

LIFE CYCLES OF CLAUSILIIDS OF POLAND – KNOWN AND UNKNOWN

TOMASZ K. MALTZ¹ and ANNA SULIKOWSKA-DROZD²

¹*Museum of Natural History, Wrocław University, Sienkiewicza 21,
50-335 Wrocław, Poland; e-mail: tomaltz@biol.uni.wroc.pl*

²*Department of Invertebrate Zoology and Hydrobiology, University of Łódź,
Banacha 12/16, 90-237 Łódź, Poland; e-mail: sulik@biol.uni.lodz.pl*

Abstract.— Among the 24 native clausiliids, 15 were subject to laboratory observations. Eleven of them were found to be oviparous, three – egg retainers and one – ovoviviparous. Batches, containing most often one to about a dozen of partly calcified, ellipsoidal or spherical eggs, appeared usually in the spring and autumn (in non-hibernating individuals throughout the year). Probably the main factors determining the onset of reproduction are humidity and temperature while the photoperiod has no significant effect. The incubation period is ca. two weeks (room temperature), the hatching is synchronous or asynchronous. Cases of intra-batch and inter-batch cannibalism were observed. The minimum time from hatching/birth till adult size is ca. 3–9 months and after further 5–8 months the snails start producing eggs/babies. Clausiliids are iteroparous. Anatomical studies on the development of the reproductive system show that just before lip completion the reproductive system is still incompletely developed. Penis, epiphallus and spermatheca develop within the first month after growth completion (which would indicate attainment of ability to copulate), and the reproductive system becomes wholly mature only after a few months. The clausiliid development strategy is probably the following: the quickest possible growth and attainment of adult size, then development of the reproductive system and attainment of sexual maturity.



Key words.— Terrestrial snails, Clausiliidae, life cycle, reproduction strategy, reproductive season, development, growth, maturity.

INTRODUCTION

Recent terrestrial malacofauna of Poland includes 174 species (Wiktor 2004) classified in 27 families. Besides the Helicidae (19% species) and the Zonitidae (11.5%), one of the numerous represented families are clausiliids with their 24 species (13.8%) assigned to nine genera in three subfamilies (Table 1) (Kerney *et al.* 1983, Riedel 1988, Wiktor 2004).

Zoogeographically, European clausiliids constitute the biggest group (54.2%), followed by Carpathian species (29.2%), while the Alpine component is represented by three (12.5%), and the boreo-montane component

by one species (4.1%) (Riedel 1988). A detailed classification is presented in Table 2. The European group includes widely distributed species found in the whole country (8 species), and some with regional ranges: *Clausilia bidentata* (lowlands of north-western Poland), *C. cruciata* and *C. parvula* (uplands and mountains) and *Balea perversa* (a few sites in the Sudetes and one in the Eastern Beskidy Mts). Alpine clausiliids: *Cochlodina costata*, *Charpentieria ornata* and *Macrogastra badia*, have only single sites in the Sudetes, whereas Carpathian species occur most of all in the south-eastern part of the country, though the range of some of them is not confined to the

Table 1. Systematic index of clausiliids of Poland (Riedel 1988, Wiktor 2004).

Family	Subfamily	Genus	Subgenus	Species
Clausiliidae	Alopiinae	<i>Cochlodina</i>	<i>Cochlodina</i>	<i>C. costata</i> (C. Pfeiffer, 1828) <i>C. laminata</i> (Montagu, 1803) <i>C. orthostoma</i> (Menke, 1828) <i>Ch. ornata</i> (Rossmässler, 1836)
		<i>Charpentieria</i>	<i>Paracochlodina</i> <i>Itala</i>	
	Clausiliinae	<i>Ruthenica</i> <i>Macrogastra</i> <i>Clausilia</i>		<i>R. filograna</i> (Rossmässler, 1836) <i>M. badia</i> (C. Pfeiffer, 1828) <i>M. latestriata</i> (A. Schmidt, 1857) <i>M. plicatula</i> (Draparnaud, 1801) <i>M. tumida</i> (Rossmässler, 1836) <i>M. ventricosa</i> (Draparnaud, 1801) <i>C. bidentata</i> (Ström, 1765) <i>C. cruciata</i> (Studer, 1820) <i>C. dubia</i> Draparnaud, 1805 <i>C. parvula</i> Férussac, 1807 <i>C. pumila</i> C. Pfeiffer, 1828
Baleinae	<i>Laciniaria</i> <i>Alinda</i> <i>Balea</i> <i>Vestia</i> <i>Bulgarica</i>	<i>Balea</i> <i>Pseudalinda</i> <i>Vestia</i> <i>Strigilecula</i>	<i>L. plicata</i> (Draparnaud, 1801) <i>A. biplicata</i> (Montagu, 1803) <i>B. perversa</i> (Linnaeus, 1758) <i>B. fallax</i> (Rossmässler, 1836) <i>B. stabilis</i> (L. Pfeiffer, 1847) <i>V. elata</i> (Rossmässler, 1836) <i>V. gulo</i> (E. A. Bielz, 1859) <i>V. turgida</i> (Rossmässler, 1836) <i>B. cana</i> (Held, 1836)	

Carpathians: *Macrogastra tumida* has a few localities in the Eastern Sudetes, and *M. latestriata* inhabits also the lowlands of north-eastern Poland. The region holds also two European species typical of upland and mountainous areas: *Cochlodina orthostoma* and *Clausilia dubia* (Riedel 1988, Wiktor 2004) (Fig. 1).

Most clausiliids (91.7%) live in natural forest habitats, some (among others *Laciniaria plicata*, *Alinda biplicata*) are found also in forest-like habitats (dense, shaded shrubs, neglected parks etc.). Only *Charpentieria ornata* and *Balea perversa* prefer more open habitats. With respect to humidity requirements only *Vestia gulo* is a typical hygrophile while the remaining ones live in mesic habitats with moderate humidity fluctuations during the vegetation season (mesophile species). *Cochlodina costata*, *Charpentieria ornata* and *Clausilia parvula* require a high calcium content in the substratum. The last two species and *Balea perversa* are petrophiles (Maltz and Pokryszko 2007) (Fig. 2).

Because of the largely man-induced environmental changes, and the resulting disappearance of natural

habitats, 13 clausiliids (54.2%) are regarded as threatened in Poland: seven are low risk species while six are endangered, of these as many as five critically (Wiktor and Riedel 2002) (Table 3).

Literature information on clausiliid life cycles is usually fragmentary and pertains only to 11 among the 24 species (Table 4). Complete data based on field observations exist only for *Vestia elata* (Piechocki 1982), the life cycle of *Balea perversa* has been partly studied (Baur 1990, Baur and Baur 1992). In the remaining cases the data pertain either to a selected aspect of clausiliid biology, e.g. copulation (Nordsieck 2005), or are fragmentary and/or problematic (Frömming 1954 – literature review, Likharev 1962, Hudec 1963, Tompa 1979a – literature review, Bulman 1996, Kuźnik-Kowalska 1998), and thus require verification.

The objective of this paper is to present and discuss laboratory-based data on 15 species of clausiliids, and pertaining, among other things, to the mode and period of reproduction (oviparity: time of egg-laying, number of eggs per batch, hatching, cannibalism; egg retention, and ovoviviparity; reproductive season in the laboratory), growth and maturation, which are crucial to

Table 2. Zoogeographic composition of clausiliids of Poland (Riedel 1988).

General division	Detailed division	Species
Boreo-Alpine	Boreo-Alpine	<i>Clausilia cruciata</i>
Alpine s. lato	E Alpine-Dinaric	<i>Cochlodina costata</i>
	E Alpine	<i>Charpentieria ornata</i> <i>Macrogaster badia</i>
Carpathian s. lato	Carpathian s. stricto	<i>Macrogaster latestriata</i> <i>Macrogaster tumida</i> <i>Balea stabilis</i> <i>Vestia gulo</i> <i>Vestia turgida</i>
		E Carpathian Carpathian-Balkan
European s. lato	European s. stricto	<i>Cochlodina laminata</i>
	E European	<i>Ruthenica filigrana</i>
	C European	<i>Macrogaster plicatula</i> <i>Macrogaster ventricosa</i>
		<i>Clausilia dubia</i> <i>Clausilia parvula</i> <i>Alinda biplicata</i>
	E and C European	<i>Clausilia pumila</i> <i>Laciniaria plicata</i>
	C and E European	<i>Cochlodina orthostoma</i>
	W European	<i>Balea perversa</i>
	N and NW European	<i>Clausilia bidentata</i>
E and SE European	<i>Bulgarica cana</i>	

protection of endangered species and at the same time make it possible to rectify problematic information presented in earlier publications.

MATERIAL AND METHODS

The studies were carried out in two institutions: Museum of Natural History, Wrocław University [1] and the Department of Invertebrate Zoology and Hydrobiology, University of Łódź [2]. Fifteen species observed in the laboratory were subject to the studies (Table 5).

Adults were kept in plastic containers of 300, 500, 700 and 1200 cm³ volume, single snails or pairs were kept in smaller containers, while other containers held groups of 5–10 individuals. Apart from the species which were introduced into the culture later (*C. orthostoma*, *C. pumila*, *C. dubia*), detailed observations involved five pairs of each *C. laminata* and *L. plicata* and 10–15 pairs of each of the remaining species.

Each tissue-lined box contained pieces of deciduous bark (*Alnus* sp., *Cerasus* sp., *Prunus* sp., *Acer* sp.,

Tilia sp., *Fagus* sp.), fragments of limestone and tufts of mosses (*Ceratodon* sp., *Atrichum* sp., *Funaria* sp., *Hypnum* sp., *Dicranum* sp., *Trichostomum* sp.). Calcium was provided in the form of writing chalk or dolomite tablets. The snails were fed leaves of lettuce, Pekingese lettuce, sometimes Italian or headed cabbage, pieces of carrot, cucumber and mushroom (champignon, chanterelle).

Humidity in the containers was practically constant and close to 100% as a result of regular spraying of the tissue, stones, bark and moss. The culture was checked every 2–3 days (when necessary daily), while total cleaning (exchange of tissue paper, container cleaning) took place twice a month. In Wrocław the culture containers were kept at room temperature (18–22°C) and natural light regime throughout the year; in Łódź the snails hibernated in a cool room: preparing for hibernation (half of October till half of November – 8–12°C), hibernation (half of November till the end of February – 3°C) and preparing for activity (March – 8–12°C). During that time the photoperiod was 8 hours light and 16 hours dark. From half of March till half of October the containers

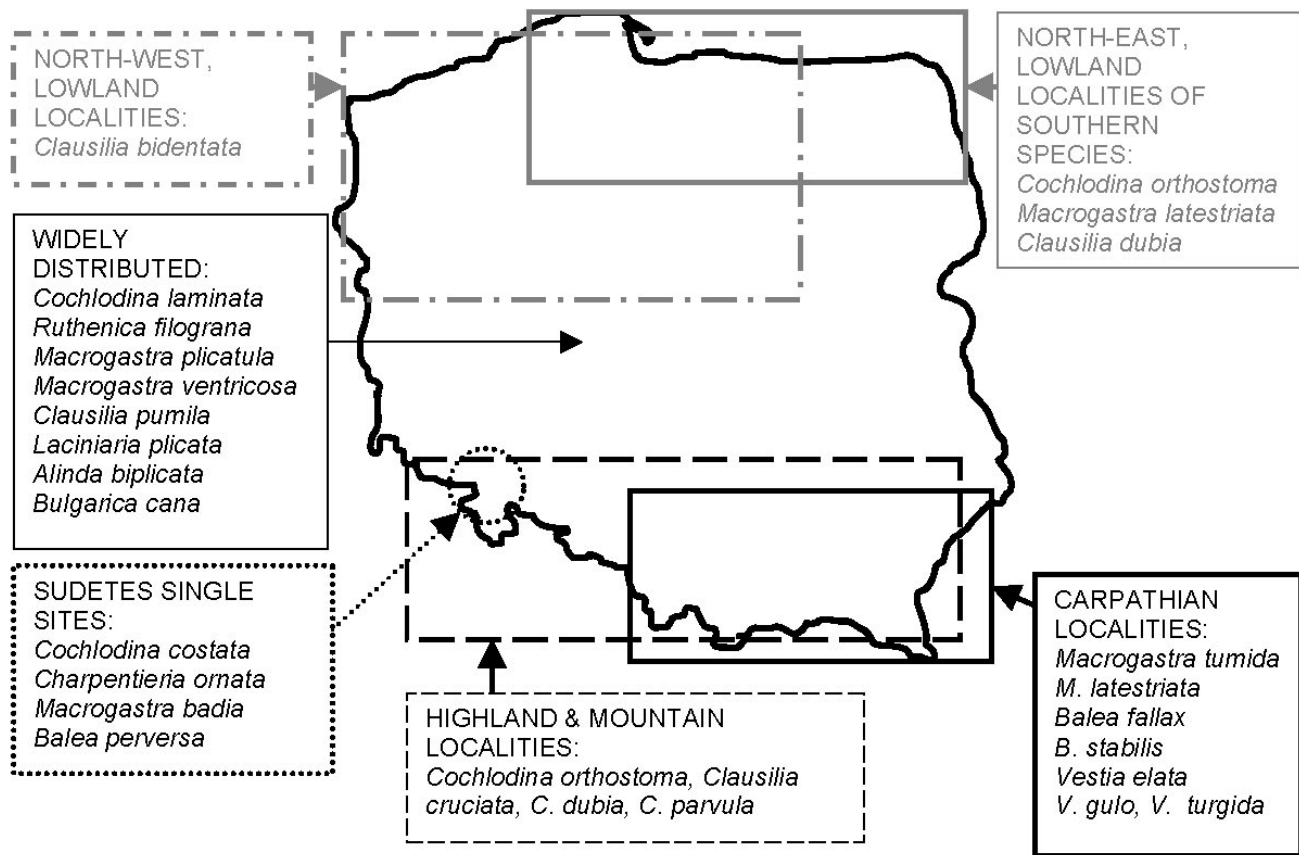


Figure 1. Clausiliid distribution in Poland.

were kept at room temperature and in natural lighting.

The aim of the laboratory observations was to ascertain the reproductive mode (oviparity/ovoviviparity), reproductive season and the effect of such factors as humidity, temperature and day length on the onset of reproduction. For oviparous species the studies included, among other things, type and size of eggs, their number per batch, preferred egg laying places, duration of incubation, hatching mode (synchronous/asynchronous), cannibalism. Because of this some of the batches were transferred to Petri dishes with humid tissue paper, some were left in containers with adults, with the egg-laying place marked. Egg major and minor diameter were measured with calibrated eye-piece in stereomicroscope Nikon SMZ-U to the nearest 0.05 mm. For ovoviviparous species the number of juveniles per litter and their shell size were determined.

Marking juveniles with nail varnish (individual marking, marking whorl increment at fortnight intervals) was used to estimate growth rate, the shortest time of attaining adult size and the quickest onset of reproduction.

The results were statistically analysed with Microsoft Excel 2000 (Nelson 1999).

In order to ascertain if attainment of ultimate shell size (completion of closing apparatus and lip, growth termination) is associated with full sexual maturity, the reproductive system was anatomically examined in adults after at least one year from lip formation; ontogenetic changes in the structure of the reproductive system were also traced. These studies included *C. laminata*, *M. ventricosa* and *A. biplicata*. Thirty adults of each species were examined: 10 one year old, 10 immediately after lip completion and 10 – 2–3 months after reaching ultimate size, and also 30 juveniles: 10 – just before body whorl formation and 10 during formation of closing apparatus and lip. The snails were preserved in 70% ethanol and dissected under stereomicroscope Nikon SMZ-U.

RESULTS

Reproductive modes

Three reproductive modes were represented among the 15 clausiliid species examined: 1) typical oviparity, 2) long egg retention and 3) typical ovoviviparity. Among the examined species, 11 (73%) (Table 6)

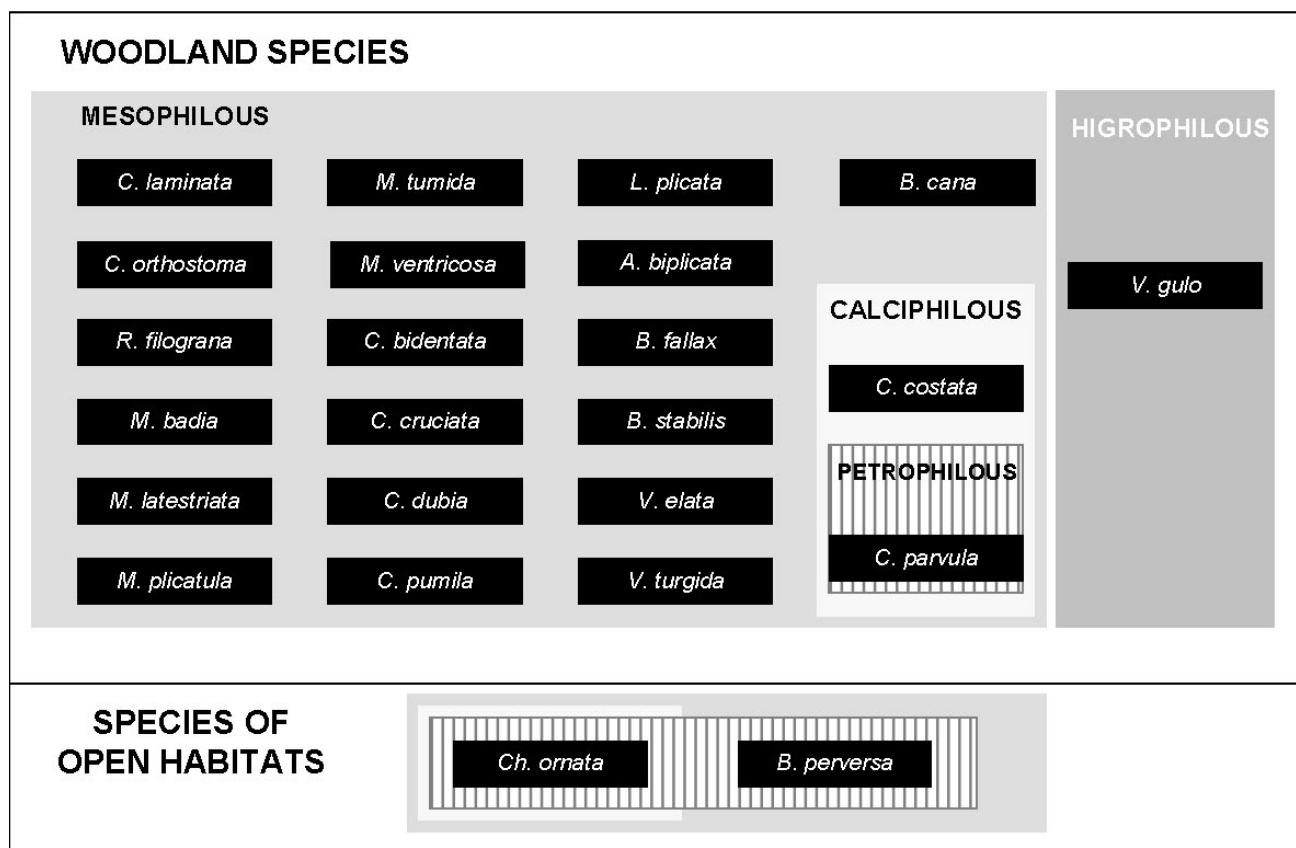


Figure 2. Ecological components.

represent the first group, three species of the genus *Vestia* (20%) – the second group and *A. biplicata* (7%) – the third group.

Eggs of the first group clausiliids are spherical or slightly elongate, partly calcified (clearly visible numerous calcium carbonate crystals, evenly distributed just below the surface) (Fig. 3). The average egg size is 1.5–1.7 × 1.4–1.6 mm, the length/width ratio being 1.14 (Table 7). Smaller eggs were found in *C. parvula* (mean size 1.19 × 1.03 mm), the largest eggs being those of *M. ventricosa* (mean 1.83 × 1.67 mm). The eggs are laid singly or in batches of two to a few or a few dozen (mean 6.54) (Table 8), in very humid places in tufts of moss, under bark and stones, sometimes in tissue paper. Some species were

observed to have very definite preferences regarding places of egg deposition (e.g. *Ch. ornata*, *M. latestriata* and *C. parvula* laid their eggs only in moss tufts, *C. laminata*, *M. tumida* and *B. stabilis* preferred bark) while other species showed no such preferences (e.g. *L. plicata*). In containers where snails were kept in pairs, when batches appeared more or less simultaneously, they were never deposited close to each other. The mean incubation time is 10–14 days (room temperature), but snails with the smallest eggs depart from the rule (*C. parvula*: 8–12 days). Hatching was usually synchronous, but in some species (*C. laminata*, *Ch. ornata*, *M. ventricosa*, *L. plicata*) in batches with many eggs it was asynchronous. In such situations intra-batch cannibalism occurred sometimes.

Table 3. Threatened species of Clausiliidae of Poland (Wiktor and Riedel 2002).

Threat Category	Species
Critically Endangered (CR)	<i>Cochlodina costata</i> , <i>Charpentieria ornata</i> , <i>Macrogastra badia</i> , <i>Balea perversa</i> , <i>Vestia elata</i>
Vulnerable (VU)	<i>Vestia turgida</i>
Near Threat (NT)	<i>Macrogastra latestriata</i> , <i>Macrogastra tumida</i> , <i>Clausilia cruciata</i> , <i>Clausilia parvula</i> , <i>Balea fallax</i> , <i>Balea stabilis</i> , <i>Vestia gulo</i>

Table 4. Life cycle knowledge of clausiliids of Poland.

Species	Field observations	Laboratory observations	Source
<i>Ruthenica filograna</i> , <i>Macrogastra plicatula</i> , <i>Macrogastra ventricosa</i> , <i>Clausilia bidentata</i> , <i>Clausilia dubia</i> , <i>Laciniaria plicata</i>	unknown	fragmentary	Frömring 1954, Likharev 1962, Tompa 1979a, Nordsieck 2005
<i>Cochlodina laminata</i> , <i>Alinda biplicata</i> , <i>Vestia turgida</i>	fragmentary	fragmentary	Frömring 1954, Likharev 1962, Tompa 1979a, Bulman 1996, Kuznik-Kowalska 1998, Nordsieck 2005
<i>Balea perversa</i>	partly known	partly known	Frömring 1954, Likharev 1962, Tompa 1979a, Baur 1990, Baur and Baur 1992
<i>Vestia elata</i>	known	fragmentary	Hudec 1963, Piechocki 1982

During such hatching earlier hatched juveniles, still within the batch, after consuming their own egg envelopes started biting other eggs' envelopes but were not interested in the contents (it seemed more like an accidental damage). When so damaged eggs contained sufficiently developed juveniles, the damage did not affect their further development; when the embryos were too small, the damage probably was the reason for their death.

Egg retainers are *V. gulo*, *V. elata* and *V. turgida*. Individuals of the first species laid typical clausiliid eggs (Fig. 3.B2), but their incubation period was shorter (7–10 days) than in oviparous species. Eggs of *V. elata* also had a typical structure (Fig. 3.5), but they always contained advanced embryos and the incubation period did not exceed four days. In the third case, when any eggs were laid, they had an unusual form: much elongated (mean 2.1×1.44 mm; length/width 1.46), flattened, jelly-like, glued together with mucus

(Fig. 4). Their incubation period was very short, of ca. two days (Table 8).

Relative egg size: ratio of mean egg length (a) to mean shell height (b) (Fig. 5) was determined for all egg-laying species. The following snail groups were distinguished: first to 12 mm mean shell height ($a/b \sim 0.15$), second from 12 to 15 mm ($a/b \sim 0.13$) and third above 15 mm ($a/b \sim 0.11$). Small snails (e.g. *C. parvula*) lay relatively the largest eggs, while large snails (e.g. *M. ventricosa*) produce relatively smaller eggs.

A positive correlation was found between the absolute egg size and the adult size. For all clausiliids laying eggs in the laboratory the Pearson coefficient (r for $p < 0.05$) was 0.49, and discounting the species with long egg retention – $r = 0.62$. For relative egg size a significant negative correlation was observed – $r = 0.74$. There was also a significant positive correlation between the mean number of eggs per batch and the mean snail size ($r = 0.83$), and a weaker

Table 5. List of species kept in laboratory, with dates of beginning of observations. 1) Museum of Natural History, Wrocław University, 2) Department of Invertebrate Zoology and Hydrobiology, University of Łódź.

Wrocław [1]		Łódź [2]	
Species	Culture	Species	Culture
<i>Ch. ornata</i>	X 2003	<i>V. gulo</i>	VII 2002
<i>M. ventricosa</i>	IX 2004	<i>M. tumida</i>	IV 2004
<i>A. biplicata</i>	IX 2004	<i>M. ventricosa</i>	IV 2004
<i>C. laminata</i>	VIII 2005	<i>V. turgida</i>	IV 2004
<i>C. parvula</i>	VIII 2005	<i>B. stabilis</i>	VII 2006
<i>M. latestriata</i>	VII 2006	<i>V. elata</i>	XII 2006
<i>L. plicata</i>	IX 2006	<i>C. pumila</i>	IV 2007
<i>C. orthostoma</i>	X 2006	<i>C. dubia</i>	VI 2007

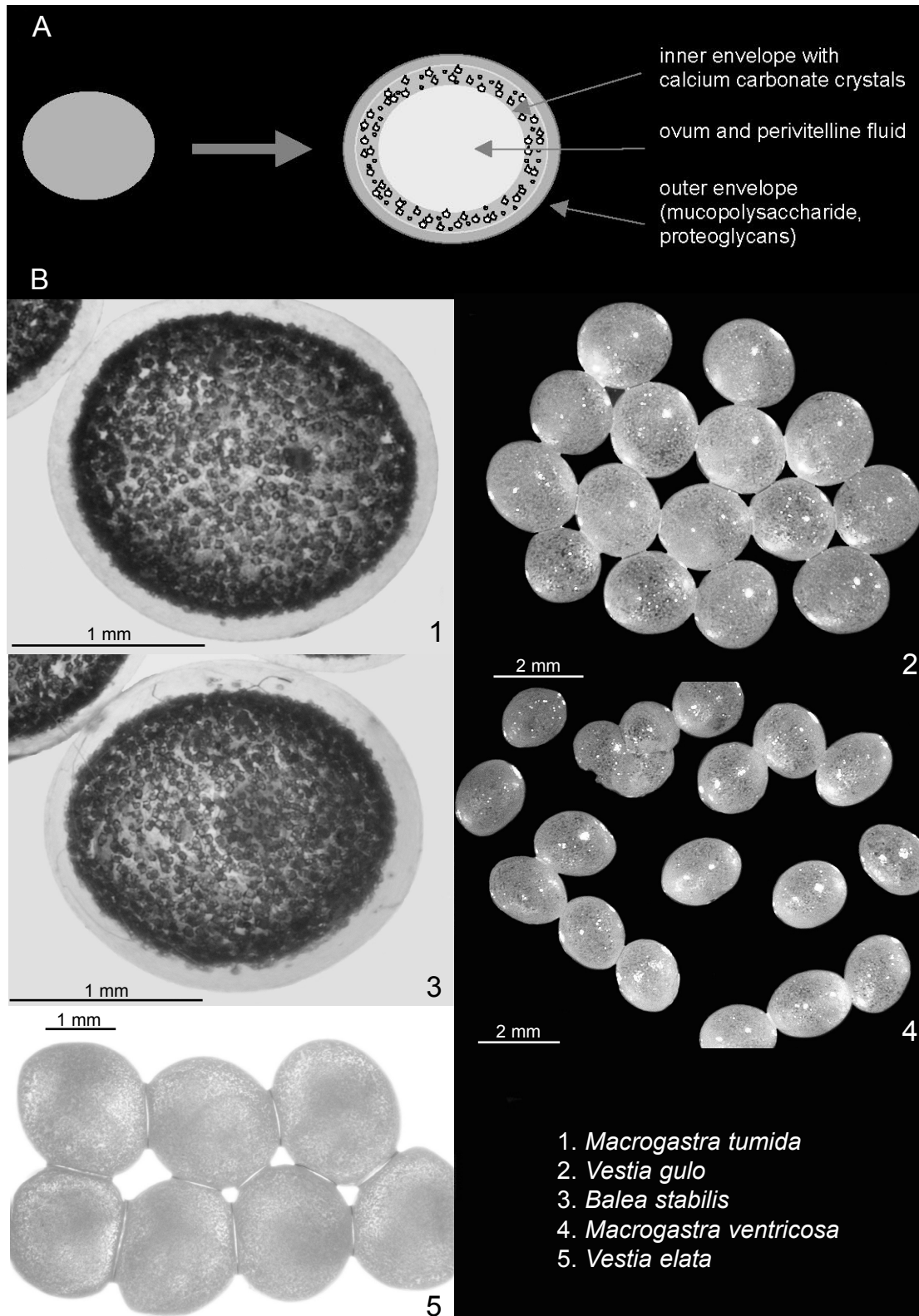


Figure 3. The first egg type: partly calcified, spherical or oval – typical of clausiliids; (A) – structure diagrammatic (according to Tompa, 1984 – slightly modified); (B1–5) – examples of eggs.

Table 6. Reproduction modes of Clausiliidae – data based on own laboratory observations.

Reproduction mode	Species
Oviparity	<i>Cochlodina laminata</i> , <i>Cochlodina orthostoma</i> , <i>Charpentieria ornata</i> , <i>Macrogastra latestriata</i> , <i>Macrogastra tumida</i> , <i>Macrogastra ventricosa</i> , <i>Clausilia dubia</i> , <i>Clausilia parvula</i> , <i>Clausilia pumila</i> , <i>Laciniaria plicata</i> , <i>Balea stabilis</i>
Egg retention	<i>Vestia elata</i> , <i>Vestia gulo</i> , <i>Vestia turgida</i>
Ovoviviparity	<i>Alinda biplicata</i>

correlation between the egg size and the number of eggs per batch ($r = 0.45$).

A. biplicata is a typically ovoviviparous clausiliid. Juveniles, with shells of 2.0–2.4 whorls (mean 2.18, \pm SE: 0.03) and 1.2–1.4 mm (mean 1.29, \pm SE: 0.01), are most often born 2–3 at a time, at most seven (mean 3.09, \pm SE: 0.29) per litter. All embryonic development inside the egg takes place inside the parent's reproductive ducts: from eggs much like those of *V. turgida*, till hatching of juveniles with completely developed embryonic shell, which then leave the parent's body (Fig. 6). No egg batches were observed.

Reproductive season

In the laboratory reproduction was intensified in the spring (III–V) and autumn (VIII–X) (Fig. 7). In those periods over 50% observed snails produced offspring (darker fields in the graph). It was also found that snails not subject to hibernation reproduced throughout the year with varied intensity. Such species as *M. latestriata*, *C. parvula* and *L. plicata* showed three reproductive peaks per year (additional reproductive period, besides the two mentioned above,

appeared on the border of autumn/winter or winter/spring). Between the reproductive periods single instances of egg/juvenile production were observed; they were mostly individuals breeding for the first time.

Hibernated snails started reproducing ca. six weeks after the temperature in the room increased above 3°C at the beginning of March. In these species the main reproductive peak fell mostly on April/May, with a minor peak at the end of August or in September. *V. turgida* was exceptional in that its reproduction was intense only from the end of April till the beginning of June.

Growth rate

Clausiliids grow from the moment of being hatched/born till completion of closing apparatus and lip (the shell has then reached its ultimate size). Growth rate in the laboratory varied between species, and three groups could be distinguished: 1) slow-growing (ca. 26–32 weeks), 2) moderately fast-growing (ca. 18–22 weeks) and 3) fast-growing (ca. 14–18 weeks) (Fig. 8). The first group includes *L. plicata*, *A. biplicata* and *B. stabilis*. The second comprises *C. laminata*,

Table 7. Egg size of 14 cultured species (mean in parenthesis).

Species	Major diameter (mm)	Minor diameter (mm)	Major to minor diameter ratio	N
<i>C. laminata</i>	1.4–2.07 (1.68)	1.36–1.85 (1.57)	1–1.26 (1.07)	73
<i>C. orthostoma</i>	1.7–2.05 (1.86)	1.59–1.7 (1.61)	1.02–1.29 (1.14)	12
<i>Ch. ornata</i>	1.3–2.05 (1.52)	1.2–1.9 (1.47)	1–1.19 (1.04)	152
<i>M. ventricosa</i>	1.3–2.51 (1.83)	1.25–2.2 (1.67)	1–1.27 (1.09)	335
<i>M. latestriata</i>	1.4–1.88 (1.58)	1.2–1.7 (1.41)	1–1.49 (1.41)	47
<i>M. tumida</i>	1.44–2.20 (1.81)	1.33–1.86 (1.6)	1–1.38 (1.14)	77
<i>C. dubia</i>	1.41–1.65 (1.5)	1.29–1.44 (1.37)	1.02–1.15 (1.09)	9
<i>C. parvula</i>	0.9–1.5 (1.19)	0.83–1.2 (1.03)	1–1.42 (1.15)	84
<i>C. pumila</i>	1.18–1.94 (1.51)	0.99–1.82 (1.27)	1–1.54 (1.19)	104
<i>L. plicata</i>	1.4–2.13 (1.75)	1.35–1.96 (1.62)	1–1.24 (1.08)	71
<i>B. stabilis</i>	1.44–2.58 (1.7)	1.29–1.79 (1.47)	1–1.7 (1.16)	53
<i>V. elata</i>	1.5–2.47 (2.08)	1.4–2.17 (1.8)	1–1.49 (1.16)	104
<i>V. gulo</i>	1.36–2.49 (1.84)	1.14–2.11 (1.67)	1–1.57 (1.1)	174
<i>V. turgida</i>	1.63–2.7 (2.1)	1.37–1.52 (1.44)	1.19–1.87 (1.46)	9

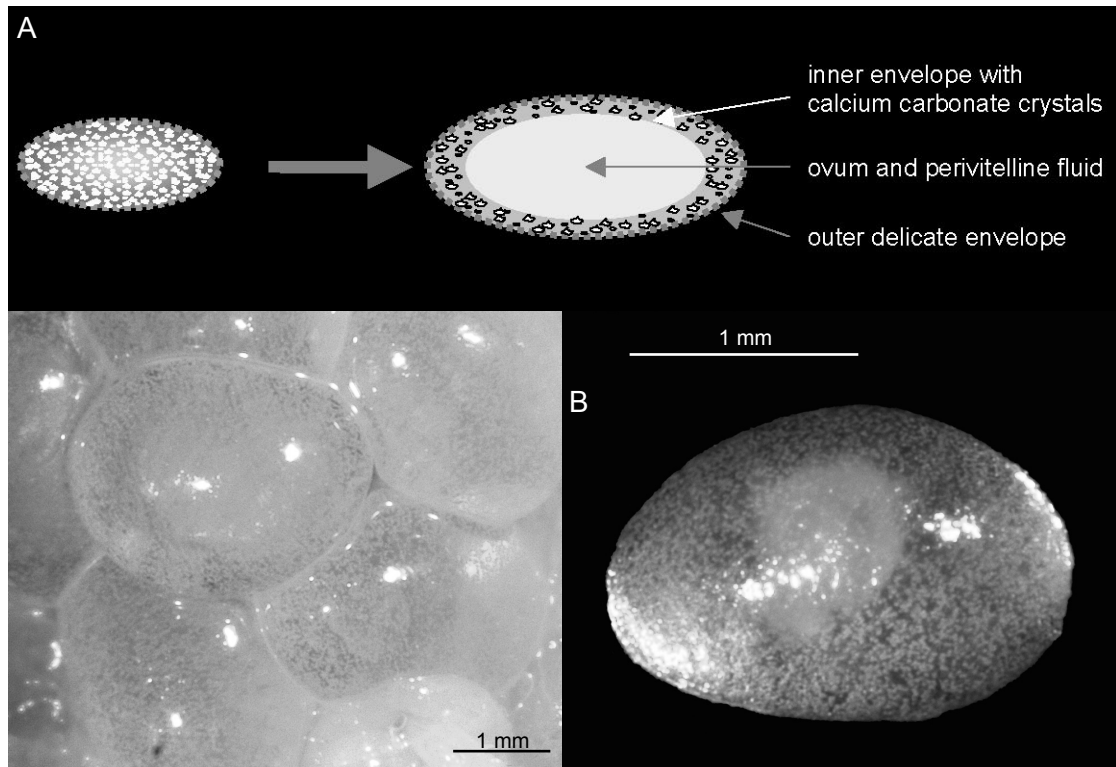


Figure 4. The second egg type: partly calcified, much flattened *Nestia turgida*; (A) structure diagrammatic (according to Tompa 1984 – slightly modified); B) example of egg.

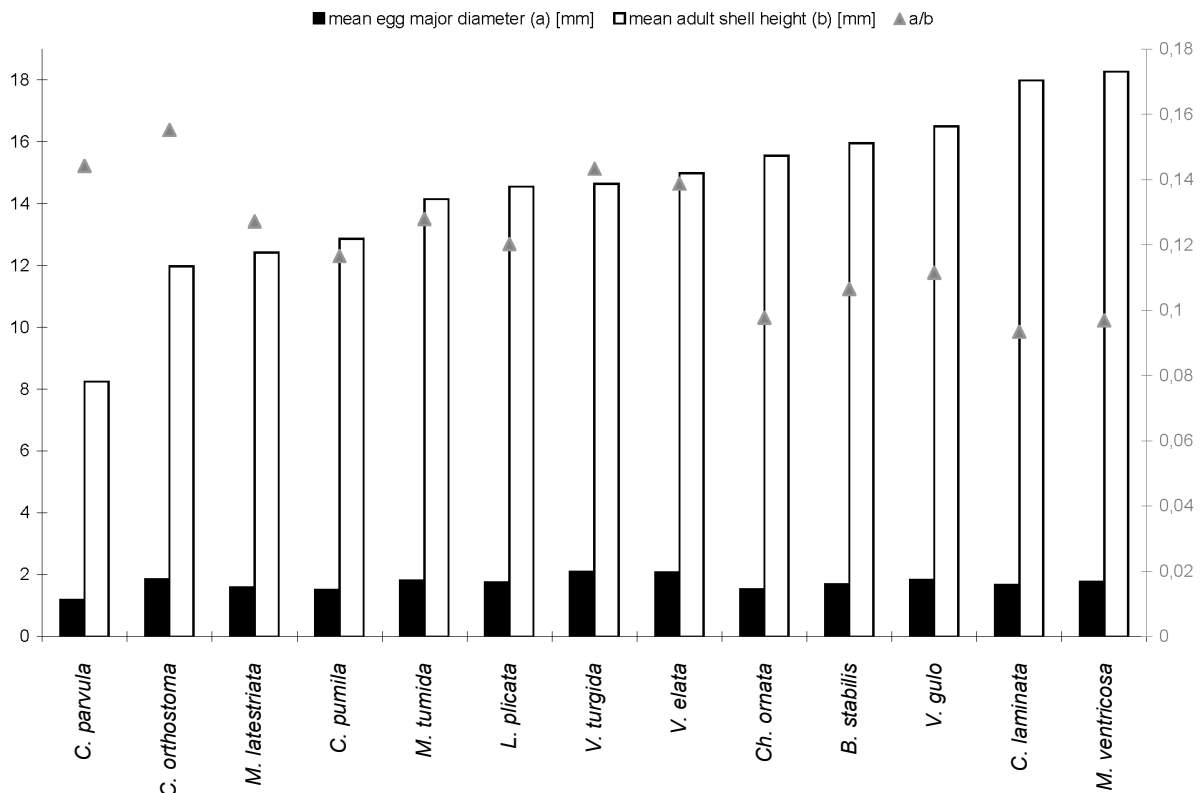


Figure 5. Relative egg size.

Table 8. Egg number per batch, incubation period (room temperature), hatching and cannibalism in 12 cultured species.

Species	Egg type	Egg number per batch	Incubation period (days)	Hatching	Cannibalism
<i>C. laminata</i>	1	5–17, mean: 10.29, N=7	12–14	asynchronous	+
<i>Ch. ornata</i>	1	1–11, mean: 4.67, N=83	10–14	asynchronous	+
<i>M. ventricosa</i>	1	1–23, mean: 8.19, N=116	12–16	asynchronous	+
<i>M. latestriata</i>	1	1–8, mean: 3.25, N=16	10–12	?	?
<i>M. tumida</i>	1	1–11, mean: 6.56, N=32	14–16	synchronous	?
<i>C. parvula</i>	1	1–9, mean: 2.42, N=57	8–12	synchronous	–
<i>C. pumila</i>	1	2–10, mean: 7.64, N=14	14–16	asynchronous	+
<i>L. plicata</i>	1	1–11, mean: 4.73, N=15	12–14	asynchronous	+
<i>B. stabilis</i>	1	1–15, mean: 8.25, N=16	10–14	?	?
<i>V. elata</i>	1	1–10, mean: 4.4, N=44	2–4	asynchronous	+
<i>V. gulo</i>	1	6–19, mean: 10.4, N=98	7–10	asynchronous	+
<i>V. turgida</i>	2	1–11, mean: 3.85, N=20	1–2	synchronous	–

Ch. ornata and *V. elata*. The third group, besides *M. latestriata*, includes other species of similar growth rate: *M. tumida*, *M. ventricosa*, *C. parvula*, *V. gulo* and *V. turgida*. In terms of weekly whorl increment, during the first two weeks the growth rate is very high in all the snails and amounts to 0.71–0.73 whorl (maximum 1–1.1) (Table 9). Later the growth becomes slower, and for slow-growing clausiliids the weekly whorl increment is then 0.18–0.37, for those of moderate growth rate – 0.18–0.4, and for fast-growing species – 0.43–0.52. Another phase of growth acceleration is observed during the last 4–6 weeks of growth: in the first group the mean increment is then 0.24–0.36, in the second group – 0.41–0.51, in the third – 0.51–0.55. The model growth curve for clausiliids shown in Fig. 9B is based on individual growth curves (Fig. 8), mean growth rate curves (Fig. 9A) and data on monthly whorl increment (Table 9); it includes three phases: rapid growth after birth/hatching, deceleration phase and another rapid phase ending with closing apparatus and lip formation.

Maturation

Though clausiliids can reach their ultimate size within a few months (the shortest time depending on the species is 3–6 months) (Fig. 10), the snails were never observed to start reproducing just after growth completion. The earliest produced offspring appeared ca. 4.5–7.5 months after shell growth completion (Fig. 10). Studies on the development of the reproductive system showed (Fig. 11) that juvenile stages, preceding the body whorl formation, had only gonads with more or less marked acini and an array of thin thread-like primordia of hermaphrodite duct, spermoviduct, vagina, vas deferens, epiphallus and penis (Fig. 11A). During formation of the body whorl with the closing appa-

ratus and lip the gonad acini were already very distinct, the diverticle (mucus gland) appeared, as well as spermatheca (27 out of 30 dissected specimens – 90%; except one *C. laminata* and two *A. biplicata*); the copulatory organ became more pronounced (Fig. 11B). In specimens which had just completed their lip, spermatheca, mucus gland, penis and epiphallus were well developed (Fig. 11C). Most specimens (21 out of 30 – 70%; except two *C. laminata*, two *M. ventricosa* and five *A. biplicata*), dissected 2–3 months after reaching their ultimate size had fully developed reproductive system, like adults one year old (Fig. 11D).

DISCUSSION

Reproductive modes

Animals show four reproductive modes: oviparity, egg retention, ovoviviparity and viviparity; for terrestrial pulmonates the first three modes have been documented, while the alleged viviparity has never been unambiguously confirmed (Tompa 1979 a, b, 1984, Heller 2001).

Oviparity is the most common mode among terrestrial pulmonates (Tompa 1984, Heller 2001); typically oviparous species lay their eggs immediately after their formation, with embryos of up to a few blastomeres (never gastrulae or older stages), within 24 to maximum 36 hours (Tompa 1979 b, 1984). Among clausiliids this mode is practiced, among others, by *Cochlodina laminata* (Frömming 1954, Likharev 1962, Bulman 1996), *Macrogastrea plicatula*, *M. lineolata* (Frömming 1954), *Laciniaria plicata* (Likharev 1962), and also by *Cristataria genezarethana* (Heller and Dolev 1994), *Albinaria coerulea*, *A. discolor*, *A. turrita* and *A. voithii* (Giokas and Mylonas

2002) as well as *Pontophaedusa funiculum* (Páll-Gergely and Németh 2008). Among the species observed in the laboratory this mode was found in *Charpentieria ornata*, *Macrogastera latestriata*, *M. tumida*, *M. ventricosa*, *Clausilia dubia*, *C. parvula*, *C. pumila*, *Balea stabilis*.

Another group includes egg retainers. The eggs are kept in the parent's reproductive ducts till the stage of gastrula or even more advanced stages; the batches may contain embryos of different development stages (Tompa 1979 b, Heller 2001). The phenomenon has been observed in members of Streptaxidae, Spiraxidae, Achatinidae, Subulinidae, Ferrusacidae, Helicodiscidae, Systrophidae, Achatinellidae, Valloniidae, Endodontidae (Tompa 1979 a, b, 1984, Baur 1989). Among the studied clausiliids the mode is practiced by members of the genus *Vestia*, a longer retention (large embryos and very short incubation) being observed in *V. elata* and *V. turgida*, compared to *V. gulo*.

Ovoviviparity (in older literature sometimes referred to as viviparity) consists in the whole embryonic development taking place inside the parent's body till hatching, and subsequently the juveniles are "born" (Tompa 1979 b, 1984, Heller 2001), or they hatch imme-

diately after egg laying (Baur 1994). The mode has been observed in members of 30 families of terrestrial pulmonates (Tompa 1979 a and literature cited therein). For clausiliids, information exists on *Macrogastera ventricosa* (Frömring 1954, Likharev 1962, Shileyko 1967, Tompa 1979 a), *Alinda biplicata* (Frömring 1954, Likharev 1962, Tompa 1979 a), *Balea perversa* (Frömring 1954, Likharev 1962, Baur A.1990, Baur B.1994, Baur and Baur 1992, Wirth *et al.* 1997), *Vestia elata* (Hudec 1963, Piechocki 1982), *V. turgida* (Tompa 1979 a), and also *Euxina tschetschenica*, *E. lessonae*, *Megaleurina derasa*, *M. reulauxi*, *Filosa filosa*, *Vestia riloensis*, *Quadriplicata quadriplicata*, *Mucronaria duboisi*, *M. pleuroptychia*, *M. gustavi* (Likharev 1962) as well as *Clausilia conchinchinensi*, *C. similis*, *Euphaedusa tetsui* and *Laciniaria strauchii* (Tompa 1979 a – literature review). Among the studied clausiliids only *Alinda biplicata* is ovoviviparous – only juveniles were observed and never egg batches. Data on the ovoviviparity of *M. ventricosa* are very doubtful. Based on laboratory observations the species is strictly oviparous – only batches of typical clausiliid eggs were observed (see – egg types), which excludes the species

Table 9. Whorl increment per week in the laboratory. Light grey fields – 1st growth phase; white fields – 2nd growth phase; dark grey field – 3rd growth phase.

Weeks	<i>L. plicata</i>	<i>Ch. ornata</i>	<i>M. latestriata</i>
2	mean: 0.73; \pm SE: 0.09 min. 0.4; max. 1.1	mean: 0.78; \pm SE: 0.07 min. 0.5; max. 1.1	mean: 0.61; \pm SE: 0.06 min. 0.4; max. 1
4	mean: 0.59; \pm SE: 0.07 min. 0.2; max. 1	mean: 0.72; \pm SE: 0.06 min. 0.5; max. 1	mean: 0.71; \pm SE: 0.07 min. 0.4; max. 0.15
6	mean: 0.37; \pm SE: 0.05 min. 0.1; max. 0.6	mean: 0.4; \pm SE: 0.08 min. 0.1; max. 0.85	mean: 0.52; \pm SE: 0.07 min. 0.25; max. 1
8	mean: 0.3; \pm SE: 0.08 min. 0.05; max. 0.7	mean: 0.36; \pm SE: 0.06 min. 0.05; max. 0.6	mean: 0.43; \pm SE: 0.05 min. 0.25; max. 0.65
10	mean: 0.26; \pm SE: 0.07 min. 0; max. 0.83	mean: 0.18; \pm SE: 0.04 min. 0; max. 0.45	mean: 0.49; \pm SE: 0.07 min. 0.1; max. 0.75
12			mean: 0.51; \pm SE: 0.04 min. 0.35; max. 0.8
14	mean: 0.22; \pm SE: 0.06 min. 0.03; max. 0.53	mean: 0.27; \pm SE: 0.06 min. 0.05; max. 0.5	mean: 0.55; \pm SE: 0.1 min. 0.1; max. 1.13
16			
18	mean: 0.2; \pm SE: 0.05 min. 0; max. 0.43	mean: 0.41; \pm SE: 0.11 min. 0; max. 0.88	
20		mean: 0.51; \pm SE: 0.06 min. 0.3; max. 1.1	
22	mean: 0.18; \pm SE: 0.05 min. 0.08; max. 0.5		
24			
26	mean: 0.24; \pm SE: 0.06 min. 0.02; max. 0.63		
28	mean: 0.36; \pm SE: 0.08 min. 0.1; max. 0.75		
30			

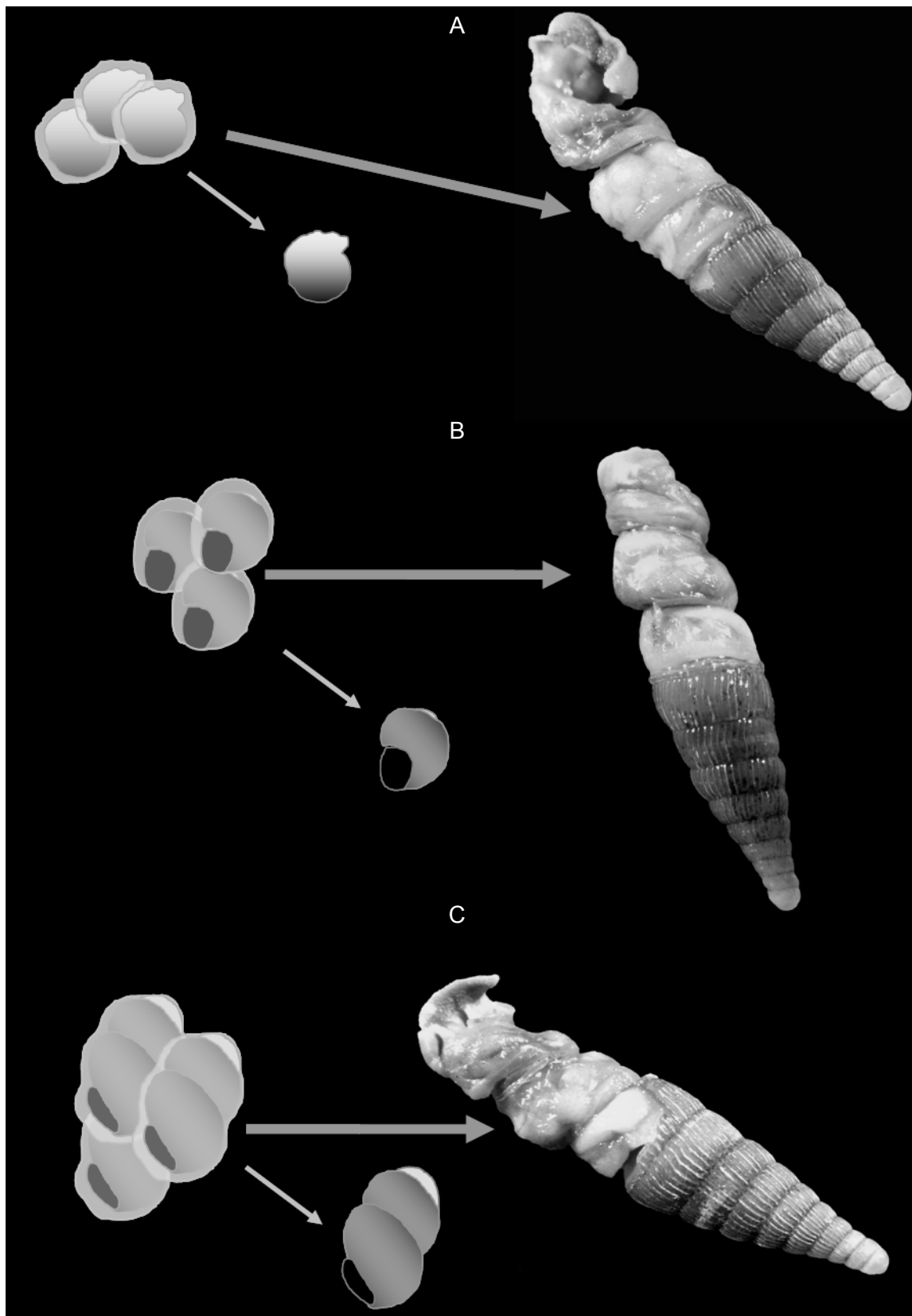


Figure 6. *Alinda biplicata*. Ovoviviparity in Clausiliidae. Examples of three development stages of embryos: (A) eggs with delicate outer envelope; (B) embryos with one whorl shell; (C) embryos with two whorl shell just before birth.

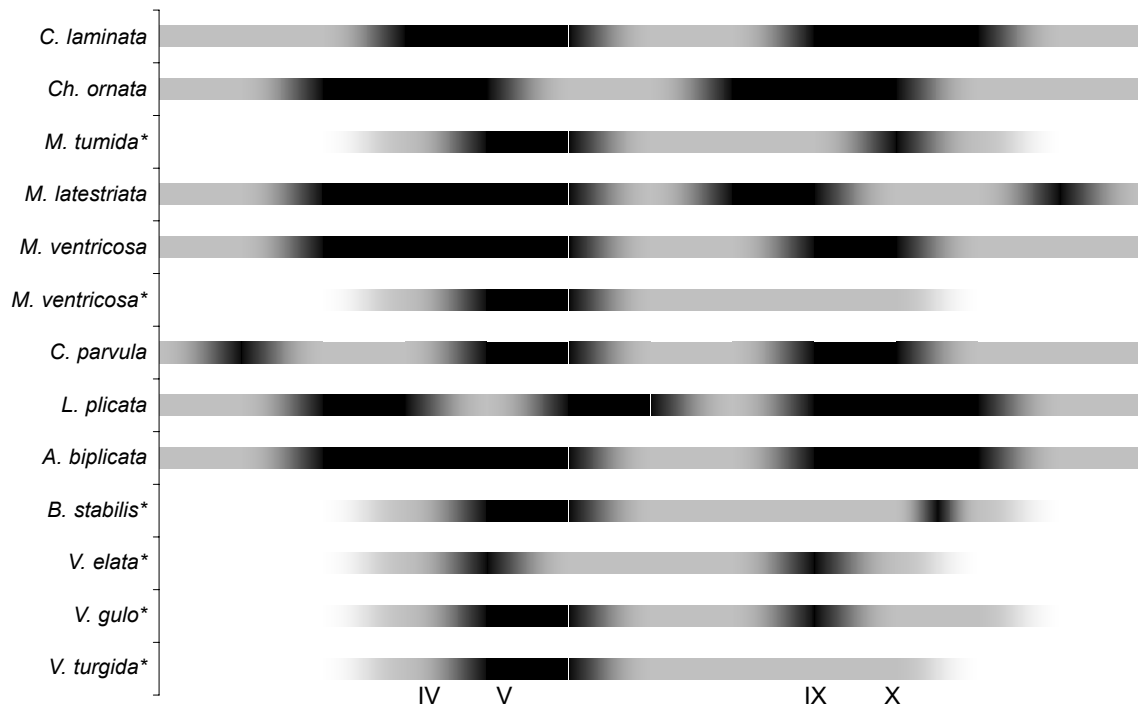


Figure 7. Reproductive season in laboratory (2007). Species marked with asterisks – inactive in winter.

from the ovoviviparous group. It is thus likely that the authors of earlier reports did not observe the moment of egg-laying and hatching (they observed only newly hatched juveniles) or the observations pertained to another species, similar to *M. ventricosa* and mistaken for it (e.g. misidentification of ovoviviparous *A. biplicata*). For many of the above species (especially in the papers of Likharev 1962, Hudec 1963 or Piechocki 1982) ovoviviparity was reported based on dissection of the reproductive system and the presence of embryos, and not on actual birth of juveniles. Eggs with embryos contained in the oviduct may only point to retention, sometimes very long. Such a situation is observed in *Vestia elata*, where laboratory observations show that the snails are not typically ovoviviparous but show a prolonged egg retention, the laid eggs containing in most cases very advanced embryos (Sulikowska-Drozd – in press). Observations on *Euxina tschetschenica*, regarded as ovoviviparous based on dissection (Likharev 1962), showed that the snail laid eggs (Kalitina 1953 after Likharev 1962), which points to a strategy similar to that employed by the members of *Vestia*. In cases when typically ovoviviparous *A. biplicata* (Frömming 1954, Likharev 1962, Tompa 1979 a) laid eggs, they failed to hatch (Loosjes 1941 after Frömming 1954) or such batches appeared rarely, only in especially favourable environmental conditions and the embryos were ready to hatch (Fechter and Faulkner 1990 after Baur 1994). Such a phenomenon could be interpreted as a "precocious birth" – making it

impossible for the juveniles to survive and develop when the embryos were in early development stages, while when they were advanced, the hatching was successful.

Several explanations have been proposed for egg retention and ovoviviparity in terrestrial snails. Such reproductive strategies may increase the offspring's chances in food competition with juveniles of oviparous snails (feeding from the beginning of the vegetation season) (Tompa 1979 b), and in areas with unstable environmental conditions decrease the offspring mortality resulting from drought and/or predation (Tompa 1984, Baur 1994, Heller 2001) and are especially advantageous for small-sized species (Heller *et al.* 1997). However, it should be considered that the retained embryos constitute a burden for the parent, which then cannot, for example, maximally contract (no ovoviviparity has been observed among slugs; Tompa 1984) and retract deep inside the shell because of the embryo-filled reproductive ducts; as a result surviving adverse conditions becomes even more difficult. In the case of clausiliids, with their elongated, spindle-shaped shells provided with a closing apparatus (clausilium), egg retention does not negatively affect the animal's drought resistance, and the shell structure rather favours such reproductive mode. Probably most clausiliid species are capable of short term egg retention, and some can retain their eggs for fairly long periods. There is also a group of species specialising in egg retention to such an extent (appropriate egg structure,

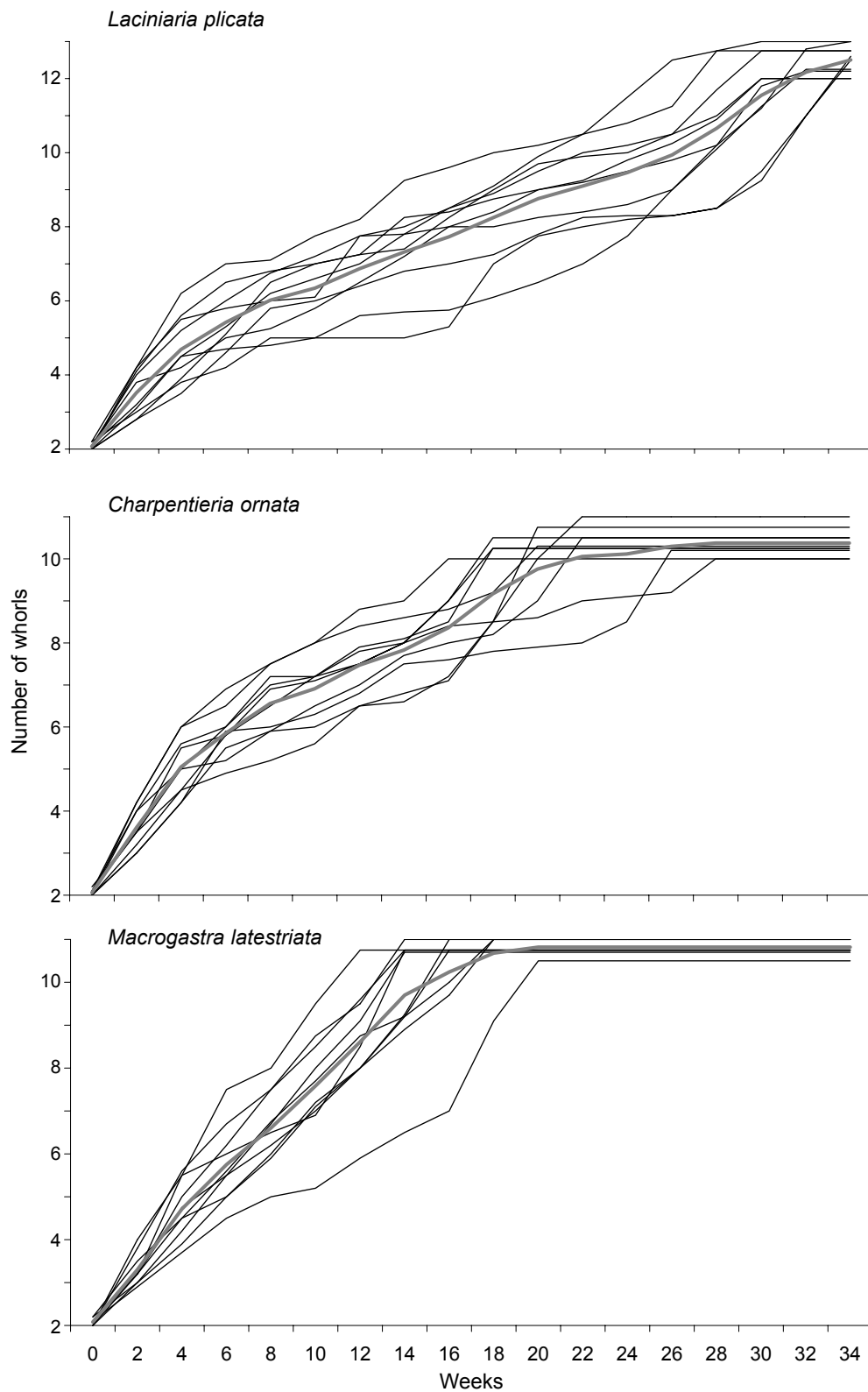


Figure 8. Growth curves of 10 selected individuals of three clausiliid species: (A) – example of slow growth; (B) – example of moderate growth rate; (C) – example of fast growth.

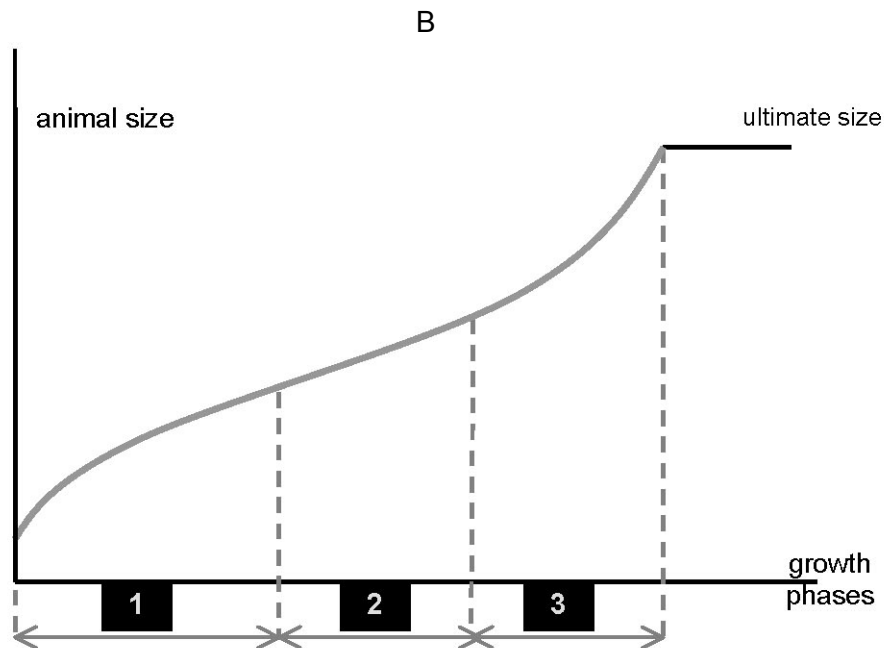
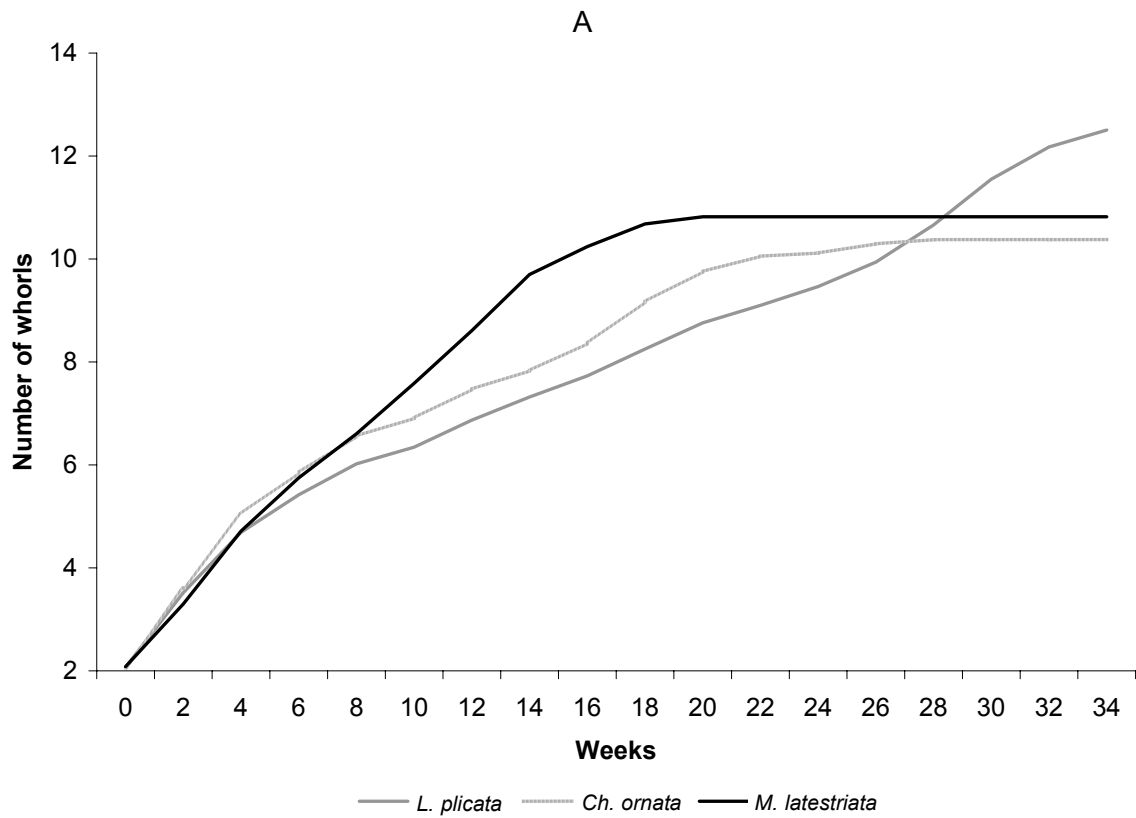


Figure 9. Clausiliidae. Growth rate: (A) – means of growth rate of three species (see fig. 10); (B) – model curve of clausiliid growth rate with three phases: 1. intense growth immediately after hatching/birth, 2. slightly slower growth, 3. quick growth including formation of closing apparatus and lip.

oviduct structure, see below), that the whole embryonic development takes place within the parent's body. Typical oviparity and typical ovoviviparity can be regarded as extremes on an axis of reproductive modes, like *r* and *K* strategies (Skelton 1994). Among the native clausiliids, three are ovoviviparous: *Ruthe-nica filograna* (Szybiak – personal communication), *Alinda biplicata* (Frömming 1954, Likharev 1962, Tompa 1979 b) and *Balea perversa* (Frömming 1954, Likharev 1962, Baur A. 1990, Baur and Baur 1992, Baur B. 1994, Wirth *et al.* 1997), another three are egg retainers (*Vestia elata*, *V. turgida* and *V. gulo*), while nine are oviparous with a possibility of short egg retention (Fig. 12).

Egg types and sizes

Contrary to aquatic snails, terrestrial gastropods lay separate eggs, each with its own envelopes (Tompa 1976). This mode of egg laying is probably associated with provision of the developing embryo with adequate supply of calcium carbonate as an adaptation to terrestrial conditions. With respect to the degree of egg envelope calcification terrestrial gastropod eggs were divided into uncalcified, partly calcified and calcified (Tompa 1976, 1984). The first type of eggs is found in e.g.

Succineidae, Vertiginidae, Arionidae, Limacidae, the second – in e.g. Agriolimacidae, Milacidae, Philomycidae, Parmacellidae, Helicidae, while the third type is produced by e.g. *Arion ater*, *Cepaea nemoralis*, and Testacellidae (Tompa 1976, 1984, Pokryszko 1990a, Heller 2001, Myzyk 2005).

The eggs of the examined clausiliids can be classified as the second type (partly calcified with clearly visible calcium carbonate crystals, rather regularly distributed just below the egg surface). Similar eggs have been observed in *Cristataria genezarethiana* (Heller and Dolev 1994). It has also been shown that some clausiliids produce calcified eggs, e.g. *Pontophaedusa funiculum* (Páll-Gergely and Németh 2008). In conditions of high humidity partly calcified eggs are resilient and spherical. They absorb and lose water easily and are susceptible to desiccation. Newly laid eggs are slightly concave (probably as a result of being tightly packed in the reproductive tracts), but soon they regain their spherical shape due to their thick external envelope. Such eggs were observed in 12 out of 14 examined species. Eggs of *V. turgida* were little resilient, very easily damaged (any attempt at transferring eggs to another place resulted in their damage), with a delicate external envelope. Very similar but much more delicate eggs with more sparsely distributed crystals

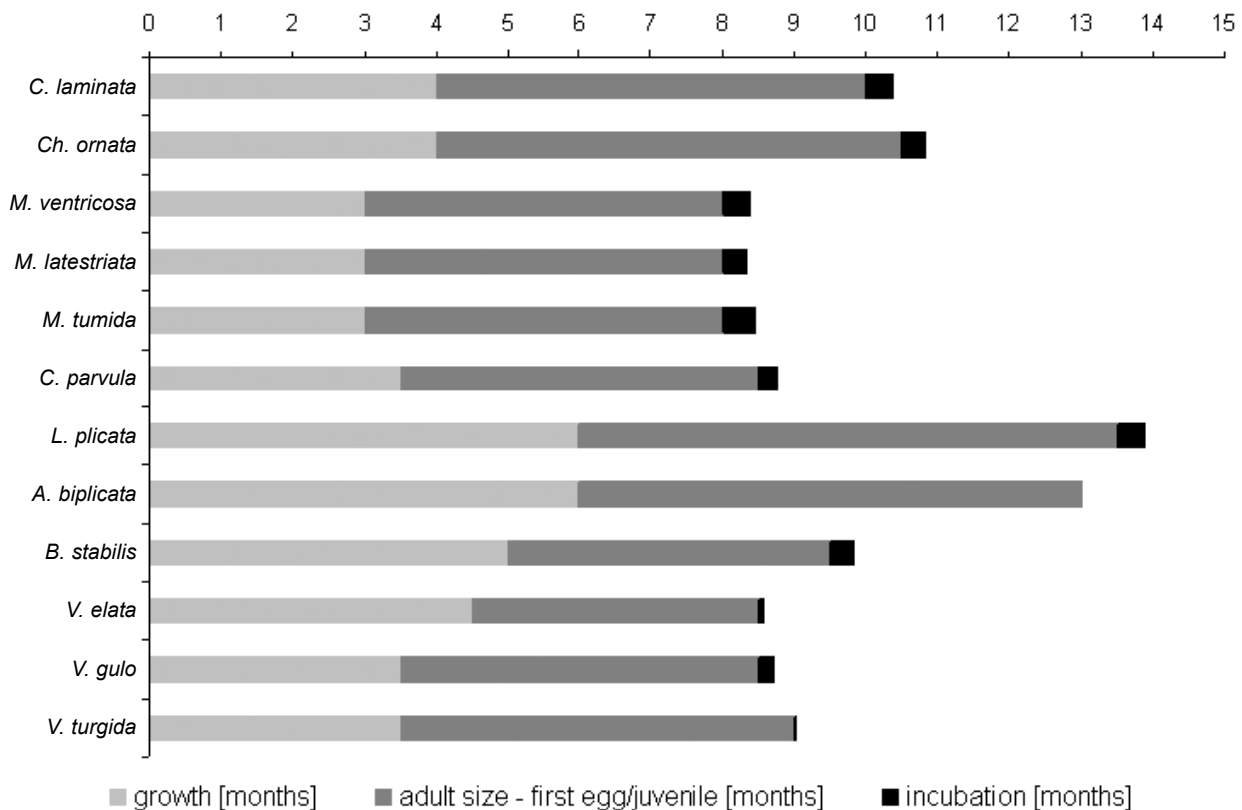


Figure 10. The quickest growth and the quickest reproduction.

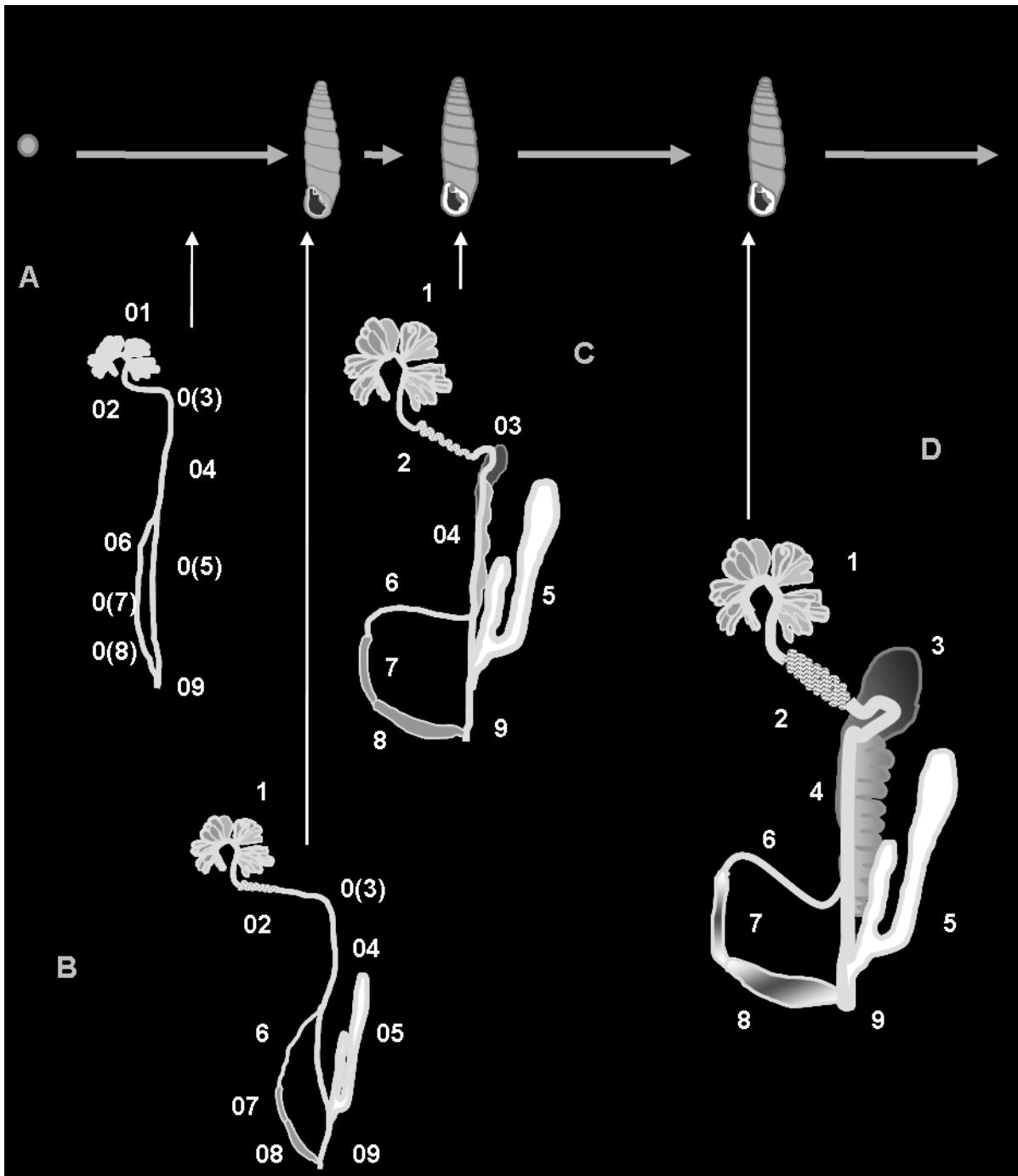


Figure 11. The reproductive system development of Clausiliidae: (A) – juvenile stage before closing apparatus formation; (B) – stage of lip formation; (C) – stage in the first month after growth completion; (D) – fully mature stage; Organ symbols: 1. gonad, 2. hermaphroditic duct, 3. albumen gland, 4. spermoviduct, 5. spermatheca & mucus gland (diverticulum), 6. vas deferens, 7. epiphallus, 8. penis, 9. atrium; Explanation for numerical symbols: 0(X) – organ absent, 0X – primordial organ, X – developed organ.

were found in uteri of some dissected, freshly killed *A. biplicata*. It can be conjectured that the reduction of the external envelope is a form of adaptation to ovoviviparity. The envelope is necessary to uncalcified or partly calcified eggs; it preserves their shape and because of its composition (mucopolysaccharides, proteoglycans) it is hygroscopic and elastic (structure close to gel-like liophilic colloid). Its formation however implies an energy expenditure on the part of the parent. If eggs are to remain in the reproductive ducts, the parent can invest less in envelope formation. The thickness of the external envelope of eggs of *M. ventricosa* (regarded as oviparous by some authors) and *V. gulo* is typical (= like in oviparous species), like in *V. elata*, while in *V. turgida* the envelope is much thinner, and in *A. biplicata* it is much reduced. The observed direction of structural transformations of partly calcified clausiliid eggs can be regarded as ovoviviparity-related. There exist, however, cases of retention of much calcified eggs (e.g. some Subulinidae or Achatinidae, *Helicodiscus* and *Ceciloides*) (Tompa 1984), which would suggest that ovoviviparity and egg retention appearing in different phylogenetic lineages might involve different adaptations, depending on the original egg type: uncalcified, partly calcified and calcified.

Egg size in terrestrial gastropods varies much among species and is significantly correlated with the adult size (Heller 2001). Among stylommatophorans the smallest eggs are produced by *Punctum pygmaeum* (eggs 0.41–0.5 mm; snail 1.2–1.5 mm) (Baur 1987 a, 1989), the largest eggs, laid by *Megalobulimus popelairianus* which reaches up to 230 mm largest shell dimension, exceed 50 mm diameter (Heller 2001). Analysis of egg and snail sizes (Heller 2001 and literature cited therein) suggests a regularity: small snails, of a shell size up to 5 mm, usually produce eggs of 0.3–0.7 mm, eggs of snails with shells exceeding 5 mm but not larger than 25 mm (medium-sized species) are usually 1–3 mm in size, while those of big snails (shell

exceeding 25 mm) – 4–20 mm. There exist literature data on only a few clausiliid species: *Macrogaster lineolata* (shell height 13–16 mm; egg 1.9–2 × 0.8–1 mm), *M. plicatula* (shell height 11–14 mm; egg 1–1.5 mm) (Frömring 1954), *Cristataria genezarethana* (shell height 20 mm; egg 1 mm) (Heller and Dolev 1994), *Cochlodina laminata* (shell height 12–20 mm; egg 1.5 mm) (Bulman 1996), or *Pontophaedusa funiculum* (egg 2.2–2.7 × 1–1.3 mm) (Páll-Gergely and Németh 2008). The egg size in the examined species (0.9–2.7 × 0.83–2.17 mm) is generally close to that reported for other clausiliids and typical for medium-sized snails. Significant interspecific differences were observed among clausiliids – the smallest species produced the smallest eggs (absolute size), while large clausiliids laid large eggs (egg major diameter in *M. ventricosa*, *B. stabilis* or *V. gulo* is by ca. 70% larger than such diameter in *C. parvula*). However, considering the relative egg size the dependence is reversed: the smallest snails lay relatively largest eggs, large snails – the smallest (for *C. parvula* the relative egg size is by ca. 29–55% larger than such size for *V. gulo*, *M. ventricosa* or *C. laminata*, and in *C. orthostoma* it is even by ca. 38–67% larger). *V. turgida*, a species with long egg retention, departs from this rule and produces extremely elongated eggs, very large in relation to the parent. The observed dependences are likely to result from an evolutionary trade-off: balancing parent's investment between producing many eggs (and thus small) and eggs large enough to ensure an adequate space for embryo development and provide building and nutritive substances. The relatively big eggs in small species point to a certain critical size below which the embryo cannot develop.

Eggs batches and their protection

The number of eggs per batch in terrestrial pulmonates varies from one to a few dozen, depending on the species (Heller 2001). Small snails, with shells up to

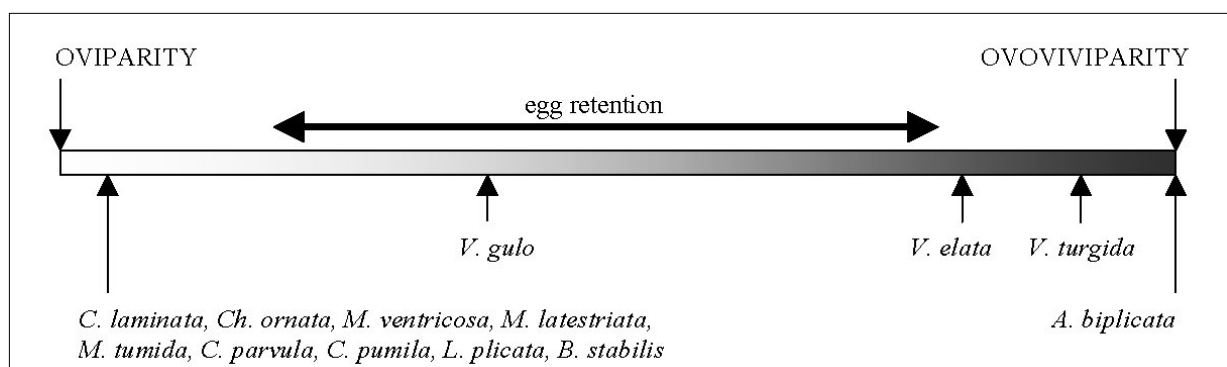


Figure 12. Reproductive modes in native clausiliids kept in laboratory.

5 mm, e.g. *Punctum pygmaeum*, *Vertigo pusilla*, *Vallonia pulchella* or *Carychium tridentatum*, lay single eggs (Whitney 1938, Baur 1989, Bulman 1990, Pokryszko 1990 b), batches of larger species (shell up to 25 mm) usually contain from one to about a dozen or sometimes few dozen eggs, e.g. *Discus rotundatus* (1–11), *D. perspectivus* (1–9), *D. ruderatus* (1–6), *Aegopinella nitidula* (1–20), *Helicella obvia* (7–30), *Helicodonta obvoluta* (9–27), *Arianta arbustorum* (20–80) (Mordan 1978, Baur 1987 b, Kuźnik-Kowalska 1999, 2005, 2006, Maltz 2003 b, Lazaridou and Chatziioannou 2005), while batches of big snails (shell exceeding 25 mm) range from about a dozen to several dozen eggs, e.g. *Helix texta* (mean 60), *H. pomatia* (24–93) or *H. lutescens* (16–67), *H. lucorum* (25–82) (Dziabaszewski 1975, Staikou *et al.* 1988, Heller and Ittiel 1990, Koralewska-Batura 1999). With respect to the number of produced eggs clausiliids are within the typical range of medium-sized snails, i.e. their batches usually range from one to about a dozen eggs, as reported for *M. lineolata* (1–11) (Frömming 1954), *C. laminata* (10–15 according to Frömming 1954; 1–25 according to Bulman 1996), *Albinaria coerulea*, *A. discolor*, *A. turrita* and *A. voithii* (5–8) (Giokas and Mylonas 2002) or *C. genezarethana* (5–11) (Heller and Dolev 1994). Similar results were obtained for the 12 examined egg-laying species (see Table 8). This is another indicator of the quality and quantity of resources the snail can invest in its offspring (Heller 2001).

Protection of eggs is rather common among terrestrial snails. It consists for example in placing batches in moss, under stones, in rock crevices, holes dug in the soil, rotting wood or covering eggs with a thick layer of mucus and, in case of tropical tree snails, in hollows at the base of branches (*Pseudachatina downesi*), on the surface of leaves (*Cryptaegis pilsbryi*) or in leaves rolled to form tubes (*Helicostyla pithogaster*) (Tompa 1984, Heller 2001). Species dwelling on the soil surface typically dig holes. Such behaviour has been observed in e.g. *Deroceras sturanyi*, *Arianta arbustorum*, *Theba pisana*, *Cepaea nemoralis*, *Helix pomatia*, *H. lutescens*, *H. aspersa*, *H. texta* (Wolda 1970, 1972, Dziabaszewski 1975, Cowie 1980, Kosińska 1980, Tompa 1984, Baur and Baur 1986, Heller and Ittiel 1990, Koralewska-Batura 1999). Species associated with rotting timber (*Helicodonta obvoluta*, *Causa holosericum*, *Isognomostoma isognomostoma*) lay their eggs in its crevices (Maltz 2003 b). Some species, when protecting their batches, show no preferences to any particular substratum (eggs are laid most often where the adults find shelter during adverse environmental conditions). Examples are *Arion rufus*, *A. subfuscus*, *A. intermedius*, *Limax maximus*, *L. cinereoniger*, *Bielzia coeruleans* (Smoleńska 1935, Riedel and Wiktor 1974, Wiktor 1989). Data on clausiliid batch

protection are very scarce and pertain to only a few species. Heller and Dolev (1994) have found that *C. genezarethana* lays its eggs under stones, in small hollows dug in the soil, 5 mm deep. Bulman (1996) has observed *C. laminata* to prefer dead timber, while Giokas and Mylonas (2002) have shown that the four species of *Albinaria* they examined placed their batches in crevices and under stones. Our laboratory observations showed that most species preferred to lay their eggs in tufts of dense moss (batches placed on the soil surface in the compact parts of the turf), on pieces of bark/rotting timber (in crevices) and under stones. Though the snails were kept in high humidity conditions, batches were deposited in places which under natural conditions would be shaded and stayed damp for a long time. The behaviour was displayed both by snails brought from the field and by those born in the laboratory. Instinctive protection of drought-sensitive eggs ensures a higher reproductive success (Tompa 1984). Covering batches with mucus is an important component of egg-laying behaviour. The mucus may: a) reduce desiccation risk, b) contain substances which prevent development of harmful microorganisms, c) repel predators (Tompa 1984), though the latter seems unlikely: there are frequent cases of consumption of eggs of one snail species by another, for example *O. cellarius* may attack batches of *C. nemoralis* (Wolda 1963 after Heller 2001). Mucus-covering does not seem to be an adequate anti-desiccation means. Mucus ensures humidity when it is hydrated, but it quickly loses water. The role of mucus may consist in gluing the eggs together into a grape-like shape which decreases the evaporation area of the batch. Additionally, mucus may convey information that the place is already occupied to conspecific individuals (analogous to information exchange during courtship). Such marking of laid eggs prevents their damage by other individuals preparing an egg-laying site or warn them against excessive density of batches which may lead to inter-batch cannibalism.

Egg retention and ovoviviparity can be regarded as another form of batch protection (see Modes of reproduction) (Baur 1994, Heller 2001).

Incubation, hatching, cannibalism

The incubation period in the examined species usually ranges from two to five weeks and depends on external conditions. Juveniles of *Helix lutescens* hatch 14 days from egg-laying (Koralewska-Batura 1999), in *Helicodonta obvoluta* incubation takes 14–31 days (Maltz 2003 b), in *Discus rotundatus*, *D. perspectivus* and *D. ruderatus* – 14–36, 24–35 and 17–34 days, respectively (Kuźnik-Kowalska 1999, 2005, 2006), and in *Deroceras sturanyi* – 13–17 days (Kosińska 1980) (data on eggs developing at 17–22°C).

Literature information on incubation of clausiliid eggs is very scanty. According to Likharev (1962) the duration of incubation in Central European clausiliids in their natural habitat ranges from three to five weeks and is weather-dependent, while Shileyko (1967) reports that in the laboratory the period is 22–28 days. Juvenile *Macrogastra lineolata* are reported to hatch in 19–34 days after egg-laying (Frömming 1954), *Cristataria genezarethana* – in three weeks (Heller and Dolev 1994), in species of the genus *Albinaria* incubation takes 2–3 weeks (Giokas and Mylonas 2002), and in *Pontophaedusa funiculum* – 9–20 days (Páll-Gergely and Németh 2008). In *Cochlodina laminata* incubation takes three weeks (Frömming 1954), but according to Bulman (1996) it is only 7–15 days (our own data point to 12–14 days and are thus close to the value reported by the latter author). Incubation of oviparous species examined by us took 8–16 days (mean 10–14) at room temperature (18–20°C). Juveniles of *C. parvula*, the species with the smallest eggs among the examined clausiliids, appeared after 8–12 days, in species producing large eggs the period was usually 12–16 days, which would suggest that, other factors being constant, the egg size, and most of all the size reached by the embryos before hatching, determine the duration of incubation. In egg-retaining clausiliids the incubation was distinctly shorter and took 7–10 days in *Vestia gulo*, 2–4 days in *V. elata* and 1–2 days in *V. turgida*. A considerable part of embryonic development in these snails takes place inside the eggs before their deposition. This is confirmed by dissection of adults collected in the field in V–VII; their oviducts contain tightly packed eggs with much advanced embryos (Sulikowska-Drozd – unpublished). In the last species the embryos are so advanced that the border between egg retention and ovoviviparity becomes blurred.

Hatching can be synchronous or asynchronous. According to Tompa (1984) reasons for the latter should be sought in a) asynchronous release of ova from the gonad (laid eggs vary in the development stages of their embryos, as observed e.g. in *Helix aspersa*) and/or b) position of the egg within the batch (central or peripheral), which may result in different development rates. Asynchronous hatching has been observed both in snails producing large batches, e.g. *Arianta arbustorum*, *Helix aspersa*, *H. lutescens*, *H. pomatia* (Tompa 1984, Baur 1987b, 1988a, 1990, Koralewska-Batura 1999), and those producing few eggs per batch, e.g. *Discus rotundatus*, *D. perspectivus*, *D. ruderatus* or *Helicodonta obvoluta* (Kuźnik-Kowalska 1999, 2005, 2006, Maltz 2003 b). Among clausiliids the only mention of asynchronous hatching pertains to *C. laminata* (Bulman 1996). Among the examined species asynchronous hatching was observed in *C. laminata*, *Ch. ornata*,

M. ventricosa and *L. plicata*, but only in the case of very large batches. According to Tompa's (1984) concept, in such situations the snails had probably accumulated a number of eggs in their reproductive tracts before egg-laying, or the duration of development was associated with different positions of eggs within the batch. Varied degree of advancement of embryos within batches is commonly observed in egg-retainers (*V. gulo*, *V. elata*) and is independent of the batch size.

Egg cannibalism is common among terrestrial pulmonates. It has been observed for example in three members of *Discus*, *Deroceras sturanyi*, *Arianta arbustorum*, *Cepaea nemoralis*, *Helix pomatia* and *H. lutescens* (Kosińska 1980, Baur 1987b, c, 1988 a, b, 1990, 1994, Baur and Baur 1986, Koralewska-Batura 1999, Kuźnik-Kowalska 1999, 2005, 2006). The behaviour has been best studied in *A. arbustorum* and the three species of *Discus*. Most probably its promoting factor is asynchronous hatching and the habit of consuming the remains of the juvenile's own egg envelope, thus using up the last of the egg-contained resources (Baur 1987b). Intra-batch cannibalism is the most frequent, however in both *A. arbustorum* and members of *Discus* attacking other batches has been observed (Baur 1987b, Kuźnik-Kowalska 2006). This is an effect of depositing batches too close to each other. It has been found that *A. arbustorum*, when preparing to lay eggs, ignores the presence of other batches which may increase the probability of cannibalistic behaviour (Baur 1988). In the case of this species it is of no significance if the cannibalised eggs originate from the same or alien batch, whether or not the eggs are fertilised and what is the development stage of the embryos (Baur 1993, 1994). The number of eggs in the batch also does not have any effect on the intensity of such behaviour (Baur and Baur 1986). *D. perspectivus*, *A. arbustorum* and *H. pomatia* consume only conspecific eggs (Baur 1988a, Baur and Baur 1986, Kuźnik-Kowalska 2005), whereas *D. rotundatus* and *D. ruderatus* consume also eggs of other, congeneric species (Kuźnik-Kowalska 2006). Older juveniles and adults of *A. arbustorum* and *H. pomatia* are not interested in eggs, while *Discus* devour eggs even when adult (Baur 1987b, 1992, Kuźnik-Kowalska 2006). Among clausiliids cannibalism has been reported only for *C. laminata* (Bulman 1996). Our observations on cannibalism in the examined species are at present only preliminary. Newly hatched juveniles consumed remains of their own envelopes and sometimes damaged those of other, unhatched eggs (when hatching was asynchronous). Embryos inside the damaged eggs were able to survive only when they were at advanced development stages. Consuming egg envelopes may be one of the reasons for differentiated growth rate among the juveniles – snails from "attacked" eggs had a smaller initial size since they were deprived of a part of the

egg-contained resources. Inter-batch cannibalism was observed only in overdensity situations (deficit of adequate egg-laying places). In some cases eggs were damaged by juveniles of another clausiliid species. Like in *A. arbustorum* and *H. pomatia*, older juveniles and adults did not consume eggs. At present it can be assumed that cannibalism is not a typically clausiliid form of investment in offspring. Such a situation occurs in *A. arbustorum* (Baur 1994, Heller 2001); increase in egg-size is impossible and the higher reproductive success is achieved through increase in the batch size, some of the eggs being nutritive.

Reproductive season

Some of temperate zone gastropods reproduce irrespective of the season, e.g. *Carychium tridentatum*, *Deroceras laeve*, *Arion subfuscus* or *A. hortensis* (Morton 1954, Riedel and Wiktor 1974, Wiktor 1989, Bulman 1990); others have a strictly determined reproductive period, e.g. *Columella edentula*, *Vertigo pusilla*, *Punctum pygmaeum*, *Discus rotundatus*, *D. perspectivus*, *D. ruderalis*, *Tandonia rustica*, *Limax cinereoniger*, *Malacolimax tenellus*, *Lehmannia marginata*, *Deroceras agreste*, *D. reticulatum*, *D. rodnae*, *D. praecox*, *Helicodonta obvoluta*, *Arianta arbustorum*, *Helix pomatia*, *H. lutescens* (Riedel and Wiktor 1974, Dziabaszewski 1975, Baur 1987a, 1989, 1990, Wiktor 1989, Pokryszko 1990a, b, Reise 1995, Koralewska-Batura 1999, Kuźnik-Kowalska 1999, 2005, 2006, Maltz 2003b). Literature data on clausiliids of the temperate zone indicate a strictly determined reproductive season: *C. laminata* both in the wild and in the laboratory reproduces in April and May and in September (Bulman 1996) or, according to Frömring (1954) – August and September (laboratory observations), *M. plicata* – in late summer, *M. lineolata* – from half of August till half of October, *C. bidentata* – in September and October (Frömring 1954; laboratory observations), *A. biplicata* – from June to August (Kuźnik-Kowalska 1998; field observations), though according to Loosjes (1941, after Frömring (1954) its reproductive period falls in April, June, July and from August to October (laboratory observations). In the wild *V. elata* reproduces mainly in June and July, sometimes the period is extended to include October (Piechocki 1982). In the laboratory *C. laminata*, *Ch. ornata*, *M. latestriata*, *M. ventricosa*, *C. parvula*, *L. plicata* and *A. biplicata* reproduced throughout the year, and thus with no distinct reproductive season. They were kept at natural photoperiod, only constant humidity and food supply being ensured. Hibernated snails reproduced from spring till autumn, but some species showed rather distinct reproductive peaks; egg-laying started ca. 4–6 weeks after the temperature was increased above 3°C. It can

be supposed that the main factors determining the onset of reproduction for temperate zone clausiliids are humidity and temperature while the day length is of no significance. It seems that in the wild the day length is also unimportant for reproduction, since according to literature data clausiliids reproduce in months of long (VI, VII) and short days (IV, X).

In the Mediterranean, with its succession of dry and wet periods, activity and thus also reproduction of terrestrial gastropods are closely associated with the rainy season. This has been observed in *Helicella obvia*, *Helix texta* or *Lauria cylindracea* (Heller and Ittiel 1990, Heller *et al.* 1997, Lazaridou and Chatziioannou 2005). Such clausiliids as *C. genezarethana*, *A. coerulea*, *A. discolor*, *A. turrita* or *A. voithii*, reproduce in the autumn and winter (October/November–December), and in favourable conditions egg-laying continues through most of the rainy season (Heller and Dolev 2004, Giokas and Mylonas 2002). Thus for Mediterranean clausiliids the decisive factors triggering reproduction would also be long-lasting, high humidity (no activity observed during sporadic rains in the dry period) and temperature. The beginning of estivation is not closely correlated with the end of rains – in both dry and wet years estivation starts in April, irrespective of the actual humidity conditions which would indicate an effect of photoperiod (Giokas and Mylonas 2002).

Growth rate

Terrestrial pulmonates include two groups of different growth patterns: species growing through life (undetermined growth), and species terminating growth and then investing resources exclusively in reproduction (determined growth). Snails of the second group include for example *Chondrina clienta*, *Helicodonta obvoluta*, *Arianta arbustorum*, *Cepaea nemoralis*, *Helix pomatia* or *H. lucorum* (Wolda 1970, 1972, Dziabaszewski 1975, Staikou *et al.* 1988, Baur 1991, Baur and Baur 1992, 1995, Maltz 2003b). Lip formation in such snails is the sign of reaching ultimate size. Clausiliids conform to this pattern: formation of closing apparatus (clausilium, system of lamellae and folds within the body whorl) and lip indicate growth termination. An exception is *Balea perversa*, with much reduced apertural barriers, which has been observed to grow also later in life (Baur and Baur 1991). Clausiliid growth can be divided in three phases, like in those members of the Helicidae which have been examined; in clausiliids the middle phase of growth is much less distinct, and the second acceleration phase is more dynamic. Such growth strategy is probably associated with the existence of the closing apparatus (reduced in some members of *Alopiia*, *Balea* or *Reinia*; Likharev 1962), which provides an additional, permanent

protection and reinforcement of aperture. In the last stage of growth resources are invested in the possibly quickest formation of apertural barriers and thus completion of growth. As a result the critical period of the body whorl formation, when the shell is very delicate, thin-walled and liable to mechanical damage, becomes shortened. The time necessary to attain ultimate size varies greatly among clausiliids: in *P. funiculum* it is 4–5 months (Páll-Gergely and Németh 2008), in *B. perversa* – 3–4.5 months (Baur and Baur 1992), in *C. laminata* – 3–12 months (Bulman 1996). In the examined species in the laboratory the growth is completed within 3–8 months depending on the species. In nearly optimum conditions (laboratory) the growth rate is maximum, dictated by the growth potential of the animal, and the differences are probably the effect of internal factors, both individual and species-specific (see Fig. 8). In the wild environmental factors, mainly humidity, temperature and duration of the vegetation season (altitude), were observed to influence growth rate. Clausiliids of areas with alternating dry and wet seasons usually need a few wet seasons to complete their growth. Members of *Albinaria* from Greece take 2–3 seasons to complete their growth (Giokas and Mylonas 2002), while *C. genezarethana* from Israel needs ca. 11 years (Heller and Dolev 1994). *B. perversa* from the Swedish island of oland reaches ultimate size in 3–4 years (Wirth *et al.* 1997), while *V. elata* from the population at Święty Krzyż (Świętokrzyskie Mts) – in about two years (Piechocki 1982). Preliminary results of field observations on *Ch. ornata* in Krowiarki (region of Klodzko) indicate a growth rate close to that reported for *V. elata*. Field observations on Carpathian populations of *V. gulo* revealed a considerable dependence between the altitude and the growth rate: at 420 m a.s.l. growth is completed in one year, at 1150 m a.s.l. – in ca. three years (Maltz and Sulikowska-Drozd unpublished). Population density is also a significant factor. Baur and Baur (1992) have shown that a higher density of *B. perversa* kept in the laboratory considerably increases the time necessary to attain ultimate size (with 5–10 individuals per dish the time was ca. 3–4.5 months, with 40 individuals – ca. one year). A similar phenomenon has been observed in *C. genezarethana*: high density and the presence of adult snails are the probable reasons for slow growth of juveniles (Heller and Dolev 1994).

Maturity

Fully developed reproductive system is one of indicators of sexual maturity. Available literature data on the ontogenetic development of this system in terrestrial pulmonates are very scanty; they pertain to a few members of the Succineidae and Vitrinidae, to *Helicodonta obvoluta* and *Helix lutescens* (Umiński

1975, Jackiewicz and Zboralska 1994, Koralewska-Batura 1994, Maltz 2003a). Individuals of *H. obvoluta* and *H. lutescens* (Helicidae s. lato) with complete shells (aperture surrounded by lip) have fully developed reproductive system and are thus sexually mature; the examined Succineidae and Vitrinidae have developed reproductive system and reproduce, continuing growth at the same time. Two strategies of maturation can be thus distinguished: simultaneous attainment of ultimate size and sexual maturity (Helicidae s. lato), and attainment of maturity which does not preclude further growth (Succineidae, Vitrinidae). Also *Discus* and *Punctum pygmeum* reach a certain critical size at which they start reproducing, and continue growing, though slowly (Baur 1989, Kuźnik-Kowalska 1999, 2005, 2006), and thus represent the second strategy. Results of laboratory observations on clausiliid growth and anatomical examination of the reproductive system in various growth classes indicate a different maturation strategy in these snails. Clausiliids which have completed growth, produce their first offspring only after 5–8 months from attainment of ultimate size which would suggest that snails with newly completed shells (including closing apparatus and lip) are not completely mature. At that stage they have well developed spermatheca and mucus gland, as well as penis and epiphallus which would suggest an ability to copulate as both donors and acceptors of sperm. Similar observations have been made on Greek *Albinaria* (Schilthuizen and Lombaerts 1994, Giokas and Mylonas 2002). Clausiliid strategy consists in temporal separation of investment in shell growth and growth of the reproductive system. In these animals the shell growth is rather equalized while in *H. obvoluta* there is a distinct deceleration phase which coincides with the beginning of reproductive system development and intense divisions in the gonad (Maltz 2003a). Energy expenditure associated with gamete production and with accumulation of resources to produce eggs considerably inhibits the growth. Growth inhibition coinciding with the onset of reproduction has also been observed in members of *Discus* which grow throughout life (Kuźnik-Kowalska 1999, 2005, 2006). Clausiliid growth strategy seems advantageous, considering their life span [based on field studies the life span of *V. elata* is at least 8 years (Piechocki 1982), *C. genezarethana* – ca. 16 years (Heller and Dolev 1994), *B. perversa* – at least 7 years (Wirth *et al.* 1997), species of the genus *Albinaria* – ca. 7 years (Giokas and Mylonas 2002), and *Ch. ornata* and *V. gulo* – at least 6 years (Maltz and Sulikowska-Drozd – unpublished)].

Our current studies on the development and activity of clausiliid gonad in annual cycle should contribute to a more complete picture of clausiliid biology.

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