Vol. 13(4): 169–175

FOLIA MALACOLOGICA

ISSN 1506-7629

The Association of Polish Malacologists
& Faculty of Biology, Adam Mickiewicz University
Poznań 2005

EGG STRUCTURE OF SOME VERTIGINID SPECIES (GASTROPODA: PULMONATA: VERTIGINIDAE)

STANISŁAW MYZYK

Sąpolno 14, 77-320 Przechlewo, Poland

ABSTRACT: Eggs of species of the genus *Vertigo*: *angustior, antivertigo, moulinsiana, pusilla, pygmaea, ronnebyensis* and *substriata* are flattened-sphaerical (lenticular), gelatinous and nearly colourless. The eggs of *V. angustior, V. pygmaea* and *V. moulinsiana* have 3 envelopes: external, gelatinous and internal. In *V. angustior* the external envelope bears sparse granules while in *V. moulinsiana* and *V. pygmaea* it is smooth. The eggs of *V. antivertigo, V. pusilla, V. ronnebyensis* and *V. substriata* are additionally surrounded with a mucus cover of variable thickness and density. The mean egg size (diameter in mm) is: *pygmaea* – 0.54, *angustior* – 0.59, *pusilla* – 0.63, *substriata* – 0.64, *antivertigo* – 0.65, *ronnebyensis* – 0.70, *moulinsiana* – 0.74. The smallest egg (0.42 mm) was laid by *V. pygmaea*, the largest (0.87 mm) by *V. moulinsiana*. Eggs of *Truncatellina cylindrica* are spherical or slightly oval, with a strongly calcified external envelope, and are 0.52-0.58 mm in diameter. Eggs of *Columella edentula* are probably calcified, flattened-oval, 0.64-0.66 × 0.69-0.71 mm, with their external envelope rugose.

KEY WORDS: land snails, Vertiginidae, reproduction, eggs

INTRODUCTION

Snail shell characters are still among the most often employed in vertiginid classification. The structure of internal organs is known in relatively few species, and the additional difficulty is caused by simplification of the reproductive organs and small body size. Studies on the reproductive system (POKRYSZKO 1990a) have shown that in this respect congeneric species differ little, and the differences become clear only at the generic level.

Literature information on life cycles and reproduction of vertiginids is scanty (POKRYSZKO 2003). The best known species is *Vertigo pusilla* (POKRYSZKO 1990b); there exist fragmentary data on some other species (POKRYSZKO 1990a, CAMERON 2003, CAMERON et al. 2003, KILLEEN 2003). General descriptions of eggs in *Vertigo* have been given by POKRYSZKO (1990a, b) and CAMERON et al. (2003); there is no information on structural details and possible interspecific differences. The egg structure may provide new characters for phylogenetic inferences, since it is associated with both structure and function of the reproductive system.

My studies included ten vertiginid species of two subfamilies: Vertigininae (genus *Vertigo*) and Truncatellininae (genera *Truncatellina* and *Columella*).

MATERIAL AND METHODS

In order to obtain eggs, the following species were kept in the laboratory in 2004–2005: *Vertigo angustior* Jeffreys, 1830, *V. antivertigo* (Draparnaud, 1801), *V. moulinsiana* (Dupuy, 1849), *V. pusilla* O. F. Müller, 1774, *V. pygmaea* (Draparnaud, 1801), *V. ronnebyensis* (Westerlund, 1871), *V. substriata* (Jeffreys, 1833), *Truncatellina cylindrica* (Férussac, 1807), *Columella edentula* (Draparnaud, 1805) and *C. aspera* Waldén, 1966. Adult or subadult individuals were collected near Sąpolno (NW. Poland – for the exact location see MYZYK 2004), and identified based on the monograph of POKRYSZKO (1990a). Maintly rotting leaves

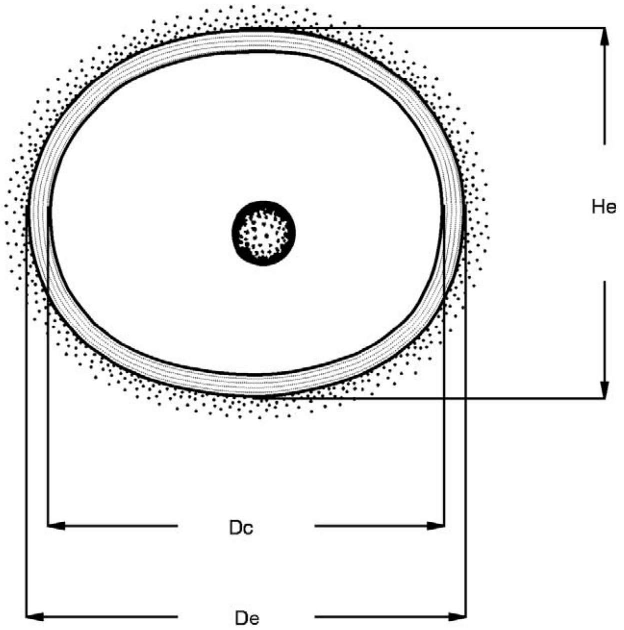


Fig. 1. Measurements: Dc – egg chamber diameter, De – egg diameter, He – egg height

of trees (*Populus tremula* L., *Quercus* sp., *Betula pendula* Roth, less often other species), collected in the places where the vertiginids occurred, were used as food. To prevent accidental transport of eggs, only leaves that could be examined thoroughly and cleaned were selected. The leaves in the containers were exchanged every few weeks, while the relative humidity was constantly high.

Since detailed checking of all the contents of containers was very time-consuming, the eggs were usually "harvested" every three to four days (rarely daily). The total number of examined eggs was ca. 3,200 eggs of *Vertigo*, 14 of *Truncatellina cylindrica* and 2 of *Columella edentula*.

The eggs were measured in the way presented in Fig. 1. When measuring diameter (De) and height (He) the mucus coating, which is present on eggs of some species, was disregarded. The eggs were measured in a large drop of water. Dry eggs very quickly shrank, while in a small drop of water the size appeared to be magnified. The thickness of envelopes was calculated as a half of the difference between the egg diameter and the chamber diameter: (De–Dc)/2. The measurements were taken with calibrated eyepiece (magnification 150 ×), to the nearest 0.01 mm. It was observed that the egg (even in water) acted as a convergent lens as a result of which the visible chamber diameter was magnified by probably 3–5%. Consequently, the chamber sizes are slightly biased towards higher values, and the envelope thickness – towards lower values.

All the figures are original.

RESULTS

GENUS *VERTIGO*

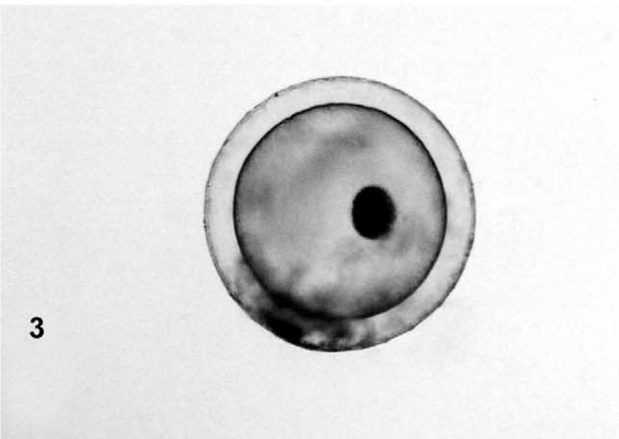
The eggs of members of the genus *Vertigo* were gelatinous, translucent and nearly colourless. Their size compared to the parent's shell was large (Figs 2–3), which confirms POKRYSZKO's data (1990a, b). They were slightly flattened (lens-like) and in top view most often regularly circular in outline (Fig. 3). Their flatness index (He/De ratio) was within 0.80–0.90 (most often ca. 0.85). Some snails (of various species), besides typical eggs, sometimes laid elongated or kidney-shaped eggs (Fig. 4); they constituted ca. 3.6% of all eggs laid.

The largest eggs were laid by *V. moulinsiana* (mean diameter 0.737 mm, range 0.55–0.87 mm), the smallest by *V. pygmaea* (mean diameter 0.540 mm, range 0.42–0.60 mm). The remaining species produced eggs of intermediate size. The intraspecific ranges of egg size were rather wide and partly overlapping. Table 1 presents measurements of eggs of typical

Table 1. Eggs size in *Vertigo*

Species	Number of measured eggs	Diameter of eggs in mm				Diameter of egg chamber in mm			
		mean	SD	minimum	maximum	mean	SD	minimum	maximum
angustior	721	0.591	0.024	0.48	0.66	0.514	0.022	0.40	0.57
pygmaea	211	0.540	0.025	0.42	0.60	0.491	0.025	0.38	0.55
moulinsiana	507	0.737	0.041	0.55	0.87	0.623	0.042	0.43	0.73
antivertigo	674	0.648	0.034	0.55	0.78	0.559	0.029	0.47	0.64
pusilla	337	0.629	0.027	0.52	0.70	0.559	0.027	0.44	0.62
ronnebyensis	237	0.699	0.024	0.58	0.78	0.622	0.025	0.49	0.70
substriata	394	0.637	0.027	0.56	0.72	0.564	0.026	0.50	0.64

structure (lenticular), Figs 5–6 – variation in egg diameter. Elongated eggs (oval, kidney-shaped) were sometimes up to 0.92 mm long (e.g. in *V. ronnebyensis*). The size of the egg cross-section (Fig. 1 – De and He) was often very close to the aperture size. All the studied species have toothed apertures; the flattening of the eggs and the absence of calcified envelopes make it possible for the eggs to get out of the shell.



Figs 2–3. *V. moulinsiana*, light microscope, 50 ×; 2 – shell; 3 – egg, top view

The eggs of *Vertigo* were covered by three (*angustior, pygmaea, moulinsiana*) or four envelopes (*antivertigo, pusilla, ronnebyensis, substriata*). The egg structure is presented diagrammatically in Fig. 7. Immediately after oviposition, the zygote, 0.10–0.16 mm in diameter, occupied a central or a slightly eccentric position. Some snails laid eggs in which the zygote was located on the margin of the egg chamber. The egg chamber was surrounded by a very thin, parchment-like internal envelope of a light brown or grey colour. Soon after oviposition, its surface often bore delicate folds. According to POKRYSZKO (1990b) the eggs do not change their size during development. According to my observations, in the last stage of embryonic development (snail with a shell visible) the egg measurements increased slightly. For example, in *V. moulinsiana* the egg diameter increased on an average by 1.8% (sporadically even by 7%), that of the egg chamber by 2.7% (sporadically even by 8%).

The gelatinous envelope filled the space between the internal and the external envelope (Figs 7, 8–11). In undamaged eggs its multilayered structure was nearly always visible (Figs 8–9). In most eggs the borders of the layers were arranged spirally, but in some, in one or more points on the periphery of the layer there were discontinuities and the layers were doubled. When broken (e.g. after hatching), the gelatinous envelope revealed an even more complicated structure (Fig. 12). The thickness of this envelope was usually the same on all the periphery. Among typical eggs (lenticular), eggs with their gelatinous envelope of uneven thickness (chamber displaced sideways, concave in one or two places) were rare. In atypical eggs (kidney-shaped) the envelope thickness was very often smaller on the convex side, compared to the concave side (Fig. 4). Eggs of *V. moulinsiana* were usually surrounded by a thick envelope (0.021–0.083 mm, mean 0.057 mm) contrary to those of *V. pygmaea*

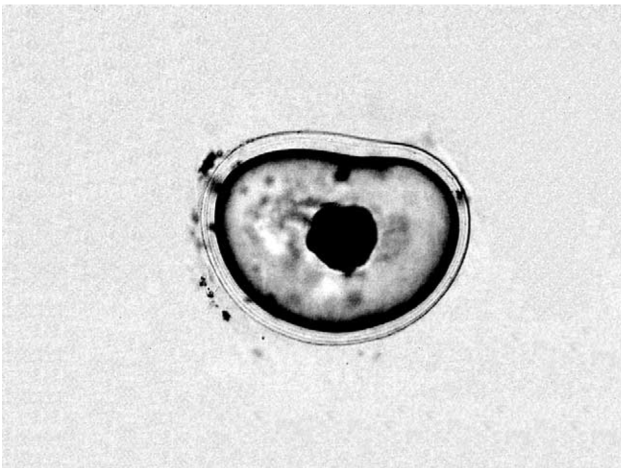
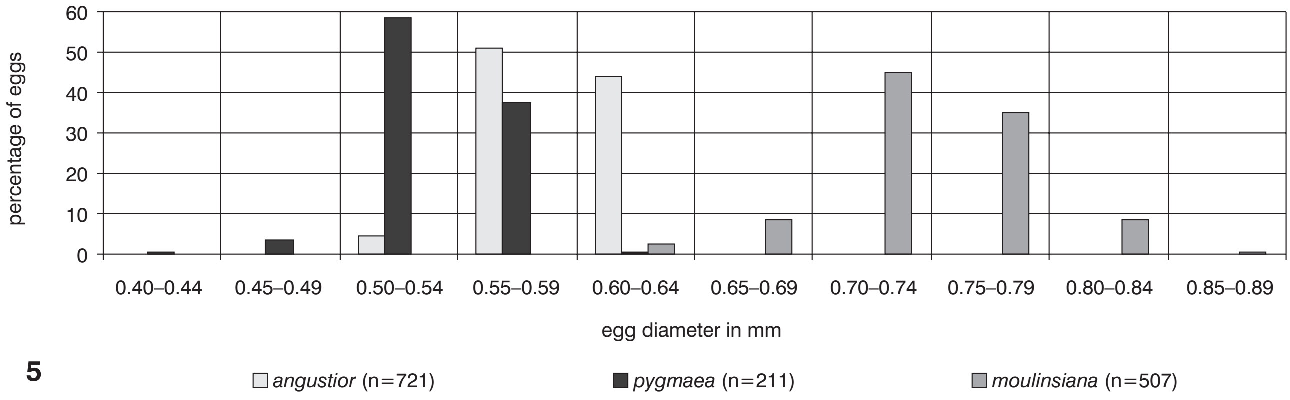
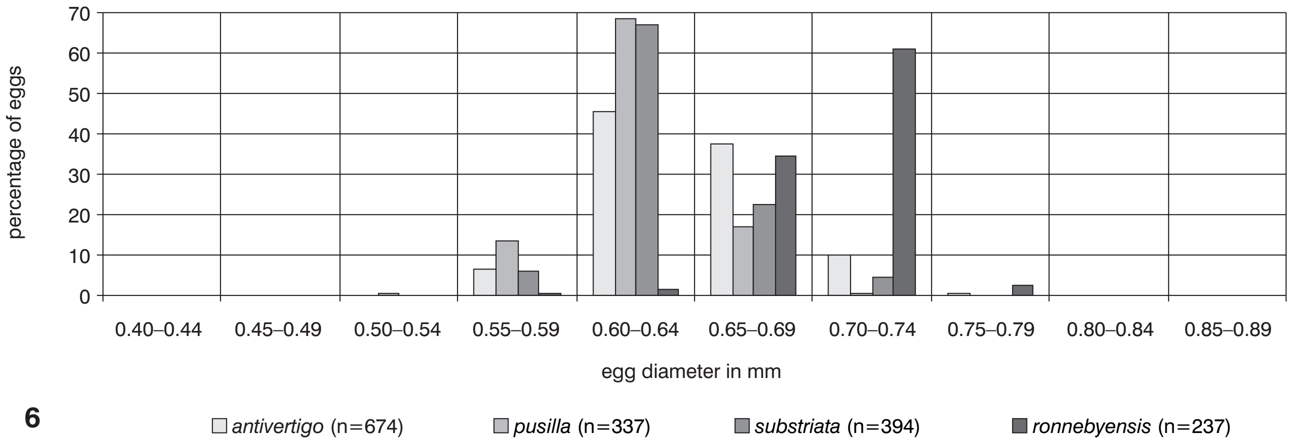


Fig. 4. Atypical, kidney-shaped egg of *V. substriata*, light microscope, 50 ×



5



6

Figs 5–6. Variation in egg diameter: 5 – eggs with three envelopes; 6 – eggs with three envelopes and mucus coating; mucus coating omitted during measurements

where it was relatively thin (0.010–0.036 mm, mean 0.025 mm). In the remaining species the envelopes

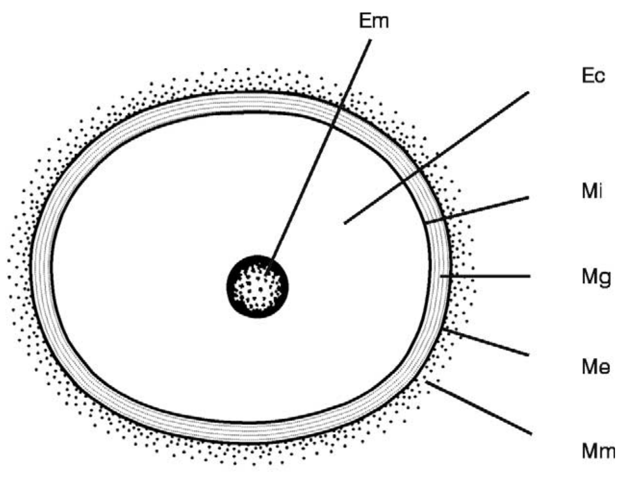
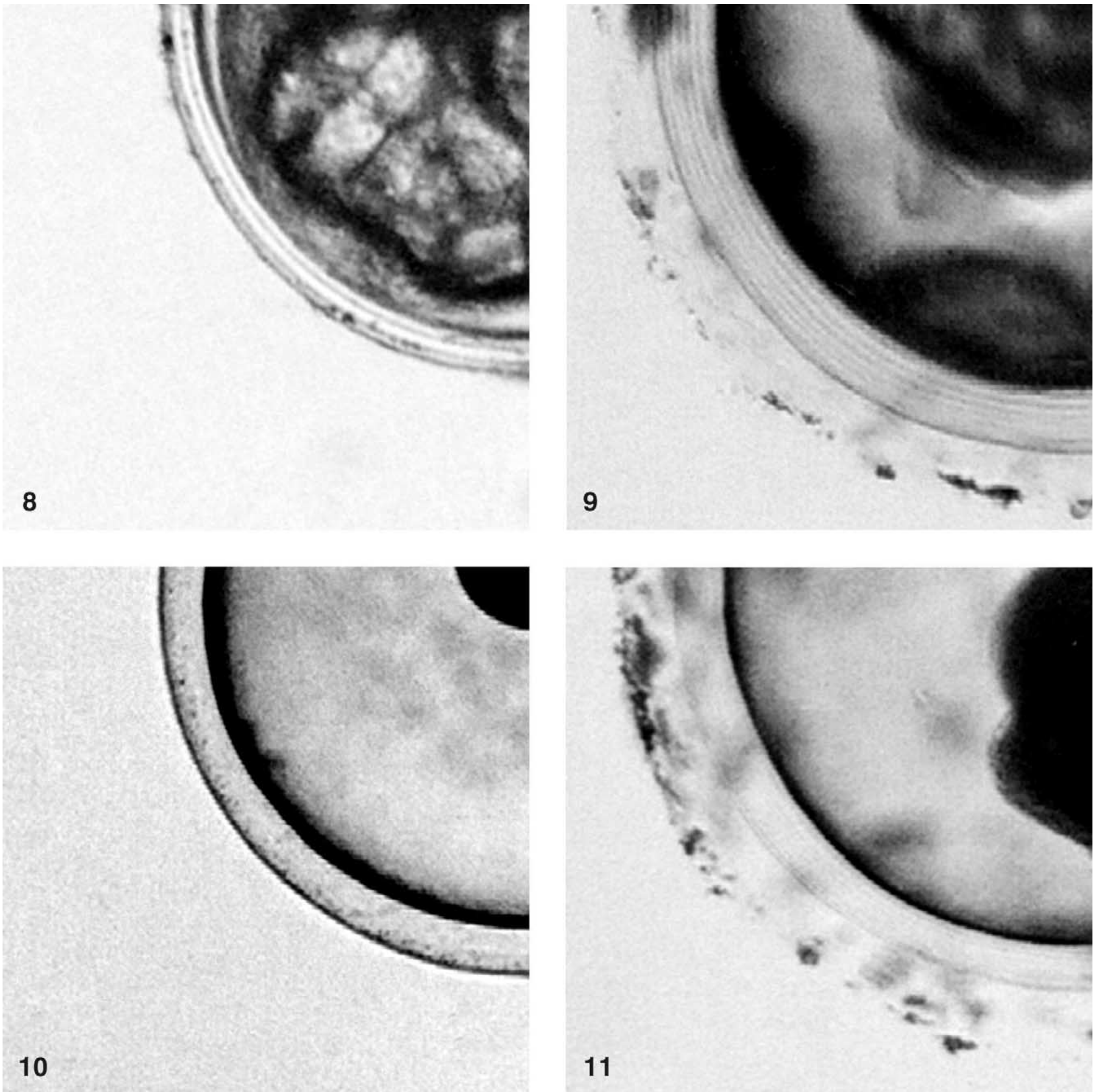


Fig. 7. *Vertigo* egg structure: Ec – egg chamber, Em – egg cell, Me – external envelope, Mg – gelatinous envelope, Mi – internal envelope, Mm – mucus coating

were of a similar mean thickness (0.035–0.044 mm) and a similar range of variation (0.021–0.073 mm). The envelope thickness and the number of visible layers showed a wide variation even between consecutive eggs produced by the same parent. In some eggs individual layers of the gelatinous envelope were of even thickness, in other eggs they became inresasingly thinner towards the outer margin of the envelope (rarely they became thicker). Only in *V. angustior*, on the side of the chamber, there was nearly always a zone with a thickness of ca. 30-65% envelope thickness, where the borders of the layers were invisible. Near the external envelope the layers had rather clear borders (2–6). Sporadically, the borders of the layers were visible on the whole thickness of the envelope (7–8 layers). In *V. moulinsiana* the number of the observed layers was the highest among all the examined species (8–20, sporadically fewer), and their borders were usually poorly marked. In *V. pygmaea* the number of layers was rather small (2–6, sporadically up to 8), whereas their borders were well visible (Fig. 8). The remaining species (*antivertigo*, *pusilla*, *ronnebyensis* and *substriata*) had a very variable number of layers in their gelatinous envelope, and the variation ranges were nearly the same. The mean thickness of the en-

Table 2. Egg envelopes in *Vertigo*

Species	Number of measured eggs	Gelatinous envelope			External envelope	Mucus coating
		Thickness in mm		Number of layers		
		mean	SD			
angustior	721	0.039	0.006	wide layer + 2–6 narrow	surface grained	absent
pygmaea	211	0.025	0.004	mostly 3–6	surface smooth	absent
moulinsiana	507	0.057	0.009	mostly 10–15	surface smooth	absent
antivertigo	674	0.044	0.007	mostly 5–9	rarely absent	generally present
pusilla	337	0.035	0.006	mostly 6–9	rarely absent	generally present
ronnebyensis	237	0.039	0.005	mostly 3–6	rarely absent	generally present
substriata	394	0.037	0.005	mostly 3–9	rarely absent	generally present



Figs 8–11. Comparison of egg envelopes, light microscope, 200 ×; 8 – *V. pygmaea*; 9 – *V. antivertigo*; 10 – *V. angustior*; 11 – *V. ronnebyensis*

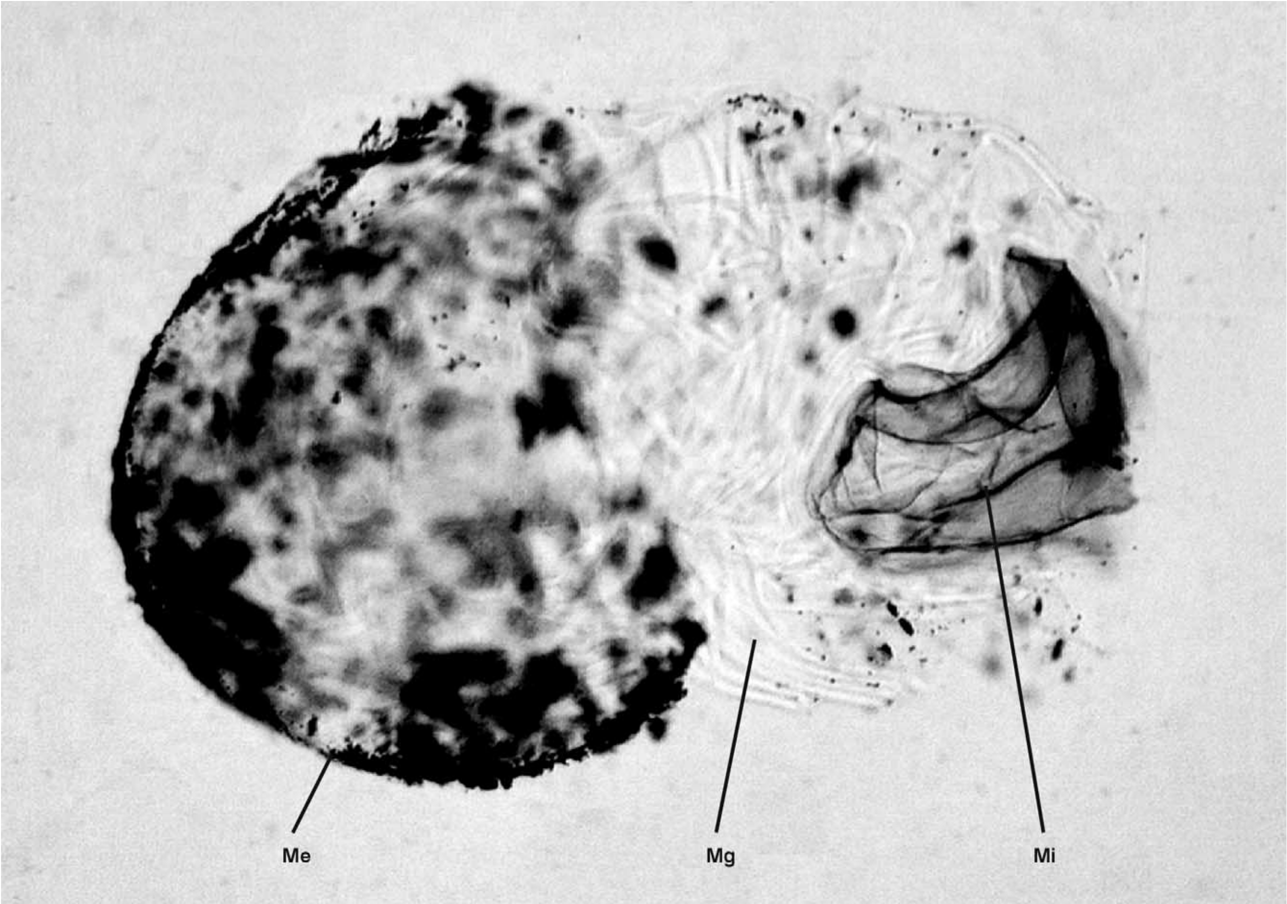


Fig. 12. *V. moulinsiana*, egg envelopes after hatching: Me – external envelope, Mg – gelatinous envelope, Mi – internal envelope; light microscope, 100 ×

velope and the most often encountered numbers of layers are presented in Table 2.

A thin and colourless external egg envelope was always present in *V. angustior*, *pygmaea* and *moulinsiana*. In *V. pygmaea* and *moulinsiana* its surface was nearly smooth. In *V. angustior* small granules or nodules (diameter ca. 0.002 mm) were scattered on its external surface. They remained on the envelope even after the completion of embryonic development and hatching. In *V. antivertigo*, *pusilla*, *ronnebyensis* and *substriata* the external envelope had a variable thickness or even was absent (the outermost layer of the gelatinous envelope adjoined the mucus coating).

The mucus coating was present only in *V. antivertigo*, *pusilla*, *ronnebyensis* and *substriata*. In some eggs it was dense, with clearly marked external border and delicate, irregular striae parallel to the external envelope. In other eggs it was rather liquid, and its presence was only noticeable thanks to contaminations sticking to it (Figs 9, 11). Its thickness was usually 0.03–0.06 mm, though in some eggs it was as thick as 0.10 mm. In atypical eggs (e.g. kidney-shaped) its thickness was often uneven, the greatest on the convex side. Some eggs of the mentioned four species seemed to be devoid of the mucus coating, or it was very thin, almost invisible. In a few cases it could be confirmed that it had been rubbed off when removing the eggs from the leaf (the coating remained on the leaf).

GENUS *TRUNCATELLINA*

Eggs laid by *Truncatellina cylindrica* had a strongly calcified external envelope and immediately after deposition were opaque, milky white. The eggs were roughly spherical or slightly oval. The spherical eggs were 0.52–0.58 mm in diameter, the measurements of the oval eggs were 0.50 × 0.55 to 0.54 × 0.59 mm. The external envelope was rather thick and, because of the calcium carbonate crystals, its surface was rough. The rate of disappearance of the crystals was associated with the stage of the embryonic development (rather fast at the veliger stage). When the embryo was dead or died at an early stage, the crystals disappeared also but much slower. After the disappearance of the crystals, the egg surface remained uneven, with densely arranged pits and convexities (resembling goose flesh). The gelatinous layer was 0.015–0.030 mm thick, and the borders of its layers were usually poorly marked or invisible.

GENUS *COLUMELLA*

Attempts at breeding *Columella* proved unsuccessful. No eggs were found in containers with *Columella aspera*, and in those with *C. edentula* only two eggs were found, containing fairly advanced embryos (shells of 1.2 and 1.25 whorls). The eggs were flattened and in top view oval in outline. Their size was 0.69 × 0.64 mm and 0.71× 0.66 mm. Their external envelope bore nodules and concavities, arranged in characteristic patterns (initially probably calcified). The gelatinous envelope was 0.07–0.08 mm thick, and its multilayered structure was poorly visible through the external envelope.

DISCUSSION

Uncalcified eggs of *Vertigo* differ clearly from the calcified eggs of *Truncatellina cylindrica* (and the probably calcified eggs of *Columella edentula*), which is in agreement with the commonly accepted division of the family into subfamilies Vertigininae and Truncatellininae.

The genus *Vertigo* was originally divided into several subgenera (for names and references see e.g. SHILEYKO 1984, POKRYSZKO & STWORZEWICZ 2001) which later, based on cladistic interpretation of conchological characters (POKRYSZKO 1990a, POKRYSZKO & STWORZEWICZ 2001) were reduced to two: *Vertilla* (5 species, including *V. angustior*) and *Vertigo* s. str. (the remaining extant and fossil species).

The eggs of the studied seven members of *Vertigo* show three, or even four, types of structure.

1. The eggs of *V. angustior* are covered by three envelopes (Fig. 10), of which the outermost is covered by fine granules (nodules?) which are absent in the remaining species, while the gelatinous envelope almost always has a fairly characteristic structure. Combined with conchological characters, it confirms the separate status of the subgenus *Vertilla*.
2. *V. pusilla* is the type species of *Vertigo* s. str. A similar egg structure is observed in *V. antivertigo*, *ronnebyensis* and *substriata*. In all these species the eggs are mucus-coated (Figs 9, 11); the mucus coating is absent in *V. angustior*, but also in *moulinsiana* and *V. pygmaea*.
3. The eggs of *V. moulinsiana* and *pygmaea* have three envelopes, like those of *V. angustior*, but their surface is always smooth. Despite the general similarity the eggs of these species differ in many details, e.g. size, thickness and structure of the gelatinous envelope (Figs 3, 8).

The differences in the egg structure between the three groups of species may indicate that the existing subgeneric classification may not entirely reflect phylogenetic relationships.

ACKNOWLEDGEMENTS

I am grateful to Prof. dr hab. BEATA M. POKRYSZKO for providing me with papers on the vertiginids and for translating the text into English.

REFERENCES

CAMERON R. A. D. 2003. Life-cycles, molluscan and botanical associations of *Vertigo angustior* and *Vertigo geyeri* (Gastropoda, Pulmonata: Vertiginidae). Heldia 5: 95–110.

CAMERON R. A. D., COLVILLE B., FALKNER G., HOLYOAK G. A., HORNUNG E., KILLEEN I. J., MOORKENS E. A., POKRYSZKO B. M., PROSCHWITZ T. VON, TATTERSFIELD P., VALOVIRTA I. 2003. Species accounts for snails of the genus *Vertigo* listed in Annex II of the Habitats Directive: *V. angustior*, *V. genesii*, *V. geyeri* and *V. moulinsiana*. Heldia 5: 151–172.

KILLEEN I. J. 2003. A review of EUHSD *Vertigo* species in England and Scotland (Gastropoda, Pulmonata: Vertiginidae). Heldia 5: 73–84.

MYZYK S. 2004. A new locality of two rare vertiginid species (Gastropoda: Pulmonata: Vertiginidae) in NW Poland. Folia Malacol. 12: 57–61.

POKRYSZKO B. M. 1990a. The Vertiginidae of Poland (Gastropoda: Pulmonata: Pupilloidea) – a systematic monograph. Ann. Zool. 43: 133–257.

POKRYSZKO B. M. 1990b. Life story and population dynamics of *Vertigo pusilla* O. F. Müller,1774 (Gastropoda: Pulmonata: Vertiginidae), with some notes on shell and genital variability. Ann. Zool. 43: 407–432.

POKRYSZKO B. M. 2003. *Vertigo* of continental Europe – autecology, threats and conservation status (Gastropoda, Pulmonata: Vertiginidae). Heldia 5: 13–25.

POKRYSZKO B. M., STWORZEWICZ E. 2001. On the subgeneric classification of *Vertigo* O. F. Müller, 1774 (Gastropoda: Pulmonata: Vertiginidae). Folia Malacol. 9: 27–35.

SHILEYKO A. A. 1984. Nazemnye mollyuski podotryada Pupillina fauny SSSR (Gastropoda, Pulmonata, Geophila). Fauna SSSR, Mollyuski 3, 3. Nauka, Leningrad.

Received: September 5th, 2005
Accepted: November 15th, 2005