AN OVERVIEW OF THE OCCURRENCE OF PAEDOMORPHOSIS IN YUGOSLAV NEWT *(TRITURUS,* SALAMANDRIDAE) POPULATIONS

DZUKIC, G_1., M.L. KALEZIC$_2$,
M- TVRTLPVOC$_3$. A. DKPRPVOC$_2$

Institute for Biological Research "Sinisa Stankovic",
29. Novembra 142, Belgrade, $_2$Institute of Zoology, Faculty of Science,
Studentski trg 16, Belgrade, $_3$Croatian Museum of natural History,
Demetrova 1, Zagreb, Yugoslavia.

INTRODUCTION

One of the newt species considered in this paper had the privilege to be the first described of all urodeles in which an alternative path in life history existed. More than 100 years ago, de Filippi (1861) found sexually mature individuals with larval characteristics of the Alpine Newt *(Triturus alpestris)* among a collection of metamorphosed newts. Since then facultative paedomorphosis, as this phenomenon is called, has been frequently discovered in many newt populations.

The Yugoslavian newt fauna consists of populations of six species: the Smooth Newt *(T. vulgaris),* the Alpine Newt *(T. alpestris),* and at least four species of the Crested Newts: *T. carnifex, T. dobrogicus, T. cristatus, T. karelinii* (Wallis and Arntzen, 1989; Kalezic et al., 1990). Thus far, most known paedomorphic populations were that of the Alpine Newt, followed by the Smooth Newt. Taking into account the whole range of these species, the occurrence of paedomorphosis in *T. alpestris* and *T. vulgaris* is most pronounced in the Yugoslavian part of their range. Among Crested Newts in Yugoslavia, only in two populations of *T. carnifex* from Montenegro possible evidence of paedomorphosis has been reported (Kalezic and Dzukic, 1990).

The objectives of this paper are to present some of the general characteristics of the occurrence of paedomophosis in Yugoslav newt populations, including a list of paedomorphic populations, their localities superimposed on the species' ranges in Yugoslavia, as well as characteristics of the newt biotopes and some consequences which paedomorphosis brings to bear on population structure and differentiation.

THE SMOOTH NEWT AND ITS PAEDOMORPHOSIS

This is the widest ranging of all European newts, occurring in west Asia too. It is also the commonest species in most parts of its range including Yugoslavia. In Yugoslavia the Smooth Newt can be found in almost all parts except the Velebit mountains and adjacent areas (Kalezic et al., 1990), and probably the western part of Macedonia (Fig. 1). Its Yugoslav vertical distribution ranges from sea level to almost 1800m above sea level (Mount Durmitor; Dzukic, 1990). The Smooth Newt is the only newt species inhabiting some Adriatic islands (Krk and Cres). Substantial morphological and genetical differentiation occurred in the Smooth Newt populations inhabiting the Balkan region during Pleistocene glaciations (Schmidtler and Schmidtler, 1983; Kalezic, 1984). At least four subspecies live in Yugoslavia: *T.v. vulgaris, T.v. meridionalis, T.v. graecus* and *T.v. dalmaticus* with probably a broad zone of gene flow between some of these subspecies (Fig. 1). The detailed distributions of these subspecies are in many respects still unknown. Also, some authorities denied the existence of *T.v. dalmaticus,* considering it to be *T.v. graecus* (e.g. Schmidtler and Schmidtler, 1983).

Up to now, paedomorphosis has been recorded in seventeen Smooth Newt populations (Table 1). (One individual with larval characteristics was enough to acknowledge the occurrence of paedomorphosis in a particular population). All paedomorphic populations, except one from the slope of Fruska Gora (No. 17), are situated in the Dinaric Carso not far from the Adriatic sea. The populations in question mainly inhabit surface water bodies which usually appear

at the sites of sinkholes and potholes with impermeable bottoms. These biotopes are fed by atmospheric rain water and occasionally by boiling springs and as such they frequently suffer a considerable lowering of water level. During severe droughts which are not uncommon in the Dinaric area, some of them occasionally dry up. As water has always been in short supply in this area, people take care of these ponds, enabling them to last. The incidence of paedomorphic individuals in such biotopes appears to be the highest, up to 50% (Kalezic and Dzukic, 1986), in comparison to other biotopes.

Other, less numerous biotopes with paedomorphic Smooth Newts include man-made ponds in fields fed by atmospheric and/or underground water and, as time passed, colonised by vegetation (Nos. 2, 5, 16, 17). Also Anthropogenetic in origin is another biotope, a drainage and irrigation canal which crosses Sinjsko polje (No. 8). To our surprise, a highly numerous Smooth Newt population occurred there with many paedomorphic individuals, living in a fairly strong water current.

THE ALPINE NEWT AND ITS PAEDOMORPHOSIS

This widely distributed European species has an extensive range in Yugoslavia too (Figure 2). It cannot be found along the coast, including Adriatic islands, lowland areas of the Danube plains, broad zones along the rivers Sava, Velika Morava, and in almost all of Macedonia. The largest populations of the Alpine Newt are to be found in hilly or mountainous districts above 700m, but sizeable colonies are also to be met within some lowland areas (less than 200m).

The Alpine Newt occurs in a wide variety of habitats in Yugoslavia. "Usual" habitats include ponds in woods, pools, lakes and snow-flowing streams in hilly or mountainous regions. However, it can be found in extremely arid environments in the Submediterranean zone at low altitude (less than 100m; Kalezic et al., 1990).

For a long time, paedomorphosis in the Alpine Newt was regarded as being invariably confined to high-altitude, deep glacial lakes or tarns. Of 22 populations in which paedomorphic individuals have so far been found, 15 were in such an environment. However, the rest of the populations inhabit Dinaric karst areas, often at quite low altitude (Nos, 2, 3, 4, 5, 6, 7, 12). Such populations are quite numerous in the Bukovica region (Kalezic et al., submitted) where they populated the same eutrophic habitat type as those of the Smooth Newt paedomorphic populations from the Submediterranean area of Yugoslavia. At one site (No. 12) paedomorphic Alpine Newts were found in relatively small shallow water bodies lying along a lost river in a karst field (Dzukic and Kalezic, 1984).

The localities inhabited by the Alpine Newt paedomorphic populations situated in high mountains were originally free of fish, which was important for the maintenance of paedomorphosis. That it was so was unfortunately confirmed a decade later when introduced trout caused the complete disappearance of newts, particularly of paedomorphic ones, in many such lakes (see present status in Table 2).

A subspecies level has been attached to many previously reported Alpine Newt populations with paedomorphic individuals. Werner (1902) started by describing a population from Prokosko Jezero (No. 10) as *T. a. reiseri.* A famous paedomorphic population from Bukumirsko Jezero (No. 20) was designated as *T. a. montenegrinus* (Radovanovic, 1951). Radovanovic (1961) described populations from Kapetanovo and Manito Jezero (No. 18, 19) as *T. a. piperianus,* and a population from Zminicko Jezero as *T. a. serdarus.* The individuals from all these populations were said to have larger and wider heads in comparison with the nominate form, besides some differences in colouring. Separate taxonomic positions of these taxa are still uncertain because of some discrepancies of results obtained by different approaches: morphological (Rocek, 1974), biochemical (Breuil and Gutllaume, 1984; Arano and Arntzen, 1987), and cytogenetical (Herrero et al, 1989).

TABLE 1

Population localities with observed paedomorphic Smooth Newt individuals, altitude, sympatry with other newt species, and present status (paedomorphic newts present +, absent –).

Locality	Altitude	Sympatry with	Present status	Reference
1. Ferlini	330 m	–	+	this study
2. Trget	195 m	–	+	this study
3. Diviska	470 m	–	+	this study
4. Bag	240 m	–	+	this study
5. Smilcic	190 m	–	+	Kalezic et al., 1987
6. Knin	(cca 300 m)	?	?	Wolterstorff, 1935
7. Sitno	175 m	–	–	Kolombatovic, 1908
8. Sinjsko polje	296 m	–	+	this study
9. Supljica	1350 m	*T. alpestris*	+	Dzukic & Kalezic, 1983
10. Kovacevica lokva	930 m	–	+	Kalezic & Dzukic, 1985
11. V. Osjecenica	990 m	–	+	Dzukic, 1981
12. Voluje oko	970 m	–	+	Kalezic & Dzukic, 1985
13. Rutesica voda	950 m	–	+	Kalezic & Dzukic, 1985
14. Dobrsko selo	250 m	*T. carnifex*	+	Kalezic & Dzukic, 1990
15. Markova lokva	220 m	*T. carnifex*	+	this study
16. Donji Stoj	0 m	*T. carnifex*	+	Kalezic & Dzukic, 1990
17. Sremska Kamenica	80 m	*T. dobrogicus*	+	Franolic & Cobic, pers. comun.

TABLE 2

Population localities with observed paedomorphic Alpine Newt individuals, altitude, sympatry with other newt species, present status (paedomorphic newt present +, absent –).

Locality	Altitutde	Sympatry with	Present status	Reference
1. Jezero pri Planini nad jezerom	1428 m	*T. vulgaris* *T. carnifex*	–	Seliskar & Pehani, 1935
2. Gucinac bunar	220 m	–	+	Tvrtkovic & Kletecki, submitted
3. Antinovic lokva	270 m	–	+	Tvrtkovic & Kletecki, submitted
4. Pajica lokva	275 m	–	+	Kalezic et al., 1990
5. Brgud	260 m	–	+	Kalezic et al., 1990
6. Grulovici	245 m	–	+	Kalezic et al., 1990
7. Suhopolje	900 m	?	?	Kolombatovic, 1908
8. Satorsko jezero	1488 m	–	+	Pocrnjic & Kosoric, 1967
9. Lokva kod koliba	930 m	–	?	Travizi, pers. comun.
10. Prokosko jezero	1640 m	–	–	Werner, 1902
11. Rujiste	1100 m	–	+	Djurovic, 1987
12. Nevesinjsko polje	850 m	*T. vulgaris*	+	Dzukic & Kalezic 1984
13. Kladopoljsko jezero	1380 m	–	?	Pocrnjic & Kosooric, 1966
14. Trnovacko jezero	1517 m	–	+	Radovanovic, 1961
15. Zminicko jezero	1285 m	*T. vulgaris*	+	Radovanovic, 1961
16. Vrazje jezero	1428 m	*T. vulgaris*	+	Pocrnjic & Kosoric, 1966

17. Zabojsko jezero	1477 m	-	-	Radovanovic & Lesnicenko, 1963
18. Manito jezero	1773 m	-	+	Radovanovic, 1961
19. Kapetanovo jezero	1678 m	-	?	Radovanovic, 1961
20. Bukumirsko jezero	1440 m	*T. vulgaris*	+	Radovanovic, 1951
21. Ridsko jezero	1970 m	?	?	Radovanovic, Col.
22. Crno jezero	2122 m	-	?	Radovanovic, Col.

DISCUSSION

We believe that the results of this paper, as well as others dealing with paedomorphosis among European newts, are in line with those in which it has been claimed that many urodele species had a notably variable life history (e.g. Duellman and Trueb, 1986). Three major life history pathways also existed in *Triturus* species. Most individuals in most populations (with a few exceptions including some Yugoslav ones) follow the ontogenetic path characterized by the metamorphosing of larvae into an immature individual which remains essentially terrestrial before reaching sexual maturity. Obligate metamorphosis may be the ancestral condition in the whole family Salamandridae if we assume that there is no evidence of paedomorphosis in *Tylotriton*, the most primitive genus of this family (see Wake and Ozeti, 1966). The second path is that followed by larvae with prolonged growth followed by attaining sexual maturity and afterwards metamorphosing into adults (immature efts are excluded). The third path is toward obligate paedomorphosis: larvae with prolonged growth mature sexually without completing metamorphosis. Whether paedomorphic individuals in Yugoslav newt populations are those from the second and/or third paths described above is still unknown. There is indirect evidence that the third path may be efficient at least in the case of the Alpine Newt in mountain lakes. Smirina and Sofianidu (1985) found that the life span of the paedomorphic and metamorphic individuals from Greek Alpine Newt populations was approximately equal. Individuals following the second path may take advantage of a favourable aquatic environment yet have the ability to metamorphose in order to escape that environment when it becomes deleterious. This might be the case with Smooth Newt and Alpine Newt populations with facultative paedomorphosis in Yugoslavia inhabiting biotopes in Submediterranean areas.

Collins (1981) did not find any correlation between the occurrence of paedomorposis and altitude in the Axolotl *(Ambystoma).* Nor did we in the case of two European newt species (see Tables 1 and 2). Also, it is obvious that the ease and frequency of metamorphosis of newt populations with facultative paedomorphosis cannot be correlated with geographical and ecological gradients as was claimed earlier (e.g. Gould, 1977). It appears that reproduction of newt individuals with larval features is a labile character and that each occurrence might be considered as an evolutionary independent event, as was suggested for ambystomatid salamanders (Shaffer and Breden, 1989). However, that newts of both species *(T. vulgaris* and *T. alpestris)* have more chance to become paedomorphic in Dinaric areas than in other parts of its range still keeps the hypothesis of ecological importance for polymorphic life history actual. Recent studies on the genetic basis of paedomorphosis in urodele species showed that the ability to become paedomorphic is under genetic control, albeit highly susceptible to environmental conditions (Harris, 1987; Semlitsch and Wilbur, 1989).

The presence of inheritable genetic variation, as shown by Semlitsch and Wilbur (1989) for *Ambystoma talpoideum,* supports the view that paedomorphosis may be an important microevolutionary mechanism (Gould, 1977; Alberch et al., 1979). Evidence that non-transforming urodeles have a significantly lower level of genetic variation than transforming was found (Shaffer and Breden, 1989). Also, paedomorphosis in newts is associated with a female-biased sex ratio (Kalezic et al., 1989), and paedomorphic-metamorphic population partitioning proved to be a significant factor that considerably increased phenotypic variation (Tucic et al., 1985; Kalezic et al., 1989). Taking into consideration two European newt species we may assume that paedomorphosis had more influence on population differentiation in the

Alpine Newt than in the Smooth Newt. It might be so because paedomorphosis in the Smooth Newt is limited to the retention of some gill structures only ("limited neoteny"; Reilly, 1987), while the same heterochronic phenomenon in the Alpine Newt retains more larval characteristics including perhaps the skull features (unpublished).

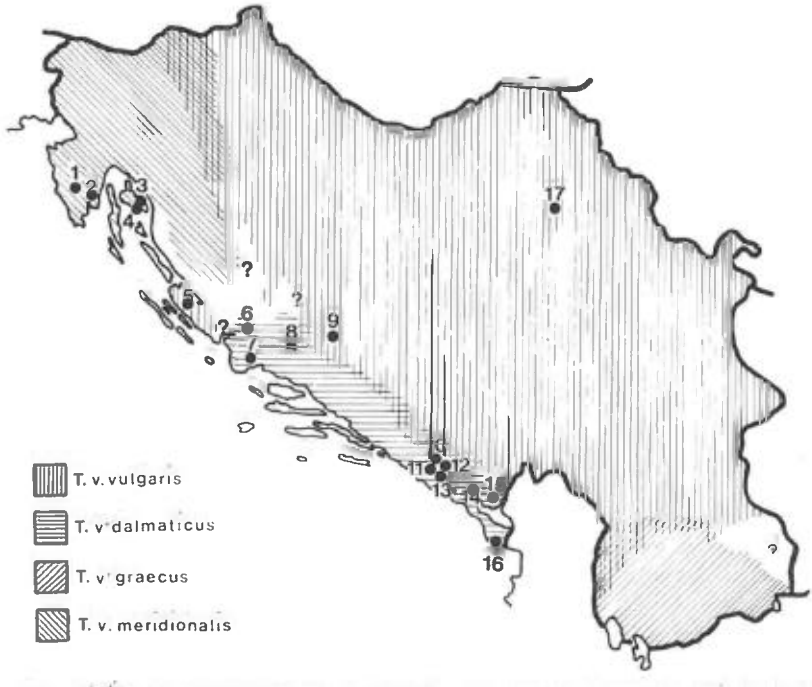

Figure 1. Map showing the distribution of the Smooth Newt taxa in Yugoslavia and the location of paedomorphic populations. For location designations see Table 1.

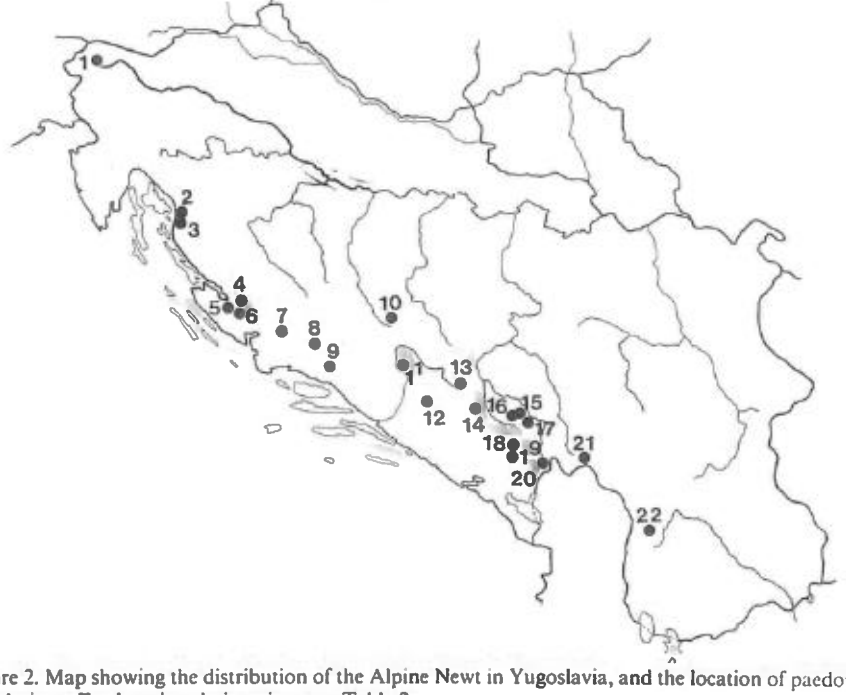

Figure 2. Map showing the distribution of the Alpine Newt in Yugoslavia, and the location of paedomorphic populations. For location designations see Table 2.

ACKNOWLEDGEMENTS

Our colleagues Ana Travizi, Zvonimir Franolic and Dragan Cobic kindly gave us access to their unpublished data on newt paedomorphosis in Yugoslavia.

REFERENCES

Arano, B. & Arntzen, J.W. (1987). Genetic differentiation in the alpine newt, *Triturus alpestris. Proc. Fourth Ord. Gen. Meet. S.E.H.* Nijmegem.

Alberch, P., Gould, S.J., Oster, G.F. & Wake, D.B. (1979). Size and shape in ontogeny and phylogeny. *Paleobiology,* **5,** 296-317.

Breuil, M. & Guillaume, C.P. (1984). Etude electrophoretique de quelques populations de Tritons alpestres neoteniques *(Triturus alpestris,* Amphibia, Caudata, Salamandridae) du sud de la Yugoslavie. *Mem. Soc. zool. Fr.,* **109** (4), 337-389.

Collins, J.P. (1981). Distrifbution, habitats and life history variation in the tiger slamander, *Amystoma tigrinum,* in east-central and southeast Arizona. *Copeia,* 1981(3), 666-675.

Djurovic, E. (1986). Novi podaci o rasprostranjenju i morfoloskim karakteristikama *Triturus alpestris* (Laurenti, 1768) (Amphibia: Urodela) u Bosni i Hercegovini. *Glas. zem. muz. BiH,* Sarajevo, NS 25-26, 201-210.

Dzukic, G. (1981). Prvi nalaz neotenicne populacije malog mrmoljka *Triturus vulgaris* (Linnaeus), 1758 u Jugoslaviji. *Glas. Republ. zavoda zast. prirode Prir. muz.* Titograd, **14,** 71-77.

Dzukic, G. (1990). The Fauna of Durmitor, 3: Amphibians and Reptiles, Materials to the fauna of Durmitor Mountain's amphibia and reptiles (Amphibia-Reptilia). *Crnogorska akademija nauka i umjetnosti, Odeljenje prirodnih nauka, knj.* **14.** Titograd.

Dzukic, G. & Kalezic, M.L. (1983). Novi nalaz neotenicnog primerka *Triturus vulgaris* (L.) u Jugoslaviji. *Arch. biol. nauka,* Beograd, **35,** 11P-12P.

Dzukic, G. & Kalezic, M.L. (1984). Neoteny in the alpine newt population from submediterranean area in Yugoslavia. *Alytes,* **3,** 11-19.

Duellman, W.E. & Trueb, L. (1986). *Biology of the Amphibia.* McGraw-Hill, New York.

Filippi, F. de (1861). Uber die larven des *Triton alpestris. Z. Zool.,* **28** (1877): Deutsche Uberzetzungvon C. von Siebold.

Gould, S.J. (1977). *Ontogeny and Phylogeny.* The Belknap Press, Cambridge.

Harris, R.N. (1987). Density-dependent paedomorphosis in the salamander *Notophthalmus viridescens dorsalis. Ecology,* **68,** 705-712.

Herrero, P., Arano, B. & Garcia de la Vega, C. (1989). Chromosome differentiation in the *Triturus alpestris* complex (Amphibia: Caudata). *Genetica,* **79,** 27-35.

Kalezic, M.L. (1984). Evolutionary divergences in the smooth newt, *Triturus vulgaris* (Urodela, Salamandridae): Electrophoretic evidence. *Amphibia-Reptilia,* **5,** 221-230.

Kalezic, M.L. & Dzukic, G. (1985). Ecological aspects of the smooth newt *(Triturus vulgaris)* paedomorphosis from Montenegro. *Arh. Biol. Nauka,* Beograd, **37,** 43-50.

Kalezic, M.L. & Dzukic, G. (1988). The Frequent Occurrence of Paedomorphosis in the Smooth Newt *(Triturus vulgaris)* Population from Submediterranean Area of Yugoslavia. *Amphibia-Reptilia,* **7,** 86-89.

Kalezic, M.L., Dzukic, G., Crnobrnja, J. & Tvrtkovic, N. (1987). On the *Triturus vulgaris schreiberi* problem: electrophoretic data. *Alytes,* **6,** 18-22.

Kalezic, M.L., Dzukic, G., Popadic, A. (1989). Paedomorphosis in Yugoslav alpine newt *(Triturus alpestris)* populations: Morphometric variability and sex ratio. *Arh. biol. nauka,* Beograd, **41,** 67-79.

Kalezic, M.L. & Dzukic, G. (1990). Evidences for paedomorphosis in the crested newt, *Triturus cristatus* Complex (Salamandridae, Urodela). *Glas. Prir. Muz. Serija B,* Beograd, **45:** 127-132.

Kalezic, M.L., Dzukic, G., Stamenkovic, S., Crnobrnja, J. (1990). Morphometrics of the crested newt *(Triturus cristatus* Complex) from Yugoslavia: Relevance for taxonomy. *Arh. biol. nauka, Beograd,* **42,** 17-37.

Kalezic, M.L., Dzukic, G., Tvrtkovic, N. (1990). Newts *(Triturus,* Salamandridae, Urodela) of the Bukovica and Ravni Kotari Regions (Yugoslavia). *Spixiana* (in press).

Kolombatovic, G. (1908). Sui Tritoni della Dalmazia. *Glas. Hrv. Prir. drustva,* **20,** 240-250.

Pocrnjic, Z. & Kosoric, Dj. (1966). New finding-sites of neotenic alpine tritons *(Triturus alpestris). Bull. Sci., Sec. 1,* **11,** 10-12.

Pocrnjic, Z. & Kosoric, Dj. (1967). New finds of the phenomenon of neoteny in the populations of alpine tritons. *Bull. Sci., Sec. A*, **12**, 7-8.

Radovanovic, M. (1951). A new race of the alpine newt from Yugoslavia. *Brit. J. Herpetol.*, **1**, 93-97.

Radovanovic, M. (1961). Neue Fundorte neotenischer Bergmolche in Jugoslawien. *Zool. Anz.*, **166**, 206-218.

Radovanovic, M. & Lesnicenko, O. (1963). Skelet glave neotenicnih tritona. *Srpska akademija nauka, Glas* CCLIII, **23**, 25-42.

Reily, S.M. (1987). Ontogeny of the Hyobranchial apparatus in the salamanders *Ambystoma talpoideum* (Ambystomatidae) and *Notophthalmus viridescens* (Salamandridae): The ecological morphology of two neotenic strategies. *J. Morph.*, **191**, 205-214.

Rocek, Z. (1974). Beitrag zur Erkennung der Neotenie des Alpen molches *Triturus alpestris* (Laurenti, 1768). *Vest. Cs. spol. zool.*, **38**, 285-294.

Schmidtler, J.J. & Schmidtler, J.F. (1983). Verbreitung, Okogieund innerartliche Gliederung von *Triturus vulgaris* in den adriatischen Kustengebieten. *Spixiana*, **1**, 229-249.

Shaffer, H.B. & Breden, F. (1989). The relationship between allozyme variation and life history: Non-transforming salamanders are less variable. *Copeia*, 1989 (4), 1016-1023.

Semlitsch, R.D. & Wilbur, H.M. (1989). Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum. Evolution*, **43**, 105-112.

Seliskar, A. & Perhani, H. (1935). Limnologische beitrage zum Problem der Amphibienneotenie (Beobachtungen an Tritonen der Triglavseen). *Verh. Inter. Verein. fur th. angew. Limn.*, **7**, 263-294.

Smirina, E.M. & lSofianidu, T. (1985). On life span of the neotenic and metamorphosed alpine newt *(Tritutus alpestris)* from high mountains of Greece. *Zoologiceskii zurnal*, **64**, 311-315.

Tucic, N., Kalezic, M.L. & Dzukic, G. (1985). Morphometric variability in the *Triturus vulgaris* population with facultative paedomorphosis. *Zool. Anz.*, **215**, 102-108.

Tvrtkovic, N. & E. Kletecki. Amphibia from North-Velebit Mts. karst area (Croatia, Yugoslavia). Submitted.

Wake, D.B. & Ozeti, N. (1969). Evolutionary relationships in the family Salamandridae. *Copeia* 1969(2), 124-137.

Wallis, G.P. & Arntzen, J.W. (1989). Mitochondrial DNA variation in the crested newt superspecies: Limited cytoplasmic gene flow among species. *Evolution*, **43**, 88-104.

Werner, F. (1902). Eine neue varietat des alpenmolches aus Bosnien. *Molge alpestris* var Reiseri. *Verh. zool. botan. Ges.*, Wien, **52**, 7-9.

Wolterstorff, W. (1935). Katalog der Amphibien-Sammlung im Museum fur Natur- und Heimatkunde zu Magdeburg. *Abh. Ber. Mus.* Magdeburg, **4**, 231-310.