



REPRODUCTIVE BIOLOGY AND GROWTH OF TWO VALLONIA SPECIES IN LABORATORY CONDITIONS (GASTROPODA: EUPULMONATA: VALLONIIDAE)

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ABSTRACT: Reproduction and growth of *Vallonia pulchella* (O. F. Müller) and *V. costata* (O. F. Müller) were studied in laboratory conditions. Their ellipsoid and singly laid eggs are among the smallest heavily calcified (mean size 0.68×0.67×0.52 and 0.69×0.67×0.54 mm in *V. pulchella* and *V. costata*, respectively). *V. pulchella* reached morphological maturity (lip completion) at 3.25–3.50 whorls (mean 3.35), 49 to 166 days after hatching (85). The first egg (sexual maturity) was laid at 3.25–3.50 whorls (3.35), 50–283 days after hatching (162). The life span ranged from 628 to 940 days (779), the time elapsing between the last egg and death was 12–184 days (111). In *V. costata* the lip was completed at 3.25–3.50 whorls (3.37), 42 to 183 days after hatching (120). The first egg was laid at 3.25–3.50 whorls (3.42), 131–290 days after hatching (193). The life span ranged from 360 to 841 days (709) and the time elapsing between the last egg and death was 11–692 days (210). The egg production rate and juvenile life span in individuals kept in isolation were the same as in those kept in pairs or larger groups. The growth pattern was similar in the two species: fast phase followed by slow phase. However, the formation of ribs on the shell surface of *V. costata* probably slowed down its growth rate. The life history traits shared by the two *Vallonia* species are determined growth, iteroparity, longevity and predominantly selfing reproductive mode. The greater lifetime fecundity, shorter incubation period, faster growth and longer life span predestine *V. pulchella* to be a better coloniser than *V. costata*.

KEY WORDS: land snails, reproduction, self-fertilisation, longevity, lifetime fecundity, growth rate

INTRODUCTION

Vallonia pulchella (O. F. Müller, 1774) and *V. costata* (O. F. Müller, 1774) are small land snails with the shell diameter not exceeding 3 mm. They are Holarctic species, widely distributed in Europe and America (GERBER 1996), introduced in South Africa (HERBERT 2010) and Israel (ROLL et al. 2009). *V. pulchella* has also been recorded in Madagascar (GERBER 1996), the Mascarene Islands (GRIFFITHS & FLORENS 2006), India (MITRA et al. 2005), China (GERBER 1996) and Australia (STANISIC 1998), whereas *V. costata* has been found in Japan (SASAKI 2008); its occurrence in Australia requires confirmation (STANISIC 1998).

They are ground-dwelling snails, rarely climbing more than a few centimetres above the soil surface. They occur in a wide variety of habitats (GERBER 1996) but become rare in the highlands (KERNEY 1999). They usually inhabit open places where they often co-occur, although *V. pulchella* prefers grassy, base-rich, humid places like meadows on floodplains, moist pastures, marshes, and dune slacks, while *V. costata* is typical of short-turfed swards, natural cliffs and scree, disused quarries and old walls (KERNEY 1999). *V. costata* can also be found in humid, close-canopy forests (HORSÁK et al. 2010), and often



selects calcium-rich sites compared to *V. pulchella*. Both species can occur abundantly in synanthropic habitats (KOSIŃSKA 1979).

The only data on the biology of *Vallonia* are WHITNEY'S (1938) observations on the reproductive cycle of *V. pulchella*, fragmentary data on the bionom-

ics of *V. pulchella* and *V. costata* (GASSIES 1849, STERKI 1893, FRÖMMING 1954), and an unpublished thesis by ISKRZYŃSKA (1986). The aim of this paper was to compare the life histories of the two closely related species, based on laboratory observations.

MATERIAL AND METHODS

The initial material for the laboratory culture (10 adults of each species) was collected on the 2nd October 2010 in the ruins of the castle Grodztwo (50°47'26.9"N, 16°02'09.6"E, 440 m a.s.l.) in Kamienna Góra (Central Sudetes, SW. Poland). Thirty five of the hatched individuals of each species constituted the original laboratory population. The laboratory observations lasted till the 30th of March 2014. The individuals of each species were distributed as follows: 15 single, 4 pairs and 3 groups of 4 snails each.

The snails were kept in Petri dishes and in containers of a size depending on the number of inhabitants (dishes of 5–10 cm diameter, and plastic containers of 6×7.5×5 cm and 12×7.5×5 cm), on humid tissue paper with litter brought from the habitat. The dishes were checked and cleaned at least once a week and during periods of intense observations (e.g. reproductive period) – every day or two. Eggs and newly hatched snails were removed to separate dishes. The snails were kept in a climatic chamber at constant conditions of temperature (day 22°C, night 18°C)

and relative humidity (80%), with a 12 : 12 h light regime (fluorescent lighting). They were fed lettuce and sometimes carrots. Water and food were supplied as needed. Dolomite tablets constituted the source of calcium.

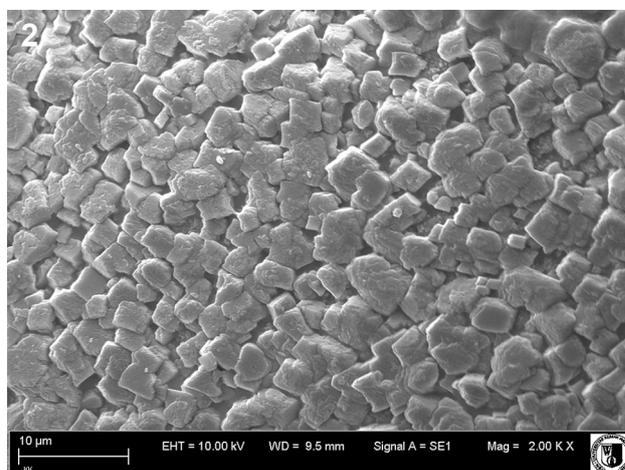
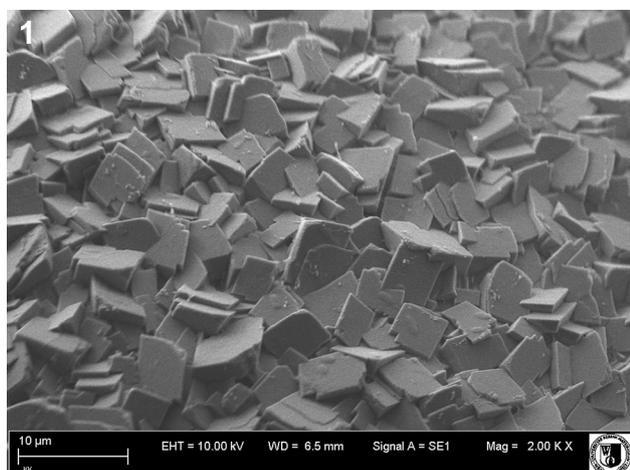
Laboratory observations included lifetime fecundity, egg-laying, egg morphometrics, incubation, hatching, growth rate, maturity and life span. Growth was assessed by counting whorls every 30 days using EHRMANN'S (1933) method. The maximum of reproduction (fecundity) was assessed by counting the total number of eggs produced by selected individuals of each species during their lifetime. Hatching success was estimated based on the hatching percentage. Two-way variance analysis (ANOVA) was applied to detect significant differences in the reproductive parameters between individuals kept singly and in pairs/groups as well as between the species.

To perform scanning electron microscope observations, the shells and egg shells of each species were gold-coated and SEM photos were taken using the microscope EVO LS 15, Zeiss.

RESULTS

In the laboratory both *V. costata* and *V. pulchella* laid eggs singly, under or between layers of damp tissue paper, on the bottom of the container, under litter and lettuce leaves. Newly laid eggs were milky-

white, ellipsoid and rather uniform in size (Table 1). The egg surface consisted of a continuous heavily calcified layer, which developed as geometric forms (Figs 1–2). The size of calcite crystals on the external



Figs 1–2. Scanning electron micrograph (SEM) of egg shells: 1 – *V. costata*, 2 – *V. pulchella*


 Table 1. Comparison of life cycle parameters between *V. costata* and *V. pulchella*

Life cycle parameter	<i>V. costata</i>			<i>V. pulchella</i>			P	
	Range	Mean	SD	n	Range	Mean		SD
Egg measurements (in mm)	0.62–0.75 × 0.58–0.75 × 0.44–0.67	0.69 × 0.67 × 0.54	0.04 × 0.04 × 0.03	87	0.58–0.75 × 0.58–0.75 × 0.44–0.62	0.68 × 0.67 × 0.52	0.05 × 0.05 × 0.04	50
No. of eggs during lifetime	6–47	19.72	10.97	25	17–60	37.71	11.77	28
Time to hatching (days)	10–35	17.76	4.28	62	10–21	13.51	3.21	37
Hatching success (%)	56.29				57.73			
Days from hatching to egg laying	131–290	192.56	57.65	25	50–283	162.48	81.96	29
Days from lip completion to egg laying	0–32	20.32	11.089	25	0–93	34.56	27.579	25
Days from hatching to lip formation	42–183	120.09	39.2	32	49–166	84.59	33.27	32
Days between first and last egg	17–506	265	191.58	25	358–780	523	139.74	28
Days between last egg and death	11–692	209.96	183.66	23	12–184	111.17	62.48	18
Newly hatched (no. of whorls)	1–1.75	1.49	0.17	30	1.4–1.75	1.59	0.11	31
Lip completion (no. of whorls)	3.25–3.5	3.37	0.08	30	3.25–3.5	3.35	0.08	21
First egg-laying (no. of whorls)	3.25–3.5	3.42	0.08	30	3.25–3.5	3.35	0.08	21
Life span (days)	360–841	709.31	182.94	16	628–940	778.83	97.63	18

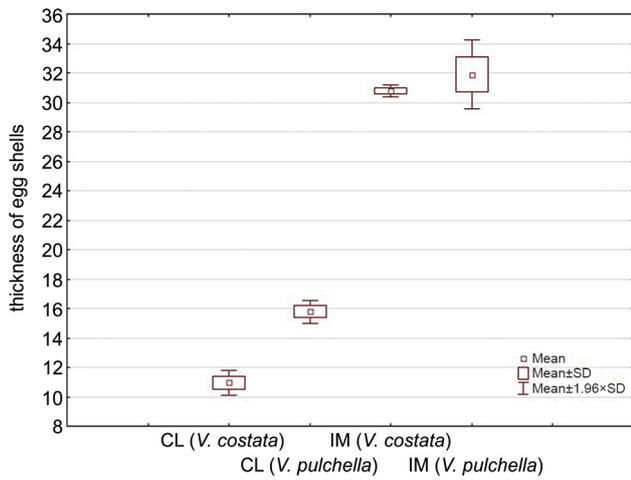


Fig. 3. Variation of calcified layer (CL) and internal egg membrane (IM) in *V. pulchella* and *V. costata*

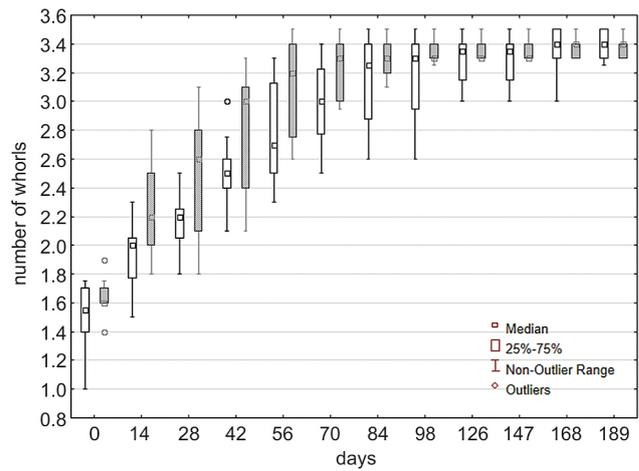
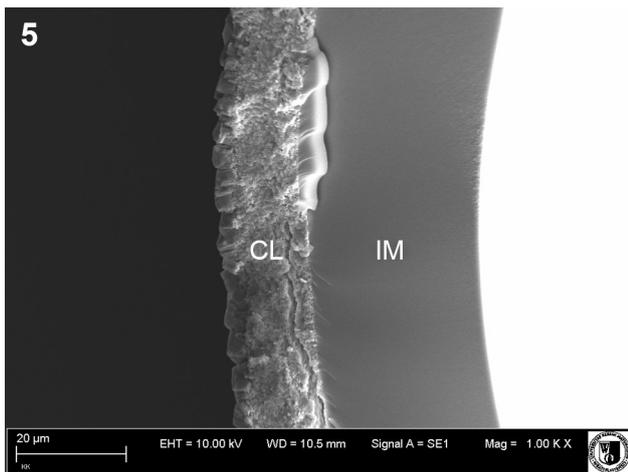
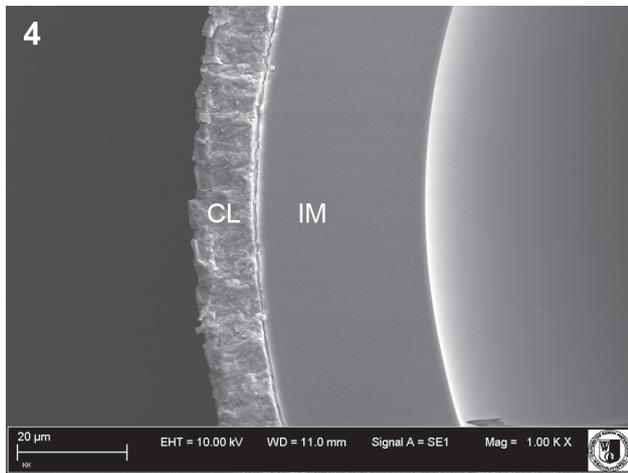


Fig. 6. Growth of 11 randomly selected individuals of *V. costata* (white) and *V. pulchella* (patterned)



Figs 4–5. Cross-sections through fractured eggs: calcified shell layer (CL), internal egg membrane (IM): 4 – *V. costata*, 5 – *V. pulchella*

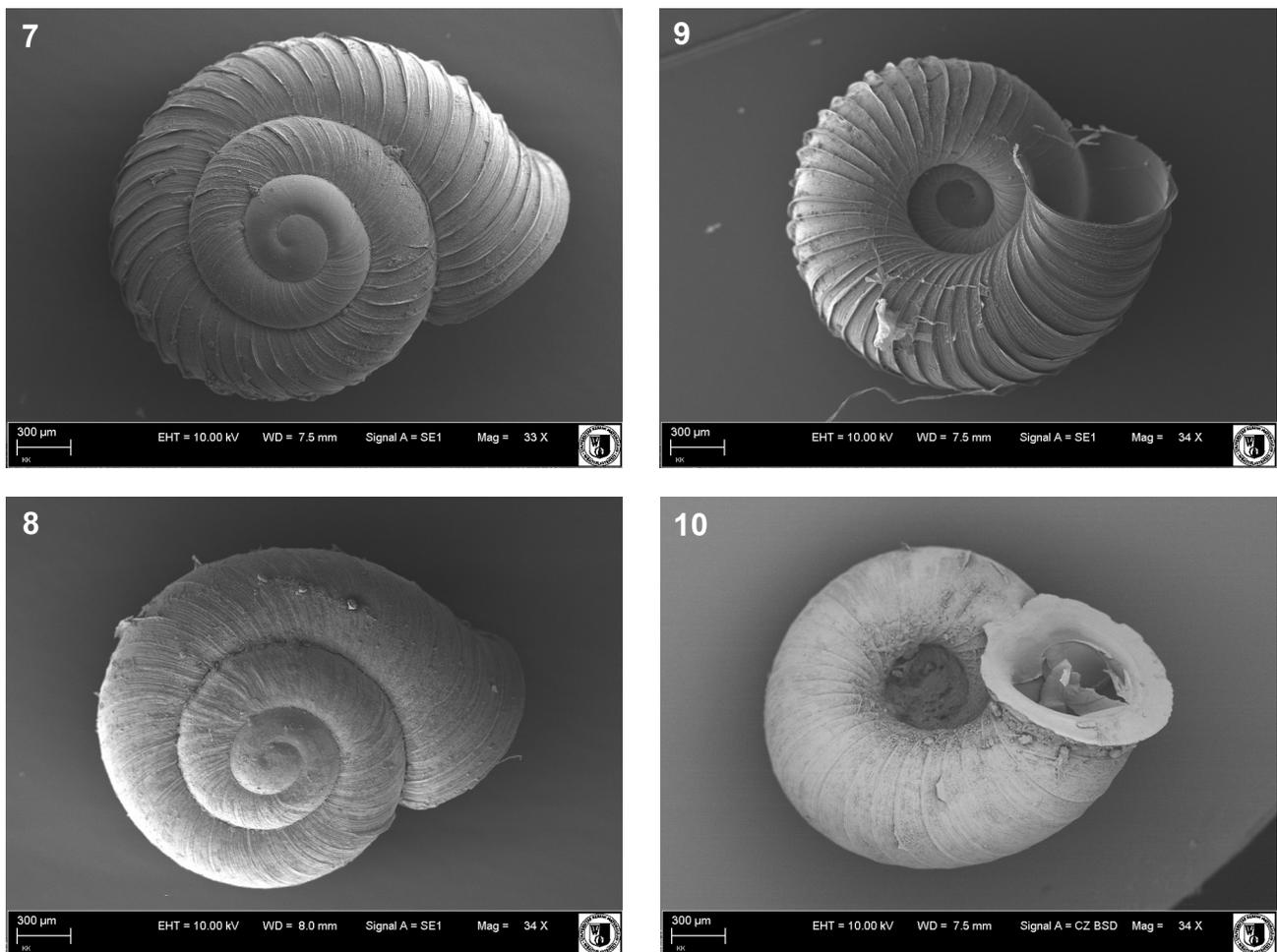
egg surface in *V. costata* ranged from 3.621 to 5.096 μm (mean = 4.198, SD = 0.432, n = 18), whereas in *V. pulchella* it varied more widely between 1.118 and 5.070 μm (mean = 2.765, SD = 1.349, n = 18). The differences were not statistically significant ($p = 0.823$). The differences in thickness of the egg shells and cross-sections through fractured eggs in *V. pulchella* and *V. costata* are shown in Figs 3–5.

There were no statistically significant differences ($p > 0.05$) in any of the studied reproduction parameters between individuals kept in isolation and those living in pairs or groups. Therefore, the results were pooled; the comparison of all the life cycle parameters between *V. costata* and *V. pulchella* is shown in Table 1.

The growth pattern in *V. costata* and *V. pulchella* was similar (Fig. 6). Two phases could be distinguished: I – fast phase in snails from 1.0 to 3.0 whorls, II – slow phase in snails above 3.0 whorls. Considerable differences were observed in the growth rate in the first phase: the mean growth rate in *V. pulchella* was faster than in *V. costata*, which showed a greater individual variation during both phases.

In *V. costata* during the fast phase formation of one whorl took 28–113 days (mean = 56.9, SD = 28.7, n = 11), while in *V. pulchella* the corresponding time was 23–53 days (mean = 38.4, SD = 11.8, n = 11). During the slow phase, *V. costata* and *V. pulchella* formed one whorl within 28–440 days (mean = 161.3, SD = 131.4, n = 11) and 28–280 days (mean = 116.0, SD = 78.6, n = 11), respectively.

The shell of *V. costata* bears regular, widely spaced, coarse ribs on both the upper and lower surfaces. During the life span of ca. 2 years (maximum 841 days, Table 1) the ribs are easily weathered, making old shells difficult to identify; the ribs are usually better preserved inside the umbilicus (Figs 7–10).



Figs 7–10. Shells of *V. costata*: 7 – apical view of fresh shell, 8 – apical view of old shell, 9 – umbilical view of fresh shell, 10 – umbilical view of old shell

DISCUSSION

All available data on the life history of *V. costata* and *V. pulchella* are summarised in Table 2. Where the same features have been studied, there is a broad measure of agreement among the studies; this study adds precision and more features.

Life strategy data are known in only 2% of all terrestrial gastropods (HELLER 2001) and for European land-snail species the proportion is ca. 6% (MALTZ 2003). Our comparative study adds to the knowledge of life histories of two closely related species of *Vallonia*. Both represent iteroparous mode of reproduction, i.e. animals reproduce during one season and then live on to reproduce again (HELLER 2001). Among land snails this kind of reproduction is common in clausiliids (MALTZ & SULIKOWSKA-DROZD 2008) and in some helicids (HELLER 2001). In molluscs iteroparous species are long-lived (HELLER 2001) and it has been also noted that short life spans are more frequent among very minute gastropods than among large ones (HELLER 1990). Both *Vallonia* species, as well as *Lauria cylindracea* (HELLER et al.

1997), are clearly exceptions to this pattern as these minute snails live longer than two years.

Uniparental reproduction is regular in *Vallonia* and was observed through several consecutive generations in this and previous studies (WHITNEY 1938, ISKRZYŃSKA 1986). Self-fertilisation was proposed as the mode of reproduction since in aphyllid individuals gametes of both sexes were simultaneously found in individual acini of hermaphroditic gland in *V. pulchella* (WHITNEY 1941). In a closely related *Acathinula aculeata* self-fertilisation was also suggested (BOYCOTT 1917, STEENBERG 1918). Our laboratory-bred *Vallonia* were aphyllid and reproduced by self-fertilisation, since we did not observe copulating snails, and egg production and juvenile life span in individuals reared in isolation were the same as in those kept in pairs or larger groups. Aphyllism is extremely common in *Vallonia* and was observed in all examined individuals of *V. pulchella* and *V. peteri* (WATSON 1920, WHITNEY 1941, AKRAMOWSKI 1976, SCHILEYKO 1984, ISKRZYŃSKA 1986), while male cop-

Table 2. Life history traits of *Vallonia* species

	<i>V. costata</i>	<i>V. pulchella</i>
	Mean egg size [mm]	
This study	0.69 × 0.67 × 0.54	0.68 × 0.67 × 0.52
ISKRZYŃSKA 1986	0.65 × 0.5	0.68 × 0.53
GUGLER 1963		0.7 × 0.9
FRÖMMING 1954	0.7–0.8	0.7–0.8
WHITNEY 1938		> 0.5
	Number of eggs during lifetime (mean)	
This study	6–47 (19.72)	17–60 (37.71)
WHITNEY 1938		30–69 (app. 59 during 3 months)
	Time to hatching [days] (mean)	
This study	10–35 (17.76)	10–21 (13.51)
ISKRZYŃSKA 1986	13–26 (20.3)	14–25 (17.6)
WHITNEY 1938		ca. 12
	Hatching success [%]	
This study	56.29	57.73
ISKRZYŃSKA 1986	83.89	74.04
	Time from hatching to lip formation [days] (mean)	
This study	42–183 (120.09)	49–166 (84.59)
ISKRZYŃSKA 1986	123–210 (162.9)	75–155 (119.7)
WHITNEY 1938		app. 59
	Time from lip completion to oviposition [days] (mean)	
This study	0–32 (20.32)	0–93 (34.56)
ISKRZYŃSKA 1986	6–52 (7.8)	0–21 (10.8)
WHITNEY 1938		4–8
	Life span [days] (mean)	
This study	360–841 (709.31)	628–940 (778.83)
ISKRZYŃSKA 1986	more than 2 years	more than 2 years

ulatory organs were recorded in the vast minority of *V. excentrica* and *V. costata* (STEENBERG 1918, WATSON 1920, GITTENBERGER 1977, SCHILEYKO 1984, BARKER 1985, GIUSTI & MANGANELLI 1986). The small number of euphallic individuals coupled with the ability to self-fertilise indicate that this mode of reproduction is predominant in both *Vallonia* species, also in the wild.

Stylommatophoran eggs show different degrees of calcification: heavily calcified, partly calcified and uncalcified (TOMPA 1976). The heavily calcified egg is sometimes viewed as an ancestral character in this group and is thought to be a terrestrial adaptation (TOMPA 1976). However, the function of the calcified shell is still debateable. Some of the smallest eggs are calcified and others are not, while it appears that the larger ones are all heavily calcified which may have to do with providing the half-liquid egg contents with mechanical support once a certain size is exceeded (TOMPA 1976). Various theories also suggest prevention of desiccation, protection from predators and physiological buffering (MAZZINI et al. 1984). In land snails the smallest hard-shelled eggs known so far belong to *Truncatellina cylindrica* (Vertiginidae) (0.52–0.58 mm, MYZYK 2005) and to *Vallonia* (Vallonidae) (not exceeding 0.9 mm, Table

2). The diameter of most calcified eggs varies from 1 mm in *Discus rotundatus* (Endodontidae) to 51 mm in *Megalobulimus popelairianus* (Acavidae) (STANDEN 1917, KUŹNIK-KOWALSKA 1999). Though the eggs of both *Vallonia* species do not differ in size, their surface structure is slightly different (Figs 1, 2), with minor differences in the size of calcite crystals (Fig. 3). TOMPA (1976) did not notice differences between the two *Vallonia* species, but found egg shell ultrastructure to be species-specific in some other closely related species.

It is commonly believed that the fecundity of minute terrestrial gastropods is limited by the fact of producing only few eggs at any one time (HELLER 2001). This, for example, is true of species which lay eggs singly: *Carychium tridentatum*, *Punctum pygmaeum* and *Vertigo* spp. (MORTON 1954, BAUR 1989, BULMAN 1990, POKRYSZKO 1990, MYZYK 2011). In these species the mean number of eggs produced per individual lifetime is small and ranges from five or six (*C. tridentatum* and *P. pygmaeum*) to 25 (*Vertigo moulinsiana*). In *V. pulchella* it is higher, with the mean number of 38 eggs. On the other hand, *D. ruderratus*, having shell diameter twice as large as *Vallonia*, lays approximately 12 eggs in 2–5 batches per lifetime (KUŹNIK-KOWALSKA 2006). Therefore, the relative



egg size, the number of eggs per batch and during lifetime depend not only on the size (HELLER 1990) but also on the longevity of adult snails. In *Vallonia* the life span is relatively long, of ca. 2 years (maximum 940 days in *V. pulchella*), while in other species it ranges from 170 days (*P. pygmaeum*) to 580 days (*D. ruderratus*). In contrast, *L. cylindracea*, a minute, litter-dwelling snail, whose life span is even longer (4–5 years in the wild), does not follow this pattern since its average number of hatchlings per adult is five to six (HELLER et al. 1997).

It is, however, known that snails with long periods of egg retention tend to produce fewer eggs per lifetime than do oviparous snails of similar size (BAUR 1989). For example, brooding clausiliids usually produce fewer offspring per reproductive event than their oviparous cousins (SULIKOWSKA-DROZD & MALTZ 2013). The same may be true of minute species with different reproductive strategies: among all known ovoviviparous or egg-retaining species the number of offspring is small and does not exceed 8 (*Pupilla muscorum*, POKRYSZKO 2001) but usually is 5–6 (*Punctum pygmaeum* or *L. cylindracea*, BAUR 1989, HELLER et al. 1997, respectively) or 3–7 (*Pyramidula pusilla*, GERMAIN 1930). In strictly oviparous species living in different habitats this number is higher, of up to ca. 38 eggs in *V. pulchella*, 20 in *V. costata*, 25 in *Vertigo moulinsiana* and 15 in *V. pusilla* (POKRYSZKO 1990, MYZYK 2011).

In the laboratory the time to hatching varied but agreed with that observed in the other studies (WHITNEY 1938, ISKRZYŃSKA 1986). Its duration depends on temperature (e.g. MYZYK 2011) or may be a consequence of a different duration of the egg retention period (SULIKOWSKA-DROZD & MALTZ 2013). In oviparous small-sized species incubation periods also vary widely (Table 2, BULMAN 1990, POKRYSZKO 1990, KUŹNIK-KOWALSKA 1999, 2006). This cannot be solely attributed to temperature differences, especially considering the constant laboratory conditions. The shells of newly hatched snails varied in the number of whorls, and their range was larger in *V. costata* than in *V. pulchella* (Table 1). Similarly as in the case of *P. bidentata* and *Discus* species (KUŹNIK-KOWALSKA 2006, KUŹNIK-KOWALSKA & ROKSELA 2009), some differences may be explained by the variation of the

non-ribbed, translucent, embryonic shell in *V. pulchella* versus hatchlings with a few ribs on definitive whorls in *V. costata* (ISKRZYŃSKA 1986).

The two species of *Vallonia* differ in their growth rate, but the growth pattern in both of them follows some general rules; the shape of growth curves is similar to other species with determined growth (MALTZ 2003, KUŹNIK-KOWALSKA & ROKSELA 2009, PROĆKÓW et al. 2013). However, the time to lip formation is longer in *V. costata* than in *V. pulchella* (Table 1). The development of regular and relatively large ribs on the shell surface of *V. costata* may explain the differences.

In several studies both *V. pulchella* and *V. costata* were regarded as pioneer species of anthropogenic sites which undergo secondary succession (BARGA-WIĘCŁAWSKA 1997, BAUCZ-MALIJ 2001, MALTZ 2009, 2011). Among terrestrial gastropods pioneer species may possess any of several life history strategies in various combinations (BENGTSSON & BAUR 1993). As seen in this study both species of *Vallonia* show very similar life cycle parameters (Table 1). Nevertheless, the higher lifetime fecundity, shorter incubation period, faster growth and longer, significantly different life span, predestine *V. pulchella* to be a better coloniser. This is recognisable in the distribution of the species. Although both have wide-temperate distributions in Holarctic, *V. pulchella* was additionally successfully introduced to Africa, Asia and Australia (GERBER 1996, STANISIC 1998, MITRA et al. 2005, GRIFFITHS & FLORENS 2006) and *V. costata* is known from South Africa and Japan (SASAKI 2008, HERBERT 2010). On the other hand, *V. costata* exhibits a wider ecological amplitude, i.e. it is usually more frequent at high altitudes in Switzerland, but in the north of the British Isles it is mainly found in coastal regions and only rarely in the highlands, but *V. pulchella* is slightly more tolerant against heat (WELTER-SCHULTES 2012).

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