SPIXIANA	19	3	315–326	München, 01. November 1996	ISSN 0341–8391

Paedomorphosis and morphometric variability: Ontogenetic allometry in European newts of the genus *Triturus*

(Amphibia, Salamandridae)

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Djorovic, A. & M. L. Kalezic (1996): Paedomorphosis and morphometric variability: Ontogenetic allometry in European newts of the genus *Triturus* (Amphibia, Salamandridae). – Spixiana **19/3:** 315-326

Using bivariate and multivariate morphometric analyses, effects of paedomorphosis on intrapopulation ontogenetic changes in size and shape of three European newt species (*Triturus vulgaris, T. alpestris* and *T. carnifex*) are studied. Samples of larvae, efts and adults of two conspecific populations of each species were considered, one with generalized life cycle, the other with paedomorphosis (in a *T. carnifex* population larvae had prolonged growth and metamorphosed during the following year). It was found that existence of an alternative life cycle rendered more complex ontogenetic picture of allometric relations of individual morphometric features, particularily in *T. vulgaris*. In this species paedomorphic individuals followed ontogenetic trajectories of larvae, while metamorphic adults deviated considerably from this trajectories. This was much less significant in *T. alpestris*, another species with high incidence of paedomorphosis, but also in *T. carnifex*, a species with less plastic life-cycle than both previous species. As in the American newts (Harris 1989), differences between non-transforming and transforming individuals in the genus *Triturus* in ontogenetic paths of size and shape changes presumably developed relatively late in ontogeny.

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Introduction

It is the commonly held view that the heterochrony, changes in the timing of developmental events during ontogeny, is among the most prominent mechanisms for phenotypic changes (e.g. McKinney 1988). Allometry, the study of size/shape relations, provides data for assessing heterohronic morphological events (Alberch et al. 1979). If paedomorphosis, sexual maturation of individuals retaining morphology that resembles subadult stages of closely related populations or species (Gould 1977), is to be studied, ontogenetic allometry is relevant. Ontogenetic allometry simply refers to changes in size and shape relationships in individuals with time (Shea 1984, Lande 1985).

Paedomorphosis is frequent in amphibians, especially in Caudata where it occurs due to change in timing of metamorphosis. Metamorphosis consistently occurs in generalized and presumably primitive form of urodele life-history; from eggs laid into aquatic environment larvae are developed and metamorphose into immature individuals (juveniles or efts) who remain mainly terrestrial before reaching sexual maturity. In many urodele species, however, there are populations with individuals following another ontogenetic pathway. Larvae here have prolonged growth, attain sexual maturity and reproduce retaining larval morphology. Immature eft stage is excluded in this path, while adults can have abandoned or delayed metamorphosis. These urodele species exhibit two adult phenotypes in natural populations. Paedomorphs are adults having such larval characteristics as: external gills and associated hyobranchial structures, an enlarged tail fins, skin often with Leydig cells and larval texture, and characteristics of larval skull. Metamorphs lack all these traits in morphology.

There is considerable interspecific variation among urodeles with paedomorphosis in the degree of retention of larval characteristics. Reilly (1987) found, studying metamorphosis of skull and hyobranchial apparatus, that paedomorphosis in *Ambystoma talpoideum* has profound effects on these osteological structures, while paedomorphosis in salamandrids (Salamandridae; *Notophthalmus viridescens, Taricha granulosa* and *Triturus vulgaris*) is mainly limited to the retention of gill structures to varying degrees. Also, it seems that urodeles species with paedomorphosis differ in the stage of somatic truncation along an ancestral size-shape trajectory (Shaffer 1984, Harris 1989).

Paedomorphosis is rather common in many species of the genus *Triturus*. The smooth newt (*Triturus vulgaris*) and the alpine newt (*Triturus alpestris*) show a high degree of paedomorphosis incidence, particularly in the submediterranean area of the Balkans (Dzukic et al. 1990). In the crested newt (*Triturus cristatus* superspecies) almost an exclusive life-history pathway leads to obligate metamorphosis; i.e. paedomorphosis is extremly rare. So far, there has been no study on paedomorphosis related ontogenetic changes in size and shape of European newts (genus *Triturus*). The main goal of this paper is to compare such intrapopulation changes in three species, *T. vulgaris, T. alpestris*, and *T. carnifex*. Populations with paedomorphosis were studied, as well as conspecific populations with obligate metamorphosis considered here as control groups. The null hypothesis in this study was that the allometric relations of paedomorphs should resemble more those of larval and juvenile individuals than those of metamorphs ones.

Materials and methods

Population Samples

Paedomorphic population of *Triturus vulgaris* from the pond of Velika Osjecenica (Vilusi, Montenegro), further designated as V1, was chosen because of high percentage of paedomorphic individuals (Tucic at al. 1985). Morphometric variables were scored on 205 larval and post-larval specimens collected from this pond. The smooth newt population from pond Česta (Vrsacki breg, Serbia) was a control population (population referred to as V2), as no evidence of paedomorphic individuals was found in the years of its inspection. When larvae from this pond were sampled (July), some were sacrifised and preserved as larval sample, while others were grown under laboratory conditions in order to provide eft sample. In the end of August the majority of larvae metamorphosed; efts were grown for two weeks in terrarium and then preserved. The total population sample contained 111 individuls.

The alpine newt population from Bukumirsko Lake (Montenegro; population referred to as A1) was selected as paedomorphic population. In this lake non-transformed individuals predominated (Radovanovic 1951). Neither larvae nor efts were found in this lake. Efts were sampled in a nearby temporary lake (Crno Lake) separated from Bukumirsko Lake only by a low moraine which presents no barrier to intensive gene flow between the newts of these lakes. We failed to collect larvae from this lake, too. The alpine newt paedomorphic population sample consisted of 169 individuals. Samples of a control alpine newt population (referred to as A2) were taken from the locality of Sirokar (Montenegro, Mt. Prokletije). From here we took a total of 166 newt specimens.

The individuals from Lokanj pond (Montenegro), referred to as C1, have plastic life-history, including the strategy of paedomorphosis (Kalezic et al. 1994). We have sampled here, besides efts and adults, overwintering larvae as well. The total population sample estimated 118 newts. The individuals of crested newts from nearby Ceklin pond are characterized by obligate metamorphosis. This population is a control one in our study and is referred to as C2. From this population morphometric characteristics of 179 individuals were measured.

Measurements

To demonstrate the size and shape changes during newts ontogenesis, the following set of 10 morphometric variables were measured to the nearest 0.1 mm using dial calipers or plastic ruler as appropriate: L: total length, Lcp: body length (measured from the snout to the front edge of cloaca), Lcd:

tail length, Lsv: snout-vent length (measured from the snout to the posterior edge of cloaca), Ltc: head width, Lc: head length (measured from the snout to the angle of the jaw), Pa: forelimb length, Pp: hindlimb length, D: distance between fore- and hindlimbs, and Lh: maximum tail height (measured at the base of the tail from dorsal to ventral edges).

Before they were mesured, the individuals used in this study had been preserved in ethanol for different period of time (from a couple of months to 7 years). In scoring morphometric traits values and their on-going statistical treatment, we may have dealt with a source of potential errors. We are aware that occasional imprecision in measuring might occur due to some morphological distortion which can affect newts during their preservation (Lee 1982, Verrell 1985). The extent of this measurer bias in our study was not determined. But, as individuals of each ontogenetic stage spent approximately the same time in conservation solution, and as it might be supposed that tissue shrinkage due to preservation was not age and paedomorphs/metamorphs dependent, we may assume that this potential error did not introduce any systematic bias into analysis.

Statistical analysis

Since we have treated ontogenetic stages (larvae, efts, adults) of the same population as different categories, obtained sets of measurements could be referred here to as "cross-sectional data" (Cock 1966). These data yield information on the average growth of individual groups. Due to marked sexual size differences in newts (Kalezic et al. 1992), sexes of paedomorphs and metamorphs were separately statistically treated.

Univariate traits were analyzed using one-way analysis of variance (ANOVA) when comparing the significance in difference between trait variability, and two-way analysis of variance when evaluating the significance of paedomorphosis and sex effects on morphometric character diversity. The used measure of bivariate allometry is the regression coefficient of logarithmically transformed data. In this analysis, Lsv was used as an independent size variable. The differences among bivariate allometric coefficients of morphometric characteristics for analyzed forms were tested by Tukey q-test for multiple slopes comparison (Zar 1984).

Patterns of morphological variation were examined by the multivariate methods of principal component analysis (PCA) done on pooled all measurments data. The first component (PC1) of this analysis, which is highly positively correlated with original data, was used as a latent size variable, while the second principal component (PC2) measures organism shape independent of size (Shea 1985, Bookstein et al. 1985 and references therein). The analysis was performed on the variance-covariance matrix (more appropriate when one deals with morphometric data than correlation matrix) of log-transformed variables (done in order to meet the assumption of homoscedascity; Zar 1974).

A test of isometry was performed by comparing PCA eigenvectors to those of an isometric vector (chi-square test; see Jolicoeur 1963). To measure relationship between bivariate and multivariate allometry, Spearman's rank correlations were calculated between the eigenvector loadings for the first component and allometric loadings of each morphometric characters.

Ontogenetic trajectories were obtained for each ontogenetic stage (larvae, juveniles and adults) by linear regression analysis of PC1 scores on PC2 scores. A rate of change in shape relative to size was estimated by the slope of the regression lines.

Results

Morphometric traits variability

The mean values (±one standard error) of 10 morphometric characters for larvae, efts, and adults (females and males were given separately within paedomorphs and metamorphs groups) of examined populations were given in Appendix for *T. vulgaris* (Tab. 1), *T. alpestris* (Tab. 2), and *T. carnifex* (Tab. 3). In the smooth and crested newt population samples efts were significantly larger than larvae individuals for most characters (ANOVA test), while such differences in the alpine newt were much less pronounced. Among the adults, in the smooth newt paedomorphic individuals were significantly smaller than metamorphic ones for both sex; such differences within alpine newt population were much less apparent.

The influence of paedomorphosis effect and sex effect on morphometric variability in the smooth newt appeared to be statistically highly significant for all characters, except for tail height (two-way ANOVA test). In the alpine newt such influences were more selective. Intersex differences in examined morphometric characters were much more pronounced in the crested newt population with obligate metamorphosis than in the population with more plastic life-history traits (ANOVA test).

Bivariate allometry

In the smooth newt population with paedomorphosis (V1) larvae retreated significantly from isometry for many characters, following with metamorphs and efts in decreasing order (Tab. 1). In paedomorphic individuals statistically significant coefficients of bivariate allometry were only in some characters (head dimensions and tail height). In the control smooth newt population (V2) all measured morphometric characters of males had isometrical growth, following by larvae where only tail height had allometric growth. Among efts and females allometry appeared in more characteristics (mainly head dimensions).

In the alpine newt population with paedomorphosis (A1), a number of characters of non-transformed females and some characters of transformed females, expressed statistically significant allometric growth (Tab. 2). Morphometric characters in males (paedomorphic and metamorphic) were almost excusively characterized by isometry. However, in the population of this species with obligate metamorphosis (A2), most characters of larvae and males were with a significant bivariate allometry. In both crested newt populations, the number of significant character allometry decreased from larvae, throught efts to females and males (Tab. 3).

Tab. 1. The significancy of allometric coefficients - testing the slope against a standard 1 - for all analysed form in smooth newt populations. n.s.: isometry; statistically significant allometry *P<0.05, **P<0.001, ***P<0.001. See text for character and population designation.

	V1						V2			
			metamorphic		paedomorphic				metamorphic	
	larvae	efts	♀♀	♂♂	♀♀	♂♂	larvae	efts	♀♀	♂♂
L	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Lcp	***	*	**	***	n.s.	n.s.	n.s.	n.s.	**	n.s.
Lcd	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ltc	***	***	*	n.s.	**	n.s.	n.s.	***	**	n.s.
Lc	**	*	***	*	**	**	n.s.	n.s.	**	n.s.
Pa	**	n.s.	***	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Pp	***	***	***	*	n.s.	n.s.	n.s.	**	n.s.	n.s.
D	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Lh	**	*	**	***	**	n.s.	*	n.s.	n.s.	n.s.

Tab. 2. The significancy of allometric coefficients - testing the slope against a standard 1 - for all analysed forms in alpine newt populations. n.s.: isometry; statistically significant allometry *P<0.05, **P<0.001, ***P<0.001. See text for character and population designation.

	A1					A2			
		metamorphic		paedomorphic				metamorphic	
	efts	♀♀	♂♂	♀♀	♂♂	larvae	efts	♀♀	♂♂
L	n.s.	n.s.	*	***	n.s.	*	n.s.	n.s.	*
Lcp	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	*
Lcd	n.s.	n.s.	n.s.	**	n.s.	*	n.s.	n.s.	*
Ltc	***	n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	n.s.
Lc	n.s.	**	n.s.	n.s.	n.s.	*	n.s.	*	***
Pa	n.s.	*	n.s.	*	n.s.	***	*	**	**
Pp	*	n.s.	n.s.	***	n.s.	*	n.s.	*	n.s.
D	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Lh	n.s.	*	*	n.s.	n.s.	*	***	n.s.	n.s.

Between-ontogenetic-stages pairwise comparisons in allometric coefficients were presented in Tab. 4 in the form of the number of statistically significant differences of nine morphometric variables versus snout-vent length for each population. In both populations of the smooth newt and control population of the alpine newt (A2) there were no statistically significant difference between bivariate coefficients of larvae and efts, but it was not the case in the crested newt populations. Among larvae and adults, most differences existed between larvae and metamorphosed males, especially in the smooth newt population with paedomorphosis (V1). In the population with paedomorphic individuals, efts and paedomorphic females differed in two of nine comparisons. In these populations there was no difference in regression coefficients between efts and metamorphosed females. The difference between efts and metamorphosed females existed in both populations of the crested newt. Efts and males differed only in the populations V1 and C1 (Tab. 4). Statistically significant differences of bivariate allometric coefficients between paedomorphs and metamorphs of the same sex were found in the smooth newt and in the alpine newt only for one character comparison (Tab. 4). Intersex differences within metamorphs existed in the smooth newt population V1, and in populations of the crested newt, while paedomorphic females and males differed in the population A1 for two bivariate relationships. Taking

Tab. 3. The significancy of allometric coefficients - testing the slope against a standard 1 - for all analysed forms in crested newt populations. n.s.: isometry; statistically significant allometry *P<0.05, **P<0.001, ***P<0.001. See text for character and population designation.

	C1				C2			
	larvae	efts	♀♀	♂♂	larvae	efts	♀♀	♂♂
L	*	*	*	*	n.s.	n.s.	n.s.	n.s.
Lcp	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Lcd	*	***	*	n.s.	n.s.	n.s.	n.s.	*
Ltc	n.s.	n.s.	n.s.	n.s.	***	**	n.s.	n.s.
Lc	**	n.s.	n.s.	n.s.	***	***	n.s.	n.s.
Pa	n.s.	**	n.s.	n.s.	*	n.s.	***	n.s.
Pp	*	n.s.	***	n.s.	*	n.s.	**	n.s.
D	*	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.
Lh	n.s.	n.s.	n.s.	*	n.s.	***	n.s.	n.s.

Tab. 4. Number of statistically significant differences between bivariate allometric coefficient (q-test) of nine morphometric characters and Lsv as independent variable of larvae, efts, paedomorphs and metamorphs (sexes were separated) in six studied populations. Abbreviations: L: larvae, E: efts, FM: metamorphic females, FP: paedomorphic females, MM: metamorphic males, MP: paedomorphic males. df: degree of freedom. See text for population designation.

	V1 df=297	V2 df=103	A1 df=168	A2 df=158	C1 df=110	C2 df=171
L/E	0	0	/	0	1	2
L/FM	1	0	/	0	0	0
L/FP	0	/	/	/	/	/
L/MM	4	1	/	0	0	1
L/MP	1	/	/	/	/	/
E/FM	0	0	0	0	2	1
E/FP	2	/	2	/	/	/
E/MM	2	0	0	0	1	0
E/MP	2	/	0	/	/	/
FM/FP	1	/	0	/	/	/
FM/MM	1	0	0	0	1	2
FM/MP	1	/	1	/	/	/
FP/MM	1	/	1	/	/	/
FP/MP	0	/	2	/	/	/
MM/MP	0	/	0	/	/	/
Total	16	1	6	0	5	6

Tab. 5. Character eigenvectors and eigenvalues derived from pooled data of larvae, efts, paedomorphs and metamorphs of the six populations. The variables used in the analysis were the logarithms of 10 morphometric characteristics. See text for character designation.

	Eigenvectors		
	PC1	PC2	PC3
L	0.31	-0.06	0.31
Lcp	0.31	-0.16	-0.03
Lcd	0.31	0.03	0.66
Lsv	0.31	-0.15	-0.02
Ltc	0.28	-0.10	-0.58
Lc	0.23	-0.16	-0.14
Pa	0.33	-0.13	-0.22
Pp	0.34	-0.14	-0.12
D	0.36	-0.15	0.18
Lh	0.35	0.92	-0.13
Eigenvalues	0.3825	0.0195	0.0031
% of variance	(93.42)	(4.77)	(0.76)

Tab. 6. Chi-square values obtained from test of isometry (comparing PCA eigenvectors based on covariance matrix with an isometric vector -arc cos $^1/_3$; total df=9). The variables used in the analysis were the logarithms of 10 morphometric characteristics. See text for character designation. P: significance of differences from isometry. *P<0.05; ***P<0.001

	V1	V2	A1	A2	C1	C2
Larvae	2.94	54.88***	/	1.66	5.95	4.88
Efts	21.06*	3.92	17.43*	2.34	8.39	3.12
♀♀ (M)	15.14	4.52	54.58***	59.56***	1.47	2.84
♂♂ (M)	9.69	4.74	18.37*	11.51	5.75	3.03
♀♀ (P)	3.09	/	58.64***	/	/	/
♂♂ (P)	4.97	/	12.67	/	/	/

Tab. 7. Spearman's rank correlation between results of bivariate and multivariate allometry. M: metamorphic individuals. P: paedomorphic individuals.

	V1	V2	A1	A2	C1	C2
Larvae	0.720*	0.418	/	0.300	0.633*	0.833**
Efts	0.500	0.284	0.979***	0.736*	0.845**	0.713*
♀♀ (M)	0.962***	0.833**	0.883**	-0.017	0.600*	0.966***
♂♂ (M)	0.950***	0.828**	0.770*	0.703*	0.946***	0.967***
♀♀ (P)	0.946**	/	0.200	/	/	/
♂♂ (P)	0.427	/	0.217	/	/	/

Tab. 8. Means and standard errors of PC1 and PC2 scores for analysed forms in the smooth newt populations. See text for population designation.

	V1		V2	
	PC1	PC2	PC1	PC2
Larvae	3.06 ± 0.06	-0.31 ± 0.03	2.67 ± 0.10	-0.40 ± 0.10
Efts	2.92 ± 0.05	-0.71 ± 0.02	2.62 ± 0.08	-0.70 ± 0.03
♀♀ (M)	4.13 ± 0.07	-0.46 ± 0.05	3.89 ± 0.08	-0.57 ± 0.05
♂♂ (M)	4.16 ± 0.09	-0.39 ± 0.04	4.05 ± 0.11	-0.36 ± 0.05
♀♀ (P)	4.04 ± 0.06	-0.37 ± 0.04	/	/
♂♂ (P)	3.10 ± 0.07	-0.38 ± 0.04	/	/

into account the total number of statistically significant differences between bivariate allometric coefficients of all nine morphometric characters in larvae, efts and adults comparisons, some trends become apparent (Tab. 4). Populations with paedomorphosis *(T. vulgaris* and *T. alpestris)* were much more different from conspecific populations with obligate metamorphosis than conspecific populations with much less differences in life-history pathways (*T. carnifex*).

Multivariate allometry and ontogenetic trajectories

All morphometric variables were positively correlated with first principal component (PC1) which explained more than 93 % of the total variability in six newt populations (Tab. 5). With the principal component two (PC2) only tail height (Lh) and tail length (Lcd) were positively correlated. PC2 component explained almost 5 % of total variability. Next principal component (PC3) took less than 1 % of total variation, and therefore was not further considered.

The results of assessing multivariate allometry on separate PCA for each forms of analyzed populations were given in tab. 6. The statistically significant differences from isometrical growth were found in paedomorphic population of the alpine newt for efts and both groups of adults, expect for paedomorphic males. In the conspecific control population (A1) such a difference was found only for females. In paedomorphic population of the smooth newt a difference from isometry was found only for efts. All forms in populations of the crested newt had a multivariate isometrical growth.

We also tested the correlation (Spearman's rank correlation) between results of bivariate and multivariate allometry (Tab. 7). These allometries were significantly correlated for metamorphic males and females (except in A2 population) in all analysed populations. Non-transformed newts, however, had decopuled bivariate and multivariate allometries, except for pedomorphic smooth newt females. When preadult stages were considered, only in smooth newt populations (efts) and in populations with obligate metamorphosis of the smooth newt and alpine newt (larvae), these allometries were not correlated.

Means and standard errors of PC2 and PC1 scores for analyzed forms (larvae, efts and adults) were given for the smooth newt (Tab. 8), the alpine newt (Tab. 9) and for the crested newt (Tab. 10). Concomitant bivariate plots of PC1 and PC2 scores and regressions for these formes were presented in Figures 1 and 2 for the populations with paedomorphosis only. The most informative way to compare obtained ontogenetic trajectories of examined newt populations was to test significance of differences of the slopes of regression lines of PC1/PC2 scores for larvae, effts, paedomorphs and metamorphs within populations (Tab. 11). Some trends in these comparisons were obvious. Larvae did not differ from efts in the rate of change in shape relative to size in any studied newt species. Larval and

Tab. 9. Means and standard errors of PC1 and PC2 scores for analysed forms in alpine newt populations. See text for population designation.

	A1		A2	
	PC1	PC2	PC1	PC2
Larvae	/	/	3.00 ± 0.06	-0.31 ± 0.03
Efts	3.06 ± 0.08	-0.71 ± 0.03	2.85 ± 0.06	-0.71 ± 0.02
♀♀ (M)	4.22 ± 0.08	-0.65 ± 0.09	4.23 ± 0.07	-0.65 ± 0.08
♂♂ (M)	4.10 ± 0.10	-0.61 ± 0.07	4.10 ± 0.06	-0.57 ± 0.04
♀♀ (P)	4.22 ± 0.08	-0.56 ± 0.09	/	/
♂♂ (P)	4.17 ± 0.09	-0.51 ± 0.07	/	/

Tab. 10. Means and standard errors of PC1 and PC2 scores for analysed forms in crested newt populations. See text for population designation.

	C1		C2	
	PC1	PC2	PC1	PC2
Larvae	4.22 ± 0.05	-0.51 ± 0.04	3.88 ± 0.09	-0.49 ± 0.04
Efts	4.28 ± 0.07	-0.60 ± 0.03	4.02 ± 0.10	-0.62 ± 0.03
♀♀ (M)	4.76 ± 0.10	-0.65 ± 0.04	4.87 ± 0.12	-0.61 ± 0.05
♂♂ (M)	4.74 ± 0.09	-0.64 ± 0.04	4.74 ± 0.11	-0.62 ± 0.03

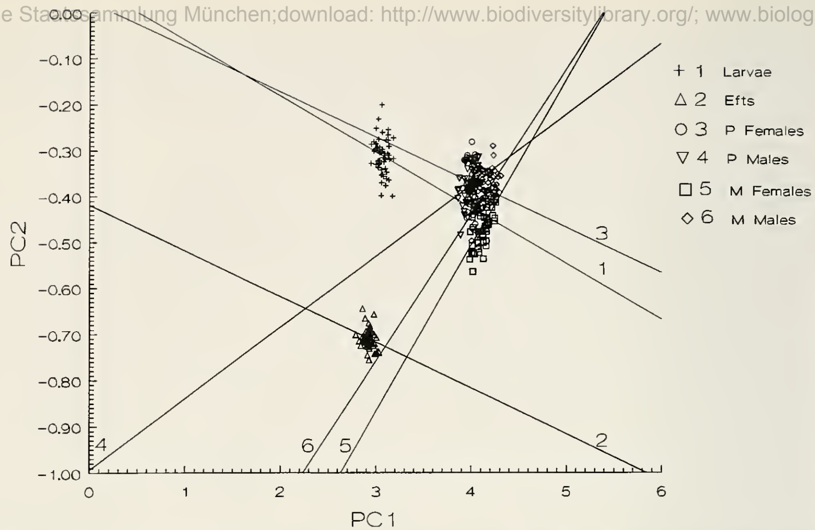

Fig. 1. Bivariate plot of PC1 and PC2 scores and regressions for larvae, efts, paedomorphs and metamorphs (sexes were separated) for the smooth newt population (V1).

paedomorphs' (both sexes) ontogenetic trajectories were not significantly different in the smooth newt; larvae, efts, and paedomorphic females have almost parallel regression lines (Fig. 1). Ontogenetic trajectories of the metamorphs and larvae of the same population showed, however, significant differences. Efts in this population had quite different trajectories from metamorphs, but not from paedomorphs. Within-adult-sex comparisons revealed only significant differences between paedomorphic and metamorphic females, but not between males. In the intersex comparisons paedomorphic females were apparently different from metamorphic males.

Tab. 11. Significancy of differences between regression coefficients (q-test) of PC1/PC2 scores of larvae, efts, paedomorphs and metamorphs (sexes were separated) in six studied populations. Abbreviations: L: larvae, E: efts, FM: metamorphic females, FP: paedomorphic females, MM: metamorphic males, MP: paedomorphic males. n.s.: non-significant, *P <0.05, ** P<0.01, *** P<0.001. df: degree of freedom. See text for population designation.

	V1 df=297	V2 df=103	A1 df=168	A2 df=158	C1 df=110	C2 df=171
L/E	n.s	n.s.	/	n.s.	n.s.	n.s.
L/FM	***	n.s	/	**	n.s.	n.s.
L/FP	n.s	/	/	/	/	/
L/MM	***	n.s.	/	n.s.	n.s.	n.s.
L/MP	n.s.	/	/	/	/	/
E/FM	***	n.s.	n.s.	***	n.s.	n.s.
E/FP	n.s.	/	n.s.	/	/	/
E/MM	***	n.s.	n.s.	n.s.	n.s.	n.s.
E/MP	n.s.	/	n.s.	/	/	/
FM/FP	***	/	n.s.	/	/	/
FM/MM	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
FM/MP	n.s.	/	n.s.	/	/	/
FP/MM	***	/	n.s.	/	/	/
FP/MP	n.s.	/	n.s.	/	/	/
MM/MP	n.s.	/	n.s.	/	/	/

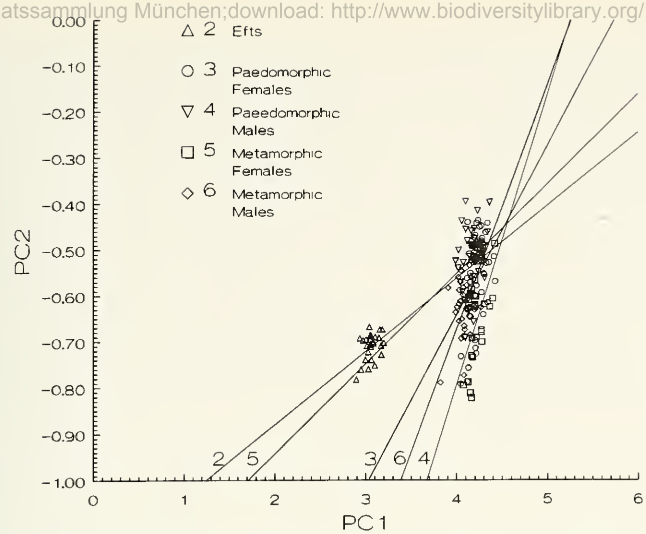

Fig. 2. Bivariate plot of PC1 and PC2 scores and regressions for larvae, efts, paedomorphs and metamorphs (sexes were separated) for the alpine newt population (A1).

Paedomorphic alpine newt population (A1), however, did not show any of such differences; there were no statistically significant differences in size and shape changes among analyzed stages, which was not the case with the control smooth newt population (V2) and with both crested newt populations (Tab. 11). In the alpine newt population with obligate metamorphosis (A2) the regression coefficient of females differed from that of larvae and efts (Tab. 11).

Discussion

A number of populations of the smooth newt (*Triturus vulgaris*) and the alpine newt (*Triturus alpestris*) from the submediterraneans of the Balkans have individuals with polymorphic phenotypes (see Dzukic et al. 1990 for review). Paedomorphs in these populations often outnumber syntopic metamorphs. Even a subspecific level has been attached to some of these alpine newt populations, including the alpine newt population with paedomorphosis studied here. This was based on phenotype differences of its paedomorphic individuals, including morphometric characters (head dimensions), in comparisons with the conspecifics of the nominotypical form which had obligate metamorphosis only.

In the crested newt (*Triturus cristatus* superspecies) there are populations in which numerous larvae have prolonged growth and metamorphose into immature juveniles during the following year. However, a few of the larvae with prolonged growth attain sexual maturity without metamorphosis, thus excluding a juvenile stage. But these individuals, contrary to other European newt species with paedomorphosis, do not stay long as paedomorphs. Up to now, in only one population of *Triturus carnifex* from Montenegro a few sexually mature newts with larval morphology have been found (Kalezic et al. 1994) - this population is included in this study (C1).

We found in this study that larvae did not differ from efts in the rate of change in shape relative to size in any studied newt species. This is another confirmation that the main size and shape changes occurred after metamorphosis, till newts attain sexual maturity (Kalezic et al. in prep.). This was established to be about three years for the newts of all three species studied here from the Balkans (Kalezic et al. in prep., Cvetkovic et al. in prep.), and for the crested newt (*T. cristatus*) from France (Francillon-Vieillot et al. 1990). During this period newts mostly reach their adult size and shape which do not change significantly afterwards. But what happened when metamorphosis is omitted from life cycle?

In the smooth newt, paedomorphic individuals followed ontogenetic trajectories of larvae from the same population, while metamorphic ones deviated from this trajectories considerably. The morphological null hypothesis postulated in this study that the size and shape of non-transforming newts was accounted for by an extention of the larval growth trajectries happened to be confirmed. The situation in the alpine newt population with paedomorphosis is much less clear probably because of inaccessibility of larvae from the population in our study. In this species trajectories of paedomorphic newts depicted no difference in comparison with trajectories of efts and, most likely, they would not do that of larvae too. But, metamorphs of the population did not deviate from this trajectories. Interestingly, the same happened with adults in other newt populations with obligate metamorphosis studied here. If any exception existed, as was the case in such a population of the alpine newt, females were those to deviate significantly from common population ontogenetic size-shape trajectories (Tab. 10). A general conclusion could be that paedomorphosis in some newt species (*T. vulgaris* in our study) has influence on ontogenetic trajectories making somehow metamorphic population counterparts different in this sense. In other cases, paedomorphosis (*T. alpestris* in our study) and more plastic life-history, i.e. prolonged larval period and omitted eft stage (*T. carnifex*), have no such effect. More plastic life-history had, however, an effect on interpopulation level; juveniles and adult males, the only sex with paedomorphic individuals from Lokanj and Ceklin ponds, appeared to be statistically significantly different in the ontogeny of size and shape changes (Kalezic et al. 1994).

Our results of bivariant analysis of shape changes during ontogeny are mainly in the line with the results of multivariate allometry. It was found that the existence of an alternative life cycle rendered more complex ontogenetic picture of allometric relations of individual morphometric features. The changes in allometric relations of paedomorphic and metamorphic individuals were particularly evident in the smooth newt. In this species paedomorphs more than metamorphs, followed the path of larval allometric coefficients. It seems also that paedomorphosis decoupled bivariate and multivariate allometries as the correspondence between these allometries at the adult stage was much more pronounced in transformed individuals than in syntopic paedomorphic individuals.

It should be pointed out here that the sample of larvae taken from the population with paedomorphosis in our study consists of individuals which would have metamorphosed, as well as of those which would have prolonged growth and reached sexual maturity without complete metamorphosis. There was no way of separating these two larvae groups. Due to this fact, as well as to using cross-sectional data instead of longitudinal ones, we were prevented from getting a clearer picture of ontogenetic allometry relations in newt populations. Nevertheless, it became apparent that in European newts, as well as in American newts (genus *Notophtalmus*, Harris 1989) small intrapopulation differences between transforming and non-transforming individuals in ontogenetic paths of size and shape changes developed, if any, and that happened relatively late in ontogeny.

Acknowledgements

We appreciate the help of Georg Dzukic, Davor Bejakovic and Ivan Aleksic in collecting specimens, as well as the help of Nikola Tucic in statistical analyses.

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Appendix

Tab. 1. Mean values and standard error (X±SE) for analyzed forms of two smooth newt populations. n: sample size. See text for character and population designation.

	V1						V2			
			metamorphic		paedomorphic				metamorphic	
	larvae (n=53) X±SE	efts (n=48) X±SE	♀♀ (n=52) X±SE	♂♂ (n=52) X±SE	♀♀ (n=52) X±SE	♂♂ (n=52) X±SE	larvae (n=27) X±SE	efts (n=34) X±SE	♀♀ (n=25) X±SE	♂♂ (n=25) X±SE
L	36.85	35.63	80.56	79.42	75.92	72.40	27.11	27.85	72.00	76.24
	±1.85	±1.88	±4.94	±4.34	±4.25	±3.88	±2.31	±2.02	±4.96	±5.48
Lcp	17.80	17.64	39.56	36.70	36.22	32.45	13.48	14.25	35.29	34.28
	±0.88	±0.73	±2.09	±1.75	±1.97	±1.56	±1.14	±0.84	±2.11	±2.38
Lcd	19.05	17.98	41.00	42.72	39.71	39.95	13.63	13.60	36.71	41.92
	±1.34	±1.38	±3.10	±2.99	±2.66	±2.85	±1.53	±1.35	±3.17	±3.69
Lsv	20.00	19.78	43.29	41.18	39.88	36.96	15.01	15.91	38.96	39.15
	±1.09	±0.84	±2.41	±2.15	±2.08	±1.61	±1.22	±0.92	±2.66	±2.77
Ltc	3.99	3.74	7.60	7.04	7.18	6.62	3.08	3.02	5.91	5.92
	±0.18	±0.13	±0.45	±0.46	±0.45	±0.34	±0.25	±0.14	±0.39	±0.42
Lc	3.03	3.22	5.56	5.77	4.81	4.89	2.53	2.74	4.96	5.20
	±0.21	±0.17	±0.31	±0.33	±0.30	±0.26	±0.24	±0.19	±0.31	±0.39
Pa	6.22	6.48	14.46	16.03	12.72	13.92	4.85	5.08	12.07	14.08
	±0.37	±0.35	±0.74	±1.26	±1.04	±0.95	±0.44	±0.43	±0.90	±1.37
Pp	5.72	6.27	14.05	16.10	12.73	13.95	4.64	4.93	11.87	14.66
	±0.32	±0.33	±0.65	±1.24	±0.81	±1.01	±0.51	±0.33	±0.94	±1.41
D	8.55	8.75	24.47	22.79	22.05	19.26	6.67	7.19	21.82	20.46
	±0.55	±0.82	±1.54	±1.30	±1.34	±1.28	±0.75	±0.49	±1.73	±1.77
Lh	4.99	1.88	8.56	10.17	9.47	9.04	3.07	1.51	5.46	9.73
	±0.45	±0.11	±1.19	±1.47	±0.94	±1.00	±0.71	±0.14	±0.70	±1.55

Tab. 2. Mean values and standard error (X±SE) for analyzed forms of two alpine newt populations. n-sample size. See text for character and population designation.

	A1					A2			
		metamorphic		paedomorphic				metamorphic	
	efts (n=26) X±SE	♀♀ (n=25) X±SE	♂♂ (n=34) X±SE	♀♀ (n=54) X±SE	♂♂ (n=34) X±SE	larvae (n=50) X±SE	efts (n=54) X±SE	♀♀ (n=27) X±SE	♂♂ (n=35) X±SE
L	37.54	87.92	74.59	82.00	76.03	32.36	31.76	90.67	77.74
	±3.34	±4.90	±4.56	±4.60	±5.04	±1.85	±1.68	±5.03	±4.10
Lcp	19.96	45.53	38.73	42.74	38.79	16.95	17.08	45.83	38.17
	±1.11	±2.95	±2.45	±2.57	±2.74	±1.00	±0.88	±2.45	±1.97
Lcd	17.58	42.39	35.86	39.26	37.23	15.41	14.68	44.83	39.57
	±2.68	±3.05	±2.58	±2.84	±3.00	±1.30	±1.00	±3.37	±2.95
Lsv	22.10	50.66	44.16	47.46	44.69	18.81	18.89	50.21	44.34
	±1.17	±2.81	±2.88	±2.98	±2.85	±1.04	±0.87	±2.42	±2.42
Ltc	4.49	9.10	8.19	10.13	9.86	4.07	3.89	8.57	7.74
	±0.19	±0.73	±0.65	±0.85	±1.16	±0.21	±0.19	±0.70	±0.52
Lc	3.47	6.36	6.05	6.21	6.03	2.89	3.11	6.13	5.89
	±0.22	±0.33	±0.44	±0.56	±0.51	±0.24	±0.21	±0.38	±0.29
Pa	7.32	16.78	16.54	17.31	17.53	6.33	6.29	16.68	15.67
	±0.46	±1.89	±1.16	±1.69	±1.28	±0.43	±0.40	±0.82	±1.05
Pp	6.98	17.03	16.31	16.64	17.14	5.75	5.85	16.31	15.41
	±0.44	±1.58	±1.28	±1.26	±1.25	±0.42	±0.46	±0.87	±0.89
D	9.95	25.38	22.78	23.39	21.88	8.61	8.84	27.20	22.24
	±0.73	±2.91	±1.86	±1.88	±1.80	±0.65	±0.53	±2.26	±1.40
Lh	2.15	6.29	6.32	7.75	8.13	4.85	1.81	6.18	6.60
	±0.21	±1.53	±1.25	±1.74	±1.45	±0.44	±0.11	±1.22	±0.82

Tab. 3. Mean values and standard error (X±SE) for analyzed forms of two crested newt populations. n: sample size. See text for character and population designation.

	C1				C2			
	larvae (n=35) X±SE	efts (n=43) X±SE	♀♀ (n=21) X±SE	♂♂ (n=19) X±SE	larvae (n=40) X±SE	efts (n=90) X±SE	♀♀ (n=29) X±SE	♂♂ (n=20) X±SE
L	83.89	89.67	130.81	123.89	64.18	73.93	142.48	122.80
	±3.53	±6.16	±9.31	±8.16	±5.50	±5.86	±12.50	±10.40
Lcp	43.00	47.19	67.71	64.43	34.63	39.98	73.80	65.26
	±1.92	±2.29	±5.40	±4.36	±2.50	±2.76	±6.16	±3.83
Lcd	40.89	42.49	63.10	59.47	29.54	33.93	68.69	57.54
	±2.27	±4.28	±4.69	±4.41	±3.82	±3.92	±7.00	±7.17
Lsv	46.69	51.51	74.43	72.57	37.14	43.72	*81.66	73.84
	±2.05	±2.43	±6.20	±4.50	±2.74	±2.94	±7.01	±4.50
Ltc	9.19	8.77	12.84	12.46	7.39	7.34	14.00	12.49
	±0.53	±0.53	±1.13	±0.96	±0.47	±0.56	±1.31	±0.75
Lc	5.91	6.26	8.30	8.09	5.05	5.54	8.79	7.93
	±0.31	±0.39	±0.68	±0.52	±0.27	±0.51	±0.73	±0.67
Pa	16.41	17.36	24.43	25.79	12.82	14.85	25.21	25.70
	±0.80	±0.81	±1.88	±2.02	±0.94	±1.10	±1.78	±2.38
Pp	16.76	17.95	24.98	26.49	12.69	14.35	25.50	26.39
	±0.77	±0.85	±1.53	±1.67	±0.89	±1.12	±1.87	±2.39
D	23.44	26.89	40.56	38.71	18.23	23.04	44.93	39.97
	±1.68	±1.76	±4.31	±2.83	±1.65	±2.17	±4.52	±3.59
Lh	8.35	7.22	9.57	9.68	6.74	5.70	11.29	10.18
	±0.83	±0.62	±1.14	±1.36	±0.79	±0.70	±1.80	±1.14