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Source: Folia Zoologica, 60(2) : 167-175

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v60.i2.a11.2011

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Folia Zool. – 60 (2): 167–175 (2011)

Shell shape and size variation in the Egyptian tortoise *Testudo kleinmanni* (Testudinidae, Testudines)

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Received 2 November 2010; Accepted 24 February 2011

Abstract. We examined 126 wild tortoises to evaluate the shell changes due to sexual dimorphism and ontogenesis by the geometric morphometrics. Adult body shape varies substantially in males and females; adults showed different ontogenetic patterns between sexes: in females the posterior portion of the carapace narrows in the dorsal view, the carapace tends to assume a pyriform shape in the lateral view, and the plastron tends to lengthen of the midline and shows a slight lateral enlargement. Male shape changes towards the posterior portion of the carapace, a bending of the seam between marginal and pleural scutes, allowing the body to assume a hemispherical shape, and ventrally, the plastron narrows strongly, posteriorly. The latter feature was mainly due to the shortening of the anal scutes, probably facilitating copulation by allowing more space to move the long tail. A wider posterior in male angulate tortoises may convey greater stability in male-to-male combat. All the ontogenetic changes suggest a modification of the plastron formula, an important feature for chelonian systematics and taxonomy.

Key words: geometric morphometrics, sexual dimorphism, ontogenesis, allometry

Introduction

The Egyptian tortoise *Testudo kleinmanni* Lortet, 1883 is the smallest representative of circum-Mediterranean *Testudo* species (Farkas et al. 1997), recently split into two species on apparent differences in shell morphology and markings: *T. kleinmanni* was restricted to areas west of the River Nile while *T. werneri* encompassed populations east of the Nile delta in Egypt and Israel (Perälä 2001). However subsequent morphometric and molecular analyses showed that the morphological differences observed among populations were intraspecific, so *T. werneri* and *T. kleinmanni* should not be considered separate species (Attum et al. 2007, Široký & Fritz 2007). Consequently, its geographic range extends along Libyan coastal regions of Tripolitania and Cyrenaica, through mainland Egypt to north of El Arish on the Sinai Peninsula, and the northern Negev Desert in Israel (Schleich et al. 1996, Fritz & Buskirk 1997, Baha El Din 2006, Sindaco & Eremcenko 2008). The range of the Egyptian tortoise has decreased considerably since the 1980s (Perälä 2001) and the species has been considered "critically endangered" (Perälä 2005), although the conservation status of *T. kleinmanni* is probably not as critical as Perälä proposed (Schneider & Schneider 2006).

In spite of the great interest in Egyptian tortoise systematics and conservation, we know little about its morphology and possible sexually dimorphic characters. Studies on morphological variation of chelonians have generally focused on variation among species or populations (McCord et al. 1990, Yasukawa et al. 1996, Lambert et al. 1998), and in some case, such as *T. kleinmanni*, a comprehensive description was never published till two years ago (see Delfino et al. 2009). Nevertheless, these studies provided important information on sexually dimorphic traits; very few other works describe the differences between male and female reproductive roles and the factors influencing

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body shape (e.g., Allison et al. 1995, Bonnet et al. 1998, Malmgren & Thollesson 1999, Valenzuela et al. 2004) or shape variation during ontogeny (Loehr et al. 2006). However, a powerful new method may improve the study of these variations in shape.

Traditional morphometric studies typically evaluate variation in animal form (size + shape) from linear, curvilinear or angular measures of size while geometric morphometrics (GM) uses complete spatial arrangements of anatomical data throughout an analysis (see review by Adams et al. 2004). In GM, coordinates of biologically definable landmarks (e.g., scute locations on a tortoise shell) are collected and non-shape variation is mathematically removed by superimposition or overlaying methods (see Material and Methods). Group differences in shape can be calculated as (a) group distances between landmarks, or (b) the warp degree between the group shapes (thin-plate spine method; Adams et al. 2004). These differences can be compared among groups using multivariate statistics and graphs (deformation grids; Adams et al. 2004). GM has been relatively recently applied to chelonians (Claude et al. 2003, Valenzuela et al. 2004, Chiari et al. 2008) and could prove to be a powerful tool for future analyses of chelonian shape.

A confiscation of Libyan *T. kleinmanni* illegally imported into Italy enabled us to quantify their morphology using GM in order to evaluate the morphological variability of the carapace and plastron. Despite the uncertain geographic origin, this does not represent a limit for the sexual dimorphism since dimorphic characters are well established characters in each population of the same species. This represents a first attempt for proposing such a study in a *Testudo* species in order to provide a basis for comparison with other species. In particular, we evaluated whether shape varied between males and females (i.e., sexual dimorphism) and between juveniles and adults (ontogenetic variation).

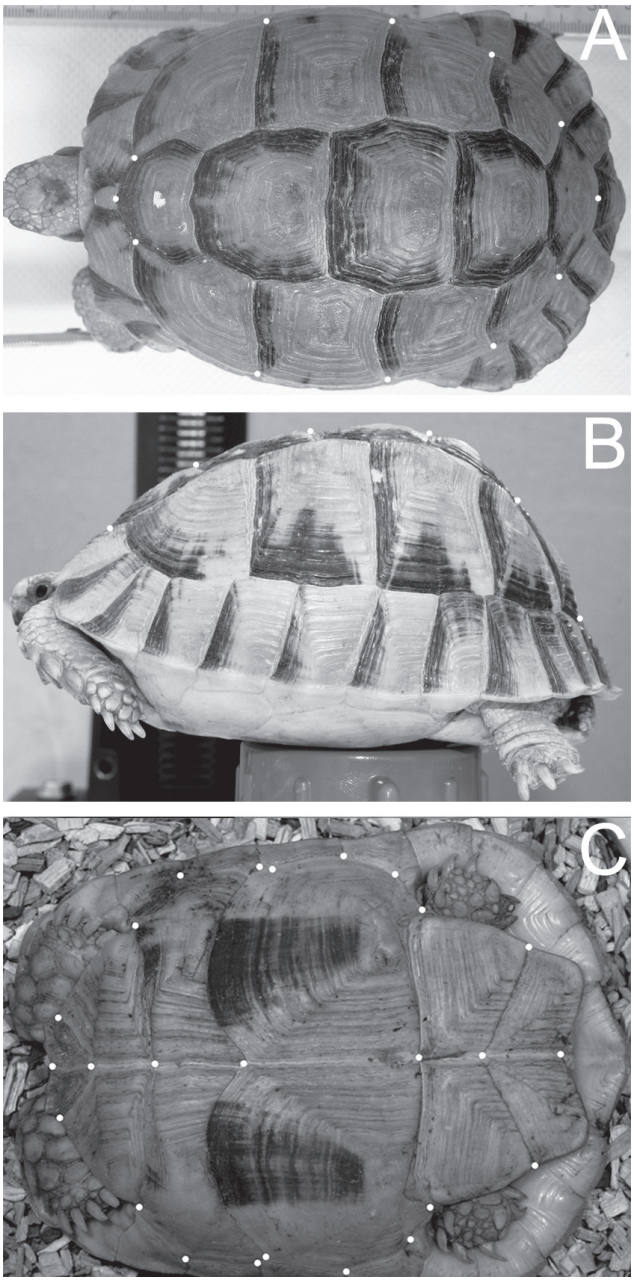


Fig. 1. *Landmarks (solid white circles) used in geometric morphometric analysis of the dorsal (A), lateral (B), and ventral (C) sides of individual* Testudo kleinmanni.

Material and Methods

Tortoises and image collection

In total 265 wild *T. kleinmanni*, were illegally-imported from an unknown Libyan locality, and confiscated September 2005 at the Fiumicino Airport, Rome, Italy. The tortoises were housed at the Bioparco of Rome, and our analysis was performed in October 2005. We selected a portion of the same sample studied by Macale et al. (2009). In detail, a total of 126 animals, were divided as follows: 39 juveniles (plastron length, PL < 90 mm), 42 adult females (PL > 130 mm), and 45 adult males (102 < PL < 110 mm) (see Fig. 1 in Macale et al. 2009). The animal numbers can vary in the different analyses since some individuals can show abnormalities in some scales due to the bad transport conditions. So we excluded some pictures without biasing our analyses since the study is supported by an adequate number of tortoises.

For each tortoise, we photographed the dorsal (DS), lateral (LS) and ventral (VS) sides, with an eight megapixel Canon 350 D SLR digital camera mounted on a tripod and placed 30 cm from each specimen.

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Each photograph included graph paper, under or behind the tortoise, for scale. To minimize spherical distortion and parallax, we used a 50 mm (f 2.5) high-resolution Canon macro lens. Images were transferred to a computer where configurations of 12, 6 and 25 two-dimensional co-planar landmarks were digitized for DS, LS and VS, respectively (Fig. 1), in geometric morphometric TpsDig (Rohlf 2004).

Image processing

After acquiring images, we firstly determined the centroid (the mean of the landmark coordinates – Slice et al. 1996) and centroid size (CS) of each tortoise. CS is a dimensionless size, and equals the square root of the sum of the squares of the distances of each landmark from the centroid (Zelditch et al. 2004). Next, we used TpsRelw software (Rohlf 2004) to mathematically remove non-shape variation (position, orientation and scale) according to Generalised Procrustes Analysis (GPA), an iterative superimposition process that calculates landmark means while minimising the least-squares differences for corresponding landmarks. This superimposition process involved (a) translating (placing) each individual's centroid at the origin, (b) scaling the individual's landmark configuration to a common size (by dividing by CS; Bookstein 1986), and (c) rotating the landmark configuration to further minimise differences between corresponding landmarks (Adams et al. 2004).

The resulting aligned coordinates of all specimens were used to quantify shape differences mathematically, using thin-plate splines (Bookstein 1991, Rohlf 1993). The splines describe how shape has been warped from parameters called partial warp scores. The partial warp scores between objects were used to quantify the deformation, to analyse and display the variation of shape differences among groups. In this way, deformation grids using thin-plate splines were used to describe graphically the patterns of shape variation among the landmarks.

Specifically, the projection of the superimposed configurations on the principal warps produced the partial-warp scores, which described their deviations from the reference configuration (a mean hypothetical configuration, i.e. the hypothetical individual with 0,0 coordinates at the centre of the output diagram) and can be used as variables in a subsequent relative warp analysis (Rohlf 1993) that corresponds to a principal components analysis of variation in a sample on the matrix of all the shape coordinates after projection in the tangent space, via the TpsRelw program. The relative warps (RWs) were computed in the full shape space (i.e., including both uniform and non-uniform components), as recommended by Bookstein (1996). TpsRelw was also used to produce deformation grids illustrating shape variation associated to the ordination. We also described the plastron formula (i.e., the rank of scute size at the midline; see Ernst et al. 2000) using the deformation grids obtained by the TpsRelw.

Allometry (i.e., shape changes during development and growth) was evaluated by using the TpsRegr to regress the parameters of the shape change functions on centroid size. TpsRegr performs a multivariate multiple regression of shape onto one or more independent variables, here the centroid size (Rohlf 2004).

Statistics

We used a one-way ANOVA and MANOVA to assess size and shape differences, respectively, among three groups: juvenile, adult males and adult females. ANOVA was (1) performed to assess differences in for all groups and (2) followed with Tukey posthoc tests for describing the hierarchy, both in CS. The CS normal distribution was first verified by the Kolmogorov-Smirnov test (data were log-transformed when not normal). MANOVA were followed with Hotelling T^2 posthoc tests for describing differences among groups. Finally, we used MANCOVA to test for differences between the regression slopes and intercepts of the two sexes.

Geometric morphometric analyses were performed using computer programs from the 'TPS' (Thin Plate Splines) series (Rohlf 2004).

Results

Centroid size (CS)

Females had the largest dorsal, lateral and ventral centroid sizes compared to males and juveniles (Fig. 2), and adult male centroid sizes were larger than those of juveniles. Differences in centroid size amongst the three groups were expected due to the existence of a certain type of data circularity.

Shape variation

The scatter plots of relative warps illustrated how shape differed among the three groups (Fig. 3). Relative warps (RW) were computed on the consensus (i.e., the reference configuration) of each specimen to show ordination and shape differences among groups. The first two RW explained 44.66 % (RW1 + RW2 = 24.69 + 19.97), 47.32 % (RW1 + RW2 = 28.45 + 18.87), and 55.58 % (RW1 + RW2 = 31.82 + 23.76) of the total variance of dorsal, lateral, and ventral views, respectively. Each of the other Relative warp scores

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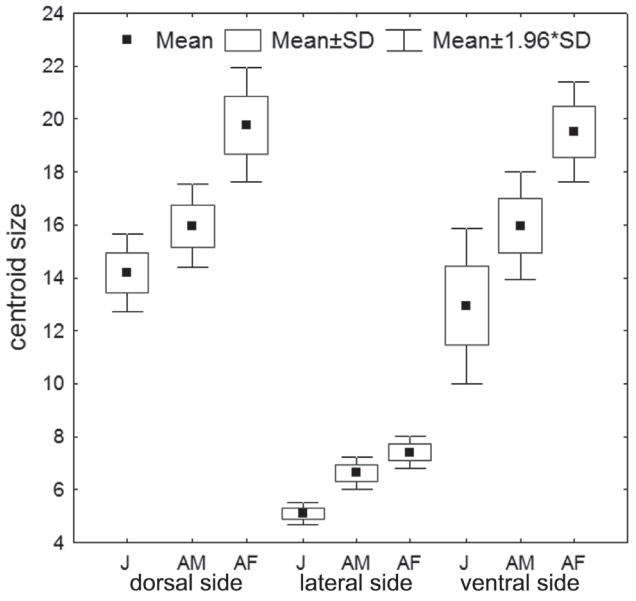


Fig. 2. *Centroid size for dorsal, lateral and ventral views of juvenile (J), adult female (AF) and adult male (AM)* T. kleinmanni *from Libya (see Table 2 for sample sizes). ANOVA were significant for each view ($F_{3, 121}$ = 53.11, 41.41, and 65.68, for dorsal, lateral and ventral, respectively; all P < 0.05). Centroid size was consistently different in Tukey posthoc tests (P < 0.05), with AF > AM > J.*

explained < 10 % of the variance.

The deformation grids demonstrated the shape shifts from juveniles to adults (Fig. 4), whose main changes depended on sex. MANOVA showed significant differences between female and male adults, between juveniles and adults, and in their interaction (sex × age; Table 1).

The Hotelling T^2 test indicated that all pairwise comparisons were significant (Table 2). We also observed three different plastron formulae, using the deformation grids of each group, among adult females (abd > an > pect > fem > hum > gul), adult males (abd > pect > an > hum > gul > fem), and juveniles (abd > an > pect > hum > gul > fem).

Allometry

For allometric analyses, multivariate regressions of dorsal, lateral and ventral shape were significantly related to the centroid size of adult females (all Wilks' $\lambda > 7.7$, $F > 8.5$, $P < 0.0005$, df1 = 2 and df2 ≥ 35) and adult males (all Wilks' $\lambda > 7.8$, $F > 6.13$, $P < 0.0005$, df1 = 2 and df2 ≥ 35). All DS, LS and VS shape changes were correlated to centroid size for females and males (all $F_{2, df2} > 6$, P was always ≤ 0.001 and df2 > 36), with slopes and intercepts differing between adult males and adult females (all $F_{2, df2} > 18$, P was always < 0.001 and df2 > 71).

Discussion

Ontogeny

Adult *T. kleinmanni* showed different ontogenetic patterns between sexes. In females, the posterior

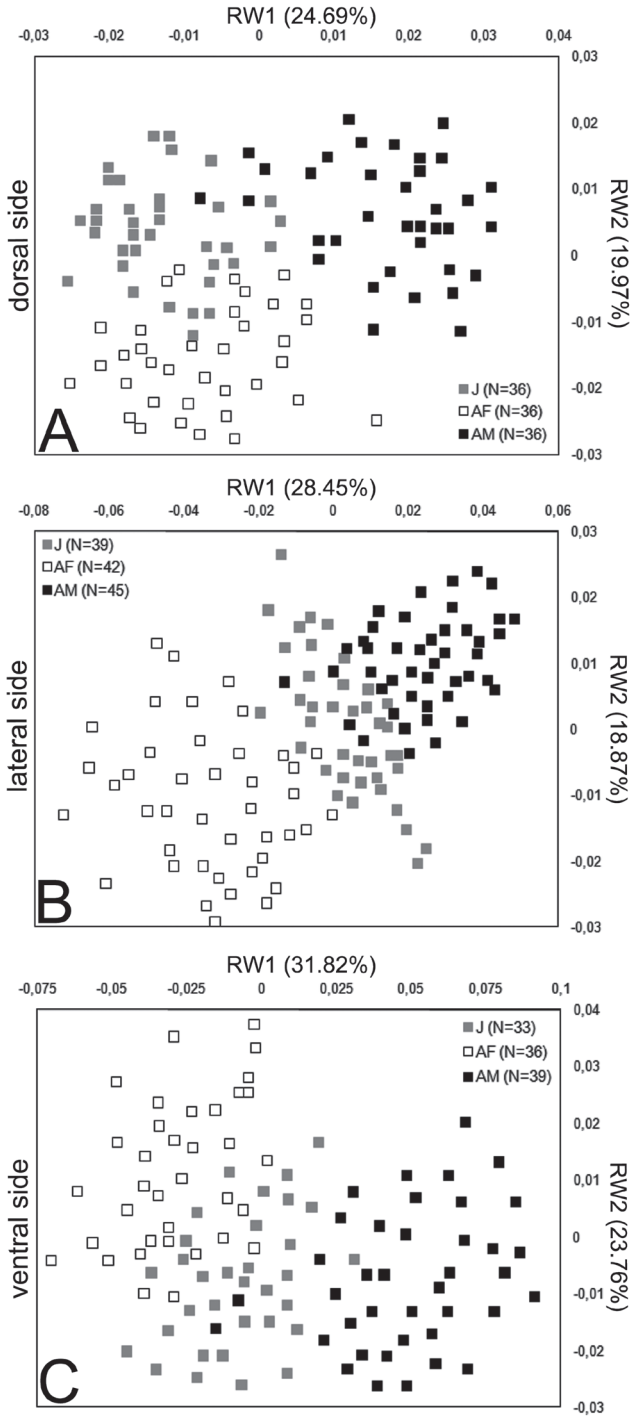


Fig. 3. *Scatter plot of the two first Relative Warp scores (RW1 and RW2) obtained from analysing the dorsal (A), lateral (B), and ventral (C) sides of the* T. kleinmanni *configurations.*

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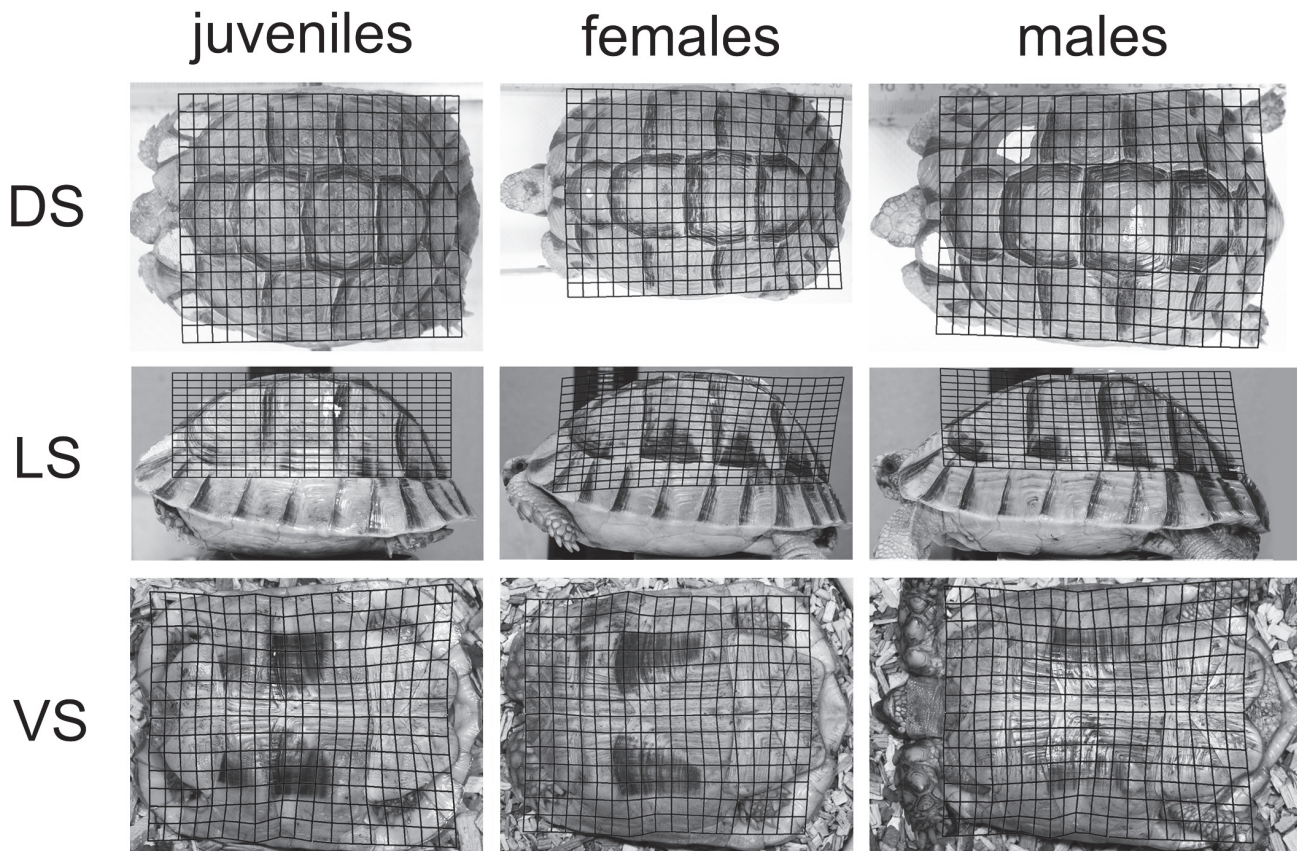


Fig. 4. *Overlay of deformation grids on respective dorsal (D), lateral (L) and ventral (V) images of a representative juvenile, adult male and adult female* T. kleinmanni *from Libya.*

Table 1. *MANOVA test results for sex, age and sex × age interaction (for the shell shape of* Testudo kleinmanni. *All effects were significant at P < 0.005.*

Shell view	Effect	Wilk's lambda	F	Df
Dorsal	sex	0.00107	55.81	2, 78
	age	0.00094	71.37	2, 124
	sex × age	0.00021	52.27	3, 124
Lateral	sex	0.00507	94.10	2, 78
	age	0.00225	57.53	2, 124
	sex × age	0.00017	57.83	3, 124
Ventral	sex	0.00344	82.51	2, 78
	age	0.00291	87.23	2, 124
	sex × age	0.00171	66.54	3, 124

portion of the carapace narrows in the dorsal view, the carapace tends to assume a pyriform shape in lateral view (Fig. 4), and the plastron tends to lengthen at the midline and shows a slight widening near the pectoral and abdominal scutes. In contrast, male shape changes towards the posterior portion of the carapace (viewed laterally), with a bending of the seam between marginal and pleural scutes and assuming a hemispherical shape, and ventrally, the plastron narrows strongly, posteriorly (Fig. 4). The latter feature was mainly due to the shortening of the anal scutes, and probably facilitates copulation by

Table 2. *Hotelling T^2 test values for comparing shell shape among groups (J = juvenile; AF = adult female; AM = adult male). All pairwise comparisons among groups showed significant differences (P < 0.05), setting time to time α by the Bonferroni correction. N = number of individuals.*

	dorsal			lateral			ventral		
	J	AF	AM	J	AF	AM	J	AF	AM
N	36	36	36	39	42	45	33	36	39
J	-	5.713	8.296	-	8.483	10.559	-	8.771	11.394
AF		-	10.772		-	12.873		-	11.473

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allowing more space to move the long tail (see also Bonnet et al. 2001, Mann et al. 2006).

This type of modification during ontogenesis in both sexes causes a different plastron formula from that proposed by Loveridge & Williams (1957), Ernst & Barbour (1989), Ernst et al. (2000), and Delfino et al. (2009), probably due to an intraspecific variability never detected before. Since plastral formulae are used in chelonian systematics and taxonomy (Ernst et al. 2000), it is important to account for sexual dimorphism and ontogenetic changes in future inter-population and systematic studies.

Sexual dimorphism

This study revealed that in the Egyptian tortoise, body shape varies due to sexual maturation and sexual dimorphism, similarly to other tortoises (Bonnet et al. 2001, Lagarde et al. 2001). The most obvious dimorphism in *T. kleinmanni* was that males were smaller than females, a trend that was reflected in all measured body parameters, suggesting the influence of the sexual selection on the Egyptian tortoise body size in.

T. kleinmanni shows the same pattern of sexual size dimorphism as most species of *Testudo*, with females being larger than males (Mlynarski 1966, Brouchko 1981, Lambert 1982, Michel & Stöck 1996, Ataev 1997, Willemsen & Hailey 1999, Bonnet et al. 2001, Lagarde et al. 2001). However, in *T. marginata*, the sister species of *T. kleinmanni* (Fritz & Bininda-Emonds 2007), males exceed females in size (Bringsøe et al. 2001). The larger female size is probably an adaptation to improve egg production (Congdon & Tinkle 1982, Wilbur & Morin 1988, Gibbons & Greene 1990, Gibbons & Lovich 1990, Forsman & Shine 1995, Loehr et al. 2006). As a consequence, the posterior body region might have enlarged, as supported by the bigger size of anal and femoral scutes in females (see also Geffen & Mendelssohn 1991). Selection for greater fecundity likely exists for female *T. kleinmanni* because they exhibit a positive correlation between clutch size and body size as do other chelonian species (Gibbons et al. 1982, Mitchell 1985, Congdon & van Loben Sels 1993, Nieuwolt-Dacanay 1997, Zuffi et al. 1999).

In contrast, suggesting biological interpretations for the male shell shape and size is very difficult, mainly due to the posterior carapace portion. In particular, the *T. kleinmanni* males have a wide the posterior carapace (also observed by Delfino et al. 2009) similar to males of other species, such as *Chersina angulata* (Mann et al. 2006). In the latter species, males fight for access to females for reproduction, and their wide posterior carapace seems to provide great stability and power in both attack and defense (Mann et al. 2006). In species with male-to-male combat, males are often larger than females (Berry & Shine 1980, Gibbons & Lovich 1990). In contrast, *T. kleinmanni* males are smaller than females, such as in other species of *Testudo* inhabiting the Mediterranean area (Loehr et al. 2006), with the above mentioned main exception of *T. marginata*. Posterior carapace width suggests that males may have wider hind leg openings than females have (see also Mann et al. 2006). This may help males increase efficiency of locomotion, which might allow them to move faster and with greater agility than females, such as in male *Testudo horsfieldi* (Bonnet et al. 2001).

Sexual and natural selection

Are the observed sexual differences a simple consequence of allometric patterns or do they reflect adaptive responses to different selective pressures? Size and shape divergence is one of the most apparent differences between males and females of a wide range of animals, including chelonians (see Bonnet et al. 2001, Lagarde et al. 2001). Divergence in growth trajectories between sexes may be influenced by concordant or opposing selective forces (e.g. sexual selection or niche divergence; see Hedrick & Temeles 1989, Shine 1994, Macale et al. 2009). In fact, sexual dimorphism in size and shape could arise from ecological differences between the sexes, from natural selection for fecundity or parental care, or from sexual selection for courtship success (Hedrick & Temeles 1989, Shine 1989, Andersson 1994).

Our results clearly showed that adults of both sexes diverge, nearby to the same extent, from the juvenile shape. It is usually accepted that in the genus *Testudo* shape changes seem due to sexual selection for courtship in males, while to natural selection for fecundity in females (Willemsen & Hailey 2003). In previous studies using only adults these two possibilities cannot be separated as the cause of shape differences between males and females (Hailey, pers. comm.). This study convincingly shows that adults of both sexes have modified shape compared to juveniles, and thus that both sexual and natural selection are probably involved in the shape of adult *T. kleinmanni*. In the case of *T. kleinmanni*, it appears that sexual selection contributes to the divergence between the two sexes. Sexual selection should favour mate searching in males, while selection for female fecundity and offspring survivorship should favour increased clutch size and egg size (Bonnet et al. 2001). If females are

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under selection to produce large clutches, they must accrue nutrients for developing follicles, making eggs, and storing body reserves, so considerable space is probably necessary to accommodate body reserves and egg follicles (Henen 1997, Bonnet et al. 2001, Loehr et al. 2006). A combination of all these features may select for larger size in females.

Sexual selection thus seems to be a stronger influence on the shape of the Egyptian tortoise than does natural selection for fecundity. It remains possible that natural selection for fecundity is important in *Testudo*, but with other outlets such as clutch frequency. The pattern of clutch dynamics in *Testudo* supports this possibility, as energy for reproduction accumulates in follicles throughout the year (Hailey & Loumbourdis 1988). Multiple clutches thus provide a means of overcoming the volume restriction of the body, rather than resulting from energy accumulation during the nesting period.

Moreover, environmental conditions (e.g., climate and substrate) and *T. kleinmanni's* digging ability may have constrained shell shape, as suggested by Mlynarski (1966). Traits that impede digging ability should experience negative selection (Bonnet et al. 2001). Because other factors might affect the direction and intensity of sexual dimorphism, and variation in environmental conditions and resources can influence growth rate and survival, quantifying the selective pressures (Shine 1990, Berrigan & Charnov 1994) and sexual differences in *T. kleinmanni* will remain complex.

Acknowledgements

We are indebted to two anonymous reviewers, Adrian Hailey, Michela Gori, Brian T. Henen, and John Measey for their helpful suggestions toward to the manuscript improvement, and to the reptile house staff of 'Fondazione Bioparco di Roma' for the logistic support.

Literature

Adams D.C., Slice D.E. & Rohlf F.J. 2004: Geometric morphometrics: ten years of progress following the 'revolution'. *Ital. J. Zool. 71: 5–16.*

Allison D.B., Paultre F., Goran M.I., Poehlman E.T. & Heymsfield S.B. 1995: Statistical considerations regarding the use of ratios to adjust data. *Int. J. Obesity Rel. Met. Dis. 19: 644–652.*

Andersson M. 1994: Sexual selection. *Princeton: Princeton University Press.*

Ataev C.A. 1997: Reptiles of the autonomous republic of Turkmenistan. *Chelonian Conserv. Biol. 2: 627–634.*

Attum O., Baha El Din S.M., Carranza S., Earley R., Arnold E.N. & Kingsbury B. 2007: An evaluation of the taxonomic validity of *Testudo werneri*. *Amphibia-Reptilia 28: 393–401.*

Baha El Din S.M. 2006: A guide to the reptiles and amphibians of Egypt. *The American University Press, Cairo.*

Berrigan D. & Charnov E.L. 1994: Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos 70: 474–478.*

Berry J.F. & Shine R. 1980: Sexual size dimorphism and sexual selection in turtles (order Testudines). *Oecologia 44: 185–191.*

Bonnet X., Shine R., Naulleau G. & Vacher-Vallas M. 1998: Sexual dimorphism in snakes: different reproductive roles favour different body plans. *Proc. R. Soc. Lond. B Biol. Sci. 265: 1–5.*

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 horsfieldi*): influence of the environment and sexual selection on body shape and mobility. *Biol. J. Linn. Soc. 72: 357–372.*

Bookstein F.L. 1986: Size and shape spaces for landmark data in two dimensions. *Stat. Sci. 1: 181–222.*

Bookstein F.L. 1991: Morphometric tools for landmark data. *Cambridge University Press, Cambridge.*

Bookstein F.L. 1996: A standard formula for the uniform shape component in landmark data. In: Marcus L.F., Corti M., Loy A., Naylor G. & Slice D. (eds.), Advances in morphometrics. *Plenum Press, New York: 153–168.*

Bringsøe H., Buskirk J.R. & Willemsen R.E. 2001: *Testudo marginata* Schoepff, 1792 – Breitrandschildkröte. In: Fritz U. (ed.), Handbuch der Reptilien und Amphibien Europas. *Aula-Verlag, Wiebelsheim: 291–334.*

Brouchko Z.K. 1981: Données sur la reproduction de la tortue d'Asie générale (*Testudo horsfieldi*) dans le sud du lac Baïkal. *Bull. Soc. Herpetol. Fr. 18: 19–23.*

Chiari Y., Wang B., Rushmeyer H. & Caccone A. 2008: Using digital images to reconstruct three-dimensional biological forms: a new tool for morphological studies. *Biol. J. Linn. Soc. 95: 425–436.*

Claude J., Paradis E., Tong H. & Auffray J.C. 2003: A geometric morphometric assessment of the effects of environment and cladogenesis on the evolution on the turtle shell. *Biol. J. Linn. Soc. 79: 485–501.*

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Congdon J.D. & Tinkle D.W. 1982: Reproductive energetics of the painted turtle (*Chrysemys picta*). *Herpetologica 38: 228–237.*
Congdon J.D. & van Loben Sels R.C. 1993: Relationships of reproductive traits and body size with attainment of sexual maturity and age in Blanding's turtles (*Emydoidea blandingii*). *J. Evol. Biol. 6: 547–557.*
Delfino M., Chesi F. & Fritz U. 2009: Shell morphology of the Egyptian tortoise, *Testudo kleinmanni* Lortet, 1883, the osteologically least-known *Testudo* species. *Zool. Studies 48: 850–860.*
Ernst C.H., Altenburg R.G.M. & Barbour R.W. 2000: Turtles of the world. World Biodiversity CD-ROM Series, Windows Version 1.2. *Expert Center for Taxonomic Identification, University of Amsterdam.*
Ernst C.H. & Barbour R.W. 1989: Turtles of the world. *Smithsonian Institution Press. Washington D.C.*
Farkas B.L., Sasvari L. & Buskirk J.R. 1997: Maximum size of the Egyptian tortoise, *Testudo kleinmanni*. *Chel. Conserv. Biol. 2: 415.*
Forsman A. & Shine R. 1995: Sexual size dimorphism in relation to frequency of reproduction in turtles (Testudines: Emydidae). *Copeia 1995: 727–729.*
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. & Buskirk J.R. 1997: The occurrence of *Testudo kleinmanni* in Tripolitania. *J. Nat. Museum (Prague), Nat. Hist. Series. 167: 143–144.*
Geffen E. & Mendelssohn H. 1991: Preliminary study on the breeding pattern of the Egyptian tortoise, *Testudo kleinmanni*, in Israel. *Herpetol. J. 1: 574–577.*
Gibbons J.W. & Greene J.L. 1990: Reproduction in the slider and other species of turtles. In: Gibbons J.W. (ed.), Life history and ecology of the slider turtle. *Smithsonian Institution Press, Washington D.C.: 124–134.*
Gibbons J.W. & Lovich J.E. 1990: Sexual dimorphism in turtles with emphasis of the slider turtle (*Trachemys scripta*). *Herpetol. Monogr. 4: 1–29.*
Gibbons J.W., Greene J.L. & Patterson K.K. 1982: Variation in reproductive patterns of freshwater turtles. *Herpetologica 35: 86–89.*
Hailey A. & Loumbourdis N.S. 1988: Egg size and shape, clutch dynamics, and reproductive effort in European tortoises. *Can. J. Zool. 66: 1527–1536.*
Hedrick A.V. & Temeles E.J. 1989: The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends Ecol. Evol. 4: 136–138.*
Henen B.T. 1997: Seasonal and annual energy budgets of female desert tortoises (*Gopherus agassizii*). *Ecology 78: 283–296.*
Lagarde F., Bonnet X., Henen B.T., Corbin J., Nagy K.A. & Naulleau G. 2001. Sexual size dimorphism in steppe tortoises (*Testudo horsfieldi*): growth, maturity, and individual variation. *Can. J. Zool. 79: 1433–1441.*
Lambert M.R.K. 1982: Studies on the growth, structure and abundance of the Mediterranean spur-thighed tortoise, *Testudo graeca*, in field populations. *J. Zool. 196: 165–189.*
Lambert M.R.K., Campbell K.L.I. & Kabigumila J.D. 1998: On growth and morphometrics of leopard tortoises, *Geochelone pardalis*, in Serengeti National Park, Tanzania, with observations on effects of bushfires and latitudinal variation in populations of eastern Africa. *Chel. Conserv. Biol. 3: 46–57.*
Loehr V.J.T., Henen B.T. & Hofmeyr M.D. 2006: Shell characteristics and sexual dimorphism in the Namaqualand speckled padloper, *Homopus signatus signatus*. *Afr. J. Herpetol. 55: 1–11.*
Loveridge A. & Williams E.E. 1957: Revision of the African tortoises and turtles of the suborder Cryptodira. *Bull. Mus. Comp. Zool. 115: 163–557.*
Macale D., Scalici M. & Venchi A. 2009: Growth of the Egyptian tortoise *Testudo kleinmanni* Lortet, 1883. *Israel J. Ethol. Evol. (Isr. J. Zool.) 55: 133–148.*
Malmgren J.C. & Thollesson M. 1999: Sexual size and shape dimorphism in two species of newts, *Triturus cristatus* and *T. vulgaris* (Caudata: Salamandridae). *J. Zool. 249: 127–136.*
Mann G.K.H., O'Riain M.J. & Hofmeyr M.D. 2006: Shaping up to fight: sexual selection influences body shape and size in the fighting tortoise (*Chersina angulata*). *J. Zool. 269: 373–379.*
McCord R.D., Strauss R.E. & Lowe C.H. 1990: Morphometric variation in *Kinosternon* turtles of the western United States and adjacent Mexico. *J. Herpetol. 24: 297–301.*
Michel S. & Stöck M. 1996: Untersuchungen zur Populationsdichte und Struktur der Steppenschildkröte *Agrionemys horfieldii* (Gray, 1844) in der südlichen Kyzyl-Kum (Usbekistan) (Reptilia: Testudines:

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Testudinidae). *Zool. Ab. Mus. Tierk. Dresden, Germany 49: 73–82.*
Mitchell J.C. 1985: Female reproductive cycle and life history attributes in a Virginia population of painted turtle *Chrysemys picta*. *J. Herpetol. 19: 218–226.*
Mlynarski M. 1966: Morphology of the shell of *Agrionemys horsfieldii*. *Acta Biol. Cracov. Ser. Zool. 9: 219–223.*
Nieuwolt-Dacanay P.M. 1997: Reproduction in the western box turtle, *Terrapene ornata luteola*. *Copeia 1997: 819–826.*
Perälä J. 2001: A new species of *Testudo* (Testudines: Testudinidae) from the Middle East, with implications for conservation. *J. Herpetol. 35: 567–582.*
Perälä J. 2005: Assessment of the threatened status of *Testudo kleinmanni* Lortet, 1883 (Testudines: Testudinidae) for the IUCN Red List. *Chel. Conserv. Biol. 4: 891–898.*
Rohlf F.J. 1993: Relative warp analysis and an example of its application to mosquito wings. In: Marcus L.F., Bello E. & Garcìa-Valdecasas A. (eds.), Contribution to morphometrics. *Museo Nacional de Ciencias Naturales, Madrid: 131–159.*
Rohlf F.J. 2004: Tps Series. Department of Ecology and Evolution. *State University of New York, Stony Brook.*
Schleich H.H., Kastle W. & Kabisch K. 1996: Amphibians and reptiles of North Africa. *Koeltz Scientific Publishers, Koenigstein.*
Schneider W. & Schneider C. 2006: Field notes on the Egyptian tortoise, *Testudo kleinmanni* Lortet, 1883 in Libya. *Radiata 15: 11–19.*
Shine R. 1989: Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol. 64: 419–431.*
Shine R. 1990: Proximate determinants of sexual differences in adult body size. *Am. Nat. 135: 278–283.*
Shine R. 1994: Sexual size dimorphism in snakes revisited. *Copeia 1994: 326–346.*
Sindaco R. & Eremcenko V.K. 2008: The reptiles of the Western Palearctic. 1. Annotated checklist and distributional atlas of the turtles, crocodiles, amphisbaeninas and lizards of Europe, North Africa, Middle East and Central Asia. *Monogr. S.H.I., Belvedere.*
Slice D.E., Bookstein F.L., Marcus F.L. & Rohlf F.J. 1996: A glossary of geometric morphometrics. In: Marcus L.F., Corti M., Loy A., Naylor G.J.P. & Slice D.E. (eds.), Advances in morphometrics. *Plenum Press, New York: 531–551.*
Široký P. & Fritz U. 2007: Is *Testudo werneri* a distinct species? *Biologia 62: 228–231.*
Valenzuela N., Adams D.C., Bowden M.R. & Gauger A.C. 2004: Geometric morphometric sex estimation for hatchling turtles: a powerful alternative for detecting subtle sexual shape dimorphism. *Copeia 4: 735–742.*
Wilbur H.M. & Morin P.J. 1988: Life history evolution in turtles. In: Gans D.C., Huey B. & Riss A. (eds.), Biology of the reptilia. Ecology B. *Academic Press, New York: 387–437.*
Willemsen R.E. & Hailey A. 1999: 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. 2003: Sexual dimorphism of body size and shell shape in European tortoises. *J. Zool. 260: 353–365.*
Yasukawa Y., Ota H. & Iverson J.B. 1996: Geographic variation and sexual size dimorphism on *Mauremys mutica* (Cantor, 1842) (Reptilia: Bataguridae), with description of a new subspecies from southern Ryukyus, Japan. *Zool. Sci. 13: 303–317.*
Zelditch M.L., Sheets H.D. & Fink W.D. 2004: Spatiotemporal reorganization of growth rates in the evolution of ontogeny. *Evolution 54: 1363–1371.*
Zuffi M.A.L., Odetti F. & Meozzi P. 1999: Body size and clutch size in the European pond turtle (*Emys orbicularis*) from central Italy. *J. Zool. 247: 139–143.*

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