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Differences in the radula of the genus *Melanopsis* in the Jordan Valley, Israel (Gastropoda: Cerithioidea: Melanopsidae)

With 4 tables and 17 figures

KRYSTYNA MAZAN-MAMCZARZ, JOSEPH HELLER & MAGDALENA SZAROWSKA

Abstract. This paper describes the radulae of five *Melanopsis* taxa from the Jordan Valley, Israel: *M. buccinoidea* OLIVIER, 1801, *M. meiostoma* HELLER & SIVAN, 2000, *M. costata costata* OLIVIER, 1804, *M. costata jordanica* ROTH, 1839, and *M. saulcyi* BOURGUIGNAT, 1853. SEM photographs are given. Interspecific differences in 15 biometrical characters were analyzed by means of descriptive statistics and Kruskal-Wallis test. To illustrate the phenetic grouping, PCA, nonmetric MDS and UPGMA cluster analysis based on the Euclidean distance were performed. Phylogenetic analysis was computed with two additive trees techniques: neighbour-joining and Fitch-Margoliash. Eight characters showing statistically significant interspecific differences were applied to reconstruct phylogeny, using MacCLADE and PAUP, and a consensus tree was found. A "phyllogram" with branch length proportional to the amount of change was constructed based on one of the MPR's. The radulae show high intraspecific variation coupled with slight interspecific differences and the overlapping variability intervals. The results confirm the conchological and allozymic distinctness of *M. costata costata*, *M. costata jordanica* and *M. saulcyi*, the distinctness of the shell morphology of *M. meiostoma*, and reveal considerable differentiation on the radula of *M. buccinoidea*.

Key words. Cerithioidea, Melanopsidae, *Melanopsis*, radula, population, variation, multivariate analysis, Israel.

Introduction

The freshwater snail genus *Melanopsis* (FÉRUSSAC, 1807) (Melanopsidae) is one of the most abundant molluscs in the Levant (GERMAIN 1921-22, TCHERNOV 1975, SCHÜTT & BILGIN 1974, BANARESCU 1990-95, GLAUBRECHT 1993). The shell is extremely variable, with smooth and costate, elongate and stout, banded and all-black forms found in a relatively small area.

In a conchometric study of *Melanopsis* in northern Israel, HELLER et al. (1999) and HELLER & SIVAN (2000) recognized four species: those with smooth shells (*M. buccinoidea* OLIVIER, 1801); smooth shells and a narrow mouth (*M. meiostoma* HELLER & SIVAN, 2000); straight-

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Authors' addresses:
Dr. Krystyna Mazan-Mamczarz and Dr. Magdalena Szarowska, Department of Malacology, Institute of Zoology, Jagiellonian University, ul. R. Ingardena 6, 30-060 Kraków, Poland; e-mail: mazan@zuk.iz.uj.edu.pl
Prof. dr. hab. Joseph Heller, Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel; e-mail: heller@vms.huji.ac.il

ribbed shells that almost always extend the entire length of the whorl (*M. costata* Olivier, 1804); and tubercle-ribbed shells that do not extend the entire length (*M. saulcyi* Bourguignat, 1853). Hybrids (characterized by very weak ribs) were found in narrow zones of contact, both between *M. buccinoidea* and *M. costata* and between *M. buccinoidea* and *M. saulcyi*. Within *M. costata* Heller et al. (1999) further recognized three subspecies: *M. c. costata* Olivier, 1804 (shell elongate), *M. c. jordanica* Roth, 1839 (shell usually stout), and *M. c. noetlingi* Bourguignat (ribs consisting of a pronounced upper tubercle, fused to a straight lower ridge).

A comparative study of the sperm (Hodgson & Heller 2000) supported the separation of *M. buccinoidea*, *M. costata*, *M. saulcyi* and *M. meisostoma*. An allozyme study (Falniowski et al. submitted) revealed that *M. c. costata*, *M. c. jordanica* and *M. saulcyi*, each of them conchometrically distinct, appeared also allozymatically as distinct biological units, though very close to each other. *M. buccinoidea* was scattered in each of the big clusters, suggesting that it is a distinct species but with some level of hybridization with other species. However, *M. meiostoma* always adjoined *M. saulcyi*, and its position as a distinct species was not confirmed.

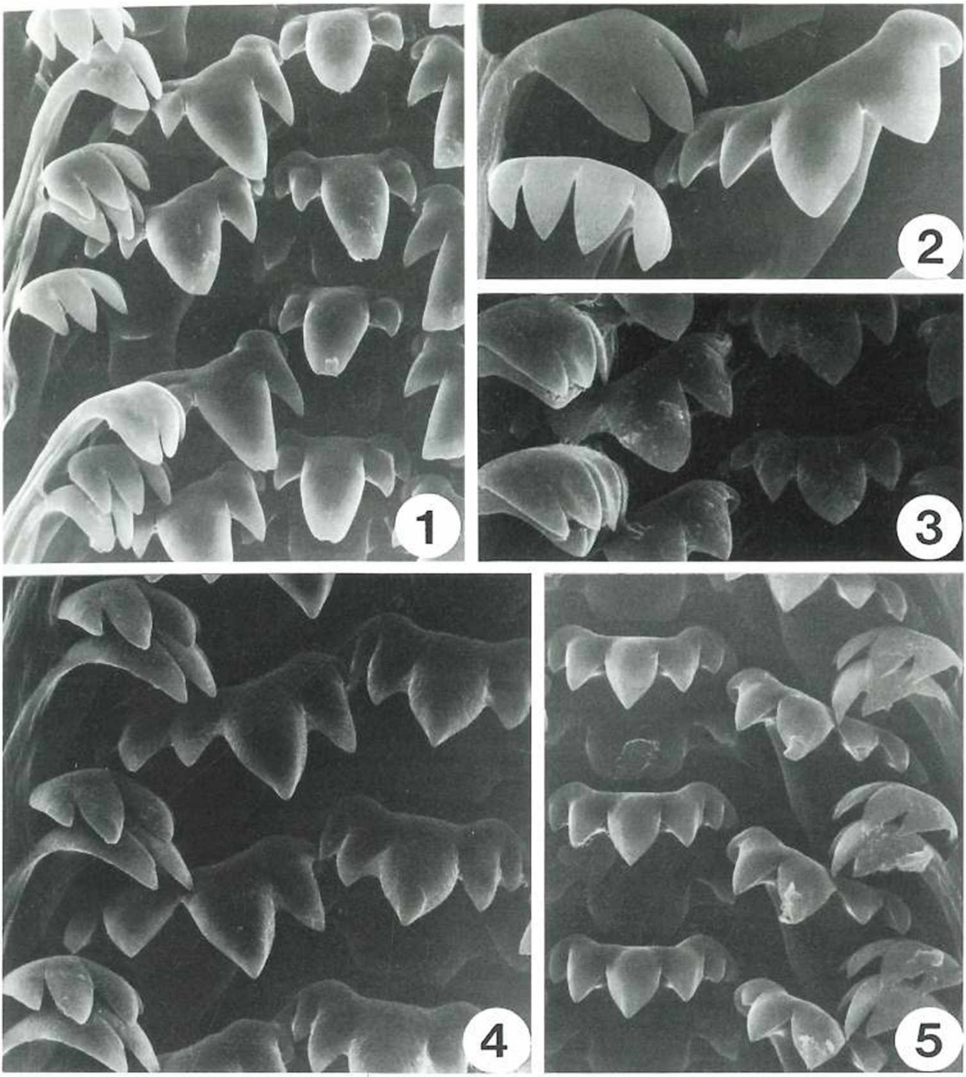
This present study explores whether *M. buccinoidea*, *M. meiostoma*, *M. c. costata*, *M. c. jordanica* and *M. saulcyi* appear as distinct biological units in another molluscan character, the radula.

Material and methods

In September 1998, 26 *Melanopsis* samples were collected at 23 localities in the Jordan Valley, Israel: 1. Enot Huga (IG 200-213); 2. En Hanatziv (IG 197-208); 3. En Raqqat, spring (IG 199-245); 4. Dan (IG 212-295); 5. Sede Eliyahu (IG 198-204); 6. Banias (IG 214-294); 7. Nahal Tavor (IG 201-223) 8. En Haruv. (IG 211-240); 9. Kinneret, Ginossar (IG 209-250); 10. Kinneret, 208 (IG 209-253); 11. Kinneret, En Raqqat (IG 199-245); 12. Kinneret, En Sheva (IG 201-252); 13. Kinneret, Ha'on (IG 208-237); 14. Kinneret, Bet Gavriel (IG 205-234); 15. Upper Jordan River, Gesher Benot Ya'aqov (IG 209-269); 16. Upper Jordan River, Gesher Lehavot (IG 209-283); 17. Upper Jordan River, Eastern Canal (IG 208-278); 18. Bet Hillel (IG 207-289); 19. Sede Nehemia (IG 208-288); 20. En Hanatziv (IG 197-208), 21. Sheluhot (IG 196-209); 22. Hamat Gader, 15 m from spring (IG 213-232); 23. Nahal Tavor (IG 201-223); 24. Enot Huga (IG 200-213); 25. Hamat Gader spring (IG 213-232); 26. En Malkoah (IG 198-198). Chosen because their populations were investigated in both the conchometric and the allozyme studies, these above enlisted localities are described in further detail by Falniowski et al. (submitted).

For this radulae study, specimens were taken whose hepato-pancreas had earlier been used for the electrophoresis study of Falniowski et al. (submitted). These specimens were kept in 70 % ethanol until they were dissected under a stereoscopic microscope; next the radulae were cleaned in CLOROX for about three minutes and rinsed for five minutes in distilled water. For each population two radulae were rinsed twice in absolute ethanol, dried, mounted with a two-sided adhesive tape on a holder, coated with gold and examined with a JSM-35 scanning electron microscope. To show teeth that were completely developed yet not deformed through usage, SEM photographs were taken from the mid section of the radula length. Other radulae (ten for each population) were put in Faure's fluid and examined and measured under a light microscope, using a calibrated ocular micrometer.

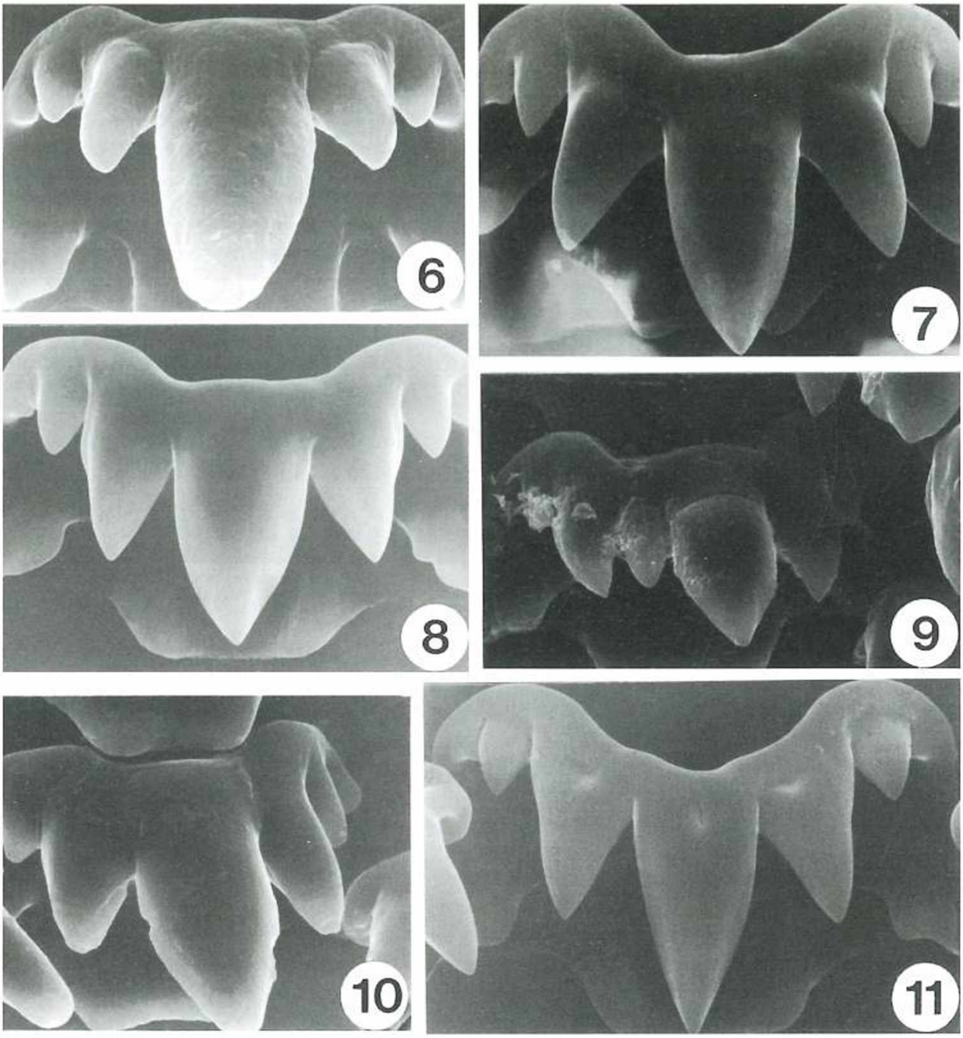
The following radula measurements were made: radula length, radula breadth, total transverse rows number, forming transverse rows number, cusps on inner edge of lateral tooth, cusps on outer edge of lateral tooth, cusps of inner marginal tooth, cusps of outer marginal tooth, rhachis breadth, central cusp on rhachis length (difference between length of central cusp and length of neighbouring cusp). To avoid the direct impact of size differences among the species, the following proportions were calculated: radula length : shell breadth, radula length : mouth height, radula breadth : radula length, total rows number : radula length and per cent of forming radula rows.



Figs 1–5: Fragments of radulae: 1 – *Melanopsis meiostoma*, half of a transverse row (500×); 2 – *M. costata costata*, lateral and marginal teeth (1000×); 3–5 – half of a transverse row: 3 – *M. costata jordanica* (750×), 4 – *M. buccinoidea* (500×), 5 – *M. saulcyi* (750×).

Descriptive statistics (Sokal & Rohlf 1996) were computed on PC microcomputer by means of the SYSTAT 5.03 for the Windows package. Then each of the radular characters was tested by the Kruskal-Wallis nonparametric test (with SYSTAT), analogous with the independent groups t-test and one-way ANOVA, for significance of differences among the studied populations.

The multivariate techniques (Bookstein et al. 1985, Jajuga 1993, Sokal & Rohlf 1996, Johnson & Wichern 1998) employed in our study included principal component analysis (PCA), nonmetric multidimensional scaling (MDS) and minimum spanning trees (MST). PCA was applied to show the structure of the data with no *a priori* assumption. It was performed for the mean values of each character for each population, to visualize the relation



Figs 6–11: Plate of a central tooth in radulae: 6–7 – *Melanopsis meiostoma* (1500×), 8 – *M. costata costata* (1500×), 9 – *M. costata jordanica* (1000×), 10 – *M. buccinoidea* (1500×), 11 – *M. saulcyi* (2000×).

ships between all of the populations together, with NTSYS (Rohlf 1994). All data were logarithmically transformed (ln+1) and standarized (according to the formula SUBYBAR + DIVSTD). The Euclidean distances between the populations and correlation between the variables were computed. Ten eigenvectors with accompanying eigenvalues, per cent of the total variability explained by the subsequent PC's eigenvectors and per cent variability explained by chance under the broken-stick model (Rohlf 1994) were extracted. Then the original data were projected into PC space, together with MST, to show local distorsions in the data. The resulting projection matrix was used as an initial configuration for the MDS, applied also with superimposed MST (NTSYS: Rohlf 1994). To illustrate phenetic relations among the populations, the UPGMA clustering techinique, based on the Euclidean distances, was calculated with NTSYS.

Multivariate analysis, although useful in visualisation of the internal and external relations of the data, can hardly be applied directly to phylogeny reconstruction. Clustering reflects overall similarity, but should rather not be applied to phylogeny reconstruction, because of its ultrametricity (Swofford & Olsen 1990, Weir 1990). The additive tree model behaves much better (Edwards & Cavalli-Sforza 1964, Cavalli-Sforza & Edwards 1967, Fitch & Margoliash 1967, Felsenstein 1984). The values of Euclidean distances were used to compute the tree of relationships among the populations, by means of FITCH of PHYLIP (Felsenstein 1990). The latter method is based on Fitch-Margoliash's algorithm (Fitch & Margoliash 1967), under the "additive tree model" (Felsenstein 1984, 1990). In Fitch-Margoliash's method the tree is drawn in the form of a phyllogram (Maddison & Maddison 1992), with the branch lengths proportional to the amount of change, thus enabling one to observe not only the tree topology, but also amounts of anagenetic evolution. The neighbour-joining technique (Saitou & Nei 1987) behaves like Fitch-Margoliash for additive data (Rohlf 1994), thus we computed, with NTSYS, also a neighbour-joining tree (Swofford & Olsen 1990, Rohlf 1994).

The continuous characters, whose values had shown statistically significant ($p = 0.01$) interspecific differences, where then recoded into discrete multistate ordered characters. Since the distributions were as a rule not normal, usually not means but medians were recoded, because of their robustness (Jajuga 1993). The medians were used as an input for the Macintosh MacCLADE (Maddison & Maddison 1992). Its Nexus-format file was processed by PAUP (Swofford 1991) to find the shortest, most parsimonious (Swofford & Olsen 1990, Weir 1990) trees. Finally, the majority-rule (set at 50 %) consensus tree was computed with PAUP, and one of the MPR's constructed, in a form of phyllogram, by means of MacCLADE. The drawings were made by means of the graphic facilities of MacCLADE and MacDRAFT 1.26.

Results

The radulae (figs 1–11) are typically taenioglossate, with the same basic pattern in all the studied species. There were always one basalcentral, with three lateral cusps on each of its sides (figs 6–11). In *Melanopsis meiostoma* the central cusp on the rhachis (figs 1, 6–7) was often, but not always, much longer then the neighbouring cusps. Such long central cusps on the rhachis were found in the other species too, but they were much rarer there than in *M. meiostoma* (tables 1, 2). Interspecific differences could be observed in the lateral and marginal teeth (figs 1–5), but they were slight and considerably variable (tables 1, 2).

In principal component analysis (PCA), the per cent of variability explained by the first three PC's was higher than that expected by chance (table 3); they thus reflected the true relationships among the populations. However, the first PC reflects size differences mainly. Therefore, the second and third eigenvectors, also explaining much of the variability (table 3) and representing mainly shape differences (Gould 1977), were used. Projection into the second and third PC space (fig. 12) separated *M. meiostoma* (population 8), and three distinct groups of populations. One group contained populations 9–14 (*M. costata jordanica*), the second comprised populations 15–19 (*M. costata costata*) and the third consisted of populations 5, 20–26 (*M. saulcyi*). On the other hand, populations 1–4, 6, 7 (*M. buccinoidea*) were scattered along the centre and mixed with both *M. saulcyi* and *M. c. costata*. Multidimensional scaling (MDS) gave the same picture as PCA (not shown).

The UPGMA clustering computed on the Euclidean distance (fig. 13), like the PCA and MDS showed the distinctness of *M. meiostoma*. Populations of *M. c. costata* formed one cluster and those of *M. c. jordanica* formed another cluster. These two clusters, each comprising a subspecies of the same species, were not joined together. The branch joining all populations of *M. c. jordanica* was included in the cluster grouping nearly all populations (except 26) representing *M. saulcyi*. On the other hand, population 26 belonging to *M. saulcyi* was joined with populations 1, 2, 7 of *M. buccinoidea*. The three remaining populations of *M. buccinoidea* were scattered in *M. saulcyi* and *M. c. costata* clusters.

Tab. 1: Descriptive statistics of the radulae (populations 1 – 13). Measurements are given in [mm]. N = 10 (except population 2, where N = 4).

Population		1	2	3	4	5	6	7	8	9	10	11	12	13
radula	min.-max.	12.70-16.60	10.80-17.00	8.00-12.90	10.00-14.70	3.20-11.20	10.70-14.10	10.40-14.70	4.70-7.90	7.70-12.90	7.40-11.40	9.80-12.20	8.20-13.10	6.90-10.80
length	mean/med.	14.99/15.30	13.87/13.85	10.11/10.35	12.32/12.50	6.83/6.30	12.35/12.20	12.70/12.40	6.30/5.90	9.84/9.80	9.06/8.90	11.03/11.15	11.27/12.25	8.99/9.50
	sd/C.V.	1.20/8.01	2.91/20.95	1.59/15.68	1.36/11.06	2.78/40.72	1.09/8.81	1.39/10.91	1.29/20.51	1.79/18.18	1.34/5.10	0.84/7.63	1.95/17.30	1.40/5.62
radula	min.-max.	0.40-0.50	0.45-0.55	0.25-0.40	0.40-0.54	0.15-0.40	0.35-0.50	0.35-0.50	0.20-0.30	0.30-0.40	0.25-0.45	0.40-0.45	0.30-0.50	0.30-0.40
breadth	mean/med.	0.45/0.45	0.52/0.55	0.32/0.32	0.45/0.45	0.24/0.22	0.43/0.45	0.41/0.40	0.25/0.25	0.35/0.35	0.35/0.32	0.42/0.40	0.44/0.50	0.35/0.35
	sd/C.V.	0.04/8.11	0.05/9.52	0.042/13.07	0.05/10.50	0.08/35.14	0.04/9.86	0.05/12.60	0.04/16.33	0.04/10.39	0.08/23.33	0.03/6.15	0.08/17.92	0.03/9.52
transv.	min.-max.	183-224	160-235	173-212	161-195	120-199	154-184	195-230	141-212	144-209	161-237	178-225	172-227	166-229
row. n.	mean/med.	203.0/201.0	203.2/209.0	190.9/192.0	176.5/176.5	158.8/64.0	165.1/162.0	213.8/212.0	163.7/162.0	188.9/193.0	186.1/183.0	198.3/196.0	201.4/204.5	192.7/190.5
total	sd/C.V.	11.22/5.53	32.00/15.75	13.44/7.04	10.60/6.00	27.79/17.50	11.72/7.10	10.38/4.86	19.09/11.66	20.81/11.02	23.78/11.29	14.30/7.21	17.63/8.75	21.20/11.00
inner	min.-max.	2-2	2-2	2-2	2-2	2-2	2-2	2-2	2-3	2-2	2-2	2-2	2-2	2-2
cusp on	mean/med.	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.1/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0
later	sd/C.V.	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.32/15.06	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
outer	min.-max.	3-4	3-3	3-4	3-4	3-4	3-5	3-4	2-4	3-5	3-4	3-5	3-5	3-4
cusp on	mean/med.	3.7/4.0	3.0/3.0	3.2/3.0	3.6/4.0	3.5/3.5	3.8/4.0	3.6/4.0	2.6/2.5	3.4/3.0	3.5/3.5	3.3/3.0	3.7/4.0	3.4/3.0
later	sd/C.V.	0.52/13.06	0.00/0.00	0.42/13.18	0.52/14.34	0.53/15.06	0.79/20.76	0.52/14.34	0.70/26.89	0.70/20.56	0.53/15.06	0.67/20.45	0.67/18.24	0.52/15.19
cusp on	min.-max.	3-4	3-4	4-6	4-5	3-7	3-4	3-4	4-5	4-8	4-6	4-5	4-5	4-5
inner	mean/med.	3.4/3.0	3.5/3.5	4.5/4.0	4.5/4.5	4.9/5.0	3.8/4.0	3.9/4.0	4.3/4.0	5.1/5.0	5.0/5.0	4.7/5.0	4.7/5.0	4.8/5.0
margin	sd/C.V.	0.48/15.19	0.58/16.50	0.71/15.71	0.53/11.71	1.29/26.26	0.42/11.10	0.32/8.11	0.48/11.23	1.20/23.47	0.47/9.43	0.48/10.27	0.48/10.28	0.42/8.78
cusp on	min.-max.	3-4	3-4	4-5	3-5	4-7	3-4	4-5	3-5	4-6	5-6	4-6	4-6	4-6
outer	mean/med.	3.3/3.0	3.75/4.0	4.3/4.0	4.3/4.0	5.2/5.0	3.7/4.0	4.2/4.0	4.0/4.0	5.5/6.0	5.5/5.5	5.1/5.0	5.1/5.0	5.3/5.0
margin	sd/C.V.	0.01/14.64	0.50/13.33	0.48/11.23	0.67/15.70	1.03/19.86	0.48/13.06	0.42/10.04	0.67/16.67	0.71/12.86	0.53/9.58	0.57/11.13	0.47/14.47	0.67/12.73
breadth	min.-max.	0.09-0.11	0.01-0.12	0.06-0.10	0.08-0.11	0.04-0.10	0.09-0.11	0.08-0.12	0.05-0.07	0.06-0.10	0.06-0.09	0.08-0.11	0.06-0.12	0.06-0.09
central	mean/med.	0.10/0.10	0.10/0.11	0.08/0.08	0.019/0.10	0.07/0.06	0.10/0.10	0.09/0.09	0.06/0.060	0.08/0.08	0.07/0.07	0.09/0.09	0.09/0.09	0.07/0.07
tooth	sd/C.V.	0.01/9.29	0.02/15.19	0.01/14.10	0.01/8.55	0.02/34.10	0.01/9.01	0.01/12.57	0.01/13.44	0.01/17.48	0.01/13.80	0.01/8.46	0.02/27.32	0.01/11.32
central	min.-max.	0.000-0.010	0.004-0.006	0.000-0.012	0.000-0.008	0.000-0.012	0.004-0.010	0.002-0.008	0.006-0.024	0.006-0.014	0.004-0.012	0.004-0.018	0.004-0.010	0.004-0.008
cusp on	mean/med.	0.005/0.005	0.004/0.004	0.006/0.004	0.004/0.004	0.004/0.004	0.007/0.006	0.004/0.004	0.016/0.017	0.010/0.010	0.007/0.007	0.010/0.010	0.007/0.007	0.006/0.006
rhachis l.	sd/C.V.	0.003/71.36	0.001/22.22	0.004/74.91	0.002/63.07	0.003/82.33	0.002/24.95	0.002/47.35	0.005/31.38	0.003/27.43	0.002/29.86	0.004/40.34	0.003/36.27	0.002/27.21
radula l./	min.-max.	1.38-1.68	1.37-1.48	1.13-1.72	0.93-1.57	0.73-1.84	1.29-1.60	1.35-1.62	1.42-1.76	0.97-1.42	0.95-1.15	0.94-1.22	1.06-1.26	0.87-1.09
/shell	mean/med.	1.52/1.52	1.44/1.45	1.40/1.36	1.38/1.40	1.27/1.25	1.42/1.42	1.49/1.49	1.59/1.60	1.21/1.21	1.07/1.09	1.12/1.14	1.19/1.22	1.02/1.05
breadth	sd/C.V.	0.09/6.25	0.047/3.24	0.19/13.24	0.13/9.56	0.28/22.02	0.11/7.58	0.08/5.34	0.14/8.54	0.15/12.21	0.07/6.76	0.09/8.40	0.06/5.44	0.08/7.38
radula l./	min.-max.	1.10-1.31	1.04-1.30	0.94-1.47	1.12-1.34	0.67-1.75	1.09-1.41	1.21-1.47	1.31-1.68	0.88-1.32	0.89-1.08	0.97-1.24	1.02-1.32	0.81-1.10
/mouth	mean/med.	1.21/1.20	1.20/1.23	1.22/1.24	1.19/1.24	1.20/11.18	1.20/1.20	1.30/1.30	1.47/1.453	1.14/1.13	1.00/1.03	1.15/1.18	1.15/1.18	1.00/1.04
height	sd/C.V.	0.07/5.62	0.11/9.20	0.16/12.86	0.12/10.17	0.28/23.16	0.10/8.24	0.07/5.68	0.14/9.15	0.15/12.87	0.07/7.11	0.10/8.26	0.10/8.83	0.10/10.41
radula	min.-max.	0.03-0.03	0.03-0.05	0.03-0.04	0.03-0.04	0.03-0.05	0.03-0.04	0.03-0.03	0.03-0.05	0.03-0.04	0.03-0.05	0.03-0.04	0.04-0.04	0.03-0.05
breadth/	mean/med.	0.03/0.03	0.04/0.04	0.03/0.03	0.04/0.04	0.04/0.04	0.03/0.03	0.03/0.03	0.04/0.04	0.04/0.04	0.04/0.04	0.04/0.04	0.04/0.04	0.04/0.04
/length	sd/C.V.	0.00/4.86	0.01/15.41	0.00/10.84	0.00/10.36	0.01/16.77	0.00/6.02	0.00/7.25	0.01/14.35	0.00/10.28	0.01/17.11	0.00/5.04	0.00/3.45	0.00/11.30
row n./	min.-max.	12.23-15.59	13.82-16.61	15.87-25.54	12.59-17.80	17.05-37.50	12.81-14.42	15.21-18.75	20.89-34.89	15.81-23.78	18.67-21.77	17.41-18.90	16.39-21.86	19.49-24.51
/radula	mean/med.	13.59/13.53	14.79/14.36	19.26/18.70	14.46/14.10	25.80/23.36	13.40/13.11	16.94/17.16	26.67/26.72	19.55/19.11	20.63/21.03	17.99/17.80	18.17/17.35	21.65/20.93
length	sd/C.V.	0.95/7.01	1.29/8.75	3.01/15.66	1.58/10.92	7.81/30.30	0.62/4.66	1.13/6.67	4.53/17.00	2.91/14.86	1.11/5.40	0.49/2.74	2.04/11.20	1.90/8.78
transv.	min.-max.	59-67	52-76	51-59	48-61	47-61	47-55	58-71	48-59	53-70	48-74	49-78	29-75	40-90
row n.	mean/med.	63.7/64.5	66.25/68.5	55.8/58.0	55.4/56.0	56.7/57.0	51.2/51.0	65.4/64.5	52.7/53.5	63.6/63.5	59.2/56.5	63.3/64.0	62.5/68.5	62.1/59.0
forming	sd/C.V.	2.83/4.44	10.14/15.31	3.16/5.66	3.57/6.44	4.19/7.39	2.25/4.34	4.06/6.21	3.43/6.52	5.34/8.39	8.24/13.92	8.96/14.15	14.55/23.27	14.42/23.22
% radula	min.-max.	27.44-33.67	31.80-33.83	24.29-33.33	28.20-35.40	30.37-47.50	28.83-33.12	27.23-33.33	25.94-36.87	32.06-36.81	25.32-35.82	22.48-39.00	13.88-35.95	20.83-39.30
forming	mean/med.	31.45/32.16	32.62/32.42	29.39/30.21	31.47/30.76	36.53/35.65	31.10/31.15	30.64/30.89	32.44/32.52	33.80/33.52	31.96/32.94	32.16/33.33	31.07/33.80	32.13/32.02
	sd/C.V.	2.02/6.44	0.86/2.65	2.87/9.76	2.49/7.92	5.97/16.33	1.79/5.76	2.13/6.95	2.97/9.17	1.63/4.83	3.61/65.00	5.47/17.02	6.74/21.68	5.74/17.86

Tab. 2: Descriptive statistics of the radulae (populations 14 – 26). Measurements are given in [mm]. N = 10.

Population		14	15	16	17	18	19	20	21	22	23	24	25	26
radula length	min.-max.	5.50-10.20	7.70-11.10	7.30-12.70	7.20-10.70	8.80-13.30	10.00-12.30	6.10-11.90	9.30-11.80	6.50-9.70	5.20-9.00	7.40-11.00	4.90-6.70	9.10-16.50
	mean/med.	8.78/8.95	9.37/9.35	10.78/11.05	9.37/9.85	11.22/11.15	11.15/11.15	9.87/10.10	10.87/11.00	7.83/7.80	7.38/7.65	9.68/10.25	5.92/6.00	12.74/12.65
	sd/C.V.	1.29/14.73	1.15/2.29	1.53/14.22	1.14/12.20	1.38/12.31	0.72/6.43	1.77/17.95	0.88/8.11	0.99/12.60	1.33/18.06	1.31/13.52	0.71/11.91	2.30/18.01
radula breadth	min.-max.	0.30-0.40	0.30-0.40	0.30-0.50	0.30-0.40	0.40-0.50	0.40-0.45	0.25-0.40	0.35-0.40	0.20-0.30	0.20-0.30	0.30-0.40	0.20-0.25	0.30-0.50
	mean/med.	0.35/0.35	0.35/0.35	0.41/0.42	0.35/0.35	0.42/0.40	0.40/0.40	0.32/0.30	0.36/0.35	0.26/0.25	0.25/0.27	0.33/0.35	0.21/0.20	0.38/0.40
	sd/C.V.	0.04/10.39	0.05/13.47	0.06/13.97	0.04/10.39	0.03/8.32	0.02/3.90	0.05/15.10	0.02/6.62	0.03/12.73	0.05/19.50	0.03/10.07	0.02/10.04	0.05/13.76
transv. row. n. total	min.-max.	153-211	150-182	152-188	155-183	154-185	158-206	129-209	186-231	164-236	145-212	176-216	158-184	189-218
	mean/med.	175.5/175.5	165.0/162.0	171.6/170.5	172.0/174.0	168.2/167.5	178.6/181.0	187.1/193.5	213.9/214.0	200.6/199.5	179.0/179.5	197.3/198.0	171.4/172.0	202.0/201.5
	sd/C.V.	18.77/10.69	13.26/8.04	11.03/6.43	9.78/5.68	10.71/6.37	13.33/7.47	22.70/12.13	16.02/7.49	25.71/12.82	21.70/12.12	11.08/5.61	8.21/4.79	9.26/4.58
inner cusp on later	min.-max.	2-2	2-2	2-2	2-2	2-2	2-2	2-2	2-2	2-2	2-2	2-2	2-2	2-2
	mean/med.	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2./2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0	2.0/2.0
	sd/C.V.	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00	0.00/0.00
outer cusp on later	min.-max.	2-4	3-4	2-4	3-4	2-4	3-4	3-5	3-4	3-4	3-4	3-4	3-4	3-4
	mean/med.	3.4/3.5	3.4/3.0	3.1/3.0	3.1/3.0	2.9/3.0	3.2/3.0	3.5/3.0	3.4/3.0	3.5/3.5	3.1/3.0	3.5/3.5	3.3/3.0	3.8/4.0
	sd/C.V.	0.70/20.56	0.52/15.19	0.57/18.31	0.32/10.20	0.57/19.57	0.42/13.18	0.71/20.20	0.52/15.19	0.53/15.06	0.32/10.20	0.53/15.06	0.48/14.64	0.42/11.10
cusp on inner margin	min.-max.	4-5	4-5	3-4	4-5	3-4	4-4	4-5	4-6	4-5	4-5	4-5	4-6	4-5
	mean/med.	4.7/5.0	4.3/4.0	3.9/4.0	4.4/4.0	3.8/4.0	4.0/4.0	4.4/4.0	5.0/5.0	4.7/5.0	4.3/4.0	4.4/4.0	5.0/5.0	4.3/4.0
	sd/C.V.	0.48/10.28	0.48/11.23	0.32/8.11	0.52/11.74	0.42/11.10	0.00/0.00	0.52/11.74	0.67/13.33	0.48/10.28	0.48/11.23	0.52/11.74	0.47/9.43	0.48/11.23
cusp on outer margin	min.-max.	5-6	4-5	4-5	4-5	3-4	4-5	4-6	5-6	5-6	4-6	4-6	5-6	4-5
	mean/med.	5.3/5.0	4.8/5.0	4.2/4.0	4.2/4.0	3.9/4.0	4.3/4.0	4.9/4.5	5.4/5.0	5.3/5.0	4.7/5.0	4.9/5.0	5.4/5.0	4.1/4.0
	sd/C.V.	0.48/9.11	0.42/8.78	0.42/10.04	0.42/10.04	0.32/8.11	0.48/11.23	0.99/20.29	0.52/9.56	0.48/9.11	0.67/14.36	0.74/15.06	0.52/9.56	0.32/7.71
breadth central tooth	min.-max.	0.05-0.08	0.07-0.10	0.07-0.11	0.06-0.08	0.08-0.11	0.08-0.10	0.06-0.09	0.08-0.10	0.05-0.07	0.05-0.08	0.06-0.09	0.04-0.06	0.06-0.10
	mean/med.	0.07/0.07	0.08/0.08	0.09/0.09	0.07/0.07	0.09/0.09	0.08/0.08	0.08/0.08	0.08/0.08	0.06/0.06	0.06/0.06	0.08/0.08	0.05/0.05	0.08/0.08
	sd/C.V.	0.01/12.09	0.01/12.44	0.01/12.88	0.01/8.18	0.01/10.85	0.01/8.51	0.01/1.23	0.01/9.01	0.01/11.40	0.01/13.06	0.01/12.67	0.01/12.10	0.01/13.80
central cusp on rhachis l.	min.-max.	0.004-0.010	0.004-0.020	0.006-0.016	0.004-0.014	0.004-0.022	0.002-0.008	0.002-0.008	0.004-0.012	0.004-0.012	0.004-0.012	0.004-0.016	0.004-0.008	0.002-0.008
	mean/med.	0.007/0.008	0.010/0.008	0.011/0.011	0.008/0.007	0.013/0.014	0.005/0.004	0.005/0.005	0.007/0.007	0.006/0.006	0.006/0.004	0.009/0.010	0.006/0.006	0.005/0.004
	sd/C.V.	0.002/25.64	0.005/52.21	0.003/31.20	0.003/40.16	0.006/42.97	0.002/44.79	0.002/46.06	0.002/29.86	0.002/41.28	0.003/47.02	0.005/54.42	0.001/25.44	0.002/35.14
radula l./ /shell breadth	min.-max.	0.92-1.20	1.01-1.42	1.06-1.39	0.92-1.54	1.11-1.37	1.32-1.68	1.05-1.47	1.15-1.47	1.12-1.43	1.06-1.63	1.15-1.62	1.16-1.52	1.16-1.82
	mean/med.	1.09/1.12	1.21/1.26	1.26/1.30	1.29/1.35	1.28/1.29	1.42/1.39	1.32/1.35	1.32/1.30	1.31/1.31	1.39/1.37	1.44/1.43	1.30/1.31	1.53/1.54
	sd/C.V.	0.09/8.70	0.13/10.96	0.12/9.67	0.18/13.69	0.07/5.44	0.11/8.06	0.12/9.47	0.10/7.58	0.08/6.48	0.18/12.86	0.15/10.44	0.12/8.88	0.19/12.11
radula l./ /mouth height	min.-max.	0.81-1.13	0.88-1.19	0.92-1.24	0.86-1.38	0.99-1.11	1.14-1.48	0.94-1.42	1.08-1.35	1.03-1.24	0.91-1.53	1.09-1.48	1.06-1.36	0.95-1.63
	mean/med.	1.02/1.02	1.05/1.05	1.09/1.09	1.19/1.24	1.06/1.06	1.27/1.25	1.18/1.17	1.21/1.21	1.12/1.12	1.21/1.19	1.25/1.28	1.20/1.23	1.28/1.28
	sd/C.V.	0.09/9.13	0.10/9.95	0.10/9.20	0.17/14.11	0.04/3.35	0.12/9.34	0.13/11.18	0.08/6.41	0.06/5.72	0.19/15.36	0.12/9.36	0.11/9.52	0.17/13.54
radula breadth/ /length	min.-max.	0.03-0.05	0.03-0.04	0.03-0.04	0.03-0.04	0.03-0.04	0.03-0.04	0.03-0.04	0.03-0.04	0.03-0.04	0.03-0.04	0.03-0.04	0.03-0.04	0.03-0.03
	mean/med.	0.04/0.04	0.04/0.04	0.04/0.04	0.04/0.04	0.04/0.04	0.04/0.04	0.03/0.03	0.03/0.03	0.03/0.03	0.03/0.03	0.03/0.03	0.04/0.04	0.03/0.03
	sd/C.V.	0.01/14.96	0.00/10.61	0.00/4.75	0.00/6.36	0.00/10.98	0.00/5.42	0.00/14.33	0.00/6.92	0.00/7.33	0.00/9.00	0.00/8.94	0.00/10.03	0.00/8.36
row n./ /radula length	min.-max.	15.94-35.45	13.87-20.91	12.99-20.82	15.66-21.90	13.08-17.50	14.71-18.39	16.52-24.97	17.67-22.00	21.03-31.25	20.89-27.88	18.44-27.43	25.69-32.69	12.30-20.77
	mean/med.	20.64/18.96	17.81/18.27	16.18/15.95	18.57/18.24	15.13/15.21	16.04/15.93	19.25/19.25	19.72/19.70	25.84/26.19	24.61/24.91	20.71/19.25	29.23/29.02	16.25/15.57
	sd/C.V.	5.55/26.86	2.23/12.51	2.21/13.63	2.12/11.41	1.47/9.73	1.11/6.93	2.47/12.82	1.22/6.21	3.67/14.19	2.69/10.93	3.01/14.54	2.80/9.58	2.51/15.44
transv. row n. forming	min.-max.	48-84	37-55	45-56	47-55	45-56	47-61	42-72	49-71	52-66	43-64	49-78	46-67	58-66
	mean/med.	61.8/59.5	49.3/51.0	50.7/51.5	51.7/52.0	52.3/53.0	53.5/54.0	60.9/63.5	63.0/65.0	60.0/58.5	56.2/57.0	63.1/65.0	56.3/56.0	62.2/61.5
	sd/C.V.	9.86/15.96	6.24/12.66	3.47/6.84	2.67/5.16	3.23/6.18	4.06/7.59	9.12/14.98	6.60/10.48	4.52/7.54	6.34/11.28	9.02/14.30	6.02/10.69	2.53/4.07
% radula forming	min.-max.	30.38-41.38	24.67-34.16	27.48-31.18	27.48-32.90	28.65-35.00	26.52-33.70	24.87-37.11	26.34-34.63	26.76-35.37	26.32-34.54	24.62-37.50	25.56-39.41	27.98-33.50
	mean/med.	35.21/35.28	29.85/30.04	29.56/29.89	30.11/29.97	31.15/30.59	30.05/29.71	32.61/32.53	29.45/28.81	30.19/28.69	31.50/31.78	32.00/32.52	32.97/32.38	30.85/30.41
	sd/C.V.	3.86/10.95	2.76/9.23	1.20/4.06	1.76/5.85	2.07/11.10	2.52/8.39	3.39/10.40	2.28/7.76	3.04/10.07	2.41/7.66	4.37/13.65	4.30/13.04	1.88/6.10

Table 3: Principal component analysis; eigenvalues and percent of variability explained. Proportions of variance expected under broken- stick model.

PC No	Eigenvalue	Percent of Variability Explained	Cumulative percent	Expected Percent
1	5.552459	37.0164	37.0164	22.1215
2	3.439691	22.9313	59.9477	15.4549
3	2.422823	16.1522	76.0998	12.1215
4	1.294768	8.6318	84.7316	9.8993
5	1.015741	6.7716	91.5032	8.2326
6	0.504577	3.3638	94.8671	6.8993
7	0.335049	2.2337	97.1007	5.7882
8	0.216672	1.4445	98.5452	4.8358
9	0.104865	0.6991	99.2443	4.0025
10	0.049728	0.3315	99.5758	3.2617

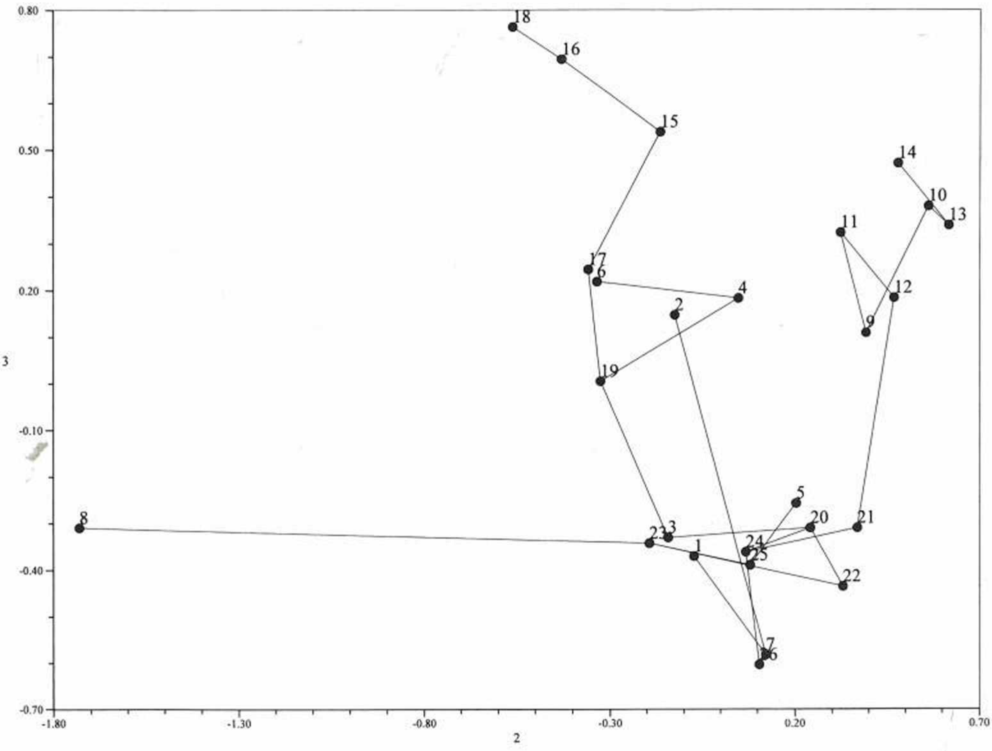


Fig. 12: Principal component analysis for mean values of each character for each population.

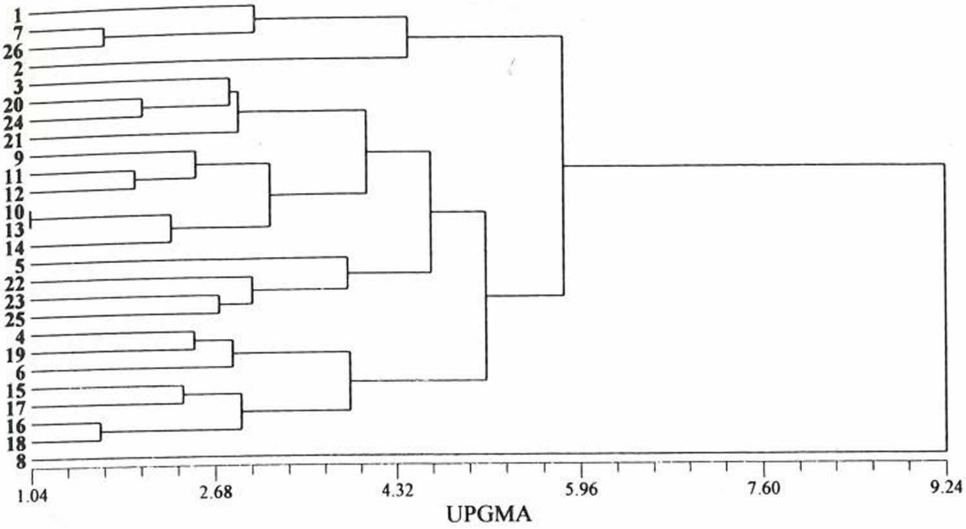


Fig. 13: UPGMA clustering ultrametric phenogram based on Euclidean distances calculated on radulae biometry characters.

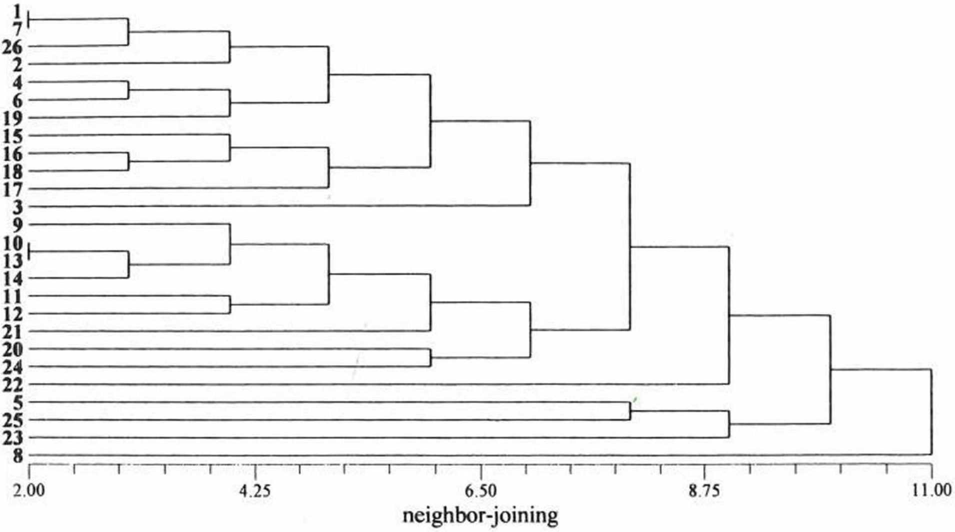


Fig. 14: Neighbour-joining additive tree based on Euclidean distances calculated on radulae biometry characters.

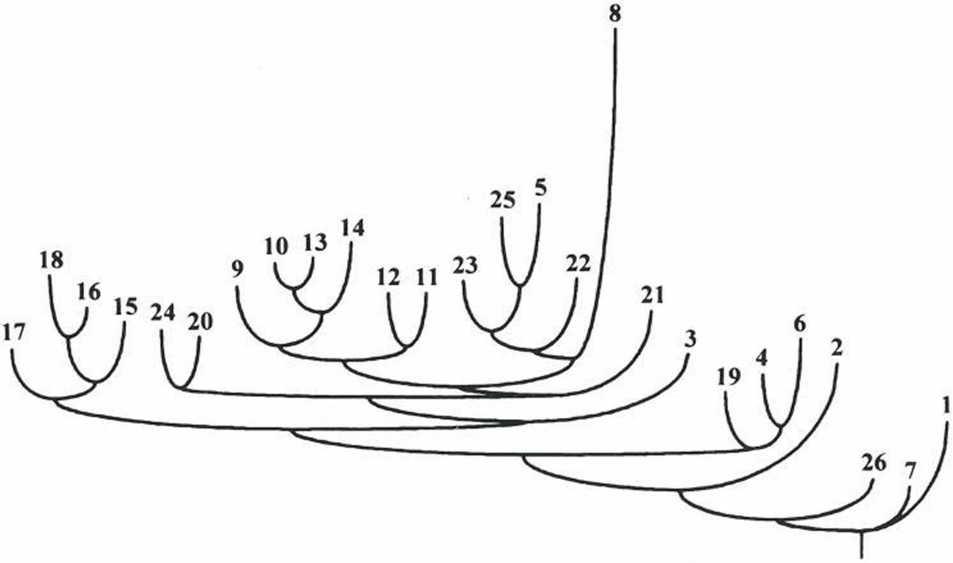


Fig. 15: Fitch-Margoliash additive tree based on Euclidean distances calculated on radulae biometry characters; sum of squares = 11.02635, average percent standard deviation = 13.04453, examined 2833 trees.

Tab. 4: Input matrix for the MacCLADE; characters and their state.

Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1	0	1	2	3	4	2	2	2	4	4	4	4	4	4	2	2	2	2	2	2	4	4	2	2	4	2
2	0	2	2	2	4	2	2	2	6	5	4	4	4	4	4	2	2	2	2	3	4	4	4	4	4	2
3	5	5	2	5	1	4	4	1	2	1	4	3	1	2	2	4	2	4	3	2	3	0	1	2	0	3
4	0	0	0	0	0	1	0	6	3	1	3	1	1	2	2	3	1	5	0	0	1	1	0	3	1	0
5	5	4	3	3	2	4	4	6	2	0	1	2	0	1	2	2	3	2	3	3	3	3	3	4	3	5
6	0	1	0	1	1	1	0	2	1	1	1	2	1	2	1	1	1	1	1	0	0	0	0	0	1	0
7	0	0	1	0	2	0	1	3	1	2	1	1	2	1	1	1	1	1	1	1	1	3	2	1	3	1
8	2	2	1	1	3	1	1	2	2	2	2	2	2	3	1	0	1	1	0	2	0	0	1	2	2	1

1 – cusps on inner marginal tooth (0 – 3.0-3.4, 1 – 3.5-3.9, 2 – 4.0-4.4, 3 – 4.5-4.9, 4 – 5.0-5.4); 2 – cusps on outer marginal tooth (0 – 3.0-3.4, 1 – 3.5-3.9, 2 – 4.0-4.4, 3 – 4.5-4.9, 4 – 5.0-5.4, 5 – 5.5-5.9, 6 – 6.0-6.4); 3 – rhachis breadth (0 – 0.050-0.059, 1 – 0.060-0.069, 2 – 0.070-0.079, 3 – 0.080-0.089, 4 – 0.090-0.099, 5 – 0.100-0.109); 4 – central cusp on rhachis length (0 – 0.004-0.005, 1 – 0.006-0.007, 2 – 0.008-0.009, 3 – 0.010-0.011, 4 – 0.012-0.013, 5 – 0.014-0.015, 6 – 0.016-0.017); 5 – radula length to shell breadth proportion (0 – 1.000-1.099, 1 – 1.100-1.199, 2 – 1.200-1.299, 3 – 1.300-1.399, 4 – 1.400-1.499, 5 – 1.500-1.599, 6 – 1.600-1.699); 6 – radula breadth to length proportion (0 – 0.030-0.034, 1 – 0.035-0.039, 2 – 0.040-0.045); 7 – total transverse rows number to radula length proportion (0 – 10.000-14.999, 1 – 15.000-19.999, 2 – 20.000-24.999, 3 – 25.000-29.999); 8 – percent of forming radula rows (0 – 28.0-29.9, 1 – 30.0-31.9, 2 – 32.0-33.9, 3 – 34.0-35.9)

Phylogenetic analysis based on the Euclidean distance was computed with two additive trees techniques: neighbour-joining (fig. 14) and Fitch-Margoliash (fig. 15). Both techniques, like the phenetic method, showed the distinctness of both *M. meiostoma* and the group of

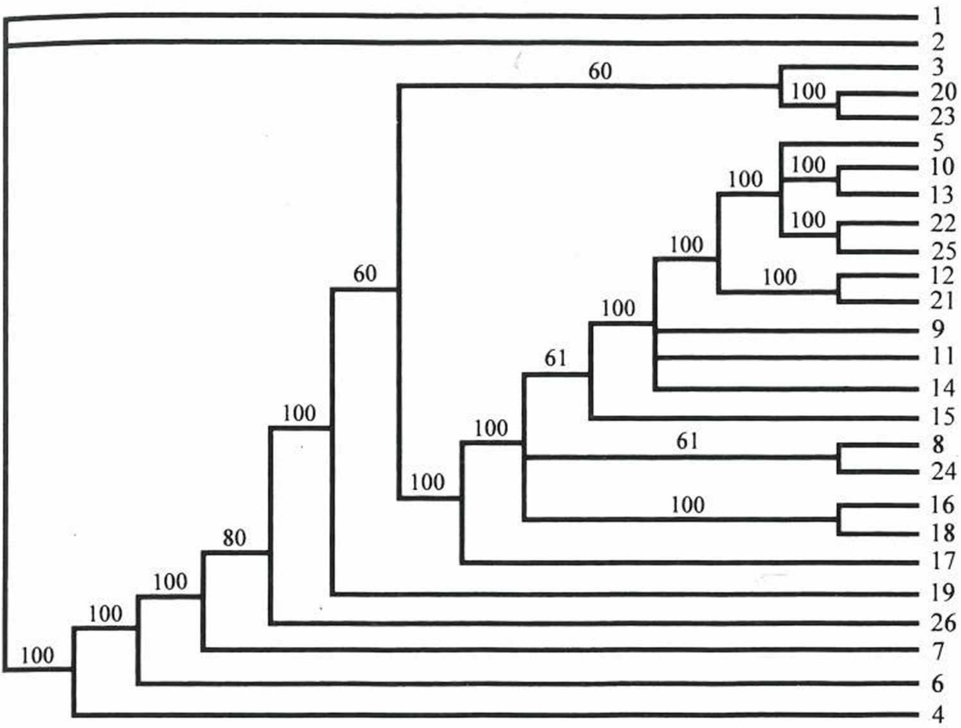


Fig. 16: Consensus tree for all found MPRs (constructed by PAUP).

closely related populations representing *M. c. jordanica*. Like in the UPGMA tree, in the neighbour-joining and the Fitch-Margoliash trees the *M. c. jordanica* cluster was contained in the *M. saulcyi* cluster (excluding population 26). In both of the phylogenetic trees, unlike in the UPGMA tree, population 19 belonging to *M. c. costata* was not joined with the branch of all the remaining populations of this taxa, but clustered together with populations 4 and 6 of *M. buccinoidea*. In comparison with the phenetic results, in both the phylogenetic trees, the populations representing *M. saulcyi* were joined less closely. Surprisingly, in the neighbour-joining tree, the populations of *M. buccinoidea* were much more close to each other and less mixed with the other populations.

From among the 15 characters (tables 1, 2) tested by the Kruskal-Wallis test, statistically significant ($p = 0.01$) interspecific differences were found in 8 (table 4), which were then used as an input for MacClade and PAUP. 176 MPRs were found, their length: 83, consistency index CI: 0.422, retention index RI: 0.684, rescaled consistency index RC: 0.289, minimum: 35, maximum: 187, and a consensus tree was constructed. The resulting tree (fig. 16) showed populations representing *M. c. jordanica* in one branch, to which the populations of *M. c. costata* were joined. All the populations of *M. saulcyi* were mixed with the latter two. These three species together formed one branch, to which the populations of *M. buccinoidea* were joined. *M. meiostoma* was connected with population 24 of *M. saulcyi*. To visualize the amount of anagenetic chance along the branches a "phyllogram" with branch length proportional to the amount of change was constructed based on one of the MPR's (fig. 17). The highest amount of change was in the clade of *M. meiostoma*.

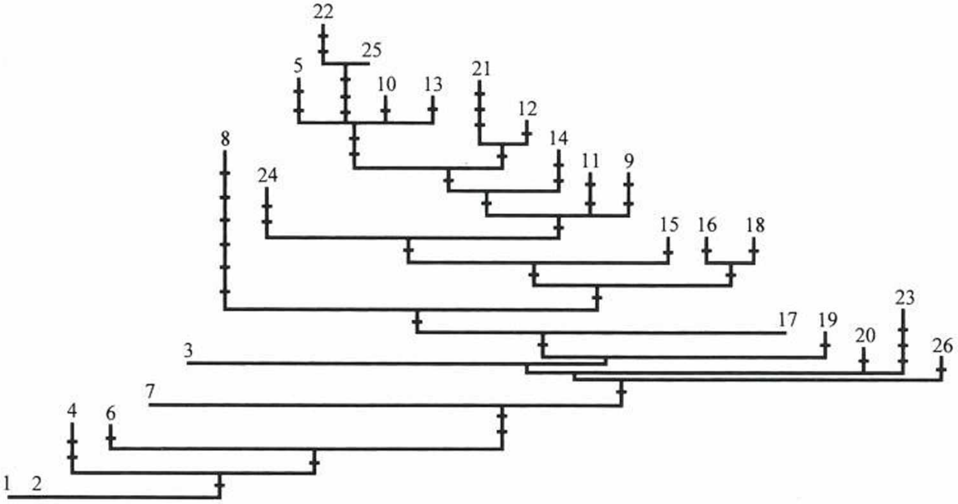


Fig. 17: "Phyllogram" with branch lengths proportional to the amount of change constructed with MacCLADE of one of the MPR's. A bar equals one change (unambiguous events only).

Discussion

The radula is one of the earliest considered anatomical structures, and its characters have for a long time been very commonly exploited in the taxonomy of Gastropoda. Once thought to be an important character, the structure soon turned out to be very variable (Roszkowski 1929, Krull 1935) and show numerous homoplasies (Davis 1979, Davis et al. 1985, Falniowski 1990b). Although the radula reflects feeding adaptations, thus gastropod macro-evolution (Fretter & Graham 1962, Purchon 1977), its usefulness in taxonomical studies is most often limited and questionable (Falniowski 1983, 1989, 1990a, b). In some cases, however, statistical analysis of quantitative radular characters may show differences that can be applied to the reconstruction of relationships among species (Falniowski et al. 1996).

In the studied *Melanopsis* taxa the radulae are very similar; the rhachidian has always seven cusps, as observed also in the other species of this genus (Bilgin 1973, Martinez-Lopez et al. 1987). Our results reveal high intraspecific variation of the radulae; coupled with slight interspecific differences and the overlapping variability intervals. However, both the multivariate analysis and the phylogenetic analysis confirm the distinctness of most of the postulated taxa.

The radulae characters showed the distinctness of *M. meiostoma*. In the radula of the population representing this species, much more often than in the radulae of the other studied populations, the central cusps on the rhachis were considerably longer than the neighbouring ones. Thus, the present study contrasts the conclusions based upon allozyme data of Falniowski et al. (submitted), and confirm the distinctness of the shell morphology of *M. meiostoma* (Heller & Sivan 2000). The conchologically and allozymatically distinct *M. costata costata*, *M. costata jordanica* and *M. saulcyi* (Heller et al. 1999, Falniowski et al. submitted) show radular distinctness, too. The radulae of the populations representing *M. c. jordanica* are more similar to *M. saulcyi* than to *M. c. costata*; they also are less variable than the radulae of all the other taxa. The distinctness of *M. c. jordanica* may be due to these snails' different feeding adaptation. Of all the studied *Melanopsis* populations, only the latter occupy stones and boulders on the stormy shores of Lake Kinneret. *M. c. costata* occurs along the river banks, within a weak current and upon a muddy substratum or submerged vegetation (HELLER et al. 1999). The differences between the radulae of these two subspecies may be an adaptation to different environmental conditions, especially to the substratum from which they scrape their food.

In *M. saulcyi* the radulae are more variable than in *M. costata*. The populations of *M. saulcyi* often co-occur with *M. buccinoidea*, and both these species inhabit a wide variety of habitats, from small trickles to springs and streams, where they occupy stones or silty mud (HELLER et al. 1999). So, the environmental stress at each locality may be a little different.

The considerable differentiation among the radulae among the populations of *M. buccinoidea*, agrees with the large allozymic differentiation of these populations (FALNIOWSKI et al. submitted). As the *M. buccinoidea* populations for this study are widely distributed, they may reveal the largest differentiation of habitat. Undoubtedly the form of a radula corresponds to the kind of substratum and food the snail lives on, but on one hand, many snail species eat the same kind of food and on the other hand, the majority of the radulae are universal inasmuch as they can take various kinds of food. Hence, there seems to be little stabilizing selection to maintain a certain form of radula.

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