Russian Journal of Herpetology Vol. 14, No. 3, 2007, pp. 177 – 190

COMPARATIVE MORPHOLOGY OF TRUNK AND SACRAL VERTEBRAE OF TAILED AMPHIBIANS OF RUSSIA AND ADJACENT COUNTRIES

Vyacheslav Yu. Ratnikov[1] **and Spartak N. Litvinchuk**[2]

Submitted September 18, 2006.

Trunk and sacral vertebrae of three species of the family Hynobiidae (*Onychodactylus fischeri*, *Ranodon sibiricus*, and *Salamandrella keyserlingii*) 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 individual variation of vertebrae of these species along the axial column and systematic descriptions of these species are given. Our comparative analysis revealed that all species studied have peculiarities which allow diagnosing them. Geographic variation in height of neurapophysis was found in *Triturus karelinii*. Specimens of the species from the Crimea and the Balkans have low neurapophyses, and newts from eastern Georgia and Dagestan are characterized by high ones.

Keywords: Salamandridae, Hynobiidae, trunk vertebrae, sacrum.

INTRODUCTION

The fauna of tailed amphibians of Russia and adjacent countries (the territory of Former Soviet Union) consists of two urodelan families. The Hynobiidae Cope, 1860 includes three species. Two species, *Onychodactylus fischeri* (Boulenger, 1886) and *Salamandrella keyserlingii*[3] Dybowski, 1870, distributed in Russia, and one species, *Ranodon sibiricus* Kessler, 1866, inhabits Kazakhstan (Borkin, 1998). The Salamandridae Goldfuss, 1820 consists of six genera occurring in Russia and adjacent countries. Newts of the former genus *Triturus* were recently divided into four distinct genera based on molecular evidence (Carranza and Amat, 2005; Frost et al., 2006; Garsia-Paris et al., 2004; Litvinchuk et al., 2005b): *Lissotriton* Bell, 1839, *Mesotriton* Bolkay, 1927, *Ommatotriton* Gray, 1850, and *Triturus* Rafinesque, 1815. Among them, four species, *Lissotriton vulgaris* (Linnaeus, 1758), *Ommatotriton ophryticus* (Berthold, 1846)[4], *Triturus cristatus* (Laurenti, 1768), and *Triturus karelinii* (Strauch, 1870), inhabit Russia, and three species, *Lissotriton montandoni* (Boulenger, 1880), *Mesotriton alpestris* (Laurenti, 1768), and *Triturus dobrogicus* (Kiritzescu, 1903) are distributed in Ukraine. The fire salamander *Salamandra salamandra* (Linnaeus, 1758) is known from western Ukraine, and the Caucasian salamander *Mertensiella caucasica* (Waga, 1876) occurs in south-western Georgia (Borkin, 1998).

For a long time, much attention has been focused upon the vertebral morphology of tailed amphibians. The first drawings of skeletons of newts and salamanders were published by Meyer (1748). Some vertebrae of urodelans were described in the first edition of famous “Ossemens Fossiles” (Cuvier, 1812). Mertens (1820) made comparative analysis of axial skeleton elements of various groups of extant tailed amphibians. This author, and later Mivart (1870), divided urodelan vertebral column into following parts: the cervical (“colli”), the trunk (“dorsi and lumbales” or “dorsal”), the sacral (“sacrales”), and the caudal (“coccyges”) ones. Up to the present time, such division has been generally accepted.

In tailed amphibians, the first vertebra (atlas) strongly differs in morphology from other vertebrae (Duellman and Trueb, 1986). The number of trunk vertebrae ranges from 11 in some salamandrids to 64 in amphiumids (Litvinchuk and Borkin, 2003). The trunk part of

[1] Voronezh State University; University sq. 1, Voronezh 394006, Russia; E-mail: vratnik@yandex.ru.

[2] Institute of Cytology, Russian Academy of Sciences; Tikhoretsky pr. 4, St. Petersburg 194064, Russia;
E-mail: slitvinchuk@yahoo.com.

[3] Recently, *Salamandrella keyserlingii* from south-eastern part of the Russian Far East was distinguished as a distinct cryptic species, *Salamandrella schrenckii* (Berman et al., 2005).

[4] Based on genetic data, subspecies *Triturus vittatus ophryticus* was erected to the status of distinct species (Litvinchuk et al., 2005b).

1026-2296/2007/1403-0177

the vertebral column could be divided into three segments distinguishing with regard to the position of the limb bases: the anterior, the middle, and the posterior ones (Litvinchuk and Borkin, 2003). The sacral part, as a rule, consists of one vertebra only. However, in few specimens, the sacrum consists of two neighboring vertebrae (Gerecht, 1929; Antipenkova, 1994). The morphology of the sacrum is similar to that of trunk vertebrae, distinguishing them by more massive rib-bearers only. The number of caudal vertebrae varies from 18 in *Salamandrella keyserlingii* to 53 in *Siren* sp. and *Mertensiella caucasica* (Antipenkova, 1994; Boulenger, 1896; Mivart, 1870). The caudal part of the axial skeleton could be divided into two segments: the caudosacral and the "true" caudal ones. The caudosacral vertebrae (usually 3, range 2 – 4) are associated with the pelvic musculature and cloaca. Anterior one or two caudosacral vertebrae are characterized by lack of haemal archs, and, therefore, are similar to trunk vertebrae (Frolich, 1991; Hilton, 1948).

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

Taxon	Locality	*N*
	Hynobiidae	
Onychodactylus fischeri	Primorskiy Kray, Russia	1
Ranodon sibiricus	Alma-Ata Province, Kazakhstan	1
Salamandrella keyserlingii	Sverdlovskaya Oblast', Russia	2
	Russia	1
	Salamandridae	
Lissotriton montandoni	Ukraine	5
Lissotriton vulgaris vulgaris	Leningradskaya Oblast', Russia	10
	Udmurtia, Russia	1
Mesotriton alpestris alpestris	The Carpathians, Ukraine	2
	Serbia	1
Mertensiella caucasica	Georgia	6
Ommatotriton ophryticus ophryticus	Tbilisi, Georgia	2
	Batumi, Georgia	1
	Krasnodarskiy Kray, Russia	6
	Sochi, Krasnodarskiy Kray, Russia	2
Salamandra salamandra salamandra	Ukraine	4
Triturus cristatus	Chur, Udmurtia, Russia	1
	Leningradskaya Oblast', Russia	5*
	Locality unknown	2
Triturus dobrogicus dobrogicus	Izmail, Odessa Province, Ukraine	3
	Vilkovo, Odessa Province, Ukraine	1
Triturus karelinii arntzeni	Treshnja, Serbia	1
Triturus karelinii karelinii	Kutuzovka, Crimea, Ukraine	5
	Crimea, Ukraine	1
	Tbilisi, Georgia	1
	Ersi, Dagestan, Russia	1

* The sample included two subadult specimens.

The vertebral morphology of hynobiids is poorly studied. Okajima (1908) was the first who described the axial column of *Onychodactylus japonicus*. Later, Deinegi (1917) studied vertebrae of *Ranodon sibiricus*. Some authors (Antipenkova, 1994; Hilton, 1948; Teege, 1957; Zhang, 1985) published short descriptions of vertebrae of *Salamandrella keyserlingii* and some other hynobiids. Fossil records of hynobiid vertebrae were described from Romania, Kazakhstan, and Russia (Averianov and Tjutkova, 1995; Ratnikov, 2002; Venczel, 1999).

Trunk vertebrae of the Salamandridae are more comprehensively studied. Various authors (e.g., Gonzalez et al., 1986; Haller-Probst and Schleich, 1994; Hilton, 1948; Mivart, 1870; Teege, 1957; Wiedersheim, 1875) published comparative analyses of vertebrae morphology of various salamandrids. Descriptions of fossil salamandrids were published in numerous paleontological studies as well (Auge and Rage, 1995; Böhme, 1983; Delfino and Bailon, 2000; Estes, 1981, 1982; Estes et al., 1967; Estes and Darevsky, 1977; Estes and Hoffstetter, 1976; Hodrova, 1984, 1985; Holman, 1995; Kotsakis, 1981; Rage and Bailon, 2005; Rage and Hossini, 2000; Ratnikov, 2002; Sanchiz and Młynarski, 1979; Sanchiz and Szyndlar, 1984).

Unfortunately, these descriptions were, as a rule, very brief. Vertebrae are the most frequent remains. In the absence of detailed comparative and biometrical studies of vertebrae of extant taxa, identification of fossils is not possible. Moreover, recently, systematics of tailed amphibians was greatly changed. Therefore, the aim of the present paper was to describe morphology of trunk and sacral vertebrae of tailed amphibians which inhabit countries of the Former Soviet Union.

MATERIAL AND METHODS

In total, sixty-four adult and two subadult specimens of three 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 Zoological Museum of Moscow State University, as well as Department of Herpetology of Zoological Institute of the Russian Academy of Sciences (St. Petersburg). Measurements of vertebrae parameters were performed with use of binocular microscope (accuracy 0.1 mm). Various authors mentioned different names for the same elements of vertebrae. As a

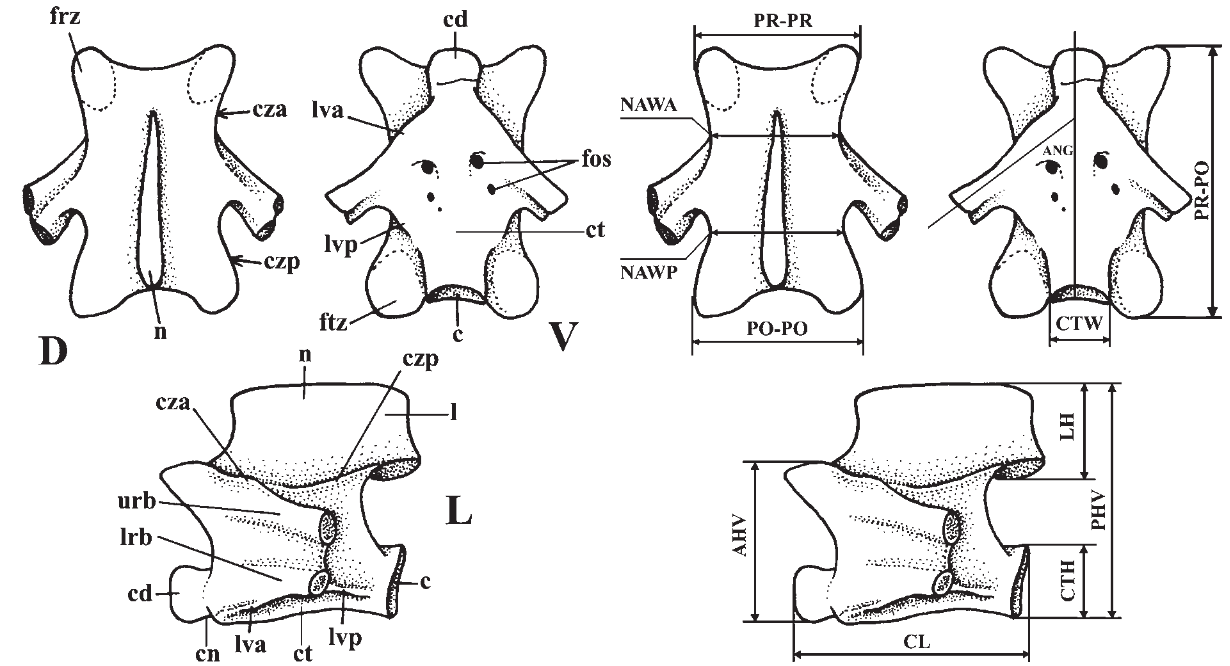

Fig. 1. The trunk and sacral vertebrae parameters names (at the left) and the scheme of measurements (at the right). D, dorsal view; V, ventral view; L, lateral view; c, cotylus; cd, condylus; cn, neck; ct, centrum; cza, anterior zygapophyseal crest; czp, posterior zygapophyseal crest; fos, subcentral foramen; frz, prezygapophyseal articular facet; ftz, postzygapophyseal articular facet; l, lamina; lrb, lower rib-bearers; lva, anterior ventral crest; lvp, posterior ventral crest; n, neurapophysis; urb, upper rib-bearers; CL, centrum length; NAWA, minimal width of neural arch before level of rib-bearers; NAWP, minimal width of neural arch behind level of rib-bearers; LH, laminae height; CTH, cotyle height; CTW, cotyle width; AHV, anterior height of vertebra; PHV, posterior height of vertebra; PR-PR, distance between lateral margins of prezygapophyseal articular facets; PO-PO, distance between lateral margins of postzygapophyseal articular facets; PR-PO, distance between anterior margin of prezygapophyseal articular facet and posterior margin of postzygapophyseal articular facet; ANG, angle between longitudinal axis of centrum and rib bearer.

basic, we applied the terminology of Rage and Hossini (2000) with minor additions from Szyndlar (1984). For detailed morphometric measurements (Fig. 1), we used, as a minimum, four vertebrae for each specimen studied: the sacral, the first trunk, the second trunk, and the largest trunk vertebrae. In some cases, we additionally measured the middle and/or last trunk vertebrae as well. The variation along axial column was studied visually. The statistical analysis was performed with use of the computer program Statistica 6.0. The significance of differences between means was estimated by the Kolmogorov–Smirnov test.

RESULTS AND DISCUSSION

Individual Variation Along Axial Column

In various groups of urodelans, the variation along axial column was studied by Averianov and Tjutkova (1995), Estes (1982), Haller-Probst and Schleich (1994) and Worthington and Wake (1972). According to these data, the vertebral length increases from the anterior to the largest trunk vertebrae, and, then, decreases from the largest trunk vertebra to the sacrum. Among representatives of various urodelan groups, which were studied by Worthington and Wake (1972), the variation of vertebral parameters in the genus *Notophtalmus* Rafinesque, 1820 was most similar to those of the Salamandridae studied by us. The vertebral length increases in the first five trunk vertebrae, remains approximately the same in the middle part of the trunk, and, then, decreases in the one or two posterior trunk vertebrae and the sacrum. In contrast to the length of vertebrae, the height of the anterior part of the neural arch decreases from the first trunk vertebra to the largest one, and then was approximately constant. The decrease of the posterior height of the neural arch is usually observed from the first trunk vertebra to the sacrum. The height of the laminae changed insignificantly. In the first trunk vertebrae, the relations between values of PR-PR and PO-PO were at random. In the next vertebrae, PR-PR was less than PO-PO, if their lengths increased across the axial column, and PR-PR

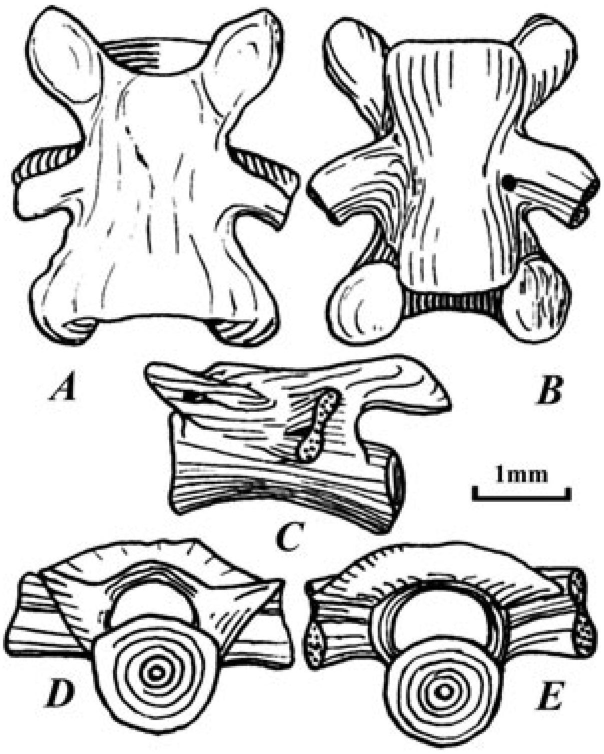

Fig. 2. Trunk vertebra of *Onychodactylus fischeri*. Here and in Figs. 3 – 13: *A*, dorsal view; *B*, ventral view; *C*, left lateral view; *D*, anterior view; *E*, posterior view.

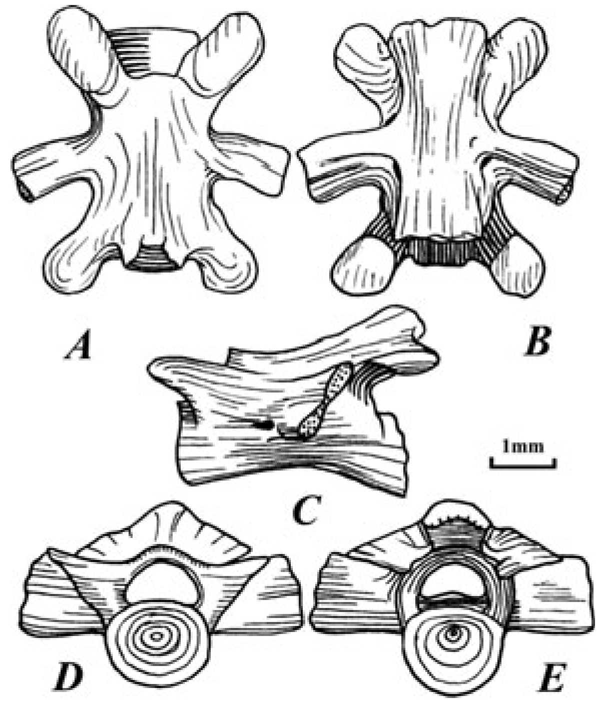

Fig. 3. Trunk vertebra of *Ranodon sibiricus*.

was higher than PO-PO, if the lengths decreased. NAWA was usually less than NAWP, except for the first trunk vertebra, where this ratio was inversed. The index LH/PO-PO decreased from the first trunk vertebra to the sacrum. The indices PO-PO/PR-PO, AHV/PR-PO, and PHV/PR-PO decreased from the first trunk vertebra to the largest one, and, then, increased from the largest trunk vertebra to the sacrum.

DESCRIPTIONS OF VERTEBRAE

Family Hynobiidae
(Figs. 2 – 4)

Number of trunk vertebrae 14 – 21. Vertebrae amphicoelous: both anterior and posterior articular surfaces of centrum concave. Articular surfaces of centrum circular (CTW/CTH = 1) or slightly oval. Subcentral foramina usually lacking. Laminae low (LH/PHV = 0.30 – 0.39) and sufficiently flat (LH/PO-PO = 0.21 – 0.39). Neurapophysis lacking or weakly developed. Posterior margin of neural arch without medial notch (view from above). Lower and upper rib-bearers are connected along their entire lengths. Zygapophyseal and ventral crests lacking. Foramen near bases of lower rib-bearers usually present.

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

Number of trunk vertebrae 19 – 21. CL up to 2.7 mm, PR-PO up to 3.6 mm. Anterior margin of neural arch concave or straight (view from above), at level of the posterior third or, rarely, middle part of prezygapophyseal articular facets. Posterior margin of neural arch straight or salient (view from above), at level before the posterior edges of postzygapophyseal articular facets. Subcentral foramina and neurapophysis lacking.

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

Number of trunk vertebrae 14 – 17. CL up to 3.7 mm (3.8 mm after Averianov and Tjutkova, 1995), PR-PO up to 4.8 mm. Anterior margin of neural arch concave, straight or salient, at level of the posterior third or fourth of prezygapophyseal articular facets. Posterior margin of neural arch concave or salient, much before level of the posterior edges of postzygapophyseal articular facets. Subcentral foramen lacking. Neurapophysis low, but clearly distinguishable, sometimes, moderate.

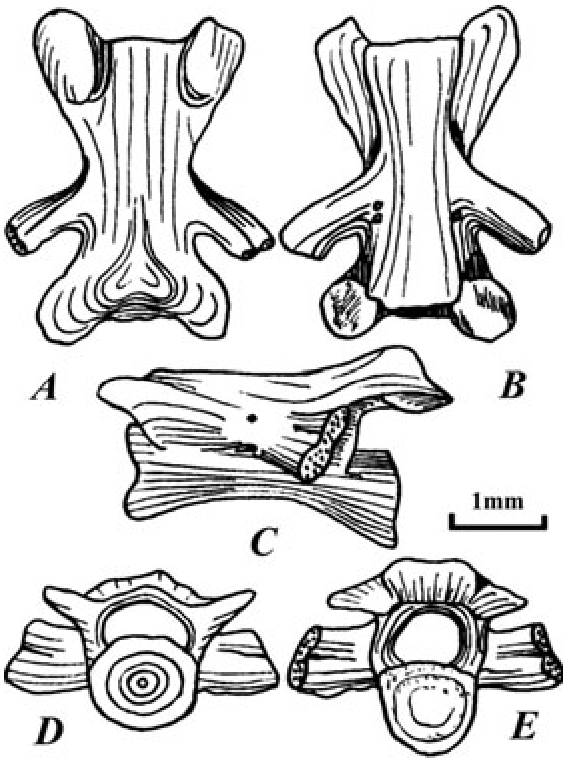

Fig. 4. Trunk vertebra (anterior) of *Salamandrella keyserlingii*.

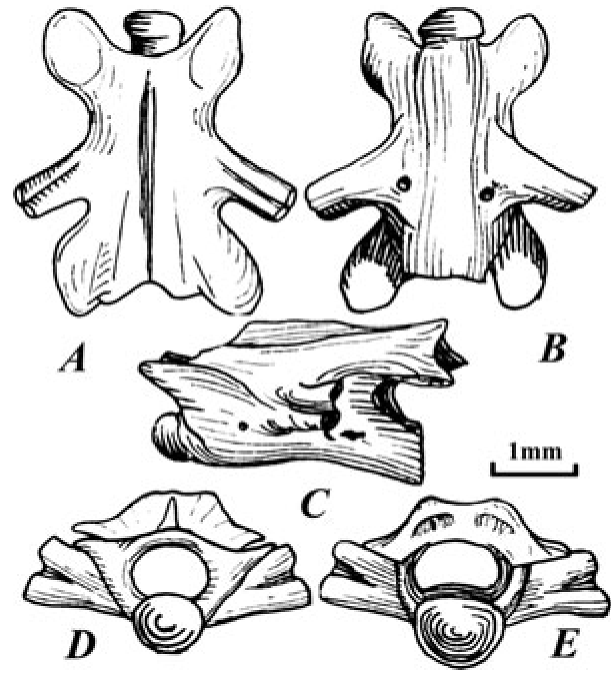

Fig. 5. Trunk vertebra of *Mertensiella caucasica*.

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

Number of trunk vertebrae 16 – 19[5]. CL up to 3.2 mm, PR-PO up to 4.0 mm. Anterior margin of neural arch concave, at level of the middle part of prezygapophyseal articular facets. In anterior trunk vertebrae, posterior margin of neural arch slightly salient, before level of the posterior edges of postzygapophyseal articular facets. In posterior trunk vertebrae and sacrum, posterior margin of neural arch deeply concave, after level of the posterior edges of postzygapophyseal articular facets. Subcentral foramen lacking. Neurapophysis low or lacking.

Family Salamandridae
(Figs. 5 – 13)

Number of trunk vertebrae 11 – 18. Vertebrae opisthocoelous (anterior articular surface of centrum convex and posterior one concave) or false opisthocoelous (a convex calcified cartilage on anterior articular surface of centrum). Subcentral foramina usually present. Articular surfaces of centra horizontally-oval (CTW/CTH < 1), sometimes round (CTW/CTH = 1). Laminae and neurapophysis heights vary significantly (LH = 0.5 – 1.9). Posterior margin of neural arch with medial notch. The zygapophyseal and ventral crests usually well developed, but sometimes lacking. Foramen near bases of lower rib-bearers usually present or replaced by several smaller foramina.

Genus *Mertensiella* Wolterstorff, 1925
Mertensiella caucasica (Fig. 5)

Number of trunk vertebrae 16. Vertebrae opisthocoelous. CL up to 4.0 mm, PR-PO up to 4.4 mm. Anterior surface of condylus uneven, neck of condylus well developed. Subcentral foramen present only in vertebrae with well developed posterior ventral crests. Neural arch low and, in the posterior part, flat, with salient laminae. Anterior margin of neural arch deeply concave, its bottom at level of the middle part of prezygapophyseal articular facets. Posterior margin of neural arch before level of the posterior edges of postzygapophyseal articular facets. Neurapophysis high, with slightly concave (sometimes, flat) and horizontal dorsal margin. Anterior margin of neurapophysis abrupt, at level of the posterior edges of prezygapophyseal articular facets. Posterior margin of neurapophysis at level of medial notch. Zygapophyseal crests weakly developed. Ventral crest varies from lacking to very broad (with large subcentral foramen).

[5] Number of trunk vertebrae in *Salamandrella schrenckii* is equal to 14 – 16 (Litvinchuk and Borkin, 2003).

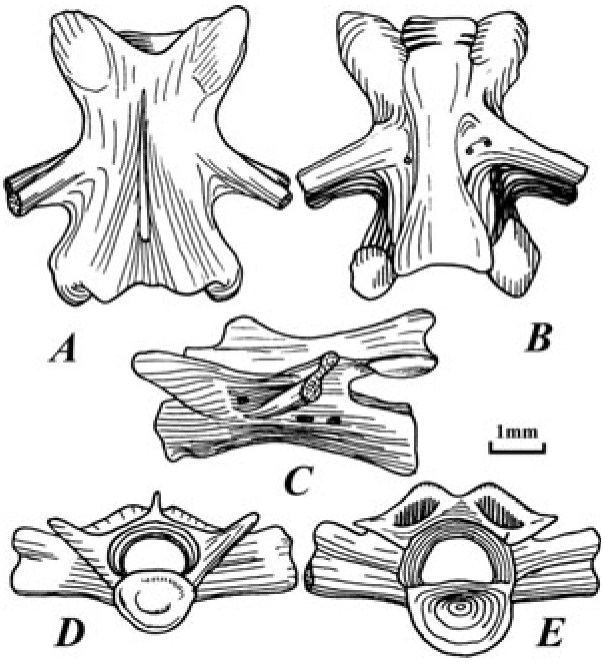

Fig. 6. Trunk vertebra of *Salamandra salamandra*.

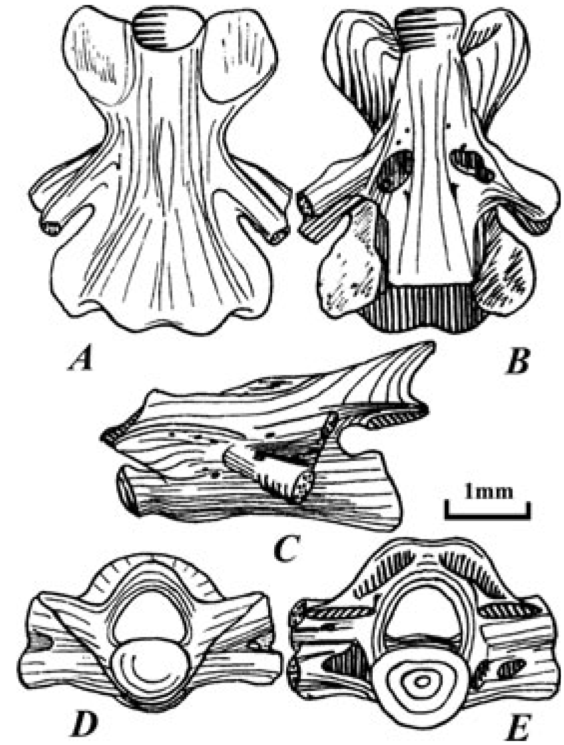

Fig. 7. Trunk vertebra of *Triturus cristatus*.

Genus *Salamandra* Laurenti, 1768
Salamandra salamandra (Fig. 6)

Number of trunk vertebrae 13 – 15. Vertebrae opisthocoelous. CL up to 5.3 mm (6.8 mm after Hodrova, 1984), PR-PO up to 6.0 mm (6.7 mm after Haller-Probst and Schleich, 1994). Anterior surface of condylus flat and anteroventrally inclined. As a rule, neck well developed, because condylus broader than rest of centrum. Subcentral foramen vary from large to almost lacking. Neural arch low, with salient laminae. Anterior margin of neural arch deeply concave, at level of the middle part of prezygapophyseal articular facets. Posterior margin of neural arch before level of the posterior edges of postzygapophyseal articular facets; sometimes, at the same level or behind these facets. Neurapophysis low or moderately high, originates behind level of the anterior margin of neural arch, well developed in the middle part of neural arch only. Dorsal margin of neurapophysis concave. Zygapophyseal crests distinctly developed. Ventral crests near bases of lower rib-bearers or along their anterior margins weakly developed.

Genus *Triturus*
(Figs. 7 – 9)

Number of trunk vertebrae 11 – 18. Vertebrae opisthocoelous. Anterior surface of condylus flat, sometimes inclined anteroventrally, neck weakly or well developed. Subcentral foramen very large or replaced by several smaller foramina. Foramen near bases of rib-bearers usually present. Neural arch low. Laminae in the posterior part of neural arch salient. Short medial notch present on the posterior margin of neural arch. Anterior margin of neural arch concave or straight, its bottom at level of the anterior third or half of prezygapophyseal articular facets. Posterior edge of neural arch at level of the posterior edges of postzygapophyseal articular facets; sometimes, behind or before these facets. The neurapophysis height varies highly.

Triturus cristatus
(Fig. 7)

Number of trunk vertebrae 14 – 16. CL up to 3.7 mm (4.6 mm for Teege, 1957), PR-PO up to 4.2 mm (4.6 mm for Haller-Probst and Schleich, 1994). Neurapophysis usually low, well developed in the middle part of neural arch only, sometimes moderately developed (in this case, reach medial notch). Posterior ventral crests distinctly developed. Anterior ventral and zygapophyseal crests lacking or weakly developed.

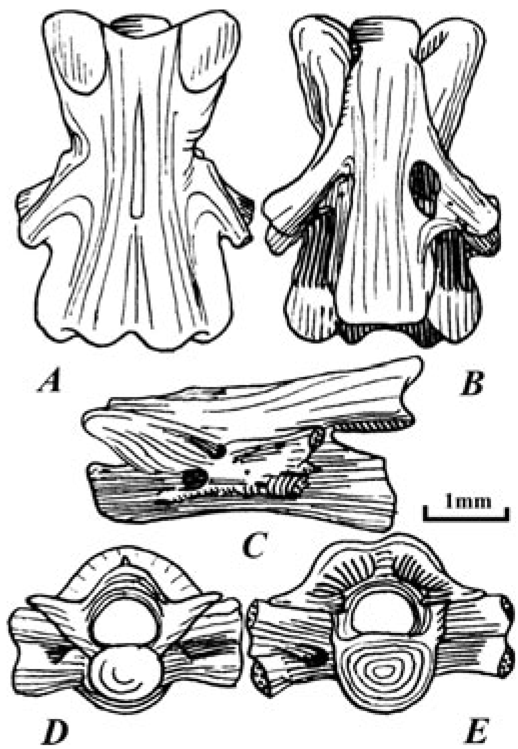

Fig. 8. Trunk vertebra of *Triturus dobrogicus*.

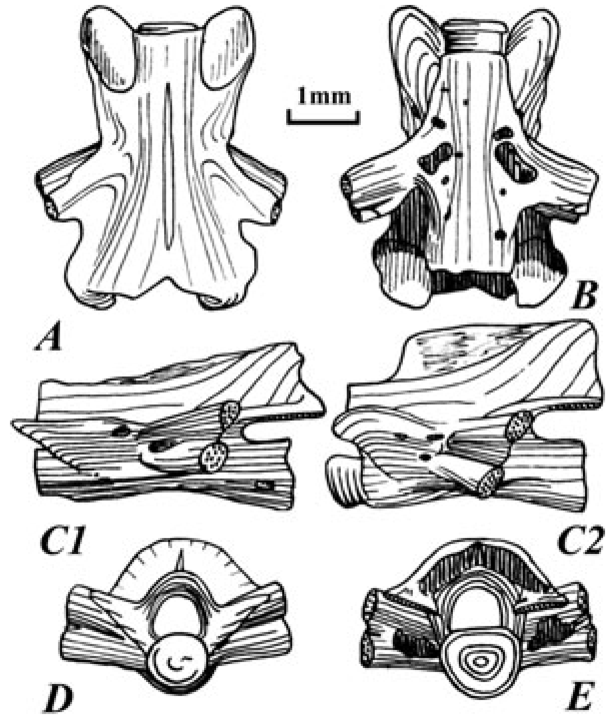

Fig. 9. Trunk vertebra of *Triturus karelinii*. *C1*, the Crimea and the Balkans; *C2*, Georgia and Dagestan.

Triturus dobrogicus (Fig. 8)

Number of trunk vertebrae 14 – 18[6]. CL up to 3.9 mm, PR-PO up to 4.3 mm. Neurapophysis usually low, well developed in the middle part of neural arch only; sometimes moderately developed (in the last case, reach medial notch). Posterior ventral crests always well developed. Anterior ventral and zygapophyseal crests lacking or weakly developed.

Triturus karelinii (Fig. 9)

Number of trunk vertebrae 11 – 15. CL up to 4.4 mm, PR-PO up to 5.2 mm. Anterior margin of neurapophysis at level of the posterior edges of prezygapophyses, posterior margin can reach medial notch. Neurapophysis low or high, with inclined anterior margin. Ventral and zygapophyseal crests weakly developed.

Genus *Mesotriton*
Mesotriton alpestris (Fig. 10)

Number of trunk vertebrae 12 – 14. Vertebrae opisthocoelous. CL up to 3.1 mm (3.5 mm after Teege,

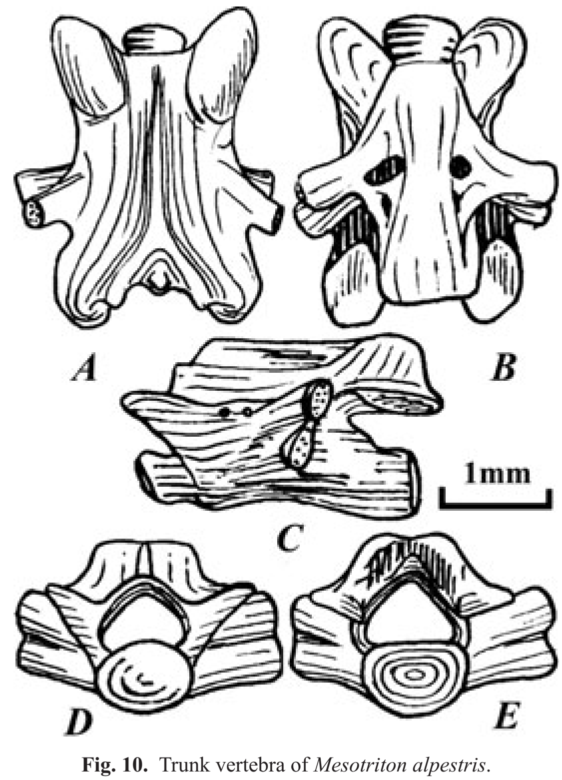

Fig. 10. Trunk vertebra of *Mesotriton alpestris*.

6 Two subspecies of *Triturus dobrogicus* are characterized by different modal number of trunk vertebrae (Litvinchuk and Borkin, 2000).

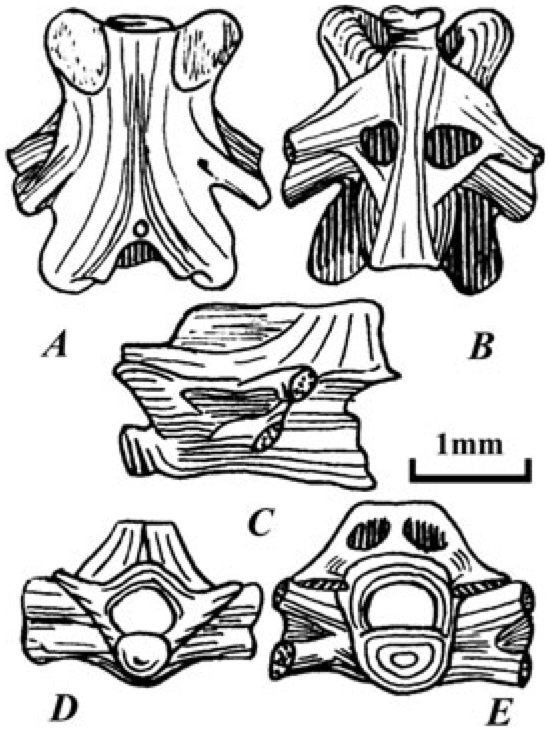

Fig. 11. Trunk vertebra of *Lissotriton montandoni*.

1957), PR-PO up to 3.6 mm (3.7 mm after Haller-Probst and Schleich, 1994). Condylus with smoothly rounded margins and flat anterior surface, strongly anteroventrally inclined, neck well developed. Subcentral foramen large or replaced by several smaller foramina. Neural arch high. Laminae in the posterior part of neural arch flat or concave. Anterior margin of neural arch straight, at level of the middle part (sometimes, anterior third) of prezygapophyseal articular facets. Posterior margin of neural arch before level of the posterior edges of postzygapophyseal articular facets; sometimes at level of the posterior edges of these facets. Medial notch in the posterior margin of neural arch broad and deep. Neurapophysis very high, with horizontal dorsal margin; reach always medial notch. Anterior margin of neurapophysis sloping, near anterior part of neural arch. Zygapophyseal and ventral crests well developed, except of anterior one or two trunk vertebrae, where crests weaker developed.

Genus *Lissotriton*
(Figs. 11 – 12)

Number of trunk vertebrae 11 – 14. Vertebrae opisthocoelous. Condylus with flat anterior surface, inclined anteroventrally, neck well or weakly developed. Subcentral foramen very large; sometimes, replaced by several smaller foramina. Neural arch high. Laminae in posterior part of neural arch flat or concave. Posterior margin of neural arch with well developed medial notch. Neurapophysis very high, with horizontal dorsal margin; reach always medial notch. Zygapophyseal and ventral crests well developed, except in anterior one or two trunk vertebrae, in which crests are weaker.

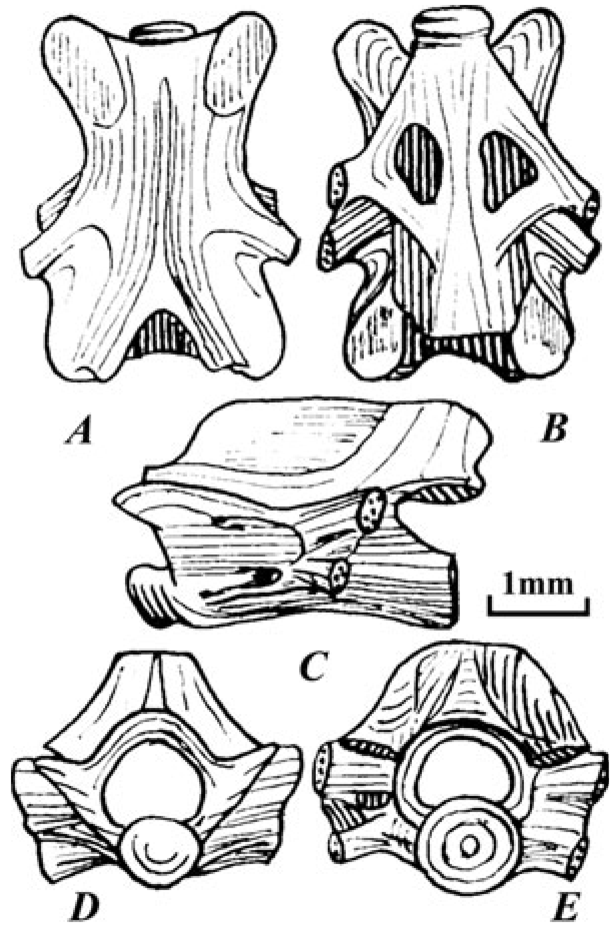

Fig. 12. Trunk vertebra of *Lissotriton vulgaris*.

Lissotriton montandoni (Fig. 11)

Number of trunk vertebrae 11 – 13. CL up to 3.4 mm, PR-PO up to 3.8 mm. Anterior margin of neural arch straight, at level of the anterior fourth of prezygapophyseal articular facets. Posterior margin of neural arch before level of the posterior edges of postzygapophyseal articular facets; sometimes, behind or at level of the posterior edges of these facets. Anterior margin of neurapophysis sloping or vertical, near or in anterior part of neural arch. Zygapophyseal and ventral crests well developed.

Lissotriton vulgaris (Fig. 12)

Number of trunk vertebrae 11 – 14[7]. CL up to 2.5 mm (2.6 mm after Haller-Probst and Schleich, 1994; Teege, 1957), PR-PO up to 2.9 mm. Anterior margin of neural arch straight, at level of the anterior fourth of prezygapophyseal articular facets. Posterior margin of neural arch before level of the posterior edges of postzygapophyseal articular facets; sometimes, behind or at level of the posterior edges of these facets. Anterior margin of neurapophysis sloping or rounded, near anterior part of neural arch. Zygapophyseal and ventral crests well developed.

Genus *Ommatotriton*
Ommatotriton ophryticus (Fig. 13)

Number of trunk vertebrae 11 – 14[8]. Vertebrae opisthocoelous. CL up to 4.4 mm, PR-PO up to 5.0 mm. Anterior surface of condylus flat. Condylus anteroventrally inclined, neck well developed. Subcentral foramen very large or replaced by several small foramina. Neural arch high. Laminae in the posterior part of neural arch flat or even concave. Medial notch in the posterior margin of neural arch deep. Anterior margin of neural arch straight, slightly salient or concave, at level of the anterior forth or middle part of prezygapophyseal articular facets. Neurapophysis very high, with horizontal dorsal margin; reach always medial notch. Anterior margin of neurapophysis vertical or abruptly sloping, near anterior part of neural arch. Posterior margin of neural arch before, behind or at the same level with the posterior edges of postzygapophyseal articular facets. Zygapophyseal and ventral crests well developed, except in anterior one or two trunk vertebrae, in which crests are weaker.

Geographic Variation in *Triturus karelinii*

We found pronounced geographic variation in *Triturus karelinii*. Specimens from the western part of the species range, including both subspecies *T. k. karelinii* (the Crimea) and *T. k. arntzeni* (the Balkans), have low neurapophyses (Fig. 9, *C1*). In contrast, *T. k. karelinii* from the eastern part of range (eastern Georgia and Dagestan) are characterized by high ones (Fig. 9, *C2*).

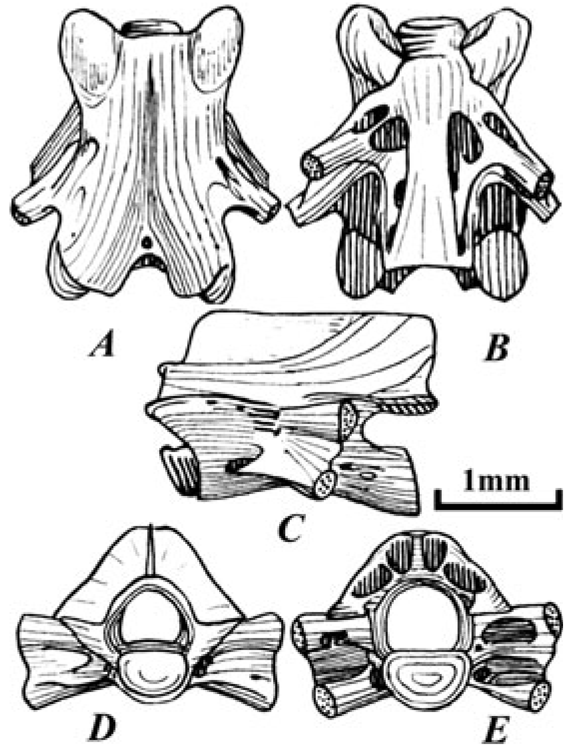

Fig. 13. Trunk vertebra of *Ommatotriton ophryticus*.

Previously, genome size differences were found between samples from the Crimea and east part of the Caucasus as well (Litvinchuk et al., 2005a).

Traditionally, vertebrae of fossil newts of the genus *Triturus* with low neurapophyses were attributed to the species of *T. cristatus* complex (i.e., *T. carnifex*, *T. cristatus*, *T. dobrogicus*, and *T. karelinii*), whereas vertebrae with high ones were referred to *T. marmoratus* complex (i.e., *T. marmoratus* and *T. pygmaeus*) (Auge and Rage, 1995; Estes, 1981; Estes and Darevsky, 1977; Estes and Hoffstetter, 1976; Hodrova, 1984; Rage and Bailon, 2005). Our data are not consistent with the previous use of this character.

Interspecies Differences

As mentioned above, the families Hynobiidae and Salamandridae can be distinguished by the nature of the intervertebral articulations (amphicoelous or opisthocoelous, respectively; Table 2).

Among the Hynobiidae, *Ranodon sibiricus* could be distinguished by visible neurapophyses and largest values for most of metrical characters (Table 3). In this species, the centrum lengths vary from 2.9 mm in the first trunk vertebra to 3.8 mm in the last one (Averianov and

[7] According to Pellarini and Papini (2000), the modal number of trunk vertebrae in *Lissotriton v. vulgaris* and *L. v. meridionalis* is different (13 and 12, respectively). However, the modal number in *L. v. vulgaris* (“*Triton taeniatus*”) from Latvia is 12 (range 11 – 13; Gerecht, 1929). According to our data, *L. v. lantzi* ($n = 3$) and *L. v. graecus* ($n = 1$) has 13 trunk vertebrae and *L. v. schmidtlerorum* ($n = 1$) has 12 ones.

[8] Two subspecies of *Ommatotriton ophryticus* are characterized by different modal number of trunk vertebrae (Litvinchuk et al., 2005b).

Tjutkova, 1995; our data). However, sometimes, the minimum length of anterior trunk vertebrae of this species was similar to length of the largest posterior trunk vertebrae of *Salamandrella keyserlingii* (Table 3). Vertebrae of *Onychodactylus fischeri* and *Salamandrella keyserlingii* were distinguished by width of the posterior part of the centrum only. This part of vertebrae in *Salamandrella keyserlingii* is usually narrower than in *Onychodactylus fischeri*. This peculiarity is reflected on values of three metrical characters (NAWP, CTH, and CTW) and the index CTW/CL (Table 3).

In the Salamandridae, differences between salamanders and newts are most obvious. According to our data, vertebrae of salamanders differ from newts by form of the condylus, form and position of the anterior and posterior edges of the neural arch and the neurapophysis.

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

Taxon	VE	PMNA	FOS	AMNA	ASCD	NA	N	CZ	LV
Onychodactylus fischeri	1	2	1	1, 2	1	1	1	1	1
Ranodon sibiricus	1	2	1	1, 2, 3	1	1	2	1	1
Salamandrella keyserlingii	1	2	1	1	1	1	1, 2	1	1
Lissotriton montandoni	2	1	3	2	1	2	3	3	3
Lissotriton vulgaris	2	1	3	2	1	2	3	3	3
Mesotriton alpestris	2	1	3	2	1	2	3	3	3
Mertensiella caucasica	2	1	1, 2	1	2	1	2	2	1, 2, 3
Ommatotriton ophryticus	2	1	3	2	1	2	3	3	3
Salamandra salamandra	2	1	1, 2, 3	1	1	1	2, 3	3	2
Triturus cristatus	2	1	3	1	1	1	2	1, 2	1, 2, 3
Triturus dobrogicus	2	1	3	1	1	1	2	1, 2	1, 2, 3
Triturus karelinii	2	1	3	1	1	1	2, 3	2	2

Note. VE, vertebrae: amphicoelous (1), opisthocoelous (2); PMNA, medial notch on posterior margin of neural arch: well developed (1), lacking (2); FOS – subcentral foramen: lacking (1), small (2), large or replaced by several smaller foramina (3); AMNA, anterior margin of neural arch: concave (1), straight (2), salient (3); ASCD, anterior surface of the condylus: flat (1), uneven (2); NA, neural arch: low (1), high (2); N, neurapophysis: lacking (1), low (2), high (3); CZ, zygapophyseal crests: lacking (1), weakly developed (2), broad (3); LV, ventral crests: lacking (1), weakly developed (2), broad (3).

TABLE 3. Variation of Morphometric Characters of Trunk and Sacral Vertebrae for Three Species of the family Hynobiidae

Character	*Onychodactylus fischeri* [1/3]	*Ranodon sibiricus* [1/4]	*Salamandrella keyserlingii* [3/12]
CL	2.3 ± 0.3 (2.1 – 2.7)	3.5 ± 0.2 (3.3 – 3.7)	2.5 ± 0.3 (2.0 – 3.2)
NAWA	1.7 ± 0.0 (1.7 – 1.7)	2.1 ± 0.1 (2.0 – 2.2)	1.5 ± 0.2 (1.2 – 1.7)
NAWP	1.7 ± 0.2 (1.6 – 1.9)	2.0 ± 0.1 (1.9 – 2.0)	1.4 ± 0.1 (1.1 – 1.6)
LH	0.8 ± 0.0 (0.8 – 0.8)	1.2 ± 0.1 (1.1 – 1.2)	0.7 ± 0.1 (0.6 – 0.8)
CTH	1.2 ± 0.1 (1.1 – 1.2)	1.4 ± 0.1 (1.2 – 1.4)	1.0 ± 0.1 (0.8 – 1.1)
CTW	1.2 ± 0.1 (1.1 – 1.3)	1.5 ± 0.1 (1.4 – 1.6)	0.9 ± 0.1 (0.8 – 1.0)
AHV	2.1 ± 0.3 (1.8 – 2.4)	2.3 ± 0.1 (2.2 – 2.4)	1.7 ± 0.2 (1.5 – 2.1)
PHV	2.4 ± 0.1 (2.3 – 2.5)	3.1 ± 0.1 (3.1 – 3.2)	2.2 ± 0.1 (2.0 – 2.4)
PR-PR	2.4 ± 0.4 (2.1 – 2.9)	3.5 ± 0.1 (3.3 – 3.6)	2.1 ± 0.3 (1.7 – 2.6)
PO-PO	2.5 ± 0.4 (2.2 – 2.9)	3.4 ± 0.2 (3.2 – 3.6)	2.0 ± 0.2 (1.7 – 2.3)
PR-PO	3.1 ± 0.5 (2.6 – 3.6)	4.5 ± 0.3 (4.1 – 4.8)	3.1 ± 0.5 (2.3 – 4.0)
ANG	54 ± 3 (50 – 56)	70 ± 7 (62 – 80)	58 ± 7 (44 – 68)
LH/PHV	0.33 ± 0.02 (0.32 – 0.35)	0.37 ± 0.02 (0.35 – 0.39)	0.33 ± 0.02 (0.30 – 0.36)
LH/PO-PO	0.33 ± 0.05 (0.28 – 0.36)	0.34 ± 0.01 (0.33 – 0.34)	0.36 ± 0.04 (0.30 – 0.41)
PO-PO/PR-PO	0.81 ± 0.04 (0.77 – 0.85)	0.75 ± 0.02 (0.73 – 0.78)	0.66 ± 0.11 (0.51 – 0.84)
AHV/PR-PO	0.70 ± 0.21 (0.50 – 0.92)	0.51 ± 0.05 (0.48 – 0.59)	0.58 ± 0.15 (0.43 – 0.91)
PHV/PR-PO	0.81 ± 0.16 (0.64 – 0.96)	0.69 ± 0.05 (0.65 – 0.76)	0.72 ± 0.14 (0.57 – 0.96)
CTW/CL	0.52 ± 0.03 (0.48 – 0.55)	0.43 ± 0.01 (0.42 – 0.44)	0.38 ± 0.05 (0.31 – 0.45)

Note. All values are mean ± standard deviation, and range (in round brackets); in square brackets, the amount of specimens/vertebrae studied. The first eleven characters are given in millimeters, and ANG is in degrees.

TABLE 4. Differences between adults of nine salamandrid species

Taxa	Character																
	CL	NAWA	NAWP	LH	CTH	CTW	AHV	PHV	PR-PR	PO-PO	PR-PO	LH/PHV	LH/PO-PO	PO-PO/PR-PO	AHV/PR-PO	PHV/PR-PO	CTW/CL
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. "–", the significance level which more than 0.05; "+", $p < 0.05$; "++", $p < 0.01$; "+++", $p < 0.001$.
M, *Mertensiella caucasica*; S, is *Salamandra salamandra*; O, *Ommatotriton ophryticus*; c, *Triturus cristatus*; d, *Triturus dobrogicus*; k, *Triturus karelinii*; m, *Lissotriton montandoni*; v, *Lissotriton vulgaris*; a, *Mesotriton alpestris*.

TABLE 5. Variation of Morphometric Characters of Trunk and Sacral Vertebrae for Nine Species of the Family Salamandridae

No.	Species	Character								
		CL	NAWA	NAWP	LH	CTH	CTW	AHV	PHV	PR-PR
1	*Mertensiella caucasica* [6/32]	3.5 ± 0.3 (2.8 – 4.0)	1.6 ± 0.2 (1.3 – 2.0)	1.7 ± 0.2 (1.4 – 2.1)	0.7 ± 0.1 (0.5 – 0.9)	0.8 ± 0.1 (0.8 – 0.9)	1.1 ± 0.1 (0.9 – 1.2)	1.5 ± 0.2 (1.3 – 1.9)	2.1 ± 0.1 (1.7 – 2.3)	2.5 ± 0.2 (2.1 – 2.9)
2	*Salamandra salamandra* [4/20]	4.4 ± 0.6 (3.5 – 5.3)	2.7 ± 0.3 (2.3 – 3.4)	2.7 ± 0.3 (2.3 – 3.3)	1.3 ± 0.2 (0.8 – 1.5)	1.3 ± 0.2 (1.0 – 1.6)	1.9 ± 0.2 (1.7 – 2.3)	2.4 ± 0.4 (1.9 – 3.3)	3.2 ± 0.4 (2.5 – 3.8)	3.7 ± 0.4 (3.1 – 4.4)
3	*Omatotriton ophryticus* [14/48]	3.5 ± 0.4 (2.9 – 4.4)	1.9 ± 0.3 (1.4 – 2.4)	2.2 ± 0.3 (1.6 – 2.8)	1.4 ± 0.3 (1.0 – 1.9)	1.0 ± 0.2 (0.7 – 1.4)	1.4 ± 0.2 (1.0 – 1.9)	1.9 ± 0.3 (1.4 – 2.5)	2.9 ± 0.5 (2.1 – 3.7)	2.8 ± 0.4 (2.0 – 3.5)
4	*Triturus cristatus* [6/32]	3.2 ± 0.4 (2.4 – 3.7)	1.5 ± 0.2 (1.0 – 1.9)	1.8 ± 0.2 (1.3 – 2.2)	1.0 ± 0.1 (0.7 – 1.2)	0.9 ± 0.1 (0.8 – 1.1)	1.1 ± 0.1 (0.9 – 1.3)	1.7 ± 0.2 (1.4 – 2.2)	2.3 ± 0.2 (1.8 – 2.8)	2.5 ± 0.3 (2.0 – 3.0)
5	*Triturus dobrogicus* [4/21]	3.2 ± 0.4 (2.5 – 3.9)	1.4 ± 0.2 (1.2 – 1.9)	1.7 ± 0.2 (1.3 – 2.2)	0.8 ± 0.1 (0.7 – 0.9)	0.9 ± 0.1 (0.8 – 1.0)	1.1 ± 0.1 (1.0 – 1.3)	1.6 ± 0.2 (1.4 – 2.0)	2.1 ± 0.2 (1.8 – 2.5)	2.2 ± 0.2 (1.8 – 2.5)
6	*Triturus karelinii** [7/40]	3.8 ± 0.3 (3.1 – 4.4)	2.2 ± 0.2 (1.9 – 2.6)	2.4 ± 0.2 (1.9 – 3.2)	1.3 ± 0.2 (1.1 – 1.8)	1.1 ± 0.1 (0.9 – 1.3)	1.4 ± 0.1 (1.2 – 1.7)	2.0 ± 0.2 (1.7 – 2.4)	2.8 ± 0.3 (2.1 – 3.7)	3.0 ± 0.2 (2.3 – 3.4)
7	*Lissotriton montandoni* [5/20]	2.5 ± 0.4 (1.8 – 3.4)	1.5 ± 0.2 (1.2 – 1.8)	1.6 ± 0.2 (1.4 – 2.0)	0.8 ± 0.1 (0.6 – 1.0)	0.8 ± 0.1 (0.6 – 0.9)	0.9 ± 0.1 (0.7 – 1.1)	1.4 ± 0.2 (1.1 – 1.8)	2.0 ± 0.2 (1.7 – 2.3)	1.9 ± 0.3 (1.5 – 2.4)
8	*Lissotriton vulgaris* [12/42]	2.1 ± 0.2 (1.7 – 2.5)	1.2 ± 0.1 (0.9 – 1.4)	1.3 ± 0.1 (1.0 – 1.6)	0.7 ± 0.1 (0.5 – 0.8)	0.6 ± 0.0 (0.6 – 0.8)	0.7 ± 0.0 (0.6 – 0.8)	1.2 ± 0.1 (0.9 – 1.5)	1.6 ± 0.2 (1.3 – 2.0)	1.5 ± 0.1 (1.3 – 1.8)
9	*Mesotriton alpestris* [3/13]	2.7 ± 0.2 (2.4 – 3.1)	1.5 ± 0.1 (1.4 – 1.7)	1.5 ± 0.2 (1.3 – 1.8)	0.8 ± 0.1 (0.6 – 0.9)	0.7 ± 0.1 (0.6 – 0.8)	0.9 ± 0.1 (0.8 – 1.0)	1.5 ± 0.2 (1.3 – 1.8)	2.0 ± 0.2 (1.7 – 2.3)	2.0 ± 0.2 (1.7 – 2.4)

Note. All values are mean ± standard deviation, and range (in round brackets); in square brackets, the amount of specimens/vertebrae studied. The first eleven characters are given in millimeters, and ANG is in degrees. * The Crimea and the Balkans.

Moreover, vertebrae of salamanders have relatively flattened and lower neural arches (Estes et al., 1967; Sanchiz and Młynarski, 1979). *Mertensiella caucasica* differs from other salamandrids by values of the indices LH/PHV, LH/PO-PO, AHV/PR-PO, and PHV/PR-PO (Tables 4 and 5). *Salamandra salamandra* is characterized by the largest vertebrae (Table 5) and differs from other Salamandridae by the indices AHV/PR-PO and CTW/CL (Table 5).

Two groups could be recognized among newts, with large and small vertebrae. The first one includes representatives of the genera *Ommatotriton* and *Triturus*; the second one consists of *Lissotriton* and *Mesotriton* (Table 5). This division correlates with total length of adults and phylogenetic relationships (Weisrock et al., 2006). The groups differed from each other by values of CTH, CTW, and PR-PO as well (Table 4). Among these newts with large vertebrae, *Ommatotriton ophryticus* differs most obviously by high neural arch and highest values of the index LH/PO-PO (Tables 4 and 5). In contrast to other newts, members of the genus *Triturus* have low neural arches with salient laminae. Among them, *Triturus karelinii* has the largest vertebrae, the most developed neurapophysis, and the broader ventral and zygapophyseal crests. Vertebrae of *Triturus cristatus* and *T. dobrogicus* are very similar and differ from each other by the indices LH/PHV and LH/PO-PO only (Table 4). Among newts with small vertebrae, *Mesotriton alpestris* differs from the species of the genus *Lissotriton* by deeper position of the anterior edge of neural arch. Two species of last genus are very similar. *Lissotriton montandoni* differs from *L. vulgaris* by the indexes PO-PO/PR-PO and CTW/CL only (Tables 4 – 5).

Acknowledgments. We wish to thank J. C. Rage (Paris), L. J. Borkin (St. Petersburg), P. P. Skuchas (St. Petersburg) and I. G. Danilov (St. Petersburg) for helpful comments, V. F. Orlova (Moscow) and E. A. Dunaev (Moscow) kindly offered the museum collections available for study. The study was partially supported by the grants of the Russian Foundation for Basic Research (No. 07-04-00694) and the President of Russian Federation (NSh.-4212.2006.4).

REFERENCES

Antipenkova T. P. (1994), "Axial skeleton," in: Vorobyeva E. I. (ed.), *The Siberian Newt* (Salamandrella keyserlingii *Dybowski*, *1870*). *Zoogeography*, *Systematics*, *Morphology*, Nauka, Moscow, pp. 153 – 158 [in Russian].

Averianov A. O. and Tjutkova K. A. (1995), "*Ranodon* cf. *sibiricus* (Amphibia, Caudata) from the Upper Pliocene of Southern Kazakhstan: the first fossil record of the family Hynobiidae," *Paläont. Z.*, **69**(1/2), 257 – 264.

Augé M. and Rage J.-C. (1995), "Le garouillas et les sites contemporains (Oligocene, MP 25) des phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertebres. 2. Amphibiens et squamates," *Paleontographica Abt. A*, **236**(1 – 6), 11 – 32.

Berman D. I., Derenko M. V., Malyarchuk B. A., Grzybowski T., Kryukov A. P., and Miścicka-Śliwka D.

TABLE 5 (continued)

No.	Character								
	PO-PO	PR-PO	ANG	LH/PHV	LH/PO-PO	PO-PO/PR-PO	AHV/PR-PO	PHV/PR-PO	CTW/CL
1	2.5 ± 0.2 (2.0 – 3.0)	3.8 ± 0.4 (3.0 – 4.4)	58 ± 7 (43 – 72)	0.32 ± 0.04 (0.26 – 0.41)	0.27 ± 0.05 (0.19 – 0.36)	0.66 ± 0.06 (0.56 – 0.81)	0.42 ± 0.09 (0.32 – 0.60)	0.56 ± 0.09 (0.46 – 0.74)	0.31 ± 0.02 (0.26 – 0.36)
2	3.6 ± 0.4 (3.1 – 4.2)	5.3 ± 0.5 (4.4 – 6.0)	69 ± 8 (56 – 82)	0.40 ± 0.03 (0.32 – 0.44)	0.35 ± 0.06 (0.25 – 0.47)	0.70 ± 0.06 (0.57 – 0.86)	0.67 ± 0.12 (0.54 – 0.91)	0.61 ± 0.11 (0.45 – 0.86)	0.45 ± 0.07 (0.33 – 0.57)
3	2.7 ± 0.4 (2.0 – 3.4)	3.8 ± 0.5 (3.2 – 5.0)	53 ± 12 (30 – 80)	0.50 ± 0.05 (0.43 – 0.68)	0.53 ± 0.08 (0.38 – 0.68)	0.71 ± 0.06 (0.59 – 0.83)	0.50 ± 0.10 (0.35 – 0.71)	0.75 ± 0.14 (0.53 – 1.06)	0.39 ± 0.04 (0.31 – 0.50)
4	2.4 ± 0.3 (1.9 – 3.0)	3.6 ± 0.4 (2.9 – 4.2)	50 ± 8 (27 – 65)	0.43 ± 0.05 (0.33 – 0.50)	0.42 ± 0.04 (0.33 – 0.50)	0.67 ± 0.05 (0.59 – 0.81)	0.49 ± 0.08 (0.36 – 0.66)	0.65 ± 0.08 (0.56 – 0.86)	0.36 ± 0.03 (0.30 – 0.43)
5	2.2 ± 0.1 (2.0 – 2.5)	3.4 ± 0.4 (2.4 – 4.3)	43 ± 7 (31 – 53)	0.37 ± 0.03 (0.29 – 0.42)	0.35 ± 0.03 (0.30 – 0.43)	0.65 ± 0.05 (0.59 – 0.83)	0.49 ± 0.10 (0.35 – 0.79)	0.62 ± 0.11 (0.49 – 0.92)	0.37 ± 0.04 (0.29 – 0.44)
6	2.9 ± 0.2 (2.4 – 3.4)	4.3 ± 0.4 (3.5 – 5.2)	54 ± 8 (32 – 65)	0.48 ± 0.04 (0.30 – 0.36)	0.46 ± 0.06 (0.38 – 0.59)	0.68 ± 0.05 (0.60 – 0.81)	0.48 ± 0.08 (0.38 – 0.66)	0.66 ± 0.12 (0.46 – 1.00)	0.37 ± 0.03 (0.31 – 0.43)
7	2.0 ± 0.2 (1.5 – 2.5)	2.7 ± 0.4 (2.0 – 3.8)	56 ± 9 (32 – 72)	0.41 ± 0.03 (0.35 – 0.47)	0.42 ± 0.06 (0.32 – 0.53)	0.72 ± 0.05 (0.64 – 0.83)	0.54 ± 0.12 (0.37 – 0.75)	0.74 ± 0.14 (0.56 – 1.05)	0.37 ± 0.04 (0.29 – 0.45)
8	1.5 ± 0.1 (1.2 – 1.7)	2.4 ± 0.2 (1.8 – 2.9)	56 ± 10 (33 – 76)	0.41 ± 0.04 (0.35 – 0.52)	0.44 ± 0.07 (0.29 – 0.62)	0.66 ± 0.04 (0.56 – 0.75)	0.52 ± 0.10 (0.38 – 0.74)	0.70 ± 0.12 (0.52 – 0.97)	0.32 ± 0.03 (0.28 – 0.39)
9	2.0 ± 0.2 (1.7 – 2.3)	3.0 ± 0.3 (2.7 – 3.6)	56 ± 10 (34 – 72)	0.41 ± 0.03 (0.35 – 0.47)	0.41 ± 0.06 (0.30 – 0.50)	0.65 ± 0.03 (0.61 – 0.72)	0.50 ± 0.07 (0.41 – 0.63)	0.65 ± 0.10 (0.55 – 0.78)	0.35 ± 0.02 (0.31 – 0.38)

(2005), "Intraspecific genetic differentiation of Siberian newt (*Salamandrella keyserlingii*, Amphibia, Caudata) and cryptic species *S. schrenkii* from the Russian south-east," *Zool. Zh.*, **84**(11), 1374 – 1388 [in Russian].

Böhme G. (1983), "Skelettreste von Amphibien (Urodela, Salientia) aus dem fossilen Tierbautensystem von Pisede bei Malchin. Teil 1. Taxonomie und Biostrationomie," *Wiss. Zeitsch. Humboldt-Univ. Berlin Math.-Nat. Reihe*, **32**(6), 657 – 670.

Borkin L. J. (1998), "Class Amphibia," in: Ananjeva N. B., Borkin L. J., Darevsky I. S., and Orlov N. L. (eds.), *Amfibii i Reptilii* [*Amphibians and Reptiles*], ABF, Moscow, pp. 19 – 174 [in Russian].

Boulenger G. A. (1896), "On some little-known Batrachians from the Caucasus," *Proc. Zool. Soc. Lond.*, 548 – 555.

Carranza S. and Amat F. (2005), "Taxonomy, biogeography and evolution of *Euproctus* (Amphibia: Salamandridae), with the resurrection of the genus *Calotriton* and the description of a new endemic species from the Iberian Peninsula," *Zool. J. Linn. Soc.*, **145**, 555 – 582.

Cuvier G. (1812), *Recherches sur les Ossemens Fossiles de Quadrupèdes, où l'on rétablit les caractères de plusieurs espèces d'animaux que les révolutions du globe paroissent avoir détruites. Tom Quatrième*, Paris.

Delfino M. and Bailon S. (2000), "Early Pleistocene herpetofauna from Cava Dell'Erba and Cava Pirro (Apulia, southern Italy)," *Herpetol. J.*, **10**, 95 – 110.

Deynegi V. A. (1917), "To the knowledge on structure and development of *Ranodon sibiricus* Kessl.," *Bull. Soc. Imp. Nat. Moscou An. 1916 N. S.*, **30**, 291 – 320 [in Russian].

Duellman W. E. and Trueb L. (1986), *Biology of Amphibians*, The John Hopkins Univ. Press.

Estes R. (1981), *Encyclopedia of Paleoherpetology. Part 2. Gymnophiona*, *Caudata*, Gustav Fisher Verlag, Stuttgart – New York.

Estes R. (1982), "Systematics and paleogeography of some fossil salamanders and frogs," *Natl. Geogr. Soc. Res. Rep.*, **14**, 191 – 210.

Estes R. and Darevsky I. (1977), "Fossil amphibians from the Miocene of the North Caucasus, USSR," *J. Pal. Soc. India*, **20**, 164 – 169.

Estes R., Hecht M., and Hoffstetter R. (1967), "Paleocene amphibians from Cernay, France," *Am. Mus. Novitates*, **2295**, 1 – 25.

Estes R. and Hoffstetter R. (1976), "Les Urodeles du Miocene de La Grive-Saint-Alban (Isere, France)," *Bull. Mus. Nat. Hist. Natur. 3 Ser. 398. Sci. Terre*, **57**, 297 – 343.

Frolich L. M. (1991), "Osteological conservatism and developmental constraint in the polymorphic 'ring species' *Ensatina eschscholtzii* (Amphibia: Plethodontidae)," *Biol. J. Linn. Soc.*, **43**, 81 – 100.

Frost D. R., Grant T., Faivovitch J. N., Bain R. H., Haas A., Haddad C. L. F. B., De Sa R. O., Channing A., Wilkinson M., Donnellan S. C., Raxworthy C. J., Cambell J. A., Blotto B. L., Moler P., Drewes R. C., Nussbaum R. A., Lynch J. D., Green D. M., and Wheeler W. C. (2006), "The amphibian tree of life," *Bull. Am. Mus. Nat. Hist.*, **297**, 1 – 370.

Garsía-París M., Montori A., and Herrero P. (2004), *Amphibia*, *Lissamphibia*, Museo de Ciencias Naturales, CSIC, Madrid.

Gerecht A. (1929), "Über die Richtung der phyletischen Wanderung der Sakralregion bei *Triton cristatus* und *Triton taeniatus*," *Bull. Soc. Biol. Lettonie*, **1**, 9 – 19.

Gonzalez J. E., Arano B., and Sanchiz B. (1986), "Anatomical variation in *Triturus* (Salamandridae)," in: Roček Z. (ed.), *Studies in Herpetology*, Prague, pp. 285 – 288.

Haller-Probst M. and Schleich H. H. (1994), "Vergleichende osteologische Untersuchungen an einigen Urodelen Eurasiens (Amphibia: Urodela, Salamandridae, Proteidae)," in: Schleich H. H. (Hrsg.), *Amphibien und Reptilien aus dem Kaenozoikum Eurasiens. Vol. 173*, Curier Forsch.-Inst. Senckenberg., Frankfurt am Main, pp. 23 – 77.

Hilton W. A. (1948), "The Vertebrae of Salamanders," *J. Ent. Zool.*, **40**(3), 47 – 65.

Hodrova M. (1984), "Salamandridae of the Upper Pliocene Ivanovce locality (Czechoslovakia)," *Acta Univ. Carol. Geol.*, **4**, 331 – 352.

Hodrova M. (1985), "Amphibia of Pliocene and Pleistocene Včelar localities (Slovakia)," *Čas. Miner. Geol.*, **30**(2), 145 – 161.

Holman J. A. (1995), "Additional amphibians from Pleistocene interglacial deposit at Purfleet, Essex," *Br. Herpetol. Soc. Bull.*, **52**, 38 – 39.

Kotsakis T. (1981), "Gli anfibi e i repttili del pleistocene del Lazio (Italia centrale)," *Geologica Rom.*, **20**, 57 – 67.

Litvinchuk S. N. and Borkin L. J. (2000), "Intraspecific taxonomy and nomenclature of the Danube crested newt, *Triturus dobrogicus*," *Amphibia–Reptilia*, **21**, 419 – 430.

Litvinchuk S. N. and Borkin L. J. (2003), "Variation in number of trunk vertebrae and in count of costal grooves in salamanders of the family Hynobiidae," *Contr. Zool.*, **72**, 195 – 209.

Litvinchuk S. N., Borkin L. J., Rosanov J. M., Skorinov D. V., Khalturin M. D., Džukić G., Kalezić M. L., and Mazanaeva L. F. (2005a), "Geographic differentiation in newts (*Triturus*) of eastern Europe: genome size, allozymes, and morphology," in: Ananjeva N. and Tsinenko O. (eds.), *Herpetologia Petropolitana*, St. Petersburg, pp. 57 – 60.

Litvinchuk S. N., Zuiderwijk A., Borkin L. J., and Rosanov J. M. (2005b), "Taxonomic status of *Triturus vittatus* (Amphibia: Salamandridae) in western Turkey: trunk vertebrae count, genome size and allozyme data," *Amphibia–Reptilia*, **26**(3), 305 – 323.

Mertens C. H. (1820), *Anatomiae Batrachiorum Prodromus sistens observationes nonnullas in osteologiam batrachiorum nostratus. Dissertatio inauguralis quam consensu illustris medicorum ordinis Halensis ut summos in medica et chirurgia honores rite adipiscatur die v. Julii ‹I›I›CCCXX publice defendet auctor Carolus Henricus Mertens, Bremanus*, Formis Friderici Grunerti filii, Halae.

Meyer J. D. (1748), *Angenehmer und nützlicher Zeit-Vertreib mit Betrachtung curioser Vorstellungen allerhand kriechender, fliegender und schwimmender, auf dem Land und im Wasser sich befindender und nährender Thiere, sowohl nach ihrer Gestalt und äusserlichen Beschaffenheit als auch nach der accuratest davon verfertigten Structur ihrer Scelete oder Bein-Körper / nebst einer deutlichen so physicalisch und anatomisch besonders aber osteologisch und mechanischen Beschreibung derselben nach der Natur gezeichnet, gemahlet, in Kupfer gestochen und verlegt von Johann Daniel Meyer, Miniatur-Mahler in Nürnberg*, Gedruckt bey Johann Joseph Fleischmann, Nürnberg.

Mivart G. (1870), "On the axial skeleton of the Urodela," *Proc. Zool. Soc. London*, 260 – 278.

Okajima K. (1908), "Die Osteology des *Onychodactylus japonicus*," *Z. Wiss. Zool.*, **91**(3), 351 – 381.

Pellarini P. and Papini L. (2000), "Differenze etologiche e morfologiche tra *Triturus vulgaris vulgaris* (Linnaeus, 1758) e *Triturus vulgaris meridionalis* (Boulenger, 1882)," in: *Atti del I Congr. Naz. della Soc. Herpetol. Italica*, Mus. Reg. Sci. Nat. Torino, pp. 347 – 351.

Rage J.-C. and Bailon S. (2005), "Amphibians and squamate reptiles from the late the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France)," *Geodiversitas*, **27**, 413 – 441.

Rage J.-C. and Hossini S. (2000), "Les Amphibiens du Miocène moyen de Sansan," *Mem. Mus. Hist. Nat.*, **183**, 177 – 217.

Ratnikov V. Yu. (2002), "Late Cenozoic amphibians and reptiles of the East-European plain," *Trudy NIIG VGU*, **10**, 1 – 138 [in Russian].

Sanchiz B. and Młynarski M. (1979), "Pliocene Salamandrids (Amphibia, Caudata) from Poland," *Acta Zool. Cracov*, **24**(4), 175 – 188.

Sanchiz B. and Szyndlar Z. (1984), "Pleistocene amphibian fauna from Kozi Grzbiet in the Holy Cross Mts.," *Acta Geol. Polon.*, **34**(1 – 2), 51 – 62.

Szyndlar Z. (1984), "Fossil snakes from Poland," *Acta Zool. Cracov.*, **28**(1), 1 – 156.

Teege M.-J. (1957), "Studien zur Entwicklung und Gestalt der Urodelenwirbel," *Z. Wiss. Zool. Abt. A*, **160**, 95 – 163.

Venczel M. (1999), "Land salamanders of the family Hynobiidae from the Neogene and Quaternary of Europe," *Amphibia–Reptilia*, **20**, 401 – 412.

Wiedersheim R. (1875), Salamandrina perspicillata *und* Geotriton fuscus*. Versuch einer vergleichenden Anatomie der Salamandrinen mit Berücksichtigung der Skelet-Verhaeltnisse*, Genua.

Weisrock D. W., Papenfuss T. J., Macey R. J., Litvinchuk S. N., Polymeni R., Ugurtaş I. H., Zhao E., and Larson A. (2006), "A molecular assessment of phylogenetic relationships and lineage accumulation rates within the family Salamandridae (Amphibia, Caudata)," *Mol. Phyl. Evol.*, **41**(2), 368 – 383.

Worthington R. D. and Wake D. B. (1972), "Patterns of regional variation in the vertebral column of terrestrial salamanders," *J. Morphol.*, **137**(3), 257 – 277.

Zhang F. (1985), "On anatomy of the skeletal system of *Liua shihi* (Liu) (Amphibia, Hynobiidae)," *Acta Herpetol. Sinica*, **4**(1), 17 – 24 [in Chinese].