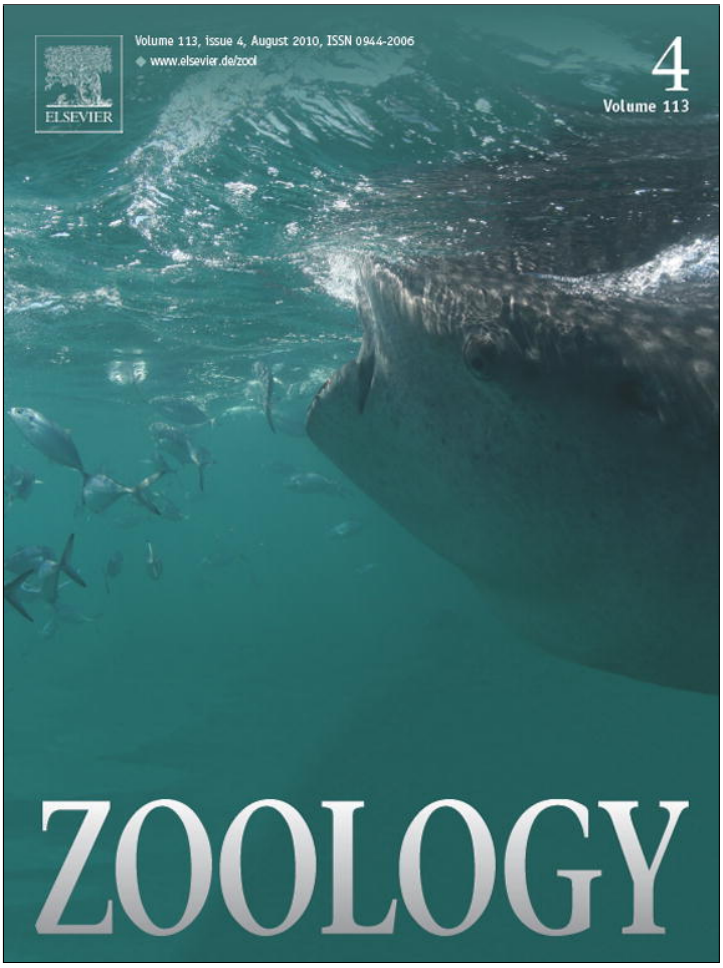
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Is sexual body shape dimorphism consistent in aquatic and terrestrial chelonians?

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Comparisons between aquatic and terrestrial species provide an opportunity to examine how sex-specific adaptations interact with the environment to influence body shape. In terrestrial female tortoises, selection for fecundity favors the development of a large internal abdominal cavity to accommodate the clutch; in conspecific males, sexual selection favors mobility with large openings in the shell. To examine to what extent such trends apply in aquatic chelonians we compared the body shape of males and females of two aquatic turtles (*Chelodina colliei* and *Mauremys leprosa*). In both species, females were larger than males. When controlled for body size, females exhibited a greater relative internal volume and a higher body condition index than males; both traits potentially correlate positively with fecundity. Males were more streamlined (hydrodynamic), and exhibited larger openings in the shell providing more space to move their longer limbs; such traits probably improve mobility and copulation ability (the males chase and grab the female for copulation). Overall, although the specific constraints imposed by terrestrial and aquatic locomotion shape the morphology of chelonians differently (aquatic turtles were flatter, hence more hydrodynamic than terrestrial tortoises), the direction for sexual shape dimorphism remained unaffected. Our main conclusion is that the direction of sexual shape dimorphism is probably more consistent than sexual size dimorphism in the animal kingdom.

1. Introduction

One important purpose of morphometric studies is to frame variations of body size and body shape within a broad evolutionary context. In addition to phylogenetic constraints (i.e. the "historical factor", Raup, 1972), it is assumed that most morphological traits result from the interactions between natural (ecological) selection and sexual selection: ecological selection favoring traits that maximize survival and maximize juvenile growth rates, sexual selection influencing morphological characteristics in ways that directly increase reproductive success (Stearns, 1977; Shine, 1990). Sexual selection and natural selection can interact in opposition or in synergy, depending upon various factors such as sex (Shine, 1989, 1990; Hedrick and Temeles, 1989; Mueller, 1990; Andersson, 1994; Arnold, 1994; Fairbairn, 1997; Chippindale et al., 2001).

Indeed, in most species the reproductive success of females and males is determined in different ways, with females being under strong selection to produce the maximum number of surviving offspring, whilst the fitness of the males is positively correlated with mating success (Dussenbury, 2000). These divergences between the sexes are considered to form the basis for the emergence of various forms of sexual dimorphism (Hedrick and Temeles, 1989; Shine, 1994; Levitan, 1996). Assessing the influence of divergent selective forces on the respective morphology of the sexes is therefore important.

Different factors such as phylogeny, allometry, phenotypic plasticity, and sexual conflicts complicate such an endeavor (Arthur, 2000; Chippindale et al., 2001; Claude et al., 2003; Kuraku et al., 2005; Tobler et al., 2008). Sexual size dimorphism (SSD, the most studied form of dimorphism between the sexes; Fairbairn et al., 2007) provides a clear illustration of such difficulties. Exceptions to broad trends weaken unequivocal explanations: any counter example to a general rule (e.g., one sex should be larger than the other in a given lineage) renders the rule incapable of embracing all situations, and calls for *ad hoc* explanations. For instance, exceptions (e.g., "reverse SSD "in birds and mammals) have been documented in different taxa generating a multiplication of alternative hypotheses for particular taxonomic groups (Ralls, 1976;

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Andersson and Norberg, 1981; Jehl and Murray, 1986; McLachlan and Allen, 1987; Mueller, 1989, 1990; Bisazza and Marin, 1995; Guerra and Drummond, 1995; Bunce et al., 2003; Sergio et al., 2007).

It has been proposed that, in most taxa, the direction of sexual dimorphism in body shape (SShD) or body plan should be easier to predict compared to sexual size dimorphism (Bonnet et al., 1998, 2001). Even in species where the average body size of males and females is indistinguishable (=absence of SSD), we may nonetheless observe predictable sex divergences in body shape (Schwarzkopf, 2005). Females should exhibit well-developed capacities to process and store nutrients for offspring production and to hold the clutch (litter), whereas males are not constrained by these reproductive requirements but may exhibit attributes associated with copulatory behavior. For example, morphological traits associated with the capacity to accommodate the progeny in the body cavity should be consistently larger in females than in males. There is a plethora of studies on sexual size dimorphism that partly address these issues; notably regarding the strong positive correlation between fecundity and body size in females (Andersson, 1994 and references therein). However, fewer studies specifically examine the question of overall body proportions per se (Allison et al., 1999; Malmgren and Thollesson, 1999; Bonnet et al., 2001; Olsson et al., 2008; Kratochvíl et al., 2003; Schulte-Hostedde et al., 2003; Schwarzkopf, 2005). Possibly because body size is positively correlated with almost all body traits (including abdomen volume), the fundamental difference between body size and body shape has been seldom considered. The complications associated with the characterization of body shape (Walker, 1997; Hulsey et al., 2008) offer a possible additional explanation for the lack of attention to SShD. Indeed, although a single descriptor of body size is conceivable (body length, body width or body mass, Peters, 1983; Brown and Maurer, 1986; LaBarbera, 1989), the description of the overall body shape requires a more comprehensive set of measurements (Walker, 1997; Bonnet et al., 1998, 2001; Allison et al., 1999). Several traits facilitate the analysis of sexual shape dimorphism, however. Large variations in adult body size with a substantial overlap between the sexes make it possible to take into account the allometric effects of size on body shape (Gould, 1966; Peters, 1983). The absence of extensive bi-parental care – the most widespread situation in the animal kingdom – simplifies the respective reproductive role of each sex (Shine, 1988, 1990).

Vertebrates with representatives living both in aquatic and terrestrial environments offer an opportunity to examine sexual body shape dimorphism under the respective constraints imposed by divergent environments (Davenport et al., 1984; Claude et al., 2003; DeSalle and Schierwater, 2007; Fish et al., 2008; Vogel, 2008). Aquatic vertebrates exhibit different morphological traits, behaviours and physiological attributes compared to their terrestrial relatives resulting in profoundly modified body shapes (Rivera et al., 2006). Chelonians (tortoises and turtles) provide a suitable model with which to examine the hypothesis that SShD might be consistent despite the strong influence of contrasted environments on morphology. In chelonians, independent lineages include both terrestrial and aquatic living forms; in addition, they do not exhibit parental care (Gaffney and Meylan, 1988). Their body shape can be assessed via measurements of the shell geometry because feeding and reproductive statuses do not modify shell dimensions. Moreover, the body plan of turtles, based on the central protective role of the carapace, has been conserved since the emergence of this group (Burke, 1989; Gaffney, 1990; Lee, 1993).

To date, sex dimorphism of the overall body shape, including the main dimensions of the shell, body mass, the size of the limbs and of the head, has been examined in two terrestrial tortoises, *Testudo horsfieldii* (Bonnet et al., 2001) and *Testudo graeca* (Ben Kaddour et al., 2008), both belonging to the pleurodire lineage. From these studies, a number of simple hypotheses have been proposed to predict the direction of sexual body shape dimorphism (Table 1). The aim of this paper is to test to what extent these hypotheses, based on a terrestrial species, are applicable in two aquatic chelonians from distinct lineages: the Australian long-neck turtle *Chelodina colliei* (Pleurodira) and the stripe-necked terrapin *Mauremys leprosa* (Cryptodira). We emphasize that our goal was not to examine the influence of divergent environments on body shape. Instead, we specifically focused on testing if the direction of sexual dimorphism for the main morphological traits was consistent across aquatic and terrestrial chelonians. Examining the different locomotor requirements and biomechanics of locomotion in aquatic versus terrestrial habitats (or differences in behavior related to habitat), although of fundamental importance, was therefore out of the scope of the present study. We also emphasize that we considered the overall shell shape using a set of morphological traits rather than focusing on an organ in isolation (considering solely head size relative to body size, for instance).

2. Materials and methods

2.1. Species and study sites

The two species of freshwater turtles involved in this study, the long-neck turtle *C. colliei* (south west of Australia) and the stripe-necked terrapin *M. leprosa* (north Africa and southern part of the Iberian peninsula), belong to different lineages, separated since the Triassic period (Gaffney and Meylan, 1988). The long-neck turtle is a pleurodire, whilst the stripe-necked terrapin is a cryptodire; consequently, the stripe-necked terrapin is more closely related to the terrestrial tortoises (e.g., genus *Testudo*) than to the other pleurodires. The long-neck turtle is a highly specialized freshwater turtle, with the longest neck of any turtle species, probably as an adaptation for piscivory and plankton feeding (Pritchard, 1979, 1984; Kuchling, 2006). The two turtle species examined nonetheless share several ecological characteristics; they are both highly aquatic, they inhabit ponds, lakes and streams and they feed principally on aquatic vertebrates and invertebrates (Meek, 1987; Cogger, 1992; Muñoz and Nicolau, 2006). The shell is elongated and narrow in both species. A concave plastron characterizes the males; and females are larger than males in both species (Kuchling, 1989; Guyot and Kuchling, 1998; Muñoz and Nicolau, 2006). Adult males typically have longer and thicker tails with more distally located cloacae than females (Kuchling, 1999).

The specimens involved in the current study were captured with a landing net in Lake Jualbup at Shenton Park in Perth (Western Australia), and in two non-permanent rivers, Oued Tensift and Oued Zat in the vicinity of Marrakech (Morocco). We selected only mature individuals where the sex can be readily determined (Meek, 1987; Kuchling, 1988, 1989; Lagarde et al., 2001; Muñoz and Nicolau, 2006). We caught 35 free-living adult long-neck turtles (16 females and 19 males) and 59 free-living adult stripe-necked terrapins (42 females and 17 males). Immediately after capture we recorded the main external morphological characteristics of each specimen (see Section 2.2). All the individuals were released at the place of capture after completion of measurements, broadly 20 min to 2 h after capture.

2.2. Measurements

For comparative purposes, in both species, we adopted the same methodology we used to study the steppe tortoise (*T. horsfieldii*; Bonnet et al., 2001) and the Greek tortoise (*T. graeca*; Ben Kaddour et al., 2008). To characterize the external morphology of the tortoises, we measured the main dimensions of the shell and the size of the

Table 1
Hypotheses on the direction of sexual body shape dimorphism in terrestrial and aquatic chelonians (derived from this table in Bonnet et al., 2001).

Traits (morphology, behavior)	Sex shape dimorphism	Fitness component
All chelonians		
Abdominal volume scaled by size	Greater in females[a]	Enhance egg carrying capacity
Body mass scaled by size	Females heavier[a]	Enhance egg production Enhance male's mobility
Openings in the shell for the limbs	More developed in males[a]	Enhance mobility (righting ability?)
Tail	Longer in males[a]	Enhance sperm transfer
Aquatic chelonians		
Carapace height	Males more flat	Enhance male's mobility Fecundity selection in females favors large volume

[a] Similarities between results gathered in a terrestrial chelonian (Bonnet et al., 2001) and the current study.

main openings in the shell. We also measured the length of the tail and the relative position of the cloaca. Linear measurements of the shell were obtained with digital callipers (precision 0.1 mm). Total body mass was obtained with an electronic scale (to 1 g). Below, we provide further details on the measurements.

2.2.1. *The shell*

Carapace length (CL) was measured as the maximal antero-posterior shell length. Carapace, or shell width was represented by two measurements: the maximal width at the level of the sixth (CW6) and eighth (CW8) marginal scute. Carapace, or shell height was the maximal height of the shell (CH). Curvilinear measurements of shell width including the plastron (CURV) were recorded in the long-neck turtle using a flexible rule at the level of the sixth marginal scute (Bonnet et al., 2001). The combination of shell length and CURV provided an easily measurable index of shell volume in the field (see Bonnet et al., 2001 for details). Plastron size was recorded in two ways: first, the maximal antero-posterior length of the plastron (Plmax); second, the minimal mid-line length of the plastron recorded in the notches (=indentations; Plmid).

2.2.2. *Shell openings*

Firstly, the comparison between the dimensions of the plastron relative to the shell provides an estimate of the space available to move the head and the legs. A relatively small plastron automatically means that more space is available between these two major components of the shell. Similarly, Plmid compared to Plmax provided another index of the indentation (opening) of the plastron. In addition, we directly measured the space available to move the tail between the posterior parts of the anal scutes (W), and between the rear parts of the plastron and the supracaudal scute (Z). This later measurement also provides the most restrictive dimension for passing eggs.

2.2.3. *Tail length and position of the cloaca*

Tail length was measured along its ventral edge, from the base of the external portion of the tail to the tail-tip. The relative position of the cloaca was recorded from the base of the tail.

2.2.4. *Body mass*

This major trait is often missing in studies focusing on tortoise morphology, notably sexual dimorphism, partly because many data sets have been collected on museum specimens. Large fluctuations of body mass independent of body size may also explain why researchers are reluctant to incorporate this trait in morphological analyses. Indeed, body mass varies significantly with physiological and nutritional status (food intake, hydration, reproduction, etc.). However, body mass scaled by size provides an integrative nutritional index: body reserves, clutch mass, and the mass of the internal organs that contribute to the overall body condition (e.g., viscera, liver, and fat bodies) are all directly influenced by food intake and energy budget and they represent a crude estimate of body reserves and reproductive output. Importantly, these traits influence locomotor and reproductive performances and are therefore directly relevant to sexual dimorphism hypotheses (Jackson, 1969; Bonnet et al., 1998, 2001; Clark et al., 2001). The calculation of body mass scaled by size provides a useful estimate of how easily mobile an individual is (heavy specimens necessarily requiring more energy during displacements; Heglund and Taylor, 1988; Johnston, 1991) and of the resources that have been invested (or are available) in internal organs and for offspring production (Henen, 1997). Interestingly, in chelonians, body mass can vary substantially independently of body volume. Such a unique situation among vertebrates offers an opportunity to examine the mobility hypothesis. In other vertebrates body volume and body mass co-vary inevitably; for instance in mammals, birds, lizards or snakes the development of a large musculature entails an increase in both body mass and body volume.

2.3. *Statistical analyses*

This study focused on predictions clearly limited to the direction of sexual body shape dimorphism for various traits (Table 1). Using a single descriptor of body size or body shape would have been antagonistic to our main goal. Consequently, we did not use integrative measurements (PCA, geometric mean, Procustes methods, etc.) in an attempt to calculate a synthetic morphometric descriptor of body shape. More comprehensive morphometric information and analyses would have been useful (e.g., numerous landmarks on the shell, plastron, head, tail and legs) to fully describe the morphology of the individuals (e.g., Stayton, 2009), but such procedures are not easily applicable to large numbers and in the field.

For our purposes, ANCOVA offers one of the most straightforward methods to test if a size-corrected morphological trait is sexually divergent or not. For example, scaling body mass relative to body size will clearly indicate if one sex is proportionally heavier than the other, enabling to assess one of our main predictions. The large variations in adult body sizes, the large overlapping between the sexes and the species, and the absence of deviations from linearity in the relationships considered (see Fig. 1 and Section 3.1) enabled us to use linear models to perform comparisons of body size (ANOVAs) and body proportions (ANCOVAs) between the sexes (Barron, 1997). We selected covariates that allowed for the testing of the hypotheses of Table 1 and that have also been used in previous studies (Bonnet et al., 2001; Willemsen and Hailey, 2003). For instance, the size of the plastron was considered relative to the length of the shell to examine if males do exhibit larger openings between these two major components of the carapace.

All data were log-transformed for statistical analyses, except ratios that were arc-sine transformed. However, mean values (±standard deviation) and ranges of variations are presented as non-transformed data in the tables and figures to facilitate comparisons between studies. We tested data distribution for normality and heteroskedasticity before completing these analyses. For broad

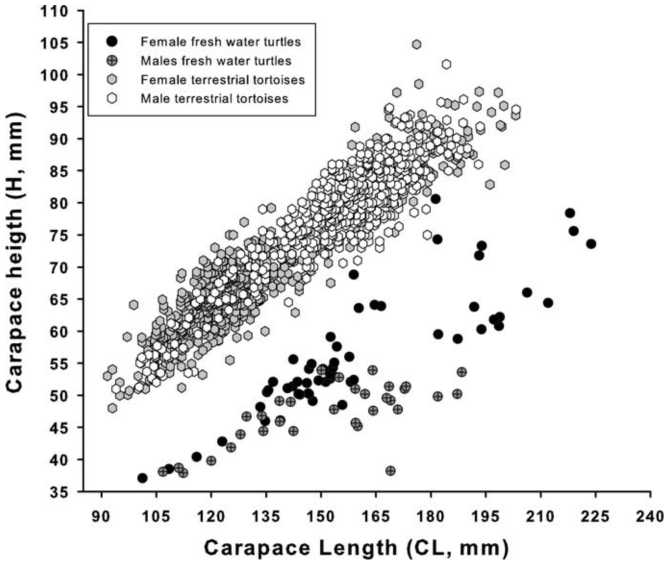

Fig. 1. Relationship between shell height (*y*-axis) and shell length (*x*-axis) in terrestrial and aquatic chelonians. Freshwater turtles exhibit a markedly flatter shell when compared with terrestrial tortoises, irrespective of phylogeny ($P < 0.001$, see text for details). In freshwater turtles, males are more streamlined compared to females ($P < 0.01$ in both long-neck turtle and stripe-necked terrapin, see text for details).

comparisons between terrestrial and aquatic chelonians, we also used the large data sets we collected on terrestrial tortoises (*T. horsfieldii*, *T. graeca*, *T. boettgeri*, and *T. hermanii*; Bonnet et al., 2001; Ben Kaddour et al., 2008; unpublished data). Means are presented with their standard error. Statistics were performed with Statistica 7.1. (StatSoft Inc., Tulsa, OK, USA) and R 2.7.1 (available at http://www.R-project.org/) softwares.

3. Results

3.1. Terrestrial versus aquatic species: general comparisons of body size and body shape

We first performed preliminary analyses on the size and shape of the turtles (aquatic) and tortoises (terrestrial) to examine if a potential strong segregation in the size distribution between the species and/or the sexes generated allometric (and thus analytical) complications. Despite important inter-individual variations within species, terrestrial and aquatic species included in the current study overlapped greatly in body size (Fig. 1 and Table 2). Similarly, the ranges of body size overlapped between the sexes (Fig. 1 and Table 2). Consequently, it was possible to test our main hypotheses about sexual body shape dimorphism in a context relatively free from major allometric complications.

Table 2
Mean carapace length ± standard deviation (in mm) for all species measured and for both sexes. The number of individuals (*N*, in brackets) and ranges of variation (range) are indicated.

Species	Sex (*N*)	Mean ± SD	Range
Chelodina colliei	F (16)	194.3 ± 21.3	153.5–223.8
	M (19)	171.6 ± 11.3	153.5–193.2
Mauremys leprosa	F (42)	148.4 ± 18.5	101.2–193.9
	M (17)	134.9 ± 17.0	106.8–164.1
Testudo horsfieldii	F (389)	154.3 ± 15.6	94.0–193.0
	M (422)	121.6 ± 11.4	91.6–152.6
Testudo graeca	F (112)	147.1 ± 25.4	100.0–188.9
	M (131)	125.0 ± 10.7	100.7–155.1
Testudo boettgeri	F (28)	173.6 ± 13.0	148.5–203.2
	M (249)	173.2 ± 14.4	116.5–205.0
Testudo hermanii	F (21)	152.9 ± 17.4	110.0–175.0
	M (18)	133.6 ± 10.8	110.0–151.0

Table 3
Morphological traits measured on two freshwater turtle species and used in statistical tests. For each trait, mean value ± standard deviation as well as the observed range of values is presented. Number of individuals (*N*, in brackets) and range of variation (range) are provided.

Trait	Species (*N*)	Mean ± SD	Range
CL	*Chelodina* (35)	182.0 ± 20.0	153.5–223.8
	Mauremys (59)	144.5 ± 101.2	101.2–193.9
CURV	*Chelodina* (32)	137.5 ± 17.9	112.0–185.0
CW6 (mm)	*Chelodina* (35)	101.6 ± 11.7	68.9–128.2
	Mauremys (59)	99.8 ± 12.8	73.6–134.9
CW8 (mm)	*Chelodina* (33)	106.0 ± 12.3	89.3–136.0
	Mauremys (59)	106.7 ± 13.7	76.5–139.4
CH (mm)	*Chelodina* (29)	56.1 ± 9.8	38.2–78.4
	Mauremys (59)	51.7 ± 9.0	37.1–80.6
Plmax (mm)	*Chelodina* (35)	149.6 ± 18.2	123.7–188.6
	Mauremys (59)	122.1 ± 17.4	84.0–170.7
Plmid (mm)	*Chelodina* (35)	144.3 ± 17.2	118.7–181.0
	Mauremys (59)	122.8 ± 18.5	85.8–173.2
Z (mm)	*Chelodina* (33)	36.0 ± 4.4	29.2–46.2
	Mauremys (59)	16.5 ± 3.2	10.9–27.1
Tail (mm)	*Chelodina* (35)	59.6 ± 12.0	27.2–78.2
	Mauremys (59)	70.5 ± 10.6	54.7–114.0
Body mass (g)	*Chelodina* (34)	756.3 ± 296.9	419–1462
	Mauremys (59)	436.7 ± 187.3	146–1006

We also examined if aquatic turtles effectively exhibited markedly different body proportions compared to their terrestrial relatives, which was a prerequisite for our main questions. Freshwater turtles exhibited a markedly flatter shell when compared with terrestrial tortoises (Fig. 1). On average, the shell height/shell length ratio (CH/CL) was 0.34 ± 0.04 (range: 0.22–0.34; $N = 88$) for aquatic turtles versus 0.52 ± 0.03 (range: 042–0.65; $N = 1197$) for terrestrial species (ANOVA with species as the main factor, shell height as the dependent variable, shell length as the independent variable: $F_{1,1280} = 2.77$; $P < 0.001$), with an almost complete segregation between the two groups despite large sample sizes. Consequently, our data set provided an appropriate context to test our main hypothesis: "Is sexual body shape dimorphism consistent in aquatic and terrestrial chelonians?"

3.2. Sexual size dimorphism in freshwater turtles

A MANOVA test was performed with the main dimensions of the shell (CL, CW6, CW8, CH, Plmax, Plmid, and body mass) as the dependent variables, and revealed strong effects for these factors: sex (Wilks $\lambda = 0.52$; $F_{8,75} = 8.76$; $P < 0.001$), species (Wilks $\lambda = 0.06$; $F_{8,75} = 138.73$; $P < 0.001$), and their interaction (Wilks $\lambda = 0.79$, $F_{8,75} = 2.45$, $P = 0.021$). The long-neck turtle was significantly larger for all traits and heavier than the stripe-necked terrapin (Table 3, $P < 0.001$ for all post hoc tests). Females were larger (hence heavier) than conspecific males in both species (Table 2, $P < 0.001$ for all post hoc tests), and the degree of sexual size dimorphism was affected by the species. As all the morphological traits above were highly inter-correlated (all $R^2 > 0.80$ and $P < 0.001$), further analyses (e.g., considering each trait separately) failed to provide information relevant to this study, therefore the associated results are not presented.

3.3. Sexual dimorphism in body shape in freshwater turtles

When controlled for body size, shell length (CL) or other shell size indexes, females and males differed for many traits in both species (Table 4). All the results were consistently oriented in the same directions. For example, the plastron was systematically relatively smaller in males (either total plastron length or

Table 4
Results of statistical tests performed on the log-transformed measures of body shape (using ANCOVA and the specified covariate) in both species of freshwater turtles (*Chelodina colliei* and *Mauremys leprosa*). The boldfaced values indicate the larger sex when the sex effect was significant (significant level: 0.05). For conciseness, this table presents a selection of analyses, given the large number of variables used (>15 morphological traits, 2 sexes, 2 species). All the analyses were performed using both a general model and separately for each species. No conflict arose between the two approaches. Bonferroni post hoc corrections were performed for each test; none of our results was altered. In addition, several measurements were available for one species. For ease of reading, un-transformed mean values are presented.

Variable	Genus	Covariate	Adjusted mean		*F*-test	*df, N*	*P*-value
			Males	Females			
Shell							
CW6	*Chelodina*	CL	102.8	99.8	2.62	1, 32	0.115
CW6	*Mauremys*	CL	97.6	**99.5**	4.14	1, 56	**0.047**
CW8	*Chelodina*	CW6	102.1	**109.1**	14.77	1, 32	**<0.001**
CW8	*Mauremys*	CW6	105.7	105.8	0.02	1, 56	0.889
CH	*Chelodina*	CL	51.3	**60.0**	17.75	1, 29	**<0.001**
CH	*Mauremys*	CL	48.9	**52.0**	10.66	1, 56	**0.002**
Openings							
Plmax	*Chelodina*	CL	145.7	**151.9**	17.32	1, 32	**<0.001**
Plmax	*Mauremys*	CL	119.5	121.3	1.84	1, 56	0.181
Plmid	*Chelodina*	Plmax	142.9	144.2	1.73	1, 32	0.198
Plmid	*Mauremys*	Plmax	118.4	**122.7**	7.87	1, 56	**0.007**
W	*Chelodina*	Plmax	**26.0**	22.6	9.13	1, 31	**0.005**
W	*Mauremys*	Plmax	21.2	19.7	0.37	1, 56	0.546
Z	*Chelodina*	CL	35.1	36.4	1.45	1, 30	0.238
Z	*Mauremys*	CL	16.0	16.3	0.17	1, 56	0.684
Z	*Chelodina*	Plmax	35.8	35.7	0.00	1, 30	0.956
Z	*Mauremys*	Plmax	16.1	16.3	0.02	1, 56	0.882
Tail							
Length	*Chelodina*	CL	**72.3**	44.8	121.4	1, 33	**<0.001**
Length	*Mauremys*	CL	**77.5**	67.0	22.31	1, 59	**<0.001**
Cloak	*Chelodina*	CL	**52.3**	30.1	138.9	1, 35	**<0.001**
Cloak	*Mauremys*	CL	**34.2**	22.7	28.08	1, 59	**<0.001**
Cloak	*Chelodina*	Tail length	**43.6**	37.4	9.38	1, 33	**0.004**
Cloak	*Mauremys*	Tail length	**31.8**	23.3	24.31	1, 59	**<0.001**
Body mass							
Mass	*Chelodina*	CL	648.0	**777.5**	35.26	1, 31	**<0.001**
Mass	*Mauremys*	CL	372.2	**413.9**	15.01	1, 56	**<0.001**
Mass	*Chelodina*	CL × CH	676.1	**758.6**	5.32	1, 24	**0.03**
Mass	*Mauremys*	CL × CH	363.1	**380.2**	4.26	1, 55	**0.042**
Mass	*Chelodina*	CL × CURV	658.9	**764.3**	22.54	1, 27	**<0.001**

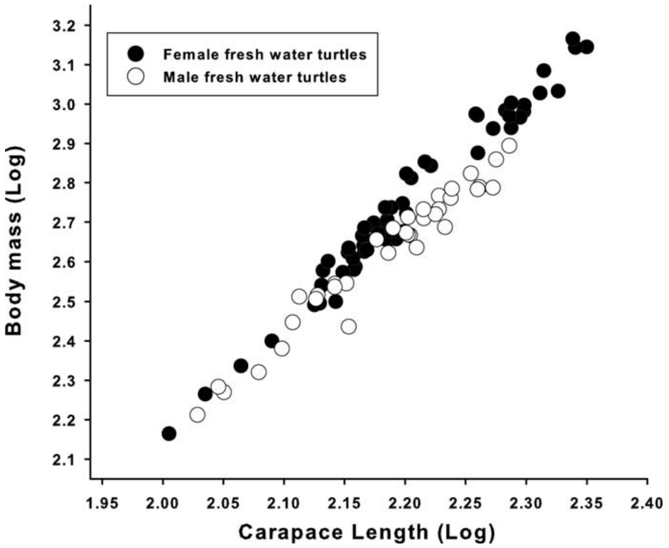

Fig. 2. Relationship between body mass (measured in g, log-transformed, *y*-axis) and shell length (in mm, log-transformed, *x*-axis) in two species of aquatic chelonians: *Chelodina colliei* and *Mauremys leprosa*. Female turtles (black circles) are relatively heavier when compared with males (open circles). The two species are not graphically separated because body sizes overlap greatly (see text for details). The clear sexual body shape dimorphism observed held true when the main dimensions of the shell (i.e., CW6, CW8, CH, Plmax, Plmid or CURV) were used separately or in various combinations, as covariates.

mid-line plastron length being significantly smaller) compared to females. On average, females were more voluminous than conspecific males: they exhibited a greater relative shell width, shell height, and a relatively larger plastron. They were also relatively heavier when body mass was controlled by the main dimensions of the shell (i.e., CL [Fig. 2], CW6, CW8, CH, Plmax, Plmid or CURV used separately or in various combinations as in index of body volume, as covariates [analyses not all shown]). Conversely, the openings in the shell were more developed in males relative to females. This result was reinforced when considering the relative larger space to move the tail in males than in females observed in the long-neck turtle, and a similar (albeit non-significant) trend for the stripe-necked terrapin. For both species, on an absolute scale, the tail was longer in males with a more posterior position of the cloaca. This sex difference in the position of the cloaca held true when the absolute difference in tail length was taken into account (Table 4).

The analyses were re-performed separately for each species to control for the variance generated by the significant differences between the species that can blunt possible subtle sex effects. This procedure enabled us to scrutinize more finely for the existence and direction of sexually dimorphic traits. The results remained unchanged (not reported) or reached significance. Notably, when the main dimensions of the shell (e.g., CL × CH, or CL × CURV; Table 4) were included, the females exhibited a higher body condition index.

4. Discussion

From a simplistic perspective, the optimal protective shape of the carapace is spheroid, a body form adopted by various taxa (e.g., hedgehogs, pangolins, woodlouses and pill millipedes). In terms of the mass/surface ratio, a spheroid offers less opportunity to predators to inflict bites (Wilbur and Morin, 1988; Stayton, 2009); it also limits evaporative water loss (Graham et al., 1995). Although the relatively round-shaped carapace of the chelonians has been conserved since the emergence of this group more than 200 million years ago, evolution produced a great diversity of forms both in living and fossil species (Burke, 1989; Gaffney, 1990). Among different factors that influence carapace shape (Gaffney and Meylan, 1988; Wilbur and Morin, 1988; Burke, 1989), life style is one of the most important (Davenport et al., 1984; Claude et al., 2003; DeSalle and Schierwater, 2007; Blob et al., 2008; Rivera, 2008). The flat body shape of freshwater turtles compared to terrestrial species as documented in the current study can be reasonably interpreted as a consequence of the strong hydrodynamic constraints imposed by the aquatic environment on distant lineages (pleurodires versus cryptodires).

Our main results, however, suggest that the massive influence imposed by contrasting environments, aquatic versus terrestrial, on chelonian morphology did not alter the major directions of sexual dimorphism in body shape. We did not find any result contradicting the predictions proposed in Table 1. Despite the relatively small sample size available for freshwater turtles, and despite the fact that most of the dimorphisms we documented were modest in absolute proportions (<10% of the size-corrected measurements on average; see Table 4), most predicted sex differences in body shape were significant. This was true for both a typical freshwater terrapin (stripe-necked terrapin) and the highly morphologically specialized long-neck turtle. Most of our results can be interpreted in terms of simple selective advantages: sexual selection in males and selection for fecundity in females.

4.1. *Sexual shape dimorphism*

When scaled by size, the abdominal volume was systematically greater in females than in males. A recent study on the stripe-necked terrapin in Spain reported similar trends with larger and more domed females that also exhibited a more closed carapace compared to males; unfortunately, body mass was not reported (Muñoz and Nicolau, 2006). A large relative abdominal volume is positively correlated with the capacity to accommodate larger clutches (or larger eggs), but it also provides more space for the internal organs (viscera, liver, etc.) that are involved in processing the energy and nutrients necessary for vitellogenesis (Brana, 1996; Henen, 1997; Bonnet et al., 1998; Zuffi and Plaitano, 2007). Similarly, when scaled by volume, females were heavier than males. Measurements of dry carapaces suggest that this difference was not due to a differential thickness of the shell but rather was a consequence of the relative density of the internal content (Bonnet et al., 2001). Although we cannot tease apart the respective contributions of stomach content, body reserves, visceral mass, clutch mass, etc. on the relative mass of the tortoises, the body condition divergence nonetheless indicates that females display a greater body mass compared to males. This might be a consequence of the maternal reproductive investment (via either income or capital breeding), the females being under selection to process and accumulate large amounts of resources (nutrients, body reserves, eggs). Alternatively, males could be under selection to be relatively less dense to maximize mobility in order to maximize the number of females they can find and fertilize. Possibly, males allocate a large proportion of their activity to sex behaviors rather than to food acquisition, this behavioral trade-off producing relatively light males as a by-product. These alternative hypotheses are not in opposition, the outcome being consistently heavy females versus light males.

Males were more streamlined than females. The flat shell of the males correlates with their smaller body volume. A relatively hydrodynamic and light body should enhance mobility and thus should be advantageous for mate searching during the reproductive season. Although field data are lacking to test these hypotheses directly, Muñoz (2004) demonstrated that during the mating season, male stripe-necked terrapins select water with female chemical odors, suggesting a greater searching activity. Other data available for chelonians show that males intensively search for females during the reproductive season (Kuchling, 1999; Lagarde et al., 2003).

The direction of sexual dimorphism in shell height (or domeness) is inconsistent between chelonian species (Bonnet et al., 2001), and *ad hoc* hypotheses are necessary to interpret SSD variations of this trait. In terrestrial tortoises where male-to-male combat generates the risk of being turned upside down, the ability of self-righting is essential. Aquatic chelonians rely on the use of their neck as a fulcrum, whilst terrestrial tortoises depend essentially on the shell geometry to flip back (Bonnet et al., 2001; Mann et al., 2006; Delmas et al., 2007; Domokos and Várkonyi, 2008). When righting does not depend on the shell geometry, or is less frequently relevant (aquatic species), domeness should be systematically more pronounced in females to provide space for the clutch. In contrast, in those species where male-to-male combat generates a strong risk of being flipped, male domeness should reach an optimal geometry (Domokos and Várkonyi, 2008), with cases where males can be even more domed than females (Bonnet et al., 2001). Interestingly, the greater dispersion of the shell height data relative to shell length displayed by the aquatic chelonians compared to tortoises suggests a greater canalization of domeness in terrestrial species (Fig. 1), a trend in accord with the notion of differential constraints proposed above.

4.2. *Sexual size dimorphism*

Interpretations related to sexual size dimorphism are more ambiguous than those associated with sexual shape dimorphism: the majority of chelonians show at least some degree of sexual size dimorphism, but not all, and both the direction and the magnitude of this trait vary considerably without clear phylogenetic pattern (Gibbons and Lovich, 1990; Ernst et al., 1998). Such instability in the SSD patterns led to various interpretations.

In most species large body size correlates with both female fecundity and male reproductive success (Wilbur and Morin, 1988; Kuchling, 1999; Wallis et al., 1999; Zuffi et al., 1999). Berry and Shine (1980) proposed that patterns of chelonian SSD correlate with habitat and mating strategy: (1) In most terrestrial species where male-to-male combat is frequent males are the larger sex, (2) in semi-aquatic species, male combat is less common, but males often forcibly inseminate females and they are usually larger, and (3) in truly aquatic species, male combat and forcible insemination are rare, and males are smaller than females. This scenario was partly supported (Yasukawa et al., 1996), but Gibbons and Lovich (1990) presented an alternative model where age and size at maturity, and continued growth after maturity play major roles. They also integrated the advantage of large size to cover greater distances in search of mates, and possibly to influence female choice. Environment also influences SSD. In terrestrial habitats where predation, desiccation and thermal stress are important, the magnitude of SSD decreases. Fitch (1981) documented a trend in large female reptiles of temperate-zone compared to tropical species: long intervals between laying events favor larger body size in females. But in contradiction to Fitch's hypothesis, in freshwater turtles (Emydidae) the degree of SSD in favor of large females was positively correlated with reproductive frequency (Forsman and Shine, 1995). In fact, sexual size dimorphism results from various combinations of the costs and benefits of the respective growth patterns, maturation schedules, reproductive frequency, survival rates, and possibly other factors (e.g., thermal); such interplay between natural and sexual selection generates complex situations (Gibbons and Lovich, 1990; Dodd, 1997).

5. Conclusion

The direction of sexual body shape dimorphism is likely more consistent than sexual size dimorphism across chelonian lineages, and such an orientation of this sex dimorphism is possibly one of the most widespread in the animal kingdom (Bonnet et al., 1998). The question of the magnitude of sex divergences in size and shape remains an unexplored issue, however. It is important to note that body shape cannot be characterized with isolated features (e.g., head size, sexual ornamentations), but that all major structural traits (such as size, mass and body proportions) should be incorporated. Finally, we propose that marine turtles probably display a typical sexual body shape dimorphism with more mobile males (larger openings in the shell, streamlined shell, relative smaller shell volume, relative longer limbs, more developed locomotor musculature, lower condition index, etc.) and relatively heavy females (larger relative abdominal volume, higher condition index and longer posterior limbs [for digging]). In order to test these hypotheses, it would be essential to collect and examine in more detail the patterns of sexual behaviors and sexual dimorphisms in a wide range of chelonians. Geometric morphometric analyses and finite element methods represent the next step in integrating the importance of selective pressures of the different habitats on the evolution of sexual body shape dimorphism (Butler et al., 2007; Stayton, 2009).

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