

## SYSTEMATIC AND PALAEOECOLOGICAL STUDY OF MIOCENE TERRESTRIAL GASTROPODS FROM ZWIERZYNIEC (SOUTHERN POLAND)

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**Abstract:** While the marine molluscs from Sarmatian deposits of the Carpathian Foredeep Basin are known in general, there is a paucity of data on the terrestrial gastropods. Recently, a rich assemblage of terrestrial snails, accompanied by freshwater species, was found in Zwierzyniec, in the north-western, marginal part of the Carpathian Foredeep. Among the 38 taxa recognised, there are 22 species found in Poland for the first time; a new clausiliid species *Triloba magurkai* Stworzewicz sp. nov. is described. Freshwater gastropods (nine Lymnaeidae species and two Planorbidae species) were presented elsewhere. The malacofauna comprises aquatic and typical hygrophilous elements from coastal wetland habitats, some xerophilous species from dry, open environments, and gastropods from an adjacent subtropical woodland.

**Key words:** terrestrial gastropods, Middle Miocene, Carpathian Foredeep Basin, systematics, palaeoecology.

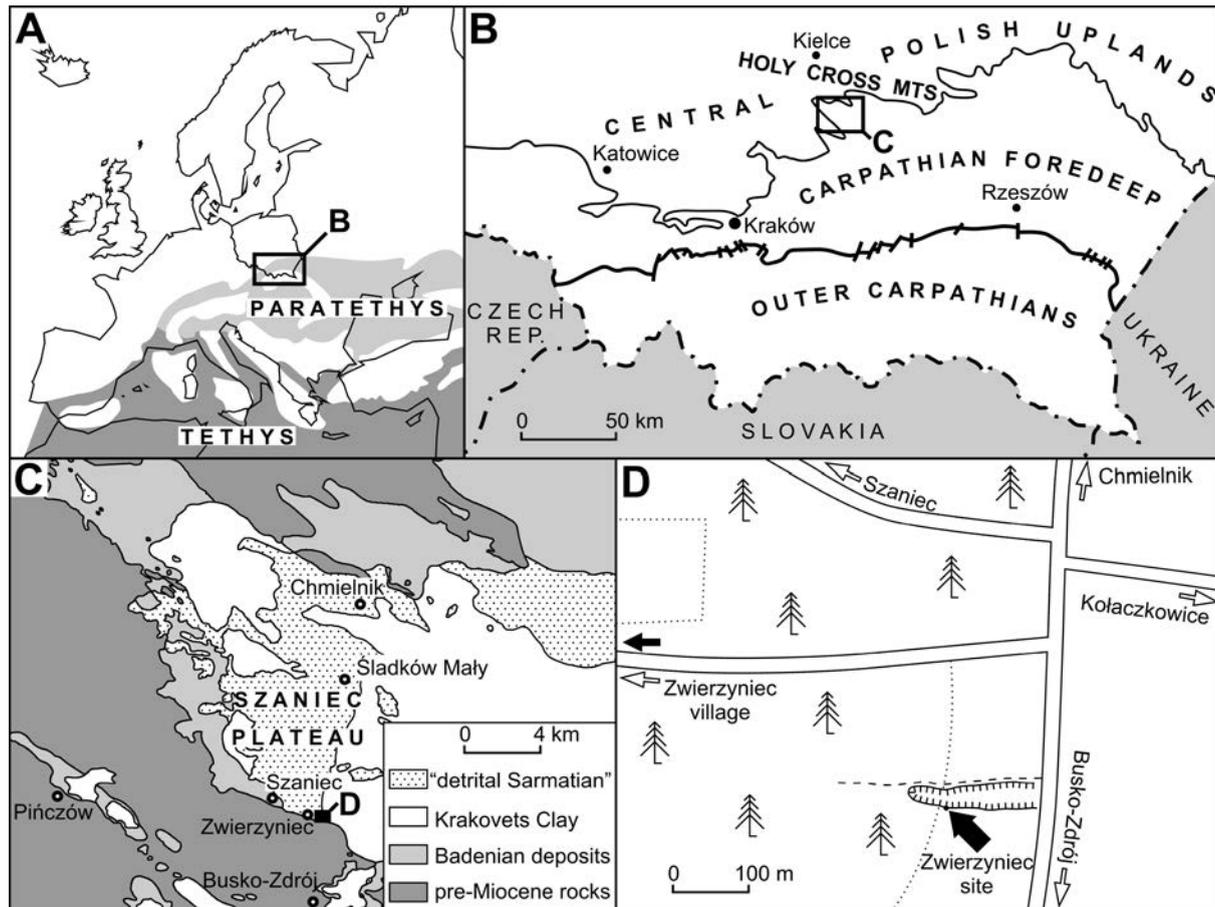
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### INTRODUCTION

During the Early Sarmatian, the Carpathian Foredeep Basin was the northernmost part of the Paratethys. The basin was filled mainly by a thick sequence of clayey deposits (Krakovets (Krakowiec) Clay of Machów Formation; see Śliwiński *et al.*, 2012), but its northern part was dominated by littoral facies, commonly called the “detrital Sarmatian” and representing the formal lithostratigraphic unit, named the Chmielnik Formation (see Alexandrowicz *et al.*, 1982). Further subdivision is based on lithostratigraphy and this distinguishes three informal lithostratigraphic units within the “detrital Sarmatian” sequence. These are called “horizons” (Rutkowski, 1976) or “complexes” (Górka, 2003, 2008b). The lower complex consists of calcareous sandstones and conglomerates and occurs only locally. The middle part is composed mainly of fine sands with thin intercalations of clays and micritic limestones. The upper complex is the most diverse, including clays, sands/sandstones and coarse gravels/conglomerates of various origins. The main source of clastic material, transported into the Sarmatian sea, was the adjoining land areas, composed of varied Mesozoic rocks and older Miocene (mainly Badenian) deposits. Some au-

thors have suggested an important role for storm-generated rip-currents in the transport of detrital material (Rutkowski, 1976; Czapowski, 1984; Czapowski and Studencka, 1990). A recent study (Górka, 2003) points to torrential rains as the main factor of transport, causing rapid washout and flooding of the adjoining land areas. As a result, some gastropod assemblages were found in several localities of this area, but that from Zwierzyniec is the most diversified.

The stratigraphic position of the sequence under discussion has remained unclear for a long time. While the foraminifer assemblages helped to determine the age as lowermost Sarmatian *Anomalinoidea dividens* Zone (Łuczkowska and Rutkowski, 1970), results based on nannofossils were less definitive, ranging from NN5 through NN5/NN6 to NN6 zones (Dudziak and Łaptaś, 1991). The most useful data seem to be those obtained from the analysis of *in situ* molluscan assemblages. The results indicate that both the “detrital Sarmatian” and the underlying clays of the Machów Formation in the area discussed represent the Lower Sarmatian (i.e. Volhynian; see Czapowski and Studencka, 1990; Studencka, in press).



**Fig. 1.** Palaeogeographical and geological background. **A.** Poland within palaeogeographical framework of the Paratethys realm. **B, C.** Geological sketch-maps of the Carpathian Foredeep and vicinity of Busko-Zdrój, respectively. **D.** Location of the gastropod-bearing site at Zwierzyniec (modified after Górka, 2003)

## GEOGRAPHICAL AND GEOLOGICAL SETTING

Zwierzyniec is situated in the north-western, marginal part of the Carpathian Foredeep (Fig. 1); its distance from the land during the Sarmatian time can be estimated at some 10 kilometres (Zastawniak, 1980). The locality is an abandoned sand-pit, situated in a densely forested gorge, about 4 km north of Busko-Zdrój, close to the Kraków – Chmielnik road (20°46'E, 50°32'N). The sandy succession at Zwierzyniec was first described by Friedberg (1928). He gave a detailed description of the profile, with special attention to the presence of the marine Sarmatian fauna.

A rich terrestrial gastropod fauna, found in the Zwierzyniec section, comes almost exclusively from deposits of the middle complex, represented by fine-grained sands with thin intercalations of micritic limestones. The section is as follows (Fig. 2).

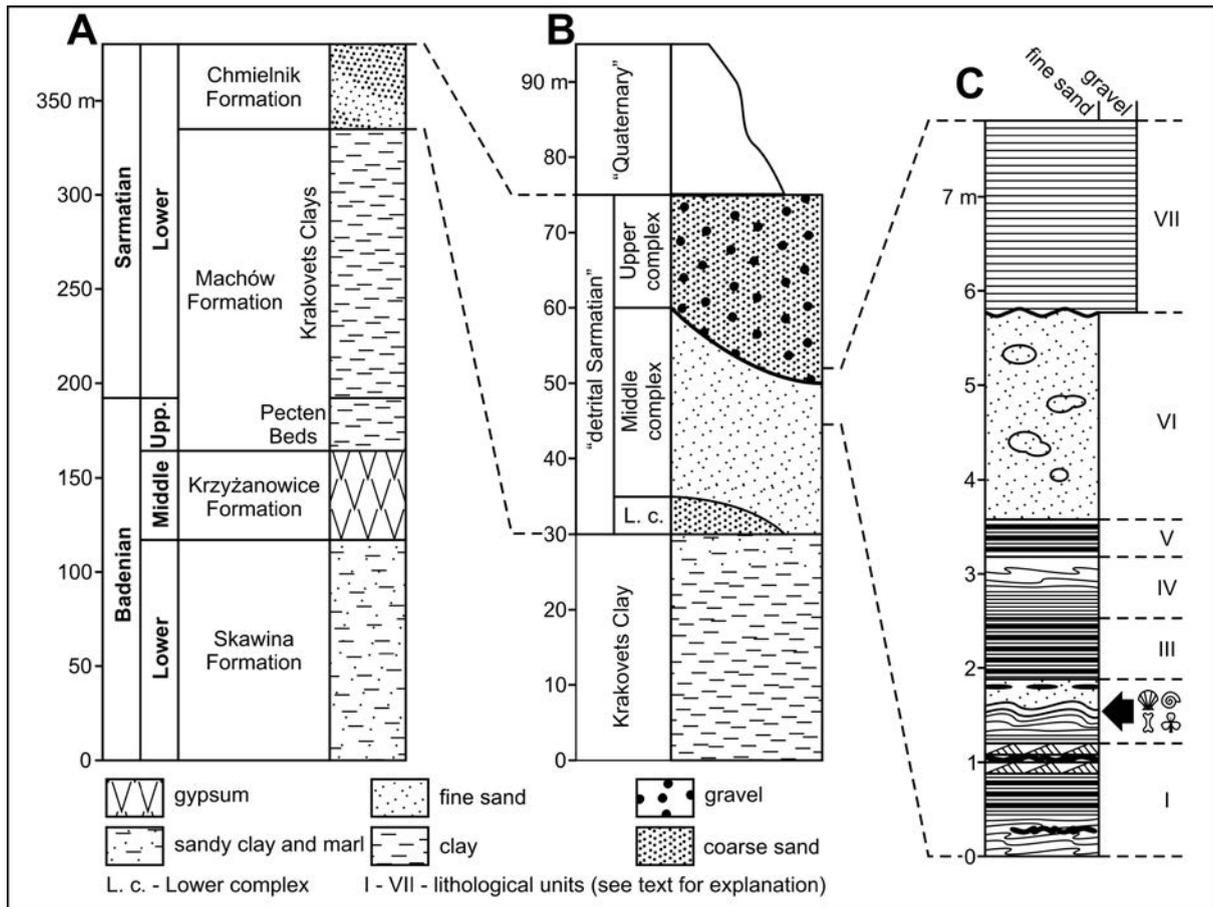
**Unit I.** Light grey quartz sand, fine- to coarse-grained, with thin intercalations of pelitic limestone. Horizontal lamination is present, but numerous syndepositional deformations are dominant. There are two horizons of coarse sand with ripple-cross stratification in the topmost part of the unit. The faunal assemblage is represented by frequent Foraminifera and Mollusca remnants; among the latter there

are abundant shells of *Plicatiforma praeplicata* (Hilber), *Maetra (Sarmatimaetra) eichwaldi* Laskarew, *Ervilia dissita* Eichwald, *E. trigonula* Sokolov, *Loripes niveus* (Eichwald). The thickness of the unit exposed is 1.2 m.

**Unit II.** Fine-grained, grey quartz sand with horizontal lamination at the base of the unit, becoming deformed and/or homogenous upward. The upper part of the unit comprises carbonate concretions, formless insertions and lenses of pelitic limestone of lacustrine origin. Marine molluscs are present as in layer 1, but terrestrial (and rarely) freshwater snails (*Anisus*, *Lymnaea*) prevail. Other terrestrial elements are small fragments of wood and rare reptile bones. The thickness of the unit varies from 0.2 to 0.7 m.

**Unit III.** Fine-grained, horizontally laminated quartz sand with thin intercalations of sandy marls of lagoonal or lacustrine origin. The upper part of the unit, composed of carbonate concretions, contains some marine gastropods and bivalves. The thickness varies between 0.6 and 0.7 m.

**Unit IV.** Fine-grained, light brown, greyish, locally yellowish quartz and carbonate sands. This unit is horizontally laminated at the base, but is homogeneous or with deformed laminae at the top (0.25 m). There are marine molluscs similar to those in layer 1, but there are also numerous small gastropods of the Hydrobiidae and Rissoidae. Freshwater, stagnophilous gastropods (*Lymnaea*, *Anisus*) and



**Fig. 2.** Litho-stratigraphical background. **A.** Synthetic profile of Miocene deposits of the study area (lithostratigraphic units after Alexandrowicz *et al.*, 1982). **B.** Profile of the "detrital Sarmatian". **C.** Lithological profile of the Zwierzyniec site with depositional structures. Stratigraphic position of the shell-bearing layer is indicated by an arrow

crushed shells of terrestrial snails (*Cepaea* sp.) occur rarely. The bed thickness is 0.65 m.

**Unit V.** Fine-grained sands with marly intercalations similar to those in layer 3. The fauna is extremely poor and composed of fragments of marine mollusc shells. The unit thickness is 0.4 m.

**Unit VI.** Fine-grained, homogenous quartz sands with numerous limy concretions. The shape of concretions is usually irregular and their dimensions vary from a few to 30 cm. The thickness is estimated as 2–2.5 m.

**Unit VII.** Fine-grained conglomerates, built predominantly of limestone clasts with a small admixture of quartz and chert grains. Within strongly lithified horizons, an indistinct lamination can be observed. The base of the unit is not exposed, and the thickness exceeds 1.5 m.

Units I to VI represent the "middle horizon" or "middle complex" (*sensu* Rutkowski, 1976; Górka, 2003, respectively) or "complex I" (*sensu* Czapowski and Studencka, 1990). The presence of bivalve assemblage – *Plicatiforma praeplacata* (Hilber), *Maetra (Sarmatimaetra) eichwaldi* Laskarew, *Ervilia dissita* Eichwald, *E. trigonula* Sokolov, *Loripes niveus* (Eichwald) – determines the age of this sequence as the lowermost part of the Early Sarmatian (i.e. early Volhynian).

Unit VII represents the "upper horizon" or "upper complex" (*sensu* Rutkowski, 1976; Górka, 2003, respectively)

or "complex I" (*sensu* Czapowski and Studencka, 1990). At the Zwierzyniec site, it is observed in the uppermost part of the profile, in the western part of the gorge. As may be presumed from observations at adjacent localities (see Czapowski and Studencka, 1990), this unit lies directly on top of "middle complex" with an erosional boundary.

## MATERIAL AND METHODS

Most of the material was collected by M. Górka during his fieldwork, over a long period in the 1980s and at the beginning of the 1990s, complemented by the first two authors in 1996. The shells and their identifiable fragments were obtained through the sieving of sandy sediments on a sieve of 0.25 mm mesh and some of the large-sized shells were taken directly from the sediment. The material was not rich, and only shells of the small-sized species were numerous and well-preserved, while zonitid and helicid shells were damaged and less numerous, with the exception of *Cepaea* shells. Freshwater snails (9 species of Lymnaeidae and 2 species of Planorbidae) were described earlier (Prisyazhnyuk *et al.*, 2006).

All of the measurements were taken with a Nikon measurescope MM-11, accuracy 0.01 mm. The following ab-

abbreviations in the text below denote shell parameters: H – shell height, B – shell breadth, h – aperture height, b – aperture breadth, HLW – last whorl height, NW – number of whorls.

The classification of the Gastropoda above the family level follows Bouchet and Rocroi (2005). Most of the material is kept at the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków, under collection numbers MI/1035– MI/1070. Only *Cepaea* and *Pseudochloritis* shells are in the collection of the Faculty of Geology, Warsaw University, abbreviated ZC C1–ZC C23 and ZC H1–ZC H4.

## RESULTS

Thirty eight taxa of terrestrial snails were identified in the sediments from Zwierzyniec (Table 1). Twenty two of them were new records for Poland. The remaining are known either from Bełchatów (Stworzewicz, 1995, 1999a, 1999b; Stworzewicz and Sołtys, 1996; Stworzewicz and Prisyazhnyuk, 1997) or from Opole (Andreae, 1902, 1904), and some from both localities. The clausilid *Triloba magurkai* Stworzewicz is described here as new. Such a great proportion of taxa, previously unknown in Poland, in the Zwierzyniec sediments is not surprising, considering the circumstances of their deposition, different from those at Bełchatów and Opole, and associated with the Paratethys shore. An unidentified species of *Myosotella*, regarded as one of the “supratidal and estuarine ellobiids” (Morton, 1955), is an indicator of maritime conditions. Pupilloids are the most frequent, particularly *Gastrocopta*, which is represented by five species and more than a hundred specimens.

**Table 1**

Gastropod taxa found in Zwierzyniec and their occurrence in the other Polish Miocene localities (the remaining species from Bełchatów and Opole are not included, only the number of species from genera found also in Zwierzyniec are recorded)

Taxa	Localities		
	Zwierzyniec	Bełchatów	Opole
<i>Pomatias rivulare</i> (Eichwald)	*	*	
<i>Carychium starobogotovi</i> Steklov	*		
<i>Carychium schlickumi schlickumi</i> Strauch	*		
<i>Carychium</i> sp.	*		
<i>Carychium</i>		10 species	4 species
<i>Myosotella</i> sp.	*		
<i>Azeca</i> aff. <i>paramonovae</i> Prisyazhnyuk	*		
<i>Azeca</i> sp.	*		
<i>Azeca</i>			2 species
<i>Pupilla steinheimensis</i> (Miller)	*		
<i>Pupilla</i> sp. ex gr. <i>iratiana</i>	*		
<i>Microstele caucasica</i> Steklov	*		

Taxa	Localities		
	Zwierzyniec	Bełchatów	Opole
<i>Microstele ikvae</i> Prisyazhnyuk	*		
<i>Microstele buryaki</i> Steklov	*		
<i>Granaria antiqua</i> (Schübler)	*		
<i>Granaria</i> sp.	*		
<i>Gastrocopta acuminata</i> (Klein)	*	*	
<i>Gastrocopta nouletiana</i> (Dupuy) sensu lato	*	*	
<i>Gastrocopta serotina</i> Ložek	*		
<i>Gastrocopta fissidens</i> (Sandberger)	*	*?	
<i>Gastrocopta</i> ex. gr. <i>didymodus</i> (Sandberger)	*		
<i>Gastrocopta</i>		2 species	3 species
<i>Leiostyla gottschicki</i> Wenz	*		
<i>Strobilops joossi</i> (Gottschick)	*	*	
<i>Strobilops</i>		5 species	2 species
<i>Vallonia subcyclophorella</i> Gottschick	*	*	
<i>Vertigo callosa</i> (Reuss)	*	*	*
<i>Vertigo protracta</i> (Sandberger)	*	*	
<i>Vertigo angulifera</i> O. Boettger	*	*	
<i>Vertigo</i>		3 species	2 species
<i>Negulus suturalis</i> (Sandberger)	*	*	*
<i>Serrulastra trolli</i> Nordsieck	*		
<i>Triloba magurkai</i> Stworzewicz n. sp.	*		
Clausiliidae			9 species
<i>Discus costatus</i> (Gottschick)	*		
<i>Helicodiscus roemeri</i> (Andreae)	*	*	*
<i>Hawaiia antiqua</i> Riedel	*		
<i>Phenacolimax suevica</i> (Sandberger)	*		
<i>Vitrea procrystallina</i> Andreae	*		*
<i>Miozonites costatus</i> (Sandberger)	*		
<i>Aegopinella</i> cf. <i>subnitens</i> (Klein)	*		
<i>Klikia giengensis</i> (Klein)	*		
<i>Pseudochloritis incrassatus</i> (Klein)	*		
<i>Cepaea sylvestrina gottschicki</i> Wenz	*		

## SYSTEMATIC PALAEOONTOLOGY

Clade LITTORINIMORPHA Golikov and Starobogotov, 1975

Family POMATIIDAE Newton, 1891

Genus *Pomatias* Studer, 1789

**Type species:** *Nerita elegans* Müller, 1774

*Pomatias rivulare* (Eichwald, 1829)

Fig. 3A

\*1829 *Cyclostoma rivularis* sp. nov. – Eichwald: p. 302.

1926 *Pomatias rivulare* (Eichwald) – Lindholm, p. 167.

1966 *Pomatias rivulare* (Eichwald) – Steklov, p. 121, pl. 1, figs 8–10.

**Material:** Two specimens and several shell fragments (MI/1035).

**Dimensions:** H = 9.6 mm, 12.35 mm; B = 7.32 mm, 10.06 mm; h = 4.36 mm, 6.16 mm; b = 4.33 mm, 5.95 mm; HLW = 7.15 mm, 9.89 mm; NW = 4.5, 4.75.

**Remarks:** The smaller shell is strikingly similar to those of *P. rivulare* from Belchatów (Bel-B, Middle Miocene) and from several Mio-Pliocene localities in Ciscaucasia (Steklov, 1966). The larger one is somewhat more elongated and the surface sculpture is more distinct. Such specimens were also found at Belchatów (Stworzewicz, 1995).

Clade EUPULMONATA J. Morton, 1955

Family ELLOBIIDAE L. Pfeiffer, 1854

Subfamily CARYCHIINAE Jeffreys, 1830

Genus *Carychium* O. F. Müller, 1774

**Type species:** *Carychium minimum* Müller, 1774

*Carychium starobogatovi* Steklov, 1966

Fig. 3B

\*1966 *Carychium starobogatovi* sp. nov. – Steklov: p. 124, fig. 40, pl. 2, fig. 14.

**Material:** Two specimens and one damaged shell (MI/1036).

**Dimensions:** H = 1.67 mm, 1.8 mm; B = 0.69 mm, 0.73 mm; h = 0.57 mm, 0.63 mm; b = 0.52 mm, 0.53 mm; HLW = 0.97 mm, 1.00 mm.

**Remarks:** The two shells are similar in outline and the weak development of aperture barriers to the specimens, described by Steklov (1966) from the Mio-Pliocene of Ciscaucasia. However one of them is distinctly larger than all of the other known shells.

*Carychium schlickumi schlickumi* Strauch, 1977

Fig. 3C

\*1977 *Carychium schlickumi schlickumi* ssp. nov. – Strauch: p. 168, pl. 16, figs 40–47, pl. 19, figs 68–70, 72–73, 75.

**Material:** Eight specimens (ML/1037).

**Dimensions:** H = 1.75–2.05 mm; B = 0.88–0.96 mm; h = 0.70–0.77 mm; b = 0.56–0.64 mm; HLW = 1.06–1.2 mm.

**Remarks:** The specimens from Zwierzyniec do not differ in the general shell outline and structure of the internal lamellae from those, known from the Pliocene of Germany (Strauch, 1977) and from the Upper Miocene of Ukraine (Steklov, 1966, p. 127, fig. 42, as *Carychium suevicum* O. Boettger), but they are generally somewhat larger.

*Carychium* sp.

**Material:** One specimen (MI/1038).

**Dimensions:** H = 1.9 mm; B = 0.86 mm; h = 0.72 mm; b = 0.63 mm; HLW = 1.12 mm.

**Remarks:** The shell outline resembles *C. nouleti*, but the structure of the internal lamellae is similar to that of *C. antiquum*. The lack of sufficient material precludes the possibility of any specific assignment.

Subfamily PYTHIINAE Odhner, 1925

Genus *Myosotella* Monterosato, 1906

**Type species:** *Auricula myosotis* Draparnaud, 1801

*Myosotella* sp.

Fig. 3D

**Material:** One fragment of shell: the last whorl with aperture (MI/1039).

**Dimensions:** B = 1.94 mm; h = 2.04 mm; b = 1.23 mm; HLW = 2.87 mm.

**Description:** The shell fragment is very thin and fine with a shiny surface and indistinct radial lines. Under higher magnification, fine pricks are visible, forming spiral lines. Below the suture, a parallel groove is marked and some vertical, thin, comma-like cavities below the groove, which are most probably hair traces. The aperture, narrowly drop-shaped, is sharpened in its upper part and rounded at the bottom. Its margin is simple in the upper half and thickened by a callus on the inner side of the bottom half. There are two lamellate teeth in the aperture. The columellar is situated on the columellar-basal transition and continues as an arcuate lamella, deflected upward around the columella. The parietal tooth is stout, situated close to the columellar margin. Both teeth enter deeply inside the body whorl (about 0.75 of whorl).

**Remarks:** The specimen from Zwierzyniec was tentatively assigned to *Myosotella* because among the genera of Ellobiidae only some *Myosotella* members share most shell features with the shell fragment discussed. These are the outline of the last whorl and aperture, teeth, and above all, the microsculpture, consisting of spiral rows of pits and one spiral row of hair traces. Ellobiids of some other genera may have hirsute whorls, but then the shape of the shell and aperture and the dentition are different (Martins, 1996). No hair traces were described in fossil representatives of the Ellobiidae (Wenz, 1920; Zilch, 1959–1960; Kókay, 2006).

In its shell form and dentition, the shell fragment is most similar to *Stoliodoma (Stoliodomopsis) glandina* (Boettger, 1874) from the Middle Oligocene, but the latter species is twice as large and it has no spiral structure or spiral groove below the suture (Wenz, 1920). On the other hand, such surface sculpture of spirally arranged small pits was described by Kókay (2006, p. 50) in *Auriculastra badeniensis* Kókay, 2006, from the Upper Badenian coal-bearing clay at Pusztamiske (Hungary), but no spiral groove below the suture or whorl traces were mentioned. Unfortunately, the dimensions of the specimens from Pusztamiske were not presented, and the holotype is somewhat different in shape (Kókay, 2006, pl. 16, figs 10–11).

This is the first record of land ellobiids in Poland, other than that of Carychiinae.

Clade STYLOMMATOPHORA Schmidt, 1855

Family COCHLICOPIDAE Pilsbry, 1900

Genus *Azeca* Fleming, 1828

**Type species:** *Helix goodalli* Férussac, 1821

*Azeca* aff. *paramonovae* Prisyazhnyuk, 1990 (in Luleva and Prisyazhnyuk, 1990)

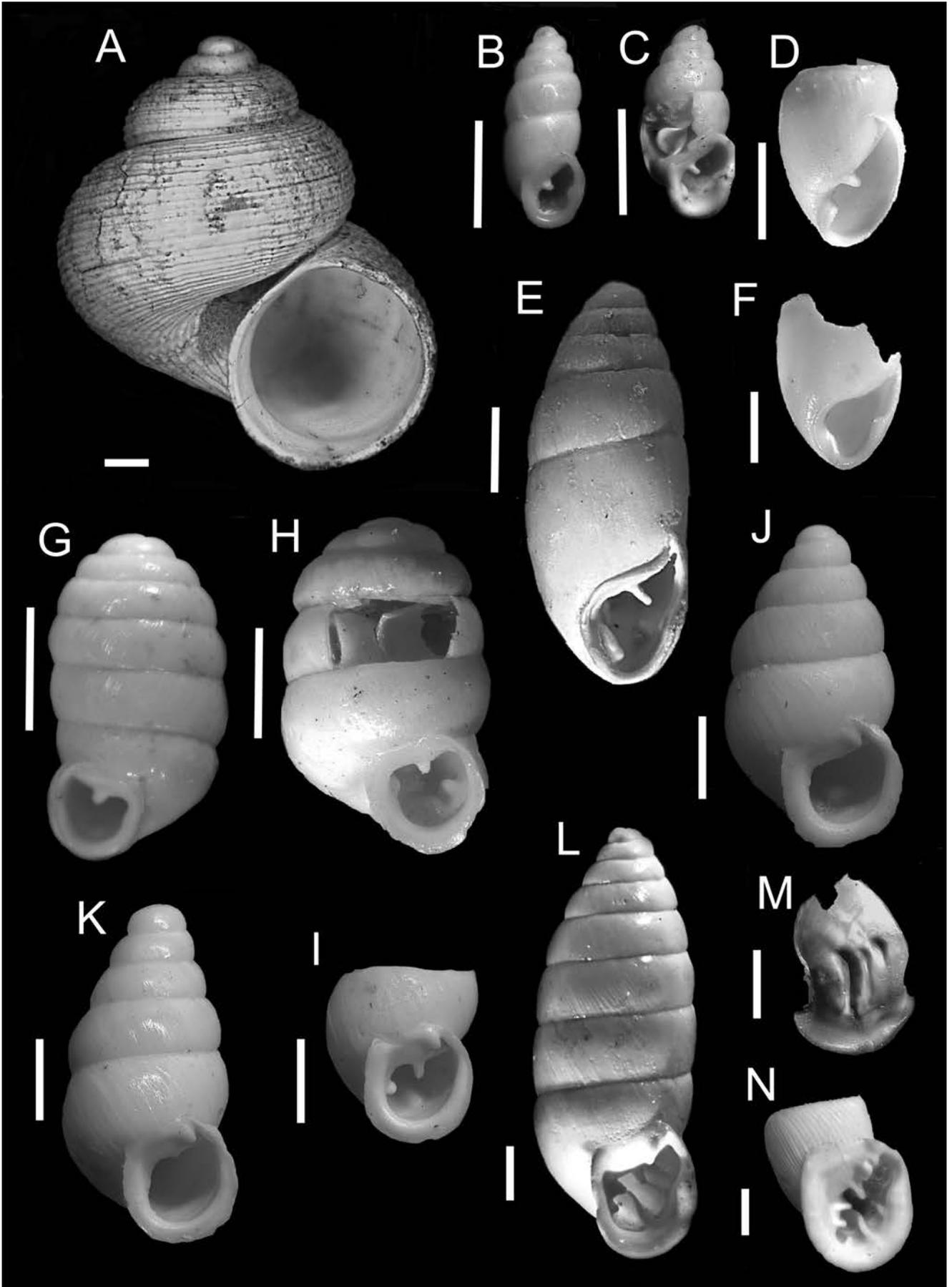
Fig. 3E

\*1990 *Azeca paramonovae* sp. nov. – Prisyazhnyuk (in Luleva and Prisyazhnyuk): p. 36, text-fig.

**Material:** One specimen and three fragments of the last whorl with an aperture (MI/1040).

**Dimensions:** H = 4.44 mm; B = 1.83–2.09 mm; h = 1.35–1.59 mm; b = 1.24–1.38 mm; HLW = 2.45–2.79 mm.

**Description:** The only well-preserved shell consists of 6 whorls. The aperture margin of all the specimens is surrounded by a cord-like edge. There are four teeth in the aperture, visible in front view. A long, lamellate parietal tooth is divided into two parts by an incision. Its outer part is shorter than the inner one, reaching more than 0.5 whorl, deep inside the shell. Of the two columellar lamellate teeth, the lower is situated close to the aperture margin, whereas the upper one, deeply set and poorly visible in front view, ascends vertically on the columella to ca. 0.3 of the body whorl height. The palatal tooth is situated in the middle of the palatal wall and does not reach the aperture margin; it is roll-like or divided by an incision into two knobs. Besides, two elongate teeth



are placed very deeply in the body whorl, at a distance of ca. 0.5 whorl from the aperture margin and they are invisible in front view.

**Remarks:** The specimens from Zwierzyniec are very distinct, because of the lower columellar tooth. In this respect, they are most similar to *Azeca paramonovae*, described from the Lower Sarmatian of Volhynia (Luleva and Prisyazhnyuk, 1990, p. 36). Moreover, they are both fusiform and the only difference is in the palatal tooth, which is very weakly marked in the specimens from Zwierzyniec and well-developed in those from Volhynia.

The only *Azeca* species, previously described from Poland, is *Azeca frechi* Andreae, 1902 from Opole (Andreae, 1902, p. 14), which has a horizontal columellar tooth, an undivided parietal one, and a distinctly smaller shell.

*Azeca* sp.  
Fig. 3F

**Material:** Two fragments of last whorl with somewhat damaged aperture (parietal tooth broken) (MI/1041).

**Dimensions:** B = 1.84 mm, 1.90 mm; h = 1.47 mm, 1.53 mm; b = 1.24 mm, 1.38 mm; HLW = 2.51 mm, 2.67 mm.

**Remarks:** The specimens differ from the preceding species in the form of the columellar teeth, particularly the lower one, which is knob-shaped. The tooth on the palatal wall is absent, but there is a tooth on the palatal margin of aperture. In addition, the cord-like edge along the aperture margin is weakly marked.

Family PUPILLIDAE Turton, 1831

Genus *Pupilla* Leach in Turton, 1831

**Type species:** *Pupa marginata* Draparnaud, 1801

*Pupilla steinheimensis* (Miller, 1900)  
Fig. 3G

\*1900 *Pupa (Pupilla) steinheimensis* sp. nov. – Miller: p. 398, pl. 7, fig. 15.

**Material:** Two specimens and five fragments including the body whorl with aperture (MI/1042).

**Dimensions:** H = 2.66 mm, 2.60 mm; B = 1.47 mm, 1.56 mm; h = 0.82 mm, 0.77 mm; b = 0.80 mm, 0.78 mm; HLW = 1.00 mm, 1.21 mm.

**Description:** Sinistral, oval-cylindrical shells consist of 6.5–7 whorls, weakly convex and separated by moderately deep sutures. The body whorl is somewhat narrower than the two above and it ascends before the aperture. The surface sculpture is composed of irregular, delicate striae, which are almost invisible. The crest is strongly marked, followed by a deep groove behind the lip and parallel to it. At the base, the crest passes into a basal keel. The aperture is semicircular, with weakly reflexed margins and thin lip, joined by a thin parietal callus. The following teeth are always present: lamellate parietal tooth; weakly developed angular tooth, which is most often in the form of a low nodule; deeply situated columellar tooth, invisible in apertural view or marked as a small nodule, continues inside the body whorl as a ridge and spirally ascends the columella. There is also a short lamellate palatal tooth.

Some shells also have a small infrapalatal tooth.

**Remarks:** The specimens from Zwierzyniec were identified as referable to *P. steinheimensis* from the upper Miocene deposits at Steinheim, despite some slight differences in apertural characters. The two specimens described by Miller (1900) have a somewhat stouter aperture margin and columellar tooth, but the scanty material from both localities does not permit the exclusion of intraspecific variation. From among the few sinistral *Pupilla* species known from the Neogene, only *P. belokrysi* Steklov, 1966 seems to be very similar in its shell form and size, as well as in the continuation of the columellar tooth, shown by Prisyazhnyuk (2008a), which is particularly characteristic of older (Karaganian) forms of this species. However, *P. belokrysi* has a somewhat less-developed aperture margin.

All other sinistral species are much smaller – *P. blainvilleana* (Dupuy, 1850) or bigger – *P. rathi* (Sandberger, 1858), *P. mutabilis* Steklov, 1966 and *P. staszicii* Łomnicki, 1886; they differ in the number of whorls, and the structure of the columellar tooth is unknown.

*Pupilla* ex gr. *iradiana* (Dupuy, 1850)  
Fig. 3H

**Material:** Two specimens (one of them damaged) and eight fragments with aperture (MI/1043).

**Dimensions:** H = 2.86 mm, 2.52 mm; B = 1.61 mm, 1.54 mm; h = 0.96 mm, 0.84 mm; b = 0.83 mm, 0.83 mm; HLW = 1.44 mm, 1.46 mm.

**Description:** Oval-cylindrical shells consist of six moderately convex whorls, covered by weakly marked, blunt, unevenly spaced radial striae. The body whorl ascends before the aperture. The crest is clearly marked and thickened toward the umbilicus, partly covering it. It is followed by a deep groove behind the lip. The aperture margins are slightly reflexed and joined by a thin or very thin parietal callus.

There are 4–5 teeth in the aperture. The lamellate parietal tooth reaches ca. 0.4 whorl deep inside the shell. The angular tooth is weakly developed in the form of a small knob, rarely elongated, but most frequently this is not perceptible. The columellar tooth is well-developed, broadened at the base. The two palatal teeth do not reach the aperture margin and the lamellate lower palatal tooth is longer than the upper, which is usually knob-shaped.

**Remarks:** *Pupilla* sp. from Zwierzyniec corresponds very closely to the description and illustration of *P. iradiana* by Dupuy (1850, p. 310, pl. 15, fig. 7) and to the more detailed redescription and drawings by Bourguignat (1881, p. 65, pl. 3, figs 83–85). However, it differs from the *P. iradiana* specimens, presented by Finger (1998, pl. 12, fig. A) and by Harzhauser *et al.* (2008, p. 49, figs 5.1–3), in the less distinct shell sculpture, stouter shell shape and more circular aperture. There is no information in Finger's paper about the dentition of *P. iradiana*. On the other hand, the specimen presented by Harzhauser *et al.* (2008) has only one small palatal tooth. Some other similar forms were described, i.e. *Pupilla iradiana eumeces* Boettger, 1884, *Pupilla iradiana maxima* Boettger, 1908 and *Pupilla iradiana suevica* Gottschick and Wenz, 1919, but their taxonomical position still remains ambiguous.

**Fig. 3.** Land gastropods from Zwierzyniec; scale bars 1 mm. **A.** *Pomatias rivulare* (Eichwald, 1829), MI/1035. **B.** *Carychium starobogatovi* Steklov, 1966, MI/1036; **C.** *Carychium schlickumi schlickumi* Strauch, 1977, MI/1037; **D.** *Myosotella* sp., MI/1039; **E.** *Azeca* aff. *paramonovae* Prisyazhnyuk, 1990 (in Luleva and Prisyazhnyuk, 1990), MI/1040; **F.** *Azeca* sp., MI/1041; **G.** *Pupilla steinheimensis* (Miller, 1900), MI/1042; **H.** *Pupilla* ex gr. *iradiana* (Dupuy, 1850), MI/1043; **I.** *Microstele caucasica* Steklov, 1966, MI/1044; **J.** *Microstele ikvae* Prisyazhnyuk, 1971, MI/1045; **K.** *Microstele buryaki* Steklov, 1966, MI/1046; **L.** *Granaria antiqua* (Schübler in Zieten, 1830), MI/1047; **M.** *G. antiqua*, teeth on palatal wall, MI/1047a; **N.** *Granaria* sp., MI/1048

Genus *Microstele* Boettger, 1886**Type species:** *Pupa moltei* O. Boettger, 1886

Among the few *Microstele* specimens from Zwierzyniec, representing three species, there is a marked trend towards weakening of the parietal, columellar and palatal teeth. Only the angular tooth remains constant. Apart from *M. caucasica*, *M. buryaki* and *M. ikvae*, there are two shell fragments with only an angular tooth present, while the remaining teeth are entirely reduced. They may represent an initial stage of transition to the younger species *M. alamellata* Steklov, 1966 which resembles *Pupoides* but the material from Zwierzyniec is insufficient to identify them. *Microstele* has not been found previously in Poland.

*Microstele caucasica* Steklov, 1966

## Fig. 3I

\*1966 *Microstele caucasica* sp. nov. – Steklov: p. 160, pl. 4, figs 84–85.

**Material:** Three fragments containing last whorl with well-preserved aperture (MI/1044).

**Dimensions:** B = 1.85–1.89 mm; h = 1.34–1.38 mm; b = 1.29–1.27 mm; HLW = 2.06–2.14 mm.

**Description:** The surface of the last whorl is very finely and irregularly striated. The umbilicus is very narrow, but open. The aperture has a reflexed and thickened margin. There are 4 teeth in the aperture: angular, deeply situated parietal and palatal, and columellar.

**Remarks:** Regarding the number and form of the teeth, the specimens from Zwierzyniec are very similar to both *M. wenzii* (Fischer, 1920) and *M. caucasica*. However, the shell breadth and aperture dimensions show that it is *M. caucasica*, which is clearly smaller than the preceding species.

*Microstele ikvae* Prisyazhnyuk, 1971

## Fig. 3J

\*1971 *Microstele ikvae* sp. nov. – Prisyazhnyuk: p. 601, fig. 1w, fig. 2.3.

**Material:** Two specimens and two fragments of the last whorl with an aperture (MI/1045).

**Dimensions:** H = 3.95 mm, 3.64 mm; B = 1.91 mm, 1.80 mm; h = 1.46 mm, 1.48 mm; b = 1.38 mm, 1.20 mm; HLW = 2.29 mm, 2.23 mm.

**Description:** Tapering shells consist of 5.5–6 whorls, very weakly and irregularly striated. The umbilicus is open and deep. The aperture margin is reflexed, with a weakly thickened lip. In the aperture, only angular and palatal teeth are well-developed; the parietal is very weak and deeply placed. The columellar tooth is vestigial, in the form of a hardly marked knob, invisible in front view, or absent.

**Remarks:** The close comparison of specimens from Zwierzyniec to those from the Lower Sarmatian deposits of Volhynia-Podolia does not raise any doubt that they are conspecific, although the former shells are somewhat smaller.

*Microstele buryaki* Steklov, 1966

## Fig. 3K

\*1966 *Microstele buryaki* sp. nov. – Steklov: p. 161, fig. 58, pl. 4, figs 86–87.

**Material:** Seven specimens (including two partly damaged) and three fragments with an aperture (MI/1046).

**Dimensions:** Given in in Table 2.

**Table 2**Dimensions of *Microstele buryaki* Steklov, 1966 (in mm)

H	3.73	3.87	3.89	3.96	4.09
B	1.81	1.88	1.83	1.85	1.82
h	1.32	1.41	1.40	1.43	1.50
b	1.21	1.34	1.28	1.25	1.30
HLW	2.05	2.15	2.01	2.08	2.13

**Description:** Elongated, tapering shells consist of 6 whorls, covered with very fine, irregular striae. The aperture has a reflected margin and a somewhat thickened lip. In the aperture, only the angular tooth is well-developed, whereas the parietal and columellar teeth are very small or vestigial and deeply situated. There is no palatal tooth.

**Remarks:** The dentition of specimens from Zwierzyniec is very similar to that of specimens from the Middle Miocene (Karagan) of Ciscaucasia (Steklov, 1966); however, the latter are somewhat bigger and less elongated.

## Family CHONDRINIDAE Steenberg, 1925

Genus *Granaria* Held, 1837**Type species:** *Pupa frumentum* Draparnaud, 1801*Granaria antiqua* (Schübler in Zieten, 1830)

## Fig. 3L, M

\*1830 *Pupa antiqua* sp. nov. – Schübler in Zieten: p. 39, pl. 29, fig. 7a–c.

1846 *Pupa Schübleri* n. nov. – Klein, p. 74, pl. 1, fig. 18.

1916 *Torquilla antiqua* (Zieten) – Gottschick and Wenz, p. 61.

1923c *Abida antiqua antiqua* (Zieten) – Wenz, p. 940.

**Material:** Three specimens (one somewhat deformed) and 23 fragments containing the last whorl with an aperture (MI/1047).

**Dimensions:** (of two complete shells and four well-preserved fragments): H = 7.95 mm, 8.0 mm; B = 2.98–3.29; h = 2.29–2.55 mm; b = 1.96–2.35 mm; H/B = 2.65, 2.66; HLW = 3.2–3.63 mm.

**Description:** Shells consist of 8.5 almost flat whorls; the embryonic whorls are smooth, the next seem to be smooth, but they are covered with poorly visible regular striae, which are more distinct on the last whorl before the aperture. There are 8–9 teeth in the aperture. The arched angularis is thickened or doubled in front by a small, knob-shaped tooth (subangularis) and joins the aperture margin; it reaches inside as far as the anterior part of the deeply situated parietal tooth. In some shells there is a short lamellate tooth (spiralis) situated beyond the inner end of the angular lamella. The parietal tooth is high lamellate and thick, situated in the middle part of the parietal wall, and reaches ca. half-whorl deep inside the shell. The columellar and subcolumellar teeth are deeply set; the former is thicker and longer than the latter. There are four teeth on the palatal wall; two long lamellate teeth (lower palatal and upper palatal) reach the inner edge of the lip and become higher within but only the lower palatal tooth is strongly developed and always clearly visible (Fig. 3M). The remaining two (infrapalatal and suprapalatal) are deeply situated and short-lamellate or knob-shaped. In some specimens, the infrapalatal tooth has a hardly marked continuation to the inner lip margin.

**Remarks:** The specimens from Zwierzyniec correspond to the figure and short description of *Pupa antiqua* from the Upper Miocene deposits at Steinheim am Aalbuch (Schübler in Zieten, 1830) and to the description of *Pupa schuebleri* (Klein, 1846), regarded by some authors as the valid name of the former species (Miller,

1900; Gottschick and Wenz, 1916) or as a separate species (Harzhauser and Binder, 2004). However, Klein (1846) wrongly interpreted the name *Pupa antiqua* as pre-occupied, arguing that Matheron (1832) gave the same name to another species (similar to *Helix tridens* Müller, 1774 = *Pupa tridens*, see Draparnaud, 1801), because he took no account of the fact that Matheron's work was published two years later (Schübler in Zieten, 1830; Matheron, 1832).

On the other hand, the specimens from Zwierzyniec differ from those, misidentified by Lueger (1981) as *G. antiqua* (see Harzhauser and Binder, 2004).

In its shell form and dentition, *G. antiqua* from Zwierzyniec is similar to *G. subvariabilis* (Sandberger), known from the Upper Oligocene and the Lower Miocene (Sandberger, 1858), but it is somewhat smaller and more distinctly striated. The H/B ratio for specimens from Hochheim is 2.52 (Boettger, 1889); for two specimens from Zwierzyniec it is 2.65 and 2.66, and the lower palatal tooth is the most developed. On the other hand, the teeth, particularly on the palatal wall, are the same in *G. antiqua* and Recent *G. variabilis* (Draparnaud, 1801). According to Boettger (1889), those three species make an evolutionary continuum *subvariabilis*–*antiqua*–*variabilis*.

This is the first Miocene record for *Granaria* in Poland.

#### *Granaria* sp.

Fig. 3N

**Material:** One fragment of last whorl with aperture and apertural barriers (MI/1048).

**Dimensions:** B = >2.70 mm; h = 2.59 mm; b = 2.28 mm; HLW = 3.5 mm.

**Remarks:** The specimen differs from those of *G. antiqua* in: 1. the distinctly, regularly striated surface of the last whorl; 2. the distinctly thickened aperture margin; 3. the subangular tooth distinctly separated from the angular; 4. the infrapalatal and upper palatal teeth, almost as long and stout as the lower palatal; and 5. the presence of a third columellar lamella above the upper columellar on the dorsal side (invisible in front view).

The specimen is most similar to the Recent *G. frumentum* (Draparnaud, 1801) and may be regarded as its ancestral form. The material is insufficient for a description of it as a new species.

#### Family GASTROCOPTIDAE Pilsbry, 1918

##### Genus *Gastrocopta* Wollaston, 1878

**Type species:** *Pupa acarus* Benson, 1856

#### *Gastrocopta acuminata* (Klein, 1846)

Fig. 4A

\*1846 *Pupa acuminata* sp. nov. – Klein: p. 75, pl. 1, fig. 19.

**Material:** Three specimens (including the larger and swollen one, regarded as *G. acuminata larteti*) and four fragments of the last whorl with an aperture (MI/1049).

**Dimensions:** H = 2.60–2.95 mm, 3.01 mm; B = 1.60–1.75 mm, 1.92 mm; h = 0.94–1.07 mm, 1.08 mm; b = 0.84–0.98 mm, 1.08 mm; HLW = 1.45–1.64 mm, 1.84 mm.

**Remarks:** The specimens from Zwierzyniec differ somewhat from the typical form of *G. acuminata*, presented in Gottschick and Wenz (1916, p. 62–64, pl. 1, fig. 4) and Schlickum (1976, p. 10, pl. 1, fig. 26), in having the interpalatal knob-shaped tooth. On the other hand, the interpalatal tooth is often observed in the specimens from Ciscaucasia (Steklov, 1966). The specimens from Zwierzyniec are within the variability range of *G. acuminata* from Bełchatów as well; some of the over 300 specimens found there have a small interpalatal tooth (Stworzewicz, 1999b).

One specimen differs from the others in having a swollen shell and less convex whorls. Such a form was described from Sansan as *G. lartetii* (Dupuy, 1850, p. 307) and subsequently was regarded as the subspecies *lartetii* of *G. acuminata* (Wenz, 1923c, p. 919). In its shell shape and the form of parieto-angular and columellar teeth, it is also similar to some specimens of *G. acuminata lartetii* from Ukraine (Brykov, Zamiechov, Bogdanovskij Karier), although in Gozhik and Prisyazhnyuk (1978, p. 89, pl. 11, figs 10, 14), specimens with basal tooth are presented.

*G. acuminata* is one of the most widespread and the longest occurring species in western and central Europe, known from the Middle Miocene to the Middle-Late Pliocene (Manganelli and Giusti, 2000).

#### *Gastrocopta nouletiana* (Dupuy, 1850) *sensu lato*

Fig. 4B

\*1850 *Pupa Nouletiana* sp. nov. – Dupuy: p. 309, pl. 15, fig. 6.

**Material:** 35 specimens and some fragments with an aperture (MI/1050).

**Remarks:** Three morphological forms of this species, widespread in Europe, were found at Zwierzyniec. They all commonly occur in the Middle-Upper Miocene deposits and are also known from Poland (Stworzewicz, 1999b).

1. The typical form, as a rule ovate with three palatal teeth, corresponds to that described by Dupuy (1950) from Sansan, that found in Bełchatów (Stworzewicz, 1999b, p. 163–164, figs 59, 61) and that from Steinheim (Gottschick and Wenz, 1919, p. 12, pl. 1, figs 22–23).

**Dimensions:** See Table 3.

**Table 3**

Dimensions of *Gastrocopta nouletiana* (Dupuy, 1850) *sensu lato*, the typical forms (in mm)

H	2.27	2.05	2.12	1.91	2.15
B	1.37	1.27	1.33	1.31	1.33
h	0.86	0.81	0.75	0.68	0.80
b	0.87	0.74	0.80	0.73	0.75
HLW	1.41	1.25	1.28	1.22	1.24
H/B	1.66	1.61	1.60	1.46	1.62

2. Ovate-elongated form with two palatal teeth; the lower one is solid and arcuate.

**Dimensions:** See Table 4.

**Table 4**

Dimensions of *Gastrocopta nouletiana* (Dupuy, 1850) *sensu lato*, ovate-elongated forms (in mm)

H	2.27	2.12	2.27	2.14	2.40
B	1.31	1.27	1.30	1.30	1.27
h	0.86	0.85	0.76	0.75	0.86
b	0.84	0.77	0.72	0.77	0.78
HLW	1.37	1.28	1.24	1.25	1.27
H/B	1.73	1.67	1.75	1.65	1.89

3. An elongated form, usually regarded as *G. nouletiana gracilidens*, with three or four palatal teeth, but the interpalatal tooth is always present (Stworzewicz, 1999b, fig. 60).

**Dimensions:** See Table 5.

**Table 5**

Dimensions of *Gastrocopta nouletiana* (Dupuy, 1850)  
*sensu lato*, elongated forms (in mm)

H	2.50	2.40	2.28	2.16	2.32
B	1.42	1.38	1.40	1.28	1.30
h	0.82	0.73	0.80	0.85	0.83
b	0.82	0.76	0.72	0.80	0.76
HLW	1.41	1.25	1.28	1.22	1.24
H/B	1.76	1.74	1.63	1.68	1.78

*Gastrocopta serotina* Ložek, 1964

Fig. 4C

\*1964 *Gastrocopta serotina* sp. nov. – Ložek: p. 194, figs 1–4.

**Material:** 36 well preserved specimens and some fragments with an aperture (MI/1051).

**Dimensions:** H = 1.66–1.73 mm and 1.90–2.42 mm; B = 1.00–1.07 mm and 1.10–1.29 mm; h = 0.54–0.64 mm and 0.66–0.84 mm; b = 0.52–0.59 mm and 0.61–0.81 mm; HLW = 0.97–1.05 mm and 1.04–1.37 mm.

**Remarks:** The specimens from Zwierzyniec are identical in their shell shape and apertural barriers to those described by Ložek (1964) from the deposits of Ctiněves (Central Bohemia). However, they vary in size (having the same number of whorls, with an average of 5) enough to distinguish two groups (see Dimensions). The larger shells predominate and they also have somewhat more massive apertural barriers.

*Gastrocopta fissidens* (Sandberger, 1863)

Fig. 4D

\*1863 *Pupa fissidens* sp. nov. – Sandberger: p. 57, pl. 5, figs 16a–c.

1875 *Pupa (Vertigo) didymodus* var. *fissidens* Sandberger – Sandberger, p. 399.

1889 *Leucochilus fissidens* (Sandberger) – Boettger, p. 285.

1914 *Leucochila fissidens* (Sandberger) – Fischer and Wenz, p. 97, pl. 6, fig. 19.

**Material:** 22 specimens and some fragments with aperture (MI/1052).

**Dimensions (of 22 specimens):** H = 1.72–2.07 mm; B = 0.96–1.11 mm; h = 0.62–0.74 mm; b = 0.61–0.70 mm; HLW = 1.02–1.18 mm; H/B = 1.79–1.90.

Detailed measurements (in mm) of 10 specimens show a continuous transition between small and large forms (Table 6).

**Table 6**

Dimensions of *Gastrocopta fissidens* (Sandberger, 1863)  
(in mm)

H	1.72	1.78	1.85	1.89	1.93	1.95	1.97	2.00	2.04	2.07
B	0.96	1.03	1.00	1.03	1.06	1.05	1.06	1.07	1.08	1.11
h	0.62	0.63	0.64	0.71	0.70	0.70	0.70	0.72	0.74	0.70
b	0.61	0.61	0.63	0.67	0.65	0.66	0.62	0.68	0.67	0.64
HLW	1.04	1.02	1.08	1.07	1.09	1.10	1.09	1.15	1.16	1.13
H/B	1.79	1.83	1.85	1.83	1.82	1.86	1.86	1.87	1.88	1.86

**Description:** Ovate-turreted shells consist of 4.75–5 convex whorls, very finely striated and separated by a distinct suture. On

the outer surface of the palatal wall, there are two dark streaks, corresponding in position to the two palatal teeth, but there is no crest. The umbilicus is open, but narrow and deep. There are 7 teeth in the aperture. The parieto-angular tooth consists of two separate, parallel parts, arcuately bent outward. The parietal portion considerably overlaps the angular portion (half a length, or even more). A small infraparietal tooth is present in all the specimens from Zwierzyniec. The columellar tooth is subhorizontal and the basal is short lamellate or knob-shaped. There are three teeth on the palatal wall; the upper one (suprapalatal tooth) is small or barely marked.

**Remarks:** The specimens from Zwierzyniec correspond generally to those described and illustrated by Sandberger (1863, p. 57, pl. 5, figs 16a–c), Wenz (in Fischer and Wenz, 1914, p. 97, pl. 6, figs 19a–b) and Wenz (1921, pl. 18, figs 20–21). Indeed, there is no infraparietal tooth in the *G. fissidens* figures of Wenz, but it is present in Sandberger's figures and in Boettger's (1889, p. 286) remarks on the *G. fissidens* specimens from Mosbach-Biebrigg and Wiesbaden (Lower Miocene). It is also distinctly marked in *G. fissidens infrapontica*, described by Wenz from Loebersdorf (Wenz, 1927, p. 47, pl. 2, fig. 8) and afterwards presented by Lueger (1981, p. 27, pl. 2, figs 20–21). The shells from Zwierzyniec come closest in shape and apertural barriers to the latter form, but also to three specimens of *G. fissidens* from Hochheim, stored at the Forschungsinstitut und Naturmuseum Senckenberg (no. 152 289/3). According to Wenz, *G. fissidens infrapontica* is smaller (H = 1.7 mm; B = 0.9 mm) than typical *G. fissidens* and has more convex whorls, but the specimen presented by Lueger (1981) is slightly bigger (H = 1.8 mm) and falls within the variability range of specimens from Zwierzyniec (see detailed measurements). Wenz's diagnosis "Diese Form unterscheidet sich von *Gastrocopta (Sinalbinula) fissidens* (Sandb) lediglich durch etwas geringere Größe und weniger hohe, etwas stärker gewölbte Umgänge" is based on one specimen only. Thus, the form described may represent one extreme of the variability range of the nominal form.

*G. fissidens* has been recorded from Poland before as *Pupa (Vertigo) didymodus* var. *fissidens* Sandberger, 1874 found in the Sarmatian sand deposits from Sobów near Tarnobrzeg (Friedberg, 1905), a locality situated not far from Zwierzyniec.

Moreover, the shells from the deposits of Belchatów, identified as *G. cf. ferdinandi* (Andreae, 1902) in Stworzewicz (1999b), are actually very large (H of 30 specimens is 1.83–2.40 mm) and somewhat more slender specimens of *G. fissidens*.

*Gastrocopta* ex gr. *didymodus* (Sandberger, 1858)

Fig. 4E

**Material:** Ten specimens and five fragments with aperture (MI/1053).

**Dimensions:** H = 1.95–2.14 mm; B = 0.92–1.07 mm; h = 0.67–0.77 mm; b = 0.63–0.72 mm; HLW = 1.08–1.24 mm; H/B = 2.0–2.18.

**Description:** Oval-cylindrical shells consist of 5–5.25 moderately convex whorls, separated by a moderately deep suture. The surface is finely, but distinctly striated. On the outer surface of the body whorl, there is a distinct crest, parallel to the aperture margin. There are 6–7 teeth in the aperture. The parieto-angular tooth consists of two parts, but they are not parallel (in contradistinction to those in *G. fissidens*), because the parietal part only slightly overlaps the angular part. Most frequently, the anterior part of the parietal tooth only reaches the posterior part of the small angular tooth. The infraparietal tooth is present in some specimens. The remaining teeth, namely the columellar, basal and palatals, are as in *G. fissidens*.

**Remarks:** At first, Sandberger (1858–1863) described both *G. didymodus* and *G. fissidens* but later (1870–75) he was uncertain,

as to whether they were two separate species. Afterwards, Boettger (1889) on the basis of the original material from Hochheim showed some important interspecific differences. First of all, the parieto-angular tooth in the former species is not “zweispaltige” like in *G. fissidens* but “zweizipfelige” (see also descriptions of the two species from Zwierzyniec and Figs 4D, E). *G. didymodus* differs from *G. fissidens* also in its clearly more cylindrical shell, less convex whorls, and distinctly marked crest. These characters are clearly visible in the specimens from Zwierzyniec, but *G. didymodus* is known only from the Upper Oligocene/Lower Miocene deposits, which are significantly older than those in Zwierzyniec. It is probable that the specimens from Zwierzyniec belong to a new species, being a direct descendant of *G. didymodus*. However, this view requires comparative studies of all species, regarded as members of the *didymodus* group, i.e. *G. obstructa* (Sandberger, 1874), *G. obstructa francofurtana* (Boettger, 1877), *G. baudoni* (Michaud, 1862) and *G. farcimen* (Sandberger, 1874).

Family LAURIIDAE Steenberg, 1925

Genus *Leiostyla* Lowe, 1852

**Type species:** *Leiostyla vincta* Lowe, 1852

*Leiostyla* cf. *gottschicki* (Wenz, 1922)

\*1922 *Lauria gottschicki* sp. nov. – Wenz: p. 107, text-fig.

**Material:** One fragment of the last whorl with partly damaged aperture and a splinter of parietal callus with parietal and angular teeth (MI/1054).

**Dimensions:** (of aperture): h = 1.06 mm; b = 1.08 mm.

**Description:** The surface of the last whorl is finely striated. The aperture margin is moderately reflexed, with a somewhat thickened lip. The umbilicus is open, but narrow and slit-like. Only one columellar tooth and two palatal teeth are visible in the preserved fragment. The two teeth, visible on the splinter of the parietal wall, continue inside the last whorl. The deeply entering columellar tooth begins on the lip and runs obliquely downwards, then bends upwards, prolonged as a large, thin lamella, parallel to the columella. The lower palatal tooth is long, rather low near the aperture, and becoming higher within. There is a small second palatal tooth above, but as the aperture margin is partly broken, its form is hard to identify.

**Remarks:** From among a few species known from the Neogene, only *L. gottschicki* described from Steinheim (Wenz, 1922) and also noted from Hollabrunn (Schütt, 1967) has such a complicated columellar tooth with the vertical part deep within the aperture. The fragment from Zwierzyniec contains only the body whorl with an aperture, so the shape and size of the shell remain unknown. Because of the complicated columellar tooth, *L. gottschicki* comes closest to the Recent Caucasian species *L. caucasica* (Pfeiffer, 1857) and *L. paulinae* (Lindholm, 1913, presented by Schileyko, 1984).

Family STROBILOPSIDAE Wenz, 1915

Genus *Strobilops* Pilsbry, 1892

**Type species:** *Helix labyrinthica* Say, 1817

*Strobilops joossi* (Gottschick, 1911)

Fig. 4F, G

\*1911 *Strobilus Joossii* sp. nov. – Gottschick: p. 502, pl. 7, figs 16a–c.

1915 *Strobilops joossi* (Gottschick) – Wenz, p. 80, fig. 9, pl. 4, figs 14a–c.

1999b *Strobilops* cf. *joossi* (Gottschick) – Stworzewicz, p. 154, figs 41–43.

**Material:** 15 specimens and 35 fragments of the last whorl with an aperture and the inner lamellae visible (MI/1055).

**Dimensions:** H = 1.32–1.77 mm; B = 1.93–2.33 mm; h = 0.58–0.79 mm; b = 0.99–1.22 mm; HLW = 0.84–1.14 mm; B/H = 1.32–1.54; NW = 4.75–5.25.

**Description:** The shell is widely coniform, with somewhat convex whorls, separated by a moderately deep suture. The embryonic whorls (1.75) are smooth and the others are sculptured, with very distinct ribs (40–55 on the last whorl), which are somewhat weaker but clearly visible at the base. The last whorl is more or less angled at the periphery. The umbilicus is open, but very narrow, and it expands abruptly, just before the aperture. The parietal lamella is higher and thicker than the infraparietal, and in contrast to the latter, it reaches the end of parietal callus. The infraparietal lamella rises inside the aperture and gradually comes level with the parietal. They both extend halfway round the last whorl. The edges of these lamellae are very weakly crenate, if at all. The interparietal lamella is absent. The columellar lamella is very weakly marked or absent. There are three basal plicae, arranged in a sequence from the shortest one near the columella, to the longest; in some specimens the third plica is equal to the second. The middle one is the most massive and the highest; generally it is rather variable.

**Remarks:** The specimens from Zwierzyniec are very close to those from Belchatów, identified as *Strobilops* cf. *joossii* (Gottschick) in Stworzewicz (1999b, figs 41–43). More material has established that the distinction among the three somewhat similar species, i.e. *S. joossii*, *S. costata* (Clessin, 1877) and *S. tiarula* (Sandberger, 1886) is clear. The latter species is intermediate in character between the two former.

The differences between the remaining strobilopsids were noted by Manganelli *et al.* (2008), who reviewed the known European Neogene species, on the basis of research on strobilopsids from Balze di Capreno.

Family VALLONIIDAE Morse, 1864

Genus *Vallonia* Risso, 1826

**Type species:** *Helix pulchella* Müller, 1774

*Vallonia subcyclophorella* Gottschick, 1911

Fig. 4H, I

\*1911 *Helix (Vallonia) subcyclophorella* sp. nov. – Gottschick: p. 503, pl. 7, figs 2–2b.

**Material:** Ten specimens and five damaged shells (MI/1056).

**Dimensions** (in brackets, those of a clearly bigger specimen): H = 0.88–1.05 (1.24) mm; B = 1.86–2.35 (2.67) mm; h = 0.76–0.9 (1.09) mm; b = 0.76–0.98 (1.17) mm; B umbilicus = 0.52–0.71 (0.86) mm; B protoconch = 0.50–0.63 (0.66) mm; NW = 3.0–3.6 (3.75).

**Remarks:** The form of the shell and aperture, as well as the surface striation of specimens from Zwierzyniec, fit very well with *V. subcyclophorella* from numerous other sites. The umbilicus of some specimens is eccentric, but according to Gerber (1996), this is not unusual in the species. *V. subcyclophorella* was widely distributed in the Miocene of Europe, and it is also known from Kazakhstan (Steklov and Tsytoich, 1967).

Family VERTIGINIDAE Fitzinger, 1833

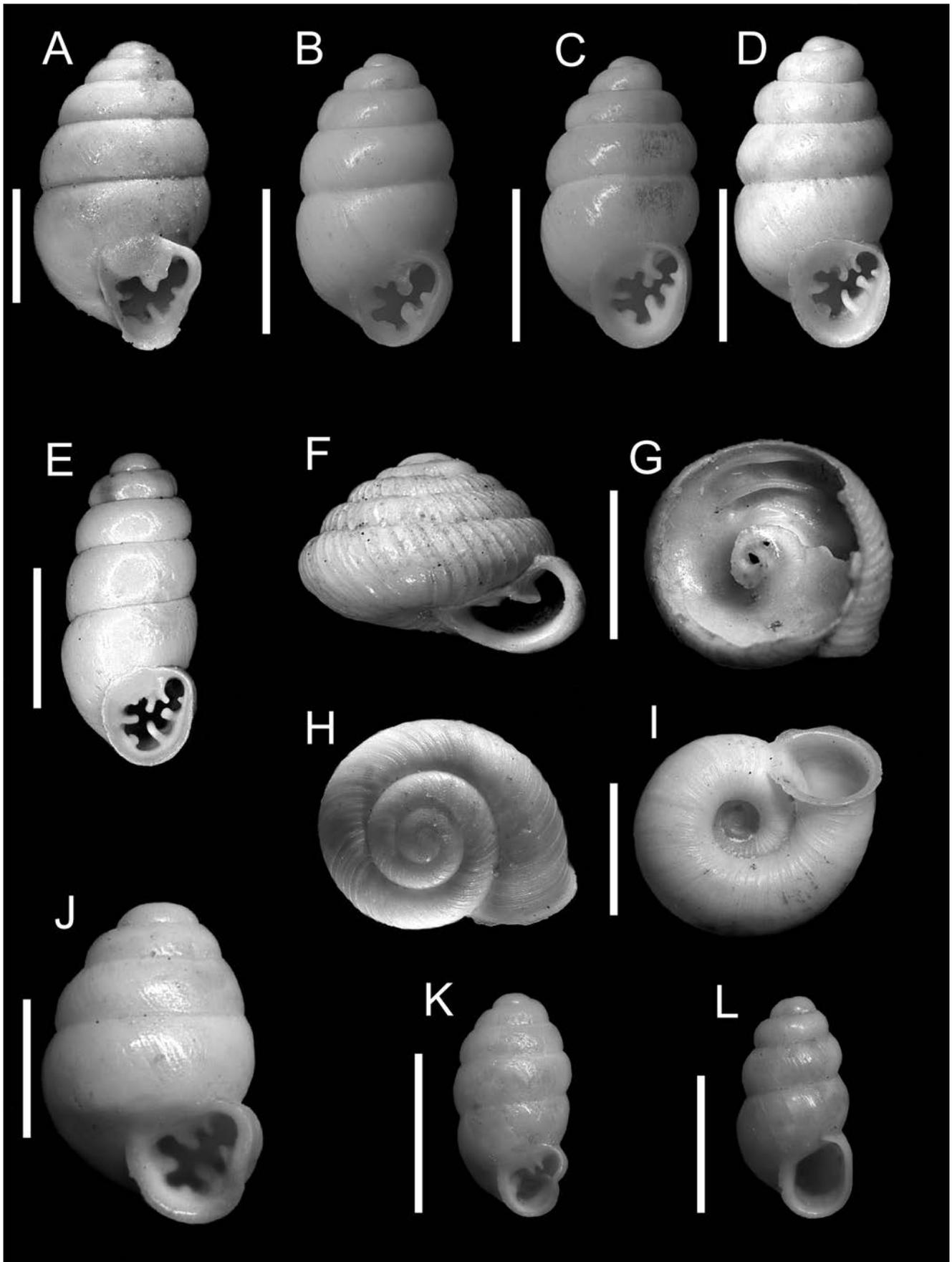
Genus *Vertigo* Müller, 1774

**Type species:** *Vertigo pusilla* Müller, 1774

*Vertigo callosa* (Reuss, 1849)

Fig. 4J

\*1849 *Pupa callosa* sp. nov. – Reuss: p. 30, pl. 3, fig. 7.



**Material:** One specimen (MI/1057).

**Dimensions:** H = 2.33 mm; B = 1.45 mm; h = 0.94 mm; b = 0.80 mm; HLW = 1.38 mm; NW = 5.25.

**Description:** The shell is ovate with poorly convex whorls. There are 6 teeth in the aperture: angular, parietal, columellar, basal and 2 palatal. The most characteristic feature is the long and thin lamellate angular tooth, located closer to the parietal callus margin than the parietal tooth, which is parallel to the former one. The columellar tooth is short, lamellate, deeply and obliquely situated, with the inner part turned upward.

**Remarks:** Because of the shell shape and size, the specimen from Zwierzyniec corresponds to *V. callosa* var. *maxima* Boettger, 1877 from Steinheim (Gottschick and Wenz, 1919, p. 14, pl. 1, fig. 27; Finger, 1998, pl. 9 fig. A), but differs from the latter in the form and location of the angular tooth and position of the columellar tooth. Almost identical specimens were found in the Lower Sarmatian and the lower part of the Middle Sarmatian deposits of Volhynia-Podolia (Ukraine).

*Vertigo protracta* (Sandberger, 1874)

\*1874 *Pupa protracta* sp. nov. – Sandberger: p. 400.

1889 *Vertigo (Alaea) protracta* (Sandberger) – Boettger, p. 300, pl. 7, fig. 5.

**Material:** One specimen and one fragment (MI/1058).

**Dimensions:** H = 1.57 mm; B = 1.05 mm; h = 0.58 mm; b = 0.60 mm; HLW = 0.97 mm.

**Remarks:** The single specimen does not differ from those, known from other Neogene localities of Europe, including that at Belchatów (Stworzewicz, 1999b).

*Vertigo angulifera* O. Boettger, 1884

Fig. 4K

\*1884 *Vertigo (Alaea) angulifera* sp. nov. – O. Boettger: p. 271, pl. 4, figs 10a–c.

**Material:** One specimen and one fragment (MI/1059).

**Dimensions:** H = 1.45 mm; B = 0.78 mm; h = 0.48 mm; b = 0.45 mm; HLW = 0.80 mm.

**Remarks:** Having a cylindrical shape, the only specimen from Zwierzyniec is most similar to *V. (Alaea) angulifera milleri* Gottschick et Wenz, 1919 from Steinheim (Sarmatian) and to some of the *V. angulifera* specimens from Belchatów (Stworzewicz, 1999b).

Genus *Negulus* Boettger, 1889

**Type species:** *Pupa reinhardti* Jickeli, 1874

*Negulus suturalis* (Sandberger, 1858)

Fig. 4L

\*1858 *Pupa suturalis* sp. nov. – Sandberger: p. 54, pl. 6, fig. 1.

1889 *Negulus lineolatus* (Al. Br.) – O. Boettger, p. 269, pl. 6, fig. 8.

1914 *Negulus suturalis* (Sandberger) – Fischer and Wenz, p. 142, pl. 5, fig. 13.

**Material:** Two specimens (MI/1060).

**Dimensions:** H = 1.7, 1.74 mm; B = 0.81, 0.86 mm; h = 0.63, 0.65 mm; b = 0.51, 0.54 mm; HLW = 1.08, 1.15 mm.

**Remarks:** The two specimens do not differ from those, known from several Neogene localities in Europe, including Belchatów and Opole (Stworzewicz, 1999b).

Family CLAUSILIIDAE Gray, 1855

Genus *Serrulastra* Nordsieck, 1981

**Type species:** *Clausilia amphiodon* Reuss, 1860

*Serrulastra trolli* Nordsieck, 1981

Fig. 5A

\*1981 *Serrulastra trolli* sp. nov. – Nordsieck: p. 76, pl. 8, fig. 17.

**Material:** Two fragments of body whorl with partly preserved lamellae and two fragments of palatal wall with an aperture (MI/1061).

**Dimensions:** H fragm = 3.63 mm, 3.60 mm; h = 2.11 mm, 2.03 mm; b = 1.58 mm, 1.70 mm.

**Description:** The body whorl is covered with strong and regular ribs, which are somewhat sparse on the dorsal side. The neck is regularly rounded. The aperture is broadly oval, with a strongly folded peristome. The superior lamella is connected with the spiral one, the inferior lamella steeply ascends and bends to the peristome, forming a bifurcation. In one specimen, there is a small fold between the branches of the bifurcation. The subcolumellar lamella reaches the peristome. The clausilian apparatus consists of three palatal plicae: a short upper plica (in one specimen it is connected with lunella), a more or less distinctly marked lunella, and a strong lower plica, which is visible inside the aperture in front view. The principal plica is very long and ends laterally. The clausilium is unknown.

**Remarks:** The two clausiliid fragments are most similar to the *Serrulastra (Serruplica)* species, described from the Middle Miocene sediments from St. Veit a.d. Triesting (Austria).

The short upper plica is separate from the lunella in only one specimen from Zwierzyniec and in both specimens the lunella is not connected with the lower plica.

Genus *Triloba* Vest, 1867

**Type species:** *Clausilia sandrii* Küster, 1847

*Triloba magurkai* Stworzewicz new species

Fig. 5B, C

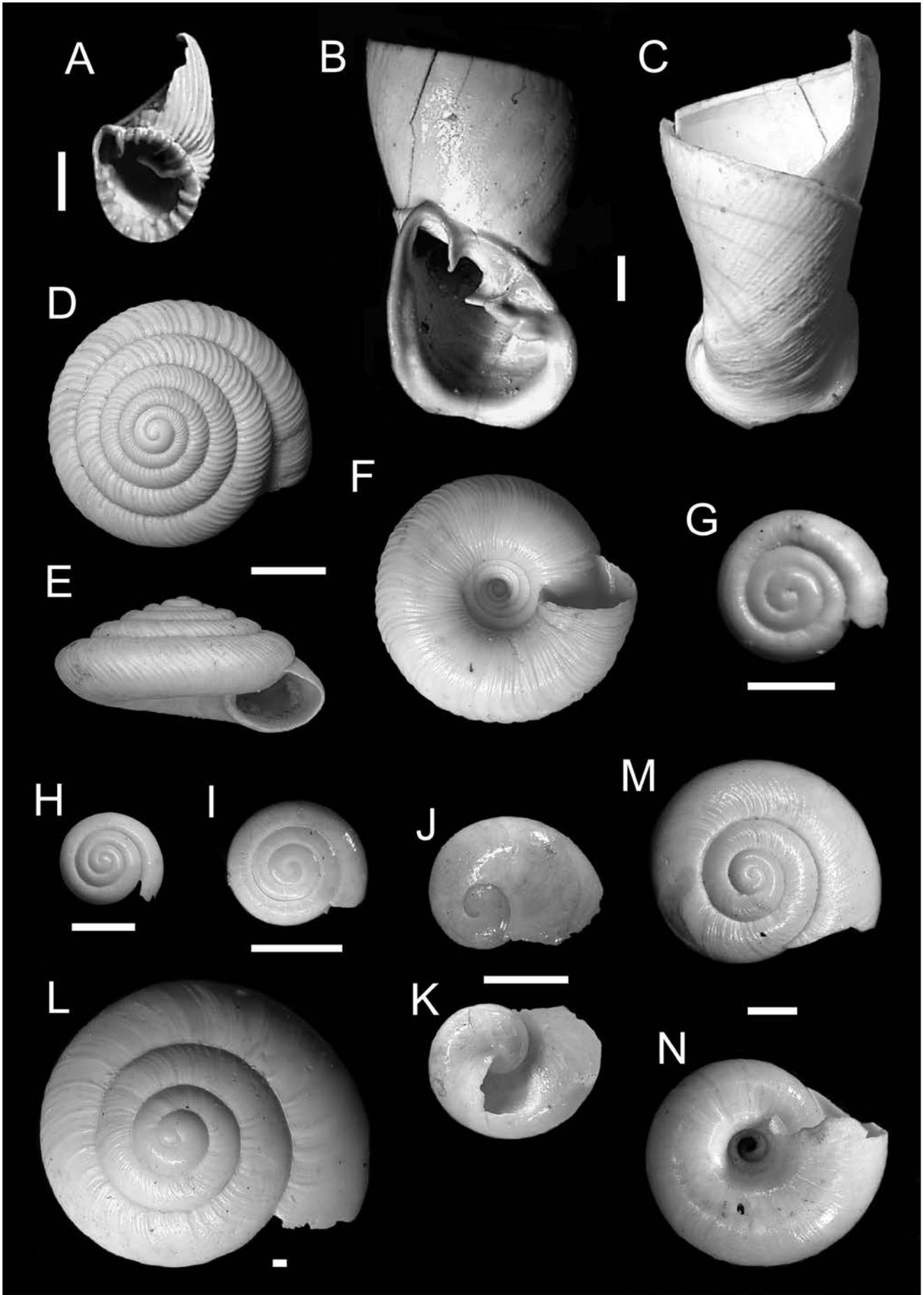
**Material:** One specimen (holotype), consisting of body whorl with an aperture (ISEA PAS, no. MI/1062).

**Dimensions:** H fragm = 8.68 mm; B = 5.45 mm; h = 5.15 mm; b = 4.40 mm.

**Type locality and type level:** Zwierzyniec, near Busko (southern Poland); fine-grained sand deposits of the Sarmatian (the upper part of the Middle Miocene, MN 7+8, ca. 12.5 Ma).

**Etymology:** Dedicated to Marcin Górka, who discovered the locality at Zwierzyniec ("magurka" is the acronym of his name in his e-mail address).

**Fig. 4.** Land gastropods from Zwierzyniec; scale bars 1 mm. **A.** *Gastrocopta acuminata* (Klein, 1846), MI/1049; **B.** *Gastrocopta nouletiana* (Dupuy, 1850), MI/1050; **C.** *Gastrocopta serotina* Ložek, 1964, MI/1051; **D.** *Gastrocopta fissidens* (Sandberger, 1863), MI/1052; **E.** *Gastrocopta* ex gr. *didymodus* (Sandberger, 1858), MI/1053; **F, G.** *Strobilops joossi* (Gottschick, 1911), MI/1055, one shell with plicae inside last whorl visible; **H, I.** *Vallonia subcyclophorella* Gottschick, 1911, MI/1056; **J.** *Vertigo callosa* (Reuss, 1849), MI/1057; **K.** *Vertigo angulifera* O. Boettger, 1884, MI/1059; **L.** *Negulus suturalis* (Sandberger, 1858), MI/1060



**Description:** The body whorl is narrowed to the aperture. Its surface is nearly smooth in front; on the dorsal side, there are weak, wrinkly striae, giving the impression of a granulated structure. The neck is rounded. The aperture is obliquely pear-shaped, with a reflexed edge and a thickened peristome, also on the parietal portion, without folds. The spiral and upper lamellae are not connected. The spiral lamella is rather weak, much weaker in the anterior part and the upper lamella is well-developed. They are situated at different distances from the columella, but they are not overlapping. The lower lamella ascends spirally and ends just before the peristome with a bipartite knot. The subcolumellar lamella is not visible in front view. There is no lunella in the clausilial apparatus; only palatal plicae are present, of which four are visible on the neck surface (Fig. 5C). The principal plica is the longest, the upper palatal plica is clearly shorter, two middle palatal plicae are the shortest (the upper one is very weakly developed, so it is not visible from without), and the lower palatal plica is longer than the two latter and arcuate. The clausilium is unknown.

**Remarks:** Regarding the dimensions of the single fragment of shell, it must belong to a rather large clausiliid species. The clausilial apparatus, without lunella, consisting of 4–5 palatal plicae, and the upper lamella, separated from spiral lamella, are characteristic of *Triloba* genus (Allopiinae) (Vest, 1867). Until quite recently, *Triloba* species have not been noted as fossils, apart from the undescribed *Triloba* n. sp., recorded from the Upper Miocene deposits at Nerezi, near Skopje in Macedonia (Nordsieck, 2007). In 2012, Schnabel described that species as *Triloba pappi*, on the basis of material, collected from Nerezi more than half of a century ago by Adolf Papp.

*Triloba magurkai* is similar to *T. pappi* with regard to dimensions of the aperture, the narrowed form of the last whorl and the clausilial apparatus of plicae-type. However, it differs in the position of the upper-spiral lamellae (the upper lamella barely reaches the spiral one, but they are not overlapping), in a well-developed principal lamella, in a different ending of lower lamella (it is not bent upwards) and in the less reflexed edge of the aperture.

*T. pappi* was found in the Upper Miocene deposits and it was regarded as “the first known fossil species of the Allopiinae from Southeast Europe” (Schnabel, 2012). The present find demonstrates that in the Middle Miocene, the group reached much further northwards.

Family DISCIDAE Thiele, 1931

Genus *Discus* Fitzinger, 1883

**Type species:** *Helix rudrata* Férussac, 1821

*Discus costatus* (Gottschick, 1911)

Fig. 5D–F

- \*1911 *Patula* (*Charopa*) *costata* sp. nov. – Gottschick: p. 501, pl. 7, figs 15a–c.
- 1916 *Pyramidula* (*Gonyodiscus*) *costata* (Gottschick) – Gottschick and Wenz, p. 29.
- 1920 *Gonyodiscus costatus* (Gottschick) – Gottschick, p. 40.
- 1998 *Discus costatus* (Gottschick) – Finger, p. 18, pl. 10, figs D–F.

**Material:** Four specimens (including 3 with broken last whorls) and fragments of 19 specimens (MI/1063).

**Dimensions** (in brackets – of damaged specimens): H = 2.43 mm (1.55, 1.83); B = 4.93 mm (3.52, 3.86); h = 1.07 mm (0.96, 0.98); b = 1.85 mm (1.30, 1.43); B umbilicus = 1.41 mm (1.0, 1.1); NW = 5.75 (4.75, 5).

**Description:** The shell is discoidal with a low coniform spire, consisting of six radially ribbed whorls with blunt keel on the periphery. The ribs become somewhat weaker at the base. There is not a distinct microsculpture on the protoconch apart from hardly visible adsutural radial wrinkles, similar to that described in *Discus pleuradrus* (Bourguignat, 1881) by Harzhauser and Binder (2004). The umbilicus is widely open, taking almost one-third of minor shell diameter, so that all the whorls, including the nucleus, are clearly visible. The aperture is widely semilunar with a simple peristome.

**Remarks:** The specimens from Zwierzyniec match those, described from the Sarmatian deposits at Steinheim and stored in the collections of the Senckenberg Museum (151372/5) and the Museum of Natural History in London. Recently, new materials, containing *D. costatus* from the *kleini* layers of the Steinheim Basin, were presented by Finger (1998).

The species has not been recorded from Poland to date.

Family HELICODISCIDAE H. B. Baker, 1927

Genus *Helicodiscus* Morse, 1864

**Type species:** *Helix lineatus* Say, 1817

*Helicodiscus* (*Helicodiscus*) *roemeri* (Andreae, 1902)

Fig. 5G

- \*1830 *Helix depressa* sp. nov. – Eichwald: p. 215.
- 1853 *Helix depressa* Eichwald – Eichwald, p. 300, pl. 11, figs 10a–d.
- 1902 *Hyalinia* (*Gyalina*) *roemeri* sp. nov. – Andreae, p. 9, fig. 3.
- 1942 *Gyalina roemeri* (Andreae) – Wenz and Edlauer, p. 93, pl. 4, fig. 12.
- 1972 *Helicodiscus eichwaldi* sp. nov. – Prisyazhnyuk, p. 132, figs a–d.
- 1979 *Helicodiscus* (*Helicodiscus*) *roemeri* (Andreae) – Schlickum, p. 69, fig. 3.
- 1997 *Helicodiscus* (*Helicodiscus*) *depressus* (Eichwald) – Stworzewicz and Prisyazhnyuk, p. 202, figs 1–4.

**Material:** One subadult specimen (MI/1064).

**Dimensions:** H = 1.10 mm; B = 2.27 mm; B umbilicus = 0.96 mm; NW = 3.

**Remarks:** The single specimen of this rare Neogene species is identical to those from other sites in Poland (Opole, Bełchatów), Austria and Ukraine. Detailed data on *H. roemeri* are included in Stworzewicz and Prisyazhnyuk (1997), where the authors presented it under the name *Helicodiscus depressus*, the species described by Eichwald (1830) as *Helix depressa* from Hołowczyńce (Podolia in Ukraine). However, Dietrich Kadolsky (pers. info., 1997) drew to the authors' attention that “...Eichwald's name is an

**Fig. 5.** Land gastropods from Zwierzyniec; scale bars 1 mm. **A.** *Serrulastra trolli* Nordsieck, 1981, MI/1061; **B, C.** *Triloba magurkai* Stworzewicz sp. nov., holotype, MI/1062, frontal and dorsal view; **D–F.** *Discus costatus* (Gottschick, 1911), MI/1063; **G.** *Helicodiscus* (*Helicodiscus*) *roemeri* (Andreae, 1902), MI/1064; **H.** *Hawaiiia antiqua* Riedel, 1963, MI/1065; **I.** *Vitrea procrystallina* Andreae, 1902, MI/1067; **J, K.** *Phenacolimax suevica* (Sandberger, 1874), MI/1066; **L.** *Miozonites costatus* (Sandberger, 1874), MI/1068; **M, N.** *Aegopinella* cf. *subnitens* (Klein, 1853), MI/1069

objective junior homonym of *Helix depressa* Montagu, 1803, Menke, 1828 and Grateloup, 1827. Therefore, it has to be replaced by *Hyalinia roemeri* Andreae 1902, the next oldest available species group name and a subjective synonym...”, afterwards placed in *Helicodiscus* (Prisyazhnyuk, 1972).

Family PRISTILOMATIDAE Cockerell, 1891

Genus *Hawaiiia* Gude, 1911

**Type species:** *Helix minuscula* Binney, 1840

*Hawaiiia antiqua* Riedel, 1963

Fig. 5H

- \*1963 *Hawaiiia antiqua* sp. nov. – Riedel: p. 37, figs 9–14.  
 1966 *Hawaiiia antiqua* Riedel – Steklov, p. 208, figs. 81–82, pl. 8, figs 161–162.  
 2008 *Hawaiiia antiqua* Riedel – Prisyazhnyuk, 2008b p. 95, pl. 3, fig. 22, pl. 5, figs 45–46.

**Material:** One subadult specimen (MI/1065).

**Dimensions:** H = 0.99 mm; B = 1.78 mm; h = 0.71 mm; b = 0.68 mm; NW = 3.5.

**Remarks:** The single specimen with a broken aperture does not differ from those described by Riedel (1963) from the Caucasus. Although the shell surface of *Hawaiiia* species has characteristic radial lines, they are barely visible on some of Riedel's type specimens, or in the specimen from Zwierzyniec.

*H. antiqua* is known from several Middle and Late Miocene sites in the Caucasus (Steklov, 1966), Podolia (Gozhik and Prisyazhnyuk, 1978) and Serbia (Prisyazhnyuk, 2008b).

This is the first record for Poland.

Family VITRINIDAE Fitzinger, 1833

Genus *Phenacolimax* Stabile, 1859

**Type species:** *Helico-Limax major* Férussac, 1807

*Phenacolimax suevica* (Sandberger, 1874)

Fig. 5J, K

- \*1874 *Vitrina suevica* sp. nov. – Sandberger: p. 602, pl. 29, fig. 27.  
 1916 *Vitrina (Phenacolimax) suevica* Sandberger – Gottschick and Wenz, p. 24.

**Material:** One specimen (MI/1066).

**Dimensions:** H = 1.16 mm; Bmax = 2.16 mm; Bmin = 1.67 mm; h = 0.92 mm; b = 1.33 mm; NW = 2.

**Remarks:** The subadult specimen is a little damaged in the apertural part. Nevertheless, it does not differ from those, described from Steinheim and known also from several sites in Ukraine (Gozhik and Prisyazhnyuk, 1978).

Family ZONITIDAE Mörch, 1864

Genus *Vitrea* Fitzinger, 1833

**Type species:** *Glischrus (Helix) diaphanus* Studer, 1820

*Vitrea procrystallina* Andreae, 1902

Fig. 5I

- \*1902 *Hyalina (Vitrea) procrystallina* sp. nov. – Andreae: p. 10, fig. 4.  
 1920 *Vitrea (Vitrea) procrystallina* Andreae – Gottschick, p. 37.

**Material:** One specimen (MI/1067).

**Dimensions:** H = 0.81 mm; B = 1.59 mm; h = 0.65 mm; b = 0.76 mm; NW = 3.5.

**Remarks:** The subadult specimen from Zwierzyniec matches the description of *V. procrystallina* from Opole, although Andreae (1902, fig. 4) showed a shell with a very narrow umbilicus. On the other hand, the specimen from Zwierzyniec does not differ from those presented from Rákosd (Gaál, 1911) and Zwiefaltendorf (Schlickum, 1976). It is a very rare species in Miocene deposits.

Genus *Miozonites* Pfeffer, 1930

**Type species:** *Helix algiroides* Reuss, 1849

*Miozonites costatus* (Sandberger, 1874)

Fig. 5L

- \*1874 *Archaeozonites costatus* sp. nov. – Sandberger: p. 604.  
 1916 *Zonites (Aegopis) costatus* (Sandberger) – Gottschick and Wenz, p. 21, pl. 1, figs 1a–c.

**Material:** One specimen (somewhat damaged) and numerous fragments (MI/1068).

**Dimensions:** H = 19 mm; B = 24.5 mm; h > 9.5 mm; b = > 12 mm; HLW = 14 mm; NW = 5.

**Remarks:** In shell form, size and surface sculpture, the specimen from Zwierzyniec corresponds to specimens from the Silvana-schichten and Hohenmemmingen (Gottschick and Wenz, 1916) and from the Karpatian deposits of the Korneuburg Basin (Niederösterreich) (Binder, 2002). This is the first record of the species in Poland.

Genus *Aegopinella* Lindholm, 1927

**Type species:** *Helix pura* Alder, 1830

*Aegopinella* cf. *subnitens* (Klein, 1853)

Fig. 5M, N

- \*1853 *Helix subnitens* sp. nov. – Klein: p. 210, pl. 5, fig. 7. partim 1875 *Hyalinia orbicularis* sp. nov. – Sandberger, p. 603, pl. 29, fig. 28.  
 1916 *Hyalinia (Polita) subnitens* (Klein) – Gottschick and Wenz, p. 23.  
 1923a *Oxychilus subnitens subnitens* (Klein) – Wenz, p. 282.  
 1976 *Aegopinella subnitens* (Klein) – Schlickum, p. 12, pl. 3, figs 39–40.

**Material:** 11 juv. and subadult specimens (2–3.75 whorls), in the most part damaged (MI/1069).

**Dimensions:** See Table 7.

**Table 7**

Dimensions of *Aegopinella* cf. *subnitens* (Klein, 1853)  
(in mm)

H	2.57	2.43	2.05	1.97	-
B	5.03	4.80	4.09	3.75	3.79
h	1.89	1.68	1.65	1.50	-
b	2.29	2.22	1.77	1.69	-
Bprot	1.12	1.05	1.08	1.04	1.11
Bumb	0.94	-	0.89	0.82	-
NW	3.75	3.75	3.25	ca.3	ca.3

**Description:** The two biggest shells have 3.75 somewhat raised whorls, covered with weak, irregular spaced growth lines, and much less visible spiral lines, with the exception of the smooth protoconch. On the basal side, this sculpture is very weakly marked. The umbilicus is open, all whorls are visible within; it takes up ca. 1/5 of the shell diameter. The aperture is ovate-semilunar.

**Remarks:** The possibility of precise identification is precluded, because of the lack of adult specimens, but the shells from Zwierzyniec match the description and figures of *A. subnitens* from Mörsingen and some other European localities (Gottschick and Wenz, 1916; Gottschick, 1920; Schlickum, 1976, 1978). On the other hand, the systematic status of *A. subnitens* requires clarification, as it is confused with some other species. Lueger (1981) illegitimately placed *A. subnitens* in synonymy of *Aegopinella orbicularis* (= *Helix orbicularis* Klein, 1846), ignoring Klein's remarks concerning the shell-surface striation of the latter species (Klein, 1846, p. 71) and the fact that Wenz (1919) transferred *Helix orbicularis* Klein to *Gonyodiscus* (*Pleurodiscus*), and then to *Pleurodiscus*, fam. Pleurodiscidae (Wenz, 1923d). Recently, the specimens, identified by Lueger (1981) as *A. orbicularis*, were assigned to *A. reussi* (Hörnnes, 1856) in Harzhauser and Binder (2004) and later to *A. reussi* (Schlosser, 1907) in Harzhauser *et al.* (2011).

This is the first record of the species in Poland, with exception of a dubious record by Woźny (1976) from Orawa – Nowy Targ Basin.

Family HELICIDAE Rafinesque, 1815

Genus *Klikia* Pilsbry, 1894

**Type species:** *Helix osculum* Thomae, 1845

*Klikia giengensis* (Klein, 1846)

Fig. 6A

- \*1846 *Helix Giengensis* sp. nov. – Klein: p. 69, pl. 1, figs 9a–b.
- 1874 *Helix* (*Gonostoma*) *osculum* var. *Giengensis* Krauss – Sandberger, p. 585, pl. 29, figs 4–4b.
- 1911 *Klikia giengensis* Krauss – Wenz, p. 85, pl. 2, figs 6–10.
- 1976 *Klikia* (*Klikia*) *giengensis* (Klein) – Schlickum, p. 16, pl. 4, fig. 58.

**Material:** One damaged specimen and seven fragments (including a fragment of body whorl with an aperture and a thickened peristome preserved) (MI/1070).

**Dimensions:** H = ca. 4.5 mm; B = ca. 8.78 mm; h = ca. 3.27 mm; b = ca. 4.43 mm; HLW = ca. 4.22 mm; NW = 5.

**Description:** The shell is flattened with a rather broadly open umbilicus, and a reflexed aperture edge with a thick peristome. The whorls are separated by a deeply incised suture and covered by very fine, dense papillae, also visible on the base.

**Remarks:** The single specimen from Zwierzyniec does not differ from those presented by Sandberger (1874), Wenz (1911) and Schlickum (1976).

Genus *Pseudochloritis* C. Boettger, 1909

**Type species:** *Helix incrassatus* Klein, 1853

*Pseudochloritis incrassata* (Klein, 1853)

Fig. 6B–D

- \*1853 *Helix incrassata* sp. nov. – Klein: p. 208, pl. 5, fig. 6.
- 1916 *Tropidomphalus incrassatus* (Klein) – Gottschick and Wenz, p. 55.
- 2008 *Pseudochloritis incrassata* (Klein) – Binder, p. 172.

**Material:** Two well-preserved specimens and over 30 fragments (ZC H1–ZC H4)

**Dimensions:** H = 14–16 mm; B = 24–26 mm; h = 9.5–12.0 mm; b = 14.0–17.5 mm; HLW = 12.5–15.0 mm; NW = 4.75–5.

**Remarks:** The shell form and size, the appearance of the umbilicus and the surface sculpture of the specimens from Zwierzyniec match those of the *P. incrassata* shells from Mörsingen, stored in the Paläontologisches Museum of Bayrische Staatssammlung Mü-

nchen (1955/4/3). Comparatively good preservation of the shells permitted analysis of the banding pattern on the whorls, particularly clearly visible in UV-light (apart from the main band located just above the periphery, there are two more – above and below the former) presented by Górka (2008a). It differs somewhat from the traces of pigment bands, observed by Binder (2008) on specimens from Mörsingen, which have only one additional band below the main one.

The species is known from many Middle Miocene sites in Europe (Wenz, 1923b; Binder, 2008), but this is the first record for Poland.

Genus *Cepaea* Held, 1837

**Type species:** *Helix nemoralis* Linnaeus, 1758

*Cepaea sylvestrina gottschicki* Wenz, 1919

Fig. 6E–G

- \*1919 *Cepaea gottschicki* sp. nov. – Wenz: p. 70.
- 1920 (1919) *Cepaea sylvestrina gottschicki* (Wenz) – Wenz: p. 152, figs 7–8.

**Material:** 48 more or less damaged specimens (ZC C1–ZC C23). **Dimensions** (of the best preserved shell, ZC C12): H = 16.0 mm; B = 20.0 mm; h = 7.5 mm; b = 10 mm; HLW = 13.5 mm; NW = 4.75.

**Remarks:** The taxonomic position of this form was uncertain, but finally Wenz (1920 (1919)) recognized the specimens from Steinheim, described previously as *C. gottschicki* (Wenz, 1919), as a subspecies of *C. sylvestrina* (Schlotheim, 1820). The form of the aperture in *C. sylvestrina* is rather variable and more or less narrowed, as in the Recent *C. nemoralis* (Linnaeus, 1758), which is regarded as a descendant of the former species (Wenz, 1920). The banding pattern of the shells from Zwierzyniec was revealed by viewing them in UV light (Górka, 2008a).

Helicidae indet.

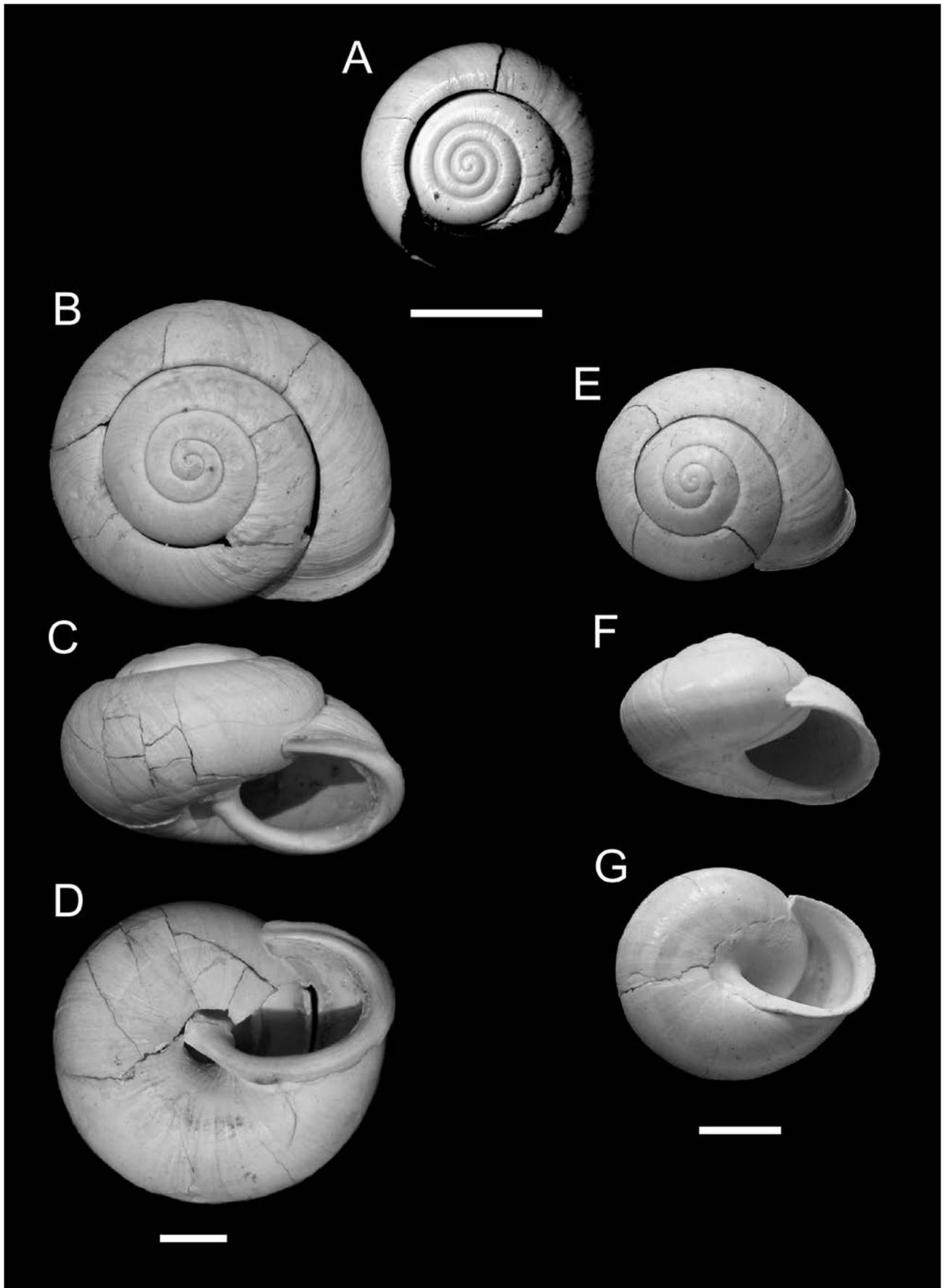
Apart from the species recognized here, some unidentifiable fragments of other shells were found. Most frequently, they are fragments of the upper part of the spire or basal parts with the umbilicus and a fragment of the aperture. Part of them probably belongs to *Protodrepanostoma* sp. or to *Helicodonta* sp. Other may represent a species of *Leucochroopsis*.

## DISCUSSION

### Palaeoenvironmental implications

The ecological requirements of extant members of the genera, which are extinct either in Europe or in Central Europe, make it possible to draw inferences about the environment that existed in the central-southern Poland of the present day during the Middle Miocene. At Zwierzyniec, terrestrial gastropods were found together with freshwater species, indicating a high degree of heterogeneity of the locality. The gastropod shells were washed down from the coast, probably by heavy rains that formed rapid torrents, discharging to the sea. The gastropod-bearing sediments might be regarded as deposits of the underwater part of a delta, and the gastropod assemblage may reflect habitats, situated both near and far away from the place of deposition.

The fact that the assemblage contains hygrophilous and xerophilous species, as well as species of shady and open places, demonstrates that they come from various habitats. Most of them represent genera which have their Recent



**Fig. 6.** Land gastropods from Zwierzyniec; scale bars 5 mm. **A.** *Klika giengensis* (Klein, 1846), MI/1070; **B–D.** *Pseudochloritis incrassata* (Klein, 1853), ZC H1; **E–G.** *Cepaea sylvestrina gottschicki* Wenz, 1919, ZC C12

members living in shrubland and/or in forests, more or less humid, and they are not limited to coastal areas (*Carychium*, *Leiostyla*, *Azeca*, *Vertigo*, *Discus*, *Helicodiscus*, *Hawaiiia*, *Phenacolimax*, *Vitrea*, Clausiliidae and some of the Helicidae). Another group consists of gastropods, which are characteristic of open, warm and dry grasslands, mostly on a calcium-rich substrate, with insolated calcareous rocks and xerophilous vegetation (*Pupilla*, *Granaria*, *Pupoides*, partly *Vallonia*). The modern distribution of *Gastrocopta* and *Strobilops* overlaps with the zone of subtropical mixed mesophytic and swamp forests, essentially evergreen, but with distinctly marked seasonal changes of temperature.

In the Zwierzyniec gastropod assemblage, there are also members of genera that are represented in modern faunas only by rare species with poorly known ecological requirements. For example, several *Microstele* species are restricted to the arid areas of tropical Africa, India and Sri Lanka (formerly Ceylon), but their ecological requirements seem to be known only for a species from Ceylon, which was found "in old posts and on palmyra trees" (Pilsbry, 1920–21). Four recent species of *Negulus* are known only from the mountain areas of tropical Africa and they were found in the leaf litter of evergreen forests, under bark, and in bushes, between 800 and 4000 m a.s.l. (Bruggen, 1994).

The only species, which unequivocally indicates a close proximity to the sea, is the unidentified species of *Myosotella*. The Recent representatives of this genus live on littoral rocks and stones, and in detritus, mainly above the high-tide mark (Martins, 1996). The other ellobiids, found in Zwierzyniec, belong to *Carychium*, a group of terrestrial snails with a preference for humid habitats, living both in forests and in meadows.

The freshwater gastropods are represented mainly by lymnaeids of the genus *Galba*, which indicate the presence of relatively small and very small water bodies (Prisyazhnyuk *et al.*, 2006).

### Remarks on biogeography

Most genera represented at Zwierzyniec have Recent representatives in southern Europe or in distant, extra-European regions. *Pomatias*, *Myosotella*, *Azeca*, *Leiostyla* and *Triloba* are recently more or less widely distributed in the Mediterranean region and in the Caucasus. The other group consists of genera, which have living members distributed nearly world-wide with the exception of Europe (*Gastrocopta*), or are restricted to North America and south-eastern Asia (*Strobilops*, *Hawaiiia*), to tropical Africa, India and Ceylon (*Microstele*), or only to tropical Africa (*Negulus*). Both groups may be regarded as remnants of a malacofauna that had a wider range during the Tertiary, and one that existed along the northern coasts of the Tethys (Stworzewicz, 1993).

The most numerous group contains the members of genera, which have extant congeners in Poland (*Carychium*, *Pupilla*, *Granaria*, *Vallonia*, *Vertigo*, *Discus*, *Vitrea*, *Aegopinella* and *Cepaea*). Only a few genera are totally extinct (*Serrulastra*, *Miozonites*, *Pseudochloritis*) and are thus less useful for biogeographical considerations.

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