Palaeobiogeographical characteristics of the Miocene land snail fauna of Poland

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A zoogeographical analysis of the Miocene land snail fauna of Poland was carried out on the basis of the author's field investigations, collections, as well as literature data. Until now about a hundred species are known from ten localities.
The distribution pattern of the genus *Gastrocopta* and a hypothesis on its origin are discussed.

Contents

Introduction

The Palaeogene/Neogene transition is characterised by substantial changes of the European faunal composition. These changes continued through Pliocene and Early Pleistocene times, and affected also the malacofaunal assemblages. The ecological changes generally followed the climatic and topographic transformations which were, in their turn, controlled by continental drift and the alpine uplift. The Neogene climatic cooling of the Northern Hemisphere and aridisation progressing from Central Asia resulted partly in the extinction and partly in a diversification of the subtropical and tropical Palaeogene malacofauna. Remainders of the Tertiary fauna survived in Poland till the Early Pleistocene (Stworzewicz, 1981).

Material and stratigraphy

Most of the Polish Miocene terrestrial mollusc species (c. 60) come from the site of Opole (Fig. 1) (Andreae, 1902a, b, 1904; Nordsieck, 1981). The age of this malacofauna was estimated by Nordsieck (based on the analysis of the Clausiliidae) as corresponding to the MN7 zone (c. 14-15 Ma BP). At the Bełchatów site up to 6000 shells belonging to c. 30 species have been found in three calcareous intercalations within a lignite sequence (Stworzewicz & Szynkiewicz, 1989), correlated with the MN4-MN9 zones determined by means of small mammal faunas. Fission-track ages on the mid-

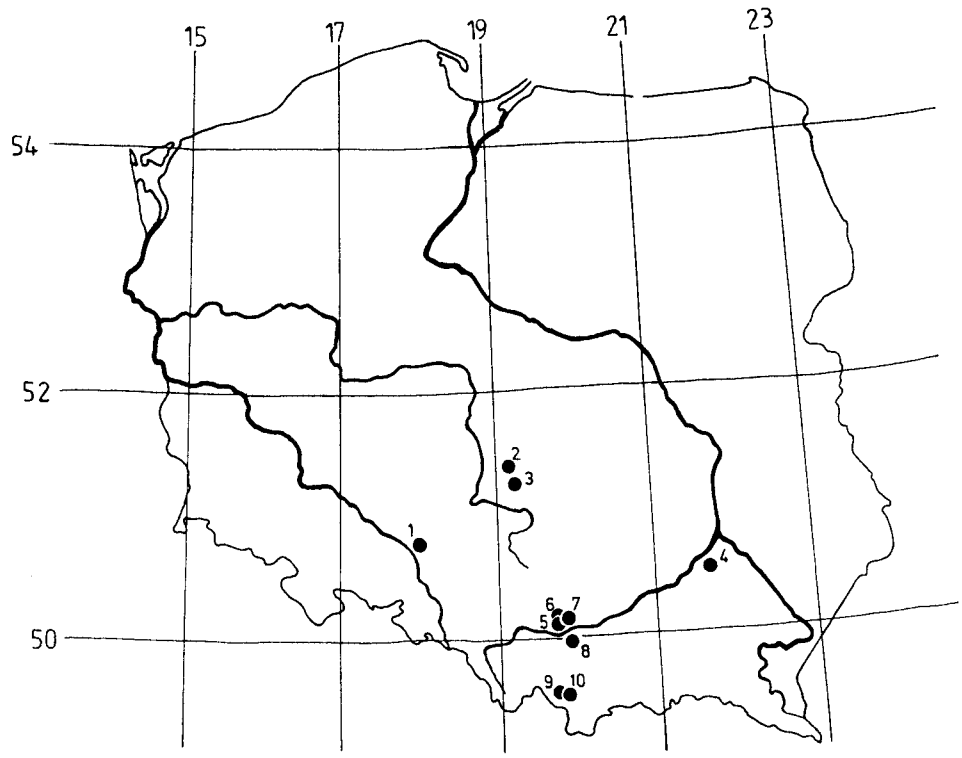

Fig. 1. Miocene localities of terrestrial gastropods in Poland. 1: Opole, 2: Bełchatów, 3: Chabielice-Kleszczów, 4: Sobów, 5: Bielany, 6: Szczyglice, 7: Witkowice, 8: Ruczaj, 9: Koniówka, 10: Czarny Dunajec.

dle and upper faunas range from 18.1 ± 1.7 to 16.5 ± 1.3 Ma BP. The malacofaunal list has not been completed so far (new samples are still under study), hence the number of species may increase. The hitherto identified malacofauna includes the species:

Pomatias bisulcatum (Zieten, 1839)
Palaina martensi (Andreae, 1902)
Renea pretiosa (Andreae, 1904)
Carychium schwageri (Reuss, 1868)
Negulus suturalis (Sandberger, 1858)
Vertigo angulifera Boettger, 1884
Vertigo callosa (Reuss, 1849)
Argna oppoliensis (Andreae, 1902)
Gastrocopta nouletiana (Dupuy, 1850)
Gastrocopta ferdinandi (Andreae, 1902)
Gastrocopta cf. *larteti* (Dupuy, 1850)
Constricta tenuisculpta (Reuss, 1861)

and furthermore representatives of the Pomatiasidae, Strobilopsidae, Vertiginidae,

Clausiliidae, Subulinidae, Oleacinidae, Endodontidae, Zonitidae, Vitrinidae, Limacidae, Milacidae, and Helicidae.

Some other data have been provided by the studies of freshwater deposits near Cracow carried out by Łomnicki (1902) and the present author (Stworzewicz, 1993). Their age corresponds to that of the lower strata from Bełchatów, i.e. the Carpathian. They contain the taxa:

Cochlostoma polonicum (Łomnicki, 1902)
Tudorella conica bielanensis (Łomnicki, 1902)
Trichia kleini kleini (von Klein, 1864)
Helicodonta involuta scabiosa (Sandberger, 1874)
cf. *Tropidomphalus extinctus* (Rambur, 1862)
Klikia giengensis bielanensis (Łomnicki, 1902)
Cepaea silvana silvana (von Klein, 1853).

Results and discussion

C. 100 species of land snails representing 54 genera and 21 families are known from the Polish Miocene (Stworzewicz, 1989). The Zonitidae, Clausiliidae and Helicidae dominate. Their proportion in the extant Polish fauna is similar, apart from the Vertiginidae which represent another important Recent group.

Discussing a zoogeographical structure of the Miocene malacofauna, it is convenient to distinguish four groups:

1. Genera extinct in Europe but extant in distant, extra-European regions: *Palaina*, *Negulus*, *Gastrocopta*, and *Strobilops*.

2. Genera extinct in Poland but extant in the Mediterranean region and the Caucasus: *Cochlostoma*, *Craspedopoma*, *Pomatias*, *Tudorella*, *Renea*, *Azeca*, *Pleurodiscus*, *Poiretia*, and *Aegopis*.

3. Totally extinct genera: *Enneopupa*, *Klikia*, *Tropidomphalus*, and *Galactochilus*.

4. Genera extant in Poland.

The first group is the most interesting one from a zoogeographical point of view. Today members of *Palaina* (Cyclophoridae) are confined to the Far East (Amur Basin, Japan, Korea), islands of the West Pacific and Australia (Queensland). In Europe this genus was represented by two species, including *Palaina martensi* which was described from Opole and is also known from Bełchatów. These species are recorded from the Late Miocene. Several specimens of *P. martensi* from Bełchatów have been collected in the upper part of the section. *Negulus* (Vertiginidae) is another genus known in Europe only as a fossil with a recorded stratigraphic range from Eocene to Late Pliocene. In Poland this genus was represented by two species: *Negulus raricostatus* (Slavik, 1869) and *N. suturalis*. They are probably closely related to *Negulus reinhardti* (Jickeli, 1874), a species living in Ethiopia (Klika, 1891). It is likely that *Negulus* migrated to Europe from the East African area through the Arabian Peninsula and the Caucasus before the opening of the Red Sea which started c. 5 Ma BP. The presence of *Negulus* sp. in Late Miocene beds of the Caucasus (Steklov, 1966) could confirm this hypothesis. But another interpretation is more probable; the presence of the living *Negulus* from Ethiopia is a remnant of a wider range before the Miocene, reaching even as far as China (Yu Wen et al., 1982). This phenomenon is also found for other

terrestrial invertebrates; for instance the species of the phyletic series *Neotrechus* (Coleoptera, Carabidae) show a close zoogeographical relation between Ethiopia and southeastern Europe (Dolomites, Dinaric Mountains), the Middle East and the Caucasus (Pawłowski & Stachowiak, 1991).

Gastrocopta is the most widespread genus of Gastrocoptinae (Vertiginidae), nowadays distributed all over the world with the exception of Europe, where it was a common element of the Cainozoic malacofauna, from the Eocene to the beginning of the Pleistocene. In the European Tertiary more than 30 species belonging to three subgenera: *Albinula*, *Sinalbinula* and *Vertigopsis* are known. Only *Albinula* and *Sinalbinula* represented by at least five species are recorded from the Polish Miocene. Another question is the systematic distinctness of the mentioned subgenera. This problem cannot be solved until the genus *Gastrocopta* is systematically revised.

Today members of *Albinula* are restricted to the middle and eastern part of North America (Fig. 2). There are some fossil records from the modern range area including its western edge (Roth, 1986). The modern range of *Sinalbinula* comprises mainly the Far East: Japan, Korea, eastern China, and Polynesia, Micronesia, Hawaii and Australia. Several localities from Central Asia, the Caucasus and Ethiopia are also reported. Pilsbry (1916-1918) suggested that *Gastrocopta* appeared in Europe originating probably from the Asian-American distribution center. This hypothesis seems hardly likely for two reasons: 1) taking into account the plate tectonic theory, it follows that there were no connections between America and Asia in Late Palaeogene-Early Neogene times; 2) in the Far East only *Sinalbinula* is represented at present (apart from *Gastrocopta* s.s., living in Ceylon and the Philippines) and there is no evidence suggesting that *Albinula* has ever occurred there.

A similar problem concerning the origin and distribution of the Strobilopsidae has been discussed by Manganelli et al. (1989), who presupposed the area of Laurasia, corresponding to present-day Europe before continental drift separated North America from Europe, as a centre of origin and dispersion for the family. For *Gastrocopta*, however, such an explanation does not seem valid, since: 1) the living members of the subgenus *Gastrocopta* s.s. in the African and American tropics display a close similarity; 2) *Gastrocopta* s.s. has been recorded from a Pliocene locality in Egypt and an Eocene one in the southwestern U.S.A. (Roth, 1986); 3) the modern range of *Gastrocopta* s.s. is extending into the tropics of both hemispheres.

Waldén (1984), considering the origin of the terrestrial mollusc fauna of the Mid-Atlantic islands stated that, among others, some extinct genera in the European Tertiary belonged to the fauna on the northern border of the Tethys Sea.

Taking all above facts into consideration, one may suggest that the genus *Gastrocopta* is a very old group which existed all along the coasts of the Tethys Ocean both in Laurasia and in Gondwana during the time that South America and Africa had a land connection. The subsequent progressive drift of Laurasia and Gondwana would be the first stage of isolation of widely distributed *Gastrocopta* (Fig. 3). This hypothesis would support the explanation of the close similarity of *Gastrocopta* species on both sides of the South Atlantic. The territory of present-day Europe could be the area of overlapping ranges of groups which speciated on the outskirts of the wide Laurasian range: *Albinula* on the North American area and *Sinalbinula* in the Far East. Later dispersion phenomena may have caused *Sinalbinula* to reach Australia (through the

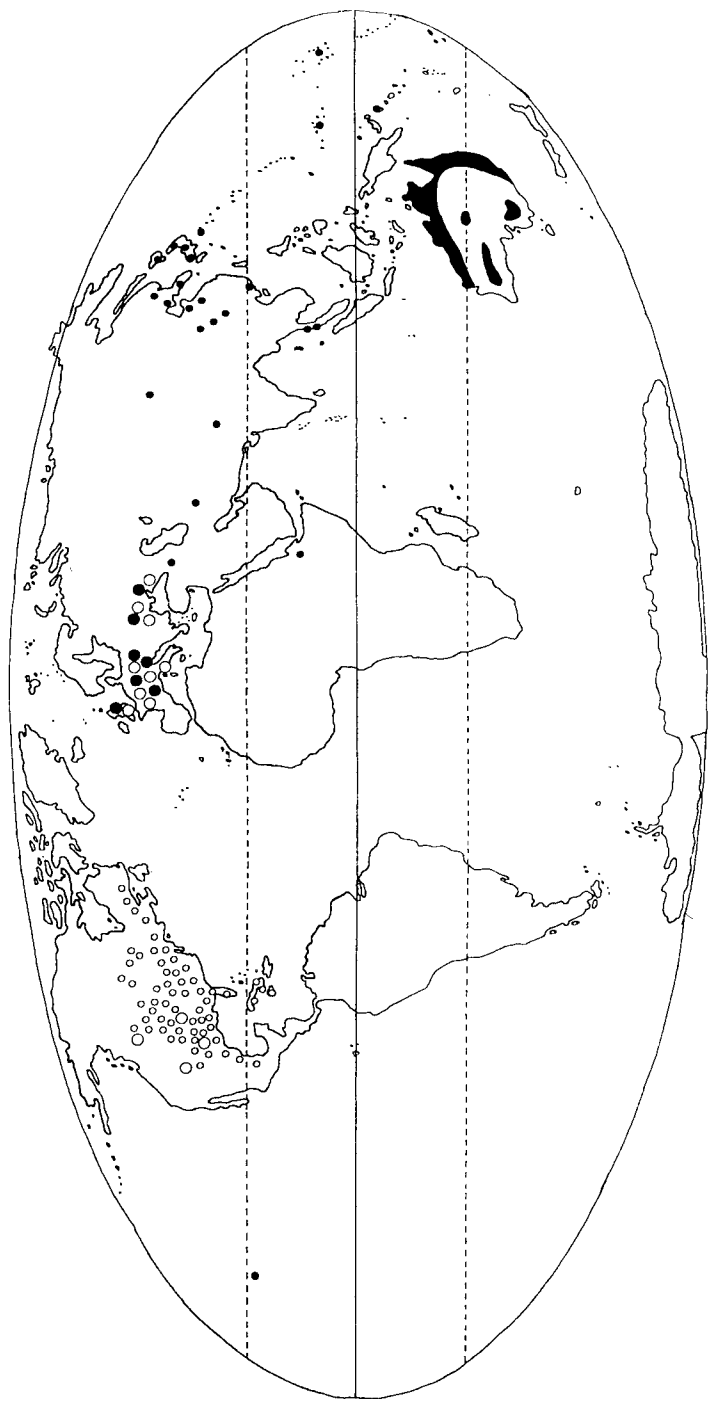

Fig. 2. Distribution pattern of *Albinula* (open circle) and *Sinalbinula* (black circle and continuous range in Australia) in the Recent fauna (small symbols) and during the Tertiary (large symbols).

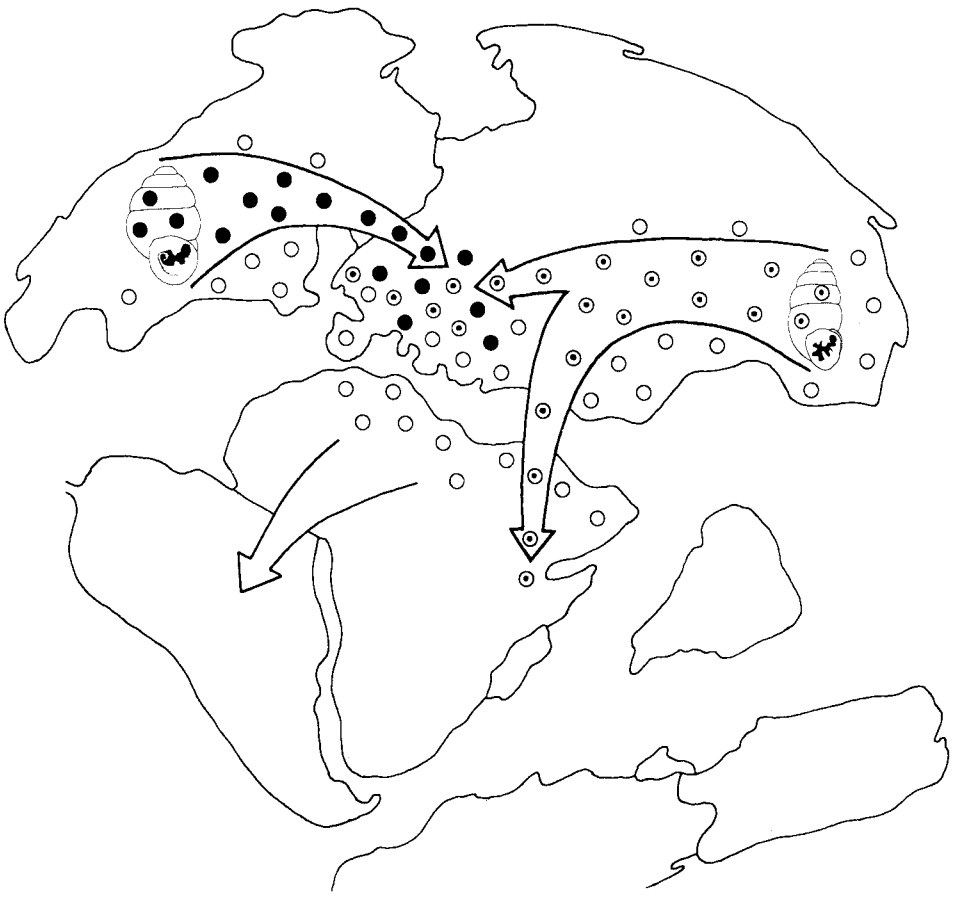

Fig. 3. Hypothetical migration of *Albinula* and *Sinalbinula* to Europe against a background of plate tectonic theory as given by van Andel (1991) and Raup & Stanley (1971).

progressive colonisation of islands between southeast Asia and Australia).

In the above mentioned paper, Manganelli et al. have considered some hypotheses on the origin and dispersion of the Strobilopsidae. It is, however, very probable that also this family originated and dispersed in the same way as *Gastrocopta* (in the second stage). The fact, that in the Tertiary both genera now living in North America (*Strobilops* s.s. and *Discostrobilops*) and in the Far East (*Eostrobilops*) (Fig. 4) were present in Europe support such inference.

The history of the malacofauna of the second group is less complicated. Their Recent occurrence in southern Europe and the Caucasus may also be regarded as a remnant of a wider distribution during the Tertiary, on the northern border of the Tethys. In the Neogene, after the climatic cooling and, later, drying, part of the mollusc fauna began to withdraw from Central Europe. Simultaneously, the ultimate formation of the Alpine-Carpathian Chain became a barrier between Central Europa and the Mediterranean Basin. The occurrence of *Poiretia* in the Mediterranean region

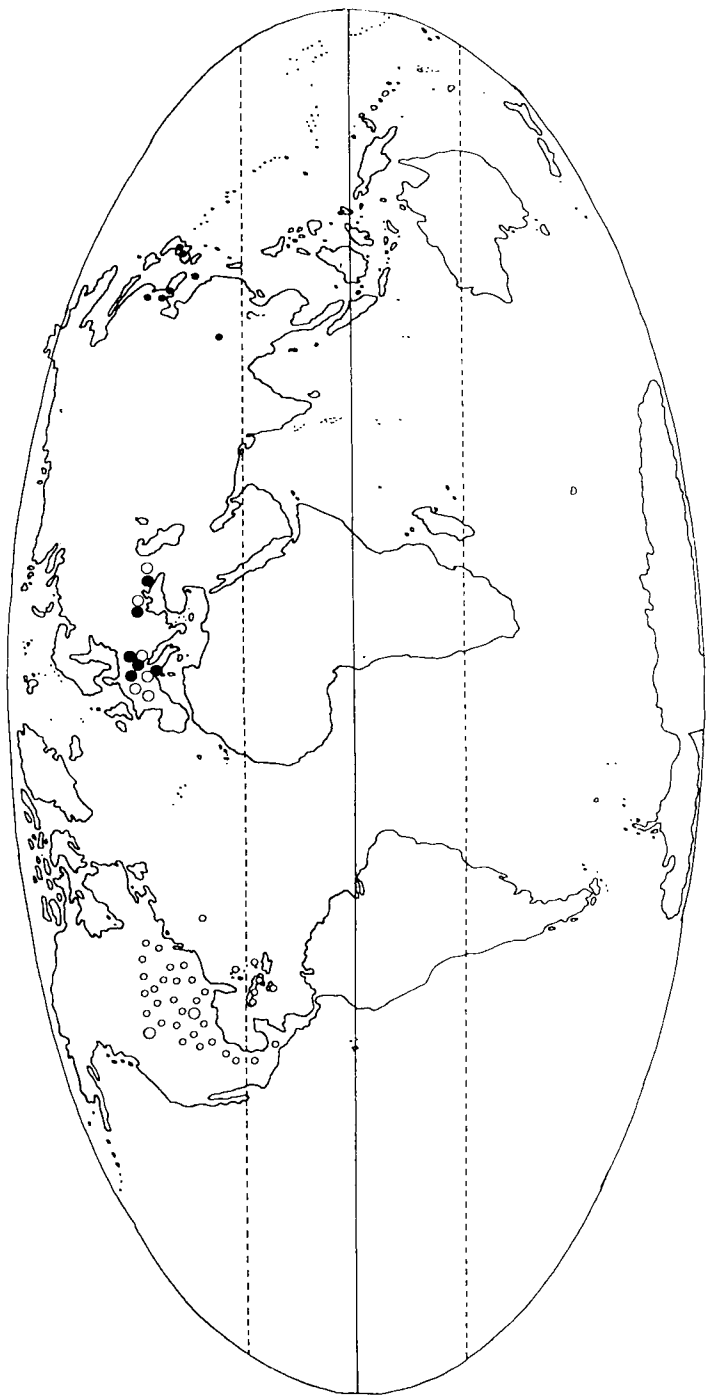

Fig. 4. Distribution pattern of some genera of Strobilopsidae in the Recent fauna (small circle) and during the Tertiary (large circle): *Strobilops* s.s. and *Discostrobilops* - open symbols, *Eostrobilops* - black symbols.

and the Caucasus (as the only living genus of the family Oleacinidae in Europe) may be regarded as a Tertiary relict, since the genus was frequently represented in the European Tertiary (including Poland). The modern range of the other Oleacinidae is restricted to Central America, the West Indies, Peru, and Brazil.

Circum-Mediterranean *Cochlostoma* and *Craspedopoma*, nowadays confined to the Canaries, Azores and Madeira, are also known from the Polish Miocene. The family Pomatiasidae is another group of snails well represented in the Polish Miocene assemblages by two genera: *Pomatias*, living in the Mediterranean Basin , western Europe and the Canary Islands, and *Tudorella* which occurs in Spain, Algeria and Minorca.

Other genera of snails lacking in the Recent mollusc fauna of Poland and known from the Miocene are: *Renea* (Aciculidae) — today distributed in the Alpine area, *Azeca* (Cochlicopidae) — in the southwestern and western part of Europe and North Africa, *Aegopis* (Zonitidae) — in southern and southeastern Europe and *Pleurodiscus* (Pleurodiscidae) — living in the Mediterranean Basin.

Considering some Miocene gastropods, which modern occurrence in Europe is commonly claimed as accidental introduction, this assumption is in need of a reinterpretation. For instance *Helicodiscus* (Endodontidae), so far regarded as a nearctic synantropic element of the European fauna, has been found also in several non-synantropic localities in Europe. In particular, this concerns *Helicodiscus (Hebetodiscus) singleyanus inermis* Baker, 1929 which was found in the Cromerian deposits of Slovakia (Ložek, 1964). Following this observation, Riedel & Wiktor (1974) have postulated a twofold origin of this snail in Europe, both as introduced and as an interglacial (or even Tertiary — E.S.) relict. Another species of *Helicodiscus* — widespread in North America —, viz. *H. (Helicodiscus) parallelus* (Say, 1821) has hitherto been found in botanic gardens of Dublin and Berlin. Several species of *Helicodiscus* are known also from the European Tertiary, including one from Poland. Schlickum (1979) supposed that *Hyalinia (Gyralina) roemeri*, described by Andreae (1902b) from Opole, represents, in fact, *Helicodiscus* and hence the genus *Helicodiscus* would be a Tertiary relict in the European fauna. Moreover, Prisyazhniuk (in: Gozhik & Prisyazhniuk, 1978) assumes that the specimens from the Miocene deposits of the Ukraine identified by him as *Helicodiscus eichwaldi* are very similar to *Hyalinia (Gyralina) roemeri*. Unfortunately, he was not able to compare his material with the holotype. A comparison of Prisyazhniuk's material with the specimens found by me in Bełchatów allows to recognise them as one and the same species.

Another representative of snails regarded as introduced to Europe, but frequently occurring in the Tertiary deposits (including the Bełchatów site), is *Opeas* (Subulinidae). Its modern range extends into the tropics and subtropics of both hemispheres. However, there is no fossil evidence suggesting that *Opeas* survived in Europe from the Tertiary.

As in the case of the extinct species, the snails of the fourth group, belonging to the living, widespread genera of the temperate climatic zone, are less distinctive from a zoogeographical point of view. On the other hand, the occurrence of living species such as *Vertigo angustior* Jeffreys, 1830 or *Vitrea crystallina* (Müller, 1774) in the Polish Miocene is noteworthy.

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