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Phalangeal formulae and ontogenetic variation of carpal morphology in *Testudo horsfieldii* and *T. hermanni**

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Abstract. We compared variation in phalangeal and carpal morphology of the Central Asian *Testudo horsfieldii*, a burrow-digging tortoise species, with its sister taxon *T. hermanni*, a Mediterranean species without extensive digging behaviour. Thirty-two *Testudo horsfieldii kazachstanica* shared the same phalangeal formula (0-2-2-1-1). The distal carpal 1 and metacarpal I as well as the pisiform were consistently lacking, sometimes also the medial centrale. Phalangeal morphology was more variable in *Testudo hermanni hermanni*. In 29 specimens four phalangeal formulae were found that differed with respect to the reduction of digit 1 (1-2-2-2-1, M-2-2-2-1, D-2-2-2-1, 0-2-2-2-1). The pisiform develops late in ontogeny and is lacking in very most juveniles and subadults. In contrast to *T. h. kazachstanica*, the medial centrale is always present. In both *T. h. kazachstanica* and *T. h. hermanni* carpalia increasingly fuse with age and size. The underlying morphological patterns differ however. The extreme character state in aged *T. h. kazachstanica* is one large solid bone element, formed by the fused intermedium, ulnare and both centralia. Aged *T. h. hermanni* have, in contrast, two separate larger carpal elements, one formed by the fused lateral and medial centralia and the other by the fused distal carpalia 1 and 2; the intermedium and ulnare never fuse with one another or with other carpalia. While a partial or complete loss of digit 1 seems to be characteristic for all *Testudo* species, we propose that the extensive fusion of carpal elements in *T. horsfieldii* is correlated with its natural history because a rigid manus could be advantageous for burrow-digging. Also the reduction of digit 4 (one phalanx present), a rare character among testudinids and not occurring in other *Testudo* species, could be linked with its mode of life.

Keywords: comparative analysis, morphology, phalangeal formula, tortoises.

Introduction

The Central Asian tortoise (*Testudo horsfieldii*) is a small to medium-sized species, reaching a maximum shell length of less than 30 cm. It occurs in dry and open landscape types, such as steppe, semi-deserts and deserts – all extreme continental climates. Unlike many tortoises, Central Asian tortoises spend a considerable part of their life in burrows, which are typically self-dug, to cope with harsh climatic conditions (e.g. Bonnet et al., 2001; Kuzmin, 2002; Lagarde et al., 2002). The morphology of the powerful forelegs of *T. horsfieldii* may be correlated with this burrowing mode of life. This species possesses fewer phalanges than any other testudinid species; the first digit is entirely lost, and in the second and fourth digit only one or two phalanges are present; in the fifth digit only one. There are only few other tortoise taxa with four digits in the manus (*Homopus areolatus*, *H. femoralis*, *Kinixys belliana nogueyi*); and, as a general rule, two phalanges occur in digits 2-4. Other burrow-digging species (*Chelonoidis chilensis*, *Geochelone sulcata*, *Gopherus* spp.) have five digits in the manus (Crumly and Sánchez-Villagra, 2004).

In a study dealing with the hand skeleton of testudinids, Crumly and Sánchez-Villagra (2004) described phalangeal formulae and report some observations on carpal morphology of four *T. horsfieldii*. In the present paper we use a distinctly larger series of *T. horsfieldii* to investigate variation of phalangeal and carpal morphology. We compare our data with the similar-sized *T. hermanni*, the sister taxon of *T. horsfieldii* (Fritz and Bininda-Emonds, 2007), and place our observations in a phylogenetic context using data from Crumly and Sánchez-

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Villagra (2004) for the other three *Testudo* species that constitute the sister group of *T. hermanni* + *T. horsfieldii* (Fritz and Bininda-Emonds, 2007). *Testudo hermanni*, although closely related with *T. horsfieldii*, is adapted to a Mediterranean climate and displays no extensive digging behaviour (Cheylan, 2001). Therefore, shared character states should reflect common ancestry whereas unique characters of *T. horsfieldii* are likely to be correlated with its natural history.

Materials and methods

Studied specimens are housed in the herpetological collection of the Museum of Zoology Dresden (Museum für Tierkunde, MTD). To avoid any possible bias of subspecies-specific variation within each species, we selected only individuals representing the same subspecies (*Testudo horsfieldii kazachstanica* and *Testudo hermanni hermanni*). Except two skeletons of *T. h. kazachstanica*, all tortoises were alcohol-preserved. According to size and external morphology (shell scutes with clear or worn-off annuli, zigzagged plastral seams or not), tortoises were assigned to three age classes (juvenile, subadult, adult). Per age class 9-12 specimens were studied for each species (32 *T. h. kazachstanica*, 29 *T. h. hermanni*; tables 1, 2). For each individual, straight line carapacial length was measured to the nearest millimetre using a calliper. Radiographies of forefeet of alcoholic specimens were taken using a Faxitron x-ray cabinet; phalangeal formulae and observed variation in carpal morphology was recorded. Where appropriate, variation was compared using the chi^2 test. Coding of phalangeal formulae follows Crumly and Sánchez-Villagra (2004). For instance, 1-2-2-2-2 indicates that one phalanx is present in the first digit; two phalanges occur in digits 2-5.

Results

Testudo horsfieldii kazachstanica

In all 32 tortoises the same phalangeal formula was found (0-2-2-1-1); the distal carpal 1 and metacarpal I as well as the pisiform were always lacking. In other respects, carpal morphology varied considerably (figs 1, 2; table 1). The three age classes differed highly significant with respect to the occurrence of fused carpalia ($p <$ 0.001, chi^2 test; $N = 61$, number of extremities). In nine of the 10 juveniles, all carpal elements were separate. Only in the largest juvenile (MTD 35742, carapace length 99 mm) the two centralia were fused in both hands. In subadult tortoises, fused and separate carpal elements occurred at approximately the same frequency while all adults had carpal elements fused. In subadults the fusion of carpals is often asymmetric. The extent of fusion increased considerably with age and size, resulting in aged adults (MTD 4908, 11130, 43913) in the extreme con-

Table 1. Variation of carpal morphology in *Testudo horsfieldii kazachstanica*. Carapacial length and age do not correspond entirely, explaining why subadults are not necessarily smaller than adults. (a) All bones separate; (b) $cl + cm$ fused; (c) $i+u$ fused; (d) $i+u+cl$ fused; (e) $i+u+cl+cm$ fused; * *cm* lacking; ** *D-5* lacking (fused with *M-V*?). Abbreviations: *cl* lateral centrale, *cm* medial centrale, *D* distal carpal, *i* intermedium, *M* metacarpal, *u* ulnare (see also fig. 1); MTD Museum of Zoology Dresden. In contrast to the findings by Crumly and Sánchez-Villagra (2004), the fourth distal carpal contacts not always intermedium and ulnare.

				Carpalia	
Age class	MTD	Sex	Carapacial length (mm)	Left	Right
Juvenile	45309	?	46	a*	?
	45311	?	57	a*	a*
	46245	?	58	a*	a*
	45310	?	67	a*	a*
	3929	?	71	a	a
	41366	?	74	a*	a
	40276	?	82	a	a
	39569	?	95	a*	a*
	3539	?	96	a	a
	35742	?	99	b	b
Subadult	28055	♂	109	a	b
	45844	♂	117	a*	a*
	7185	♂	119	c**	c**
	43335	♂	120	a	b
	3928	♂	122	c	?
	3932	♂	122	c*	c*
	3934	♂	123	a	a
	7184	♂	123	c**	a
	43336	♂	130	a*	a
	3930	♂	134	a	c*
	11131	♀	124	c	a
	3935	♀	127	c	c
Adult	3936	♂	117	c*	c*
	3937	♂	118	d*	d*
	3931	♂	119	d*	d*
	43913	♂	119	e	e
	11130	♂	135	e	e
	38233	♂	136	d*	d*
	11125	♀	172	c*	c*
	11127	♀	172	?	d*
	11128	♀	178	d*	d*
	4908	♀	205	e	c

Table 2. Variation of phalangeal formulae of the manus and carpal morphology in *Testudo hermanni hermanni*. Reduced phalangeal formulae in bold; M-2-2-2-1 indicates that phalanx 1 (*P-1*) is lacking but *M-1* and *D-1* present; D-2-2-2-1, *P-1* and *M-1* lacking but *D-1* present; 0-2-2-2-1, digit 1 entirely lacking (*P-1*, *M-1* and *D-1* lacking). (A) All carpalia and metacarpalia separate; (B) *cl* + *cm* fused; (C) *D-1* + *D-2* fused; (D) *D-1* + *M-1* fused; ^{p} pisiform present. For abbreviations, see also table 1.

Age class	MTD	Sex	Carapacial length (mm)	Phalangeal formula		Carpalia	
				Left	Right	Left	Right
Juvenile	44883	?	45	**M-2-2-2-1**	**M-2-2-2-1**	A	A
	31466	?	54	1-2-2-2-1	1-2-2-2-1	A	A
	44882	?	56	1-2-2-2-1	1-2-2-2-1	A	A
	36949	?	67	1-2-2-2-1	1-2-2-2-1	A	A
	36950	?	67	**0-2-2-2-1**	**D-2-2-2-1**	A	A
	36952	?	67	1-2-2-2-1	**D-2-2-2-1**	A	A
	36959	?	69	1-2-2-2-1	**M-2-2-2-1**	A^{p}	A
	39112	?	74	**0-2-2-2-1**	**0-2-2-2-1**	A	A
	36948	?	76	**0-2-2-2-1**	**0-2-2-2-1**	A	A
	32834	?	78	1-2-2-2-1	1-2-2-2-1	A	D
Subadult	32833	♂	94	**0-2-2-2-1**	?	B	?
	42904	♂	98	1-2-2-2-1	1-2-2-2-1	B,C	B,C
	39772	♂	100	1-2-2-2-1	**0-2-2-2-1**	A	B
	41969	♂	103	1-2-2-2-1	1-2-2-2-1	B	B
	41970	♂	104	**D-2-2-2-1**	**D-2-2-2-1**	A	A
	39773	♀	97	1-2-2-2-1	1-2-2-2-1	A	B
	36942	♀	106	1-2-2-2-1	1-2-2-2-1	A	B
	40533	♀	118	1-2-2-2-1	**D-2-2-2-1**	A	A
	36941	♀	125	1-2-2-2-1	1-2-2-2-1	D	A
Adult	39771	♂	105	1-2-2-2-1	1-2-2-2-1	B,C^{p}	B,C^{p}
	39770	♂	114	**M-2-2-2-1**	**D-2-2-2-1**	C	B^{p}
	39769	♂	118	1-2-2-2-1	1-2-2-2-1	B,C^{p}	B,C^{p}
	46140	♂	126	1-2-2-2-1	1-2-2-2-1	C^{p}	C^{p}
	46135	♂	131	1-2-2-2-1	1-2-2-2-1	C^{p}	B,C^{p}
	46138	♂	133	1-2-2-2-1	1-2-2-2-1	B^{p}	B,C^{p}
	46139	♂	135	1-2-2-2-1	1-2-2-2-1	C^{p}	B,C^{p}
	45835	♀	146	**0-2-2-2-1**	**0-2-2-2-1**	B	B
	40647	♀	148	?	**0-2-2-2-1**	?	A^{p}
	46137	♀	154	1-2-2-2-1	**D-2-2-2-1**	B,C^{p}	B,C

dition of a solid large bone element formed by the intermedium, ulnare and both centralia. The presence or absence of the medial centrale differed between the three age classes significantly ($p < 0.05$); however, when the individual age classes are compared with one another, a significant difference occurred only between subadults and adults ($p < 0.01$), suggestive of no age-dependent variation. In MTD 7184 and 7185, subadult tortoises, the distal carpal 5 was lacking, perhaps due to fusion with metacarpal V.

Testudo hermanni hermanni *and comparison*

In the 29 studied *T. h. hermanni* four phalangeal formulae occurred that differ with respect to the reduction of digit 1 (table 2). In some cases, digit 1 was entirely lacking, including the first distal carpal and the first metacarpal. In other cases only the first distal carpal alone or the first distal carpal and the first metacarpal were present. Asymmetric characters states were quite frequent. Except one juvenile (MTD 36959, carapace length 69 mm), pisiforms were present only in adult tortoises. In contrast to *T. h. kazachstanica*, the medial centrale was much better developed (fig. 1) and always present.

In both species, fusion of carpalia increased with age and size. All juvenile *T. h. hermanni* except the largest one (MTD 32834, carapace

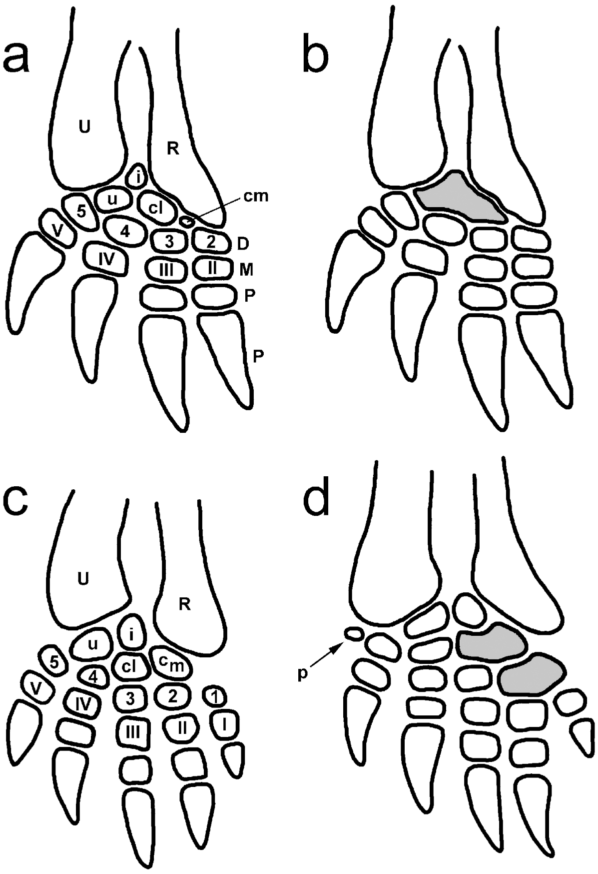

Figure 1. Right manus of *Testudo horsfieldii kazachstanica* (a: juvenile, b: adult; phalangeal formula: 0-2-2-1-1) and *Testudo hermanni hermanni* (c: juvenile, d: adult; phalangeal formula: 1-2-2-2-1). Note larger medial centrale in juvenile *T. h. hermanni* and distinct fusion patterns in both species. Fused bone elements, grey. Arrow indicates pisiform in adult *T. h. hermanni*. Abbreviations: *U* ulna, *R* radius, *i* intermedium, *u* ulnare, *cl* lateral centrale, *cm* medial centrale, *p* pisiform, *D* distal carpalia (1/2-5), *M* metacarpalia (I/II-V), *P* phalanges.

length 78 mm) had all bones separate, while distinctly more subadults and adults had some bones fused. Percentages of tortoises with separate and fused bones in the three age classes resembled the frequencies of character states of *T. h. kazachstanica* (fig. 2). The underlying morphological patterns differed in both species however. The lateral and medial centralia fused in both. But in *T. h. hermanni* the distal carpals 1 and 2 fused; a character never occurring in *T. h. kazachstanica* that generally lacks the first distal carpal. Moreover, while in *T. h. kazachstanica* bone fusion resulted in the end in one large solid element formed by intermedium, ulnare and one or both centralia (fig. 1; table 1), fusion of bones was less extensive in *T. h. hermanni*. Aged *T. h. hermanni* (except those lacking digit 1 entirely) still had two separate large carpal elements, one formed by the fused lateral and medial centralia and the other by the fused distal carpalia 1 and 2; intermedium and ulnare remained in this species always separate. Only in MTD 32834 (juvenile) and 36941 (subadult) the first distal carpal was fused with the first metacarpal.

Discussion

Crumly and Sánchez-Villagra (2004) found more variation in phalangeal formulae of the

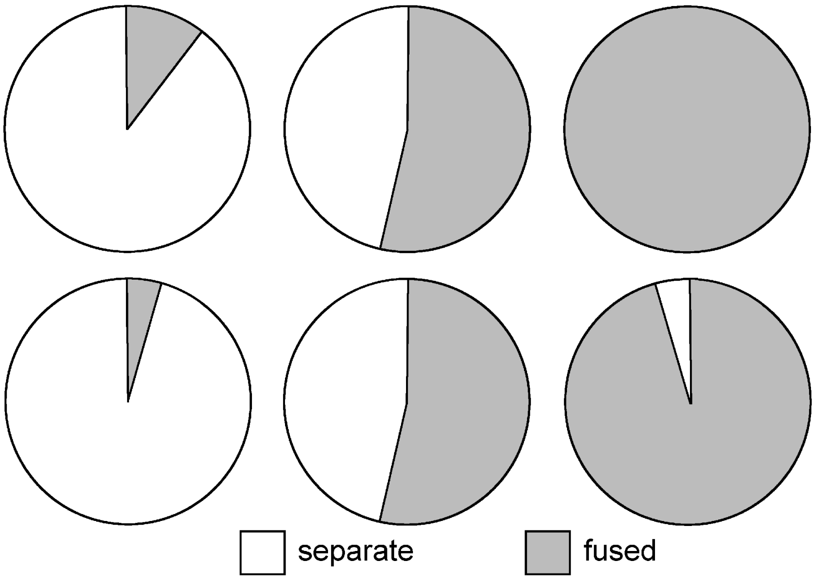

Figure 2. Frequency distribution (percentages) of separate versus fused carpals or metacarpals in age classes of *Testudo horsfieldii kazachstanica* (top) and *Testudo hermanni hermanni* (bottom). From left to right: juveniles, subadults, adults. Differences between all age classes are statistically significant (chi^2 test; *T. h. kazachstanica*: juveniles vs. subadults $p < 0.01$, juveniles vs. adults $p < 0.001$, subadults vs. adults $p < 0.001$, $N = 61$, number of extremities; *T. h. hermanni*: juveniles vs. subadults $p < 0.01$, juveniles vs. adults $p < 0.001$, subadults vs. adults $p < 0.01$, $N = 56$ extremities).

manus of *Testudo horsfieldii* (0-2/1-2-2/1-1) and less variation in *T. hermanni* (1-2-2-2-1) than we did. While in *T. hermanni* the greater variation (table 2) is easily explained by our larger sample of 29 specimens opposed to three tortoises studied by Crumly and Sánchez-Villagra (2004), this cannot be valid for *T. horsfieldii*. All of our 32 *T. horsfieldii* consistently have the formula 0-2-2-1-1. In contrast, using only four tortoises, Crumly and Sánchez-Villagra (2004) reported that a phalanx may also be lost in the second digit and a second phalanx may occur in the fourth digit. This difference may correspond, like in *Kinixys belliana* (Crumly and Sánchez-Villagra, 2004), with subspecific differentiation. Our specimens represent all *T. h. kazachstanica* whereas the subspecies allocation of the Central Asian tortoises examined by Crumly and Sánchez-Villagra (2004) was not reported. Currently, three subspecies are recognized within *T. horsfieldii* (*T. h. horsfieldii*, *T. h. kazachstanica*, *T. h. rustamovi*; Fritz and Havaš, 2007); at least *T. h. kazachstanica* and *T. h. rustamovi* are genetically distinct and differ by an uncorrected *p* distance of approximately 2.5% in the mitochondrial cytochrome *b* gene (Fritz et al., 2005).

Testudo horsfieldii is known to spend a considerable time of its life in self-dug burrows (in Uzbekistan nine months of the year; Lagarde et al., 2002); also abandoned burrows of other animals are used and extended (Kuzmin, 2002). This suggests extensive morphological adaptation to burrowing. In fact, a flattened shell like in *T. horsfieldii* also occurs in other burrow-digging tortoises (*Chelonoidis chilensis*, *Geochelone sulcata*, *Gopherus* spp., some populations of *Testudo graeca armeniaca*; Villiers, 1958; Lambert, 1993; Ernst et al., 1994, 2000; Cabrera, 1998; Fritz et al., 2007). However, in none of the other burrowing taxa has phalangeal reduction reached the extent of *T. horsfieldii*; *Ch. chilensis* even has two phalanges in all five fingers (Crumly and Sánchez-Villagra, 2004). Taking into account that partial or complete loss of the first finger occurs in all other *Testudo* species (Crumly and Sánchez-Villagra, 2004; this study), the entire reduction of the first digit in *T. horsfieldii* is not necessarily linked with its burrowing mode of life; in contrast, the reduction of digit 4 could be. There are only two other tortoise species with only one phalanx in digit 4 (*Gopherus berlandieri*, *Kinixys belliana*; Crumly and Sánchez-Villagra, 2004), one of which (*G. berlandieri*) is known to dig short tunnels and shallow depressions, so-called pallets (Ernst et al., 1994, 2000).

Clearly, the differences in carpal fusion patterns of *T. horsfieldii* and its sister taxon *T. hermanni* are likely to be correlated with their different modes of life. In *T. hermanni* the fused bones occur in that part of the hand being exposed to the greatest mechanical strain during walking. The different location and extent of fused bones in *T. horsfieldii* suggest another selective force. It is plausible that a more rigid hand skeleton and wrist are useful for excavating burrows, explaining why carpalia fuse more extensively in *T. horsfieldii* than in *T. hermanni*, a species without extensive digging behaviour. It would be worthwhile to compare carpal morphology of other burrow-digging species to test this hypothesis.

Our study highlights that it is imperative to study different ontogenetic stages for understanding variation in carpal morphology. For instance, Perälä (2002) pointed out that intermedium and ulnare are fused in "*Agrionemys kazachstanica*" and separate in "*A. rustamovi*" and used this difference as an argument for elevating those subspecies of *T. horsfieldii* to full species level. Our study provides evidence that fusion of carpal bones increases considerably during ontogeny, suggesting that the observation of Perälä (2002) is based on tortoises of different age.

Considerable ontogenetic variation also occurs regarding the presence or absence of a pisiform in *T. h. hermanni*. The nearly complete lack of this bone in juveniles and subadults implies that this element ossifies relatively late in ontogeny.

Although underlying patterns differ, in both studied tortoise species carpalia increasingly fuse with age; a similar observation was also made in a terrestrial geoemydid terrapin (*Cuora galbinifrons*; Fritz et al., 2006). It would be interesting to know whether carpalia also fuse in aquatic terrapins. If not, this would argue again for a correlation with the mode of life, as it is the case with a significant reduction of phalanges that is observed only in terrestrial or semiterrestrial chelonians (Cryptodira: Emydidae: Minx, 1992; Geoemydidae: Fritz et al., 2006; Ludwig et al., 2007; Testudinidae: Crumly, 1985; Crumly and Sánchez-Villagra, 2004; Pleurodira: Pelomedusidae: *Pelomedusa subrufa*: Sánchez-Villagra et al., 2007). In aquatic pleurodirans fused distal carpals occur however (Sánchez-Villagra et al., 2007).

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References

Bonnet, X., Lagarde, F., Henen, B.T., Corbin, J., Nagy, K.A., Naulleau, G., Balhoul, K., Chastel, O., Legrand, A., Cambag, R. (2001): Sexual dimorphism in steppe tortoises (*Testudo horsfieldii*): influence of the environment and sexual selection on body shape and mobility. Biol. J. Linn. Soc. **72**: 357-372.

Cabrera, M.R. (1998): Las tortugas continentales de Sudamérica austral. Córdoba, Privately Printed.

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

Crumly, C.R. (1985): A hypothesis for the relationships of land tortoise genera (family Testudinidae). Stud. Geol. Salmant., Vol. Esp. **1** (Stud. Palaeocheloniol. **I**, 1984): 115-124.

Crumly, C.R., Sánchez-Villagra, M.R. (2004): Patterns of variation in the phalangeal formulae of land tortoises (Testudinidae): developmental constraint, size, and phylogenetic history. J. Exp. Zool. (Mol. Develop. Evol.) **302B**: 134-146.

Ernst, C.H., Lovich, J.E., Barbour, R.W. (1994): Turtles of the United States and Canada. Washington and London, Smithsonian Institution Press.

Ernst, C.H., Altenburg, R.G.M., Barbour, R.W. (2000): Turtles of the World. World Biodiversity Database, CD-ROM Series, Windows Version 1.2. Amsterdam, Biodiversity Center of ETI.

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., Petzold, A., Auer, M. (2006): Osteology in the *Cuora galbinifrons* complex suggests conspecifity of *C. bourreti* and *C. galbinifrons*, with notes on shell osteology and phalangeal formulae within the Geoemydidae. Amphibia-Reptilia **27**: 195-205.

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., 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., Havaš, P. (2007): Checklist of Chelonians of the World. Bonn and Dresden, German Federal Ministry of Environment, Nature Conservation and Nuclear Safety and Museum of Zoology Dresden.

Kuzmin, S.L. (2002): The Turtles of Russia and Other Ex-Soviet Republics. Frankfurt am Main, Chimaira.

Lagarde, F., Bonnet, X., Nagy, K., Henen, B., Corbin, J., Naulleau, G. (2002): A short spring before a long jump: the ecological challenge in the steppe tortoise (*Testudo horsfieldi*). Can. J. Zool. **80**: 493-502.

Lambert, M.R.K. (1993): On growth, sexual dimorphism, and the general ecology of the African spurred tortoise, *Geochelone sulcata*, in Mali. Chelon. Conserv. Biol. **1**: 37-46.

Ludwig, M., Auer, M., Fritz, U. (2007): Phalangeal formulae of geoemydid terrapins (*Batagur*, *Callagur*, *Hardella*, *Heosemys*, *Kachuga*, *Orlitia*, *Pangshura*, *Rhinoclemmys*) reflect distinct modes of life. Amphibia-Reptilia **28**: 574-576.

Minx, P. (1992): Variation in phalangeal formulae in the turtle genus *Terrapene*. J. Herpetol. **26**: 234-238.

Perälä, J. (2002): Biodiversity in relatively neglected taxa of *Testudo* L., 1758 s. l. Chelonii **3**: 40-53.

Sánchez-Villagra, M., Winkler, J.D., Wurst, L. (2007): Autopodial skeleton evolution in side-necked turtles (Pleurodira). Acta Zool. **88**: 199-209.

Villiers, A. (1958): Tortues et crocodiles de l'Afrique noire française. Init. Afric. **15**: 1-354.

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