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ATLANTAL VERTEBRAE OF TAILED AMPHIBIANS OF RUSSIA AND ADJACENT COUNTRIES

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Morphology of atlantal vertebrae of four species of the family Hynobiidae (*Onychodactylus fischeri*, *Ranodon sibiricus*, *Salamandrella keyserlingii*, and *Salamandrella schrenkii*) and nine species of the family Salamandridae (*Lissotriton montandoni*, *Lissotriton vulgaris*, *Mertensiella caucasica*, *Mesotriton alpestris*, *Ommatotriton ophryticus*, *Salamandra salamandra*, *Triturus cristatus*, *Triturus dobrogicus*, and *Triturus karelinii*) were studied. Analysis of variation of vertebrae of these species and systematic descriptions of these species are given. Our comparative analysis revealed that all species studied have peculiarities which allow diagnosing them.

Keywords: atlantal vertebra, morphology, Hynobiidae, Salamandridae, Caudata.

INTRODUCTION

The morphology of atlantal vertebrae (i.e., atlases, cervical or first corporal vertebrae) of tailed amphibians is poorly studied although it appears to be of interest for purposes of identification. Very brief descriptions and/or drawings of atlases of some hynobiids and salamandrids were previously published (Antipenkova, 1994; Deynegi, 1917; Francis, 1934; Haller-Probst and Schleich, 1994; Herre, 1935; Hilton, 1948; Hoffman, 1878; Mivart, 1870; Okajima, 1908; Teege, 1957; Wiedersheim, 1875; Zhang, 1985). Paleontological records of atlantal vertebrae of urodelans are relatively frequent (Delfino and Bailon, 2000; Estes, 1981; Estes and Hoffstetter, 1976; Rage and Bailon, 2005; Rage and Hossini, 2000; Sanchiz, 1998; Sanchiz and Młynarski, 1979). However, insufficiently described morphology of atlases of recent urodelans prevents study of fossil species. Therefore, the aim of the present paper is to describe morphology of atlantal vertebrae of tailed amphibians inhabiting Russia and adjacent countries (the Former Soviet Union).

MATERIAL AND METHODS

In total, seventy seven specimens of four species of Hynobiidae and nine species of Salamandridae were studied (Table 1). The materials are kept in the herpetological collections of the Voronezh State University and Department of Herpetology of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia). Measurements of vertebrae parameters were performed with use of binocular microscope (accuracy 0.1 mm). As a basis, we applied the terminology of Haller-Probst and Schleich (1994). The scheme of measurements is given in Fig. 1. The statistical analysis was performed with use of Statistica 6.0. The significance of differences between means was estimated by the Kolmogorov – Smirnov test.

RESULTS AND DISCUSSION

Descriptions of Atlantal Vertebrae

Family Hynobiidae Cope, 1860

(Figs. 2 – 5)

Ventral surface of centrum with rare foramina. Processus odontoideus massive, wedge-shaped, with weakly-concave dorsal surface. In posterior view, dorsal part of neural arch as a rule thin, although some specimens show marked thickness (NATH/H = 0.15 – 0.24). In lateral view, neural arch with horizontal dorsal margin. Neurapophysis replaced by bulge of neural arch. Secondary dorsal and lateral crests absent or weakly defined. In dorsal view, posterior margins of postzygapophyseal articular facets posterior to the posterior edge of neural arch.

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TABLE 1. List of Taxa, Sample Localities, and Numbers of Specimens Studied (*N*)

Species	Locality	*N*
	Hynobiidae	
Onychodactylus fischeri	Primorskiy Kray, Russia	1
Ranodon sibiricus	Borokhudzir River, Alma-Ata Province, Kazakhstan	1
Salamandrella keyserlingii	Sverdlovskaya Oblast', Russia	2
–"–	Russia	1
Salamandrella schrenkii	South of Primorskiy Kray, Russia	1
	Salamandridae	
Lissotriton montandoni	The Carpathians, Ukraine	5
Lissotriton vulgaris vulgaris	Gatchina, Leningradskaya Oblast', Russia	15
–"–	Udmurtia, Russia	1
–"–	Grodno Province, Byelorussia	2
Lissotriton vulgaris lantzi	Tbilisi, Georgia	1
Mesotriton alpestris alpestris	The Carpathians, Ukraine	2
–"–	Serbia	1
Mertensiella caucasica	Georgia	6
Ommatotriton ophryticus ophryticus	Tbilisi, Georgia	2
–"–	Goryachiy Klyuch, Krasnodar Kray, Russia	6
–"–	Sochi, Russia	1
Salamandra salamandra salamandra	The Carpathians, Ukraine	5
Triturus cristatus	Chur, Udmurtia, Russia	2
–"–	Elizavetino, Leningradskaya Oblast', Russia	7[1]
–"–	Unknown locality	2
Triturus dobrogicus dobrogicus	Izmail, Odessa Province, Ukraine	3
–"–	Vilkovo, Odessa Province, Ukraine	3[2]
Triturus karelinii arntzeni	Treshnja, Serbia and Montenegro	1
Triturus karelinii karelinii	Kutuzovka, Crimea, Ukraine	5
–"–	Kuybyshevo, Crimea, Ukraine	1
–"–	Tbilisi, Georgia	1
–"–	Ersi, Dagestan, Russia	1

[1] The sample includes two subadult specimens.
[2] The sample includes a subadult specimen.

Genus *Onychodactylus* Tschudi, 1838
***Onychodactylus fischeri* (Boulenger, 1886)**
(Fig. 2)

CL is 2.3 mm. Processus odontoideus slightly narrower than cotylus (POW/CTW = 0.91) and much narrower than neural canal (POW/CNW = 0.63). In dorsal view, anterior edge of neural arch slightly uneven with wide median lobe. In both anterior and posterior views, neural canal rounded with dorsal slight narrowing. In dorsal view, bulge on neural arch clearly widened near posterior edge (T-shaped).

Genus *Ranodon* Kessler, 1866
***Ranodon sibiricus* Kessler, 1866**
(Fig. 3)

CL is 3.3 mm (3.9 mm after Averianov and Tjutkova, 1995). Processus odontoideus slightly wider than cotylus (POW/CTW = 1.15) and much narrower than neural canal (POW/CNW = 0.75). In dorsal view, anterior edge of neural arch slightly uneven with wide median lobe. In anterior view, neural canal subtriangular with dorsal sharpening, in posterior one, rounded. In dorsal view, bulge on neural arch not widened near posterior edge.

Genus *Salamandrella* Dybowski, 1870
(Figs. 4 – 5)

In dorsal view, anterior edge of neural arch curved with lacking or slightly expressed median lobe. In both anterior and posterior views, neural canal subtriangular with dorsal narrowing. In dorsal view, bulge on neural arch usually sharply widened near both anterior and posterior edges.

***Salamandrella keyserlingii* Dybowski, 1870**
(Fig. 4)

CL up to 2.6 mm. Processus odontoideus clearly wider than cotylus (POW/CTW = 1.22 – 1.38) and much narrower than neural canal (POW/CNW = 0.73). In dorsal view, anterior widening of bulge on neural arch narrower or equal to posterior widening.

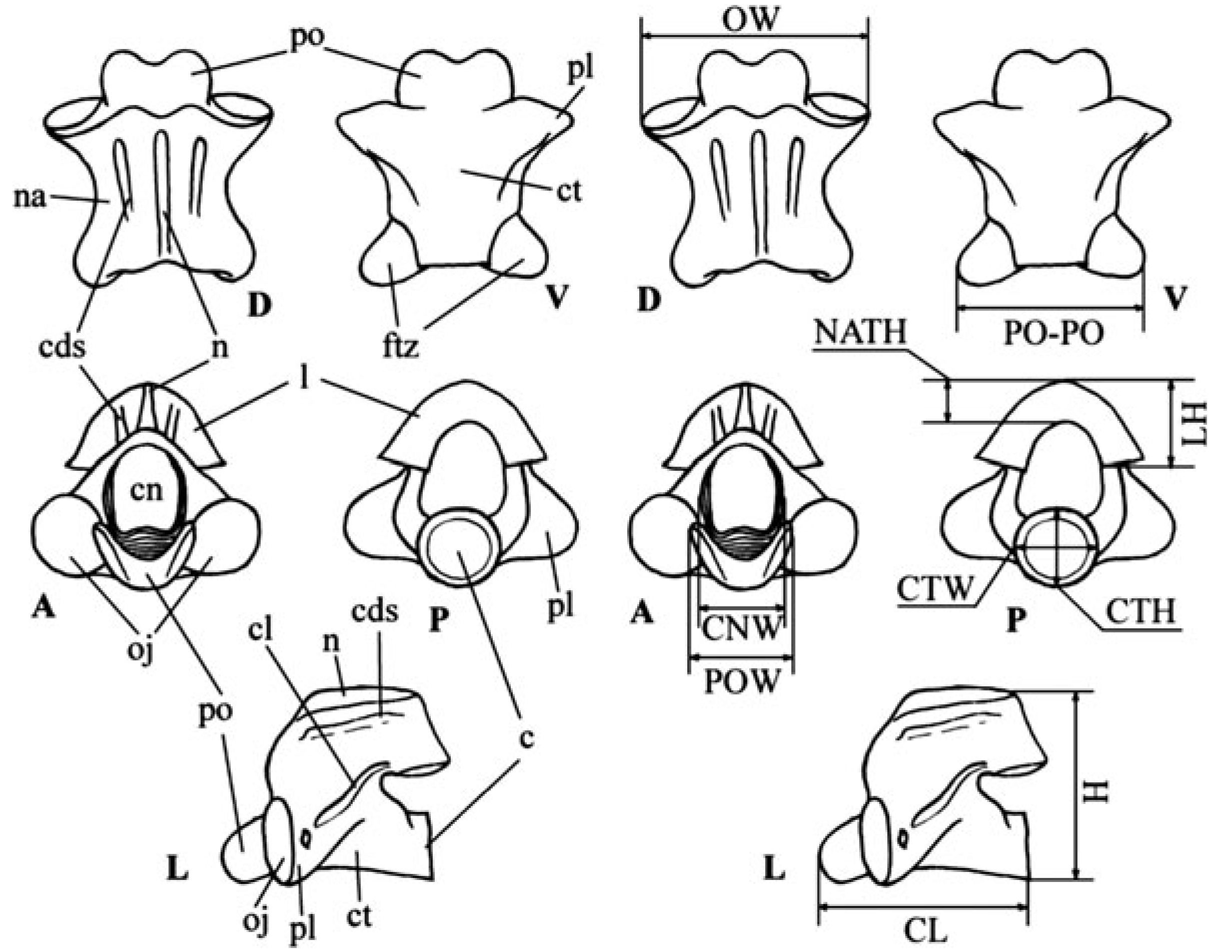

Fig. 1. The anatomical terms (left) and measurements (right) used in the present paper. D, dorsal view; V, ventral view; L, lateral view; A, anterior view; P, posterior view; c , centrum; cds, secondary dorsal crest; cl, lateral crest; cn, neural canal; ct, cotylus; ftz, postzygapophyseal articular facet; l, lamina; n, neurapophysis; na, neural arch; oj, occipital joint; pl, processus lateralis; po, processus odontoideus; CL, central length; CNW, canalis neuralis width; CTH, cotyle height; CTW, cotyle width; H, posterior height of vertebra; LH, laminae height; NATH, neural arch thickness; OW, occipital width; PO-PO, distance between lateral margins of postzygapophyseal articular facets; POW, processus odontoideus width.

***Salamandrella schrenkii* (Strauch, 1870)**
(Fig. 5)

CL is 2.1 mm. Width of processus odontoideus obviously wider than cotylus width (POW/CTW = 1.22) and smaller than neural canal width (POW/CNW = 0.85). In dorsal view, anterior widening of bulge on neural arch obviously wider than posterior widening (Y-shaped).

Family Salamandridae
(Figs. 6 – 14)

Ventral surface of centrum with rare or frequent foramina. Processus odontoideus thin, gutter-shaped, with two ventro-lateral articular surfaces. In posterior view, dorsal part of neural arch as a rule thick, although some specimens has reduced thickness (usually NATH/H = 0.21 – 0.27, range 0.13 – 0.33). In lateral view, dorsal margin of neural arch horizontal or rising caudally. Neurapophysis (instead of very thick bulge in hynobiids) usually present. Secondary dorsal and lateral crests lacking in some salamandrid species, but well developed in the other ones. In dorsal view, posterior margins of postzygapophyseal articular facets posterior to the posterior edge of neural arch.

Genus *Mertensiella* Wolterstorff, 1925
***Mertensiella caucasica* (Waga, 1876)**
(Fig. 6)

CL up to 3.2 mm. Ventral surface of centrum with rare foramina. Processus odontoideus much wider than cotylus (POW/CTW = 1.30 – 1.88) and as a rule as wide as neural canal (in average POW/CNW = 0.98,

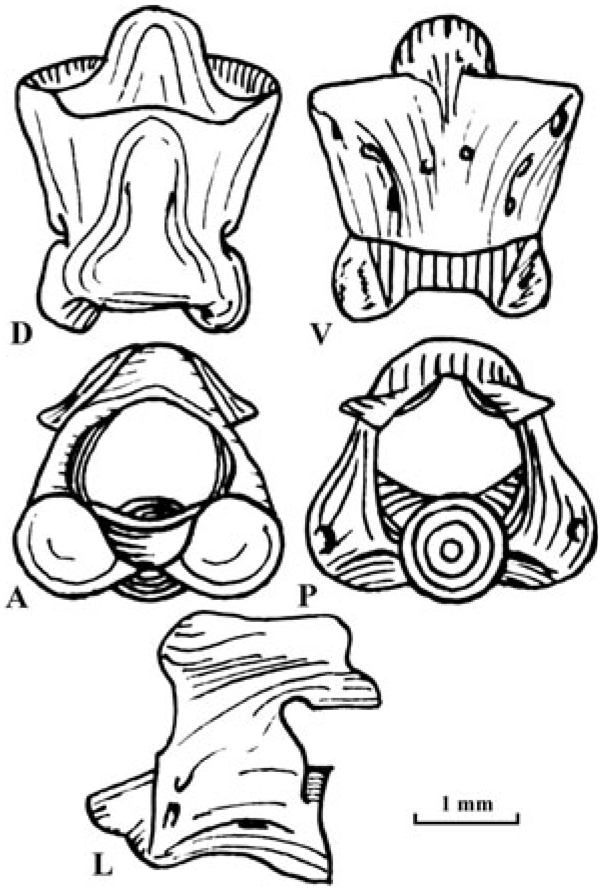

Fig. 2. Atlantal vertebra of *Onychodactylus fischeri*. Here and thereafter: D is dorsal view; V is ventral view; L is left lateral view; A is anterior view; P is posterior view.

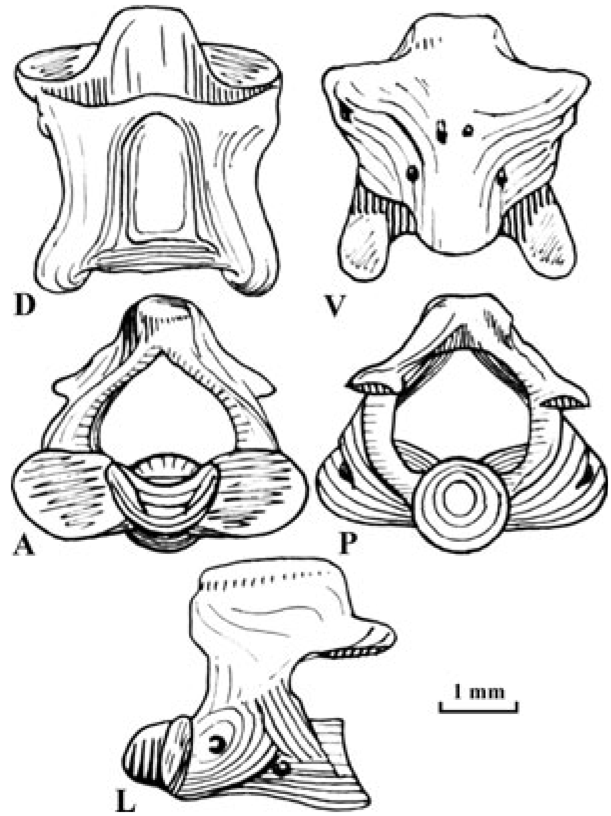

Fig. 3. Atlantal vertebra of *Ranodon sibiricus*.

range 0.87 – 1.00). In the anterior part of the neural arch, but somewhat distant from the anterior margin, is a well visible (in lateral view) transverse prominence. In lateral view, dorsal margin of neural arch horizontal and posterior to this prominence. In dorsal view, anterior edge of neural arch prominent, sometimes with a small medial notch. Neurapophysis very thin and low, weakly visible, very variable at length, sometimes reaching the posterior margin of neural arch. Secondary dorsal and lateral crests absent. In dorsal view, posterior edge of neural arch concave and bearing a small ctenoid prominence in the sagittal plane. Neural canal rounded, sometimes with dorsal narrowing in anterior view. In posterior view, dorsal part of the posterior border of neural arch thin and slightly prominent.

Genus *Salamandra* Laurenti, 1768
***Salamandra salamandra* (Linnaeus, 1758)**
(Fig. 7)

CL up to 5.6 mm. Ventral surface of centrum with rare foramina. Processus odontoideus as wide or wider than cotylus (POW/CTW = 1.00 – 1.32) and neural canal (POW/CNW = 1.00 – 1.24). In lateral view, dorsal margin of neural arch horizontal. In dorsal view, anterior edge of neural arch wavy, with medial bay, and sometimes with small prominence. Neurapophysis very thick and high, in anterior part forms two branches which diverge anteriorly. Secondary dorsal crests absent. Lateral crests absent or weakly developed. Well visible depressions with small or, sometimes, large foramina posterior to lateral crests. In lateral view, large foramen present in upper part of lateral crests, near occipital articular facets. In dorsal view, posterior edge of neural arch has a deep median notch. Neural canal narrow and high with some dorsal narrowing. In posterior view, dorsal part of neural arch moderately thick and sharply convex.

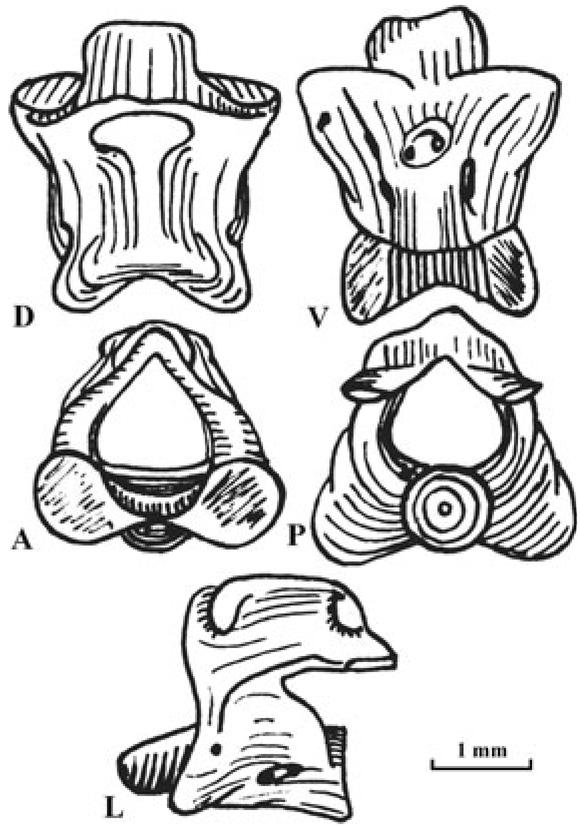

Fig. 4. Atlantal vertebra of *Salamandrella keyserlingii*.

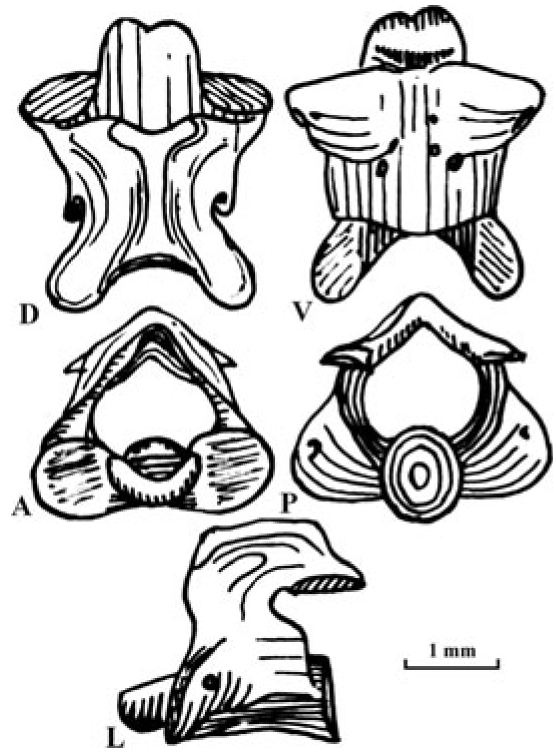

Fig. 5. Atlantal vertebra of *Salamandrella schrenkii*.

Genus *Mesotriton* Bolkay, 1927
***Mesotriton alpestris* (Laurenti, 1768)**
(Fig. 8)

CL up to 2.6 mm. Ventral surface of centrum with rare foramina. Processus odontoideus wider than cotylus (POW/CTW = 1.22 – 1.67), but narrower than neural canal (POW/CNW = 0.84 – 0.95). In lateral view, dorsal margin of neural arch inclined (rising caudally, about 30° to centrum axis). In dorsal view, anterior edge of neural arch wavy, with broad medial bay. Neurapophysis thin and low in anterior part, almost absent in medial part, then rises and becomes twice higher than in anterior part. Secondary dorsal crests weakly developed; distance between them reduced backward. Lateral crests well developed. In dorsal view, posterior edge of neural arch has a shallow medial notch subdivided by a small ctenoid prominence in the sagittal plane. Neural canal rounded. In posterior view, dorsal part of neural arch moderately thick and rounded.

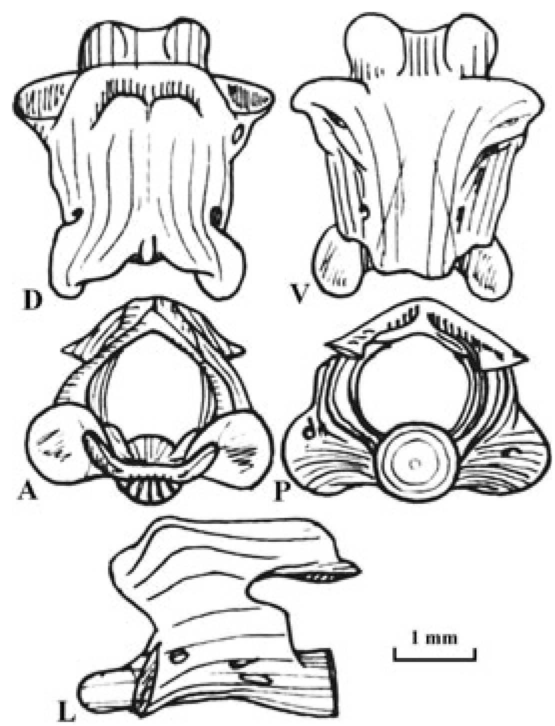

Fig. 6. Atlantal vertebra of *Mertensiella caucasica*.

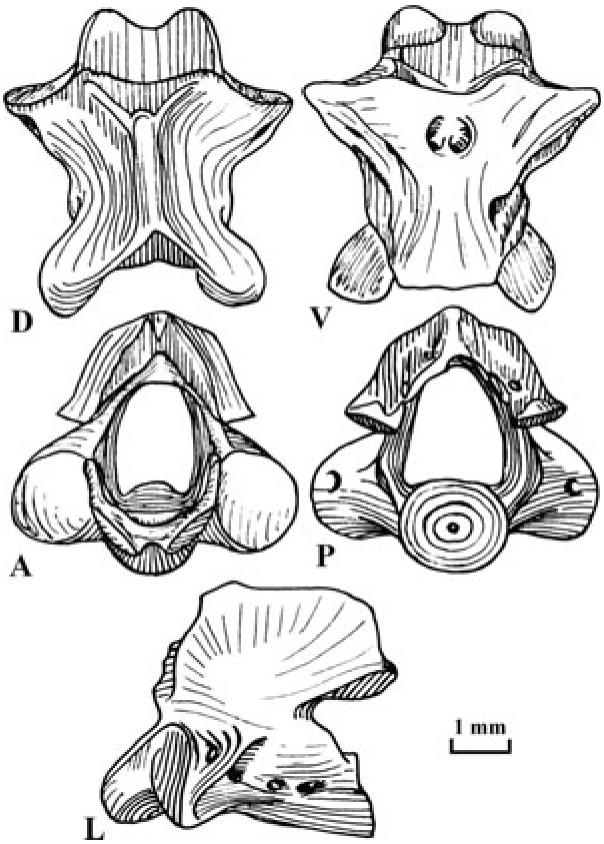

Fig. 7. Atlantal vertebra of *Salamandra salamandra*.

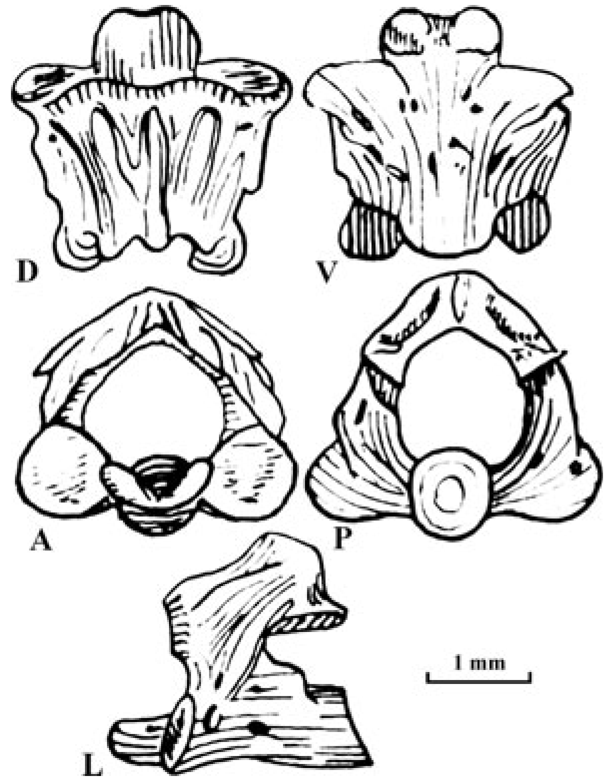

Fig. 8. Atlantal vertebra of *Mesotriton alpestris*.

Genus *Triturus* Rafinesque, 1815

(Figs. 9 – 11)

Ventral surface of centrum and lateral processes with frequent foramina. In lateral view, dorsal margin of neural arch inclined. In dorsal view, anterior edge of neural arch prominent or wavy, with shallow medial notch. In dorsal view, posterior margin of neural arch slightly-wavy. Secondary dorsal crests extend nearly parallel at a large distance from each other. Lateral crests well developed. Neural canal nearly rounded.

Triturus cristatus (Laurenti, 1768)

(Fig. 9)

CL up to 3.1 mm. Width of processus odontoideus nearly equal to that of cotylus (POW/CTW = = 0.91 – 1.14), but smaller than neural canal width (POW/CNW = 0.69 – 0.92). In lateral view, dorsal margin of neural arch inclined (rising caudally, about 30° to centrum axis). Neurapophysis low in anterior part and absent in medial and posterior parts. Secondary dorsal crests low and can extend to posterior edge of neural arch. In posterior view, dorsal part of neural arch moderately thick and trapezoid. Processes lateralis can bear deep grooves.

Triturus dobrogicus (Kiritzescu, 1903)

(Fig. 10)

CL up to 2.6 mm. Width of processus odontoideus nearly equal to that of cotylus (POW/CTW = = 0.89 – 1.16), but smaller than neural canal width (POW/CNW = 0.64 – 0.92). In lateral view, dorsal margin of neural arch inclined (rising caudally, no more than 30° to centrum axis). Neurapophysis low and thick in anterior part and absent in medial and posterior parts. Low and thick secondary dorsal crests not extending to posterior edge of neural arch. In posterior view, dorsal part of neural arch moderately thick and trapezoid. Processes lateralis without grooves.

Triturus karelinii (Strauch, 1870)

(Fig. 11)

CL up to 3.3 mm. As a rule, width of processus odontoideus nearly equal to that of cotylus (POW/CTW =

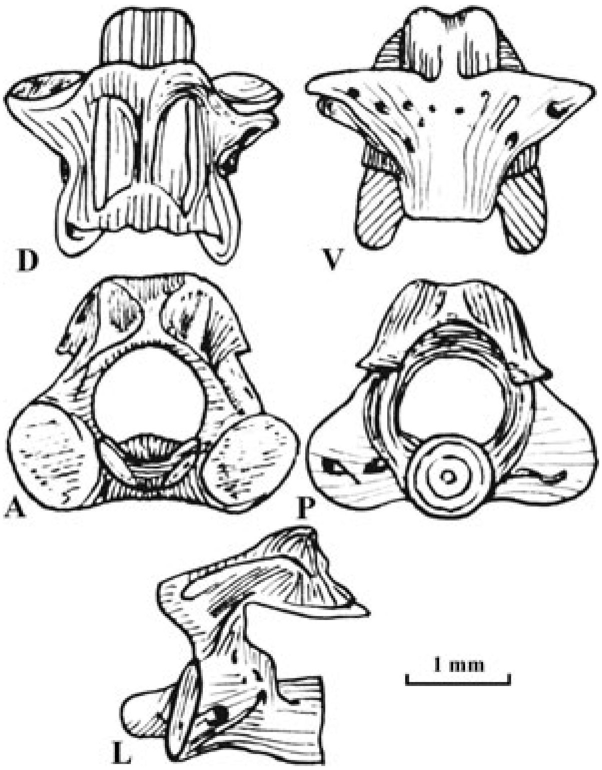

Fig. 9. Atlantal vertebra of *Triturus cristatus*.

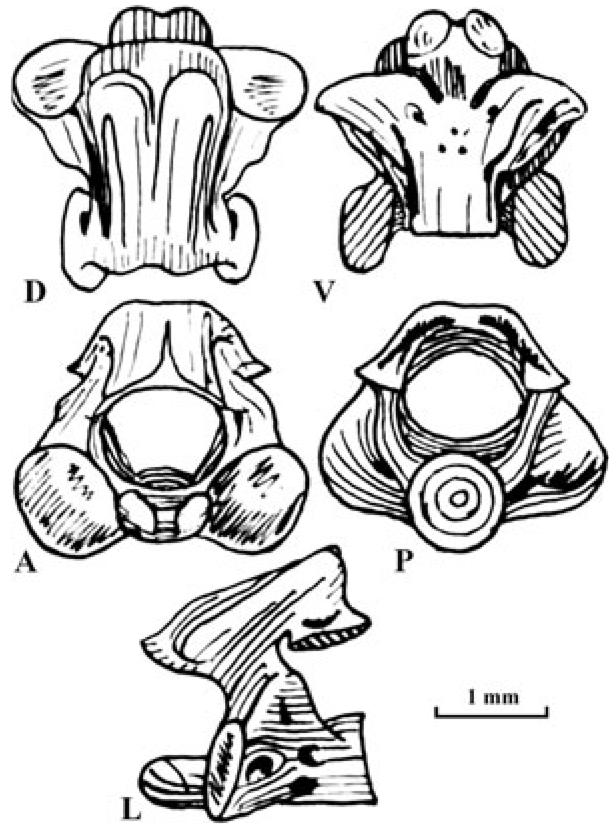

Fig. 10. Atlantal vertebra of *Triturus dobrogicus*.

= 0.93 – 1.29), but smaller than neural canal width (POW/CNW = 0.69 – 1.00). In lateral view, dorsal margin of neural arch inclined (rising caudally, up to 45° to centrum axis). Neurapophysis low in anterior and medial parts, and replaced by slightly expressed triangular area in posterior part. High secondary dorsal crests extend to posterior edge of neural arch. Frequently, lateral crests have wavy margins. In posterior view, dorsal part of neural arch thick, arched with several nearly straight segments. Posterior surfaces of processes lateralis bear numerous small crests.

Genus *Lissotriton* Bell, 1839
(Figs. 12 – 13)

Ventral surface of centrum can bear small asymmetric crests. Width of processus odontoideus slightly larger than that of cotylus (in average POW/CTW = = 1.15) and much smaller than neural canal width (mean POW/CNW = 0.75). In lateral view, anterior part of dorsal margin of neural arch inclined (rising caudally, about 30° to centrum axis). In dorsal view, anterior part of neural arch wavy, with shallow medial bay. Neurapophysis low or, sometimes, almost invisible. Secondary dorsal crests low and extend at a short distance from each other to eminent triangular area in posterior edge of neural arch. Position and height of secondary dorsal crests can be variable: high or low, close and parallel to each other or distance between them reduced backward. Lateral crests well developed. In dorsal view, posterior edge of neural arch has a deep median bay subdivided by a small ctenoid prominence in the sagittal plane. Neural canal nearly circular, it diameter much more than cotylus height. In posterior view, dorsal part of neural arch thin or moderately thick, subtriangular or trapezoid.

***Lissotriton montandoni* (Boulenger, 1880)**
(Fig. 12)

CL up to 2.2 mm. Ventral surface of centrum with several foramina. Processus odontoideus wider than cotylus (POW/CTW = 1.05 – 1.29) and narrower than neural canal (mean POW/CNW = 0.75 – 0.91). Lateral crests begin near posterior edges of processes lateralis. Large foramina present near anterior edges of processes lateralis.

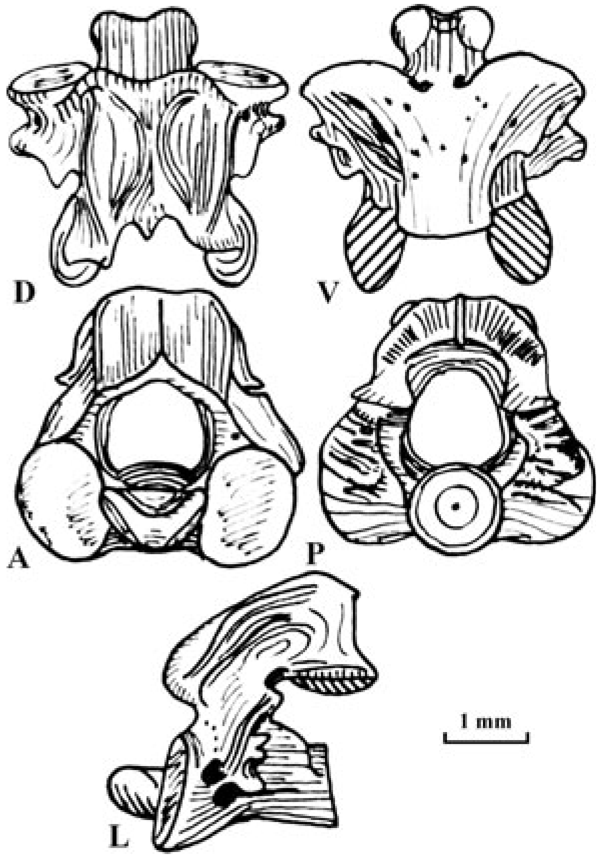

Fig. 11. Atlantal vertebra of *Triturus karelinii*.

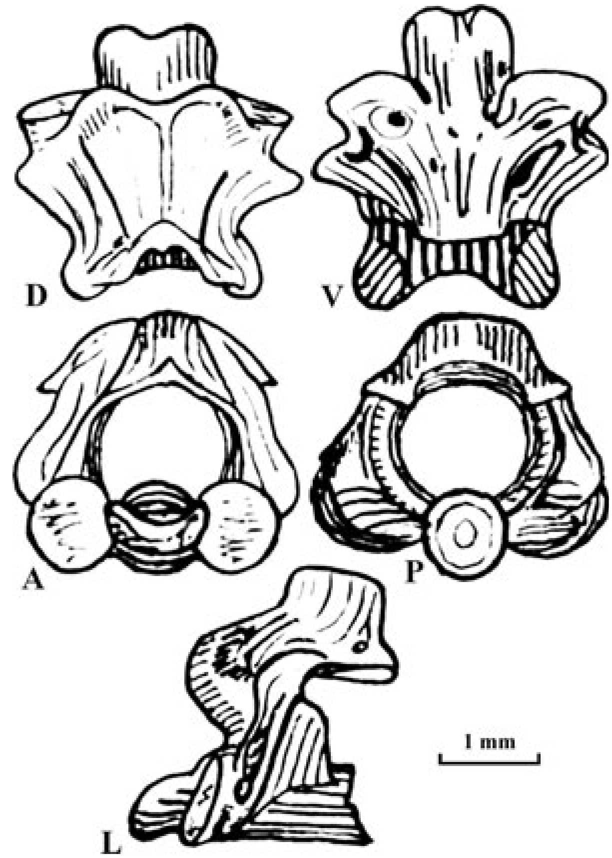

Fig. 12. Atlantal vertebra of *Lissotriton montandoni*.

Lissotriton vulgaris **(Linnaeus, 1758)**
(Fig. 13)

CL up to 2.0 mm (2.2 mm after Haller-Probst and Schleich, 1994). Ventral surface of centrum with frequent foramina. Processus odontoideus usually markedly wider than cotylus (POW/CTW = 1.23 – 1.70) and narrower than neural canal (mean POW/CNW = = 0.70 – 0.95). Lateral crests begin on anterior edges of processes lateralis near occipital articular facets. Posterior surfaces of processes lateralis have small and large foramina, crests or long grooves.

Genus *Ommatotriton* Gray, 1850
Ommatotriton ophryticus **(Berthold, 1846)**
(Fig. 14)

CL up to 3.8 mm. Ventral surface of centrum with frequent foramina. Processus odontoideus markedly wider than cotylus (POW/CTW = 1.21 – 1.55) and approximately as wide as neural canal (mean POW/CNW = 0.87 – 1.33). In lateral view, dorsal margin of neural arch inclined (rising caudally, about 30° to centrum axis). In dorsal view, anterior part of neural arch weakly wavy, with wide and shallow median bay. Neurapophysis low and thin in anterior and middle parts and absent in posterior one. Secondary dorsal crests have different length, as a rule, distance between them reduced backward, but sometimes can extend nearly parallel at a large distance from each other. Lateral crests well developed and begin near occipital articular facets. In dorsal view, posterior edge of neural arch has deep median bay divided by a small ctenoid prominence in the sagittal plane. Neural canal rounded. In posterior view, dorsal part of neural arch thick and trapezoid.

Interspecies differences

The families Hynobiidae and Salamandridae can be clearly distinguished by the shape of the processus odontoideus (wedge- and gutter-shaped, respectively; Table 2). Additionally, neurapophyses are absent in hynobiids and replaced by bulge (Table 2).

Among the Hynobiidae, all four species studied differ from each other by the form of the bulge on the neu-

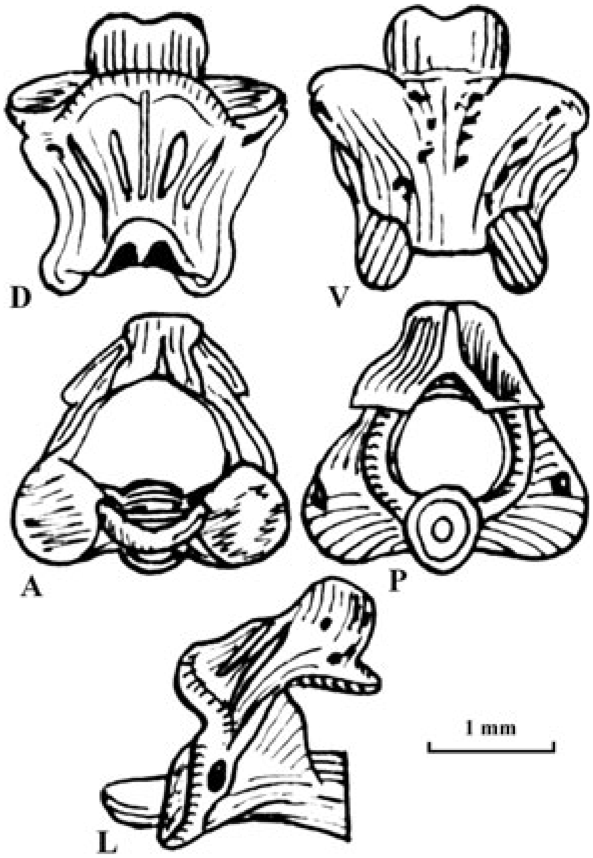

Fig. 13. Atlantal vertebra of *Lissotriton vulgaris*.

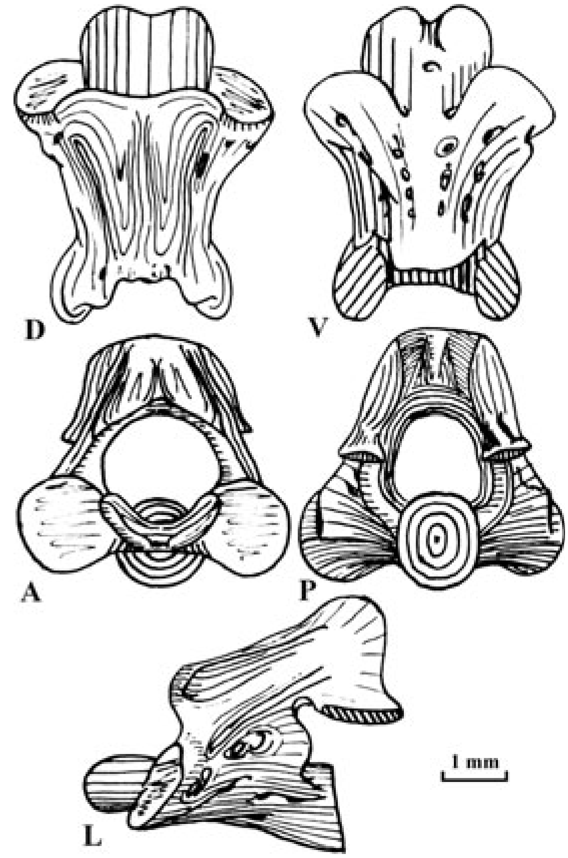

Fig. 14. Atlantal vertebra of *Ommatotriton ophryticus*.

TABLE 2. Variation of Some Characters of Atlantal Vertebrae for Twelve Species of Hynobiidae and Salamandridae

Taxon	PO	N	DMNA	SDC	LC	FC	NC
Onychodactylus fischeri	1	1	1	1	1	1	1
Ranodon sibiricus	1	1	1	1	1	1	2
Salamandrella keyserlingii	1	1	1	1	1	1	2
Salamandrella schrenkii	1	1	1	1	1	1	2
Mertensiella caucasica	2	2	1	1	1	1	1
Salamandra salamandra	2	3	1	1	1	1	3
Mesotriton alpestris	2	2	2	2	2	1	1
Lissotriton montandoni	2	2	2	2	2	1	1
Lissotriton vulgaris	2	2	2	2	2	1	1
Triturus cristatus	2	2	2	2	2	2	1
Triturus dobrogicus	2	2	2	2	2	2	1
Triturus karelinii	2	2	2	2	2	2	1
Ommatotriton ophryticus	2	2	2	2	2	2	1

Note. FC, foramina on ventral surface of centrum: rare (1), frequent (2); PO, processus odontoides: massive, wedge-shaped, with weakly-concave dorsal surface (1), thin, gutter-shaped, with two ventro-lateral articular surfaces (2); DMNA, dorsal margin of neural arch: horizontal (1), inclined (2); N, neurapophysis: replaced by bulge (1), low (2), high (3); SDC, secondary dorsal crests: lacking (1), present (2); LC, lateral crests: lacking (1), high (2); NC, neural arch in anterior view: nearly rounded (1), subtriangular with dorsal sharpening (2), vertically elongated with some dorsal narrowing (3).

TABLE 3. Variation of Morphometric Characters (mm, mean ± standard deviation, and range) of Atlantal Vertebrae in Adult Specimens of Species of the Families Hynobiidae and Salamandridae

Taxon	*n*	CL	OW	POW	CNW	H	PO-PO	LH	NATH	CTH	CTW
					Hynobiidae						
Onychodactylus fischeri	1	2.3	2.6	1.0	1.6	2.6	2.1	0.9	0.4	1.2	1.1
Ranodon sibiricus	1	3.3	3.5	1.5	2.0	3.5	3.2	1.5	0.8	1.3	1.3
Salamandrella keyserlingii	3	2.3 ± 0.3 (2.1 – 2.6)	2.6 ± 0.3 (2.4 – 2.9)	1.1 ± 0.1 (1.1 – 1.2)	1.4 ± 0.2 (1.2 – 1.5)	2.4 ± 0.1 (2.3 – 2.6)	1.9 ± 0.2 (1.8 – 2.2)	0.9 ± 0.1 (0.9 – 1.0)	0.5 ± 0.1 (0.4 – 0.6)	0.9 ± 0.1 (0.8 – 1.0)	0.9 ± 0.1 (0.8 – 0.9)
Salamandrella schrenkii	1	2.1	2.5	1.1	1.3	2.2	2.0	0.7	0.4	0.9	0.9
					Salamandridae						
Lissotriton montandoni	5	2.3 ± 0.3 (1.9 – 2.7)	2.3 ± 0.2 (2.0 – 2.7)	1.1 ± 0.2 (0.9 – 1.4)	1.2 ± 0.1 (1.1 – 1.2)	2.3 ± 0.2 (2.1 – 2.5)	1.7 ± 0.2 (1.5 – 2.0)	0.9 ± 0.2 (0.7 – 1.1)	0.4 ± 0.1 (0.4 – 0.6)	0.8 ± 0.1 (0.7 – 1.0)	0.8 ± 0.1 (0.7 – 0.9)
Lissotriton vulgaris	19	1.8 ± 0.1 (1.7 – 2.0)	2.0 ± 0.1 (1.9 – 2.2)	0.9 ± 0.1 (0.8 – 1.0)	1.1 ± 0.1 (1.0 – 1.2)	1.9 ± 0.1 (1.7 – 2.1)	1.4 ± 0.1 (1.2 – 1.6)	0.7 ± 0.1 (0.6 – 0.9)	0.4 ± 0.1 (0.3 – 0.6)	0.6 ± 0.0 (0.6 – 0.7)	0.6 ± 0.0 (0.5 – 0.7)
Mertensiella caucasica	6	2.9 ± 0.2 (2.6 – 3.2)	3.0 ± 0.1 (2.9 – 3.1)	1.5 ± 0.1 (1.3 – 1.6)	1.5 ± 0.0 (1.5 – 1.6)	2.4 ± 0.1 (2.4 – 2.5)	2.4 ± 0.3 (2.1 – 2.8)	0.8 ± 0.0 (0.8 – 0.9)	0.5 ± 0.1 (0.4 – 0.6)	0.8 ± 0.0 (0.8 – 0.9)	0.9 ± 0.1 (0.8 – 1.0)
Mesotriton alpestris	3	2.4 ± 0.2 (2.2 – 2.6)	2.4 ± 0.1 (2.3 – 2.5)	1.1 ± 0.0 (1.1 – 1.1)	1.2 ± 0.1 (1.1 – 1.3)	2.3 ± 0.2 (2.2 – 2.5)	1.9 ± 0.2 (1.8 – 2.1)	0.9 ± 0.0 (0.9 – 1.0)	0.6 ± 0.1 (0.5 – 0.7)	0.8 ± 0.1 (0.7 – 0.8)	0.9 ± 0.0 (0.9 – 0.9)
Ommatotriton ophryticus	9	3.3 ± 0.4 (2.7 – 3.8)	3.3 ± 0.4 (2.7 – 3.8)	1.6 ± 0.2 (1.3 – 1.8)	1.5 ± 0.1 (1.4 – 1.6)	3.4 ± 0.5 (2.7 – 3.8)	2.5 ± 0.3 (2.0 – 2.9)	1.6 ± 0.3 (1.2 – 2.0)	1.0 ± 0.2 (0.6 – 1.3)	1.1 ± 0.2 (0.9 – 1.4)	1.2 ± 0.2 (0.9 – 1.5)
Salamandra salamandra	5	4.5 ± 0.6 (4.0 – 5.6)	5.1 ± 0.4 (4.5 – 5.7)	2.2 ± 0.3 (1.9 – 2.5)	1.8 ± 0.2 (1.6 – 2.1)	4.2 ± 0.3 (3.9 – 4.5)	3.6 ± 0.4 (3.0 – 4.1)	2.0 ± 0.1 (1.8 – 2.1)	1.1 ± 0.1 (1.0 – 1.2)	1.5 ± 0.2 (1.2 – 1.8)	1.9 ± 0.1 (1.8 – 2.1)
Triturus cristatus	9	2.5 ± 0.3 (2.3 – 3.1)	3.2 ± 0.3 (2.8 – 3.8)	1.1 ± 0.1 (1.0 – 1.2)	1.3 ± 0.1 (1.2 – 1.5)	2.8 ± 0.2 (2.5 – 3.1)	2.3 ± 0.2 (2.0 – 2.8)	1.1 ± 0.2 (0.9 – 1.5)	0.6 ± 0.1 (0.5 – 0.7)	1.0 ± 0.1 (0.9 – 1.2)	1.1 ± 0.1 (0.9 – 1.2)
Triturus dobrogicus	5	2.2 ± 0.3 (2.0 – 2.6)	2.7 ± 0.4 (2.2 – 3.1)	1.0 ± 0.1 (0.8 – 1.1)	1.3 ± 0.1 (1.2 – 1.5)	2.5 ± 0.2 (2.3 – 2.7)	1.9 ± 0.3 (1.6 – 2.1)	0.9 ± 0.1 (0.7 – 1.0)	0.5 ± 0.0 (0.5 – 0.6)	1.0 ± 0.0 (0.9 – 1.0)	1.0 ± 0.1 (0.9 – 1.1)
Triturus karelinii	9	3.0 ± 0.3 (2.6 – 3.5)	3.7 ± 0.3 (3.3 – 4.1)	1.4 ± 0.2 (1.1 – 1.8)	1.6 ± 0.2 (1.4 – 1.8)	3.3 ± 0.2 (3.1 – 3.6)	2.8 ± 0.3 (2.5 – 3.2)	1.6 ± 0.2 (1.3 – 1.8)	0.9 ± 0.2 (0.8 – 1.2)	1.2 ± 0.1 (1.0 – 1.4)	1.3 ± 0.1 (1.0 – 1.4)

TABLE 4. Variation of Morphometric Indices (mean ± standard deviation, and range) of Atlantal Vertebrae in Adult Specimens of Species of the families Hynobiidae and Salamandridae

Taxon	*n*	H/CL	CL/OW	POW/CNW	PO-PO/H	LH/H	NATH/H	NATH/LH	CTH/CTW	POW/CTW
					Hynobiidae					
Onychodactylus fischeri	1	0.39	0.88	0.63	0.79	0.35	0.15	0.44	1.09	0.91
Ranodon sibiricus	1	0.45	0.94	0.75	0.91	0.43	0.23	0.53	1.00	1.15
Salamandrella keyserlingii	3	0.40 ± 0.02 (0.38 – 0.43)	0.90 ± 0.01 (0.89 – 0.92)	0.82 ± 0.09 (0.73 – 0.92)	0.80 ± 0.06 (0.75 – 0.86)	0.38 ± 0.02 (0.35 – 0.39)	0.19 ± 0.04 (0.16 – 0.24)	0.49 ± 0.11(0.40 – 0.61)	1.02 ± 0.12 (0.89 – 1.11)	1.31 ± 0.08 (1.22 – 1.38)
Salamandrella schrenkii	1	0.33	0.86	0.85	0.91	0.32	0.16	0.50	0.94	1.22
					Salamandridae					
Lissotriton montandoni	5	0.40 ± 0.05 (0.32 – 0.45)	1.00 ± 0.03 (0.95 – 1.05)	0.86 ± 0.10 (0.75 – 1.00)	0.74 ± 0.08 (0.65 – 0.86)	0.41 ± 0.07 (0.30 – 0.47)	0.19 ± 0.03 (0.17 – 0.24)	0.48 ± 0.08 (0.40 – 0.57)	1.00 ± 0.07 (0.88 – 1.06)	1.21 ± 0.09 (1.06 – 1.29)
Lissotriton vulgaris	19	0.41 ± 0.05 (0.33 – 0.50)	0.91 ± 0.04 (0.80 – 1.00)	0.81 ± 0.07 (0.70 – 0.95)	0.75 ± 0.06 (0.64 – 0.91)	0.39 ± 0.04 (0.32 – 0.47)	0.20 ± 0.03 (0.14 – 0.26)	0.50 ± 0.07 (0.40 – 0.62)	0.99 ± 0.07 (0.92 – 1.20)	1.46 ± 0.14 (1.23 – 1.70)
Mertensiella caucasica	6	0.28 ± 0.02 (0.27 – 0.31)	0.97 ± 0.05 (0.88 – 1.03)	0.98 ± 0.04 (0.87 – 1.00)	1.00 ± 0.13 (0.84 – 1.19)	0.34 ± 0.02 (0.32 – 0.37)	0.21 ± 0.03 (0.16 – 0.24)	0.61 ± 0.10 (0.50 – 0.75)	0.90 ± 0.07 (0.80 – 1.00)	1.63 ± 0.19 (1.30 – 1.88)
Mesotriton alpestris	3	0.39 ± 0.04 (0.35 – 0.41)	0.99 ± 0.09 (0.92 – 1.08)	0.88 ± 0.06 (0.85 – 0.95)	0.81 ± 0.03 (0.78 – 0.84)	0.39 ± 0.03 (0.36 – 0.41)	0.24 ± 0.04 (0.20 – 0.27)	0.62 ± 0.13 (0.47 – 0.72)	0.85 ± 0.06 (0.78 – 0.89)	1.20 ± 0.03 (1.17 – 1.22)
Salamandra salamandra	5	0.42 ± 0.04 (0.36 – 0.48)	0.92 ± 0.04 (0.89 – 0.98)	1.24 ± 0.20 (1.00 – 1.56)	0.85 ± 0.07 (0.75 – 0.93)	0.47 ± 0.01 (0.45 – 0.48)	0.26 ± 0.03 (0.23 – 0.29)	0.56 ± 0.05 (0.50 – 0.61)	0.80 ± 0.10 (0.67 – 0.95)	1.15 ± 0.16 (1.00 – 1.32)
Ommatotriton ophryticus	9	0.47 ± 0.05 (0.42 – 0.56)	1.00 ± 0.05 (0.96 – 1.09)	1.06 ± 0.14 (0.87 – 1.21)	0.74 ± 0.04 (0.68 – 0.79)	0.47 ± 0.03 (0.42 – 0.53)	0.29 ± 0.04 (0.22 – 0.34)	0.63 ± 0.06 (0.50 – 0.71)	0.97 ± 0.07 (0.87 – 1.09)	1.36 ± 0.14 (1.13 – 1.55)

TABLE 4 (continued)

Taxon	*n*	H/CL	CL/OW	POW/CNW	PO-PO/H	LH/H	NATH/H	NATH/LH	CTH/CTW	POW/CTW
Triturus cristatus	9	0.45 ± 0.07 (0.38 – 0.58)	0.80 ± 0.05 (0.71 – 0.87)	0.82 ± 0.08 (0.67 – 0.92)	0.81 ± 0.06 (0.71 – 0.90)	0.41 ± 0.04 (0.35 – 0.48)	0.22 ± 0.02 (0.19 – 0.25)	0.55 ± 0.05 (0.47 – 0.64)	0.99 ± 0.06 (0.91 – 1.10)	1.03 ± 0.07 (0.91 – 1.14)
Triturus dobrogicus	5	0.39 ± 0.02 (0.35 – 0.41)	0.82 ± 0.06 (0.75 – 0.91)	0.79 ± 0.12 (0.66 – 0.92)	0.74 ± 0.08 (0.64 – 0.84)	0.34 ± 0.03 (0.30 – 0.38)	0.21 ± 0.02 (0.19 – 0.23)	0.61 ± 0.07 (0.56 – 0.71)	0.97 ± 0.04 (0.90 – 1.00)	1.03 ± 0.11 (0.89 – 1.16)
Triturus karelinii	9	0.52 ± 0.05 (0.43 – 0.60)	0.82 ± 0.06 (0.73 – 0.89)	0.87 ± 0.09 (0.69 – 1.00)	0.89 ± 0.06 (0.79 – 0.95)	0.47 ± 0.03 (0.41 – 0.51)	0.28 ± 0.03 (0.23 – 0.33)	0.59 ± 0.06 (0.50 – 0.67)	0.94 ± 0.06 (0.86 – 1.00)	1.09 ± 0.11 (0.93 – 1.29)

TABLE 5. Differences between atlantal vertebrae of adults of nine salamandrid species ($p > 0.05$ is "–"; $p < 0.05$ is "+"; $p < 0.01$ is "++"; $p < 0.001$ is "+++").

Taxa	Character																		
	CL	OW	POW	CNW	H	PO-PO	LH	NATH	CTH	CTW	H/CL	CL/OW	POW/CNW	PO-PO/H	LH/H	NATH/H	NATH/LH	CTH/CTW	POW/CTW
M/S	++	++	++	+	++	++	++	++	++	++	++	–	–	–	++	+	–	–	+
M/O	–	–	–	–	++	–	++	++	++	–	++	–	–	++	++	++	–	–	+
M/c	+	–	++	++	++	–	++	–	++	–	++	++	+	+	++	–	–	–	++
M/d	+	–	++	++	–	++	–	–	++	–	++	+	+	+	–	–	–	–	++
M/k	–	++	+	–	++	–	++	++	++	++	++	++	+	+	++	++	–	–	++
M/m	+	++	++	++	–	++	–	–	–	–	++	–	–	+	–	–	–	–	++
M/v	+++	+++	+++	+++	+++	+++	–	–	+++	+++	+++	+	++	+++	++	–	–	+	+
M/a	–	+	+	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	+
S/O	++	++	++	+	++	++	–	–	+	++	–	+	–	+	–	–	–	+	–
S/c	++	++	++	++	++	++	++	++	++	++	–	++	++	–	+	+	–	+	–
S/d	+	+	+	+	+	+	+	+	+	+	–	–	+	–	+	+	–	–	–
S/k	++	++	++	–	++	+	+	–	+	++	+	+	+	–	–	–	–	+	–
S/m	+	+	+	+	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–
S/v	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	–	–	+++	+	++	++	–	+	++
S/a	+	+	+	+	+	+	+	+	+	+	–	–	+	–	+	–	–	–	–
O/c	++	–	+++	+	–	–	+	++	–	–	–	+++	++	+	+	++	+	–	++
O/d	++	–	++	+	+	+	++	+	–	–	++	++	+	–	++	+	–	–	+
O/k	–	–	–	–	–	–	–	–	–	–	+	+++	+	++	–	–	–	–	++
O/m	+	+	++	++	++	++	++	+	–	+	–	–	–	–	–	+	+	–	–
O/v	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+	+++	+++	–	++	+++	++	–	–
O/a	+	+	+	+	+	–	+	–	+	–	+	–	–	–	+	–	–	–	–
c/d	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+	–	–	–	–
c/k	+	+	++	+	++	++	++	+++	+	++	+	–	–	–	+	++	–	–	–
c/m	–	++	–	+	+	++	–	+	+	+	–	++	–	–	–	+	–	–	+
c/v	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	–	+++	–	+	–	–	–	–	+++
c/a	–	+	–	–	–	–	–	–	+	–	–	+	–	–	–	–	–	+	+
d/k	+	++	+	+	++	++	++	++	+	+	++	–	–	–	++	++	–	–	–
d/m	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–
d/v	++	+++	–	++	+++	+++	–	++	+++	+++	–	+	–	–	–	–	+	–	+++
d/a	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	–	–	+	+
k/m	+	++	+	++	++	++	++	++	++	++	+	++	–	+	–	+	–	–	–
k/v	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	++	–	+++	++	+++	+	–	+++
k/a	–	+	–	+	+	+	+	+	+	+	+	+	–	–	–	–	–	–	–
m/v	+	–	–	–	++	++	–	–	+++	+++	–	++	–	–	–	–	–	–	++
m/a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
v/a	+	+	+	–	+	+	–	+	+	+	–	–	–	–	–	–	–	+	+

Note. M, *Mertensiella caucasica*; S, *Salamandra salamandra*; O, *Ommatotriton ophryticus*; c, *Triturus cristatus*; d, *Triturus dobrogicus*; k, *Triturus karelinii*; m, *Lissotriton montandoni*; v, *Lissotriton vulgaris*; a, *Mesotriton alpestris*.

ral arch. However, we did not study within-species variation and, therefore, some of these differences might result from individual variation.

In the Salamandridae, differences between salamanders and newts are most obvious. In lateral view, the dorsal margin of neural arch is nearly horizontal in salamanders and inclined in newts (Table 2). Additionally, secondary dorsal and lateral crests are completely lacking in salamanders and clearly expressed in newts. *Mertensiella caucasica* well differs from other species by the shape of the neural arch, the presence of a peculiar transverse prominence and very thin and wide processus odontoideus (Table 2). *Salamandra salamandra* well differs from all other taxa by the marked length of the centrum (Tables 3 and 4) and by high and anteriorly deeply forked neurapophysis (Table 2).

Among newts, *Ommatotriton ophryticus* clearly differs by the very thick and trapezoid dorsal part of the neural arch. *Mesotriton alpestris* has low and wide secondary dorsal crests and well developed lateral crests. The representatives of the genus *Lissotriton* also have well developed lateral crests, but secondary dorsal crests extend at a short distance from each other. The two species of the genus differ from each other by the position of the anterior edges of lateral crests: they originate near the posterior edges of the processes lateralis in *L. montandoni* and on the anterior edges in *L. vulgaris*. Additionally, the latter species differ from other newts by very small vertebrae (Tables 3 and 5). The genus *Triturus* is characterized by well developed secondary dorsal crests. In *Triturus karelinii*, these crests are markedly higher than in the two other species of the genus. Additionally, *Triturus karelinii* is differed by larger vertebrae and three indices H/CL, LH/H, and NATH/H (Tables 3 – 5). Atlases of two other species, *T. cristatus* and *T. dobrogicus*, are very similar and differ from each other by the presence, in the former, or absence, in the latter, of small grooves and crests on the posterior margins of the lateral processes, and values of PO-PO and index LH/H (Tables 3 – 5).

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