First evidence of a paedomorphic population of the smooth newt (*Lissotriton vulgaris*) in the Czech Republic

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Abstract. Facultative paedomorphosis is an environmentally induced polymorphism that is well known for many caudate species including newts. Although facultative paedomorphosis has been documented in some smooth-newt populations, records of entirely paedomorphic populations outside the Balkans are limited. Here we present the first evidence of a paedomorphic population of the smooth newt in the Czech Republic with discussion of potential causes that need to be further tested.

Keywords. Facultative paedomorphosis, urodeles, "Triturus", Central Europe.

Facultative paedomorphosis, the case of phenotypic heterochrony when some sexually mature individuals from a population (or some populations of a species) retain some states of larval morphology, has been widely documented for many caudates (review in Denoël et al., 2005; Laudet, 2011). In Europe, facultative paedomorphosis regularly occurs in newts (former genus "Triturus") with high frequency in the Alpine newt (Ichthyosaura alpestris), especially in some areas of the Balkans and Alps (Denoël et al., 2001). Beside the Alpine newt paedomorphosis has also been recorded in other newt species (summarized by Wells, 2007): Lissotriton helveticus, L. italicus, L. vulgaris, Triturus cristatus, T. macedonicus, and Ommatotriton ophryticus (Başkale et al., 2011). In the smooth newt (L. vulgaris), this phenomenon is also relatively common, although usually only a small part of a population or single individuals are paedomorphic. Cases of peadomorphosis in the smooth newt have been reported from various places within almost the whole distribution range (review in Schmidtler and Franzen, 2004), but entirely paedomorphic populations of *L. vulgaris* are rarely reported (Dely, 1967; Dolmen, 1981; Denoël et al., 2009). One such population from northern Hungary was described like a different subspecies, *Triturus vulgaris tataiensis* (Dely, 1967), but validity of this subspecies was rejected (Raxworthy, 1990).

Here, we report a presumably almost completely paedomorphic population of *L. vulgaris* from the Czech Republic. This is the first formally reported recent record of urodelan paedomorphosis for the country. Paedomorphic smooth newts (Fig. 1) were discovered (by VG and VJ) on 28 April 2012 in a water reservoir in Stará Lysá (50°13'31.6"N, 14°47'57.1"E, ~190 m a.s.l.). The finding place is situated in "Polabí", which is a lowland area along the Labe (Elbe) River in the Central Bohemian Region. This part of the Czech Republic is one of the warmest, with dry and mild winters and average annual temperature between 8-9 °C (Quitt, 1971). The local landscape

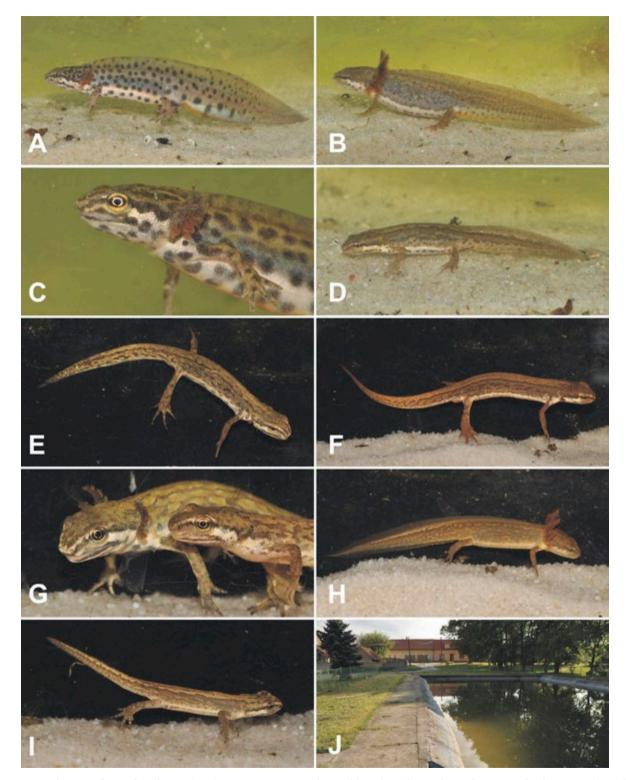


Fig. 1. Smooth newts observed in the Stará Lysá water reservoir, Czech Republic: A) Paedomorphic male in nuptial colouration; B) paedomorphic female in nuptial colouration; C) close-up view on another paedomorphic male showing the structure of gills; D) aquatic immature specimen with open gill slits (A-D photographed on 7 May 2012); E) paedomorphic male, and F) female later in the season with already reduced gills; G) different pair (adult male and female) demonstrating variation in the level of persistence of larval traits; H) immature paedomorphic specimen with large gills; I) metamorph-like aquatic immature specimen with open gill slits (E-I photographed on 23 August 2012); J) Stará Lysá water reservoir.

has been historically used for agriculture and so the locality is from three quarters surrounded by crop fields and from one quarter by a relatively dry cultivated pine forest (cf. Covaciu-Marcov et al., 2011).

Newts inhabit a water reservoir (originally used for fire protection) sized 25×15 m with maximal water depth of 1.5 m made from concrete blocks (Fig. 1J). Shorter sides of the reservoir are formed by vertical walls while longer sides slope in approximate 45°. The reservoir is supplied from a deep borehole (~60 m), and water is changed approximately once per three years and occasionally refilled (last change in 2010; V. Vaněk, pers. comm.). No fish were observed. The reservoir is without vegetation, only filamentous algae grow later in the season over submerged objects and newts use them for wrapping eggs. Apart from newts, several adult individuals of marsh frogs (Pelophylax ridibundus) were observed and their numerous offspring later in the season. The water is rich on planktonic micro-crustaceans. Generally, the reservoir meets conditions for occurrence of paedomorphic newts: does not freeze to the bottom in winter, do not dry in summer, few predators (no fish), abundant food resources (Litvinchuk et al., 1996; Denoël and Poncin, 2001).

The locality has been visited in several occasions (April, May, July, August, September, October 2012), and opportunistic visual surveys and dip-netting have been done. Paedomorphic individuals were observed during all visits, with a visually assessed abundance in the spring. During the assumed peak of reproductive season (7 May 2012), we observed 70 adult smooth newt individuals when counting specimens visible along the reservoir walls during one walk around the tank. Except of two seemingly metamorphic females (but without success to catch them and inspect for morphology) and one almost metamorphic juvenile (but with open gill slits; Fig. 1D), all individuals were clearly paedomorphic (Fig. 1A-C) and only three of them were males. Sex ratio bias toward the females is common in paedomorphic individuals of this species (e.g., Kalezić and Džukić, 1986; Litvinchuk et al., 1996; Çiçek and Ayaz, 2011), however the observed ratio is unusual. Also situations when paedomorphic smooth newts outnumber metamorphic individuals have been only rarely reported (e.g., Kalezić and Džukić, 1986; Rot-Nikcević et al., 2000) compared to the more common metamorph-biased population ratio in this species (e.g., Banks, 1985; Kalezić and Džukić, 1985; Çiçek and Ayaz, 2011). However, it is important to mention that we cannot make clear conclusion about the ratio of peadomorphs vs. metamorphs in our smooth-newt population as we did not make a quantitative survey. Potential bias toward paedomorphs might be also caused by differences in behaviour of the morphs with respect to the relatively high water depth. During the spring visits, many paedomorphic newts were resting in the water column along the walls to 50 cm below water surface and were easily counted.

To observe reproductive behaviour, three paedomorphic individuals (one male, two females) were taken into captivity (7 May 2012). Water temperature in the aquarium ranged 16.7-19. 4 °C and newts were kept under natural light conditions. The newts were housed together in an aquarium ($50 \times 25 \times 25$ cm) filled by settled tap water and with several waterweed plants (*Egeria densa*). During the following days we had observed the male's courtship behaviour (fan display), which is in newts similar for both morphs (Denoël, 2002), and deposition of eggs by both females. As we expected (cf. Banks, 1985; Litvinchuk et al., 1996; Litvinchuk, 2001), the male metamorphosed after 19 days, followed by the females which metamorphosed after 42 and 45 days in captivity, respectively (including closed gill slits).

Later in the season (23 August 2012), all captured adults (Table 1) were already almost without crests and fin appendices, and with small, sometimes rather rudimental gills, nonetheless, still in aquatic phase and with open gill slits (Fig. 1E-G). Immature individuals, according to the body size and shape and level of development of the cloaca, were of two types: some had large gills and fins (Fig. 1H), while some others resembled the adults, but being substantially smaller, by having rudimentary gills or only open gill slits (Fig. 1I). Beside these paedomorphic specimens (open gill slits as a common character), some typical larvae were also observed. It seems that adult individuals reduce their larval traits (gills) toward the winter (cf. Denoël, 2003). However, it is currently unknown if the same individuals grow the larval traits again in the next season. A study of the demographic structure is currently ongoing using the capture-markrecapture method and shall shed more light onto this and other questions in near future.

Despite relatively strong evidence for the beneficial role of facultative paedomorphosis as an alternative

Table 1. Morphometric characteristics in cm (SVL - snout-vent length, Lt - length of tail, Dbl - distance between front and hind limbs) of adult peadomorphic smooth newts (females n = 7; males n = 3) from Stará Lysá, Czech Republic.

		mean	min.	max.	SD
females	SVL	3.45	3.13	3.82	0.27
	Lt	3.10	2.80	3.47	0.22
	Dbl	1.69	1.41	1.93	0.18
males	SVL	3.68	3.34	4.01	0.34
	Lt	3.50	3.19	3.82	0.32
	Dbl	1.67	1.57	1.77	0.10

ontogenetic pathway in many tailed amphibians, importance and influence of particular factors lying behind its evolution is not fully resolved. Whilst paedomorphosis can be a highly heritable trait (e.g., Harris et al., 1990; Voss et al., 2003), the occurrence of facultative paedomorphosis in individuals and its maintenance in a population is most probably a result of interplay between genotype and heterogeneity of the environment (reviewed by Denoël et al., 2005). Among many factors, streambed or pond-bank structures (Bennett and Chippindale, 2006), slow desiccation rate (Semlitsch et al., 1990), and high food availability in water (Ryan and Semlitsch, 2003) have been observed to induce occurrence of paedomorphs and the maintenance of resulted polyphenism in a population. All the above-listed factors, particularly high food availability and resource partitioning between different phenotypes seem to be feasible as possible factors responsible for the maintenance of paedomorphosis in our smooth-newt population. Retention of larval feeding apparatus in paedomorphs may allow more efficient foraging on plankton and aquatic prey (Whiteman et al., 1996; Denoël, 2004). As a result, both microhabitat segregation and utilization of different food has been observed in particular morphs, with paedomorphs mainly foraging on plankton and distributed in both shallow and deep parts of water column compared to foremost shallower distributed metamorphs (Denoël and Joly, 2001; Denoël and Schabetsberger, 2003). As the water reservoir is rich in planktonic micro-crustaceans and areas of deep water column, we suppose the predominance of paedomorphs in our population to be inherent in these factors. It is however worth noting that predominance of paedomorphs in our smooth newt population could also be a result of an environmental-hormonal interplay, as both stress and steroid hormones were observed to significantly affect metamorphosis of larvae and paedomorphs to the adult stage (reviewed by Laudet, 2011). Detailed endocrinological studies are needed to shed light on these proximate mechanisms.

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REFERENCES

- Banks, B. (1985): Observations on neoteny in the smooth newt. Br. Herpetol. Soc. Bull. **12**: 37-38.
- Başkale, E., Sayim, F., Kaya, U. (2011): Body size and reproductive characteristics of paedomorphic and metamorphic individuals of the northern banded newt (*Ommatotriton ophryticus*). Acta Herpetol. 6: 19-25.
- Bennett, R.M., Chippindale, P. T. (2006): Streambed microstructure predicts evolution of development and life history mode in the plethodontid salamander *Eurycea tynerensis*. BMC Biol. 4: 1-12.
- Çiçek, K., Ayaz, D. (2011): New data on facultative paedomorphism of the smooth newt, *Lissotriton vulgaris*, in Western Anatolia, Turkey. J. Freshwater Ecol. 26: 99-103.
- Covaciu-Marcov, S.D., Sas, I., Cicort-Lucaciu, A.Ş., Bogdan, H.V. (2011): *Lissotrion vulgaris* paedomorphs in south-western Romania: a consequence of a human modified habitat? Acta Herpetol. 6: 15-18.
- Dely, O.G. (1967): Neuere Angaben zur Kenntnis des neotenischen Teichmolches (*Triturus vulgaris* L.). Acta Zool. Acad. Sci. Hungar. **13**: 253-270.
- Denoël, M. (2002): Paedomorphosis in the Alpine newt (*Triturus alpestris*): decoupling behavioural and morphological change. Behav. Ecol. Sociobiol., **52**: 394-399.
- Denoël, M. (2003): How do paedomorphic newts cope with lake drying? Ecography, **26**: 405-410.
- Denoël, M. (2004): Feeding performance in heterochronic Alpine newts is consistent with trophic habits and maintenance of polymorphism. Ethology 110: 127-136.
- Denoël, M., Joly, P. (2001): Adaptive significance of facultative paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): resource partitioning in an alpine lake. Freshw. Biol. **46**: 1387-1396.
- Denoël, M., Poncin, P. (2001): The effect of food on growth and metamorphosis of paedomorphs *Triturus alpestris apuanus*. Archiv. Hydrobiol. **152**: 661-670.
- Denoël, M., Schabetsberger, R. (2003): Resource partitioning in two heterochronic populations of Greek Alpine newts, *Triturus alpestris veluchiensis*. Acta Oecol. 24: 55-64.
- Denoël, M., Joly, P., Whiteman, H.H. (2005): Evolutionary ecology of facultative paedomorphosis in newts and salamanders. Biol. Rev. **80**: 663-671.
- Denoël, M., Duguet R., Džukić, G., Kalezić, M.L., Mazzotti S. (2001): Biogeography and ecology of paedomorphosis in *Triturus alpestris* (Amphibia, Caudata). J. Biogeogr. 28: 1271-1280.
- Denoël, M., Ficetola, G.F., Ćirović, R., Radović, D., Džukić, G., Kalezić, M.L., Vukov T.D. (2009): A mul-

ti-scale approach to facultative paedomorphosis of European newts in the Montenegrin karst: distribution pattern, environmental variables and conservation. Biol. Conserv. **142**: 509-517.

- Dolmen, D. (1981): Distribution and habitat of the Smooth Newt, *Triturus vulgaris* (L.), and the warty newt, *T. cristatus* (Laurenti), in Norway. Proc. Eur. Herp. Symp. Oxford **1980**: 127-139.
- Harris, R.N., Semlitsch, R.D., Wilbur, H.M., Fauth, J.E., (1990): Local variation in the genetic-basis of pedomorphosis in the salamander *Ambystoma talpoideum*. Evolution 44: 1588-1603.
- Kalezić, M.L., Džukić, G. (1985): Ecological aspects of the smooth newt (*Triturus vulgaris*) paedomorphosis from Montenegro. Arhiv. Bioloških. Nauka, Beograd 37: 43-50.
- Kalezić, M.L., Džukić, G. (1986): The frequent occurence of paedomorphosis in the smooth newt (*Triturus vulgaris*) population from the Submediterranean area of Yugoslavia. Amphibia-Reptilia 7: 86-89.
- Laudet, V. (2011): The origins and evolution of vertebrate metamorphosis. Curr. Biol. **21**: 726-737.
- Litvinchuk, S.N. (2001): First record of paedomorphosis for the smooth newt (*Triturus vulgaris*) from Ukraine. Russ. J. Herpetol. 8: 77-78.
- Litvinchuk, S.N., Rudyk, A.M., Borkin, L.J. (1996): Observation of paedomorphic newts (*Triturus vulgaris*) from the former Soviet union. Russ. J. Herpetol. **3**: 39-48.
- Quitt, E. (1971): Klimatické oblasti Československa. Academia. Studia Geographica, GÚ ČSAV., Brno.

- Raxworthy, C.J. (1990): A review of the smooth newt (*Triturus vulgaris*) subspecies, including an identification key. Herpetol. J. 1: 481-492.
- Ryan, T.J., Semlitsch, R.D. (2003): Growth and life cycle polymorphism in the salamander *Ambystoma talpoideum*. Biol. J. Linn. Soc. (London) **80**: 639-646.
- Rot-Nikcević, I., Kalezić, M.L., Džukić, G. (2000): Paedogenesis, life history traits and sexual dimorphism: a study case of the smooth newt, *Triturus vulgaris*, from Pannonia. Folia Zool. **49**: 41-52.
- Schmidtler, J.F., Franzen M. (2004): Triturus vulgaris Linnaeus, 1758 – Teichmolch. In: Handbuch der Reptilien und Amphibien Europas, Bd. 4/2b, Schwanzlurche (Urodela) IIb, pp. 847-967. Grossenbacher, K., Thiesmeier B., Eds, Aula Verlag, Wiesbaden.
- Semlitsch, R.D., Harris, R.N., Wilbur, H.M. (1990): Paedomorphosis in *Ambystoma talpoideum*: maintenance of population variation and alternative life-history pathways. Evolution 44: 1604-1613.
- Voss, S.R., Prudic, K.L., Oliver, J.C., Shaffer, H.B. (2003): Candidate gene analysis of metamorphic timing in ambystomatid salamanders. Mol. Ecol. 12: 1217–1223.
- Wells, K.D. (2007): The Ecology and Behavior of Amphibians. The University of Chicago Press, Chicago and London.
- Whiteman, H.H., Wissinger, S.A., Brown, W.S. (1996): Growth and foraging consequence of facultative paedomorphosis in the tiger salamander *Ambystoma tigrinum nebulosum*. Evol. Ecol. **10**: 433-446.