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PHENETIC RELATIONSHIP BETWEEN *Podarcis muralis muralis* (LAURENTI, 1768) AND *Podarcis muralis maculiventris* (WERNER, 1891) (LACERTIDAE, REPTILIA) IN A TRANSITION ZONE

NINA DE LUCA

Louisiana Universities Marine Consortium
8124 Hwy 56, Chauvin, LA 70344, USA

IRENA GRBAC

Croatian Natural History Museum
HR-10000 Zagreb, Demetrova 1, Croatia

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In this paper we present an analysis of phenetic relationship between two subspecies of Common Wall Lizard *Podarcis muralis* (LAURENTI, 1768) in the supposedly transition zone in the town of Rijeka and its vicinity (Croatia, Northern Adriatic Coast). A total of 96 adult specimens was investigated, using univariate methods (ANOVA and Mann-Whitney U-test) and multivariate cluster-analysis, based on 43 external morphological characters.

A considerable amount of phenotypic dissimilarity was found between specimens from the town of Rijeka and specimens from the nearby area of Grobnik. The Grobnik population can be described as nominotypic, continentally adapted *Podarcis muralis muralis*, while Rijeka samples showed much closer phenetic similarity to *Podarcis muralis maculiventris* populations from the narrow coastal zone of the Istrian Peninsula. Although recognized as *P. muralis maculiventris* in a sense of conventional subspecies concept, substantial evidence supports the hypothesis of the hybrid character of the Rijeka population. The Rijeka population shows, for example, greater morphological variability and appearance of *muralis*-specific color and pattern character states. Cluster analysis showed, therefore, incomplete morphological separation between Rijeka and Grobnik specimens. These two populations also differ substantially in their habitat and climatic preferences. Population differentiation may be caused by a corresponding change in environmental conditions, which are particularly evident in this region along the transect from the Adriatic Coast to the coastal mountains.

New evidence for the presence of *P. muralis maculiventris* on the eastern coast of the Istrian Peninsula is also discussed. This evidence seems to further support the hypothesis that *P. m. maculiventris* appears in climatically favorable habitats in the narrow coastal zone of the Istrian Peninsula, while *P. m. muralis* inhabits cooler habitats, mostly further away from the coast.

Key words: *Podarcis muralis*, lacertid lizards, intraspecific variability, phenetic relationships, transition zone, Croatia, univariate morphometrics, multivariate morphometrics

De Luca, N. & Grbac, I.: Fenetički odnos između *Podarcis muralis muralis* (LAURENTI, 1708) i *Podarcis muralis maculiventris* (WERNER, 1891) (gušterice, gmazovi) u jednoj zoni hibridizacije. Nat. Croat. Vol 4, Br. 2, 81–105, 1995, Zagreb

U ovom članku analiziramo fenetički odnos između dviju podvrsta obične zidne gušterice *Podarcis muralis* (LAURENTI, 1768) u hipotetičkoj zoni hibridizacije, u gradu Rijeci i njegovoj bliskoj okolici. Istraživanje je provedeno na ukupno 96 odraslih jedinki uz uporabu univarijantnih statističkih metoda (ANOVA i Mann-Whitney U- test) i multivarijantnom metodom grupiranja, na temelju 43 vanjske morfološke značajke.

Znatna fenotipska različnost utvrđena je između primjeraka iz grada Rijeke i onih s obližnjeg područja na Grobniku. Grobnička populacija može se opisati kao nominotipska, kontinentalno prilagođena *Podarcis muralis muralis*, dok su riječki primjerci pokazali mnogo veću fenetičku sličnost s *Podarcis muralis maculiventris* populacijama s uskoga obalnog pojasa istarskog poluotoka. Iako je određena kao *P. muralis maculiventris* u smislu uobičajenoga poimanja podvrste, temeljni uvid podupire hipotezu o hibridnosti riječke populacije. Riječka populacija pokazuje npr. veću morfološku varijabilnost te specifičnu *muralis* obojenost i osobitosti u izgledu. Analiza niza značajki ukazala je, međutim, na nepotpunu morfološku odijeljenost riječkih i grobničkih primjeraka. Te dvije populacije također se bitno razlikuju izborom obitavališta i klimatskih uvjeta. Populacijska diferencijacija možda je prouzročena odgovarajućim promjenama u okolišu što se naročito opaža u tom području koje se proteže od jadranske obale do primorskih planina.

Raspravlja se i o očitoj prisutnosti *P. muralis maculiventris* ma istočnoj obali istarskog poluotoka. Kako se čini, to ide u prilog hipotezi da se *P. m. maculiventris* pojavljuje u klimatski povoljnijim obitavalištima u uskome obalnom pojasu Istre, a da *P. m. muralis* nastava hladnija, od obale udaljenija područja.

Ključne riječi: *Podarcis muralis*, Lacertidae, intraspecifička varijabilnost, fenetički odnosi, zona hibridizacije, Hrvatska, univarijantna morfometrija, multivarijantna morfometrija

INTRODUCTION

Podarcis muralis (LAURENTI, 1768) is one of the most common small lacertid lizards in the European herpetofauna. Its widespread distribution includes Western and Central Europe, as well as Eastern and Southern Europe (GRUSCHWITZ & BÖHME 1986). The northernmost population was found in Netherlands (STRIJBOSCH et al. 1980), while the southernmost population was found on the Peloponese Peninsula in Greece. *Podarcis muralis* inhabits, as its vernacular and scientific names suggest, mostly rocky surfaces of natural or anthropogenic origin. This species is well adapted to different climatic conditions and habitat types, ranging from European high mountains to Mediterranean coastal regions.

Large diversity of habitats corresponds well to large intraspecific variability. Numerous varieties and subspecies have been recognized so far (SCHREIBER 1912; BOULENGER 1920; MERTENS & WERMUTH 1960). Subspecies descriptions, however, have usually been based on only a few characters and an inadequate number of specimens. Today, only 6 subspecies are considered valid: *P. m. muralis*, *P. m. brogniardi*, *P. m. merremia*, *P. m. nigriventris*, *P. m. maculiventris* and *P. m. albanica*. Some subspecies, however, including even the nominotypic subspecies, are not as yet adequately investigated and doubts about their validity still exist (GRUSCHWITZ & BÖHME 1986). Western populations have been studied more extensively (KLEMMER 1964; SAINT GIRONS & DUGUY 1970; BOAG 1973; STRIJBOSCH et al. 1980; CHEYLAN 1975, 1988), while eastern populations remain poorly known (WERNER 1891; KRAMER & MERTENS 1938; BOLKAY 1919, 1928). The taxonomic evaluation of this species, however, cannot be carried out adequately without detailed taxonomic and ecological studies of eastern and southeastern populations (GRUSCHWITZ & BÖHME 1986).

One of the subspecies that deserves a more detailed investigation is certainly *Podarcis muralis maculiventris* (WERNER, 1891). This subspecies is established for the region of northern Italy, southernmost Switzerland, and coastal areas of the northern Adriatic Sea (GRUSCHWITZ & BÖHME 1986). Basic description of the subspecies has been established long ago (WERNER 1891; KRAMER & MERTENS 1938). *P. muralis maculiventris* seems to be phenetically and phylogenetically close to the Italian Mediterranean subspecies *P. m. nigriventris* (GRUSCHWITZ & BÖHME 1986). Northern and northeastern *maculiventris* populations, however, are in contact with widely distributed and continentally adapted nominotypic subspecies *P. m. muralis* (LAURENTI, 1768). Both *muralis* and *maculiventris* coexist in the northern coastal region of Croatia, more precisely, in Istrian Peninsula and along the coast to the southernmost findings of *maculiventris* in Senj (WERNER 1891; MOSAUER & WALLIS 1924; KARAMAN 1921, 1939; WETTSTEIN 1928; KRAMER & MERTENS 1938; TADDEI 1950; RUCNER & RUCNER 1971; LILGE & WICKER 1972; BRELIH 1963; BRELIH & DŽUKIĆ 1974; BRUNO 1980; HENLE 1985) (Fig. 1b). *Maculiventris* is distributed mostly in a narrow coastal zone, while *muralis* prefer cooler habitats further away from the coast.

In spite of the known areas, their spatial and phenetic relationship is still poorly known (GRUSCHWITZ & BÖHME 1986). Thus, detailed taxonomic studies of these two subspecies seem necessary for any further description and analysis, as well as for the evaluation of the taxonomic status of the species as a whole. Furthermore, phenetic studies of these populations in the contact zone may provide valuable informations on the possible hybridization between the two subspecies and, consequently, some additional evidence in support of their taxonomic validity.

The investigation has been focused, therefore, on the region where both subspecies seem to coexist and possible hybrid populations are likely to occur. The town of Rijeka and the surrounding areas were chosen for two reasons. First, both *maculiventris* and *muralis* have been found in this area (WERNER 1891; KARAMAN 1921). Second, according to their zoogeographical status, these populations could represent transition stage between phenetically and ecologically different *maculiventris* population from the narrow coastal zone of Istrian Peninsula and nominotypic *muralis* population, widely distributed throughout the Dinarid mountains.

In this study, we provide the preliminary results of univariate and multivariate morphometric analysis of these populations. Also, morphology, zoogeography and ecology of *P. m. muralis* and *P. m. maculiventris* in the northern coastal region of Croatia are discussed in greater details.

MATERIAL AND METHODS

The study area

The town of Rijeka is situated on the northern Adriatic coast, more precisely, on the northernmost edge of the Kvarner Bay (Fig. 1). Climatic conditions of the region can be described as submediterranean: an average annual temperature is 14.2 °C, while an overage annual rainfall is 1431 mm. In the northern background of Rijeka, called Grobničko Polje, elevation gradually becomes higher, making the beginning of the Gorski Kotar Mountains. Higher elevation results in lower temperatures and higher annual precipitation. Consequently, vegetation also gradually changes, from warmer *Carpinetum orientalis croaticum* zone, to cooler *Seslerio-Ostryetum* zone (BERTOVIĆ 1975).

Sampling effort has been focused on the town itself, as well as its background, with the main goal to cover gradually higher altitudes and diverse habitats.

Material

Specimens were collected on 11 localities (Fig. 1 and Tab. 1). A total of 96 adult specimens was analyzed (54 males and 42 females, respectively), 89 which were collected during 1990. Animals were preserved and have been kept in the Herpetological Collection of the Department of Zoology, University of Zagreb, Croatia. An additional sample of 7 adult specimens was also analysed: 3 animals were found in the same collection, and 4 in the collection of the Croatian Natural History Museum in Zagreb.

Methods

Initially, each specimen was surveyed for 54 external morphological characters. After preliminary analysis of their between-locality variation and type of distribution, 43 external morphological characters were selected for further analysis. Characters were chosen in a way that well represent a wide range of external morphological characteristics of the species, and divided as follows: 19 biometric characters (measured in mm), 14 meristic characters (number of scales of the pileus and the pholidosis) and 10 ordered characters (*sensu* THORPE 1975, 1976). After preliminary examination, each ordered character was converted into a certain number of character states. The character state for each specimen was determined twice, using in-

dependent estimates. All the characters are listed in Table 2, with the character codes used consequently throughout the paper.

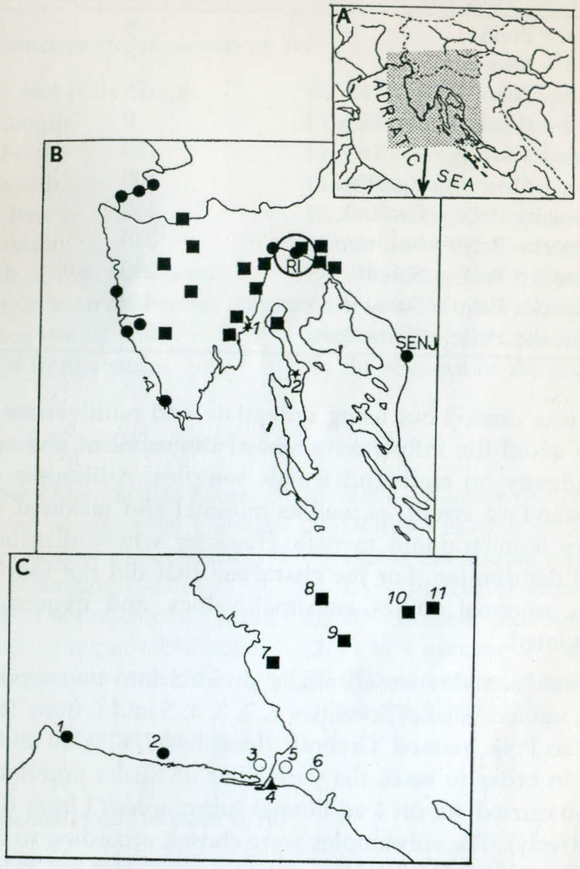


Fig. 1. Distribution of *Podarcis muralis muralis* and *Podarcis muralis maculiventris* in the Northern Adriatic Region of Croatia and Slovenia:

A. The region inhabited with both subspecies

B. Distribution of both subspecies (encircled region represents the study area):
solid circles – *P. m. maculiventris*
solid squares – P. m. muralis
stars – new findings of P. m. maculiventris (1-Rabac, 2-town Cres)

C. Study area with sampling localities; (numbers correspond to those in Table 1):
– solid circles – 'Rijeka-Bivio' (RB) (1-Bivio, 2-Kantrida)
– open circles – 'Rijeka-Trsat' (RT) (3-Belveder, 5-Trsat, 6-Orjentovo Igralište)
– triangle – 'Rijeka-Gradsko Kupalište' (RG) (4-Gradsko Kupaliste)
– solid squares – 'Grobnik' (GR) (7-Grobnik, 8-Podhum, 9-Soboli, 10-Soboli-Kamenjak, 11-Kamenjak)

Table 1. Sampling localities of the 96 specimens of the Common Wall Lizard *P. muralis* (LAURENTI, 1768) in the town of Rijeka and its vicinity

No.	Locality	Elevation (m)	No. of Specimens
1.	Rijeka – Bivio	0	40
2.	Rijeka – Kantrida	0	7
3.	Rijeka – Belveder	78	9
4.	Rijeka – Gradsko Kupaliste	0	17
5.	Rijeka – Trsat	150	4
6.	Rijeka – Orjentovo Igraliste	100	8
7.	Grobnicko Polje – Grobnik	450	3
8.	Grobnicko Polje – Podhum	370	2
9.	Grobnicko Polje – Soboli	290	3
10.	Grobnicko Polje – Soboli-Kamenjak	470	1
11.	Grobnicko Polje – Kamenjak	578	2

The analysis was carried out using univariate and multivariate statistical methods. In order to avoid the influence of sexual dimorphism, the analysis was performed independently on male and female samples. Arithmetic means, standard deviations and standard errors, as well as minimal and maximal values, were calculated for every biometric and meristic character whose distribution conformed with the normal distribution. For the characters that did not follow normal distribution, medians, minimal values, maximal values, and frequencies of character states were calculated.

Male and female samples were initially divided into two separate subsamples: the town Rijeka, named 'Rijeka' (localities 1, 2, 3, 4, 5 and 6 from Table 1 and Figure 1c) and Grobničko Polje, named 'Grobnik' (localities 7, 8, 9, 10 and 11 from Table 1 and Figure 1c). In order to asses the variability of Rijeka population, a univariate analysis was also carried out on 4 additional subsamples (3 from Rijeka, and 1 from Grobnik, respectively). The subsamples were chosen according to the distances and elevations as follows:

1. Rijeka-Bivio ('RB', localities 1 and 2 from Table 1 and Figure 1c),
2. Rijeka-Trsat ('RT', localities 3, 5 and 6 from Table 1 and Figure 1c),
3. Rijeka-Gradsko Kupalište ('RG', locality 4 from Table 1 and Figure 1c),
4. Grobnik ('GR', localities 7, 8, 9, 10 and 11 from Table 1 and Figure 1c).

Comparison between specimens from those compound localities were calculated by means of one-way ANOVA for biometric and meristic characters. The significance level of $p = 0.05$ was used. Additionally, the LSD multiple range test was used in order to test the significance between pairs of localities. Kruskal-Wallis one-way analysis by ranks was used to calculate significance of the difference between all the localities for ordered characters ($p < 0.05$). Also, the difference between paired samples was calculated using Mann-Whitney U-test. The univariate analysis was carried out using Statgraphics Plus (Version 7, 1993).

Table 2. Taxonomic characters and its codes used in univariate and multivariate analysis of phenetic relationship between *P. muralis muralis* and *P. m. maculiventris* (all the measurements are made in mm, for two-sided characters arithmetic mean was used). Description of the scaling of ordered characters into character states is also shown.

A. Biometric characters (total number = 19)

1. **DGT** – head and body length
2. **DG** – head length
3. **VG** – head height
4. **SG** – head width
5. **DP** – pileus length
6. **SP** – pileus width
7. **DIN** – length of internasal scale
8. **SIN** – width of internasal scale
9. **DF** – length of frontal scale
10. **SF** – width of frontal scale
11. **DFP** – length of frontparietal scale
12. **SFP** – width of frontoparietal scale
13. **DIP** – length of interparietal scale
14. **SIP** – width of interparietal scale
15. **DO** – length of occipital scale
16. **SO** – width of occipital scale
17. **SN** – length of the joint margin between left and right supranasal scale
18. **DA** – length of the anal scale
19. **SA** – width of the anal scale

B. Meristic characters (total number = 14)

20. **SCL** – number of supraciliar scales
21. **GSCL** – number of supraciliar granules
22. **PO** – number of postocular scales
23. **T** – number of temporal scales
24. **ST** – number of supratemporal scales
25. **SLU** – number of upper labial scales
26. **GUL** – number of chin shields (gular scales)
27. **COLL** – number of collar shields
28. **VEN** – number of ventral shields
29. **DORS** – number of dorsal scales across the middle of the trunk
30. **PA** – number of preanal scales
31. **PF** – number of femoral pores
32. **FEM** – number of femoral scales
33. **SDL** – number of subdigital lamellas on the 4^{th} toe

C. Ordered characters (total number = 10)

34. **MASS** – size of the masseteric scale (in 7 character states):

1 – it is impossible to distinguish between masseteric scale and temporal scales on the both left and right side of the head
2 – on the one side of the head like "1", while on the other side small, but clearly different in size in relation to temporal scales
3 – on the both left and right side of the head small, but slightly larger than temporal scales
4 – on one side of the head small, while on the other side much larger than temporal scales
5 – on the both left and right side of the head much larger than temporal scales
6 – on one side of the head much larger than temporal scales, while on the other side so large that make clearly more than 50% of temporal surface

35. SLA – number of upper labial scales in front of subocular scale (in 6 character states): – each category equals number of scales. This character was considered as ordered, because it was not normally distributed. If left and right side number was different, consequently larger number was used.

36. RCOLL – level of serration of the rear collar margin (in 4 character states)
1 – rear collar margin is completely straight
2 – rear collar margin is very slightly serrated
3 – rear collar margin is clearly serrated
4 – rear collar margin is very strongly serrated

37. IDORS – level of appearance of keeling on dorsal scales (in 4 character states)
1 – dorsal scales are completely smooth and flat
2 – dorsal scales are very slightly keeled
3 – dorsal scales are clearly keeled
4 – dorsal scales are very strongly keeled

38. ODORS – dorsal color and pattern (in 6 character states)
1 – dorsal color brownish, without any pattern between temporal stripes
2 – dorsal color brownish, with some small dark spots, and without occipital line in the middle between temporal stripes
3 – dorsal color brownish, with small number of dark spots, and with dark occipital line along the back between temporal stripes
4 – dorsal color brownish, with a lot of dark spots, and with dark occipital line between temporal stripes
5 – dorsal color brownish or olive-greenish, with well developed dark pattern between temporal stripes, that can sometimes be clearly reticulated; basic color and dark pattern alternate evenly
6 – dark pattern very well developed and continuously strongly reticulated along the head, back and flanks; while basic color hardly visible, usually olive-greenish

39. OBOK – temporal stripes color and pattern (in 4 character states)
1 – temporal stripes are continuos and uniformly dark, while maxillar stripes are hardly visible or completely missing
2 – temporal and maxillar stripes are continuos and clearly separated from each other, both may have slightly serrated margins
3 – temporal and maxillar stripes clearly separated from each other, both have strongly serrated margins
4 – temporal and maxillar stripes not separated from each other and make reticular pattern together with head and back reticular pattern (i.e. ODORS character state 6)

40. OVENT – ventral pattern (in 4 character states)
1 – without or with just a few dark spots on throat and belly
2 – more dark spots on throat and belly, especially on the left and the right side of ventral scales
3 – a lot of dark spots on the whole surface of throat and belly,
4 – dark spots join together in larger dark markings, covering clearly more of 50% of throat and belly

41. TBVEN – ventral color (in 3 character states)
1 – throat and belly whitish or yellowish
2 – throat and belly clearly orange and slightly reddish-brown, continuously or in spots
3 – throat and belly clearly reddish-brown

42. PP – appearance of blue spots on the flanks (in 3 character states)
1 – no blue spots on flanks
2 – blue spots clearly visible, but small and scarce
3 – blue spots on flanks numerous and large

43. PN – appearance and relation between the scales around nostrils (in 6 character states)
1 – only one postnasal scale on every side of the head, supranasal and frenal scale not in contact (typical for the pileus of *P. muralis*)
2 – on one side of the head like 1, while on the other side supranasal scale in contact with frenal scale
3 – on the both left and right side of the head supranasal scale in contact with frenal scale
4 – on one side of the head like 3, while on the other side two postnasal scales
5 – on one side of the head like 1, while on the other side two postnasal scales
6 – two postnasal scales on the both left and right side of the head

Multivariate analysis was carried out between all specimens, using an average taxonomic distance dissimilarity matrix (ROHLF 1993), which was calculated from standardized data matrix. 'Unit-variance' standardization method was used (THORPE 1976, 1980a). UPGMA and 'Complete linkage' clustering method (SNEATH & SOKAL 1973; DUNN & EVERITT 1982) were applied, in order to asses phenetic relationships between the specimens. Although clustering methods are not always helpful in description of geographic variability, they are of great value for initial detection of phenetic relationships (THORPE 1979, DUNN & EVERITT 1982). UPGMA method usually well represents relationship based on morphological data sets (SNEATH & SOKAL 1973). Complete linkage method is considered to be an appropriate method for grouping closely related objects (ROHLF 1993). In order to increase the validity of cluster analysis, Stinebrickner consensus tree between both UPGMA i 'Complete linkage' trees was constructed (ROHLF 1993). All multivariate procedures were carried out in NTSYS-pc Version 1.8 (ROHLF 1993). For now, having in mind relatively small number of specimens from Grobnik and relatively large gaps between localities, the use of some advanced multivariate techniques on pooled localities, such as ordination techniques, does not seem to be appropriate.

RESULTS

The results of descriptive statistical analysis for males (Tab. 3a) show that 'Rijeka' males are generally larger than those from Grobnik. However, only height and width of the head, width of the pileus and length of the frontal scale, were found

Table 3. Results of the descriptive statistics for Common Wall Lizard *Podarcis muralis*, males (RI – Rijeka sample, N=45; GR – Grobnik sample, N=9; Mean = arithmetic mean, SD = standard deviation, SE = standard error, MIN = minimal value, MAX = maximal value; for character codes see Table 2)

A. Biometric and meristic characters

CHARACTER	Mean		SD		SE		MIN		MAX	
	RI	GR	RI	GR	RI	GR	RI	GR	RI	GR
DGT	61.66	58.78	3.99	2.70	0.60	0.90	54.00	55.00	68.00	64.00
DG	16.11	15.35	1.04	0.63	0.16	0.21	13.33	14.28	17.95	16.46
VG	8.51	7.57	0.80	0.98	0.12	0.33	6.94	6.39	9.66	9.66
SG	10.30	9.28	0.66	0.49	0.10	0.16	8.98	8.30	11.83	9.93
DP	15.43	14.69	0.90	0.69	0.13	0.23	13.46	13.46	17.41	15.78
SP	7.66	7.03	0.53	0.23	0.08	0.08	6.80	6.66	9.25	7.34
DIN	2.42	2.37	0.26	0.26	0.04	0.09	1.77	2.04	3.13	2.99
SIN	2.62	2.52	0.28	0.13	0.04	0.04	1.43	2.31	3.13	2.72
DF	4.42	4.12	0.31	0.29	0.05	0.10	3.54	3.67	5.03	4.49
SF	2.78	2.75	0.20	0.18	0.03	0.06	2.38	2.45	3.13	2.99
DFP	3.77	3.56	0.34	0.30	0.05	0.10	3.10	3.13	4.35	4.08
SFP	2.40	2.35	0.17	0.14	0.03	0.05	1.98	2.14	2.86	2.69
DIP	2.07	2.42	0.34	0.34	0.05	0.11	1.43	1.63	2.72	2.99
SIP	1.22	1.25	0.18	0.16	0.03	0.05	0.82	0.95	1.50	1.50
DO	1.39	1.36	0.30	0.37	0.04	0.12	0.68	1.09	2.24	2.31
SO	1.48	1.30	0.28	0.19	0.04	0.06	0.82	0.95	2.04	1.70
SN	0.27	0.38	0.10	0.11	0.02	0.04	0.00	0.17	0.46	0.58
DA	2.11	2.12	0.35	0.60	0.05	0.20	1.50	0.82	3.54	3.13
SA	4.03	4.11	0.51	0.36	0.08	0.12	2.38	3.54	5.03	4.76
SCL	5.37	4.94	0.61	0.44	0.09	0.15	4.00	4.00	7.00	5.50
GSCL	10.66	9.28	2.87	1.49	0.43	0.50	7.00	8.00	19.50	13.00
PO	3.80	3.83	0.63	0.62	0.09	0.21	2.50	3.00	5.50	5.00
T	46.57	46.78	11.49	6.55	1.71	2.18	25.50	36.00	93.50	57.00
ST	4.84	4.78	0.94	0.63	0.14	0.21	2.00	4.00	7.50	6.00
SLU	7.44	7.50	0.47	0.53	0.07	0.18	7.00	6.50	8.50	8.00
GUL	24.60	23.33	2.49	1.76	0.37	0.59	20.00	20.00	31.00	26.00
COLL	10.00	9.67	1.01	0.94	0.15	0.31	8.00	8.00	12.00	11.00
VEN	23.73	23.28	1.12	1.08	0.17	0.36	22.00	21.00	26.00	24.50
DORS	56.40	51.22	3.27	2.35	0.49	0.78	50.00	48.00	65.00	56.00
PA	7.18	7.00	1.08	1.05	0.16	0.35	6.00	6.00	10.00	9.00
PF	20.17	16.78	1.98	0.71	0.30	0.24	15.50	15.50	23.50	18.00
FEM	4.76	3.89	0.65	0.39	0.10	0.13	3.50	3.00	6.00	4.50
SDL	28.79	25.94	2.02	0.93	0.30	0.31	25.00	24.00	33.00	27.00

Table 3 cont.

B. Ordered Characters

Char. State / CHARACTER	1		2		3		4		5		6		7		Median	
	RI	GR	RI	GR	RI	GR	RI	GR	RI	GR	RI	GR	RI	GR	RI	GR
MASS	1	0	1	0	2	1	2	0	11	1	4	1	24	6	7	7
%	2.22	0.00	2.22	0.00	4.44	11.11	4.44	0.00	24.44	11.11	8.89	11.11	53.33	66.67		
SLA	0	0	0	0	0	0	27	9	18	0	0	0	/	/	4	4
%	0.00	0.00	0.00	0.00	0.00	0.00	60.00	100.00	40.00	0.00	0.00	0.00	/	/		
RCOLL	8	1	17	3	20	5	0	0	/	/	/	/	/	/	2	3
%	17.78	11.11	37.78	33.33	44.44	55.56	0.00	0.00	/	/	/	/	/	/		
IDORS	0	0	27	0	18	8	0	1	/	/	/	/	/	/	2	3
%	0.00	0.00	60.00	0.00	40.00	88.89	0.00	11.11	/	/	/	/	/	/		
ODORS	1	1	9	4	8	2	13	0	13	2	1	0	/	/	4	2
%	2.22	11.11	20.00	44.44	17.78	22.22	28.89	0.00	28.89	22.22	2.22	0.00	/	/		
OBOK	0	4	0	0	1	0	44	5	/	/	/	/	/	/	4	4
%	0.00	44.44	0.00	0.00	2.22	0.00	97.78	55.56	/	/	/	/	/	/		
OVENT	5	4	24	1	15	4	1	0	/	/	/	/	/	/	2	2
%	11.11	44.44	53.33	11.11	33.33	44.44	2.22	0.00	/	/	/	/	/	/		
TBVEN	31	1	10	1	4	7	/	/	/	/	/	/	/	/	1	3
%	68.89	11.11	22.22	11.11	8.89	77.78	/	/	/	/	/	/	/	/		
PP	7	2	11	7	27	0	/	/	/	/	/	/	/	/	3	2
%	15.56	22.22	24.44	77.78	60.00	0.00	/	/	/	/	/	/	/	/		
PN	35	5	1	1	0	2	0	0	6	1	3	0	/	/	1	1
%	77.78	55.56	2.22	11.11	0.00	22.22	0.00	0.00	13.33	11.11	6.67	0.00	/	/		

to be significantly larger (ANOVA, $p < 0.05$, Tab. 5a). Exemptions are the interparietal scale and the joint margin between supranasal scales, which were significantly larger in the 'Grobnik' sample. The values of meristic characters are generally higher in 'Rijeka' males, significantly higher for dorsal scales, femoral scales, femoral pores, and subdigital lamellas. Variability expressed by the standard deviations and minimal and maximal character values (Tab. 3a) was also greater for specimens from Rijeka. A similar pattern has been found for biometric and meristic characters in females (Tab. 4a). Head dimensions, number of dorsal scales, femoral pores, femoral scales and subdigital lamellas were significantly higher in all female samples from Rijeka (ANOVA, $p < 0.05$, Tab. 5b). The number of temporal scales and supratemporal scales, however, was slightly higher in 'Grobnik' females.

Differences in ordered characters were much more obvious between males, especially in color and its pattern (Tab. 3b and Fig. 2a). The males from Rijeka show color and pattern similar to *maculiventris* type: 68.89 % of the specimens have white-colored belly, 60 % of the specimens show numerous bright blue spots on flanks (character state 3) and almost all specimens have heavily reticulated flanks (character state 4). Also, 60 % of specimens have strongly developed dorsal pattern (character states 4, 5 and 6). Surprisingly, there were only 33.33 % of males from Rijeka population with strong dark spotted belly pattern, typical for *maculiventris* coloring. 'Grobnik' males show color and pattern typical for *muralis*: small number of blue spots on flanks (77.78 % specimens), bright reddish-brown belly (77.78 %) and slightly developed back pattern (character states 1, 2 and 3 in 77.77 % specimens). The difference is also evident in the shape of the dorsal scales: they are much more keeled in 'Grobnik' males (all specimens with character state 3 and 4) than in 'Rijeka' males (60 % with character state 2). However, differences in ordered characters between the 'Grobnik' sample and 3 'Rijeka' samples appear to be significant only for ventral basic color, flanks pattern and blue spots, as well as shape of dorsal scales (Tab. 5a).

Differences in ordered characters between females were less pronounced (Tab. 4b and Fig. 2b), although obvious for color and pattern characters. In 'Rijeka' sample some specimens have blue spots on flanks (14.29 %) and dark spots on the belly (22.86 %), which is not the case with 'Grobnik' females. Surprisingly, in contrast to typical *maculiventris* belly color, 20 % of the 'Rijeka' females have typical *'muralis'* orange or reddish-brown belly. Some females from the Rijeka sample have 4 and 5 dorsal color and pattern character state (17.14 %), which have not been found in any female from Grobnik. According to the results of Mann-Whitney U-test (Tab. 5b), differences are significant between some groups from Rijeka and Grobnik females for dorsal and ventral color and pattern, as well as for blue spots on the flanks.

Based on 3 samples from Rijeka and one from Grobnik, ANOVA and Mann-Whitney U-tests showed significantly higher differences between any of the Rijeka samples and the Grobnik sample, in comparison to the differences within the 3 Rijeka samples (Tab. 5). Consequently, it appears that population differentiation is substantially higher between Rijeka and Grobnik, than within Rijeka. That is espe-

Table 4. Results of the descriptive statistics for females (RI – Rijeka sample, N=34; GR – Grobnik sample, N=7); (Mean = arithmetic mean, SD = standard deviation, SE = standard error, MIN = minimal value, MAX = maximal value, for character codes see Table 2)

A. Biometric and meristic characters										
CHARACTER	Mean		SD		SE		MIN		MAX	
	RI	GR	RI	GR	RI	GR	RI	GR	RI	GR
DGT	58.06	56.93	3.98	3.53	0.67	1.33	52.00	52.00	67.00	64.00
DG	13.61	12.54	0.96	0.52	0.16	0.20	11.97	11.70	15.50	13.53
VG	6.84	6.54	0.68	0.36	0.11	0.13	5.71	5.78	8.30	6.94
SG	8.41	8.16	0.62	0.46	0.11	0.17	7.21	7.62	9.52	8.98
DP	12.95	12.14	0.91	0.57	0.15	0.21	11.70	11.02	14.96	13.06
SP	6.48	6.13	0.39	0.35	0.07	0.13	5.71	5.44	7.21	6.66
DIN	2.13	2.01	0.30	0.17	0.05	0.06	1.29	1.77	2.58	2.18
SIN	2.32	2.27	0.26	0.19	0.04	0.07	1.50	2.04	2.72	2.58
DF	3.68	3.51	0.40	0.23	0.07	0.09	2.45	3.13	4.28	3.96
SF	2.44	2.33	0.18	0.11	0.03	0.04	2.11	2.18	2.86	2.58
DFP	3.14	2.89	0.30	0.16	0.05	0.06	2.52	2.65	3.74	3.19
SFP	2.13	2.03	0.15	0.17	0.03	0.07	1.84	1.63	2.45	2.18
DIP	1.75	1.97	0.36	0.18	0.06	0.07	0.68	1.63	2.58	2.18
SIP	1.30	1.08	0.37	0.15	0.06	0.06	0.82	0.88	2.52	1.29
DO	1.06	0.89	0.34	0.17	0.06	0.06	0.41	0.68	2.38	1.22
SO	1.37	1.29	0.30	0.22	0.05	0.08	0.82	0.88	1.90	1.50
SN	0.27	0.29	0.09	0.08	0.02	0.03	0.00	0.17	0.46	0.35
DA	2.22	2.27	0.25	0.20	0.04	0.08	1.63	2.04	2.72	2.72
SA	3.33	3.56	0.42	0.44	0.07	0.17	2.31	3.13	4.08	4.35
SCL	5.36	5.14	0.41	0.23	0.07	0.09	5.00	5.00	6.00	5.50
GSCL	9.67	8.43	1.71	0.98	0.29	0.37	7.00	7.50	14.00	10.50
PO	3.97	3.71	0.73	0.52	0.12	0.20	3.00	3.00	6.50	4.50
T	40.80	43.79	9.97	6.29	1.69	2.38	26.50	35.00	68.50	53.00
ST	5.11	5.29	0.78	0.25	0.13	0.09	3.50	5.00	7.00	5.50
SLU	7.39	7.21	0.55	0.36	0.09	0.14	6.50	7.00	8.50	8.00
GUL	23.66	22.71	1.87	1.91	0.32	0.72	21.00	20.00	30.00	26.00
COLL	9.49	9.29	0.81	1.39	0.14	0.52	7.00	7.00	11.00	11.00
VEN	26.51	26.14	1.38	0.83	0.23	0.31	23.00	25.00	28.50	27.00
DORS	52.91	46.83	3.97	1.96	0.67	0.74	42.00	44.00	60.00	50.00
PA	6.80	6.86	0.95	1.12	0.16	0.43	6.00	5.00	9.00	8.00
PF	19.00	16.43	1.83	1.18	0.31	0.45	13.50	14.00	23.00	18.00
FEM	4.29	3.36	0.56	0.44	0.10	0.17	3.00	3.00	5.00	4.00
SDL	28.59	23.36	1.61	0.99	0.27	0.37	24.00	21.50	33.00	24.50

Table 4 cont.

B. Ordered Characters

Char. State	1		2		3		4		5		6		7		Median	
CHARACTER	RI	GR	RI	GR	RI	GR	RI	GR	RI	GR	RI	GR	RI	GR	RI	GR
MASS	0	0	0	0	3	0	3	0	6	4	3	2	20	1	7	5
%	0.00	0.00	0.00	0.00	8.57	0.00	8.57	0.00	17.14	57.14	8.57	28.57	57.14	14.29		
SLA	0	0	0	0	0	0	25	6	9	1	1	0	/	/	4	4
%	0.00	0.00	0.00	0.00	0.00	0.00	71.43	85.71	25.71	14.29	2.86	0.00	/	/		
RCOLL	11	0	16	6	8	1	0	0	/	/	/	/	/	/	2	2
%	31.43	0.00	45.71	85.71	22.86	14.29	0.00	0.00	/	/	/	/	/	/		
IDORS	2	0	25	6	8	1	0	0	/	/	/	/	/	/	2	2
%	5.71	0.00	71.43	85.71	22.86	14.29	0.00	0.00	/	/	/	/	/	/		
ODORS	0	2	8	4	21	1	3	0	3	0	0	0	/	/	3	2
%	0.00	28.57	22.86	57.14	60.00	14.29	8.57	0.00	8.57	0.00	0.00	0.00	/	/		
OBOK	3	6	6	1	19	0	7	0	/	/	/	/	/	/	3	1
%	8.57	85.71	17.14	14.29	54.29	0.00	20.00	0.00	/	/	/	/	/	/		
OVENT	27	7	7	0	1	0	0	0	/	/	/	/	/	/	1	1
%	77.14	100.00	20.00	0.00	2.86	0.00	0.00	0.00	/	/	/	/	/	/		
TBVEN	28	7	6	0	1	0	/	/	/	/	/	/	/	/	1	1
%	80.00	100.00	17.14	0.00	2.86	0.00	/	/	/	/	/	/	/	/		
PP	23	7	7	0	5	0	/	/	/	/	/	/	/	/	1	1
%	65.71	100.00	20.00	0.00	14.29	0.00	/	/	/	/	/	/	/	/		
PN	21	6	0	0	0	0	0	0	6	0	8	1	/	/	1	1
%	60.00	85.71	0.00	0.00	0.00	0.00	0.00	0.00	17.14	0.00	22.86	14.29	/	/		

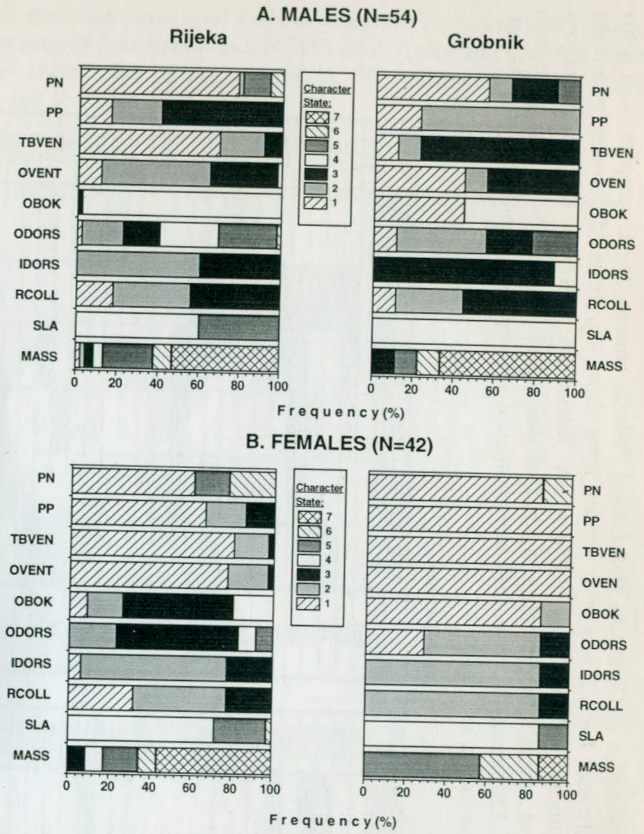


Fig. 2. A comparison of the character state frequencies for ordered characters between the Rijeka samples and the Grobnik samples (a – males; b – females)

cially true for males, where the total frequency of significantly different characters does not exceed 0.13 in a comparison of Rijeka samples. In contrast, a comparison of any Rijeka sample with Grobnik sample, gives the frequency in a range from 0.308 (Gradsko Kupalište-Grobnik) to 0.385 (Bivio-Grobnik). This is not so obvious for females, where comparison within two Rijeka subsamples (Bivio-Trsat) showed larger frequency (0.256) than comparison between any of the Rijeka samples and the Grobnik sample (Gradsko Kupalište-Grobnik = 0.128). Overall, 10 characters in males and 4 in females are significantly different between Grobnik sample and all three Rijeka samples. It should be pointed out that the number of femoral pores, the number of femoral scales, and the number of subdigital lamellas on the 4th toe can be used as new distinctive characters between the two subspecies, since their values differ significantly in both males and females.

According to the cluster-analysis, males from Grobnik tend to group in one cluster. That tendency is more obvious in 'Complete linkage' tree (Fig. 3a) than in UPGMA tree, where two Grobnik males were clustered in distinct groups. Stinebrickner consensus tree also clearly shows 'Grobnik' cluster, as well as two unclassified

Table 5. Taxonomic characters comparison among 4 samples of Common Wall Lizard *Podarcis muralis* (three samples from town Rijeka and one from Grobnik) using univariate significance tests. Boxes with vertical lines show significant difference (p) among 'Rijeka' samples. Boxes with oblique lines show significant difference (p) between any 'Rijeka' and 'Grobnik' sample. Average p is calculated by means of ANOVA (for biometric and meristic characters) and Kruskal-Wallis test (for ordered characters); each pair of samples were tested by means of ANOVA – LSD multiple range test (for biometric and meristic characters) and Mann-Whitney U-test (for ordered characters). For character codes see Table 2.

A. MALES (N=54)

CHARACTERS	BIVIO - TRSAT	BIVIO - GRAD.KUP.	TRSAT - GRAD.KUP.	BIVIO - GROBNIK	TRSAT - GROBNIK	GRAD.KUP.- GROBNIK	Average p
DGT							0.407
DG							0.408
VG							0.014
SG							0.015
DP							0.098
SP							0.048
DIN							0.89
SIN							0.436
DF							0.044
SF							0.601
DFP							0.349
SFP							0.167
DIP							0.001
SIP							0.288
DO							0.236
SO							0.058
SN							0.069
DA							0.336
SA							0.28
GSCL							0.41
PO							0.904
T							0.776
ST							0.298
GUL							0.066
COLL							0.586
VEN							0.393
DORS							0.001
PF							<0.00001
FEM							0.041
SDL							0.003
MASS							0.065
RCOLL							0.458
IDORS							0.0018
ODORS							0.233
OBOK							0.0007
OVENT							0.383
TBVEN							0.00031
PP							0.0089
PN							0.576
TOTAL NO.	1	5	2	15	14	12	/
FREQUENCY	0.026	0.128	0.051	0.385	0.359	0.308	/

B. FEMALES (N=42)

CHARACTERS	BIVIO - TRSAT	BIVIO - GRAD.KUP	TRSAT - GRAD.KUP	BIVIO - GROBNIK	TRSAT - GROBNIK	GRAD.KUP.- GROBNIK	Average p
DGT							0.552
DG							0.009
VG							0.09
SG							0.054
DP							0.019
SP							0.076
DIN							0.32
SIN							0.277
DF							0.179
SF							0.48
DFP							0.117
SFP							0.016
DIP							0.225
SIP							0.406
DO							0.639
SO							0.567
SN							0.357
DA							0.282
SA							0.032
GSCL							0.03
PO							0.649
T							0.069
ST							0.602
GUL							0.432
COLL							0.455
VEN							0.011
DORS							0.006
PF							0.0016
FEM							0.0012
SDL							<0.00001
MASS							0.047
RCOLL							0.6
IDORS							0.83
ODORS							0.0025
OBOK							0.00023
OVENT							<0.00001
TBVEN							0.45
PP							0.00007
PN							0.082
TOTAL NO.	10	5	9	11	14	5	/
FREQUENCY	0.256	0.128	0.231	0.282	0.359	0.128	/

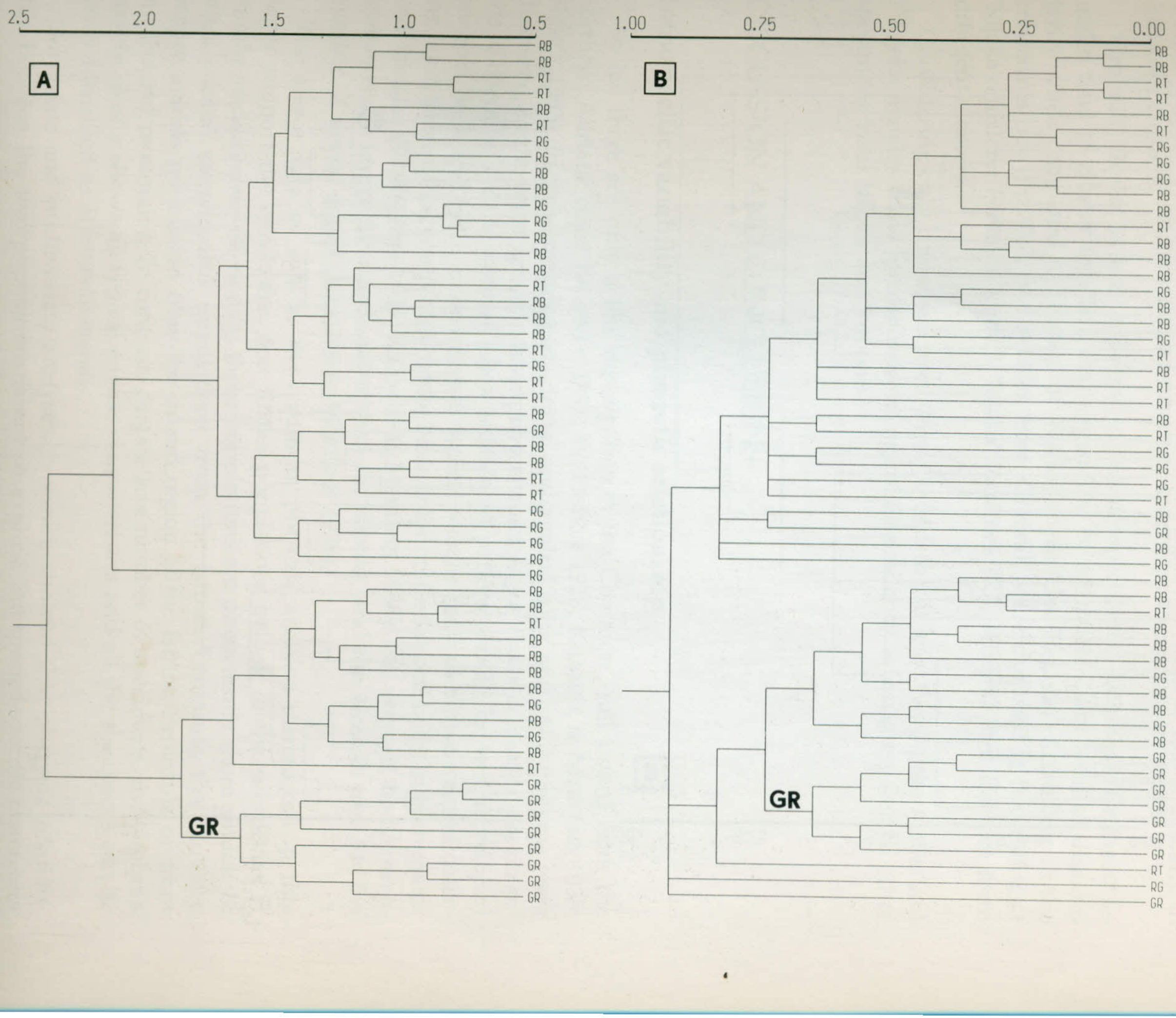
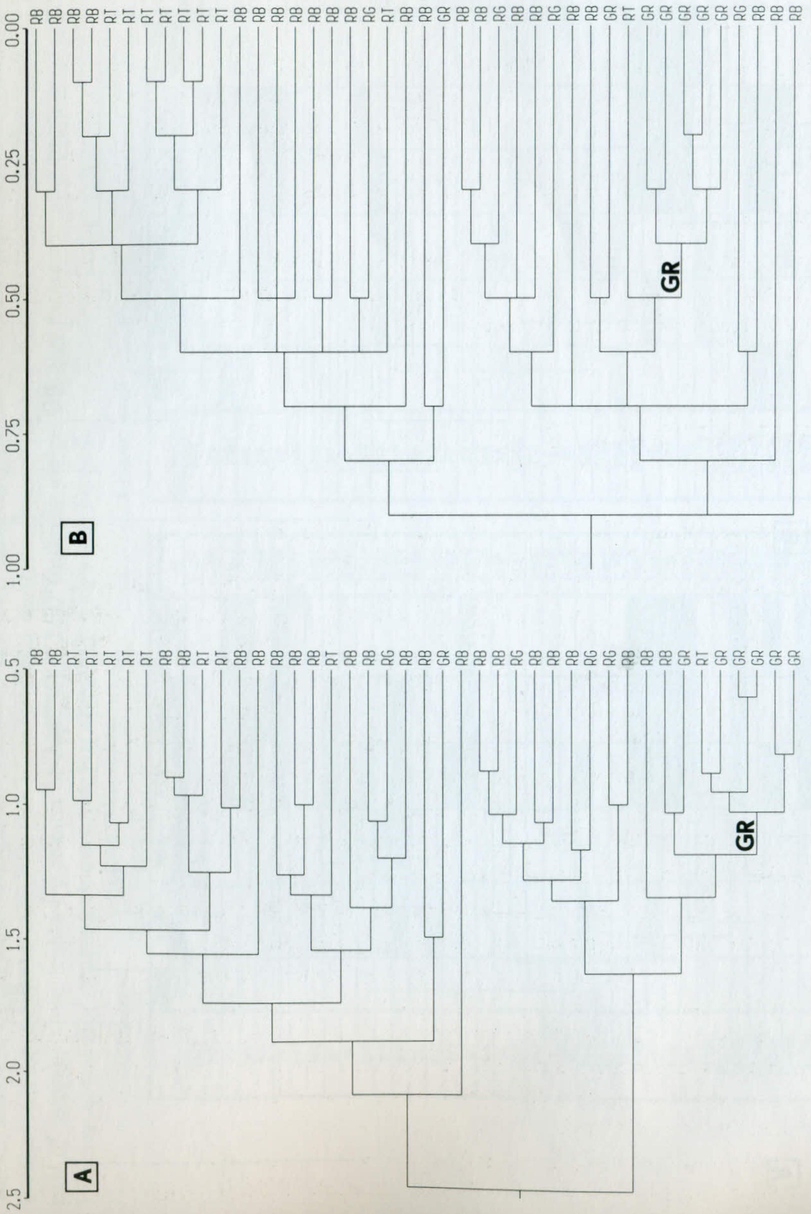


Fig. 3. Cluster analysis of all male specimens of *Podarcis muralis*. A. 'Complete linkage tree', and B. Stinebrickner consensus tree between UPGMA and 'Complete linkage' trees (Origin of every specimen is shown: RB = Rijeka – Bivio, RT = Rijeka – Trsat, RG = Rijeka – Gradsko Kupalište, GR = Grobnik)

Fig. 4. Cluster analysis of all female specimens of *Podarcis muralis*. A. 'Complete linkage tree', and B. Stinebrickner consensus tree between UPGMA and 'Complete linkage' trees (Origin of every specimen is shown: RB = Rijeka – Bivio, RT = Rijeka – Trsat, RG = Rijeka – Gradsko Kupalište, GR = Grobnik)



Grobnik males (Fig. 3b). 'Grobnik' cluster is separated from those combined from 'Rijeka' specimens on slightly lower level of dissimilarity than some 'Rijeka' clusters between themselves. It is evident, however, that those highly distinct clusters are composed from only two 'Rijeka' males (in 'Complete linkage' tree only one, Fig. 3a), that showed greater dissimilarity in comparison with all other specimens. Males from 3 'Rijeka' localities (RB, RT and RG) were clustered more or less irregularly in different clusters.

'Grobnik' cluster is less apparent in female specimens. Although 'Grobnik' females tend to cluster together, that appears to be on much lower level of dissimilarity when compared to clusters of 'Rijeka' specimens (Fig. 4a). According to the consensus tree (Fig. 4b), two females from 'Grobnik' were clustered in two different 'Rijeka' clusters. Females from 3 'Rijeka' localities (RB, RT and RG) did not form different clusters.

Considering only consensus trees (Figs. 3b and 4b), at least two Rijeka males and 7 Rijeka females show greater morphological dissimilarity, when compared to other specimens from Rijeka and Grobnik.

DISCUSSION AND CONCLUSIONS

Intraspecific variability and phenetic relationship

So far, there are only a few descriptions of the Common Wall Lizard from the northern Adriatic coast (WERNER 1891; WETTSTEIN 1928; KRAMER & MERTENS 1938; HENLE 1985). In those descriptions dorsal and ventral color and color patterns were described as the most specific descriptive characters for *Podarcis muralis maculiventris*. Generally, a dark spotted, often reticulated pattern should be well developed on both back and belly. In contrast to typical *muralis* reddish-brown ventral coloring, *maculiventris* has completely white basic color on throat and belly, in both males and females (WETTSTEIN 1928; KRAMER & MERTENS 1938). On average, body measurements are larger for *maculiventris* than for *muralis*, and the same is true for the number of dorsal scales (KRAMER & MERTENS 1938).

The above data as well as the results of phenetic analysis carried out in this paper support the conclusion that Rijeka populations belong to the subspecies *P. muralis maculiventris*. Obviously, those populations are phenetically more similar to other coastal *maculiventris* populations from the Istrian Peninsula than to any known *muralis* population from the inland region of the Istrian Peninsula or from the Dinarid mountains. In contrast, despite low number of specimens, the Grobnik sample clearly shows all typical *muralis* characteristics and all the specimens can be easily identified as *P. muralis muralis*.

Univariate and multivariate analyses, however, showed that phenetic relationship between the two populations is not so explicit. Subspecies-specific characters are not so frequently present in Rijeka samples, as it should be expected from typical *maculiventris* population (WERNER, 1891; KRAMER & MERTENS 1938; GRUSCHWITZ & BÖHME 1986). Also, overall phenetic variability is greater among Rijeka specimens, than within typical coastal northern Adriatic *maculiventris* populations described so far (KRAMER & MERTENS 1938; DE LUCA in prep.), and of Grobnik specimens investigated here. Furthermore, the number of significantly different characters between Rijeka and Grobnik specimens appears to be considerably smaller than between other known *muralis* and *maculiventris* populations (DE LUCA in prep.). Moreover, some of the Rijeka specimens cluster on a higher dissimilarity level than all other specimens investigated, including the Grobnik cluster itself. Evidently, clusters are not as clearly separated as it might be expected for two distinct subspecies (THORPE 1979). Accordingly, the great amount of phenetic variability within Rijeka populations, and incomplete morphological separation between Rijeka and Grobnik specimens, seem to point out that 'Rijeka' population may be a hybrid population. Specimens from Rijeka that showing greater dissimilarity in comparison to all other specimens, including those from Grobnik, could be recognized as intermediates. Intermediate populations usually show greater variability because of the gene flow from both neighboring phenetically distinct populations (THORPE 1979). The reddish-brown belly that was found in the Rijeka population represents clear evidence of the presence of some *muralis* genes. Previously, KRAMER & MERTENS (1938) and MERTENS (1956) pointed out that *muralis x maculiventris* F1 hybrids mostly express *maculiventris*-typical color and pattern, which is consistent with our results.

Although it is difficult to find a general workable criteria for subspecies recognition (THORPE 1979, 1980b, 1984), we think that the Rijeka population, despite its intermediate character, should be stated as *P. muralis maculiventris*. There are two reasons for that: first, phenotypically and ecologically this population is much more similar to other *maculiventris* populations described so far. Second, this should be done for practical taxonomic reasons until more detailed taxonomic investigation of subspecific differentiation of *P. muralis* are completed.

Distribution and habitat preferences

Our results clearly indicate the existence of a contact population in the town of Rijeka, between phenotypically different *maculiventris* and *muralis* populations. Despite the hybrid character of the Rijeka population, specimens from Grobnik are clearly members of typical, wide-ranging and continentally adapted *P. muralis muralis* populations from the Dinarid mountains (KARAMAN 1921, 1939; HENLE 1985). Along the eastern coast of the Istrian Peninsula most of the specimens collected were described as *P. m. muralis* (SCHERER 1902; MOSAUER & WALLIS 1924; KARAMAN 1921, 1939; KRAMER & MERTENS 1938; HENLE 1985), and along the western coastline as *P. m. maculiventris* (KRAMER & MERTENS 1938; TADDEI 1950; PEAKER & PEAKER 1968; LILGE & WICKER 1972; BRELIH & DŽUKIĆ 1974; HENLE 1985). Unfortunately, most of the available literature data suffer of lack of detailed description of specimens collected, which renders subspecific determination unclear. HENLE (1985) pointed out that the border between the two subspecies is located along the western coast of the Istrian Peninsula. However, new evidence has been recently found for the existence of *maculiventris* population in the town of Rabac on the eastern coast of the Istrian Peninsula, and in the town of Cres, on the island of Cres (Fig. 1b, DE LUCA, in prep.). Therefore, areal configuration of both *muralis* and *maculiventris* are likely to be much more 'patchy' than was previously known. Inland region of the Istrian Peninsula seems to be more favorable for *muralis* populations (MOSAUER & WALLIS 1924; KRAMER & MERTENS 1938; SCHMIDTLER 1977; HENLE 1985). Furthermore, the easternmost *maculiventris* finding in Senj, although reported in the literature (WETTSTEIN 1928) has not been confirmed recently. If the Senj population does not exist (or has never existed), the Rijeka population is the easternmost population of *P. muralis maculiventris*. It is not surprising, therefore, that it shows hybrid characteristics and great morphological variability.

The populations of *maculiventris* and *muralis* differ clearly in their habitat requirements, especially with respect to climatic conditions. *P. m. muralis* is adapted to cooler, moderate to high mountain continental climate, as it was previously indicated by various authors (KRAMER & MERTENS 1938; GRUSCHWITZ & BÖHME 1986), and confirmed by our field investigations. Larger and strongly pigmented *maculiventris* prefers warmer, Mediterranean rocky habitats, often of anthropogenic origin (WERNER 1891; KRAMER & MERTENS 1938; GRUSCHWITZ & BÖHME 1986). Dense populations were found in the town of Rijeka on the walls of an old castle and on the rocky beaches, very close to the sea level. Moreover, clearly ecologically distinctive populations of both subspecies were recently found on the island of Cres (Fig. 1b, DE LUCA in prep.; RUCNER & RUCNER 1971). Even if complete distribution is not yet known, the distribution pattern established so far could be well explained by different habitat preferences of both subspecies. *P. m. maculiventris* populations are likely to exist along narrow coastal zone on climatic favorable habitats, with the easternmost population in the town of Rijeka, while *P. m. muralis* is inhabiting mostly cooler habitats, further away from the coast.

Subspecific differentiation

The hybrid characteristics of the Rijeka population clearly indicate the presence of the intergradation zone between the two subspecies. It is still difficult, however, to explain the processes of subspecies differentiation in this region. Apparently, southern populations of *P. muralis*, adapted to warm climate, tend to be larger and more strongly pigmented than continentally adapted populations. This is the case with the recognized subspecies *P. muralis nigriventris* (probably closely related to *P. m. maculiventris*) and *P. muralis albanica*, as well as one doubtful subspecies *P. muralis colosii* (GRUSCHWITZ & BÖHME 1986). Thus, larger body size and stronger pigmentation in populations of *Podarcis muralis* are likely to be the consequence of adaptation process.

In the species entire range, only a few isolated montane populations from the Iberian Peninsula and the Apeninian Peninsula, as well as populations from the Monte Gargano, can be characterized with greater probability as glacial relics (GRUSCHWITZ & BÖHME 1986). Speculations about the relict character of some southern Balkanian populations, related to *P. muralis albanica,* also exist (GRUSCHWITZ & BÖHME 1986). If we assume, however, that Pleistocene glaciation divided a continuous areal of *Podarcis muralis* in the northern Adriatic coastal region to such an extent to cause subspecific differentiation, recent transition zone appears to be the result of secondary contact rather than primary differentiation.

The Rijeka population may also represents one of the cases of primary intergradation belts, caused by a corresponding change in environmental conditions. If we consider strongly different habitat preferences between the two subspecies, this hypothesis may be more likely than the previous one. Since environmental conditions change rapidly from Mediterranean to continental, the climate-based ecogenetic scenario seems probable. Accordingly, different degrees of introgression probably exist elsewhere along the contact zone between two subspecies. Some new data (DE LUCA in prep.), however, indicate an advanced degree of subspecies separation in areas where a hybrid zone has not been established.

In any case, the existence of both subspecies may be well explained by differences in habitat preferences. Despite the gene flow that increases similarity between populations, natural selection pressure seems to be strong enough to preserve different populations. They can still be recognized as different conventional subspecies, even if they are not consistently on the same level of dissimilarity. Detailed investigation would probably support the hypothesis that subspecies differentiation is primarily the consequence of climatic factors, that change rapidly along the transect from the Adriatic coast to the mountains of Gorski Kotar. Still, further taxonomic investigation of the populations from the entire eastern part of the species distribution range seems to be necessary to fully explain processes of subspecific differentiation of *P. muralis* in this region.

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SAŽETAK

Fenetički odnos između *Podarcis muralis muralis* (LAURENTI, 1708) i *Podarcis muralis maculiventris* (WERNER, 1891) (gušterice, gmazovi) u jednoj zoni hibridizacije

N. De Luca & I. Grbac

Zidna gušterica *Podarcis muralis* (LAURENTI, 1768) prebiva na području Istre i sjevernoga, povijesnoga Hrvatskog Primorja u dvije podvrste: kao kontinentalno adaptirana nominalna podvrsta *Podarcis muralis muralis* i mediteranski adaptirana podvrsta *Podarcis muralis maculiventris* (WERNER, 1891). U ovom radu istraženi su intraspecifička varijabilnost i fenetički odnosi izmedu dvije podvrste u području grada Rijeke i okolice, koji su odabrani kao zone moguće hibridizacije. Univarijantnim statističkim analizama i multivarijantnim metodama grupiranja obrađene su 43 morfološke značajke na 96 adultnih životinja, uključujući biometrijske značajke, značajke pileusa i folidoze, te obojenost.

Utvrđena je značajna fenotipska različitost između primjeraka iz grada Rijeke i primjeraka iz Grobničkog polja. Udio signifikantno različitih značajki bio je veći između grobničkog i riječkih uzoraka, nego unutar tri riječka uzorka. Tendencija životinja iz Grobničkog polja da formiraju izdvojenu grupu, vidljiva iz rezultata cluster-analize, osobito je izražena u mužjaka.

Grobnička populacija pripada nominantnoj podvrsti *P. m. muralis* a riječke populacije pokazuju značajno veću fenetičku srodnost s istarskom podvrstom *P. m. maculiventris*. Iako mogu biti svrstani u navedenu podvrstu u okvirima konvecionalnog subspecijskog koncepta, riječki uzorci pokazali su značajke hibridne populacije: veliku morfološku varijabilnost i pojavljivanje tipičnih *"muralis"* značajki obojenosti.

Grobničke i riječke populacije razlikuju se i po izboru staništa, osobito s obzirom na njihove klimatske značajke. Uzimajući u obzir postojeće i novootkrivene zoogeografske podatke i fenotipsku analizu, može se zaključiti da područje grada Rijeke predstavlja zonu hibridizacije između dvije podvrste. Fenotipski različite populacije nastale su najvjerojatnije kao posljedica klimatskih promjena na odgovarajućim staništima, na kojima su procesi prirodne selekcije djelovali snažnije od protoka gena između susjednih populacija.

Na temelju postojećih i novih nalaza može se zaključiti da populacije *P. m. maculiventris* nastanjuju pretežno klimatski toplija staništa uzduž istarske obale do Rijeke a da su populacije *P. m. muralis* vezane uz hladnija staništa, uglavnom podalje od toplog obalnog pojasa.