Acta Geologica Polonica, Vol. 58 (2008), No. 1, pp. 105-111

Shell colour pattern in two fossil helicid snails, *Tropidomphalus incrassatus* (KLEIN, 1853) and *Cepaea sylvestrina gottschicki* WENZ, 1919, from the Middle Miocene of Poland

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ABSTRACT:

GÓRKA, M. 2008. Shell colour pattern in two fossil helicid snails, *Tropidomphalus incrassatus* (KLEIN, 1853) and *Cepaea sylvestrina gottschicki* WENZ, 1919, from the Middle Miocene of Poland. *Acta Geologica Polonica*, **58** (1), 105-111. Warszawa.

Two fossil helicid snails, *Tropidomphalus incrassatus* (KLEIN, 1853) and *Cepaea sylvestrina gottschicki* WENZ, 1919, from the "detrital Sarmatian" (Middle Miocene) of the northernmost part of the Fore-Carpathian Depression were macroscopically analysed in daylight and UV-light to reveal the original shell colour pattern. The analysis shows a high degree of polymorphism in *C. sylvestrina gottschicki*, similar to that in the extant species *Cepaea nemoralis* (LINNAEUS, 1758) and *Cepaea hortensis* (O.F. MÜLLER, 1774), and results in the recognition of eight different banding patterns, at least four of which have never been presented before. The banding type in *T. incrassatus* shows strong convergence with that in the extant representatives of the Campylaeinae. It is suggested that restoration of the original shell colour pattern may serve as a useful tool in palaeoecological reconstructions.

Key words: Shell pattern, UV-light, Helicidae, *Tropidomphalus*, *Cepaea*, Miocene, Poland.

INTRODUCTION

The aim of the present paper is to restore the original shell colour and banding of the two fossil helicid snails, *Tropidomphalus incrassatus* (KLEIN, 1853) and *Cepaea sylvestrina gottschicki* WENZ, 1919. The restoration is based on observations of fossil specimens in daylight and UV-light, followed by comparison with relevant extant taxa.

Pigments are substances that occur commonly in every tissue of the animal body and skeleton (the shell in particular). Unfortunately, they are quite unstable, and disappear rapidly from the skeletons during the diagenesis of biotic material (FOX & VEVERS 1960, BLUMER 1965, TICHY 1980, CURRY 1999). Because of this, the preservation of natural pigmentation in fossils is usually a unique feature. Nevertheless, it was observed in many groups of shell-bearing invertebrates, such as brachiopods (see KAYSER 1871, RICHTER 1919, BIERNAT 1984, BALIŃSKI 1985, BLODGETT & *al*. 1988) and molluscs (e.g. YOCHELSON & KŘÍŽ 1974; BAŁUK 1975, 1995; TICHY 1980; KELLEY & SWANN 1988; GATTO 1993), including terrestrial snails (SANDBERGER 1870-75, ZILCH 1959-60, SCHLICKUM & STRAUCH 1970, CALLAPEZ 1999, BINDER 2002).

Within the taxa of terrestrial snails investigated, the presence of pigments was previously recorded in fossil specimens of the genera *Tropidomphalus* and *Cepaea*

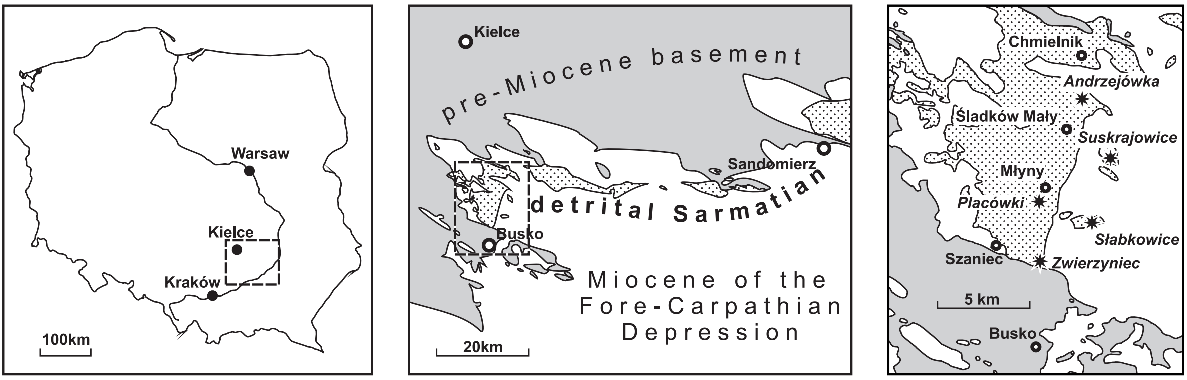


Fig. 1. Location of the discussed helicid-bearing sites (asterisked) within the "detrital Sarmatian" (Middle Miocene) of Poland

(see Sandberger 1870-75; Wenz 1920a, b; Zilch 1959-60; Groiss 1968; Kókay 2006), including the species *T. incrassatus* (see Sandberger 1870-75) and *C. sylvestrina* (see Sandberger 1870-75, Wenz 1920b, Groiss 1968) presented in this study.

In some cases, when the shell pigmentation is invisible in daylight, it may still be observed using UV-light. Pigments or their remnants, if present, show a very specific fluorescence (see Fox & Vevers 1960, Curry 1999). This particular phenomenon, sometimes referred to as a "cryptochromy" (Gatto 1993), was reported in different groups of fossil invertebrates, e.g. brachiopods (Curry 1999), and marine gastropods (Havas-Bohn 1966, Lorenz 1992).

MATERIAL AND METHODS

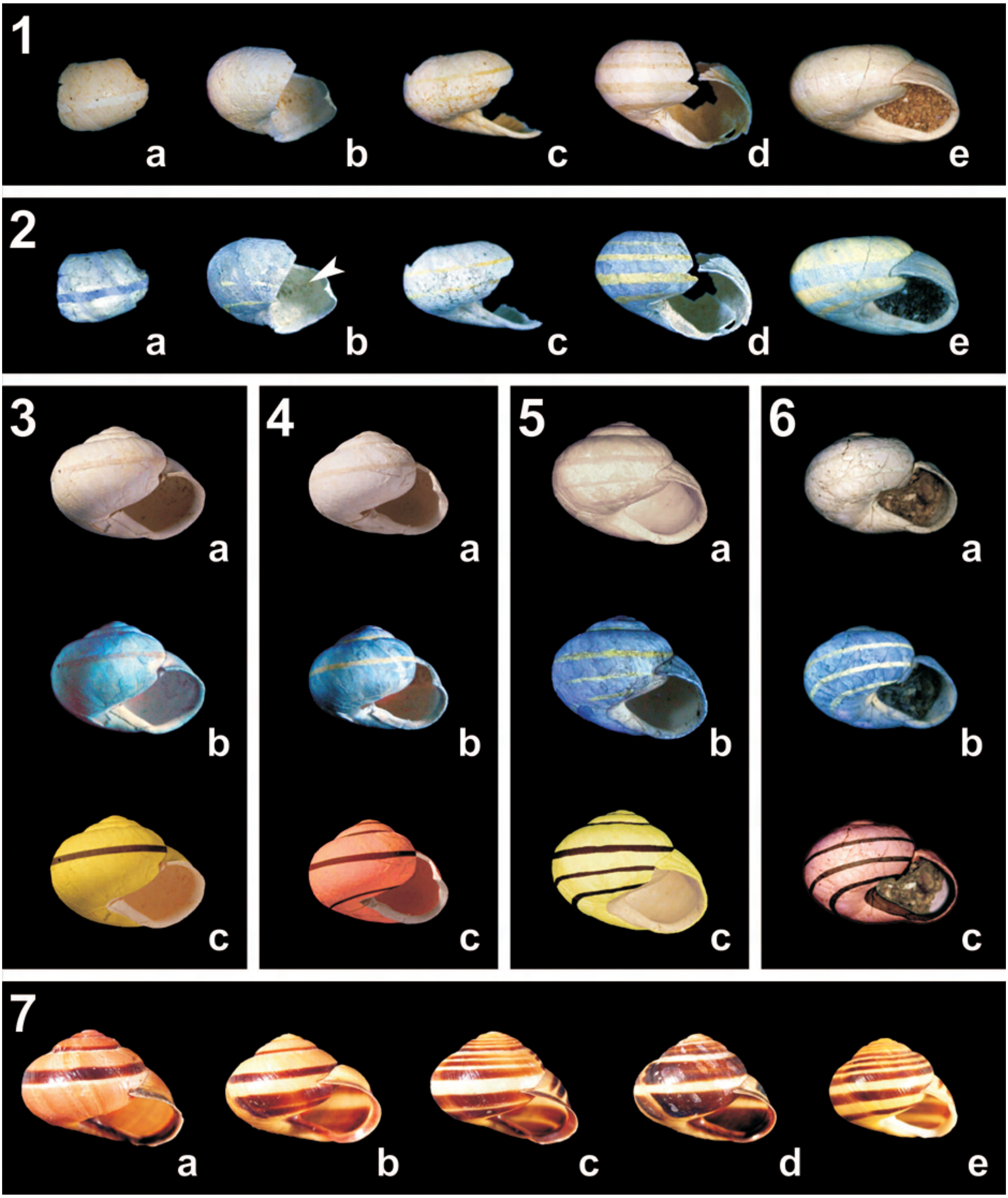
Along the northern margins of the Fore-Carpathian Depression in southern Poland there is a narrow belt of Middle Miocene (Early Sarmatian, see Łuczkowska & Rutkowski 1970, Rutkowski 1976) shallow marine facies known as the "detrital Sarmatian" (Text-fig. 1). This facies, of terrigenous origin, is a source of relatively numerous fossils of land animals. Besides rare vertebrate remains, terrestrial and freshwater molluscs were found (Zastawniak 1980, Stworzewicz & Prisyazhnyuk 1997, Prysjazhnjuk & *al*. 2006, Prisyazhnyuk & *al*. *in prep*.). This "detrital Sarmatian" facies yielded the two fossil Helicidae species investigated in this study. The first belongs to the extinct genus *Tropidomphalus* of the subfamily Campylaeinae, the numerous members of which are still living in Europe (Zilch 1969-70). The genus *Cepaea* of the subfamily Helicinae is still represented by four European species, among which *C. nemoralis* (Linnaeus, 1758) seems to be the closest extant relative of *C. sylvestrina gottschicki* Wenz, 1919 (see Gottschick 1920; Wenz 1920a, b; Boettger & Wenz 1921). The author's fieldwork over a long period has resulted in the collection of 148 specimens (or their fragments) of *Tropidomphalus incrassatus* and 127 specimens of *Cepaea sylvestrina gottschicki*. The richest material was collected at three sites (Text-fig. 1): Słabkowice (Slab), Suskrajowice (SUS-X), and Zwierzyniec (ZC), while in two other localities (Placówki near Młyny, and Andrzejówka) only single shell fragments were found. Unfortunately, most of the specimens were incomplete and strongly fragmented; only a few of them were either almost complete or the state of their preservation enabled the shell to be reconstructed by bonding the component fragments together with glue. Considerable differences in the preservation of the shell were noticed between the sites. At Słabkowice the shells were fragile and "chalky", whereas those from Suskrajowice were strongly abraded, and the shells from Zwierzyniec (or their fragments) were usually hard and glossy.

Fig. 2. *Cepaea sylvestrina gottschicki* Wenz, 1919, from the "detrital Sarmatian" of Poland. **1** – *C. sylvestrina gottschicki* in daylight to show state of preservation and banding morphs: a – morph (123)(45), specimen ZC C11, Zwierzyniec; b – morph 00045, specimen SUS-X C14, Suskrajowice; c – morph 00340, specimen SUS-X C10, Suskrajowice; d – morph 02345, specimen Slab C7, Słabkowice; e – morph (123)45, specimen SUS-X C5, Suskrajowice. **2** – Same specimens in UV-light, the arrow indicates the yellowish fluorescence on the whole inner surface of the body whorl. **3** – *C. sylvestrina gottschicki*, morph 00300, specimen Slab C2: a – in daylight, b – in UV-light, c – restoration of shell colour pattern, with presumed dark yellow background. **4** – *C. sylvestrina gottschicki*, morph 00305, specimen Slab C10: a – in daylight, b – in UV-light, c – restoration of shell colour pattern, with presumed dark pink background. **5** – *C. sylvestrina gottschicki*, morph 00345, specimen Slab C8: a – in daylight, b – in UV-light, c – restoration of shell colour pattern, with presumed pale yellow background. **6** – *C. sylvestrina gottschicki*, morph 00345, specimen Slab C1: a – in daylight, b – in UV-light, c – restoration of shell colour pattern, with presumed faint pink background and a dark aperture. **7** – Some representatives of extant species of *Cepaea*: a – *C. nemoralis*, morph 00300, dark pink; b – *C. nemoralis*, morph 003(45), dark yellow, c – *C. nemoralis*, morph 12345, pale yellow; d – *C. nemoralis*, morph (123)(45), faint pink; e – *C. hortensis*, morph 12345, yellow. All specimens × 1.25

The main method of restoration of the original colour and banding was macroscopic observation of the shells in daylight. This method was usually sufficient, but in uncertain cases these studies were followed by exposing the shells to UV-light, to enhance or even to discover their hidden colour and banding patterns. The source of UV-light was a standard Wood's mercury UVA lamp (EMITA VP-60).

EFFECTS

Observations in daylight showed no traces of the original coloration of the shell background in *Cepaea sylvestrina gottschicki* WENZ, 1919. The presence of bands depended strongly on the source of the shell (the collecting site) and the local diagenesis. Bands on the shells from Zwierzyniec and Słabkowice were



clearly visible while the bands on the specimens from Suskrajowice were hardly discernible (Text-figs 2.1-2.6). In most cases, it was only when exposed to UV-light that shells from Suskrajowice displayed their banding. In UV-light the bands usually showed a yellow to orange fluorescence, while the background of the shell showed blue to violet colours. Studies on *C. sylvestrina gottschicki* specimens with the complete banding pattern preserved (i.e. 82 of a total 127 specimens or fragments) enabled eight banding patterns to be distinguished (Text-figs 2.1-2.6), with up to five bands, sometimes fused, present. Among these patterns, there are "mid-banded" - 00300, "trifasciate" - 00345, and six varieties of "five-banded" - 00340, 00305, 00045, 02345, (123)45 and (123)(45), where "0" means the lack of band in that position and brackets symbolize the fusion of bands, according to the scheme proposed by CAIN & SHEPPARD (1950). It was also observed that yellowish fluorescence was noticeable not only in the bands but also in the aperture area. The yellow colour was visible on the lip, callus and columella, and also on the whole inner surface of the body whorl (arrowed in Text-fig. 2.2b, see also Text-figs 2.3b, 2.4b, and 2.5b).

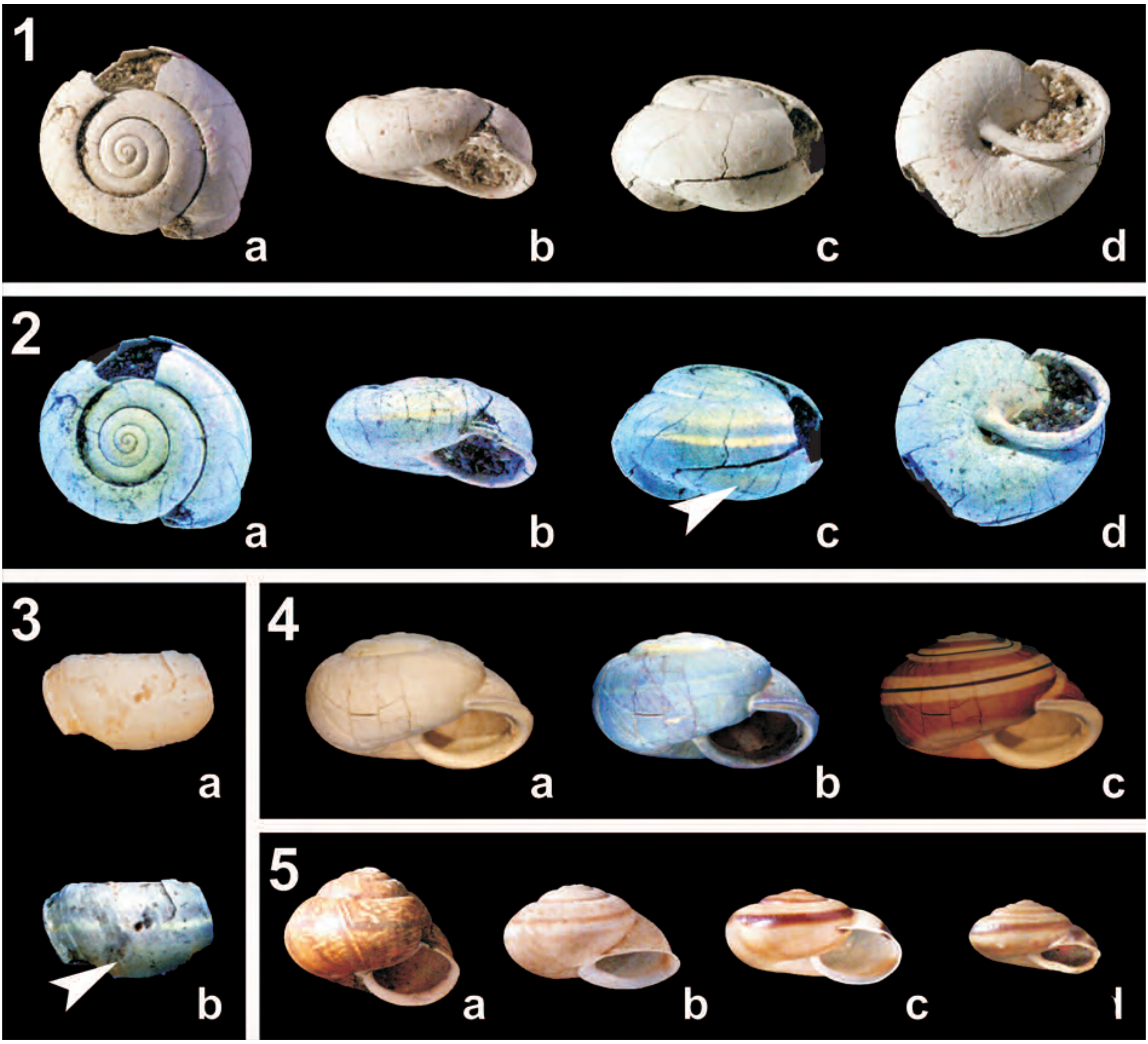


Fig. 3. *Tropidomphalus incrassatus* (KLEIN, 1853) from the "detrital Sarmatian" of Poland. **1** – *T. incrassatus* in daylight, specimen Slab H13: a – top view; b – front view; c – view of the last whorl; d – bottom view. **2** – Same specimen in UV-light, the lower diffuse band is arrowed. **3** – *T. incrassatus*, specimen ZC H4: a – in daylight; b – in UV-light, the lower diffuse band is arrowed. **4** – *T. incrassatus*, specimen ZC H1: a – in daylight; b – in UV-light, note the weak fluorescence of the specimen; c – restoration of shell colour pattern. **5** – Some representatives of extant Campylaeinae species: a – *Arianta arbustorum* (LINNAEUS, 1758), Poland; b – *Helicigona sp*., Croatia; c – *Chilostoma faustinum* (ROSSMÄSSLER, 1835), Poland; d – *Chilostoma squamatinum* (ROSSMÄSSLER, 1835), France. All specimens × 1.25

In *Tropidomphalus incrassatus* (KLEIN, 1853), observations of the shells in daylight, irrespective of the collecting site, showed no traces of coloration or banding (Text-figs 3.1a-d, 3.3a and 3.4a). This changed dramatically when some of the shells were exposed to UV-light, revealing the presence of differentiated bands, with a distinct main band, located on the periphery of the whorl, at some 3/5 of its height. Two additional bands were also observed, located above and below the main (peripheral) band (Text-figs 3.2c and 3.3b). The additional bands were indistinct (diffuse), so they could be easily regarded as darkened zones of the shell rather than normal bands. It is noteworthy that the presence of the lower additional band was not mentioned by previous authors (see e.g. SANDBERGER 1870-1875). As in *Cepaea sylvestrina gottschicki*, similar fluorescence (in this case faint pink) of the aperture area was also observed in *Tropidomphalus incrassatus* (Text-fig. 3.2b, d).

CONCLUSIONS

The presence of up to five (sometimes fused) bands was observed in *Cepaea sylvestrina gottschicki* WENZ, 1919; these banding patterns are astonishingly similar to those in two extant species, *Cepaea nemoralis* (LINNAEUS, 1758) and *Cepaea hortensis* (O.F. MÜLLER, 1774), which are highly polymorphic (see e.g. CAIN & SHEPPARD 1950, JONES & *al*. 1977). It is also noteworthy that the presence of 00300, 00340, 00305 and 00045 banding morphs had never been recorded previously in *C. sylvestrina gottschicki*. According to SANDBERGER's description (SANDBERGER 1870-1875), the banding of this subspecies (referred to as *Helix sylvestrina* V. ZIETEN, 1830) comprises no less than three, and up to five bands. A lower number of bands (morph 00040) has hitherto been observed only in the subspecies *C. sylvestrina suevica* GROISS, 1968 (see GROISS 1968, fig. 2.3a-c).

The percentage distribution of *C. sylvestrina gottschicki* morphs shows a predominance of "trifasciate" (i.e. 00345) specimens, irrespective of the site. There is also a similarity in the percentage composition of the morphs at two of the sites: Suskrajowice and Słabkowice, while at Zwierzyniec the lack of "mid-banded" (i.e. 00300) morphs is conspicuous (see Text-fig. 4).

While the fluorescence of the bands is undoubtedly caused by remnants of the original dark pigment, it is still unclear what causes the fluorescence of the whole aperture area. In *C. nemoralis*, the only living *Cepaea* species with a dark aperture (see Text-fig. 2.7a-d), and closely related to *C. sylvestrina gottschicki*, the dark pigment is situated only in the lip and callus, not inside the body whorl (except for traces of bands visible through the semi-transparent shell; see Text-fig. 2.7b-d). In *C. sylvestrina gottschicki*, the yellowish colour is visible over the whole inner surface of the body whorl (arrowed in Text-fig. 2.2b, see also Text-figs 2.3b, 2.4b, and 2.5b), which may suggest that the fluorescence here is due to the presence of the inner (nacreous/lamellar) layer of the shell, not the dark pigment. The general appearance of the aperture of *C. sylvestrina gottschicki* should then resemble that of the extant species *C. hortensis* (see Text-figs 2.3-2.5 and 2.7e)

However, it is still possible that the fluorescence of the inner layer strongly obscures the original dark pigmentation of the aperture, which could then resemble that of *C. nemoralis*, as suggested in one of the author's restorations (see Text-fig. 2.6).

The original colour of the shell background, although impossible to recognize directly (see also COOK 1998), was most probably similar to that of *C. nemoralis*: ranging from pale yellow to dark pink or even brown (see e.g. CAIN & SHEPPARD 1950, JONES & *al*. 1977) (see Text-figs 2.3-2.6).

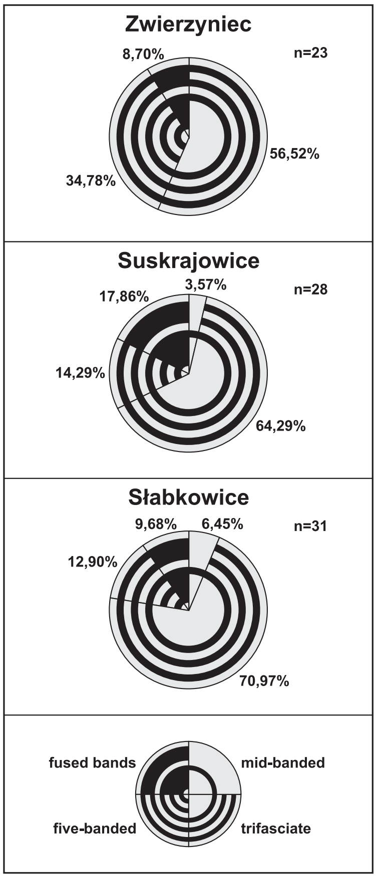


Fig. 4. Percentage distribution of banding morphs of *Cepaea sylvestrina gottschicki* WENZ, 1919, from the discussed sites of the "detrital Sarmatian" of Poland

The presence of the peripheral band observed in *Tropidomphalus incrassatus* is a feature widely known among the Campylaeinae (see Text-fig. 3.5). The occurrence of additional bands that was noticed during the present studies (see Text-figs 3.2c and 3.3b) is also quite common in that subfamily (see Text-figs 3.5b-d). The aperture area of *Tropidomphalus incrassatus*, despite the distinct fluorescence, was most probably white (see Text-fig. 3.4c), as in most of the relevant extant genera. The original colour of the shell was certainly similar to that in most of the extant Campylaeinae – ranging from white, through beige, to light brown (see Text-figs 3.4c and 3.5b-d).

Restoration of fossil shell colour pattern is not always possible to achieve due to the low preservation potential of the original pigment, and may not be useful in traditional palaeontological taxonomic work. Neverthless, it is still a very helpful tool in studies on fossil molluscs, particularly those of terrestrial habitat. When used in palaeoecological reconstructions, comparison of fossil shell colour patterns with those documented in the numerous studies on extant species (see e.g. CAIN & SHEPPARD 1950, JONES & *al*. 1977) may unveil such detailed environmental issues as: type of surface, humidity, temperature or insolation. A separate study devoted to environmental parameters is currently in preparation.

Acknowledgements

The most sincere thanks are offered to Dr. Ewa STWORZEWICZ (Institute of Systematics and Evolution of Animals PAS, Kraków, Poland) and Dr. Eugene V. KOZMINSKY (Zoological Institute RAS, St. Petersburg, Russia) for reviewing the manuscript and for their valuable critical comments and remarks on the taxonomy. A great appreciation is expressed to Dr. Krzysztof NEJBERT and Dr. Sławomir ILNICKI (both Institute of Geology, University of Warsaw, Poland) who kindly supported UVA lamps.

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Manuscript submitted: 10th January 2007
Revision version accepted: 20th December 2007