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THE COMPARISON OF CRANIAL OSTEOLOGY OF *Neurergus microspilotus* AND *Salamandra infraimmaculata semenovi* (AMPHIBIA: SALAMANDRIDAE)

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Cranial osteology characters of *Neurergus microspilotus* collected from Kavat River, Paveh, Kermanshah Province and *Salamandra infraimmaculata semenovi* from Sarvabad, Kurdistan Province, western Iran, have been described and compared based on 10 dry skull preparations. Individual characters within each of these two species discussed and compared together. Prominent differences between skulls of the two species observed are as follows: individual bones thickness, maxillary dentition, shape of the frontal, parietal and premaxillary bones, morphology of the palatines and associated structures. In *S. i. semenovi* the most parts of skull are not being completely ossified and have a membranous structure and even in the ossified parts the elements have no solidity this may due in part to more evolutionary primitive status of compare to *Neurergus*. The frontal bone in *N. microspilotus* is ossified with a projection towards the orbit which creates a ring by cartilaginous part as frontosquamosal ring. However, the frontosquamosal bone structure is absent in *S. i. semenovi*. Almost all skull elements of *N. microspilotus* are mineralized but this is not the case with *S. i. semenovi*.

Keywords: *Neurergus microspilotus*, *Salamandra infraimmaculata semenovi*, skull, comparative osteology.

INTRODUCTION

In Iran, the suborder Salamandriodea is represented by a single family, Salamandridae, and three genera, *Triturus*, *Neurergus*, and *Salamandra* (Baloutch and Kami, 1995). The genus *Neurergus* has a relatively wide geographic distribution, ranging from western Iran (Zagros Mountains) and extending into Iraq and southern Turkey (Baloutch and Kami, 1995; Cope, 1862). Sharifi and Assadian (2002) demonstrated that *N. microspilotus* occurs in several highland streams in the mid Zagros Mountains, but highly vulnerable to the changes occurring in the area. The genus *Neurergus* is comprised of four species: *N. strauchi* (Steindachner, 1887); *N. crocatus* (Cope, 1862); *N. microspilotus* (Nesterov, 1916); and *N. kaiseri* (Schmidt, 1952).

The genus *Salamandra* encompasses six species: *Salamandra algira* Bedriaga, 1883; *S. salamandra* (Linnaeus, 1758); *S. corsica* Savi, 1838; *S. infraimmaculata* (Martens, 1885); *S. lanzai* Nascetti, Andreone, Capula et Bullini, 1988; and *S. atra* Laurenti, 1768 (Steinfartz et al. 2000). *Salamandra infraimmaculata* has been divided into three subspecies: *S. i. infraimmaculata* Joger and Steinfartz, 1995; *S. i.* orientalis Joger and Steinfartz, 1995; and *S. i. semenovi* Joger and Steinfartz, 1995 (Degani, 1996). Nesterov (1916) reported the existence of *S. i. semenovi* in Siyah Guves Village near the Iraqi border. Most recently this subspecies, *S. i. semenovi*, has been found in mountainous areas around Sarvabad city and Marivan in Kurdistan Province (Rastegar-Pouyani and Faizi, 2006).

These two taxa, *N. microspilotus* and *S. i. semenovi*, have been studied in Iran for their reproduction, geographic distribution and variation (Rastegar-Pouyani and Assadian, 2003; Sharifi and Assadian, 2002, 2003). However, so far, no study has been done on description of skull characteristics and also the peculiarities of comparative osteological characteristics of these two salamandrid species. With these in mind, the main objective of this study is to compare the size, shape and connection of the skull bones between *N. microspilotus* and *S. i. semenovi*.

MATERIAL AND METHODS

Specimens of *N. microspilotus* (three males and three females) and *S. i. semenovi* (three males and three

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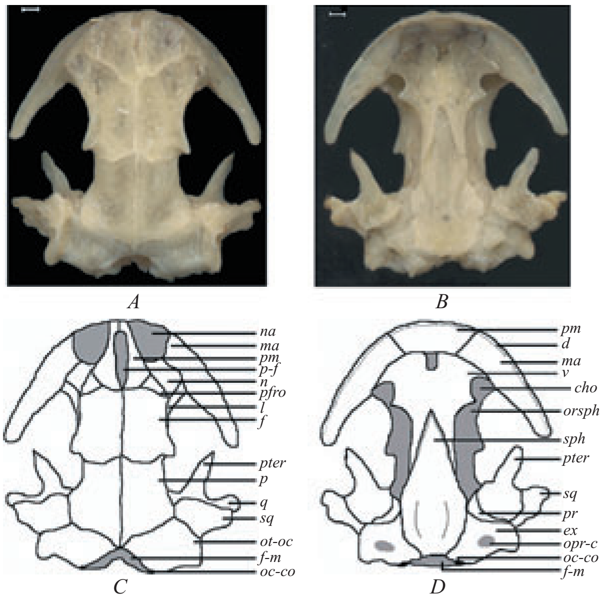

Fig. 1. Dorsal (*A*, *C*) and ventral (*B*, *D*) views of the skull of *Neurergus microspilotus*. Scans (*A*, *B*) and explanatory drawings (*C*, *D*). See *Material and Methods* for details of image preparation. **Abbreviations:** *c*, cartilage; *cho*, choana; *d*, dentary; *ex*, exoccipital; *f*, frontal; *f-m*, foramen magnum; *fs*, frontosquamosal; *l*, lacrimal; *ma*, maxilla; *n*, nasal; *no*, nostril; *o-f*, optic foramen; *oc-co*, occipital condyle; *opr-c*, operculum; *orsph*, orbitosphenoid; *ot-oc*, otic-occipital; *p*, parietal; *p-f*, premaxilla foramen; *pfro*, prefrontal; *pm*, premaxilla; *pr*, prootic; *ps-d*, parasphenoid dentary; *pter*, pterygoid; *q*, quadrate; *sph*, sphenoid; *sph-d*, sphenoid-dentary; *sq*, squamosal; *v*, vomer (Duellman and Schlager, 2004). Scale bar is 1 mm.

females) were collected in Kermanshah and Kurdistan provinces respectively, during field work in 2000 – 2005. Only adult specimens were used in this study. The specimens were prepared according to standard methods of skull preparation (e.g., Ehmcke and Clemen, 2006). Following preparation, specimens were labeled and scanned in lateral, dorsal and ventral views using a scanner Ginus (color page HR7X slim) and Olympus loop equipped with DP12 digital camera. This instrument is able to show the cranial characteristics with high quality. A comparative study between *N. microspilotus* and *S. i. semenovi* was carried out based on some descriptive and standard morphological characters with different states in cranial characters of amphibian's skull (Romer and Parsons, 1977).

RESULTS

Neurergus microspilotus

Skull (Fig. 1). The premaxillae are paired and nearly triangular dorsally. The pars dorsalis of premaxillae are distinctly and widely separated from one another by a midline fontanelle, they are separated by a groove that starts in the top of nasal opening and continues forward to pars dentalis. This groove further goes toward the antroventral part of the palate to form a hole (pore) in the vomer bone. The premaxilla contacts the prefrontal and frontal posteriorly, and participates to form the nasal cavity laterally. The maxilla completes the arch of the upper jaw that borders the nostril at the anterior part and meets the nasal and lacrimal bones medially. The nasal bones are nearly subrectangular and completely separated from each other by the premaxillae. They border the nostril anteriorly and contact the prefrontals posteromedially and lacrimals posterolaterally. The prefrontal is rather triangular in shape, the anterior part of the bone meeting the pars dorsalis anteromedially and nasal anterolaterally. It is bordered posteromedially by frontal. The lacrimal is a small triangular bone bordered by maxilla, prefrontal and nasal bones. It participates in forming the orbit cavity. The frontal is flat and trapezoid that makes a posterolateral projection. This projection binds to squamosal by a very tiny cartilage to form a ring. The frontal meets the prefrontal anterolaterally and premaxilla anteriorly, and parietal posteriorly. The parietal is relatively flat with small curvature in the posterolateral region towards the orbit cavity. The parietals are slightly larger than the frontals and complete the roof of the skull. The two parts of parietal having convergence toward the foramen magnum. The squamosal is nearly a rectangular that lying on the dorsal side of the quadrate, becoming closely fixed with it to form a lateral projection. The base of the skull is ossified. The vomers form a bony floor to the nasal cavity, flattened towards nostrils, and form choanas near the maxillae. The vomer articulates with the premaxilla (pars dentalis) and maxilla anteriorly and laterally respectively. Near the premaxilla, the vomer has a medial foramen that opens into the braincase. Pterygoids with relatively triangular depression on ventral surface from basicranial towards orbital foramen. The parasphenoid bears teeth along its lateral borders. These teeth are sharp and pointed. Teeth rows are getting close together anteriorly. The parasphenoid is the largest bone in the skull. The quadrate is a small bone located in anterior side of squamosal. The orbitosphenoid is thin and delicate bone forming two posterolateral parts of the orbit. The orbitosphenoid is located in the orbital region and makes an optic foramen posteriorly to pass of the optic nerves into the cranial cavity. The orbitosphenoid joints exoccipital ventroposteriorly.

Size of otic capsule is small to moderate and otic region of the braincase containing fenestra ovalis that is not expanded laterally. The exoccipital forms the poste-

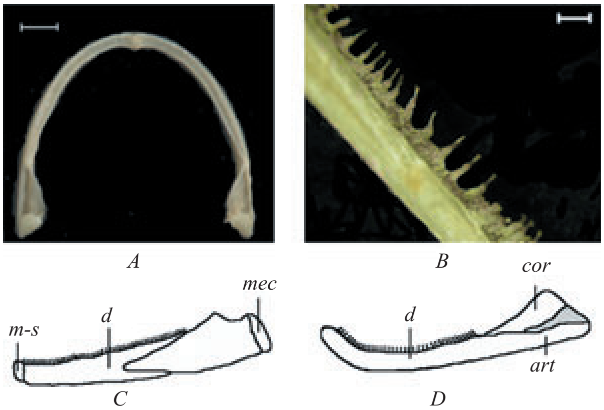

Fig. 2. Lower jaw of *Neurergus microspilotus* in dorsal view, scan (*A*); anterior part of the right jaw ramus in medial view, scan (*B*); right ramus of the lower jaw in medial (*C*) and lateral (*D*) views, explanatory drawings. See *Material and Methods* for details of image preparation. **Abbreviations:** *art*, articular; *cor*, coronoid process; *den*, dentary; *mec*, meckel s cartilage; *m-s*, mandibular symphysis; *prti*, prearticular (Duellman and Schlager, 2004). Scale bars are 2 (*A*) and 0.2 mm (*B*).

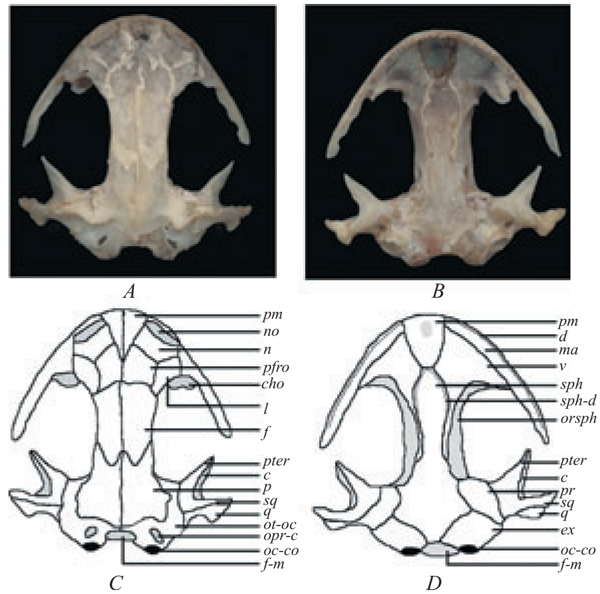

Fig. 3. Dorsal (*A*, *C*) and ventral (*B*, *D*) views of the skull of *S. i. semenovi*. Scans (*A*, *B*) and explanatory drawings (*C*, *D*). See *Material and Methods* for details of image preparation. For abbreviations see Fig. 1. Scale bar is 2 mm.

rior part of the skull base. Exoccipitals are trapezoid-shaped ventrally, paired but never meet at midline. They contact with the parietal anteriorly and squamosal laterally.

Mandible (Fig. 2*A*). Includes articular, dentary and coronoid. The shape of the lower jaw (mandible) as a whole is a simple solid bony arch. The dentary forms the main element of the mandible. The two parts of the mandible are connected medially by mandibular symphysis which is cartilaginous. Teeth are weakly connected with mandible and located on the dentary bone.

Dentitions (Fig. 2*B* – *D*). The number of maxillary and parasphenoid teeth is presented in Table 1. The vomerian teeth are absent. The teeth of the lower jaw are loosely attached to the bone.

Salamandra infraimmaculata semenovi (Nesterov, 1916)

Skull (Fig. 3). The observations on skull of *Salamandra* showed that the structure of skull is not compact and its mineralization is weak. Parts of snout are soft and made of cartilage, poorly ossified. The upper jaw is composed of paired premaxillae which at the rostral tip of the skull being laterally adjacent. The premaxillary pars dentalis overlaps the laterally positioned maxillaries, each narrow maxillary bone forms a broad process, which themselves extended posterolaterally to the level of the center of each orbit. The dorsal maxillary process ending in two lobes directed posterodorsally up to the frontals, laterally also touching the nasal and prefrontal. Each nasal is as long as the prefrontal plus width of lacrimal. The nasal meets the maxilla laterally, premaxilla medially and lacrimal and prefrontal posteriorly. The prefrontal is rectangular, by separating nasal from frontal, meets the nasal, and lacrimal laterally, premaxilla medially and frontal posteriorly. The lacrimal is a long and slender element, rectangular and enters the margin of orbit laterally, contacts the nasal anteriorly, prefrontal medially and frontal posteriorly. The frontal is large and smooth, completely ossified, with a little obliquation an-

TABLE 1. The Number of Examined Skulls, Mandibular, and Parasphenoid Teeth in *Neurergus microspilotus* and *Salamandra infraimmaculata semenovi*

Species	Number of skulls examined	Number of teeth on each half mandible	Number of parasphenoid on each side
Neurergus microspilotus	6	70 – 75	37 – 40
Salamandra infraimmaculata semenovi	6	35 – 37	37 – 40

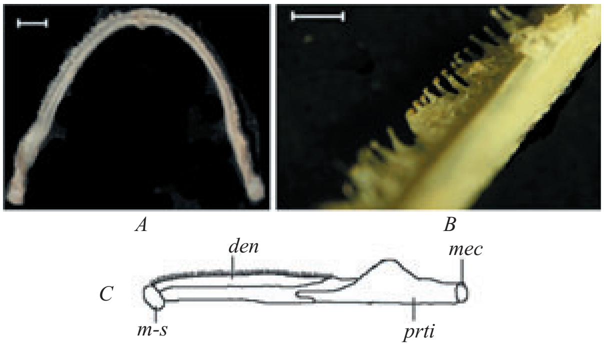

Fig. 4. Lower jaw view of *S. i. semenovi* in dorsal view, scan (*A*); part of the right jaw ramus in medial view, scan (*B*); right ramus of the lower jaw in medial (*C*) view, explanatory drawing. See *Material and Methods* for details of image preparation. For abbreviations see Fig. 2. Scale bars are 1 (*A*) and 0.4 mm (*B*).

teromedially, enters the orbit laterally, meets the prefrontal and lacrimal anteriorly and parietal posteriorly. The parietal is smooth and flattened. It enters the orbits laterally, contacts frontals anteriorly, and overlaps the prootic-exooccipitals posteriorly; where it meets squamosal to form a crest. The squamosal is almost vertical, producing a sharp nodule, dorsally; it meets parietal anteriorly, exoccipital posteriorly and joins quadrate ventrally. Mineralization of the palate and associated structures is weak in the anterior portion of the skull. The vomer bone is arch-shaped, becomes wider towards the nostril, forms choana near the maxilla, and a tangent with the orbit. The vomer bone just makes a pit near the premaxilla, between the nasals that is the beginning of braincase. This pit is long and oval shaped. The pterygoid consists of an ossified portion posteriorly and cartilaginous portions anteriorly in its end points.

The parasphenoid teeth begin on the edge of the bone that is S-shaped and it is one of the best diagnostic features of the genus. The parasphenoid is divided into two parts laterally, not well ossified, membranous in some parts. The parasphenoid teeth are located in anterior and marginal surfaces of parasphenoid. There is a rather big optic foramen located in the posterior part of the orbitosphenoid. The parasphenoid bone contacts with the exoccipital posterodorsally. Orbitosphenoid ossification was absent in the examined specimens.

Exoccipital is paired in ending parts of skull; it meets prootic laterally, and parasphenoid anteriorly. The prootic is located between parasphenoid and squamosal; it meets parasphenoid medially and exoccipital laterally. The caudal portion of exoccipital bone is thin and gracile. It meets foramen magnum posteriorly, parietal anteriorly and squamosal laterally, where it forms a cavity. Occipital condyles form the margin of foramen magnum. Occipital condyles are located at the posterior end of the exoccipital bones, being short and firm.

Mandible (Fig. 4*A*). The mandible is composed of articular, coronoid process, dentary, meckel s cartilage, mandibular symphysis, prearticular. Lower jaw is firm and elongated, with the same thickness throughout its whole parts. The two parts of dentary join to form mandibular symphysis anteriorly, lower jaw forms articular bone which is trigonal-shaped, the tip upward and the base towards mandible. The articular is not being firm; a part of it that connects to the upper part of mandible is membranous and semi-cartilaginous. Toward mandible externally, the prearticular produces the coronoid process that is an extra part.

Dentitions (Fig. 4*B*, *C*). Teeth are loosely connected with mandible and located on the dentary bone. The teeth occur on jaw rim inwardly close to the maxillary bone, marginal teeth are pleurodont and are situated in a continuous groove. They are thin, cylindrical and transparent with a distinct crown and pedicel, crowns separated to some extent. The number of the teeth is shown in Table 1.

DISCUSSION (A COMPARATIVE APPROACH)

For decades the urodele skull has been the subject of numerous comparative studies (Noble, 1931; Ehmcke and Clemen, 2000, 2006). Most skull structures of the mentioned salamanders are still poorly understood and the study of the species skull is still an active field. One of the earliest investigations to describe the skull in any detail was made by Duges (1834). As well, Stadtmuller (1924) has undertaken a complete and detailed reinvestigation of the development of the skull of some salamandrids and his works have been accepted as a basis for further investigations on the subject. The structure of ossified elements of the skull as modified by metamorphosis is a key aspect in urodele systematics (e.g., Wilder, 1925; Noble, 1931; Laurent, 1947; Regal, 1966; Hanken and Hall, 1993). The skulls of six spices of plethodontid salamanders of the genus *Bolitoglossa* were comparatively analyzed by Ehmcke and Clemen (2006). Differences in head and body form, adult size, cranial osteology, and maxillary and vomerian teeth counts separate species of the genus *Bolitoglossa* Duméril et Bibron, 1854 (James and David, 2005). Two cranial characters that provide synapomorphies for subgroups of salamandrids (Titus and Larson, 1995) include: presence of a frontosquamosal arch as a derived characteristic found in all the newts (except *Triturus* Rafinesque,

1815) but in no other salamandrids. And also fusion of the premaxillary bones is a synapomorphy of all the newts excluding the genera *Pleurodeles* Michahelles, 1830, *Salamandrina* Fitzinger, 1826, and *Tylototriton* Anderson, 1871. Although this character has arisen independently in other salamanders (Wake and Larson, 1987). Other cranial characteristics show more complex patterns of evolution in the Salamandridae. Differences in cranial osteology, maxillary and vomerian teeth counts separate all the recognized taxa of salamandrids from one another (James and David, 2005).

The skulls of the species presented in this study are different so that the skull structures and bony elements are more compact and more mineralized in *Neurergus microspilotus* than in *Salamandra infraimmaculata semenovi*.

The *N. microspilotus* skull being smaller, upper part of it is flattened and the snout being shorter; all of the skull parts are almost mineralized bony; although a small part of it is still cartilaginous. The skull roof in *N. microspilotus* having some overlapped parts. On the other hand, the skull of *S. i. semenovi* being larger and higher than that of *N. microspilotus*, and its upper part is arch-shaped.

The skull is generally broader in *S. i. semenovi* than in *N. microspilotus*. The cranial characters and the number of characters of N. micropilotus show a general similarity to those of *S. i. semenovi*, but there are several noteworthy differences as well, of these, the following differences may be mentioned. The prefrontal is triangular in *N. microspilotus* but squarish in *S. i. semenovi*. The frontal is enlarged in *N. microspilotus* with an ossified process in orbit side that connects to the squamosal by a cartilaginous part and forms a ring in the corner of orbit; the ending part of the frontal is W-shaped with a little overlap towards the parietal in *S. i. semenovi*. The frontal in the connection site with parietal in *S. i. semenovi* becomes elliptical, continued to the middle of head. The parietal in *N. microspilotus* is flat, broad and covers a small part of lateral margin of orbit, but in *S. i. semenovi* it is elongated and most part of the lateral edge of the eye is covered by it. The orbit in *S. i. semenovi* is larger than that of *N. microspilotus*. The occipital in *N. microspilotus* is protracted into two directions with a little connection, but in *S. i. semenovi* the incline of these two pieces of bone to the extremes is markedly decreased and the degree of their connection significantly increased. The pterygoid in *N. microspilotus* is short and weakly cartilaginous, whereas this bone in *S. i. semenovi* is larger, narrow and a great part of it is cartilaginous. The form of the palatal bones in both species showing prominent differences, so that the mouth floor is short in *N. microspilotus* and long in *S. i. semenovi*. The premaxilla in *N. microspilotus* is distinct and ossified but in *S. i. semenovi* it is unmarked, soft and membranous. The vomer in *N. microspilotus* is distinct and in the proximal part of the bone there is a pore that opens upward. In *S. infraimmaculata semenovi* there is no prominent frontier between premaxilla and vomerian bones. The sphenoid forms a part of the skull contacting the orbit. Related to the form of dentition, since there are just slight differences in shape of the teeth in various regions of the mouth, so dentition is termed homodont. The parasphenoid teeth seem to serve and retain the roof of the mouth in both species. There is a foramen between the two parts of premaxillary bones in *N. microspilotus* that opens out into the palate, while there is no foramen in *S. i. semenovi* and the two parts of premaxilla are fused together. In *S. i. semenovi*, there is a relatively large distance between the nostrils, and premaxillae are almost triangular, but in *N. microspilotus* the base of premaxillae are upward and distance between nostrils is small and nostrils are tangent together that is where both parts of premaxilla are narrow. In *N. microspilotus* the maxillary bone is more flattened and thicker than that of *S. i. semenovi*. The nasal bone is long and is elongated in the length of skull roof in *N. microspilotus*, but in *S. i. semenovi* the nasal bone is elongated horizontally in the skull roof.

The frontosquamosal arch is present in *N. microspilotus* (Fig. 1*A*), but absent in *S. i. semenovi*. Naylor (1978) has suggested that the frontosquamosal arch of newts is an anti-predator adaptation designed to add structural support to the skull and protect retracted eyes. The skull of *Salamandra* showed that its structure not being compact and mineralization is weak; parts of snout are soft transparent, and often tend to be flexible. In a similar study, it is shown that the skull of the plethodontid salamanders is membranous and flexible (Ehmcke and Clemen, 2006).

In short, our study shows that there are distinct differences in cranial osteology between the two studied genera and species of the Iranian Plateau salamandrids (i.e., *Neurergus microspilotus* and *S. i. semenovi*). Less ossification in *S. i. semenovi* agrees with the primitive position of this taxon comparing to more derived taxon, *Neurergus*, based on Steinfartz et al., 2007. To conclude, our data correspond to the recent phylogenetic and evolutionary studies of Salamandridae in that *S. i. semenovi* is a more primitive taxon than *N. microspilotus*.

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REFERENCES

Baloutch M. and Kami H. G. (1995), "Amphibians of Iran," *Tehran University Publications 2250*, **177**, 91 – 99.

Degani G. (1996), Salamandra salamandra *at the Southern Limit of its Distribution*, Laser Pages Publishing Ltd.

Duellman E. W. and Schlager N. (2004), *Animal Life Encyclopedia. Second Edition. Vol. 6. Amphibians*, In association with the American Zoo and Aquarium Association.

Duges A. (1834), "Recherches sur osteologie et la myologie des Batraciens a leurs differens ages," part II, 155, Paris.

Ehmcke J. and Clemen G. (2000), "The structure and development of the skull of Costa Rican plethodontid salamanders (Amphibia: Urodela)," *Ann. Anat.*, **182**, 537 – 547.

Ehmcke J. and Clemen G. (2006), "The skull structure of six species of Mesoamerican plethodontid salamanders (Amphibia: Urodela)," *Ann. Anat.*, **185**, 235 – 261.

Hanken J. and Hall B. (1993), "Mechanisms of skull diversity and evolution," in: J. Hanken and B. K. Hall (eds.), *The Skull. Vol. 3. Functional and Evolutionary Mechanisms*, Univ. Chicago Press, Chicago and London, pp. 1 – 36.

James H. and David B. (2005), "The solution to the large Black Salamander Problem (genus *Bolitoglossa*) in Costa Rica and Panama," *Copeia*, **2005**(2), 227 – 245.

Joger U. and Steinfartz S. (1994), "Zur subspezifischen Gliederung der südiberischen Feuersalamander (*Salamandra salamandra*-Komplex)," *Abh. Ber. Naturkunde*, **17**, 83 – 98.

Joger U. and Steinfartz S. (1995), " Protein electrophoretic of taxonomic problems in East Miditerranean *Salamandra* (Urodela: Salamandridae)," in: Lorente et al. (eds.), *Scientia Herpetologica*, pp. 33 – 36.

Laurent R. (1947), "La disposition des dents vomeriennes t chez les Urodeles superieurs et son importance phylogenetique," *Bull. Mus. Roy. d'Hist. Nat. Belg.*, **23**, 1 – 4.

Naylor B. G. (1978), "The frontosquamosal arch of newts as a defense against predators," *Can. J. Zool.*, **56**, 2211 – 2216.

Nesterov P. V. (1916), "Tri novykh khvostatykh amfibii is Kurdistana (Drei neue Formen von Amphibien aus Kurdistan)," *Ann. Mus. Zool. Acad. Sci. Petrograd*, **21**, 1 – 30.

Noble G. K. (1931), *The Biology of the Amphibians. Edition 1995*, Dover Publications, Inc.

Rastegar-Pouyani N. and Assadian S. (2003), "Analysis of geographic variation in *Neurergus microspilotus* (Caudata: Salamandridae)," in: *Proc. of the 11th Iranian Biol. Conf., August 23 – 25, 2003*, Urmia University, Urmia, Iran.

Rastegar-Pouyani N. and Faizi H. (2006), "On a collection of the Near East Fire Salamander, *Salamandra infraimmaculata semenovi* (Salamandridae), from Kurdistan province, Western Iran," *Zool. Middle East*, **37**, 115 – 118.

Regal P. J. (1966), "Feeding specializations and the terrestrial salamanders," *Evolution*, **20**, 392 – 407.

Romer A. Sh. and Parsons T. (1997), *The Vertebrate Body. 5th Edition*, W. B. Saunders Company.

Sharifi M. and Assadian S. (2002), "Distribution and conservation of *Neurergus microspilotus*," *Asiatic Herpetol. Res.*, **10**, 224 – 229.

Sharifi M. and Assadian S. (2005), "The reproductive cycle of *Neurergus microspilotus* in western Iran," *Russ. J. Herpetol.*, **12**(1), 63 – 68.

Stadtmuller F. (1924), "Über Entwichlung und Bau der papillenformigen Erhebungen (Filterfortsatze) auf den Branchialbogen der Salamandriden Larven, Zeitschr," *Morphol. Antropol.*, **24**, 125 – 156.

Steinfartz S., Veith M., and Tautz D. (2000), "Mitochondrial sequence analysis of *Salamandra* taxa suggests old splits of major lineages and postglacial recolonizations of Central Europe from distinct source populations of *Salamandra salamandra*," *Mol. Ecol.*, 9, 397 – 410.

Steinfartz S., Vicario S., Arntzen Jw., and Caccone A. (2007), "A Bayesian approach on molecules and behavior: reconsidering phylogenetic and evolutionary patterns of the Salamandridae with emphasis on *Triturus* newts," *J. Exp. Zool.*, **308**, 139 – 162.

Titus T. A. and Larson A. (1995), "A molecular phylogenetic perspective on the evolutionary radiation of the salamander family Salamandridae," *Syst. Biol.*, **44**, 125 – 151.

Wake D. B. and Larson A. (1987), "Multidimensional analysis of an evolving lineage," *Science*, **238**, 42 – 48.

Wilder I. (1925), *The Morphology of Amphibian Metamorphosis*, Smith College, Northampton, Mass.