevis* (Ald.) as well as by hygrophilous species: *Vertigo genesii* (Gredl.) and *Vertigo geyeri* (Lindh.).

This fauna developed in shallow and intensively overgrown, permanent lakes (Fig. 2T_{II}). It is characteristic of cold climate and corresponds to the Late Glacial (Fig. 3).

The assemblage with *Pisidium obtusale lapponicum* (Pol) is a malacocoenosis poor in species composition, consisting chiefly of aquatic species, among which the forms living in small, very shallow, intensively overgrown and temporarily disappearing water bodies, typical for a cold climate. Apart from the nominal taxon, there are also oligothermic forms: *Pisidium lilljeborgii* (Cless.) and *Pisidium stewarti* (Pat.) as well as species of wide thermal tolerance: *Galba truncatula* (Müll.) and *Radix baltica* (L.). Terrestrial species are few and they are most often represented by hygrophilous and oligothermic snails as *Vertigo genesii* (Gredl.) (Fig. 2T_{II}). This malacocoenosis is typical of Late Glacial, particularly of the Younger Dryas. It also occurs rarely at the beginning of the Holocene. It does not appear in its younger part, starting from the Boreal Phase (Fig. 3).

The assemblage with *Gyraulus laevis* (Gl) is characterised for its abundant occurrence of oligothermic aquatic snails. Apart from the most characteristic nominal taxon, there are also *Pisidium obtusale lapponicum* (Cless.) as well as other species of wide thermal tolerance such as: *Radix baltica* (L.), *Galba truncatula* (Müll.) and others. The terrestrial fauna with prevalence of oligothermic species: *Vertigo genesii* (Gredl.), *Vertigo geyeri* (Lindh.) and mesophilous species usually appears as admixture, although even up to 40% (Fig. 2T_{II}). This assemblage is characteristic for small, shallow but not drying lakes of a cold climate. The assemblage with *Gyraulus laevis* is characteristic for warmer phases of the Late Glacial or the beginning of the Holocene. In the upper part of the Holocene, the nominal species occurs extraordinarily rarely (Fig. 3).

Assemblages with predominant of species typical for permanent open water bodies (LA)

The assemblage with Lymnaeidae (Ly) is a rich and diversified malacocoenosis, consisting chiefly of aquatic species of wide ecological tolerance, inhabiting permanent water bodies: *Radix baltica* (L.), *Stagnicola turricula* (Held), *Stagnicola palustris* (Müll.), *Pisidium casertanum* (Poli.), and many other species. Forms typical of small water bodies: *Acroloxus lacustris* (L.), *Gyraulus albus* (Müll.), and sometimes even forms typical for temporarily drying zones: *Galba truncatula* (Müll.) appear as admixture. Terrestrial species are either absent or appear only as single shells (Fig. 2T_{III}). The composition and structure of this association are very variable and depend closely on nature of the water body. The assemblage with Lymnaeidae develops during the whole Holocene, both in small, shallow and intensively overgrown lakes and in larger lakes of different trophism (Fig. 3).

The assemblage with *Bithynia tentaculata* (Bt) is one of the most characteristic and most commonly occurring associations in lake carbonate sediments. In this malacocoenosis, the most important species is *Bithynia tentaculata* (L.) which is sometimes accompanied by numerous forms characteristic for permanent water bodies (Fig. 2T_{III}). The fauna with *Bithynia tentaculata* is typical for semi-open lakes, partly overgrown with reeds. There are 2 types of it. The first one is

characterized by predominance of opercula over shells and is indicative of presence of compact reeds. The second type indicates prevalence of shell over opercula and corresponds to the littoral zone of the lake (Steenberg, 1917; S. W. Alexandrowicz, 1999a). The admixture of terrestrial fauna is usually minor. This assemblage is often found in early and mid-Holocene deposits. It occurs only occasionally in the Late Glacial formations (Fig. 3).

The assemblage with *Valvata piscinalis* (Vpi) has a poor composition indicated by predominance of nominal species, accompanied by euryecological bivalves: *Pisidium casertanum* (Poli.), *Pisidium subtruncatum* (Malm), and snails – *Bithynia tentaculata* (L.) (both shells and opercula). Terrestrial species are practically absent (Fig. 2T_{III}). This association usually develops in deeper parts of the lakes, on a muddy bottom without rooted vegetation. The fauna with *Valvata piscinalis* occurs both in Late Glacial and Holocene sediments. In the latter case, it is usually more diversified in its species composition (Fig. 3).

The assemblage with *Pisidium milium* (Pm) is predominated by bivalves of the *Sphaeridae* family. Apart from the nominal taxon, the most frequently are: *Pisidium casertanum* (Poli.), *Pisidium subtruncatum* (Malm), and *Sphaerium corneum* (L.) as well as *Pisidium henslowanum* (Shep.) and *Pisidium supinum* (A. Schmidt). Warmer phases are indicated by presence of *Pisidium moitessierianum* (Pal.). Aquatic snails are more rare and are represented by lake forms: *Bithynia tentaculata* (L.) and *Stagnicola turricula* (Held), while terrestrial species are absent (Fig. 2T_{III}). This assemblage is typical of open lake water bodies where it lives in the zones characterized by poor vegetation, both above the water surface and immersed. The malacocoenosis with *Pisidium milium* occurs exclusively in the Holocene sediments (Fig. 3).

The assemblage with *Pisidium nitidum* (Pn) is indicated by major proportion of bivalves among which a major role is played by *Pisidium nitidum* (Jen.), *Pisidium amnicum* (Müll.), *Pisidium casertanum* (Poli.) and *Pisidium subtruncatum* (Malm). Aquatic snails are rare while the admixture of terrestrial forms does not exceed 20% (Fig. 2T_{III}). This malacocoenosis is distinct for its large contents of species that require running water. Such fauna develops in lowland rivers with slow current, or in bottom parts of large lakes, in the zones in which the currents occur. The assemblage with *Pisidium nitidum* was found in the sediments allocated to Late Glacial, and to early and mid-Holocene (Fig. 3).

The assemblage with *Dreissena polymorpha* (Dp) is predominated by the nominal species up to 95%. This assemblage occurs in lakes, characteristic for its different nature and trophy. The nominal species is remarkably euryecological, but it prefers particularly to colonise hard surface zones (cobble, shells of large bivalves as *Unio* or *Anodonta* genera, anthropogenic hydrotechnical structures) where it develops huge populations (Stańczykowska, 1977) (Fig. 2T_{III}). Presence of *Dreissena polymorpha* (Pall.) in the sediments indicates their young age. This form was introduced accidentally into Poland and has been recorded there since the beginning of the 19th century (W.P. Alexandrowicz and S.W. Alexandrowicz, 2010) (Fig. 3).

The assemblage with *Potamopyrgus antipodarum* (Pa) forms a poor association, predominated by the nominal spe-

cies, accompanied by other aquatic forms typical for lakes: *Radix baltica* (L.), *Stagnicola turricula* (Held), *Bithynia tentaculata* (L.), as well as species typical for temporarily dried-up zones as *Galba truncatula* (Müll.) (Fig. 2T_{III}). *Potamopyrgus antipodarum* (Gray) is a young immigrant, recorded in Poland since 1933 (W.P. Alexandrowicz and S.W. Alexandrowicz, 2010) and it is therefore a good age indicator (Fig. 3).

DISCUSSION

The mollusc assemblages develop in definite habitats. Their nature depends on two principal factors. The first one is climate which determines geological processes and living conditions in a regional scale. Within the most recent 15 000 years, two periods, utterly different from the viewpoint of climatic conditions, can be distinguished. The older period covers a termination of the last glaciation i.e. the Late Glacial. It was a cold phase with two warmer fluctuations (Bølling and Allerød) which were only very weakly indicated in malacological successions of carbonate lake sediments. This period was associated with progressing deglaciation, when massive melting of dead ice blocks led to the emergence of lakes and swamps. The younger period corresponds with the Holocene when several colder stages are occurred, separated by warmer fluctuations. The Holocene is not only represented by developing lakes but, in many cases, also by their overgrowing, shallowing and gradual disappearance (e.g. Starkel, 1977; Ralska-Jasiewiczowa and Starkel, 1988; Ralska-Jasiewiczowa, 1989; Birks and Birks, 1989).

Local conditions are the second principal factor that determines development and variability of malacocoenoses. Great diversity of habitats can result in occurrence of utterly different faunistic assemblages in sediments of the same age. The Late Glacial is associated with occurrence of relatively poor malacocoenoses. These are characterised by significant proportion of oligothermic species and forms of wide ecological tolerance as well as with occurrence of high numbers of molluscs living in shallow water bodies, boggy zones and open terrestrial habitats. The faunas of the Holocene are usually more diversified and include also species with high ecological requirements. The taxa associated with large water bodies and shaded terrestrial habitats are also common.

It is possible to distinguish three types of malacological successions in the analysed material, indicating diversification of habitats and stratigraphic sequences of fauna assemblages. These analyses of such sequences were attempted only rarely (S. W. Alexandrowicz, 1983a; W. P. Alexandrowicz, 1997, 2004), although they provide ample grounds for interpretations and reconstructions of palaeoenvironments as well as their changes in time.

Type A is indicated by domination of assemblages with major proportion of terrestrial molluscs. They are rare in lake deposits, but much more often in calcareous tufas in northern Poland (Skompski, 1961; Brykczyński and Skompski, 1979) as well as in the south (W. P. Alexandrowicz, 2004). The sequence starts with a malacocoenosis predominated by oligothermic terrestrial species preferring open habitats (assemblage with *Pupilla loessica*). In the final part of the Late Glacial, the hygrophilous assemblages (chiefly the

fauna with *Vertigo genesii*) became increasingly important as well as associations typical for small, shallow and densely overgrown water bodies (assemblage with *Pisidium stewarti* and with *Pisidium obtusale lapponicum*). Starting from the early Holocene, the proportion of aquatic and swamp taxa declines gradually and shadow-loving, open-country and mesophilous snails take over (Fig. 4).

The aforementioned sequence is a record of evolution of small water bodies which emerged at the end of the Late Glacial as an effect of melting of small dead ice blocks. Small and shallow lakes were rapidly filled with sediments and transformed into swamps. Such transformation took place during the Younger Dryas or during the early Holocene. From the beginning of the Atlantic Phase, progressive drying and replacement of moist swampy habitats by drier grassland and/or forest habitats occurred (Fig. 4).

Type B is the most frequent one of the malacofauna assemblage in carbonate lake sediments (W.P. Alexandrowicz, 1999, 2007). This sequence begins with a phase predominated by open terrestrial habitats of tundra type. Characteristic features of this interval include occurrence of oligothermic assemblages with *Pupilla loessica* (on drier sites) or with *Vertigo parcedentata* (moist and waterlogged biotopes). In younger Late Glacial, a phase of peat bog development is commonly observed. Presence of characteristic malacocoenosis with *Vertigo genesii* is linked to this period. In waterlogged areas, there were small, shallow and much overgrown melt-out lakes, inhabited by associations with *Pisidium stewarti* and *Pisidium obtusale lapponicum*. Progressive melting of large dead ice blocks during the Younger Dryas and at the beginning of the Holocene led to transformation of these habitats into major lakes. This stage is associated with occurrence of rich assemblages of aquatic molluscs, particularly with *Bithynia tentaculata*. It is also a stage of intensive accumulation of carbonate sediments, a thickness of which may even exceed 10 m. Lacustrine chalk and calcareous gyttja gradually filled lake basins, leading to their disappearance. The final stage of filling of the lakes resulted in their transformation into peat bogs. This is confirmed by presence of peat layers overlying the carbonate sediments. The molluscan communities show also evident changes. The assemblages with prevalence of species typical of lakes are replaced by associations dominated by taxa of shallow and intensively overgrown, sometimes even episodic water bodies (assemblage with *Valvata cristata*). In the late Holocene, these waterlogged zones were transformed into terrestrial habitats, either open (assemblage with *Vallonia pulchella*) or shaded (assemblage with shadow-loving species) (Fig. 4).

Type C succession is characteristic for large lakes. These water bodies developed from extensive cave-in lakes, resulting from melting dead ice blocks and formed as late as in the Late Glacial. This stage is associated with occurrence of assemblages with minor proportion of terrestrial species e.g. fauna with *Valvata piscinalis*. A domination of aquatic molluscs maintains throughout the whole Holocene. The changes of water level in lakes (Ralska-Jasiewiczowa and Starkel, 1988; Wojciechowski, 1999, 2000) were marked by periodic occurrence of assemblages with greater proportions of taxa typical of shallow water bodies (assemblage with *Valvata cristata*) or even waterlogged terrestrial habitats (assem-

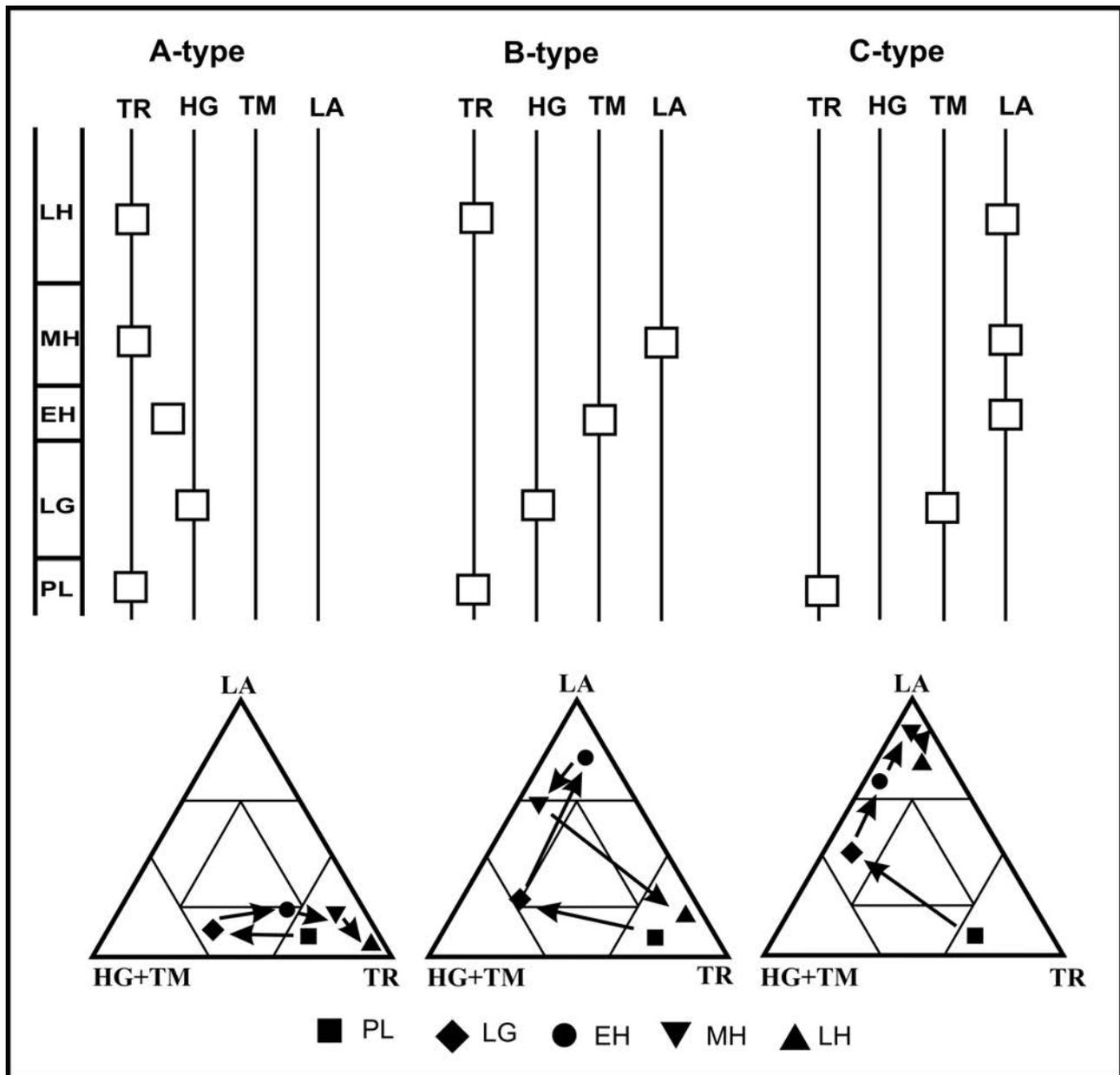


Fig. 4. Successions of molluscan assemblages from lake sediments in North Poland. A-type, B-type, C-type – successions of assemblages described in text: PL – Pleniglacial, LG – Late Glacial, EH – Early Holocene, MH – Middle Holocene, LH – Late Holocene, TR – terrestrial environments, HG – moist environments, TM – temporary bodies of water, LA – permanent bodies of water (lakes).

blage with *Perforatella bidentata*). In the top part of the sequence of lake sediments, the assemblages with *Potamopyrgus antipodarum* and with *Dreissena polymorpha* occur and indicate a human impact (Fig. 4).

CONCLUSIONS

On the basis of the analysis of features and sequences pertaining to molluscan assemblages occurring in lacustrine chalk and calcareous gyttja, it was possible to compile the scheme of evolution of lake water bodies. The oldest molluscan assemblages document the pre-lacustrine terrestrial phase, corresponding to the end of Pleniglacial, and with early Late Glacial. The malacoenoses indicate presence of open habitats with varying moisture levels, from dry Arctic

steppe-like habitats to moist and waterlogged tundra biotopes. The first stage of lake development is connected with a warming of the Alleröd Interphase. Massive melting of dead ice blocks led to emergence of numerous melt-out lakes (e.g. W. P. Alexandrowicz, 1999, 2007; Wojciechowski, 1999, 2000). Thus extensive but shallow and intensively overgrowing water bodies were inhabited by relatively poor molluscan assemblages with predominant oligothermic species. During the Younger Dryas, many of these water bodies were completely filled with sediments and transformed into peat bogs. A characteristic assemblage with *Vertigo genesii* regarded as indicator of the aforementioned phase is associated with these habitats (Lozek, 1964; S. W. Alexandrowicz, 1987; Limondin-Lozouet, 1992; Krolopp and Sümegei, 1993; S. W. Alexandrowicz and W. P. Alexandrowicz, 1995; W. P.

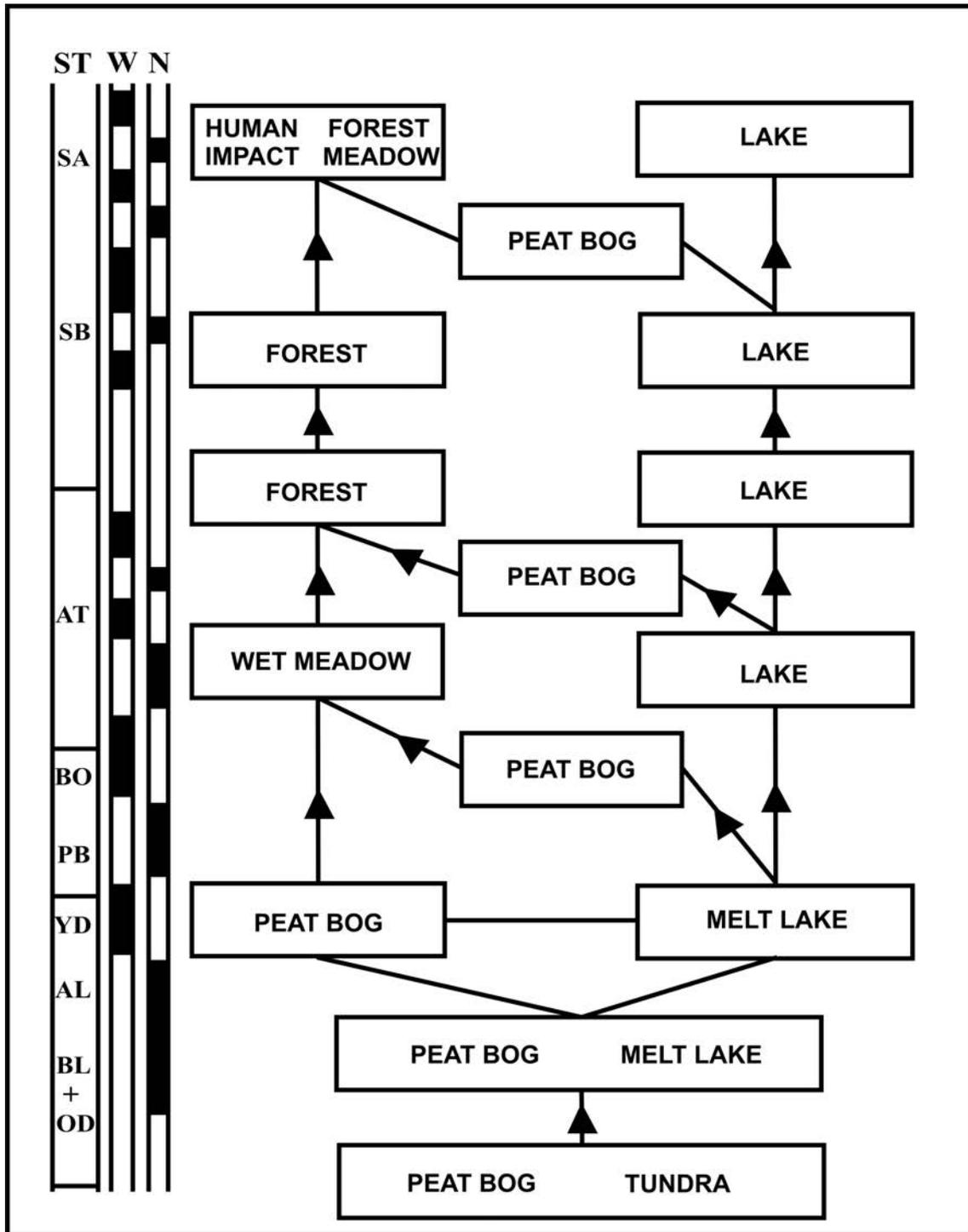


Fig. 5. Fig. 5. Late Glacial and Holocene environmental changes in North Poland in the light of malacological analysis of calcareous lake sediments. ST. stratigraphy: BL+OD – Older Dryas and Brilling AL – Alleröd, YD – Younger Dryas, PB – Preboreal Phase, BO – Boreal Phase, AT – Atlantic Phase, SB – Subboreal Phase, SA – Subatlantic Phase (subdivision of Holocene based on Starkel (1977)); W – high-level water periods (after: Wojciechowski, 1999, 2000), N – low-level water (after: Wojciechowski, 1999, 2000).

Alexandrowicz, 1997, 1999, 2004). On the other hand, however, the declining period of the Late Glacial was indicated by rising water levels in lakes. This phenomenon, observed in almost entire northern Poland (Wojciechowski, 1999, 2000) can be connected with gradually moister climate. Owing to that, many melt-out lakes were transformed into larger and deeper lakes, in which carbonate deposition was initi-

ated. A beginning of the Holocene was indicated by rapid warming that determined a subsequent stage of lake water bodies. Decreasing precipitation resulted in a drop of water level in lakes (Ralska-Jasiewiczowa and Starkel, 1988; Wojciechowski, 1999, 2000). This fact, in combination with gradual fillings of lake basins with sediments resulted in disappearance of many shallow lakes and in peat bogs emerging

in their places. During mid- and late Holocene these peat bogs were transformed into grassland and forest biotopes. The aforementioned drop of water level were much less pronounced in large lakes, in which deposition of lacustrine chalk and calcareous gyttja with rich and diverse molluscan assemblages has been continued throughout early and mid-Holocene. During late Holocene, a remarkable slowing down and in many cases, disappearance of carbonate sedimentation occurred. Climate changes reflected in changing water levels in lakes are also common during this period (Ralska-Jasiewiczowa and Starkel, 1988; Wojciechowski, 1999, 2000). During the last one hundred years, human impact has become more and more noticeable in the environment. It is marked in malacocoenoses in lake sediments either by impoverishment of species composition resulting from progressive eutrophication or by occurrence of expansive species alien to Polish fauna that indicate anthropogenic migrations (Fig. 5).

Changes in molluscan assemblages enable distinguishing of several episodes of peat bog development and disappearance of lake water bodies. These occurred in the declining part of the Younger Dryas, beginning of the Atlantic Phase and in the Subatlantic Phase (Fig. 5). These episodes evidently coincide with phases of lower water levels in lakes (e.g. Starkel, 1977; Ralska-Jasiewiczowa and Starkel, 1988; Wojciechowski, 1999, 2000).

Reconstruction of the evolution of lake water bodies in northern Poland, based on analysis of molluscan assemblages, supplements similar reconstructions and patterns defined under different methods and published in numerous studies, both in Poland (e.g. Goslar *et al.*, 1993; Starkel *et al.*, 1996; Żurek and Pazdur, 1999; Wojciechowski, 1999, 2000) and in northern Europe (e.g. Mania, 1973; Mania and Toepfer, 1973; Sunderlau, 1975; Griffiths *et al.*, 1994; Magny and Ruffaldi, 1995).

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