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Comparative humeral morphology of some Eurasian tailed amphibians (Amphibia, Urodela) for palaeontological studies

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RATNIKOV V. 2015. Comparative humeral morphology of some Eurasian tailed amphibians (Amphibia, Urodela) for palaeontological studies. *Acta zool. cracov*., **58**(1): 101-119.

Abstract. Humeri of 14 tailed amphibian species are described: *Onychodactylus fischeri* (BOULENGER, 1886), *Salamandrella keyserlingii* DYBOWSKI, 1870, *Salamandrella tridactyla* (NIKOLSKII, 1905), *Ichthyosaura alpestris* (LAURENTI, 1768), *Lissotriton lantzi* (WOLTERSTORFF, 1914), *Lissotriton montandoni* (BOULENGER, 1880), *Lissotriton vulgaris* (LINNAEUS, 1758), *Ommatotriton ophryticus* (BERTHOLD, 1846), *Pleurodeles waltl* MICHAHELLES, 1830, *Triturus cristatus* (LAURENTI, 1768), *Triturus dobrogicus* (KIRITZESCU, 1903), *Triturus karelini* (STRAUCH, 1870), *Mertensiella caucasica* (WAGA, 1876), *Salamandra salamandra* (LINNAEUS, 1758). Morphological characteristics and indices (ratios) almost always permit the distinction of tailed amphibian genera. Specific identification is more difficult because interspecific differences are insignificant.

Key words: humeri, identification, Amphibia, Urodela, Hynobiidae, Pleurodelinae, Salamandrinae.

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I. INTRODUCTION

Fossil remains of recent species of tailed amphibians are known mainly by vertebrae. This likely results from their relatively high number in a skeleton. In addition to vertebrae, large bones of limbs are sometimes also preserved, because they are more massive than other bones of the skeleton (RATNIKOV 2010).

Humeri are distinctive owing to the complexity of their morphology, which should promote identification of fossil material to low taxonomic levels. However, the rare descriptions of paleontologic findings do not give sufficient criteria for identification.

HODROVA (1984) studied material from the Upper Pliocene of Ivanovce (West Slovakia) and attributed the found humeri to *Salamandra salamandra* (LINNAEUS, 1758), *Triturus cristatus* (LAURENTI, 1768) and *Triturus* cf. *alpestris* (LAURENTI, 1768). Identifications were based on overall similarity of the morphology and sizes of fossil bones with modern comparative specimens. The detailed description and comparison with other species were not given.

AVERIANOV (1995) described remains of *Ranodon* cf. *sibiricus* KESSLER 1866, including two fragments of humeri, from the Upper Pliocene of Kiikbai, Southern Kazakhstan. He pointed out the difference of the fossil bones from modern representatives of Salamandridae, and also noticed the small morphological difference between the fossil samples and *Ranodon sibiricus*.

RATNIKOV (1997, 2002, 2010) attributed fragments of the humeri from the Lower Neopleistocene (=Lower Middle Pleistocene) of Kuznetsovka (Russia) to *Salamandrella* sp. because they differ from modern representatives of Salamandridae, are similar to *Salamandrella keyserlingii* DYBOWSKI, 1870 and attribution to other genera of Hynobiidae appeared to be less probable.

In my opinion, such tentative paleontologic identifications are connected with an absence of sufficient osteological collections available to paleontologists and with an absence of special comparative studies on the bones of modern tailed amphibians. This article is devoted to the research of morphological differences between humeri of the species available in my comparative collection with the aim of expanding our knowledge of tailed amphibian humeri.

II. MATERIAL AND METHODS

The systematics of FROST (2013) are used in this work. In total, 10 specimens of three species of Hynobiidae and 100 specimens of eleven species of Salamandridae were studied (Table I). All humeri were cleaned from muscles and sinews by scalpel. Specimens were studied under binocular microscope. The materials are kept in the comparative osteological collections of the Geological Faculty of the Voronezh State University.

As a basis for descriptions I applied the terminology of FRANCIS (1934). I have also added some new terms: a proximal notch of dorsal crest, posterior and anterior ridges on distal edge of ventral crest, and proximal and distal parts of the humerus (Fig. 1). For more accurate correlation of various parts of the bone I measured some elements and calculated some indices (the ratios of elements) (Tables II and III). Measurements of the humeri parameters were performed with the use of binocular microscope micrometer (accuracy 0.1 mm). The scheme of measurements is given in Fig. 2. Ratios of various bone element sizes (indices) were calculated in program Excel. Images of bones were obtained by a Digital Camera for Microscope (DCM300) and then processed in Photoshop.

III. GENERAL REMARKS

During the study it was found that not all the marked elements, measurements and indices have diagnostic value. Detection of the border between bone and cartilage on the humeri proximal ends is difficult, leading to subjectivity of L, D and V characterization (see Fig. 2A). Parameters L-D and L-V is considered more objective. However, the values of their measurements (L-D) - (L-V) have not showed stable tendencies in any taxa.

Table I

List of taxa, localities, and number of specimens studied (*N*)

Taxon	Locality	N
Hynobiidae		
Onychodactylus fischeri (BOULENGER, 1886)	Primorskiy Kray, Russia	1
Salamandrella keyserlingii DYBOWSKI, 1870	Sverdlovskaya Oblast', Russia	2
	Magadanskaya Oblast', Russia	4
	Russia	2
Salamandrella tridactyla (NIKOLSKII, 1905)	South of Primorskiy Kray, Russia	1
Salamandridae		
Ichthyosaura alpestris (LAURENTI, 1768)	The Carpathians, Ukraine	2
	Serbia	1
	L'vovskaya Oblast', Ukraine	6
Lissotriton lantzi (WOLTERSTORFF, 1914)	Tbilisi, Georgia	1
	Abkhazia	2
	The Caucasus	1
Lissotriton montandoni (BOULENGER, 1880)	The Carpathians, Ukraine	3
	L'vovskaya Oblast', Ukraine	13
	Locality unknown	2
Lissotriton vulgaris (LINNAEUS, 1758)	Leningradskaya Oblast', Russia	13
	Udmurtia, Russia	1
	Grodno Province, Byelorussia	2
Ommatotriton ophryticus (BERTHOLD, 1846)	Krasnodarskiy Kray, Russia	6
	Tbilisi, Georgia	3
	Batumi, Georgia	1
	Sochi, Krasnodarskiy Kray, Russia	2
Pleurodeles waltl MICHAHELLES, 1830	Locality unknown	1
Triturus cristatus (LAURENTI, 1768)	Leningradskaya Oblast', Russia	10
	Udmurtia, Russia	2
	Locality unknown	2
Triturus dobrogicus (KIRITZESCU, 1903)	Izmail, Odessa Province, Ukraine	3
	Vilkovo, Odessa Province, Ukraine	2
Triturus karelini (STRAUCH, 1870)	Crimea, Ukraine	6
	Tbilisi, Georgia	1
	Ersi, Dagestan, Russia	1
	Treshnja, Serbia	1
Mertensiella caucasica (WAGA, 1876)	Georgia	6
Salamandra salamandra (LINNAEUS, 1758)	The Carpathians, Ukraine	6

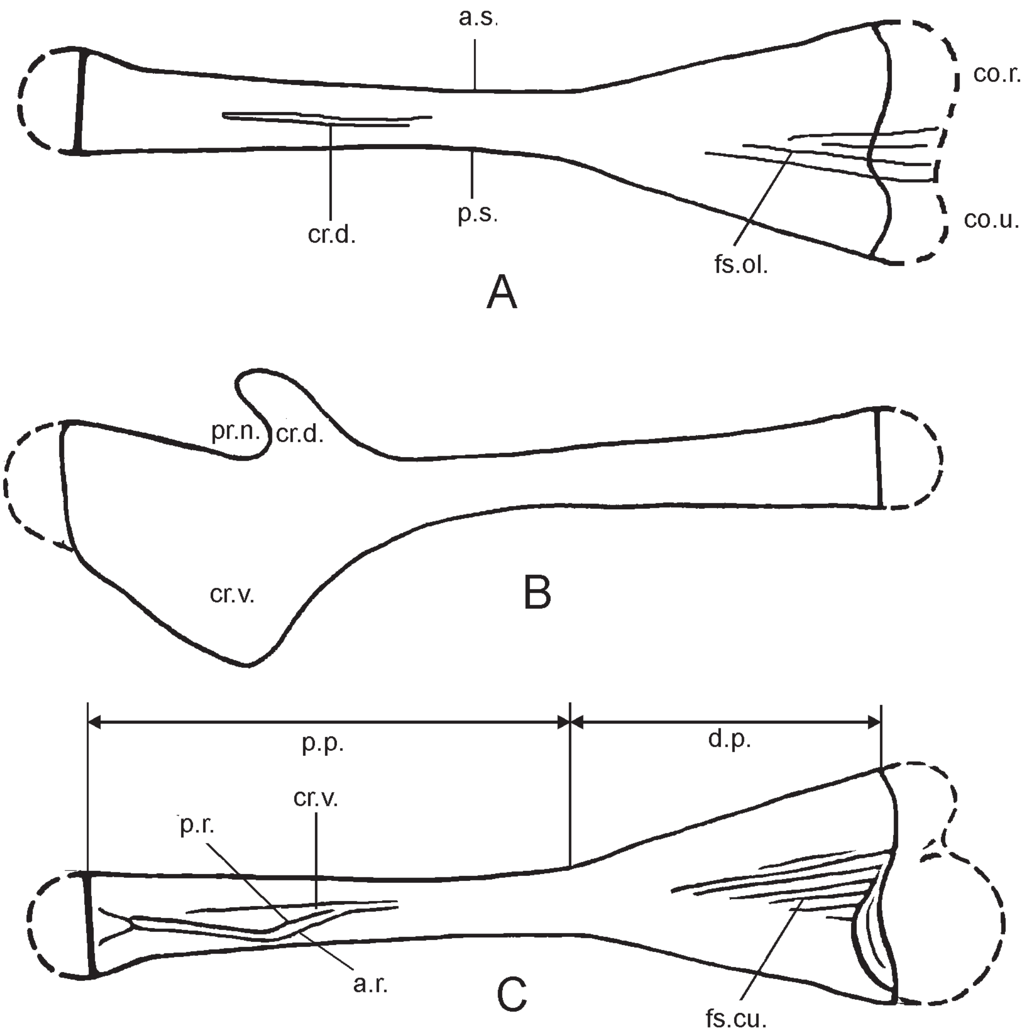

Fig. 1. Structure of the humerus (sensu FRANCIS 1934 with additions): A – right humerus, dorsal view, B – right humerus, posterior view; C – right humerus, ventral view; a.r. – anterior ridge of crista ventralis, a.s. – anterior side of the humerus, co.r. – condylus radialis, co.u. – condylus ulnaris, cr.d. – crista dorsalis, cr.v. – crista ventralis, d.p. – distal part of the humerus, fs.ol. – fossa olecranon, fs.cu. – fossa cubitalis, p.p. – proximal part of the humerus, p.r. – posterior ridge of crista ventralis, p.s. – posterior side of the humerus, pr.n. – proximal notch of crista dorsalis.

Comparative sizes between the distal (Wd) and the proximal (Wp = Hcd+Hv) bone widenings are not stable in most of the Salamandridae. All specimens of the species *Mertensiella caucasica* have the distal width larger than that of the proximal one. On the contrary, Hynobiidae have larger distal width because of undeveloped crista dorsalis.

Table II

Variation of measurements of humeri (mm) in 14 species of tailed amphibians (N – quantity of bones measured).

Species	N	L	D	V	L-D	L-V	Hcd	Hv	d	Tv	Th	Wd	Wp
Onychodactylus fischeri	2	7.2-7.3	–	1.3	–	5.9-6	–	1.5	–	0.55	0.55	2	1.5
Salamandrella keyserlingii	16	4.0-7.3	0.9-1.8	0.8-1.7	3.1-5.7	3.05-5.8	0.1-0.2	1.1-1.9	–	0.4-0.7	0.4-0.65	1.3-2.45	1.2-2.2
Salamandrella tridactyla	2	6.8-6.9	1.7-1.9	1.7-1.8	4.9-5.2	5.1	0.15-0.2	1.85-1.9	–	0.6	0.5	2.2	2.0-2.1
Ichthyosaura alpestris	17	5.6-7.4	0.8-1.4	0.7-1.3	4.3-6.2	4.6-6.1	0.4-0.65	1.2-1.6	0.0-0.2	0.4-0.6	0.4-0.55	1.6-1.95	1.65-2.0
Lissotriton lantzi	8	5.0-5.6	0.7-1.45	0.5-1.0	4.3-4.7	4.1-4.8	0.2-0.5	0.9-1.2	0.0-0.15	0.35-0.4	0.3-0.4	1.3-1.5	1.3-1.6
Lissotriton montandoni	35	5.1-7.0	0.7-1.25	0.7-1.6	4.4-5.6	4.4-5.6	0.2-0.6	1.1-1.65	0.0-0.2	0.4-0.5	0.35-0.5	1.6-2.1	1.5-2.2
Lissotriton vulgaris	26	3.8-5.7	0.4-0.9	0.3-0.9	3.2-5.0	3.25-5.0	0.25-0.5	0.8-1.1	0.05-0.3	0.25-0.4	0.25-0.4	1.1-1.45	1.1-1.5
Ommatotriton ophryticus	24	7.5-11.7	1.1-2.5	1.0-2.3	5.8-9.3	6.5-9.4	0.5-1.0	1.7-2.4	0.0-0.65	0.55-0.7	0.5-0.8	2.3-3.3	2.2-3.4
Pleurodeles waltl	2	6.8-7.0	1.4	1.4-1.6	5.4-5.6	5.4	0.5	1.7	0.15-0.2	0.45	0.45-0.5	1.8-1.85	2.2
Triturus cristatus	28	4.1-8.7	0.5-1.9	0.5-2.0	3.5-7.2	3.5-7.1	0.3-0.7	0.75-1.8	0.0-0.3	0.25-0.7	0.2-0.6	1.1-2.5	1.1-2.4
Triturus dobrogicus	10	4.7-7.8	1.05-1.3	0.9-1.3	3.6-6.8	3.7-6.8	0.3-0.6	0.85-1.3	0.0-0.25	0.32-0.6	0.3-0.6	1.2-1.75	1.2-1.85
Triturus karelini	18	8.4-10.0	1.0-1.8	1.0-1.8	6.9-8.6	6.7-8.3	0.6-0.8	1.7-2.3	0.1-0.3	0.6-0.8	0.5-0.7	2.2-2.85	2.4-3.0
Mertensiella caucasica	9	7.0-8.7	0.9-1.6	0.8-1.5	5.7-7.4	5.8-7.6	0.3-0.5	1.4-1.7	0.0-0.1	0.5-0.55	0.45-0.55	1.75-2.1	1.7-2.0
Salamandra salamandra	11	10.2-14	1.1-2.5	1.8-2.5	9.1-11.5	7.9-12.2	1.0-1.6	3.0-3.5	0.0-0.55	0.8-1.1	0.7-1.1	3.6-4.4	4.2-4.9

Sometimes the form of the dorsal crest changes in various individuals of one species (Fig. 3). Conspicuous differences can occur even between the right and left humerus of one individual. The form of dorsal crest offers more than one variant of its width measurement (w) fairly often. Therefore this parameter has been excluded from examination.

Table III

Variations of indexes of humeral bones in 14 species of tailed amphibians (N – number of bones measured).

Species	N	L/Wp	L/Wd	L-D/Wp	L-D/Wd	Wd/Th	(L-D)/ /Th	Tv/Hcd
Onychodactylus fischeri	2	4.8-4.87	3.6-3.65	–	–	3.64	–	–
Salamandrella keyserlingii	16	3.11-4.0	2.8-3.5	2.13-3.02	2.16-2.63	2.8-4.55	7.75-11.8	2.5-7.0
Salamandrella tridactyla	2	3.24-3.45	3.09-3.14	2.33-2.6	2.23-2.36	4.4	9.8-10.4	3.0-4.0
Ichthyosaura alpestris	17	3.11-3.7	3.24-4.11	2.39-3.1	2.58-3.44	3.27-4.88	9.2-12.4	0.8-1.5
Lissotriton lantzi	8	3.19-3.92	3.33-4.31	2.69-3.36	2.87-3.54	3.5-4.29	9.25-12.57	0.8-1.75
Lissotriton montandoni	35	2.83-4.0	3.19-4.0	2.43-3.07	2.57-3.24	3.2-5.0	9.8-13.5	0.73-2.25
Lissotriton vulgaris	26	3.13-4.25	3.15-4.42	2.69-3.92	2.69-3.92	3.13-5.2	10.67-16.33	0.6-1.2
Ommatotriton ophryticus	24	3.1-4.26	3.15-3.9	2.47-3.57	2.52-3.15	3.5-5.5	10.38-15.5	0.7-1.27
Pleurodeles waltl	2	3.09-3.18	3.68-3.89	2.45-2.55	2.92-3.11	3.7-4.0	10.8-12.44	0.9
Triturus cristatus	28	3.2-4.48	3.28-4.22	2.65-3.79	2.6-3.44	3.6-5.5	10.2-18	0.63-1.67
Triturus dobrogicus	10	3.24-4.8	3.92-4.73	2.65-4.0	3.0-4.12	2.55-4.0	8.18-14.25	0.83-1.33
Triturus karelini	18	3.21-3.8	3.26-4.0	2.69-3.14	2.8-3.44	3.43-5.0	9.86-15.4	0.75-1.4
Mertensiella caucasica	9	3.68-4.58	3.6-4.35	3.0-3.94	2.85-3.71	3.5-4.67	10.55-16.22	1.1-1.83
Salamandra salamandra	11	2.43-3.19	2.8-3.5	2.13-2.48	2.32-2.88	3.6-5.5	9.1-12.75	0.56-0.9

The change of the minimum bone thickness in the perpendicular planes (Tv-Th) also has not showed stable tendencies in any taxa. However, it should be noted that these parameters are not attached to any specific place on the bone, and appear in various positions in different specimens. The index Wd/Th in all species studied fluctuates around

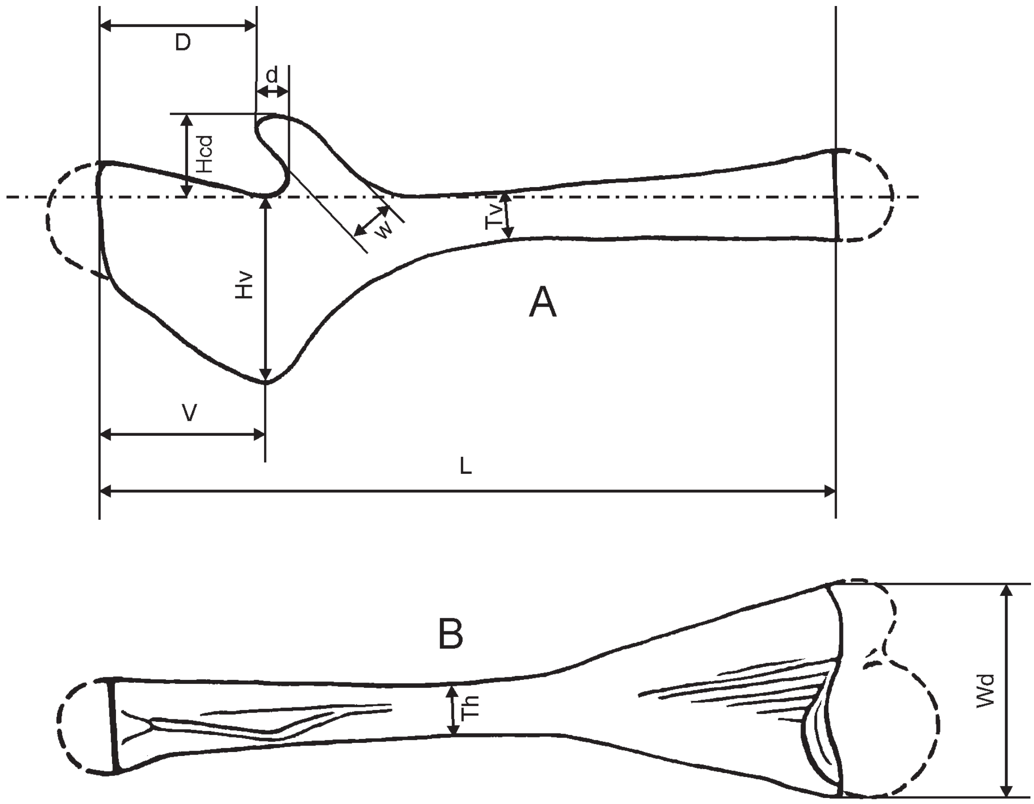

Fig. 2. Measurements of the humerus: A – posterior view, B – ventral view; D – distance from the proximal end of osseous humerus to proximal end of crista dorsalis, d – depth of proximal notch of crista dorsalis, Hcd – height of crista dorsalis, Hv – distance from dorsal side of the humerus to the lowest point of crista ventralis, L – length of osseous humerus, V – distance from the proximal end of osseous humerus to the lowest point of crista ventralis, Th – minimal thickness of the bone in horizontal plane, Tv – minimal thickness of the bone in vertical plane, w – width of crista dorsalis, Wd – width of distal end of osseous humerus.

the interval 3.5-4, deviating in one or the other side, and shows considerable overlapping values.

Expansion toward the distal bone end can be quite abrupt. In such case the border between the distal and proximal parts is visible, and it is possible to estimate their relative length. At the studied samples the length of the distal part was equal to, lesser, or much shorter than the proximal one. But in many forms the expansion begins very smoothly near the crista ventralis and consequently it is not clear where the distal part of the bone begins. Therefore this parameter could be estimated within a smaller part of the samples.

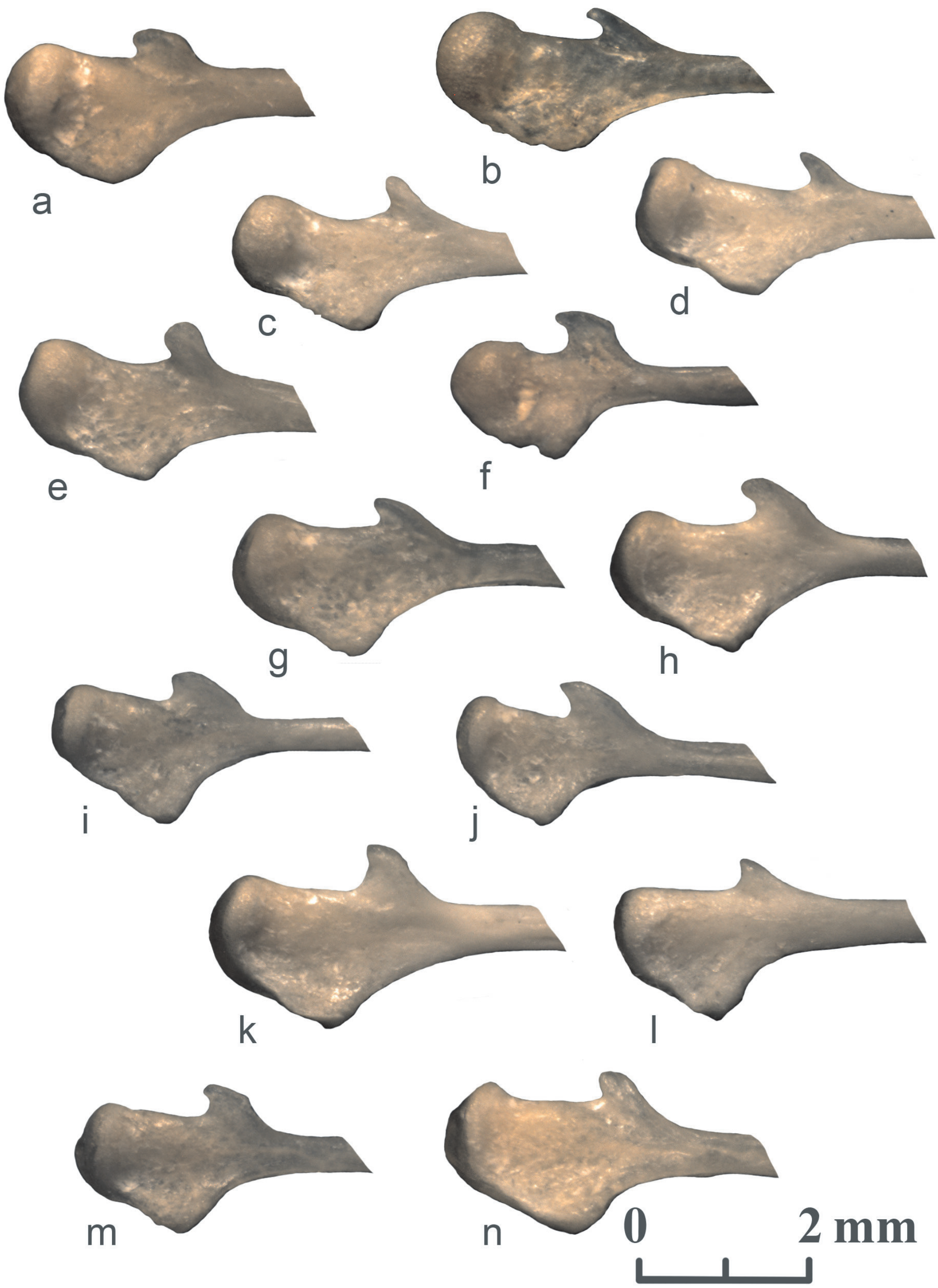

Fig. 3. Variations of crista dorsalis form in Salamandridae: a-e – *Ichthyosaura alpestris*; f-n – *Lissotriton montandoni*.

IV. DESCRIPTION OF THE HUMERI

Hynobiidae COPE, 1859

Fig. 4

Crista dorsalis is not developed or poorly developed. Posterior and anterior ridges on crista ventralis are not developed. Distal width is greater than proximal one.

Onychodactylus TSCHUDI, 1838

Onychodactylus fischeri (BOULENGER, 1886)

Fig. 4 a-c

Length about 7.3 mm. Longitudinal axis of the bone straight. The bone dorsal edge is weakly bent ventrally at the distal end and dorsally at the proximal one (weakly S-shaped). Crista dorsalis is undeveloped. The length of distal part does not exceed the proximal one. Fossa olecranon is appreciable; fossa cubitalis is very short and appreciable directly before condylus radialis.

Salamandrella DYBOWSKI, 1870

Fig. 4 d-i

Longitudinal axis of the bone is convex. The bone dorsal edge is usually considerably convex. Crista dorsalis looks as a small prominence extended along posterior edge of the bone; its height is much less than the minimum thickness of the bone (index Tv/Hcd exceeds 2.5). Proximal notch of crista dorsalis is absent.

Salamandrella keyserlingii DYBOWSKI, 1870

Fig. 4 d-f

Length up to 7.3 mm. Distal part of the bone is visibly smaller than the proximal one. Fossa olecranon is almost undeveloped, fossa cubitalis is appreciable.

Salamandrella tridactyla (NIKOLSKII, 1905)

Fig. 4 g-i

Length about 6.9 mm. Lengths of distal and proximal bone parts are approximately equal. Fossa olecranon is appreciable and almost symmetric, fossa cubitalis is almost undeveloped.

Salamandridae GOLDFUSS, 1820

Figs 5-8

Longitudinal axis of the bone is straight. Crista dorsalis is high, usually spike-like (AVERIANOV, 1995) and displaced caudally from the bone axis; its height is greater to somewhat lesser than the minimum thickness of the bone: index Tv/Hcd does not exceed 2 (Tabl. 3). Proximal notch of crista dorsalis is, as a rule, present, but sometimes lacking. Fossa cubitalis has a subtriangular form.

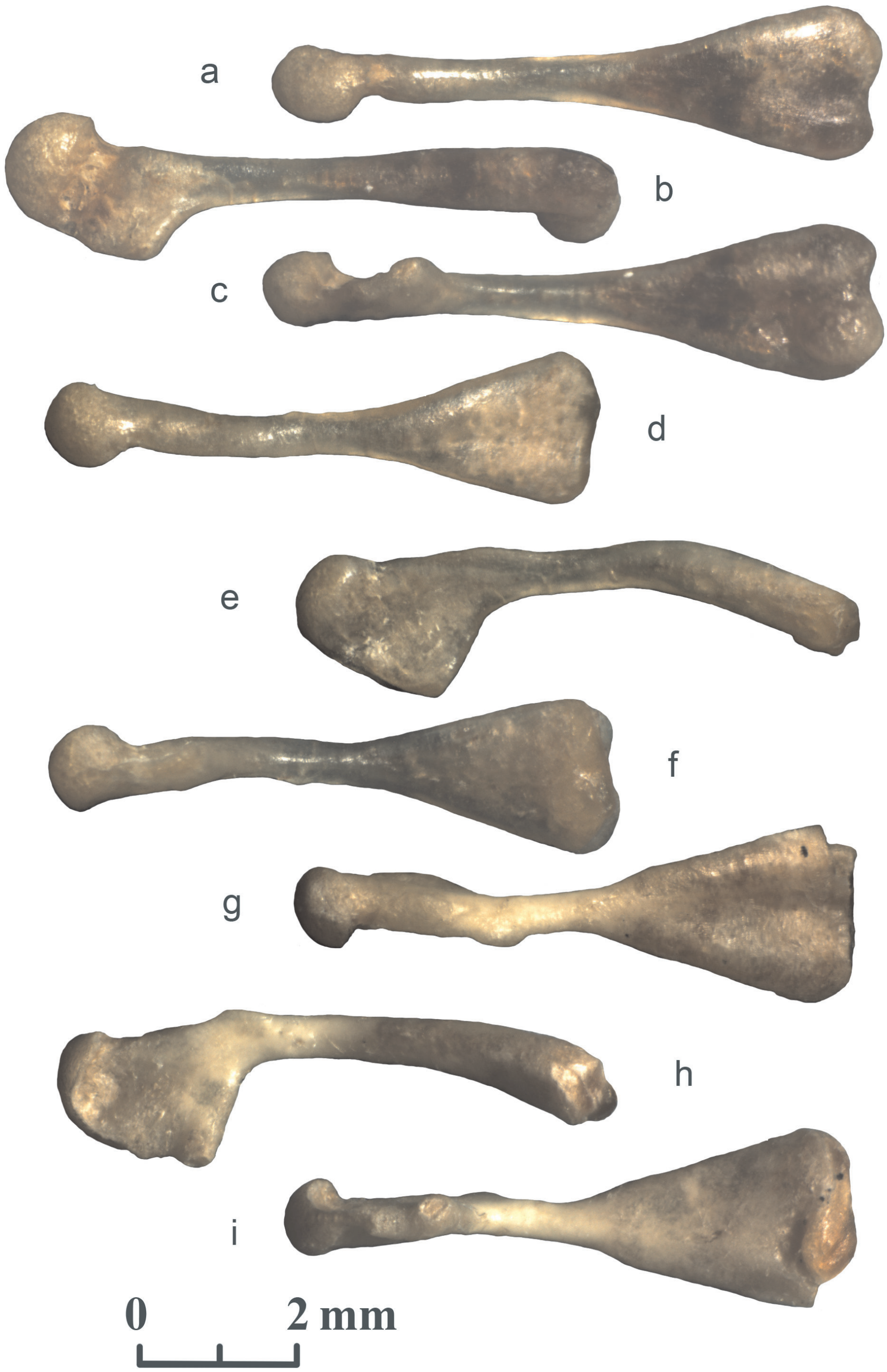

Fig. 4. Right humeri of Hynobiidae: a-c – *Onychodactylus fischeri*; d-f – *Salamandrella keyserlingii*; *g-i* – *Salamandrella tridactyla*; a, d, g – dorsal view; b, e, h – posterior view; c, f, i – ventral view.

Pleurodelinae TSCHUDI, 1838

Ichthyosaura SONNINI DE MANONCOURT and LATREILLE, 1801

Ichthyosaura alpestris (LAURENTI, 1768)

Fig. 5 a-c

Length up to 7.4 mm. The proximal notch of crista dorsalis is usually present. The dorsal edge is weakly concave or straight. A posterior ridge on the crista ventralis is distinctly higher than the anterior one. Size of the distal part in comparison with the proximal one is not clear or the distal part is not longer than the proximal one. Fossa olecranon is absent or poorly developed, fossa cubitalis is deep, usually long.

Lissotriton BELL, 1839

Fig. 5 d-l

The proximal notch of crista dorsalis is usually present. Two ridges on crista ventralis are of identical height or posterior ridge is distinctly higher than the anterior one. Fossa olecranon is absent or poorly developed, fossa cubitalis is long.

Lissotriton lantzi (WOLTERSTORFF, 1914)

Fig. 5 d-f

Length up to 5.6 mm. The proximal notch of crista dorsalis is usually present. The dorsal edge is weakly concave. Distal and proximal parts of the bone cannot be delimited or they show different ratios. Fossa cubitalis is appreciable.

Lissotriton montandoni (BOULENGER, 1880)

Fig. 5 g-i

Length up to 7.0 mm. The proximal notch of crista dorsalis is usually present. The dorsal edge is weakly concave or rarely straight. The distal edge of crista ventralis is slanting. Distal and proximal parts of the bone cannot be delimited. Fossa cubitalis is deep.

Lissotriton vulgaris (LINNAEUS, 1758)

Fig. 5 j-l

Length up to 5.7 mm. Proximal notch of crista dorsalis is present. The dorsal edge is weakly concave. Distal and proximal parts of the bone cannot be delimited or the distal part is smaller than proximal one. Fossa cubitalis is deep or at least distinct.

Ommatotriton GRAY, 1850

Ommatotriton ophryticus (BERTHOLD, 1846)

Fig. 6 a-c

Length up to 11.7 mm. The proximal notch of crista dorsalis is present. The dorsal edge is weakly concave. The distal edge of crista ventralis is slanting. The posterior ridge on

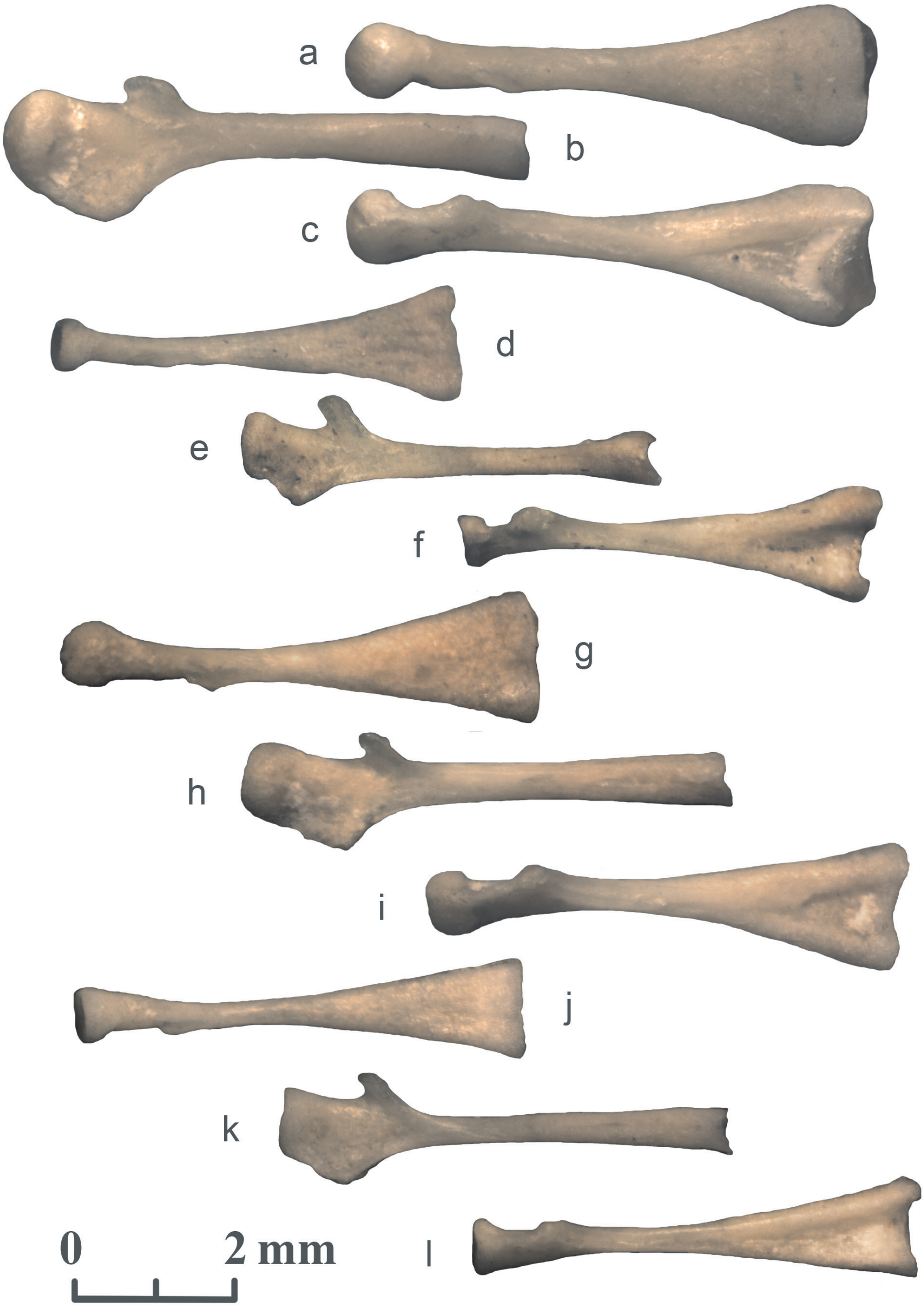

Fig. 5. Right humeri of Pleurodelinae: a-c – *Ichthyosaura alpestris*; d-f – *Lissotriton lantzi*; g-i – *Lissotriton montandoni*; j-l – *Lissotriton vulgaris*; a, d, g, j – dorsal view; b, e, h, k – posterior view; c, f, i, l – ventral view.

crista ventralis is appreciably higher than the anterior or they are of same height. Distal and proximal parts of the bone cannot be delimited. Fossa olecranon can be weakly developed or distinct, wide, or narrow and long. Fossa cubitalis is rather deep and long.

Pleurodeles MICHAHELLES, 1830

Pleurodeles waltl MICHAHELLES, 1830

Fig. 6 d-f

Length about 7.0 mm. The proximal notch of crista dorsalis is present. The dorsal edge is S-shaped. Crista dorsalis is short, high, with an overhanging proximal end. The distal edge of crista ventralis is thinned. The distal part of the bone is much smaller than proximal one. Fossa olecranon is distinct, wide; fossa cubitalis is not deep. There is a groove traceable along the posterior side of the bone on its distal end.

Triturus RAFINESQUE, 1815

Fig. 7

Crista dorsalis is short, high, with an overhanging proximal end. The posterior ridge on the crista ventralis is distinctly higher than the anterior one or they are of same height. The distal part is much smaller than the proximal one or they cannot be delimited. Fossa olecranon is usually distinct, long, but sometimes can be lacking.

Triturus cristatus (LAURENTI, 1768)

Fig. 7 a-c

Length up to 8.7 mm. The bone dorsal edge is S-shaped or concave. The posterior ridge on crista ventralis is appreciably higher than the anterior one or they are of same height. Fossa cubitalis is rather deep, but in juvenile individuals it is weakly developed.

Triturus dobrogicus (KIRITZESCU, 1903)

Fig. 7 d-f

Length up to 7.8 mm. The bone dorsal edge is S-shaped. The posterior ridge of crista ventralis is appreciably higher than the anterior one. Fossa cubitalis is rather deep, long.

Triturus karelini (STRAUCH, 1870)

Fig. 7 g-i

Length up to 10.0 mm. The bone dorsal edge is S-shaped or concave. The posterior ridge of crista ventralis is appreciably higher than the anterior one. Fossa cubitalis is rather deep, long.

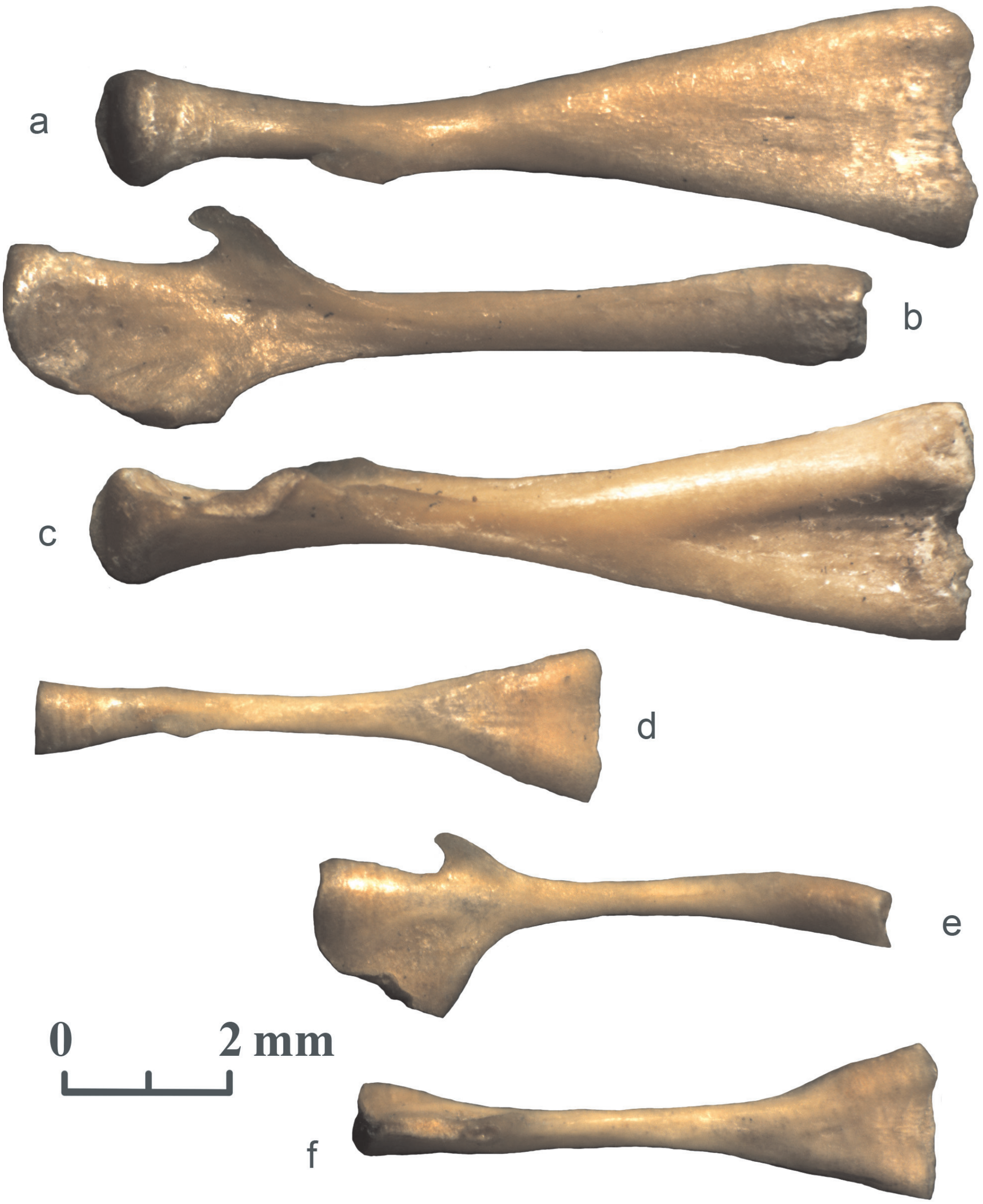

Fig. 6. Right humeri of Pleurodelinae: a-c – *Ommatotriton ophryticus*; d-f – *Pleurodeles waltl*; a, d – dorsal view; b, e – posterior view; c, f – ventral view.

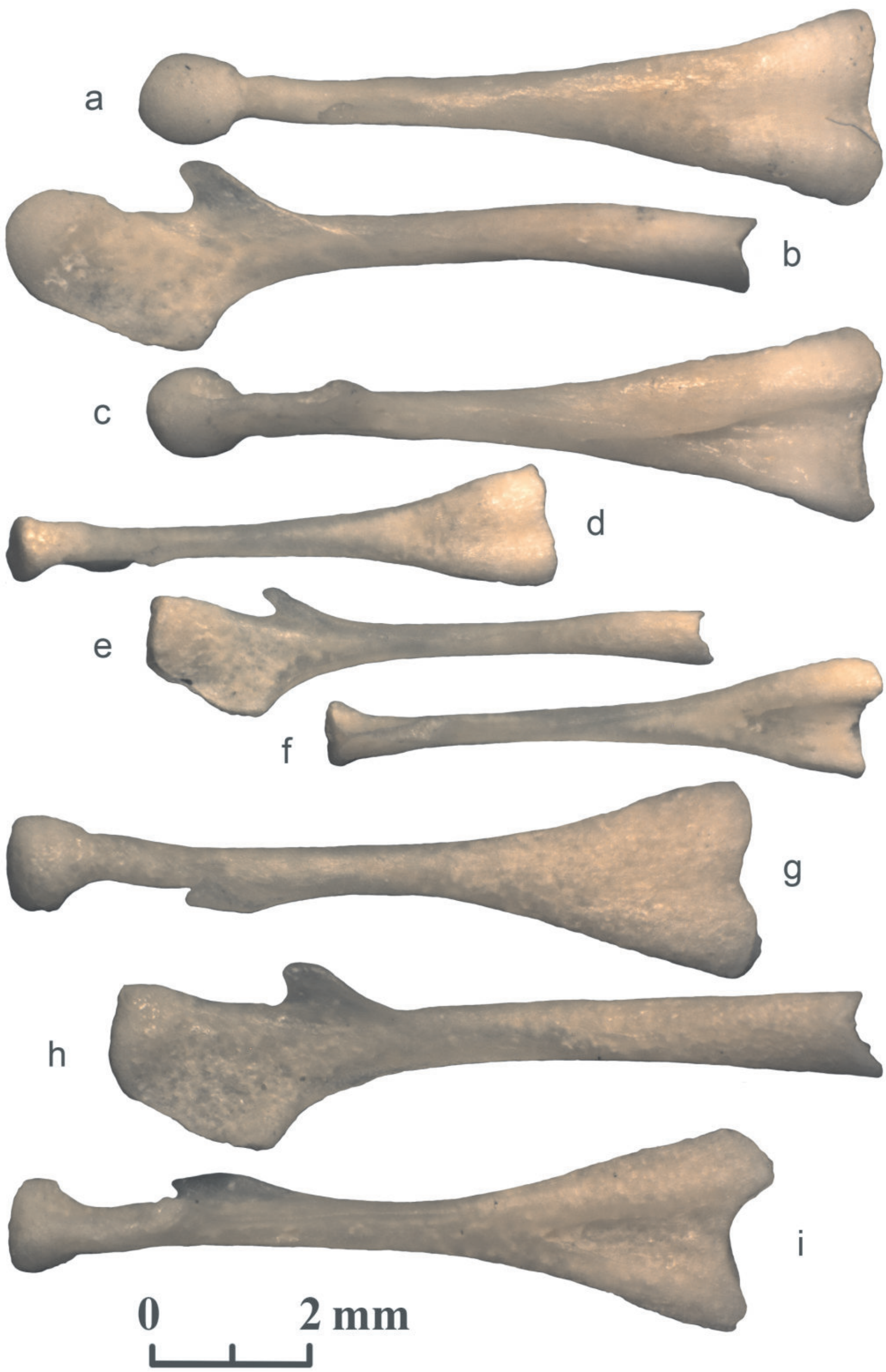

Fig. 7. Right humeri of Pleurodelinae: a-c – *Triturus cristatus*; d-f – *Triturus dobrogicus*; *g-i* – *Triturus karelini*; a, d, g – dorsal view; b, e, h – posterior view; c, f, i – ventral view.

Salamandrinae GOLDFUSS, 1820

Mertensiella WOLTERSTORFF, 1925

Mertensiella caucasica (WAGA, 1876)

Fig. 8 a-c

Length up to 8.7 mm. The dorsal edge is almost straight or weakly convex. Crista dorsalis is short, rather high and usually slightly displaced from the bone axis to posterior edge. The proximal notch of crista dorsalis is absent or very small. The distal edge of crista ventralis is steep, with a small posterior ridge. The distal part of the bone is much smaller than the proximal one. Fossa olecranon is distinct, long. Fossa cubitalis is deep and short. There are two shallow asymmetrical furrows leading from the distal end of the bone along the posterior and anterior sides as far as its midpoint.

Salamandra GARSAULT, 1764

Salamandra salamandra (LINNAEUS, 1758)

Fig. 8 d-f

Length up to 14.0 mm. The proximal notch of the crista dorsalis is usually present. The bone dorsal edge is concave. Crista dorsalis is short, high. A posterior ridge can be developed on the distal edge of the crista ventralis. Distal and proximal parts of the bone cannot be delimited. Fossa olecranon is distinct, long. Fossa cubitalis is rather deep, long.

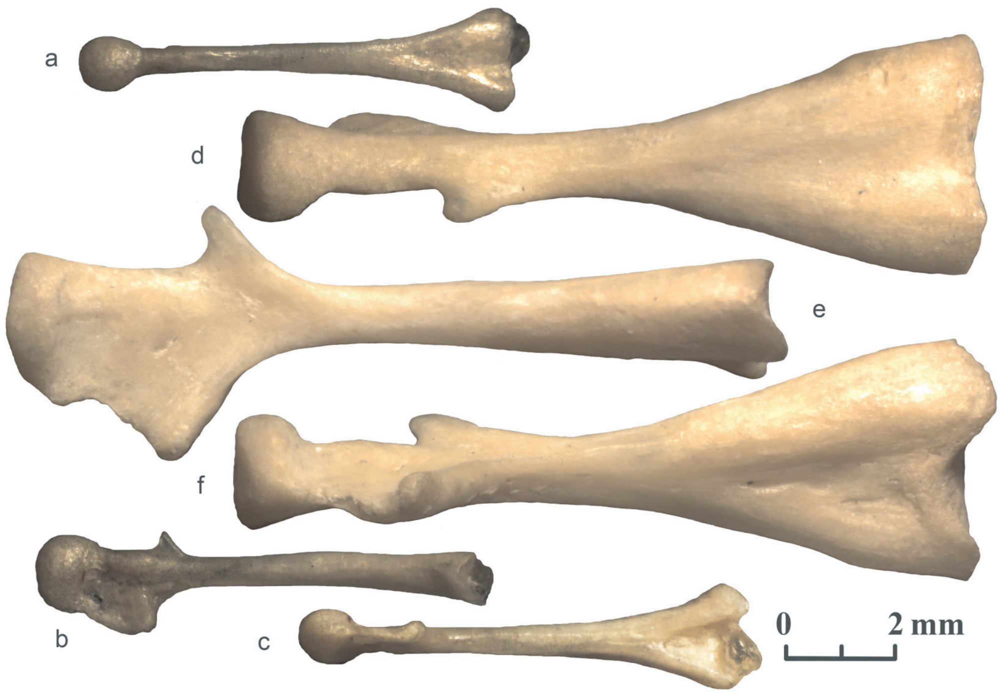

Fig. 8. Right humeri of Salamandrinae: a-c – *Mertensiella caucasica*; d-f – *Salamandra salamandra*; a, d – dorsal view; b, e – posterior view; c, f – ventral view.

V. CONCLUSIONS

The distinctions found in the morphology of the bones, briefly specified in Table IV, allow for definition of the systematic affiliation of fossil humeri.

Absence or weak development of the crista dorsalis distinguishes the family Hynobiidae from Salamandridae which have this structure well developed. Among the Hynobiidae the convex bone dorsal edge distinguishes *Salamandrella* from *Onychodactylus* with its S-shaped form. The latter is also characterized by high values of indices L/Wp and L/Wd (Table III). However, I had only one individual of *Onychodactylus fischeri* and consequently no data about intraspecific variability of these features. The distal part of this bone in *Salamandrella keyserlingii* is apparently smaller than the proximal one whereas they are approximately equal in *Salamandrella tridactyla*. In addition the fossa olecranon and fossa cubitalis are developed to various degrees. Unfortunately, I had only one individual of the latter species, and these conclusions are not supported sufficiently.

Table IV

Morphological characters of some bone elements in studied species of tailed amphibians. CD – crista dorsalis: 1 – low, 2 – high; PR - proximal notch of crista dorsalis: 1 – present, 2 – usually present, 3 – absent; DE – form of dorsal edge: 1 – S-shaped, 2 – convex, 3 – concave, 4 – straight; DP – size of humeral distal part in comparison with proximal one: 1 – smaller, 2 – equal, 3 – not clear; FO – fossa olecranon: 1 – visible, 2 – weakly developed, 3 – lacking; FC – fossa cubitalis: 1 - weakly developed, 2 – visible, 3 – deep; APR – anterior and posterior ridges on distal edge of ventral crest: 1 – posterior higher than anterior, 2 – of equal height, 3 – anterior higher than posterior, 4 – absent, 5 – only posterior present

Species	CD	PR	DE	DP	FO	FC	APR
Onychodactylus fischeri	–	–	1	1 or 2	1	2	–
Salamandrella keyserlingii	1	–	2	1	2	2	–
Salamandrella tridactyla	1	–	2	2	1	1	–
Ichthyosaura alpestris	2	2	3	3	3 or 2	3	1
Lissotriton lantzi	2	2	3	3	3 or 2	2	2 or 1
Lissotriton montandoni	2	2	3	3	3 or 2	3	2 or 1
Lissotriton vulgaris	2	1	3	3	3 or 2	3 or 2	2 or 3
Ommatotriton ophryticus	2	1	3	3	1	3	1 or 2
Pleurodeles waltl	2	1	1	1	1	2	4
Triturus cristatus	2	1	3 or 1	1 or 3	1 or 3	3	1 or 2
Triturus dobrogicus	2	1	1	1 or 3	1 or 3	3	1
Triturus karelini	2	1	3 or 1	1 or 3	1	3	1
Mertensiella caucasica	2	3	4 or 2	1	1	3	5
Salamandra salamandra	2	2	3	3	1	2	5

Essential differences between Pleurodelinae and Salamandrinae have not been revealed, whereas their genera sometimes differ. Humeri of *Mertensiella caucasica* are characterized by a very short distal part, a short crista dorsalis, and a steep distal edge of crista ventralis with a small posterior ridge. There are also characteristic asymmetrical furrows on the posterior and anterior sides of the bone. Humeri of *Salamandra salamandra* are largest (up to 14 mm), have a short high crista dorsalis and the smallest indices L/Wp, L/Wd, (L-D)/Wp and (L-D)/Wd. Among them the index (L-D)/Wp has a smallest number of overlapping values with other species (Table III).

Among tritons, *Lissotriton lantzi* and *Lissotriton vulgaris* are distinguished by their small sizes (up to 5.7 mm). Their humeri are very similar and differ only by a degree of development of the anterior and posterior ridges on crista ventralis in extreme variants, and in the values of an index (L-D)/Th, which overlaps only partially (Table III). The third representative of the genus *Lissotriton, L. montandoni,* is medium size (up to 7 mm) and a comparatively slanting distal edge of crista ventralis. Similar sizes (up to 7. 4 mm) and indices are observed in *Ichthyosaura alpestris*, but this bone looks more massive than among the *Lissotriton* species.

Representatives of the genus *Triturus* are usually of medium sizes (up to 7-8 mm), though the humeri of *Triturus karelini* can reach lengths of 10 mm. All of them have a short, high crista dorsalis usually with a hanging proximal end, and two ridges on crista ventralis, the posterior ridge being usually distinctly higher than anterior one. Interspecific differences are insignificant.

Humeri of *Ommatotriton ophryticus* are largest among tritons (up to 11.7 mm) and have a slanting distal edge of crista ventralis. Humeri of *Pleurodeles waltl* differ by a pointed distal edge of the crista ventralis, a short distal part of the bone, and a groove on its posterior side. However, I had only one individual of this species and therefore these observations are only preliminary.

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REFERENCES

AVERIANOV O. 1995. *Ranodon* cf. *sibiricus* (Amphibia, Caudata) from the Upper Pliocene of Southern Kazakhstan: the first fossil record of the family Hynobiidae. *Paläontologische Zeitschrift*, **69**: 257-264.

BELL T. 1839. History of British reptilies. London, 142 pp.

BERTHOLD A.A.1846. Mitteilung über das Vorkommen von Tritonen am Kaukasus. *Nachrichten von der Georg-Augusts-Universität und der Königl. Gesellschaft der Wissenschaften zu Göttingen*, **12**: 188-190.

BOULENGER G.A. 1886. First report on additions to the batrachian collection in the Natural-History Museum. *Proceedings of the Zoological Society of London,* **June 29**: 414-416.

COPE E. D. 1859. On the primary divisions of the Salamandridae, with descriptions of two new species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **11**: 122-128.

DYBOWSKI B. 1870. Beitrag zur Kenntnis der Wassermolche Sibiriens. *Verhandllungen der kaiserlich-kongiglichen zoologish-botanischen Gesellschaft in Wien*, **20**: 237-242.

FRANCIS E. 1934. The Anatomy of the Salamander. Clarendon Press, Oxford, 381 pp.

FROST D. R. 2013. Amphibian Species of the World: an Online Reference. Version 5.6 (9 January 2013). Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA.

GARSAULT F. A. P. 1764. Les Figures des Plantes et Animaux d'Usage en Médecine, Décrits dans la Matière Médicale de Mr. Geoffroy Médecin, Dessinés d'après Nature. Niquet scrip. [Tome 5]. [4], index 20 pp., pls. 644–729. Paris. Paris: Mrs. Defehrt, Prevost, Duflos, Martinet &c.

GOLDFUSS G. A. 1820. Handbuch der Zoologie. *Zweite Abtheilung*. Nürnburg: Johann Leonhard Schrag.

GRAY J. E. 1850. Catalogue of the Specimens of Amphibia in the Collection of the British Museum. Part II. Batrachia Gradientia, etc. Printed by Order of the Trustees. London: Spottiswoodes and Shaw.

HODROVA M. 1984. Salamandridae of the Upper Pliocene Ivanovce locality (Czechoslovakia). *Acta Universitatis Carolinae – Geologica,* **4**: 331-352.

KESSLER K. F. 1866. Wassermolchs aus Westsibirien. *Bulletin de la Société Impériale des Naturalistes de Moscou*, **39**: 126-131.

KIRITZESCU C. 1903. Contributions à la faune des batraciens de Roumanie. *Buletinul Societatii de Sciinte din Bucuresci*, România, **12**: 243-265.

LAURENTI J. N. 1768. Specimen medicum, exihibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austriacorum. Vienna: typ. J.T. Trattnern, 214 pp.

LINNAEUS C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis (ed. 10). Holmia: L. Salvii, 823 pp.

MICHAHELLES C. 1830. Neue südeuropäische Amphibien. *Isis von Oken*, **23**: 189-195.

NIKOLSKII A.M. 1905. Herpetologica Rossica. *Zapiski Imperatorskoi Akademii nauk po fiziko-matematicheskomu otdeleniyu. Ser. 8*, **17**(1): 1-518.

RAFINESQUE C. S. 1815. Analyse de la nature ou tableau de l'Univers et des corps organizes. Palerme, 224 pp.

RATNIKOV V. Yu. 1997. Novye dannye o herpetofaune mestonakhozhdeniya Kuznetsovka v Tambovskoi oblasti [New data on the herpetofauna of Kuznetsovka locality in Tambov region]. *Izvestiya Vuzov. Geologiya i Razvedka*, **1**: 26-32. [In Russian].

RATNIKOV V. Yu. 2002. Pozdnekainozoiskiye zemnovodnye i cheshuichatye presmykayushchiesya Vostochno-Evropeiskoi ravniny [Late Cenozoic amphibians and reptiles of the East-European plain]. *Trudy nauchno-issledovatelskogo instituta geologii Voronezhskogo universiteta*, **10**, 1-138. [In Russian].

RATNIKOV V. Yu. 2010. A review of tailed amphibian remains from the Late Cenozoic deposits of the East European Plain. *Russian Journal of Herpetology*, **17(**1): 59-66.

SONNINI C.-S., LATREILLE P.-A. 1801 "An. X". Histoire Naturelle des Reptiles, avec Figures dissinées d'après Nature. Volume 4. Paris: Deterville.

STRAUCH A. A. 1870. Revision der Salamandriden-Gattungen nebst Beschreibung einiger oder weniger bekannten Arten dieser Familie. *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg, Ser. 7*, **16**(4): 1-110.

TSCHUDI J. J. 1838. Classification der Batrachier, mit Berucksichtigung der fossilen Thiere dieser Abteilung der Reptilien. Neuchâtel. Buchdruck. v. Petitpierre, 103 pp.

WAGA A. S. 1876. Nouvelle espèce de Salamandride. *Revue et Magasin de Zoologie Pure et Appliquée. Serie 3*. Paris **4**: 326-328.

WOLTERSTORFF W. 1914. Zwei neue Tritonenformen der palarctischen Region. *Abhandlungen und Berichte aus dem Museum für Natur- und Heimatkunde zu Magdeburg*, **2**: 371-381.