Acta Herpetologica 7(2): 253-262, 2012

Morphological variability of the Hermann's tortoise (*Testudo hermanni*) in the Central Balkans

Katarina Ljubisavljević[1], Georg Džukić[1], Tanja D. Vukov[1], Miloš L. Kalezić[1,2]

[1] *Department of Evolutionary Biology, Institute for Biological Research "Siniša Stanković", University of Belgrade, Bulevar Despota Stefana 142, 11060 Belgrade, Serbia. Corresponding author.* E-mail: katarina.ljubisavljevic@ibiss.bg.ac.rs

[2] *Institute of Zoology, Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia*

Submitted on: 2012, 9th May; revised on: 2012, 4th June; accepted on: 2012, 10th July.

Abstract. Variation in a number of morphological characters were analysed in five populations of *Testudo hermanni* from Serbia and Montenegro. Tortoises from Serbia appeared significantly larger than those from Montenegro. An insular population of Montenegro was distinct due to its extremely small body size and mass and dark plastral pigmentation. Although the majority of tortoises had the supracaudal scute divided, many tortoises had the scute undivided. Effects of possible genetic divergence and/or adaptation to different environmental conditions on observed morphological variation were discussed.

Keywords. Land tortoises, Balkan Peninsula, morphological characteristics, plastral pigmentation, supracaudal scute.

INTRODUCTION

In the last decade, there has been a great deal of interest in the phylogeny, morphology and taxonomy of the land tortoises (Testudinidae) of the western Palaearctic (Van der Kuyl et al., 2002; Perälä, 2002a; Fritz et al., 2005, 2006, 2007, 2009; de Lapparent de Broin et al., 2006a, b; Parham et al., 2006; Fritz and Bininda-Edmonds, 2007). One *Testudo* species, the Hermann's tortoise (*T. hermanni* Gmelin, 1789) with a patchy distribution in the northern Mediterranean (Bour, 1997; Cheylan, 2001), is a particularly intriguing example for the complicated situation. It was placed in another genus by some authors (de Lapparent de Broin et al., 2006a, b) while others elevated its two subspecies to full species (*T. hermanni, T. boettgeri*) and recognized Dalmatian populations as a third species (*T. hercegovinensis*; Perälä, 2002b, 2004; Bour, 2004). Although these changes were not widely accepted (Fritz et al., 2006; Parham et al., 2006; Fritz and Bininda-Edmonds, 2007), the Balkan Peninsula yet appeared as a particularly important and intriguing area for the complex pattern of diversi-

ISSN 1827-9635 (print)
ISSN 1827-9643 (online)

fication within *T. hermanni*. Thus, the higher genetic diversity within the Balkan subspecies *T. h. boettgeri* compared with that in the western Mediterranean *T. h. hermanni* was found to be probably related to existence of several refugia in the Balkan Peninsula during the Pleistocene glaciations (Van der Kuyl et al., 2002; Fritz et al., 2006).

Up to now, the studies on populations of *T. hermanni* in the region of the central part of the Balkan Peninsula (Serbia and Montenegro) included aspects related to their ecology (Meek and Inskeep, 1981; Meek, 1985, 1989), sexual dimorphism (Đorđević et al., 2011) and commercial export and the impact of overharvesting (Ljubisavljević et al., 2011). However, some basic analyses, such as main morphological characteristics and their geographic variability, are still lacking.

Considering these facts, the main aim of this paper is to provide basic data about morphological characteristics of the Hermann's tortoise in the Central Balkans and to depict their variation pattern.

MATERIALS AND METHODS

Morphological parameters were analysed using five samples from Serbia and Montenegro (Fig. 1): 1. Limljani in Montenegro (42°12'N, 19°06'E, 156 m a.s.l.); 2. Starčevo Island in Lake Skadar in Montenegro (42°11'N, 19°13'E, 15 m a.s.l.); 3. Eastern Serbia (localities: Stara Brza, 44°28'N, 22°27'E, 67 m a.s.l.; Petrovo Selo, 44°37'N, 22°27'E, 435 m a.s.l. and Vratna monastery, 44°23'N,

Fig. 1. Map showing the distribution range of *T. hermanni* in the former Yugoslavia (shaded area) with the numbers referring to sampling areas for the examination of morphological variation (according to Ljubisavljević et al., 2011). 1. Limljani; 2. Starčevo Island; 3. Eastern Serbia; 4. Central Serbia; 5. Southern Serbia.

22°21'E, 165 m a.s.l.); 4. Central Serbia (localities: Kolare, 43°54'N, 21°14'E, 160 m a.s.l. and Ivković monastery 43°52'N, 21°13'E, 218 m a.s.l.); 5. Southern Serbia (locality: Starac Mt., 42°20'N, 21°52'E, 810 m a.s.l.). Samples from several populations at distinct localities in the eastern and central parts of Serbia were grouped together to obtain sufficient data for analysis.

Tortoises were spotted by walking through the habitat during daylight hours (9-18 h). They were measured and weighed in the field as described by Stubbs et al. (1984), photographed, and then released immediately afterwards at the point of capture. Sex was determined by plastral concavity and by the presence of larger tails in males in specimens larger than 10 cm carapace length. All animals smaller than 10 cm carapace length were considered to be juveniles (Stubbs et al., 1984) and were excluded from analysis because of possible ontogenetic variation in morphology (Guyot and Devaux, 1997). Since the size at maturity in *T. hermanni* varies substantially among localities (Willemsen and Hailey, 1999a), individuals were classified as male or female rather than as subadult, adult male or adult female (see Willemsen and Hailey, 2002).

The following quantitative parameters were recorded: M – body mass; SCL – midline straight carapace length, from the front of the nuchal scute, to the rear of the carapace; CW – carapace width (at widest point); CH – carapace height, the maximum vertical height from carapace to plastron. Mechanical calipers (0.1 mm precision) was used for measuring SCL, while other linear measurements were taken to the nearest mm using specially constructed at-bed calipers, a "tortometer" (Stubbs et al., 1984). M was taken with an electronic balance (1 g accuracy).

We considered as qualitative characteristics the supracaudal scute (undivided, divided) and the extent of plastral black pigmentation in eleven states distinguished by the degree and fragmentation of pigmentation on plastral plates (Fig. 2). This was done according to modified scheme of Guyot and Devaux (1997).

Descriptive statistics (mean, standard error, range) for quantitative traits, and percentages of states for each qualitative trait were calculated. For subsequent analyses, quantitative characters were log-transformed to ensure data normality and to generate homogeneous variances (Sokal and Rohlf, 1981). After assessing the normality of the distribution (Kolmogorov-Smirnov test) and homogeneity of variances (Bartlett test) the existence of significant geographic (among-localities) variation and sexual dimorphism was tested by analysis of variance (ANOVA) for SCL and by analysis of covariance (ANCOVA, with SCL as covariate) for other quantitative traits. Williams' corrected G test on actual counts was performed to examine differences in qualitative characters between sexes and among localities.

For quantitative traits, the Tukey HSD test for unequal sample sizes was used for average comparisons between samples. Preliminary analyses revealed no significant sex related variations in the frequencies of qualitative traits (Williams' corrected G test, $P > 0.05$, for all comparisons), and therefore, data from both sexes of the same sample were pooled for further analyses. All statistical analyses were performed using the computer package Statistica® (STATISTICA for Windows. StatSoft, Inc., Tulsa, OK).

RESULTS

Body size variation

Descriptive statistics of body size measurements of adult females and males from population samples are presented in Table 1. Sexual dimorphism in samples from Montenegro appeared to be weak and was limited to a significant intersexual difference in the CH and CW in Limljani population. On the other hand, samples from Serbia consistently showed significant sexual differences for SCL and CW. Overall, females had for all characters significantly higher values than males.

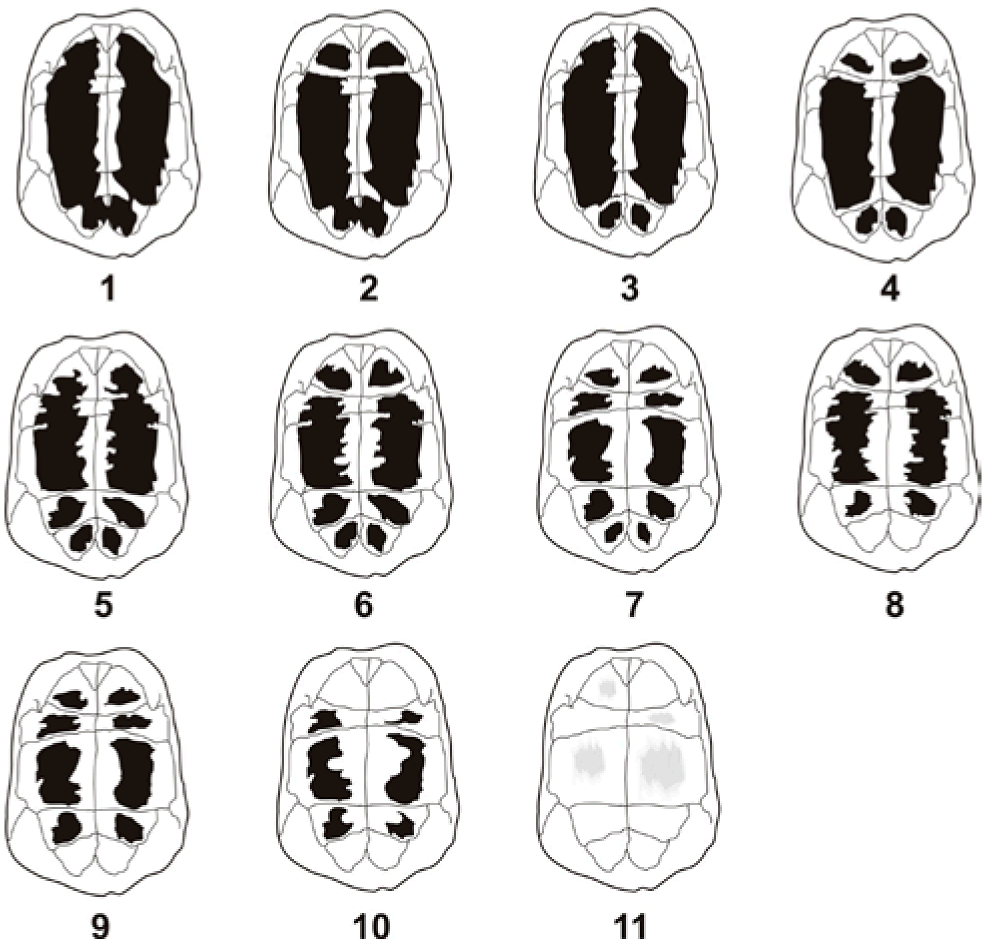

Fig. 2. Range of black plastral pigmentation (modified scheme of Guyot and Devaux, 1997): (1) continuous black pigmentation; (2) black spots on humeral scutes are isolated; (3) black spots on anal scutes are isolated; (4) black spots on anal and humeral scutes are isolated; (5) black spots on anal and femoral scutes are isolated; (6) black spots on anal, humeral and femoral scutes are isolated (7) black spots are isolated on each scute and reduced in size; (8) black spots are lacking on anal scutes, while on humeral and femoral scutes are isolated; (9) black spots are lacking on anal scutes, while on other scutes are isolated and reduced in size; (10) black spots are lacking on anal and humeral scutes, while on other scutes are isolated and reduced in size; (11) black pigmentation is lacking.

In females, statistically significant differences among samples were found for SCL, and M with SCL held constant (ANOVA, SCL: $F_{4,61} = 17.61$, $P << 0.001$; ANCOVA, M: $F_{4,60} = 7.18$, $P < 0.001$). Paired testing between the samples revealed significant differences in all comparisons (Tukey HSD test, $P < 0.001$) for M, while SCL significantly differed between samples from Montenegro and Serbia (Tukey HSD test, $P < 0.01$ in all comparisons). For this character, samples from Serbia showed significantly larger values compared with the samples from Montenegro.

Table 1. Descriptive statistics of quantitative characters of male and female *T. hermanni* from Serbia and Montenegro. Mean values of mass (M) are given in grams; all other measures are expressed in millimeters. It is also reported the statistical significance of differences between sexes (P) tested by ANOVA (for SCL) and ANCOVA with SCL as covariate (for other characters): ns, non significant; *, P < 0.05; **, P < 0.01; ***, P < 0.001. Abbreviations of characters are given in "Materials and Methods".

Character	Site	Males Mean ± SE (n; range)	Females Mean ± SE (n; range)	P
M	Limljani	800.00 ± 115.77 (8; 320.00 – 1350.00)	1016.48 ± 51.30 (21; 316.00 – 1420.00)	ns
	Starčevo Island	525.57 ± 80.84 (7; 288.00 – 805.00)	747.78 ± 120.22 (9; 258.00 – 1250.00)	ns
	Eastern Serbia	1146.00 ± 67.24 (15; 425.00 – 1550.00)	1577.94 ± 93.44 (18; 298.00 – 2035.00)	ns
	Central Serbia	1114.09 ± 71.72 (11; 650.00 – 1435.00)	1808.33 ± 87.64 (9; 1375.00 – 2160.00)	ns
	Southern Serbia	1237.50 ± 100.11 (10; 755.00 – 1685.00)	2025.56 ± 177.02 (9; 1080.00 – 2790.00)	*
CW	Limljani	119.50 ± 5.63 (8; 90.00 – 139.00)	125.14 ± 2.67 (21; 83.00 – 145.00)	*
	Starčevo Island	107.00 ± 8.09 (7; 79.00 – 138.00)	113.22 ± 7.50 (9; 82.00 – 143.00)	ns
	Eastern Serbia	149.25 ± 3.04 (16; 114.00 – 162.00)	155.56 ± 4.96 (18; 89.00 – 175.00)	**
	Central Serbia	151.00 ± 4.74 (11; 116.00 – 170.00)	165.11 ± 2.68 (9; 149.00 – 175.00)	***
	Southern Serbia	153.50 ± 4.57 (10; 130.00 – 173.00)	166.22 ± 5.17 (9; 137.00 – 185.00)	***
SCL	Limljani	151.00 ± 8.48 (8; 108.00 – 182.00)	164.62 ± 3.74 (21; 106.00 – 188.00)	ns
	Starčevo Island	132.57 ± 8.42 (7; 104.00 – 164.00)	145.67 ± 10.21 (9; 101.00 – 188.00)	ns
	Eastern Serbia	177.13 ± 4.35 (16; 126.00 – 206.00)	203.89 ± 6.11 (18; 108.00 – 229.00)	**
	Central Serbia	173.73 ± 4.11 (11; 143.00 – 193.00)	211.56 ± 3.82 (9; 195.00 – 229.00)	***
	Southern Serbia	182.80 ± 6.38 (10; 148.00 – 208.00)	218.11 ± 8.52 (9; 170.00 – 247.00)	**
CH	Limljani	77.38 ± 3.54 (8; 59.00 – 91.00)	86.67 ± 1.68 (21; 63.00 – 97.00)	**
	Starčevo Island	67.86 ± 3.28 (7; 57.00 – 79.00)	74.89 ± 4.23 (9; 56.00 – 89.00)	ns
	Eastern Serbia	89.44 ± 2.06 (16; 64.00 – 97.00)	86.67 ± 1.68 (18; 57.00 – 120.00)	ns
	Central Serbia	88.73 ± 2.31 (11; 75.00 – 98.00)	103.11 ± 2.23 (9; 93.00 – 113.00)	ns
	Southern Serbia	96.90 ± 3.48 (10; 77.00 – 111.00)	108.56 ± 4.18 (9; 88.00 – 126.00)	ns

In males, there were also significant differences in SCL between the samples (ANOVA, SCL: $F_{4,57} = 10.34$, $P < 0.001$), with the males from Starčevo Island (Montenegro) showing significantly lower values than Serbian samples (Tukey HSD test, $P < 0.01$). In addition, CW and CH significantly differed between the samples when SCL held constant (ANCOVA, CW: $F_{4,45} = 7.18$, $P < 0.001$; CH: $F_{4,45} = 3.09$, $P = 0.02$). Paired testing between the samples revealed significant differences in all comparisons for CH (Tukey HSD test, $P < 0.01$), while CW significantly differed between samples from Montenegro and Serbia (Tukey HSD test, $P < 0.001$ in all comparisons). For this variable, samples from Serbia showed significantly larger values than samples from Montenegro.

Qualitative characteristics

There was no statistically significant variance among samples with respect to the condition of the supracaudal scute ($G = 2.99$, $df = 4$, $P > 0.05$). In all samples, a divided scute prevailed, although an undivided scute also occurred in a considerable frequency (mean: 23.6%; SE: 7.5%; range: 14.3-33.3%).

The extent of plastral black pigmentation did not significantly vary among the samples ($G = 38.87$, $df = 40$, $P > 0.05$). Pairwise comparisons revealed a significant difference

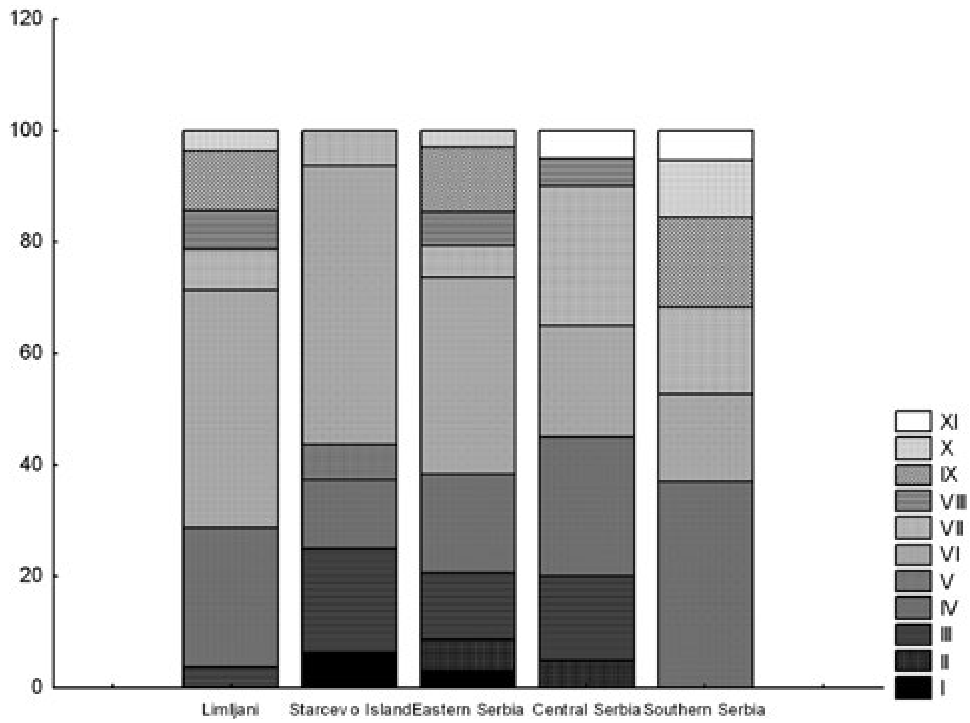

Fig. 3. Relative frequency (%) of black plastral pigmentation patterns in the five samples of *T. hermanni.* Shading corresponds to plastral pigmentation codes given in Fig. 2.

between the samples from Starčevo Island and Southern Serbia (G = 16.54, df = 8, P = 0.03) in that tortoises from the island had more dark pigmentation, and tortoises from Southern Serbia had lower and distinctly fragmented pigmentation. States 1, 2 and 3 were evident in 25% of specimens from Starčevo Island, but not in the sample from Southern Serbia; there were no states 9, 10 and 11 in the sample from the island, while in the sample from Southern Serbia they were present in approximately 32% of specimens. The highest heterogeneity was found in the sample from eastern Serbia, where nine out of 11 states were present, while the lowest was in samples from Starčevo Island and Southern Serbia, with six states in each. The fragmentation and reduced pigmentation were most evident in the sample from Southern Serbia (Fig. 3).

DISCUSSION

Population-specific variation and phenotypic plasticity in *Testudo* species are common (Guyot and Devaux, 1997; Široký and Fritz, 2007; Fritz et al., 2009). Accordingly, our results that the condition of the supracaudal scute previously considered as reliable diagnostic character for distinguishing *T. hermanni* (divided scute) and *T. graeca* (undivided scute) is variable, match this pattern. Other authors also indicated the presence of undivided scute in *T. hermanni* populations (Radovanović, 1941; Meek and Inskeep, 1981; Cheylan, 2001), thus limiting its reliability for taxonomic purposes. However, body size distinction between Serbian and Montenegrin populations of *T. hermanni boettgeri* may reflect molecular differences within this taxon, corresponding with the parapatric ranges of two mitochondrial haplotypes (B13 for Adriatic coast and B1 for inland Balkan populations; Fritz et al., 2006). The initial differentiation within *T. h. boettgeri* yet suggests limited gene flow, although the distribution gap corresponds to the zone of high mountains between Serbia and Montenegro, which represents major barriers in spreading of *T. hermanni* (Fritz et al., 2006). An alternative but not mutually exclusive hypothesis is that the variation in adult size of *T. hermanni* is adaptive, owing to variation in adult survival rates (e.g., larger the size and higher the survival) as suggested by Willemsen and Hailey (2001). In addition, the larger body size in Serbian vs. Montenegrin samples matches Bergmann's rule, as suggested previously for this species (Willemsen and Hailey, 1999a; Sacchi et al., 2007) and other chelonians (Ashton and Feldman, 2003). However, although the size and mass of tortoises from Serbia fit the latitudinal pattern presented in Willemsen and Hailey (1999a), the southern Serbian population appeared to be larger than the more northern ones. Although our survey was partly limited, due to a few samples of a modest size, our data could be in agreement with Willemsen and Hailey's (1999a) suggestion that body dimensions may reach a maximum north of Greece and then the energetic and thermoregulation may limit body size further north.

The insular Montenegrin population is characterized by small body size and mass and very dark plastral pigmentation. It appeared noticeably smaller than other mainland populations of the same subspecies (Willemsen and Hailey, 1999a; Cheylan, 2001), but within the range of some Adriatic populations (Meek and Inskeep, 1981; Meek, 1985, 1989). The presence of small-sized tortoises along the Adriatic coast could be explained by larger adult mortality correlated with higher environmental temperature causing the more frequent fires than in inland areas (Willemsen and Hailey, 1999a). Besides, the Starčevo population could also be the example of an "island dwarfism" prevalent generally in larger vertebrates (Lomolino, 2005) as well as in turtles (Georges, 1985; Aponte et al., 2003; Lomolino, 2005). This phenomenon is caused by limited resources and predatory release and is especially pronounced on smaller islands (Lomolino, 2005). Although the small islands of the Skadar lake are of relatively recent, postglacial origin (Stanković, 1976) it is known that genetic bottlenecks or environmental pressure can lead to substantial morphological changes in island tortoises over a short period of time (Georges, 1985; Aponte et al., 2003). On the other hand, there are many examples that such size differences in chelonians are not limited to island populations (e.g., Fritz et al., 2010, 2012). Considerable size differences may exist in different geographic regions within the same clade and could be the result of general phenotypic plasticity that appeared to play the major role in shaping external morphology of tortoises (Fritz et al., 2005, 2007, 2010, 2012).

Great inter- and intrapopulation variability in plastral pigmentation has already been observed among populations of *T. h. boettgeri* (Guyot and Devaux, 1997; Willemsen and Hailey, 1999b). Generally, isolation and/or climate may influence the origin and maintenance of high levels of melanism (Bittner and King, 2003). Increased dark plastral pigmentation in the southern populations of the Hermann's tortoise has been explained by thermal advantage in increasing heat loss to the substrate by infrared radiation during activity (Willemsen and Hailey, 1999b). In addition, darker pigmentation could be the result of genetic drift in small insular tortoise populations (Georges, 1982). It seems that both factors can play a role in the small-bodied southern insular population in Montenegro.

ACKNOWLEDGEMENTS

We would like to acknowledge the constructive improvements suggested by two anonymous reviewers and Marco Mangiacotti. We thank Miroslav Marković for help in the field and Ljiljana Tomović for valuable suggestions. This study was supported financially by the Serbian Ministry of Education and Science, grant no 173043.

REFERENCES

Aponte, C., Barreto, G., Terborgh, J. (2003): Consequences of habitat fragmentation of age structure and life history in a tortoise population. Biotropica **35**: 550-555.

Ashton, K.G., Feldman, C.R. (2003): Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. Evolution **57**: 1151-1163.

Bittner, T.D., King, R.B. (2003): Gene flow and melanism in garter snakes revisited: a comparison of molecular markers and island vs. coalescent models. Biol. J. Linn. Soc. **79**: 389-399.

Bour, R. (1997): *Testudo hermanni*. In: Atlas of Amphibians and Reptiles in Europe, p. 178-179. Gasc, J.P., Cabela, A., Crnobrnja-Isailović, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez Rica, J.P., Maurin, H., Oliveira, M.E., Sofianidou, T.S., Veith, M., Zuiderwijk, A., Eds, Societas Europaea Herpetologica and Museum National d'Histoire Naturelle (IEGB/SPN), Paris.

Bour, R. (2004): A new character for the identification of populations of the Hermann's tortoise, *Testudo hermanni* Gmelin, 1789. Salamandra **40**: 59-66.

Cheylan, M. (2001): *Testudo hermanni* Gmelin, 1789 - Griechische Landschildkröte. In: Handbuch der Reptilien und Amphibien Europas, Bd. 3/IIIA, Schildkröten I, pp. 179-289. Fritz, U., Ed, Aula-Verlag, Wiebelsheim.

Đorđević, S., Đurakić, M., Golubović, A., Ajtić, R., Tomović, L.M., Bonnet, X. (2011): Sexual body size and body shape dimorphism of *Testudo hermanni* in central and eastern Serbia. Amphibia-Reptilia **32**: 445-458.

Fritz, U., Široký, P., Kami, H., Wink, M. (2005): Environmentally caused dwarfism or a valid species – Is *Testudo weissingeri* Bour, 1996 a distinct evolutionary lineage? New evidence from mitochondrial and nuclear genomic markers. Mol. Phylogenet. Evol. **37**: 389-401.

Fritz, U., Auer, M., Bertolero, A., Cheylan, M., Fattizzo, T., Hundsdörfer, A.K., Martín Sampayo, M., Pretus, J.L., Široký, P., Wink, M. (2006): A rangewide phylogeography of Hermann's tortoise, *Testudo hermanni* (Reptilia: Testudines: Testudinidae): implications for taxonomy. Zool. Scr. **35**: 531-543.

Fritz, U., Bininda-Emonds, O.R.P. (2007): When genes meet nomenclature: Tortoise phylogeny and the shifting generic concepts of *Testudo* and *Geochelone*. Zoology **110**: 298-307.

Fritz, U., Hundsdörfer, A.K., Široký, P., Auer, M., Kami, H., Lehmann, J., Mazanaeva, L.F., Türkozan, O., Wink, M. (2007): Phenotypic plasticity leads to incongruence between morphology-based taxonomy and genetic differentiation in western Palaearctic tortoises (*Testudo graeca* complex; Testudines, Testudinidae). Amphibia-Reptilia **28**: 97-121.

Fritz, U., Harris, D.J., Fahd, S., Rouag, R., Graciá Martínez, E., Giménez Casalduero, A., Široký, P., Kalboussi, M., Jdeidi, T.B., Hundsdörfer, A.K. (2009): Mitochondrial phylogeography of *Testudo graeca* in the Western Mediterranean: old complex divergence in North Africa and recent arrival in Europe. Amphibia-Reptilia **30**: 63-80.

Fritz, U., Daniels, S.R., Hofmeyr, M.D., González, J., Barrio-Amorós, C.L., Široký, P., Hundsdörfer, A.K., Stuckas, H. (2010): Mitochondrial phylogeography and subspecies of the wide-ranging sub-Saharan leopard tortoise *Stigmochelys pardalis* (Testudines: Testudinidae) – a case study for the pitfalls of pseudogenes and GenBank sequences. J. Zool. Sys. Evol. Res **48**: 348-359.

Fritz, U., Alcalde, L., Vargas-Ramírez, M., Goode, E.V., Fabius-Turoblin, D.U., Praschag, P. (2012): Northern genetic richness and southern purity, but just one species in the *Chelonoidis chilensis* complex. Zool. Scr. **41**: 220-232.

Georges, A., (1982): Ecological studies of Krefft's River Tortoise, *Emydum krefftii* (Gray), from Fraser Island, Queensland. Unpublished doctoral dissertation. University of Queensland, Brisbane.

Georges, A. (1985): Reproduction and reduced body size of reptiles in unproductive insular environments. In: Biology of Australasian Frogs and Reptiles, pp. 311-318. Grigg, G., Shine, R., Ehmann, H., Eds, Surrey Beatty and Sons, Sydney.

Guyot, G., Devaux, B. (1997): Variation in shell morphology and color of Hermann's tortoise, *Testudo hermanni*, in southern Europe. Chelonian Conserv. Biol. **2**: 390-395.

de Lapparent de Broin, F., Bour, R., Parham, J.F., Perälä, J. (2006a): *Eurotestudo*, a new genus for the species *Testudo hermanni* Gmelin, 1789. C.R. Palevol. **5**: 803-811.

de Lapparent de Broin, F., Bour, R., Perälä J. (2006b): Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): First part. Ann. Pal. **92**: 385-386.
Ljubisavljević, K., Džukić, G., Kalezić, M.L. (2011): The commercial export of the land tortoises (*Testudo* spp.) from the territory of the former Yugoslavia: a historical review and the impact of overharvesting on wild populations. North-West. J. Zool. **7**: 250-260.
Lomolino, M.V. (2005): Body size evolution in insular vertebrates: generality of the island rule. J. Biogeogr. **32**: 1683-1699.
Meek, R. (1985): Aspects of the ecology of *Testudo hermanni* in southern Yugoslavia. Brit. J. Herpetol. **6**: 437-445.
Meek, R. (1989): The comparative population ecology of Hermann's tortoise, *Testudo hermanni* in Croatia and Montenegro, Yugoslavia. Herpetol. J. **1**: 404-414.
Meek, R., Inskeep, R. (1981): Aspects of the field biology of a population of Hermann's tortoise (*Testudo hermanni*) in southern Yugoslavia. Brit. J. Herpetol. **6**: 159-164.
Parham, J.F., Macey, J.R., Papenfuss, T.J., Feldman, C.R., Türkozan, O., Polymeni, R., Boore, J. (2006): The phylogeny of Mediterranean tortoises and their close relatives based on complete mitochondrial genome sequences from museum specimens. Mol. Phylogenet. Evol. **38**: 50-64.
Perälä, J. (2002a): The genus *Testudo* (Testudines: Testudinidae): phylogenetic inferences. Chelonii **3**: 32-39.
Perälä, J. (2002b): Biodiversity in relatively neglected taxa of *Testudo* L., 1758 s. l. Chelonii **3**: 40-53.
Perälä, J. (2004): *Testudo hercegovinensis* Werner, 1899. Manouria **7**: 19-20.
Radovanović, M. (1941): Zur Kenntnis der herpetofauna des Balkans. Zool. Anz. **136**: 145-159.
Sacchi, R., Pupin, F., Rosa, D.P., Fasola, M. (2007): Bergmann's rule and the Italian Hermann's tortoises (*Testudo hermanni*): latitudinal variations of size and shape. Amphibia-Reptilia **28**: 43-50.
Široký, P., Fritz, U. (2007): Is *Testudo werneri* a distinct species? Biologia **62**: 228-231.
Sokal, R.R., Rohlf, F.J. (1981): Biometry. Freeman, San Francisco.
Stanković, S. (1976): Jezera sveta. Mala biblioteka Srpskog geografskog društva, Beograd.
Stubbs, D., Hailey, A., Pulford, E., Tyler, W. (1984): Population ecology of European tortoises: review of field techniques. Amphibia-Reptilia **5**: 57-68.
Van der Kuyl, A.C., Ballasina, D.L.P., Dekker, J.T., Maas, J., Willemsen, R.E., Goudsmit, J. (2002): Phylogenetic relationships among the species of the genus *Testudo* (Testudines: Testudinidae) inferred from mitochondrial 12S rRNA gene sequences. Mol. Phylogenet. Evol. **22**: 174-183.
Willemsen, R.E., Hailey, A. (1999a): Variation of adult body size of the tortoise *Testudo hermanni* in Greece: proximate and ultimate causes. J. Zool. **248**: 379-396.
Willemsen, R.E., Hailey, A. (1999b): A latitudinal cline of dark plastral pigmentation in the tortoise *Testudo hermanni* in Greece. Herpetol. J. **9**: 125-132.
Willemsen, R.E., Hailey, A. (2001): Variation in adult survival rate of the tortoise *Testudo hermanni* in Greece: implications for evolution of body size. J. Zool. **255**: 43-53.
Willemsen, R.E., Hailey, A. (2002): Body mass condition in Greek tortoises: regional and interspecific variation. Herpetol. J. **12**: 105-114.