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Evidence for post-natal instability of head scalation in the meadow viper (*Vipera ursinii*) – patterns and taxonomic implications

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Abstract. In Squamates, head meristic characters are commonly used in analyses of intraspecific variability, systematics and phylogeny. Taxonomic significance of head scales is based on the assumption that discrete values of particular scales are set at birth and stable during individual ontogeny. In this paper, we analysed ontogenic changes of head scalation in a population of meadow viper (*Vipera ursinii*), based on multiple recaptures of marked individuals. Our results show that changes of cephalic scales occur both in immatures and in adults; the frequency of occurrence of change in the sample of re-photographed individuals was 52.2%. Oligomerisation was the most frequent change, found in 39.1% of re-photographed individuals. Changes in shape of cephalic plates as well as polymerisation were recorded in 30.4% of re-photographed individuals. Results of the log-linear analyses indicated no relation either between scale change and sex or between scale change and growth. Although we do not suggest that meristic characters of head scales are completely inadequate for taxonomic use, we point out the need for taking into account the ontogenic trajectories of these characters when analysing intra- and interpopulation variability, in systematics and phylogeny.

Keywords: Balkans, head scalation, ontogeny, taxonomy, *Vipera ursinii*.

Introduction

Among the multiple morphological traits used for classifying Squamata, head scalation is supposed to be one of the most relevant and reliable at both subspecific and supraspecific levels (Nilson et al., 1994; Crochet et al., 2003; Wuster and Broadley, 2003; Manier, 2004; Sanders et al., 2006). This is based on the assumption that discrete values of particular scalation character(s) are set at birth and cannot change thereafter (Shine et al., 2005). Developmental trajectories of meristic traits in adult reptiles would not be determined by the size of the animal (or its age), but by the embryological differentiation rate of the character, or the time at which this character stopped differentiating (Maderson et al., 1978). In fact, scales and scale hinges seem to become differentiated and their topography established during embryogenesis (stage seven, according to Maderson, 1965). The only changes in scalation that arise post-natally are in reaction to large injuries, which activate scale neogenesis in the integument and eventually may provoke alterations in the size, shape, distribution and number of the reformed units (Maderson et al., 1978). Concerning pileus scales, for example, unexpected structure ("pileus anomalies" or "pileus abnormalities") was supposed to be the consequence of error or accident(s) in the developmental process (i.e. during embryonic development only and fixed upon birth) or the result of environmental stress during development or the expression of an extreme genotype (Soule and Cuzin-Roudy, 1982). For example, severe aberrant head scalation in *Vipera ursinii rakosiensis*, were considered as to be the consequence of low genetic variability (see fig. 1. – Újvári et al., 2002).

Regarding snakes, head scales are frequently used in taxonomy, even recently (e.g. Wüster and Broadley, 2003; Malhotra and Thorpe, 2004; Manier, 2004; Sanders et al., 2004, 2006).

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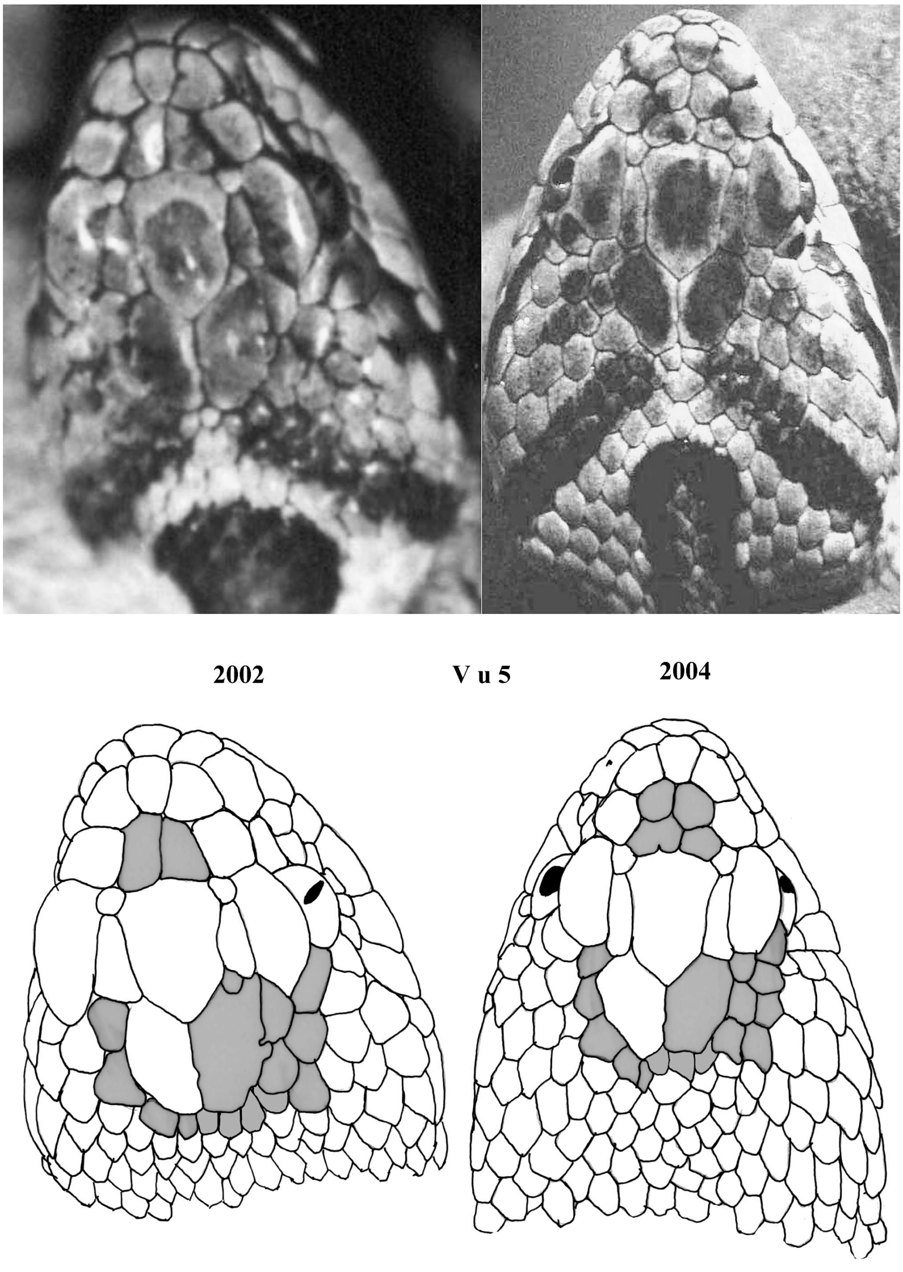

Figure 1. Photographs (top) and corresponding drawings (bottom) of head scales changes (dorsal side of the head) in individual no. 5 of meadow viper at first capture (year 2002) and after two years (year 2004). Recorded types of head scales changes: 1, 2, 3.

Within the family Viperidae, the degree of accretion of dorsal cephalic scales may differ greatly, both within and among populations (Joger and Stümpel, 2005, and references therein). Despite this, head and/or body meristic characters are commonly used when analysing the intraspecific variability of vipers or when new taxa are described (e.g. Böhme and Joger, 1983; Joger et al., 1988; Billing et al., 1990; Nilson et al., 1994; Nilson and Andrén, 1988, 2001; Zuffi and Bonnet, 1999; Zuffi, 2002; Tomović and Džukić, 2003; Brito et al., 2006; Tomović, 2006). Furthermore, several meristic traits (scalation characters, e.g. number of supra- and sublabial scales, presence of large head scales) have been used in phylogenetic analyses of different viperid taxa (e.g. Kramer, 1961; Saint-Girons, 1978; Marx et al., 1988; Nilson et al., 1994; Nilson and Andrén, 2001).

The phenomenon of post-natal changes of head scales could, however, constitute an alternative explanation to some scalation pattern observed in squamates, particularly in snakes, but, as far as we are aware, has not previously reported in the literature. That defined the main goals of this paper – 1) to establish whether head scalation actually changes throughout life in a viper population based on multiple recaptures of marked individuals; 2) if true, to determine which is the degree and pattern of such change; and 3) to derive which implications such a pattern might have for taxonomic studies.

Material and methods

The meadow viper (*Vipera ursinii macrops*) was studied at approximately 1680 m a.s.l., on the south-western slope of Bjelasica Mt. (National Park "Biogradska Gora") in eastern Montenegro (latitude N 42°54′15″, longitude E 19°37′15″). A detailed description of study area is provided in Tomović et al. (2004). The study was conducted between 2002 and 2006. The total area surveyed covered approximately 10 ha, from 1651 to 1728 m altitude. All vipers were photographed (head from above and from both sides, as well as dorsal colour pattern) at the first capture, individually marked by scale clipping, and released after this procedure. Immatures were identified by body length, less than 24.5 cm and 31.5 cm of the snout-vent length (SVL), for males and females of *V. u. ursinii* respectively – Baron, 1997. Age of immatures captured in the wild was recalculated on the basis of similarity in SVL with the recaptured ones of known age e.g. those born under the laboratory conditions. Cephalic scales change was noticed during the regular checking of the photos of individual markings in year 2004, and since then, every recaptured specimen was regularly re-photographed and checked for changes. We categorised changes in head scalation into three classes: **1** – polymerisation (one scale divided in two or more); **2** – oligomerisation (two or more scales fused into one); **3** – shape changes in cephalic scales.

Log-linear models (Jobson, 1992) were use to determine if there was consistent sexual and/or ontogenic patterns regarding the scale changes found. Due to the low sample size we grouped the ontogenic changes into three types: **a** – individuals remaining immature (not adults) between two markings; **b** – individuals changing from immature to adults; **c** – individuals being adults in the two markings. We considered the presence or absence of head scalation changes and then we tested each scale change type separately. An overall model involving all three scale changes could not be performed due to sample size. All calculations were performed by Statistica version 7.1.

Results

During our study, 53 of 159 specimens were recaptured two or more times (33.3%) and 23 of them were re-photographed (14.5% of total or 43.4% of recaptured). Among them, 12 specimens displayed head scalation changes (52.2% of re-photographed – figs 1-5) (table 1).

Oligomerisation (type 2) was the most frequent type of change among the analysed specimens. It was found in 9 of 23 meadow vipers that were re-photographed (39.1%). Changes in shape of cephalic scales (type 3) as well as polymerisation (type 1) were recorded in 7 of 23 re-photographed individuals (30.4%).

Of the total of 23 re-photographed specimens, there were 20 females and 3 males, sex-ratio being biased to females (6.7:1, $\chi^2_{Yates} = 3.85$, $p = 0.05$). However, the sex-ratio of sample of specimens with head scales changes (10 females, 2 males) did not differ from that of the total (5:1, $\chi^2_{Yates} = 0.05$, $p = 0.83$, n.s.).

Results of the log-linear analyses (table 2) reinforce such results since all four models indicated no relation either between scale change (considered as a whole or separately) and sex or between scale change and growth.

Discussion

Concerning types of head scales change detected in this study, there is no specific information in the literature about possible causes for their occurrence. Roytberg (1991, 1994a,b) in his studies on morphological variability in some lacertid lizards, detected higher occurrence of oligomerisation in regard to polymerisation and mentioned that oligomerisation of homologous organs and structures was one of

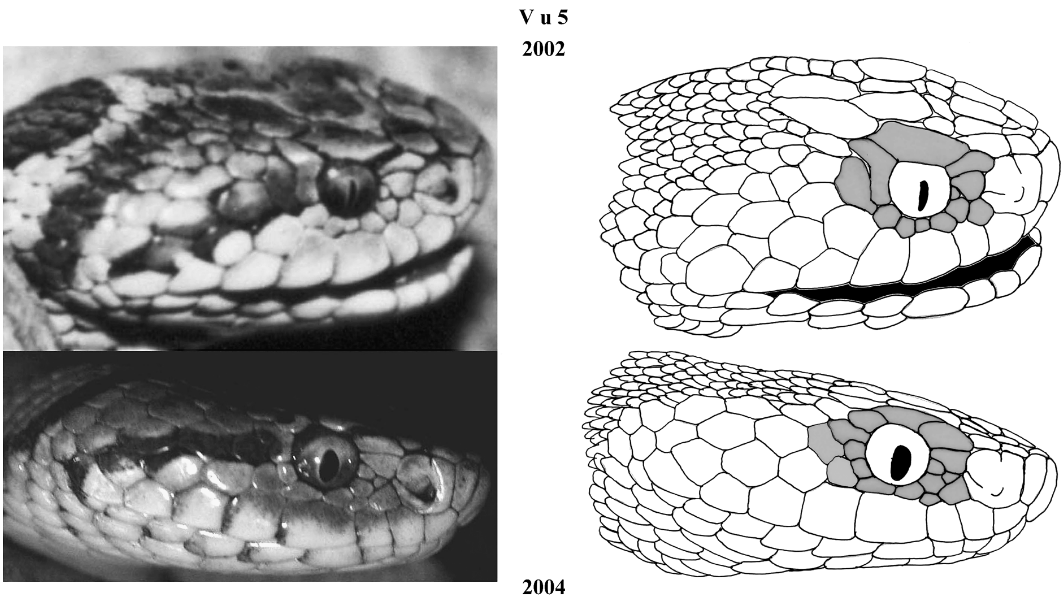

Figure 2. Photographs (left) and corresponding drawings (right) of head scales changes (right side of the head) in individual no. 5 of meadow viper at first capture (year 2002) and after two years (year 2004). Recorded types of head scales changes: 1, 2, 3.

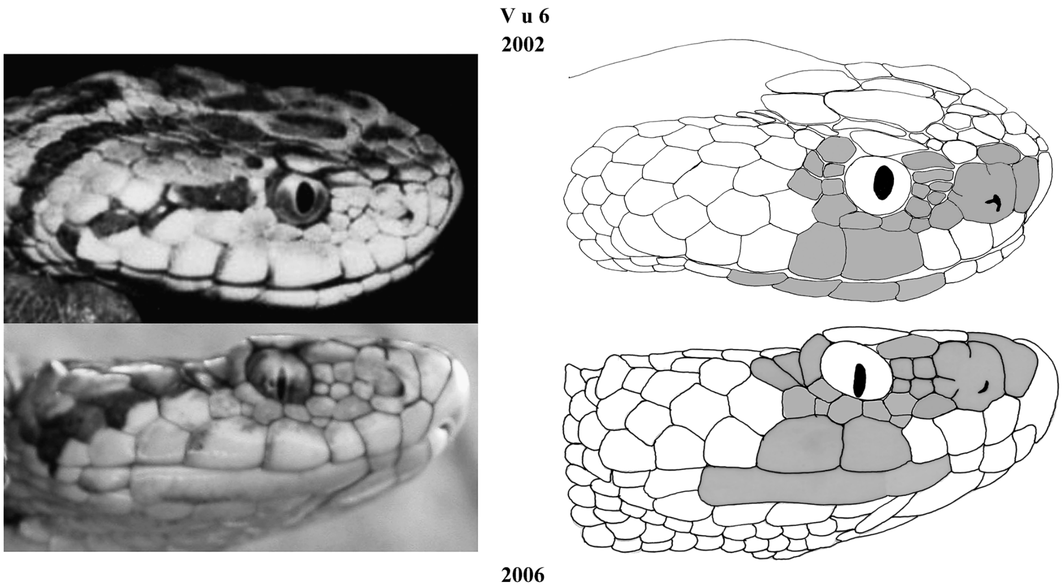

Figure 3. Photographs (left) and corresponding drawings (right) of head scales changes (right side of the head) in individual no. 6 of meadow viper at first capture (year 2002) and after four years (year 2006). Recorded types of head scales changes: 2, 3.

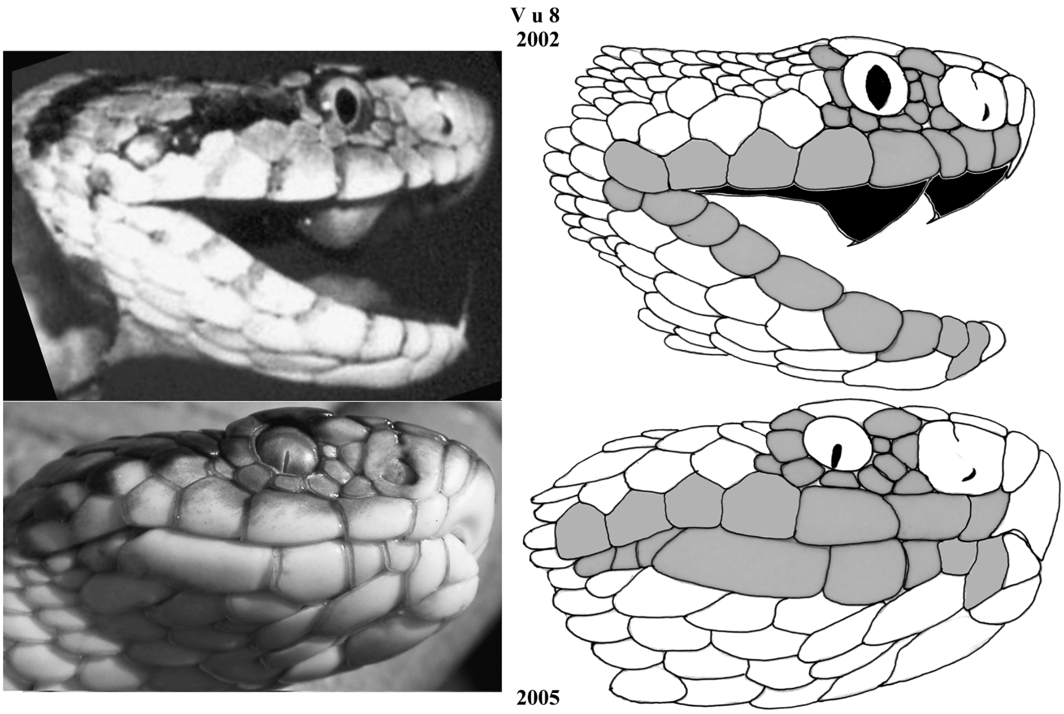

Figure 4. Photographs (left) and corresponding drawings (right) of head scales changes (right side of the head) in individual no. 8 of meadow viper at first capture (year 2002) and after three years (year 2005). Recorded types of head scales changes: 2, 3.

the general tendencies in morphological evolution (but see Bruschi et al., 2006 for the lacertid *Podarcis tiliguerta*). It is supposed that this tendency occurred also in the evolution of reptile integument, through replacement of small, simple and numerous dermal elements by large and metameric ones.

Nevertheless, there are numerous examples (at least, within viperids) that both oligomerisation and polymerisation were detected as apomorphic characters within certain clades (e.g. Kramer, 1961; Marx and Rabb, 1970, 1972; Saint-Girons, 1978; Marx et al., 1988; Nilson et al., 1994; Nilson and Andrén, 2001). For instance, absence of large dorsal head shields are considered as derived (Saint-Girons, 1978; Obst, 1983). Thus, within the *Pelias* group (*sensu* Obst, 1983), *V. berus* and *V. seoanei* are much more "oligomerised" than *V. ursinii*, while all *Pelias* species are much more "oligomerised" than members of *Rhinaspis* group (e.g. *V. latastei* or *V. ammodytes* – *sensu* Obst, 1983). On the other hand, medium numbers of supralabial and sublabial scales (eight to nine – Nilson et al., 1994) are considered plesiomorphic, while much reduced or increased numbers are considered apomorphic (Kramer, 1961; Marx and Rabb, 1970, 1972; Saint-Girons, 1978; Nilson et al., 1994). In the viper population we studied, no consistent pattern of covariation between scale change and size increase or sex emerged.

Regeneration of scales as a result of a response to trauma of integument is common in squamates (Maderson et al., 1978). However, this explanation must be discarded for this case since "neogenic scales are never regular, and there is no restoration of geometric patterning except on regenerated tails" (Maderson et al., 1978). Also, the frequency of head scales changes in our sample is so high (52.2%) that we could not treat them as "anomalies" (i.e. deviations from "normal" forms). This suggests that head scales variation throughout one indi-

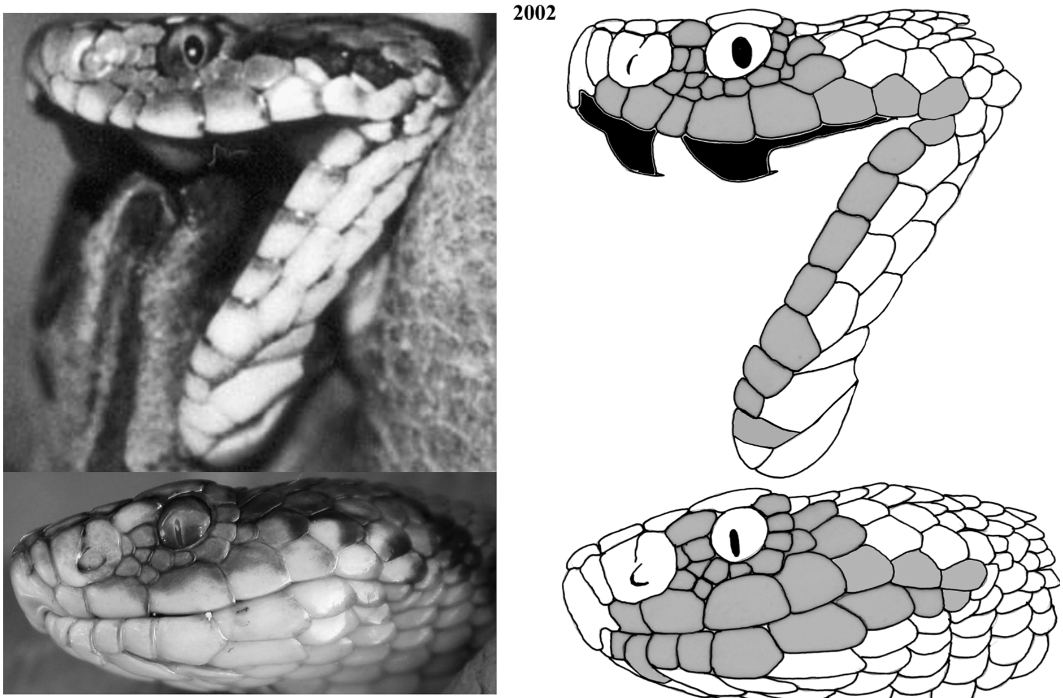

Figure 5. Photographs (left) and corresponding drawings (right) of head scales changes (left side of the head) in individual no. 8 of meadow viper at first capture (year 2002) and after three years (year 2005). Recorded types of head scales changes: 2, 3.

vidual's life is not anecdotic but a generalised phenomenon, at least in the viper population studied. On the basis of observed data about frequency of occurrence of head scales changes in both sexes, we infer that they could be equally distributed between sexes in the population of meadow viper.

Here it is important to distinguish between scalation changes at different levels: phylogenetic (between species or species groups), interpopulational, inter-individual and ontogenic (within the same individual). It is worth noting that the usefulness of head scale characters at each level depends on those levels under it. That is, head scales changing easily between populations cannot be used for phylogenetic purposes; those very variable between individuals will show poor resolution between populations and phylogroups; and, last but not least, those head scales labile in the ontogeny will be inadequate for identifying individuals, populations or species.

Traditionally, cephalic scales in squamates has been considered individual "finger-printings" (i.e. not variable in ontogeny). On the other hand, numerous experimental and field studies show that one of the most important abiotic influences on both the rate and the trajectory of embryonic differentiation in squamates is temperature – thermal regimes during embryogenesis can affect phenotypic traits of the offspring, such as body size, scalation and/or asymmetry in morphological trait (e.g. Shine and Harlow, 1996; Shine et al., 1997; Osypka and Arnold, 2000; Flatt et al., 2001; Arnold and Peterson, 2002; Zhdanova and Zakharov, 2006). Other studies showed that some additional environmental factors (e.g. reduced precipitation and altitude, and increased temperature) are correlated with higher number (Brown et al., 1991;

Table 1. Data of re-photographed individual specimens with ($n = 12$) and without head scales changes ($n = 11$) in studied population of meadow viper. Ind. no. – marking number of individual specimen; SVL – snout to vent length; class (age) – age in years; type of head scales changes: 1 – polymerisation, 2 – oligomerisation, 3 – shape changes.

Ind. no.	Sex	First photographed	Class (Age) (Baron, 1997)	SVL (in cm)	Rephoto-graphed	Class (Age) (Baron, 1997)	SVL (in cm)	Period (in years)	Type of head scales changes
5	female	2002	adult (+4)	41.5	2004	adult (+6)	44.7	2	1, 2, 3
6	female	2002	adult (+4)	40.4	2006	adult (+8)	41.4	4	2, 3
8	female	2002	immature (2-3)	23.3	2005	adult (5-6)	35.7	3	2, 3
29	female	2003	adult (+4)	40.7	2005	adult (+6)	42.6	2	1
52	female	2003	adult (+4)	34.0	2006	adult (+7)	39.2	3	3
55	female	2003	immature (3-4)	28.7	2006	adult (6-7)	35.8	3	1, 2
80	male	2004	adult (+3)	37.3	2006	adult (+5)	37.8	2	2, 3
111	male	2005	adult (+3)	26.8	2006	adult (+4)	29.9	1	2
112	female	2005	adult (+4)	37.7	2006	adult (+5)	41.1	1	1, 2, 3
126	female	2005	adult (+4)	35.1	2006	adult (+5)	37.4	1	1, 2, 3
132	female	2005	immature (+1)	16.3	2006	immature (+2)	20.1	1	1
133	female	2005	adult (+4)	36.6	2006	adult (+5)	37.8	1	1, 2
3	female	2002	adult (+4)	34.9	2003	adult (+5)	39.0	1	no
21	female	2002	immature (3-4)	27.1	2006	adult (7-8)	35.5	4	no
22	female	2003	adult (+4)	33.6	2006	adult (+7)	40.5	3	no
38	female	2003	immature (3-4)	30.0	2005	adult (5-6)	40.4	2	no
42	female	2003	immature (2-3)	23.1	2004	immature (3-4)	27.7	1	no
51	male	2003	immature (2-3)	23.4	2005	adult (4-5)	28.6	2	no
56	female	2003	adult (+4)	31.3	2005	adult (+6)	36.4	2	no
58	female	2003	adult (+4)	42.6	2006	adult (+7)	43.2	3	no
67	female	2003	immature (3-4)	26.3	2006	adult (6-7)	37.6	3	no
83	female	2004	adult (+4)	38.0	2006	adult (+6)	41.4	2	no
129	female	2005	adult (+4)	31.4	2006	adult (+5)	36.4	1	no

Table 2. Log-linear models analysing the variation of the head scales changes with sex and ontogeny. Cl. change: class change (a – individuals remaining immature; b – individuals changing from immature to adults; c – individuals being adults in the two markings). Sc. change: scale change (yes/no). 1 – polymerisation; 2 – oligomerisation; 3 – shape changes.

Var.	Log-linear model	Interaction with:						Model fit (max. likelihood)		
		Sex			Class change					
		χ^2	d.f.	p	χ^2	d.f.	p	χ^2	d.f.	p
Sc. change	sex/class change	0.03	1	0.86	1.69	2	0.43	3.02	8	0.93
1	sex/class change	0.31	1	0.58	0.75	2	0.69	4.43	8	0.83
2	sex/class change	0.56	1	0.46	1.30	2	0.52	3.90	8	0.87
3	sex/class change	0.17	1	0.68	0.83	2	0.66	4.43	8	0.82

Malhotra and Thorpe, 1997; Sanders et al., 2004) or lower number of scales of the head, body and tail (Horton, 1972; Lister, 1976). For such studies only experimental work could disentangle the effects of local adaptation and phenotypic plasticity.

Since our results showed that ontogenic changes of head scales occur in the post-natal phase (even in mature individuals), we conclude that the effects of factors promoting their intra- and/or interpopulation variability are much more prolonged than previously believed (possibly during the whole ontogeny). Such changeable elements are to be considered phenotypically plastic structures and, consequently, not appropriate for use in taxonomic analyses. The other question, whether there is genetic variability for phenotypic plasticity of these traits in certain population (Pigliucci, 2005; Pigliucci et al., 2006), cannot be solved on the basis of the simple information presented here, and needs further research.

In summary, we have shown that some of the head scalation characters of meadow viper, that were previously used taxonomically, display post-embryonic ontogenic variation. Present results may represent a challenge for viper taxonomists. Although, interspecific variation in structure of head scales is usually higher than the ontogenic changes reported here (see Joger and Stümpel, 2005, and references therein), many infraspecific taxa were described using small sets of specimens and minor scale variations which could be ontogenetically labile. Namely, many of the members of the *Vipera ursinii* complex have been described on the basis of minimal head scales differences (Nilson and Andrén, 1988, 2001; Dely and Joger, 2005, and references therein). Although we do not suggest that meristic characters are completely inadequate for taxonomic use, we emphasize the potential error in basing taxonomic decisions on few meristic traits and demonstrate the need for taking into account the ontogenic trajectories of these characters when analysing intra- and interpopulation variability of the populations.

Further studies should be addressed to other populations of *V. ursinii* and to other *Vipera* species in order to investigate the extension of ontogenic changes of head scales, as well as to have a better understanding of the nature and evolutionary significance of this phenomenon. Meanwhile, a word of caution is to be sent to those using cephalic scales for systematics in vipers.

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