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NATURAL HISTORY NOTES

Discovery and description of a novel sexual weapon in the world's most widely-studied freshwater turtle

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Abstract

Sexually coercive reproductive tactics are widespread among animals, where one sex employs specialized structures, called sexual weapons, to harass, intimidate, and/or physically force the other sex to mate. Painted turtles (*Chrysemys picta*) have been extremely well-studied over the last two centuries, and their mating system has been described as female choice based on male courtship display. The present study arises from observation that males seemingly have more protracted and serrated anterior marginal scutes than females. We hypothesized that the anterior carapace is sexually dimorphic, and that this morphology is a weapon used by males in coercive mating. We quantified anterior carapacial morphology using geometric morphometric analysis of digital photographs, drawing on samples of painted turtles from North American museum collections and our field site in Algonquin Provincial Park. We found that the anterior carapace of males had a significantly more serrated and projected shape compared to females, consistent with the sexual weapon hypothesis. Additionally, anterior carapacial shape was more strongly related to body size in males. Behavioural field observations strongly suggest that males use this morphology as a weapon to harm females during reproduction. The present study complements and strengthens the recent hypothesis that male painted turtles engage in coercion as an alternative reproductive tactic, questioning the long-understood paradigm of exclusive female choice in this well-studied species. Our study invites new avenues of research on the evolution of female harm in a system with extreme selection on female longevity and for which operational sex ratios vary among populations. Further, our work underlines how basic natural history observations can transform our understanding of well-studied systems.

Keywords Animal armament · Geometric morphometrics · Mating strategy · Sexual dimorphism · Female harm · Female resistance

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Deborah M. Hawkshaw and Patrick D. Moldowan have contributed equally to this work.

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Introduction

Sexual selection theory attempts to explain conspicuous, sexually dimorphic, and seemingly costly traits (Arnqvist and Rowe 2005). Theory proposes that traits reducing an organism's survival will be favoured by selection if they sufficiently increase reproductive success. In systems where members of one sex compete for access to members of the other sex, traits that enhance access to the limiting sex, usually females, are sexually selected (Darwin 1871). In some systems, males have evolved traits that serve to force copulation with females, which often result in female harm (Smuts and Smuts 1993) but can increase male reproductive success (Clutton-Brock and Parker 1995). These traits can include morphological structures, termed sexual weapons, which act in concert with behavioural traits to physically injure females to gain their acquiescence or to improve reproductive success (Kodric-Brown et al. 1984; Rico-Guevara and Hurme 2019). Many examples of sexual weapons exist: the spines on the intromittent organ of male cowpea weevils (*Callosobruchus maculatus*), for instance, damage the reproductive tract of females while providing male reproductive benefits (Crudgington and Siva-Jothy 2000), and male gopher tortoises (*Gopherus polyphemus*) have been observed ramming females with their modified gular scute during courting (Auffenberg 1966) to promote acquiescence.

The painted turtle, *Chrysemys* spp. (Testudines: Emydidae), is arguably the most thoroughly studied freshwater turtle in the world (Ernst and Lovich 2009; Legler and Vogt 2013; Lovich and Ennen 2013). Within the genus *Chrysemys*, two species are currently recognized (Crother 2012): southern painted turtle (*C. dorsalis* Agassiz 1857) and painted turtle (*C. picta* Schneider 1783), with the latter divided into three subspecies, western painted turtle (*C. p. bellii* Gray 1831), midland painted turtle (*C. p. marginata* Agassiz 1857), and eastern painted turtle (*C. p. picta* Schneider 1783) (Starkey et al. 2003; TTWG 2014). Many sexually dimorphic characters are known in these taxa, including larger female body size and carapace height, longer male forelimb claws and pre-cloacal tail length, and head shape differences between the sexes (Ernst and Lovich 2009; Moldowan et al. 2016b). For over a century, the mating system of the painted turtle was thought to be well understood: observations by Maynard (1869) led to the view that female choice characterizes the mating strategy of the painted turtle. Females select males based on a courtship display (titillation) involving the use of their elongated foreclaws (Darwin 1871 citing Maynard 1869; Berry and Shine 1980; Ernst and Lovich 2009). The few isolated observations of male–female antagonism that had otherwise been reported received little attention (Gibbons 1968; Roddewig 2014). Recent research, however, has hypothesized that male coercion is an alternative reproductive tactic in this group. During bouts of sexual coercion, males restrain females by biting them on the head or neck with their prominent bicuspid tomiodonts, which are tooth-like cusps positioned medially on the upper jaw (Moldowan et al. 2016a, b). Next, males engage in a novel shell-clattering behaviour (Moldowan 2014), where the anterior edges of both male and female carapaces are forcefully and repeatedly rammed together (Video S1). Males will also ram and grind their anterior carapace into the anterior shell opening of females and directly into their head and neck, resulting in wounding to females (Video S1; Fig. 2; Moldowan et al., in review; Moldowan 2014). Interestingly, historical and contemporary morphological descriptions have documented variation in anterior carapacial morphology across all *Chrysemys* taxa (Fig. 1a, Table S1), but despite over one thousand studies on *Chrysemys picta* alone, the structural variation has been overlooked as a possible sexual weapon, and has never been quantified in a sex-specific context.

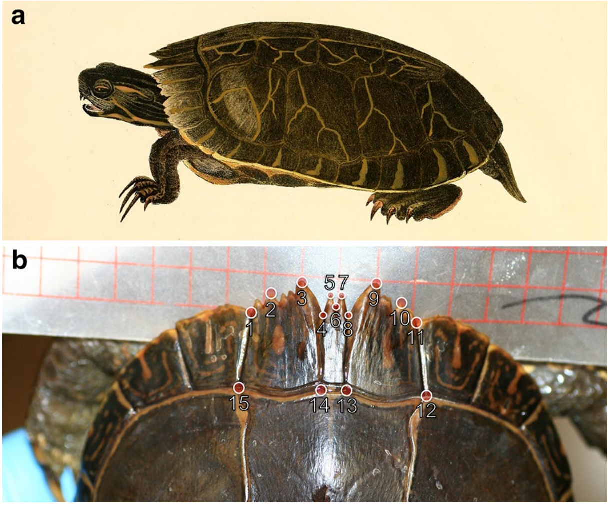

Fig. 1 Anterior carapace morphology in the painted turtle, *Chrysemys* spp. **a** Historical plate drawing of adult male *Emys oregoniensis* (=*Chrysemys picta bellii*, western painted turtle) from Holbrook (1836–1840). Sex of specimen not explicitly stated by Holbrook, but inferred to be male from illustrated sexual dimorphisms, including elongated foreclaws, thick tail base, and shallow carapace height. Note the prominent bicuspid tomiodonts, projecting spear-shaped cervical scute, and highly serrated and projecting anterior marginal scutes. **b** Location of anterior carapace landmarks used in geometric morphometric analysis. Landmarks encompass the forked cervical scute and the first marginal scute to the left and right. See Table S2 for a description of landmark positions. Grid scale in photograph is 6 mm × 6 mm

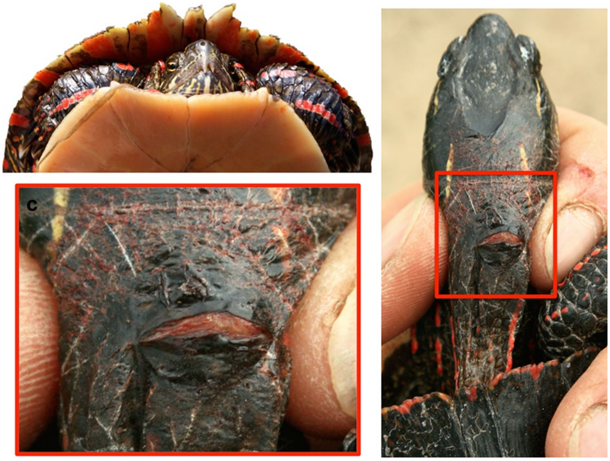

Fig. 2 Anterior carapace as a sexual weapon in the painted turtle, *Chrysemys* spp. **a** Male midland painted turtle (*C. p. marginata*) demonstrating strongly projecting and jagged cervical scute and flanking marginal scutes, as well as prominent bicuspid tomiodonts (Ontario, Canada). **b** Female midland painted turtle with deep wound on dorsal neck caused by bludgeoning (shell clattering) from the anterior carapace of a male. **c** Inset of neck wound. Note the two parallel short gash wounds anterior to the large open wound. The parallel gashes are caused by the sexually size dimorphic, bicuspid tomiodonts of males during sexual coercion (Figs. 1a, 2a; Moldowan et al. 2016a, b). See video S1 for example of how coercive behaviour leads to wounding. Photo (**a**) courtesy Cortney LeGros, and photos (**b**)/(**c**) by Patrick D. Moldowan

We investigated whether the cervical scute and adjacent marginal scutes of painted turtles are sexually dimorphic, and whether the extent of dimorphism is related to body size. To assess carapacial dimorphism, geometric morphometric analysis compared anterior carapace shape between males and females across taxa. If sexually selective mechanisms are acting, we predicted (1) that the anterior carapace would be sexually dimorphic, with male cervical and adjacent marginal scutes having more projections and serrations (i.e., greater shape complexity) compared to females. Further, consistent with the morphological expectations of sexual weapons (Rico-Guevara and Hurme 2019) we predicted that (2) the dimorphism would originate in the bone, rather than solely existing in the overlying keratinous scute.

Methods

Study sampling

We analysed anterior carapace morphology of both live and museum specimens of painted turtles. Live painted turtles (*C. p. marginata*) were sampled from several study sites in Algonquin Provincial Park, Ontario, Canada (45°34′N, 78°41′W). This sampling was a part of an ongoing long-term study of turtle life history and demography. Male and female painted turtles were collected using dip nets from canoes or were captured with baited hoop traps. Upon capture, individuals were transported and processed in the field laboratory at the Algonquin Wildlife Research Station. Specimens representing *C. dorsalis*, *C. p. marginata*, *C. p. picta* and *C. p. bellii* were sampled from herpetological collections at the Yale Peabody Museum of Natural History (New Haven, CT), Cornell University (Ithaca, NY), American Museum of Natural History (New York, NY), Smithsonian Institute (Washington, DC), Carnegie Museum of Natural History (Pittsburgh, PA) and Florida Museum of Natural History (Gainesville, FL).

The anterior carapace of all live and museum specimens was photographed by PDM using a Canon Rebel XTi digital SLR camera equipped with either an 18–55 mm Canon zoom lens or a 90 mm Sigma macro lens. All photographs were taken against a 6 mm × 6 mm grid as a reference scale. Midline plastron length (MidPL) of specimens was measured using Vernier calipers (to the nearest 0.1 mm) to serve as a body size metric. Midline plastron length was recorded as the straight-line measurement extending from between the gular (first plastral) scutes at the anterior to between the anal (sixth plastral) scutes at the posterior (Method H, Iverson and Lewis 2018). Specimen sex was determined based on the presence or absence of multiple sexually dimorphic characters (foreclaw elongation, carapace height, body size, head shape, and pre-cloacal tail length; Ernst and Lovich 2009; Moldowan et al. 2016b).

Geometric morphometric analysis

We used a landmark-based geometric morphometric analysis to quantify and compare anterior carapacial shape between male and female painted turtles. This approach involved assigning Cartesian coordinates to biologically definable landmarks to establish the shape of the structure of interest (Polly 2012; Adams et al. 2013). The cervical scute and first marginal scutes to the left and right of the cervical scute (Fig. 1) were of interest for this study because these landmarks represent the majority of observed variation in anterior carapacial morphology.

Also, the anteromedial carapace of the turtle shell, including the area underlying the cervical scute and first marginal scutes, originates from a common bone (nuchal bone), which is derived from cleithra, dorsal elements of the ancestral tetrapod pectoral girdle (Lyson et al. 2013). A total of 15 landmarks on the anterior carapace (Fig. 1b, Table S2) were digitized using the software tpsDig2 on 540 individual painted turtles. Landmarking of specimens was conducted blindly with respect to sex to eliminate observer bias.

Geometric morphometric analysis controls for body size (Bookstein 1986; Adams et al. 2004) thereby addressing size scaling differences due to sexual size dimorphism in painted turtles. All sets of specimen landmarks underwent Generalized Procrustes Analysis (GPA) to superimpose (translate, scale, and rotate) them on to a common coordinate system (Gower 1975; Rohlf and Slice 1990). The rigidity of the carapace (dermal bone overlain by keratin) is well suited for this analysis as landmarks maintain fixed positions and are not expected to differ between live and preserved specimens. Geometric morphometrics requires all individuals to have the same landmarks. Thus, only individuals with a forked cervical scute morphology were included in geometric morphometric analysis. This morphology represented the dominant cervical scute morphology in our sample of painted turtles with 73% of males and 62% of females possessing this morphology. We do not expect this to have biased our test of sexual dimorphism: both sexes demonstrate the forked morphology and we are principally concerned here with examining dimorphism of the projections and serrations of the anterior marginal scutes.

Once landmarked, a Procrustes ANCOVA (Goodall 1991) was conducted to assess the difference in anterior carapacial shape between the sexes while accounting for body size. Additional taxa-specific Procrustes ANCOVAs were preformed to assess whether sex differences in anterior carapacial shape existed in each taxon. In all analyses, sex, MidPL, and their interaction (Sex × MidPL) were included as model effects. In cases where the interaction between sex and size were non-significant, the interaction term was subsequently removed from the model. The resulting models where then used to assess allometric trends in cervical and adjacent marginal scute shape. In addition to comparing allometries of males and females in each taxon, sex-specific allometric trends were compared between each taxon. The allometric patterns were then visualized by regressing predicted shape values (first principal component scores of fitted model values) against MidPL (Adams and Nistri 2010). Analysis was conducted using the Geomorph (version 3.1.2, Adams and Otárola-Castillo 2012) package for R statistical software (R Development Core Team 2017). All results were considered statistically significant at $\alpha < 0.05$.

Carapacial structure

We qualitatively examined osteological specimens (n = ~100 specimens, across sexes and ontogeny) and radiographed (n = 3) whole adult specimens to evaluate the morphological structure of the nuchal bone (cervical scute) and adjacent peripheral bones (marginal scutes). These methods allowed us to describe the contribution of the keratin scute and underlying dermal bone in forming the projections and serrations of the anterior carapace.

Results

Geometric morphometric analysis

A total of 540 (males = 297, females = 238) individuals underwent landmarking and geometric morphometric analysis. A plot of the distance between each individual's landmark configurations compared to the sample mean revealed 10 outliers that fell outside the upper quartile (Figure S1). The images and landmarking of the 10 outliers were inspected and 5 were excluded from analysis based on a natural carapacial deformity and/or blurry imaging. Across all individuals sampled, regardless of taxa, anterior carapace shape of males was significantly different from that of females (ANCOVA, main effect of Sex, $F_{1,531} = 18.7$, $p = 0.001$). In males, the medial edge of first anterior marginal scutes (landmarks 3 and 9; defined in Fig. 1b, Table S2) projected farther out to the left and right, respectively (Fig. 3c), and the anterior-most points of the cervical scute (landmarks 5 and 7; Fig. 1b, Table S2) were also further anteriorly projected, resulting in deeper indentations where the cervical scute meets adjacent marginal scutes (Figs. 2a, 3c). Males also demonstrated a slightly deeper medial notch (fork depth) on the cervical scute (landmark 6; Fig. 3c).

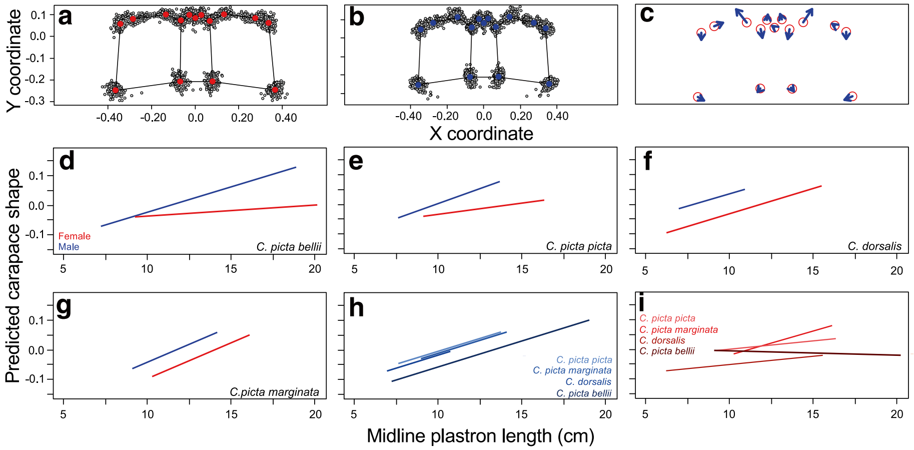

Fig. 3 Mean shape configuration of the anterior carapace, and relationships between anterior carapace shape and body size for male and female painted turtle (*Chrysemys* spp.). Averaged anterior carapace shape of **a** male (in red) and **b** female (in blue) painted turtles; blue/red dots represent the averaged location of each landmark point and grey dots represent variation in landmark location across all turtles of the same sex. **c** Mean shape of male painted turtle anterior carapace shape compared against the mean shape of females. Open red dots represent the averaged location of female anterior carapace landmarks, and blue vectors represent the relative position of male landmarks. Note, in particular, the divergence in female and male carapacial shape at landmarks points 3, 4, 8, and 9 (Fig. 1b), resulting in a more projecting and serrated anteromedial carapacial shape of male painted turtles. Vectors are magnified by a factor of two for ease of visualization. **d–g** Regression plots of predicted anterior carapace shape scores and body size (log midline plastron length) of males (blue) and females (red): **d** *C. picta bellii*, **e** *C. p. picta,* **f** *C. dorsalis* and **g** *C. p. marginata*. **h–i** Regression plots of predicted anterior carapace shape scores and body size (log midline plastron length) for **h** male and **i** female painted turtles

Taxa-specific patterns in carapacial dimorphism

In taxa-specific analyses, males and females had significantly different anterior carapacial shapes in *C. dorsalis* (ANCOVA, main effect of Sex, $F_{1,75}=3.21$, $p=0.016$), *C. p. picta* (ANCOVA, main effect of Sex, $F_{1,301}=10.7$, $p=0.001$), and *C. p. bellii* (ANCOVA, main effect of Sex, $F_{1,110}=4.45$, $p=0.003$). In our interaction model we did not find a significantly different carapacial shape between male and female *C. p. marginata* (ANCOVA, main effect of Sex, $F_{1,33}=1.74$, $p=0.135$), although sample size was relatively small.

Body size and carapacial shape

In all taxa, size was significantly associated with carapacial shape (ANCOVA, main effect of MidPL, $p=0.001$). Further, the association between size and shape significantly differed between males and females in *C. p. bellii* and *C. p. picta* (ANCOVA, Sex × MidPL interaction, $F_{1,110}=4.19$, $p=0.001$ and $F_{1,301}=2.71$, $p=0.014$ respectively), but not in *C. dorsalis* (ANCOVA, Sex × MidPL interaction, $F_{1,75}=1.28$, $p=0.225$) and *C. p. marginata* (ANCOVA, Sex × MidPL interaction, $F_{1,33}=0.85$, $p=0.447$). In *C. p. bellii* and *C. p. picta*, males exhibit a steeper allometric trend compared to females (Fig. 3d, e). At smaller body sizes, males and females of *C. p. bellii* (Fig. 3d) and *C. p. picta* (Fig. 3e) have similar anterior carapace morphology. However, the carapacial morphology diverges between the sexes as body size increases, with the anterior edge of the carapace projecting farther into the shape space and having increasingly deeper notches in males compared to females. By contrast, *C. dorsalis* and *C. picta marginata* exhibit common allometric trends between the sexes (Fig. 3f, g); as body size increases, both males and females have an increasingly projected and deeply notched carapace. Despite similar allometric trends between the sexes of *C. dorsalis* and *C. p. marginata*, male carapacial morphology is more projected and deeply notched across all body sizes in these taxa.

Sex-specific patterns in carapacial shape

In sex-specific analyses, males across all taxa exhibited common allometric trends (ANCOVA, Taxa × MidPL interaction, $F_{3,289}=1.49$, $p=0.082$; Fig. 3h). Carapacial shape (i.e., scute projection and depth of notches) increased with body size in males of all taxa (Fig. 3h). Taxa and midline plastron length were significant predictors of male carapacial shape (ANCOVA, $F_{3,289}=6.45$, $p=0.001$ and $F_{1,289}=25.0$, $p=0.001$, respectively).

In contrast to males, female *Chrysemys* demonstrated significantly different allometric trends across taxa (ANCOVA, Taxa × MidPL interaction, $F_{3,230}=2.14$, $p=0.002$; Fig. 3i). In female *C. dorsalis*, *C. p. marginata,* and *C. p. picta*, carapacial shape increases with body size. In this regard, *C. p. marginata* exhibits the steepest allometric slope while *C. dorsalis* and *C. p. picta* exhibit similar, shallower slopes (Fig. 3i). However, *C. p. bellii* demonstrated a negative association between shape and body size (Fig. 3i) with anterior carapacial shape becoming flatter as body size increased. Despite this negative association in *C. p bellii*, the anterior carapace shape in this taxa is always more projected compared to that of *C. dorsalis* (Fig. 3i). Taxa and MidPL were found to be significant predictors of female carapacial shape (ANCOVA, $F_{3,230}=8.28$, $p=0.001$ and $F_{1,230}=8.07$, $p=0.001$, respectively).

Carapacial structure

Observational study of osteological specimens and radiographs of the anterior carapace demonstrated that the keratin scute of the carapace traces the shape of the underlying dermal bone (Figure S2). Thus, the observed projections and serrations of the anterior carapace have their origins in the bone and are replicated or, in some cases, exaggerated by the overlying keratin scute.

Discussion

The painted turtle is arguably the most widely-studied species of freshwater turtle in the world (Ernst and Lovich 2009; Legler and Vogt 2013; Lovich and Ennen 2013), and yet the present study describes and quantifies a hitherto overlooked dimorphism in this species, one that may be central to its mating system. Specifically, we investigated and compared the shape of the anterior carapacial scutes of males and females using geometric morphometric analysis. Anterior carapace shape differed significantly between the sexes, with the leading edge of the anterior carapace being more projected and deeply notched in males, especially in larger males (Fig. 3). We propose that the increased projection of male anterior carapacial morphology in painted turtles may be advantageous in achieving female acquiescence, as male–male combat has not been directly observed in painted turtles. In midland painted turtles (*C. p. marginata*) from Algonquin Park, fresh neck wounds are found on both sexes but are significantly more frequent on females, particularly during the breeding season (Moldowan 2014; Moldowan et al., in review), suggesting that male aggression is primarily directed towards females during periods of reproduction (Fig. 2). Although we cannot completely rule out the possibility that the anterior carapace could be used against other males to gain access to females or for some other combative purpose (Moldowan et al., in. review), the dimorphism described herein is consistent with a recent review of sexual weapons across animal taxa (Rico-Guevara and Hurme 2019): the armament is exaggerated in males relative to females, it is paired and near the head, and observational study demonstrates that the weapon is a skeletal modification (Figure S2). Further, the male morphology described herein bears a likeness to the morphology of the gular scute(s) of males of multiple tortoise species (e.g., *Astrochelys yniphora*, *Centrochelys sulcata*, *Chersina angulata*, *Gopherus* spp.), which are relatively projected in males (McRae et al. 1981; Tuma 2016) and used as weapons for female harassment during courtship (Auffenberg 1966, Auffenberg 1977; Branch 1984; Tuma 2016) and/or male–male combat (Miller 1955; Douglass and Layne 1978; Branch 1984; Mann et al. 2006).

In their seminal work on Testudine mating strategies, Berry and Shine (1980) dismiss coercion as a reliable mating strategy in turtles with female-size bias, particularly those that are highly mobile and open-water swimmers, such as *Chrysemys* (among most Emydidae). We provide evidence to the contrary. Shifts in mating strategies are predicted to be likely in species with indeterminant growth (Thomas 2002), as the size of mature males is variable, and the strategy that maximizes mating success could differ across body sizes (Koga and Murai 1997; Angeloni and Bradbury 1999; Leary et al. 2005). In the present study, anterior carapace shape was related to body size for both males and females, but the complexity of carapacial morphology (i.e., development of sexual weaponry) is relatively pronounced in males, and is more strongly and consistently related to body size in males. The similarity of anterior carapace shape trajectories across body size in males could be a result of a common selective pressure towards a more serrated and projected shape compared to females, consistent with the sexual weapon hypothesis. Larger body sizes, combined with enlarged sexual weapons, would likely enhance the ability of males to promote female acquiescence and/or forceful insemination (Shine and Mason 2005). Interestingly, the length and gap width of the bicuspid tomiodonts (tooth-like cusps of the Testudine beak) also increase with body size in *C. p. marginata*, but are larger in males across all post-maturity body sizes, putatively to help restrain the female during bouts of coercion (Fig. 2; Moldowan et al. 2016a, b).

It is a strength and a weakness of the present study that museum specimens spanning a range of taxa were used. On the one hand, we can argue that the male morphology described herein is widely observed, as trends were generally consistent across taxa (Fig. 3). On the other hand, the museum specimens were from a mixture of populations that differ in life histories (i.e., age and size at maturity), limiting our ability to examine the true extent of divergence in any one population, and whether divergence relates precisely to size at maturity or the size of other secondary sexual structures (foreclaws and bicuspid tomiodonts) used during reproduction. An additional methodological consideration is the use of camera lenses with differing focal lengths. Although effort was made to maintain a consistent lens-specimen distance, unintended deviations could have ultimately produced variation in measurements, and may be a source measurement error in the dataset. Nevertheless, the findings of this study complement behavioural observations of painted turtles from long-term field study in Algonquin Provincial Park, where use of the anterior carapace along with bicuspid tomiodonts during bouts of coercive mating has been found to produce lacerations and wounds on females (Fig. 2, Video S1; Moldowan 2014; Moldowan et al. 2016b; Moldowan et al., in review).

The new sexual weapon described herein naturally gives rise to many questions. The first is whether inflicting physical harm on females increases male paternity, as would be necessary for the anterior carapace morphology to evolve as a sexual weapon. Relatedly, if coercive mating is not uncommon, then do males have a mechanism of paternity assurance? Another major question is whether females adopt strategies to resist copulation with aggressive males, and whether resistance also comes at a cost to female fitness (Smuts and Smuts 1993; Golubović et al. 2018). We suggest that the evolution of female harm and female resistance is particularly intriguing to study in this model system, as there is extreme selection on female longevity (Congdon et al. 2003), and operational sex ratios—which affect the degree of mate competition (Weir et al. 2011)—are typically stable within, but vary widely between, turtle populations due to temperature-dependent sex determination (e.g., Algonquin Park, Ontario, 3♀:1♂; Edwin S. George Reserve, Michigan 1♀:2.6♂). Many more general questions arise as well, particularly regarding whether there is coordination of reproductive morphology (foreclaws and bicuspid tomiodonts/anterior carapace) and reproductive behaviour (courtship and coercion, respectively), perhaps arising as a hormone-mediated response during ontogeny. Further investigation in this system could also leverage the annotated genome that is available for this species (Shaffer et al. 2013).

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