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Tracing the viviparid evolution: radular characters (Gastropoda: Architaenioglossa: Viviparidae)

With 15 SEM Photographs, 2 Figures and 2 Tables

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Abstract. The paper describes the radulae of five European viviparid species: *Viviparus acerosus* BOURGUIGNAT, 1862; *V. ater* (CRISTOFORI et JAN, 1832); *V. contectus* (MILLET, 1813); *V. hellenicus* (CLESSIN, 1879); and *V. viviparus* (LINNAEUS, 1758). SEM photographs and radula statistics are given. Eight characters showing statistically significant ($p = 0.01$) interspecific differences in their states are recorded into multistate characters and the most parsimonious reconstructions (MPR) based on the radular characters is found by PAUP (Phylogeny Reconstruction Using Parsimony) and MacCLADE. From among the eight characters the ancestral states of four are detected on the basis of ontogenetic data and the inferred evolution of the characters is described. In the inferred phylogeny *V. contectus* and *V. ater* are primitive and distant from the other three species; *V. hellenicus* cannot be a subspecies of *V. ater*. Despite that they can hybridize, *V. contectus* and *V. viviparus* are the most distant species.

Kurzfassung. **Auf den Spuren der Evolution der Viviparidae: Merkmale der Radula (Gastropoda: Architaenioglossa: Viviparidae).** - Die Arbeit beschreibt die Radulae von fünf europäischen Arten der Viviparidae: *Viviparus acerosus* BOURGUIGNAT, 1862; *V. ater* (CRISTOFORI et JAN, 1832); *V. contectus* (MILLET, 1813); *V. hellenicus* (CLESSIN, 1879); und *V. viviparus* (LINNAEUS, 1758). REM-Photos und Datenstatistiken zur Radula werden vorgelegt. Acht Merkmale mit statistisch signifikanten ($p = 0.01$) interspezifischen Unterschieden der Merkmalszustände werden zu multiplen Merkmalszuständen rekodiert, die effizienteste Rekonstruktion (MPR) wird mittels der phylogenetischen Analyseprogramme PAUP and MacCLADE ermittelt. Aus den acht Merkmalen werden die ancestralen Merkmalszustände von vier Merkmalen auf der Basis ontogenetischer Daten ermittelt, die daraus zu schließende Evolution der Merkmale wird beschrieben. In der daraus abgeleiteten Phylogenie sind *V. contectus* und *V. ater* primitive, von den anderen drei Arten entfernt stehende Taxa; *V. hellenicus* kann keine Subspezies von *V. ater* sein. Trotzdem sie miteinander Hybriden bilden können, sind *V. contectus* und *V. viviparus* die am weitesten voneinander entfernt stehenden Arten.

Introduction

The relationships of the Architaenioglossa, to which the family Viviparidae belongs, are not clear (HASZPRUNAR, 1988). The same concerns the interrelationships of the old and archaic family. There are a few characters that discriminate species, the morphological distinctness of which is hardly recognizable in many cases (FALNIOWSKI, 1989a, 1990a). Recently an undoubtedly hybrid specimen (*Viviparus contectus* x *V. viviparus*) has been found (FALNIOWSKI, KOZIK & SZAROWSKA, 1993). It seems that evolution within the Viviparidae has slightly affected the morphological characters, thus the speciation events have brought about only a minor morphological change. To test the above hypothesis and explain the relationships

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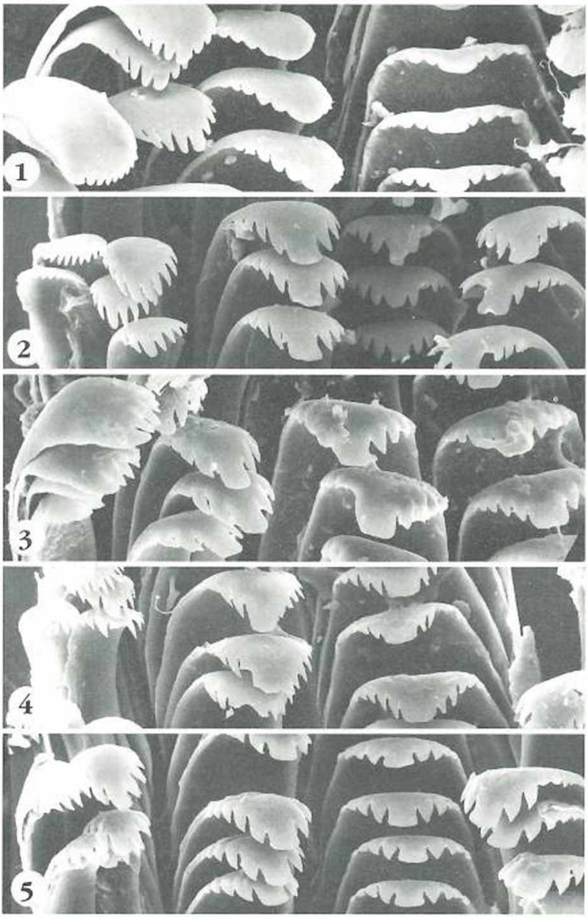


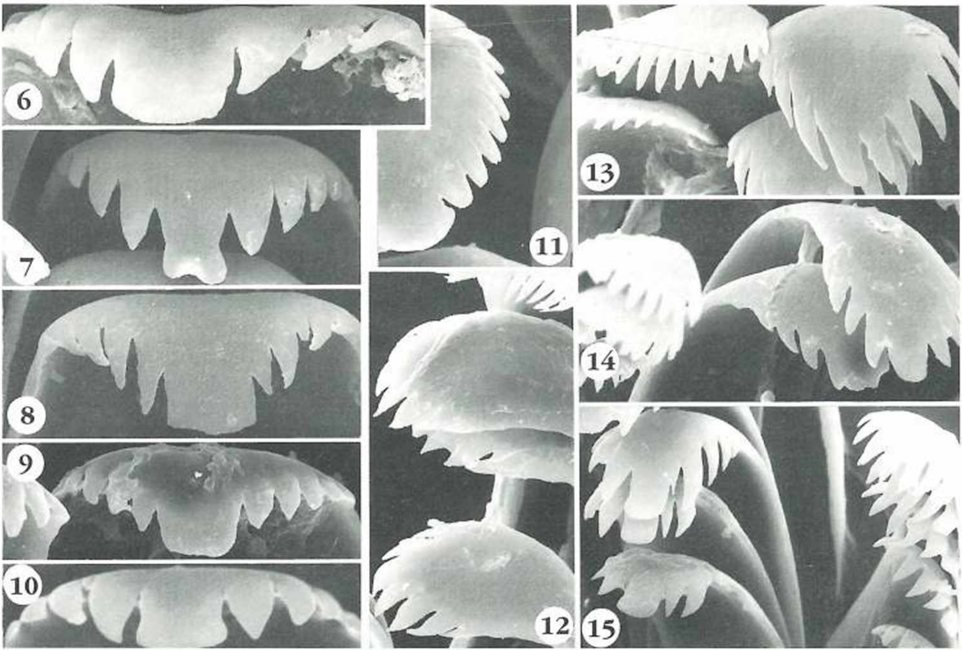
Figs. 1-5: Radula of *Viviparus*, half of a transverse row (200x): 1 - *V. contectus*, 2 - *V. viviparus*, 3 - *V. acerosus*, 4 - *V. ater*, 5 - *V. hellenicus*.

among chosen European species, we have combined morphological and electrophoretic (allozymic) studies. The following viviparid species have been considered: *Viviparus acerosus* BOURGUIGNAT, 1862; *V. ater* (CRISTOFORI et JAN, 1832); *V. contectus* (MILLET, 1813); *V. hellenicus* (CLESSIN, 1879); and *V. viviparus* (LINNAEUS, 1758). The present paper describes the results of the radular studies.

The radulae of the Polish species (*V. contectus* and *V. viviparus*) are described by FALNIOWSKI (1989a, b, 1990a). The variability ranges of the two species are wide and overlapping, which is coupled with only minor interspecific differences in cusp shape and number. Thus, the second aim of the paper is a methodological one: can such characters support a phylogenetic inference?

Material and methods

Numerous specimens of *Viviparus contectus* (MILLET, 1813) and *V. viviparus* (LINNAEUS, 1758) were collected from various localities in Poland. For the radular studies *V. contectus* from small ponds near Kielce, and *V. viviparus* from the Radunia River were chosen. *V.*



Figs. 6-15: Fragments of radulae of *Viviparus*: 6-10 - plate of central tooth: 6 - *V. contectus* (600x), 7 - *V. viviparus* (600x), 8 - *V. ater* (600x), 9 - *V. acerosus* (400x), 10 - *V. hellenicus* (600x); 11-15 - fragments of marginal teeth: 11 - *V. contectus* (outer, 600x), 12 - *V. ater* (400x), 13 - *V. viviparus* (600x), 14 - *V. acerosus* (400x), 15 - *V. hellenicus* (400x).

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, the 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. The gastropods were dissected under a stereoscopic microscope, and the buccal mass was boiled in 10 % KOH. Then the radulae were cleansed in CLOROX for 10 minutes, next rinsed for 15 minutes in distiled water. For each species five radulae were rinsed twice in absolute ethanol, dried, mounted with a two-sided adhesive tape on a holder and coated with gold. The material was examined with a Jeol JSM-35 scanning electron microscope. SEM photographs were taken at a half of the radula length to show the teeth that were completely developed yet not deformed through usage. Other radulae were put in Faure's fluid and examined and measured under a light microscope. For each species 10 radulae were measured by means of an ocular micrometer.

Descriptive statistics (Table 1) was performed on a Macintosh IIvx microcomputer using the SYSTAT 5.2.1 package (Wilkinson, Hill & Vang, 1992). Since the samples were scarce, and the distribution of the variables, especially the countable characters (Sokal & Rohlf, 1987), was apparently not normal, both parametric univariate techniques and multivariate techniques had to be abandoned. On the other hand, there was no cause to contradict both the continuity and one distribution shape for every studied populations (species). Thus we applied Kruskal-Wallis nonparametric tests (with SYSTAT), analogous with the independent groups t-test and one-way ANOVA for each character. No statistically significant sexual dimorphism found in the radular characters of every species, comparisons were made for each pair of species, regardless of the sexes. The characters, the states of which had shown statistically significant ($p = 0.01$) interspecific differences, were then recoded into multistate characters. Since the distributions were as a rule not normal, usually not means but medians were recoded, because of the robustness of the latter (with a breakdown point as high as 0.5: Jajuga, 1993). The medians were used as an input for the Macintosh MacCLADE (Maddison & Maddison, 1992). Its Nexus-format file was proces-

Table 1: Descriptive statistics of the radulae of the studied viviparid species.

		V.acerosus		V.ater		V.contectus		V.hellenicus		V.viviparus	
		m	f	m	f	m	f	m	f	m	f
	n	6	4	5	5	4	6	4	6	6	4
radula	min./max.	5.30-6.10	5.30-6.30	4.00-5.10	4.00-4.90	4.70-7.20	4.10-5.80	3.20-3.60	2.50-3.60	3.90-4.80	2.70-4.00
length	mean/med.	5.77/5.80	5.73/5.65	4.38/2.20	4.64/4.80	5.45/4.95	5.03/5.05	3.48/3.55	3.30/3.40	4.20/4.10	3.30/3.25
	sd/C.V.	0.29/0.05	0.46/0.08	0.44/0.10	0.38/0.08	1.17/0.22	0.63/0.13	0.19/0.05	0.41/0.12	0.31/0.07	0.55/0.17
radula	min./max.	0.80-0.90	0.90-0.90	0.60-0.70	0.60-0.70	0.70-1.00	0.70-0.80	0.50-0.50	0.50-0.50	0.40-0.70	0.40-0.50
breadth	mean/med.	0.87/0.90	0.90/0.90	0.62/0.60	0.62/0.60	0.80/0.75	0.75/0.75	0.50/0.50	0.50/0.50	0.55/0.55	0.48/0.50
	sd/C.V.	0.05/0.06	0.00/0.00	0.04/0.07	0.04/0.07	0.14/0.18	0.05/0.07	0.00/0.00	0.00/0.00	0.10/0.19	0.05/0.11
transv.	min./max.	76-91	79-93	76-88	80-88	84-148	66-92	70-75	70-77	70-83	70-72
row n	mean/med.	83.5/83.5	84.3/82.5	82.2/81.0	85.2/87.0	102.5/89.0	81.5/82	73.5/74.5	73.2/72.0	74.0/72.5	71.0/71.0
	sd/C.V.	6.66/0.08	6.08/0.07	4.82/0.06	3.27/0.04	30.44/0.30	9.75/0.12	2.38/0.03	3.06/0.04	5.18/0.07	1.15/0.02
cusp on	min./max.	4.00-4.50	4.00-4.50	4.50-5.00	4.00-4.50	4.50-5.00	4.00-5.00	4.00-4.00	4.00-4.50	4.00-4.50	4.50-4.50
rhachis	mean/med.	4.25/4.25	4.13/4.00	4.70/4.50	4.40/4.50	4.88/5.00	4.50/4.50	4.00/4.00	4.17/4.00	4.33/4.50	4.50/4.50
	sd/C.V.	0.27/0.06	0.25/0.06	0.27/0.06	0.22/0.05	0.25/0.05	0.45/0.10	0.00/0.00	0.26/0.06	0.26/0.06	0.00/0.00
inner	min./max.	3.00-4.00	3.00-4.00	4.00-5.00	4.00-5.00	4.00-5.00	4.00-5.00	3.00-4.00	3.00-4.00	3.00-5.00	4.00-5.00
cusp	mean/med.	3.33/3.00	3.50/3.50	4.40/4.00	4.20/4.00	4.75/5.00	4.50/4.50	3.25/3.00	3.33/3.00	4.00/4.00	4.50/4.50
on later	sd/C.V.	0.52/0.15	0.58/0.17	0.55/0.12	0.45/0.11	0.50/0.11	0.55/0.12	0.50/0.15	0.52/0.15	0.89/0.22	0.58/0.13
outer	min./max.	3.00-5.00	3.00-4.00	4.00-4.00	4.00-4.00	4.00-4.00	3.00-4.00	4.00-4.00	4.00-4.00	3.00-4.00	3.00-4.00
cusp	mean/med.	3.67/3.50	3.75/4.00	4.00/4.00	4.00-4.00	4.00-4.00	3.83/4.00	4.00/4.00	4.00/4.00	3.83/4.00	3.75/4.00
on later	sd/C.V.	0.82/0.22	0.50/0.13	0.00/0.00	0.00/0.00	0.00/0.00	0.41/0.11	0.00/0.00	0.00/0.00	0.41/0.11	0.50/0.13
cusp on	min./max.	7.00-9.00	7.00-8.00	8.00-9.00	8.00-9.00	9.00-11.00	9.00-11.00	7.00-10.00	7.00-9.00	9.00-10.00	9.00-10.00
inner	mean/med.	8.17/8.00	7.50/7.50	8.40/8.00	8.40/8.00	10.0/10.0	10.33/10.5	9.00/9.50	8.00/8.00	9.67/10.00	9.25/9.00
margin	sd/C.V.	0.75/0.09	0.58/0.08	0.55/0.07	0.55/0.07	0.82/0.08	0.82/0.08	1.41/0.16	0.63/0.08	0.52/0.05	0.50/0.05
cusp on	min./max.	7.00-10.00	8.00-10.00	8.00-9.00	8.00-10.00	10.0-10.0	9.00-10.00	6.00-7.00	6.00-9.00	7.00-8.00	7.00-8.00
outer	mean/med.	8.33/8.00	9.25/9.50	8.60/9.00	9.20/9.00	10.0/10.0	9.33/9.00	6.50/6.50	7.33/7.50	7.67/8.00	7.75/8.00
margin	sd/C.V.	1.37/0.16	0.96/0.10	0.55/0.06	0.84/0.09	0.00/0.00	0.52/0.06	0.58/0.09	1.21/0.17	0.52/0.07	0.50/0.06
radula/	min./max.	0.14-0.15	0.13-0.14	0.15-0.16	0.15-0.17	0.20-0.28	0.21-0.26	0.16-0.20	0.14-0.19	0.16-0.20	0.19-0.21
/shell	mean/med.	0.15/0.15	0.14/0.14	0.16/0.16	0.16/0.16	0.24/0.24	0.23/0.24	0.17/0.16	0.17/0.18	0.18/0.19	0.19/0.19
length	sd/C.V.	0.01/0.04	0.00/0.03	0.01/0.04	0.01/0.04	0.03/0.13	0.02/0.08	0.02/0.13	0.02/0.10	0.01/0.08	0.01/0.06
radula	min./max.	0.14-0.16	0.14-0.17	0.13-0.15	0.12-0.15	0.14-0.16	0.14-0.17	0.14-0.16	0.14-0.20	0.10-0.15	0.13-0.16
breadth	mean/med.	0.15/0.15	0.16/0.16	0.14/0.14	0.13/0.13	0.15/0.15	0.15/0.15	0.14/0.14	0.15/0.15	0.13/0.14	0.15/0.15
/length	sd/C.V.	0.01/0.06	0.01/0.08	0.01/0.05	0.01/0.09	0.01/0.06	0.00/0.08	0.01/0.06	0.02/0.15	0.02/0.15	0.02/0.10
row n/	min./max.	0.63-0.75	0.65-0.72	0.47-0.63	0.50-0.56	0.49-0.60	0.54-0.74	0.43-0.51	0.36-0.48	0.54-0.59	0.38-0.56
/rad len	mean/med.	0.69/0.68	0.68/0.67	0.53/0.52	0.54/0.55	0.54/0.54	0.62/0.61	0.47/0.48	0.45/0.47	0.57/0.57	0.46/0.46
* 10	sd/C.V.	0.04/0.06	0.03/0.04	0.06/0.12	0.03/0.05	0.04/0.08	0.07/0.12	0.04/0.08	0.05/0.10	0.02/0.03	0.08/0.16

	V.acerosus	V.ater	V.contectus	V.hellenicus	V.viviparus
radula breadth (1)	0	1	2	3	3
transverse row number (2)	1	1	1	0	0
number of lateral cusps on rhachis (3)	0	1	1	0	0
cusps on inner edge of lateral tooth (4)	0	2	2	0	1
cusps on inner marginal tooth (5)	0	0	1	0	1
cusps on outer marginal tooth (6)	1	2	2	1	0
radula length/shell length proportion (7)	0	1	2	1	1
transverse row breadth (8)	2	1	1	0	1

character states: 0 - narrow, 1 - rather narrow, 2 - rather broad, 3 - broad; (2): 0 - approximately 73 rows, 1 - approximately 84 - 90 rows; (3): 0 - to 4.5, 1 - to 5; (4): 0 - 3 - 4 cusps, 1 - 3 - 5 cusps, 2 - 4 - 5 cusps; (5): 0 - 7 - 10 cusps, 1 - 9 - 11 cusps; (6): 0 - 7 - 8 cusps, 1 - 6 - 10 cusps, 2 - 8 - 10 cusps; (7): approximately: 0 - 0.14, 1 - 0.16 - 0. 19, 2 - 0.24; (8): median: 0 - 0.047 mm, 1 - 0.055 - 0.058 mm, 2 - 0.068 mm

Table 2: Input matrix for the MacCLADE - characters and their state.

sed by PAUP (Swofford, 1991) with the exhaustive search option to find the shortest, most parsimonious (Swofford & Olsen, 1990; Weir, 1990) tree. The latter was then processed by MacCLADE to analyze the character evolution and print cladograms.

Results

Characters

The radulae (Figs. 1-15) are typically taenioglossate, showing basically the same pattern in all the studied species (Figs. 1-5). The rhachis (Figs. 6-10) has no basal cusps. In *V. hellenicus* the lateral cusps on the rhachis (Figs. 5 and 10) are somewhat broader and more massive than in the other species (Figs. 1-4 and 6-9). Similar interspecific differences can be observed for the lateral and marginal teeth (Figs. 1-5 and 11-15), but all the differences are slight and not constant because of their considerable variability.

The measurements of radula length and breadth as well as the counts of the transverse rows and of cusps on a given tooth are summarized in Table 1. To avoid the direct impact of size differences among the species, three proportions were calculated for each case: radula : shell length, radula breadth : radula length, row number : radula length (Table 1). All the 11 biometrical parameters were tested for sexual dimorphisms for each species, by means of Kruskal-Wallis test, and no sexual dimorphism was found. Therefore the following analyzes were performed for both sexes together.

From among the 11 characters (Table 1) tested by the Kruskal-Wallis test, statistically significant (significance level 1%) interspecific differences were found in eight (Table 2). For each character the test results determined a character-state grouping. The descriptions and distributions of the character states, given in Table 2, were used as an input for MacCLADE and PAUP. The resulting tree is presented in Fig. 16.

Character evolution

To analyze character evolution as well as phylogeny not introducing a pure intuitional bias and/or circular logic, the tree must be rooted. This is usually accomplished by outgroup comparisons. However, one has to have such an outgrouper(s), and an improperly chosen outgroup may cause serious problems (e.g. WILEY, 1981; SWOFFORD & OLSEN, 1990). With the Viviparidae it was impossible for us to find an adequate outgroup. Therefore the only way to polarize at least part of the characters was to use ontogenetic data. Fortunately, found in the brood pouch, the embryos of those viviparid (ovo-viviparid) gastropods are available in various stages. The embryonic radulae of each species were examined and the presumptive ancestral (plesiomorphic) states were found for four of the characters (cusp numbers). The polarity of the other four states were to be estimated indirectly, from the inferred phylogeny rooted by the distribution of the former four character states.

Character (1) - radula breadth, with three states, seems unordered. The state „broad“ is a synapomorphy of *V. hellenicus* and *V. viviparus*, but which of the other three states is ancestral cannot be decided unequivocally. It must be stressed that Equivocal Cycling (MADDISON & MADDISON, 1992) has resulted in 13 equivocal reconstructions of this character evolution. On the other hand, the states of the character are neither distinct nor objectively distinguishable although separated by statistically significant discontinuities, so the character is of minor usefulness in the reliable reconstruction of the phylogeny and thus was weighted lower than the other characters (0.5 instead of 1).

Character (2) - number of transverse rows, with two states, is ordered. Unequivocally *V. hellenicus* and *V. viviparus* share the reduction of the row number as a synapomorphy, while a higher number of rows is a primitive character state.

Character (3) - number of lateral cusps on the rhachis, with two states, is apparently an ordered character. In the embryonic radulae the number oscillates between 5 and 6 in young embryos, so the reduction of the number seems derived. Therefore *V. acerosus*, *V. hellenicus* and *V. viviparus* share a synapomorphic reduction, and *V. contectus* and *V. ater* are plesiomorphic as to the character. For this character, like for character (2), Equivocal Cycling (MADDISON & MADDISON, 1992) has shown only one possible reconstruction.

Character (4) - number of cusps on the inner edge of a lateral tooth, with three states,

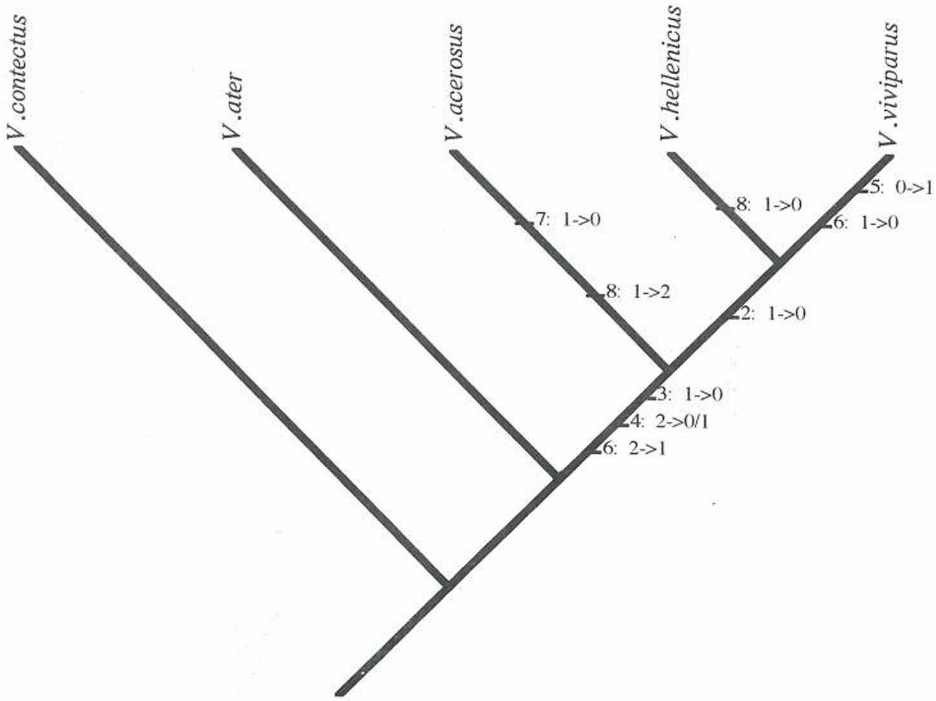


Fig. 16: Cladogram resulting from PAUP (exhaustive search option - the one tree found), only the unambiguous changes marked on the branches.

seems an ordered character. In the embryonic radulae the number varies between 5 and 6 in young embryos, so the interpreting of the reduction as an apomorphy seems justified. The reduction is the most advanced in *V. acerosus* and *V. hellenicus*, but it can be either a synapomorphy or parallelism. *V. contectus* and *V. ater* share a symplesiomorphic primitive state, and *V. viviparus* is autapomorphic.

Character (5) - number of cusps on an inner marginal tooth, with two states, seems an ordered character. Each of the two states can be primitive according to Equivocal Cycling, but the radulae of the young embryos have 10-16 cusps, thus the reduction from 9-11 to 7-10 is probably a derived state. Hence *V. acerosus, V. ater* and *V. hellenicus* share a synapomorphic reduction, *V. contectus* has a primitive state, but the same primitive state in *V. viviparus* may be an effect of the reversed evolution (paedomorphosis ?).

Character (6) - number of cusps on an outer marginal tooth, with three states, may be either ordered or unordered. The number observed in the radulae of young embryos is 10-15. Thus, for this character also, reduction seems a derived state. *V. contectus* and *V. ater* share a symplesiomorphic state, *V. acerosus* and *V. hellenicus* a synapomorphy, while *V. viviparus* is autapomorphic.

Character (7) - proportion of radula length to shell height, with three states, seems an ordered character. Indirectly, from the tree topology rooted on the basis of cusp ontogenetic data, the evolutionary trend to reduce the proportion can be deduced. The most primitive is proportionally the longest radula of *V. contectus*, the shortest one of *V. acerosus* is an autapomorphy, and the other three species share a synapomorphic moderately advanced reduction.

Character (8) - breadth of a transverse row (proportion of radula length in mm to transverse row number), with three states, is an unordered character. Unequivocally, state 1 (middle of the overall range) is primitive. The evolution in both directions has affected the proportion, resulting in two autapomorphies, so the character in uninformative to relationships weighting.

Inferred phylogeny

The PAUP runs with the exhaustive search option (SWOFFORD, 1991) have resulted in one tree (Fig. 16) rooted according to the ontogenetic criteria described above, characterized by the following statistics: tree length 16, 15-16 changes, minimum 14, maximum 20 changes, consistency index (MADDISON & MADDISON, 1992): 0.875, retention index: 0.667, rescaled consistency index: 0.583. The relatively low values of the above indices reflect the relatively low number of parallelisms and reversals in the character evolution during the inferred phylogenetic process.

The evolution pattern considered in the most rigourous way, i.e. based on unambiguous character changes only, presents the cladogram in Fig. 16. The most primitive *V. contectus* and *V. ater* are not separated by any unambiguous change. Three changes distinguish the clade with the other three studied species. Within the clade two unambiguous changes are inferred on the branch terminated with *V. acerosus*, and one distinguishes the two-species clade. Within the latter, one change along the branch terminated with *V. hellenicus*, and two along the one terminated with *V. viviparus*, are found.

To summarize not only the unambiguous changes, and to visualize the amount of evolutionary change within the various clades of the inferred phylogeny, a „phylogram" (MADDISON & MADDISON, 1992) with a vertical branch length scaled proportional to the amount of anagenetic change, has been constructed (Fig. 17). It clearly distinguishes the primitive and relatively close species: *V. contectus* and *V. ater*, from the more advanced and differentiated group of the other three species, out of which *V. viviparus* and *V. hellenicus* are the most advanced.

Discussion

The radula is the first applied anatomical structure in taxonomical studies on the Gastropoda (e.g. DYBOWSKI, 1884; for references see FALNIOWSKI, 1989a, 1990a). Although the radula reflects feeding adaptation, thus gastropod macro-evolution (FRETTER & GRAHAM, 1962; PURCHON, 1977), its usefulness in relationships weighting is often restricted and problematic, because of its considerable variation and numerous homoplasies (FALNIOWSKI, 1983, 1990a, b). In the viviparids studied all the radulae are basically the same, the interspecific differences slight and variability intervals overlapping. Results of the earlier studies based on two of the five viviparids in question (*V. contectus* and *V. viviparus*: FALNIOWSKI, 1989a, b, 1990a) are similar to the ones of this study. On the other hand, the results of statistical and parsimony-based analysis, as presented above, are promising. The inferred phylogeny is internally consistent, but of course it is to be compared with what can be deduced from other morphological as well as molecular data.

Although ontogeny need not exactly reflect phylogeny, it usually does in the way that derived character states appear later in ontogeny than primitive ones (e.g. WILEY, 1981). Thus ontogenetic data, although less often used as an outgroup criterion, can successfully be exploited to detect a character state polarity. The reduction of the cusp number on all the radula teeth seems almost a general rule, observed not only in the Viviparidae but also in the pulmonate, basommatophoran Lymnaeidae (ROSZKOWSKI, 1927; FELIKSIAK, 1939; FALNIOWSKI, 1983).

Another evolutionary trend observed within the inferred phylogeny is the reduction of radula length. It is visible in the reduction of transverse row number in the most advanced

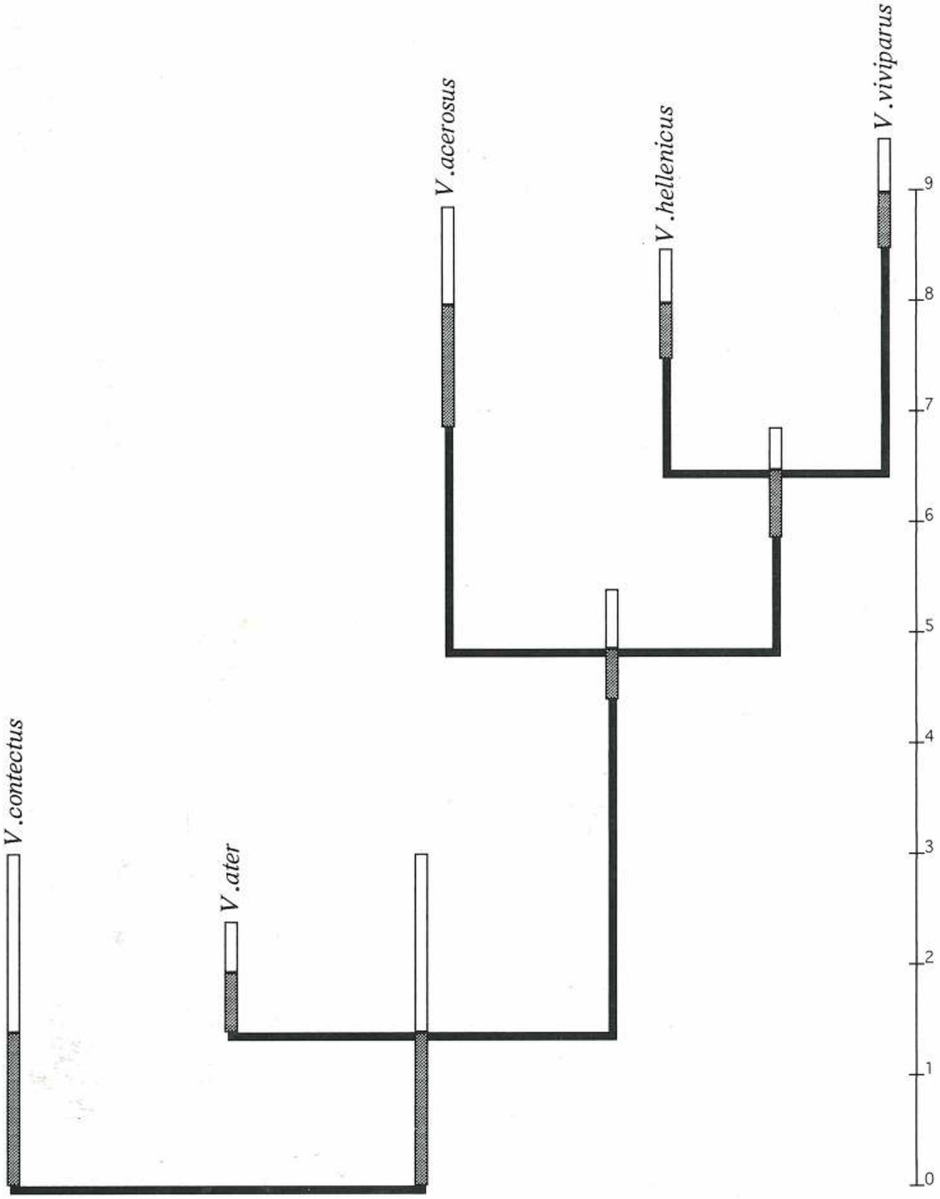


Fig. 17: The same tree as in Fig. 16, generated by MacCLADE as a „phylogram“, i.e. the branch lengths made proportional to the amount of evolutionary change along a branch (to the scale on the right, in steps). Black vertical parts on the branches reflect minimum possible changes; shaded parts, average possible changes; white bars, maximum possible changes (steps).

species. However, it may partly be due to the smaller dimensions of the gastropods. On the other hand, the same tendency is observed in the proportion of the radula length to the shell height, which means the reduction of the proportional length of the radula. The two tendencies may have the same background: the evolutionary progress of the ciliary, filtratory feeding mechanism of viviparids (COOK, 1949; FRETTER & GRAHAM, 1962) must have resulted in the diminishing importance of the radula. The size reduction of the latter is therefore not surprising.

The inferred phylogeny shows the longest distance between *V. contectus* and *V. viviparus*, despite the observed hybridization. This confirms our earlier hypothesis (FALNIOWSKI, KOZIK & SZAROWSKA, 1993) that the two species are so distant in time from their common ancestor that the isolating mechanisms have become not effective enough to prevent hybridization.

The inferred phylogeny clearly indicates that the relationships between *V. ater* and *V. hellenicus* are quite distant. Contrary to what is acknowledged by some authors (e.g. SCHÜTT, 1962: *Viviparus ater hellenicus* WESTERLUND, 1886) the latter surely cannot be a subspecies of the former.

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