

### Embryonic shells of *Viviparus* - what they may tell us about taxonomy and phylogeny? (Gastropoda: Architaenioglossa: Viviparidae)

With 18 SEM Photographs, 2 Figures and 1 Table

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**Abstract.** The paper describes the embryonic shells of five European viviparid species: *Viviparus acerosus* BOURGUIGNAT, 1862; *V. ater* (CRISTOFORI et JAN, 1832); *V. contextus* (MILLET, 1813); *V. hellenicus* (CLESSIN, 1879); and *V. viviparus* (LINNAEUS, 1758). Several interspecific differences are described, photographed and listed in a table. They indicate the species distinctness of *V. hellenicus* earlier regarded as a subspecies of *V. ater*. On the other hand, the described characters present numerous autapomorphies, and, two different most parsimonious reconstructions (MPR) having been found, they are hardly useful in phylogeny reconstruction.

**Kurzfassung.** Embryonale Schalen von *Viviparus* - was können sie uns zur Taxonomie und Phylogenie aussagen? (Gastropoda: Architaenioglossa: Viviparidae). - Die Arbeit beschreibt die embryonalen Schalen von fünf europäischen Arten der Viviparidae: *Viviparus acerosus* BOURGUIGNAT, 1862; *V. ater* (CRISTOFORI et JAN, 1832); *V. contextus* (MILLET, 1813); *V. hellenicus* (CLESSIN, 1879); und *V. viviparus* (LINNAEUS, 1758). Verschiedene interspezifische Unterschiede werden beschrieben, abgebildet und in einer Tabelle aufgelistet. Sie zeigen die spezifische Verschiedenheit von *V. hellenicus*, welche früher als eine Subspezies von *V. ater* angesehen wurde. Andererseits zeigen die beschriebenen Merkmale zahlreiche Autapomorphien, und, wie mittels zweier verschiedener effizientester Rekonstruktionen (MPR) festgestellt, sie sind kaum von Nutzen zur Rekonstruktion der Phylogenie.

#### Introduction

In phylogenetic studies the holomorphology of a species-group, with as many semaphoronts (HENNIG, 1966; WILEY, 1981) as possible is to be considered. Hence, it seems profitable to examine embryonic shell characters. The Viviparidae that bear their embryos in the brood pouches are especially convenient for such studies. Secondly, there are not many characters discriminating species and reflecting evolutionary paths within this old and archaic (HASZPRUNAR, 1988) gastropod family, so any source of „new“ characters should be taken into account. FALNIOWSKI (1989a, b, 1990a) describes the adult shell surface of two Polish viviparid species. FRETTER & GRAHAM (1962) describe two rows of bristles formed on the embryonic/young postembryonic shells by two lobes of the mantle in *V. contextus*, both the lobes and bristles being rudimentary in *V. viviparus*.

The present study deals with the embryonic shells of the five European viviparids: *Viviparus acerosus* BOURGUIGNAT, 1862; *V. ater* (CRISTOFORI et JAN, 1832); *V. contextus* (MILLET, 1813); *V. hellenicus* (CLESSIN, 1879); and *V. viviparus* (LINNAEUS, 1758). The questions are:

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(1) are there interspecific differences among the studied species?; (2) if at all, how does the embryonic shell morphology reflect phylogeny?

### Material and methods

Numerous specimens of *Viviparus contectus* (MILLET, 1813) and *V. viviparus* (LINNAEUS, 1758) were collected from various localities in Poland. For the embryonic shell studies *V. contectus* from Gardno Lake, and *V. viviparus* from the Trzesiecko Lake were chosen. *V. acerosus* BOURGUIGNAT, 1862 were collected from drainage canals (Zupny kanal) by the Danube River north of Calovo (SW Slovakia). *V. ater* (CRISTOFORI et JAN, 1832) were collected at Sirmione, south coast of the Garda Lake (North Italy); *V. hellenicus* (CLESSIN, 1879) were picked from the Trichonis Lake near Agrinio (West Greece).

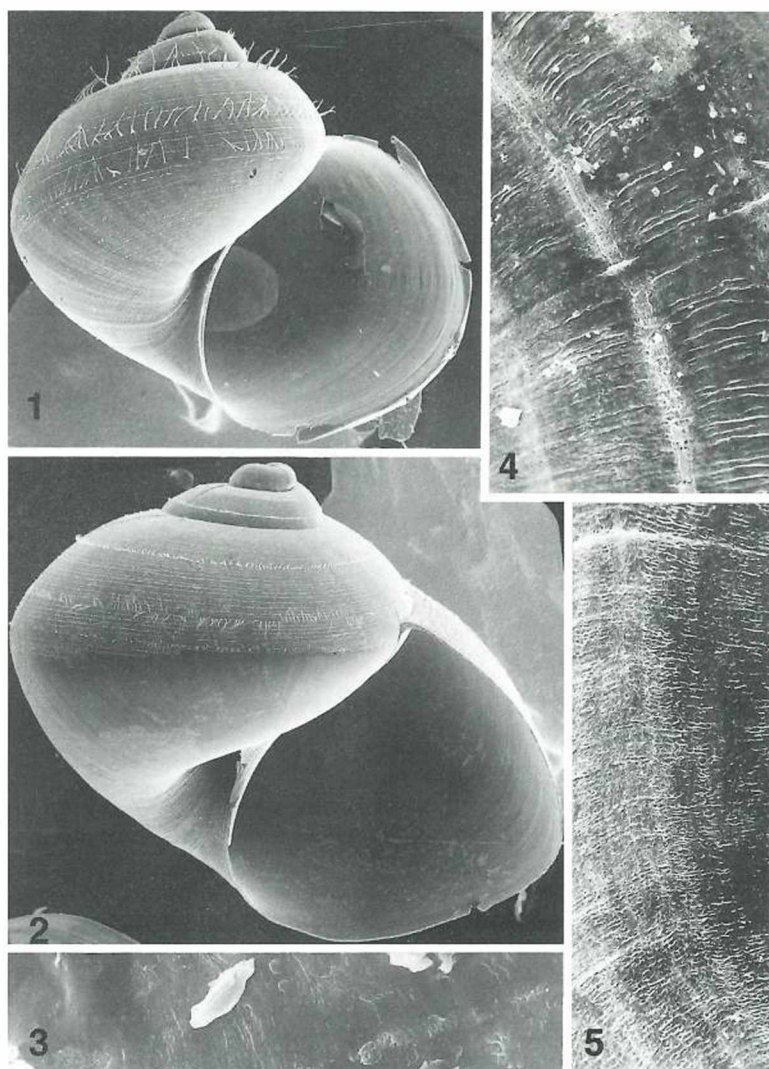
The gastropods were fixed in 4 % formalin, and then kept in 70% ethanol. They were dissected under a stereoscopic microscope; the embryo shells from the brood pouches were cleansed in CLOROX for 10 minutes, next rinsed for 15 minutes in distilled water. For each species five shells were rinsed twice in absolute ethanol, dried, glued onto a holder and coated with gold. The material was examined with a Jeol JSM-35 scanning electron microscope.

The resulting character states were used as an input for the Macintosh MacCLADE (MADDISON & MADDISON, 1992). Its Nexus-format file was processed using PAUP (SWOFFORD, 1991) with the exhaustive search option to find the shortest, most parsimonious (SWOFFORD & OLSEN, 1990; WEIR, 1990) tree. The latter were then processed using MacCLADE to analyze the evolution and print cladograms.

### Results

The shell characters showing interspecific differences, and their states for each species, are listed in Table 1. The embryonic shells are similar in outline (Figs. 1-2 and 6), spheroid with a narrow spire in all the studied species with the exception of *V. hellenicus* (Fig. 7), the shell of which is ovishaped, relatively narrow, with a broad spire. The umbilicus may be very broad (Fig. 2), broad (Fig. 1), or narrow (Figs. 6-7), partly covered (Figs. 6-7) or exposed (Figs. 1-2). The shells are slightly calcified, thin-walled, translucent and pigmentless, horn-coloured in all species (Figs. 1-2 and 6) except *V. hellenicus* (Fig. 7), the shells of which are well calcified, thick-walled, opaque and rich brownish-pigmented. The protoconchs of all the species are similar in outline (Figs. 10-13) and bear no characteristic sculpture.

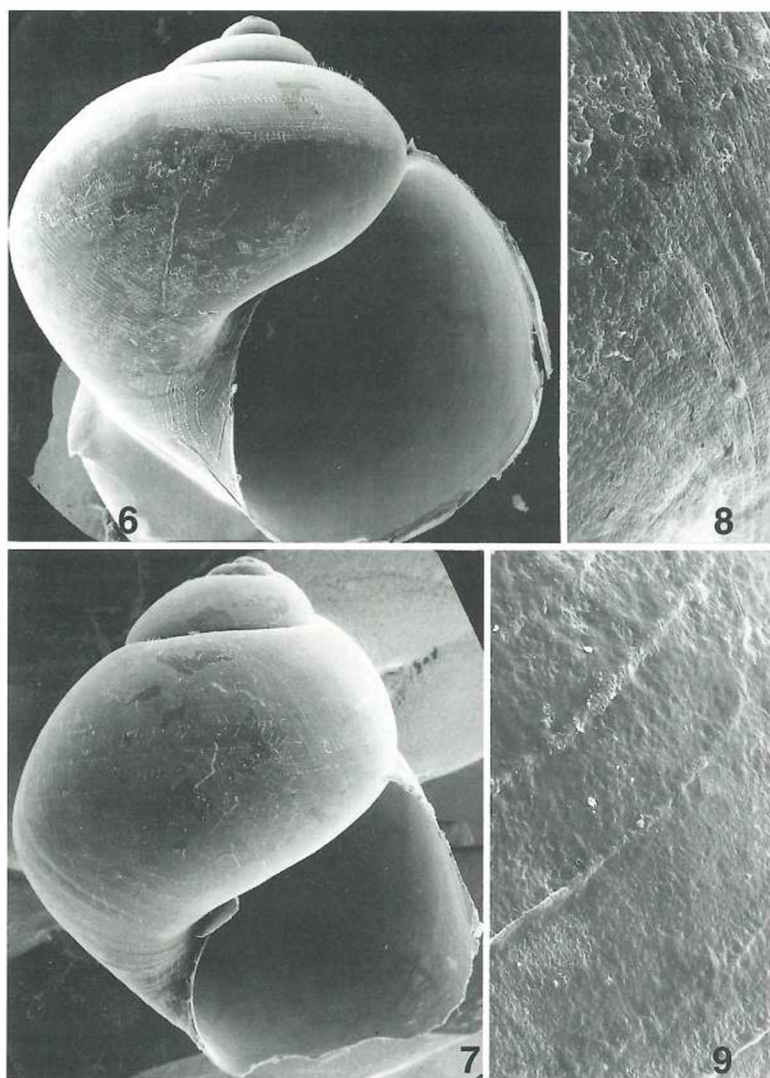
The shell surface at the region nearby the apical whorls (Figs. 3-5 and 8-9) is fine-sculptured with variously developed and densely arranged spiral and radial lines in all the species (Figs. 3-5 and 8) except *V. hellenicus*, the sculpture of which is not dense (Fig. 9). The sculpture of the surface of the later whorls (Figs. 1-2, 6-7 and 14-18) presents a varied spiral and radial pattern including growth lines, spiral lines, and bristles. The radial sculpture is interspecifically varied, from conspicuous (Figs. 1, 10 and 14) to not conspicuous (Figs. 2, 6, 16 and 17) or even vestigial (Figs. 7 and 18). Similarly, the spiral striae (Table 1) may be prominent, apparently elevated (Figs. 16 and 17) or flat but not necessarily worse visible than the prominent ones (Figs. 14 and 15). In one species they are vestigial (Fig. 18). The bristles (Figs. 1-2, 6-7 and 14-18) also differ interspecifically. In general, two kinds of bristles can be distinguished: main bristles and accessory ones (Figs. 1-2). The above discrimination seems justified since the two kinds of the bristles are potentially not homologous in the strict sense: both are formed by the mantle edge, but not at the same region of it; namely the main bristles are formed by the lobes mentioned by FRETTER & GRAHAM (1962) while the accessory ones are created outside the lobes. In *V. contectus* only the main bristles are long (Figs. 1 and 14), moderately long in two other species (Figs. 2, 6 and 16-17; Table 1), short in *V. viviparus* (Fig. 15); in *V. hellenicus* they are long but flat and rudimentary (Figs. 7 and 18). Three of the studied species have accessory bristles (Figs. 1-2 and 6) besides main ones (Table 1).



Figs. 1-5: Shells of viviparid embryos. 1-2 - habitus (10x): 1 - *Viviparus contextus*, 2 - *V. acerosus*; 3-5 - surface of initial (apical) whorl (300x): 3 - *V. acerosus*, 4 - *V. viviparus*, 5 - *V. contextus*.

The distribution of characters states the infraspecific variability ranges of which do not overlap (Table 1) was an input to MacCLADE. Preliminary analysis of the character evolution by means of MacCLADE has shown that it is only for character (2): umbilicus breadth that a transformation series can be determined without introducing circular logic. Hence, only character (2) has been assumed to be ordered and all the others to be unordered. The file was processed by PAUP with the exhaustive search option (SWOFFORD, 1991). Two MPRs (Fig. 19) have been found, their length 17, consistency index 0.882, retention index 0.600, rescaled consistency index 0.529, min. 15, max. 20. The above statistics indicates a low amount of homoplasies. The reconstructions, however, are quite different from each



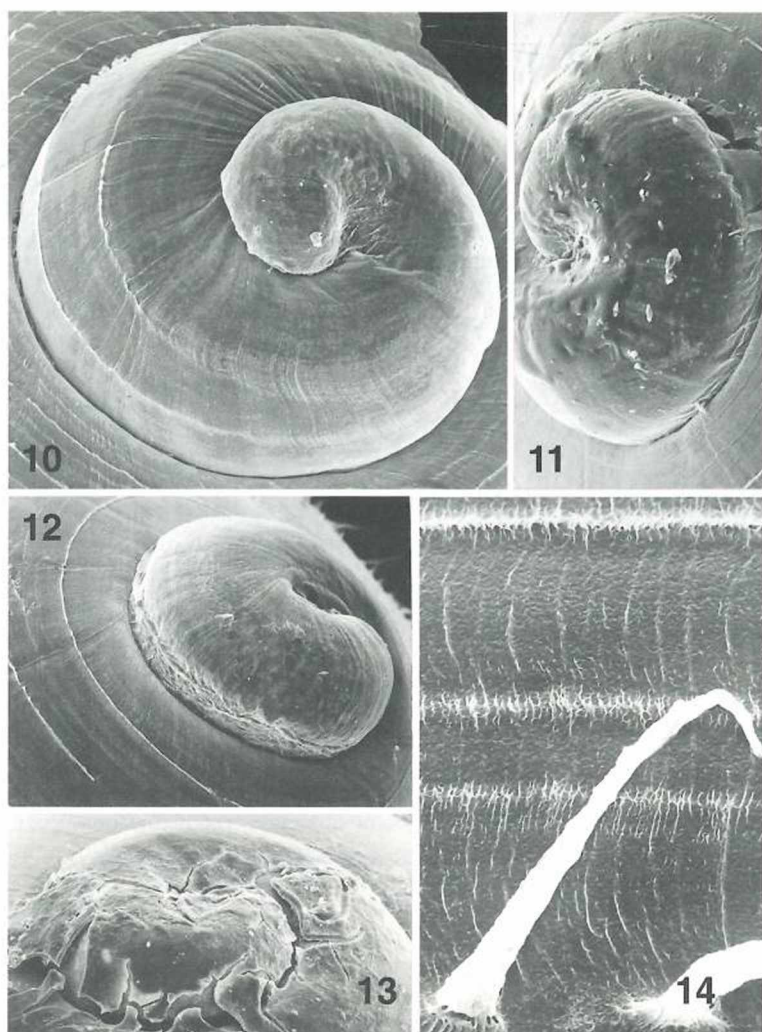


Figs. 6-9: Shells of viviparid embryos. 6-7 - habitus (10x): 6 - *Viviparus ater*, 7 - *V. hellenicus*; 8-9 - surface of initial (apical) whorl (300x): 8 - *V. ater*, 9 - *V. hellenicus*.

other and the consensus tree (constructed by PAUP) presents unresolved polytomies. To visualize the amount of anagenetic change along the branches a „phylogram“ (MADDISON & MADDISON, 1992), the branch lengths proportional to the amount of change (unambiguous events only), has been constructed (Fig. 20).

### Discussion

The thick-walled and well calcified shells of *V. hellenicus* may reflect an ecologically determined variability, since the Trichonis Lake is warm and extremely rich in calcium. Similar modifications of the shell seem rather common in that lake (FALNIOWSKI, ECONOMOU-AMILLI

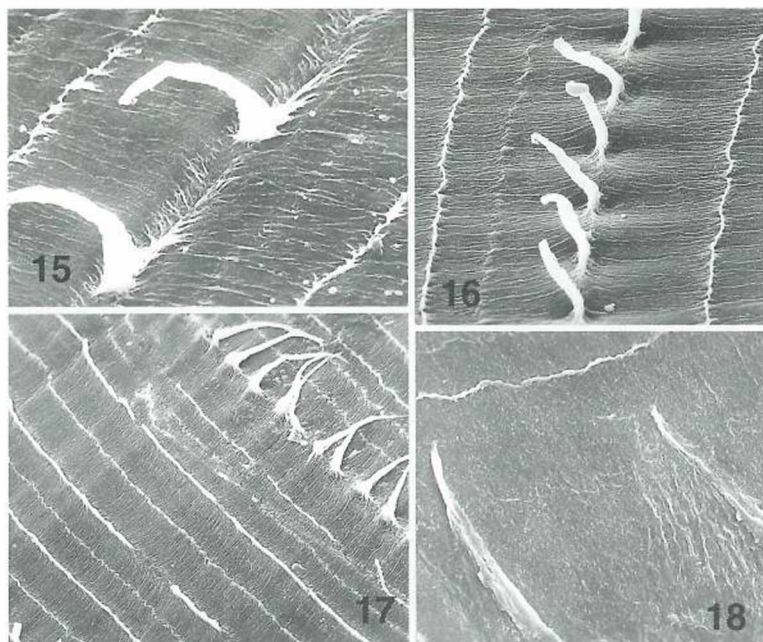


Figs. 10-14: Shells of viviparid embryos. 10-13 - habitus of apical whorls (60x): 10 - *Viviparus contectus*, 11 - *V. acerosus*, 12 - *V. ater*, 13 - *V. hellenicus*; 14 - surface of later embryonic whorls, *V. contectus* (500x).

& ANAGNOSTIDIS, 1988). On the other hand, none such calcification was observed in *V. ater* from the Garda Lake that is similar calcium-rich but not so warm. Any reasonable explanation of the other observed interspecific differences cannot be given.

As it is clear from the above description, photographs and Table 1, the answer to question (1) is: yes, there are interspecific differences between the embryonic shells of the studied species. They can be used in the determination of young specimens and/or embryos, as well as in concluding as to the species separateness. The above results contradict the acknowledging of *V. hellenicus* (CLESSIN, 1879) to be a subspecies of *V. ater* (e.g. SCHÜTT, 1962: *Viviparus ater hellenicus* WESTERLUND, 1886). However, it is not easy to give an explicit answer to question (2).





Figs. 15-18: Surface of later embryonic whorls of *Viviparus*. 15 - *V. viviparus* (500x), 16 - *V. ater* (300x), 17 - *V. acerosus* (150x), 18 - *V. hellenicus* (500x).

Cladists (HENNIG, 1966; WILEY, 1981) and modern evolutionary systematists consider synapomorphies as the only acceptable basis for phylogeny reconstruction. Even considering hypothetical synapomorphies, as the character polarities remain unknown, the number of synapomorphies traced in the studied case is apparently low. From among the ten characters, five must be excluded from phylogeny analysis as uninformative. On the other hand, there are unusually numerous autapomorphies or, more precisely (unknown polarities problem again), character states not shared by at least two species. In fact, only *V. ater* has no such character state, *V. acerosus*, *V. contectus* and *V. viviparus* have one unique character state each, but *V. hellenicus* as many as six (Table 1). The amount of change along the clade terminated with that species is strikingly high, when compared with the other clades (Fig. 20). However, this tells us nothing about the relationships of this species to the others: the latter is clearly visible in the two MPRs found (Fig. 19) showing two different placements of the *V. hellenicus* clade within the group. This clearly reflects, on a taxon- and character-restricted scale, one of the main pitfalls of parsimony and cladistics: a clade representing a relatively high number of unique modifications can be placed almost anywhere within the inferred phylogeny. And in the studied case with no „external data“ (MADDISON & MADDISON, 1992) neither phylogeny nor character evolution can be reconstructed rationally since it is impossible to choose between the inferred MPRs.

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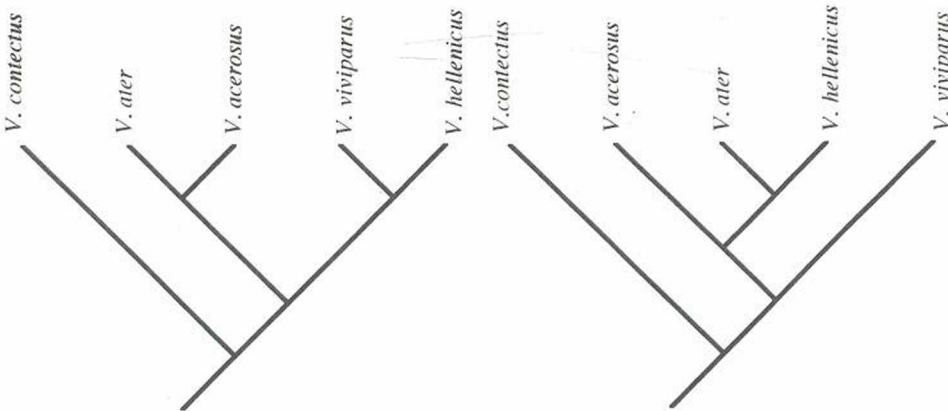


Fig. 19: Two MPRs obtained by the exhaustive search runs by PAUP and drawn with MacCLADE.

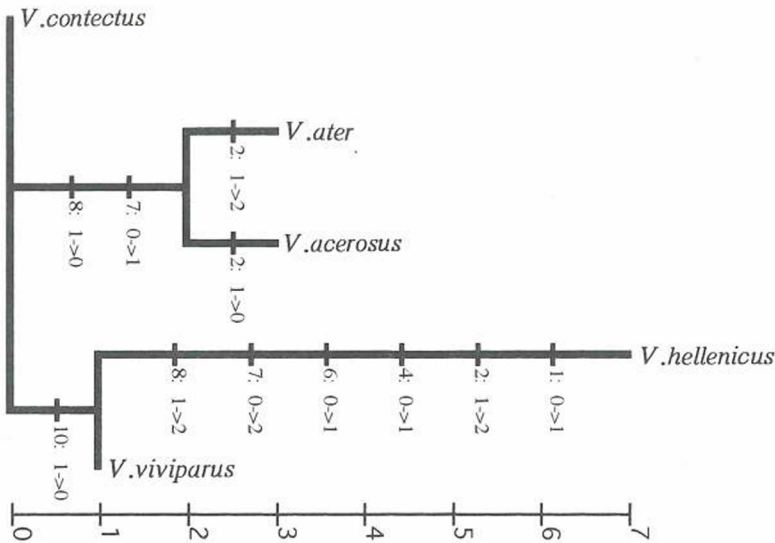


Fig. 20: „Phylogram“ with branch lengths proportional to the amount of change, constructed with MacCLADE of one of the two MPRs presented in Fig. 19. A bar equals one change (unambiguous events only).

	V.acerosus	V.ater	V.contectus	V.hellenicus	V.viviparus
shell outline (1)	0	0	0	1	0
umbilicus (2)	0	2	1	2	1
umbilicus partly covered (3)	0	1	0	1	1
shell thick, calcified heavy, pigmented (4)	0	0	0	1	0
whorl surface (5)	0	0	1	0	0
sculpture on earlier whorls (6)	0	0	0	1	0
later whorl radial sculpture(7)	1	1	0	2	0
later whorl spiral striae (8)	0	0	1	2	1
main bristles (9)	1	1	0	3	2
accessory bristles (10)	1	1	1	0	0

character states: (1): 0 - sphaeroid, 1 - ovi-shaped; (2): 0 - very broad, 1 - broad, 2 - narrow; (3): 0 - no, 1 - yes; (4): 0 - no, 1 - yes; (5): 0 - uniformly convex, 1 - slightly ridged; (6): 0 - dense, 1 - not dense; (7): 0 - conspicuous, 1 - not conspicuous, 2 - vestigial; (8): 0 - prominent, 1 - flat, 2 - vestigial; (9) - 0 - long, 1 - moderately long, 2 - short, 3 - long but flat and rudimentary; (10) - 0 - absent, 1 - present

Tab. 1: Embryonic shell characters and their states.

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