



Variation in cross-sectional horn shape within and among rhinoceros beetle species

ERIN L. MCCULLOUGH^{1,2*}, KIMBERLY J. LEDGER¹ and TALIA Y. MOORE³

¹Division of Biological Sciences, University of Montana, Missoula, MT, 59812, USA

²Centre for Evolutionary Biology, University of Western Australia, Crawley, WA, 6009, Australia

³Department of Organismic and Evolutionary Biology, Harvard University, Concord Field Station, Bedford, MA, 01730, USA

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Sexual selection has equipped male rhinoceros beetles with large horns on their head and prothorax to aid in battle over access to females. Horns are used to pry and dislodge opponents from resource sites that attract females, so an optimal horn should be able both to withstand the high stresses imposed during fights, and to resist deflection in response to these loads. We examined the cross-sectional morphology of horns using micro-computed tomography scanning to determine how horn structure changes with horn length to withstand the different fighting loads. Specifically, we measured the second moment of area of horns within and among rhinoceros beetle species to assess whether changes in cross-sectional morphology accompany changes in body size in order to maintain high strength and stiffness during fights. We find that the second moment of area of horns increases with body size both intra-specifically and inter-specifically, and that these relationships closely fit those predicted if horns have been selected to be strong and stiff fighting structures. Our results therefore support the hypothesis that rhinoceros beetle horns are structurally adapted for combat. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **115**: 810–817.

ADDITIONAL KEYWORDS: dynastinae – functional morphology – micro-CT scanning – sexual selection – weapons.

INTRODUCTION

The horns of male rhinoceros beetles are among the most impressive structures in the animal kingdom (Darwin, 1871; Arrow, 1951). These rigid, cuticular outgrowths of the beetle's head and prothorax can exceed the length of the rest of the body (e.g. the prothoracic horn of *Dynastes hercules*; Arrow, 1951; Mizunuma, 1999), and are used as weapons in fierce battles with rival males over access to females (Beebe, 1944; Eberhard, 1980; Siva-Jothy, 1987; Hongo, 2003). Species vary dramatically in the shape and size of their horns, but little information is known about why beetle horns are so diverse.

Given that horns are weapons, and thus functional structures that need to perform well in combat, the most intuitive and compelling explanation for horn diversity is that it reflects adaptations to different fighting styles (Geist, 1966; Kitchener, 1991;

Lundrigan, 1996; Caro *et al.*, 2003; McCullough, Tobalske & Emlen, 2014). However, it is unclear how different fighting styles may drive corresponding changes in horn design, because the mechanical properties of beetle horns are still poorly understood.

In all species studied to date, male rhinoceros beetles insert their head horn underneath an opponent to pry him off contested resource sites (Beebe, 1947; Eberhard, 1980; Siva-Jothy, 1987; Hongo, 2003). A horn can therefore be modelled as a cantilever beam that is fixed at the beetle's head and loaded at the tip with fighting forces (Kitchener, 1985, 1991; see also Discussion). When an initially straight horn is loaded at the tip in a fight, the horn bends into a curve, which creates tensile and compressive forces on the upper and lower surfaces of the horn, respectively, and thereby induces tensile and compressive stresses in the horn cuticle. According to beam theory (Gordon, 1976; Wainwright *et al.*, 1976), the maximum stress (force per area) in a horn during a fight is:

*Corresponding author. E-mail: mccullough.e@gmail.com

$$\sigma = \frac{FLR}{I} \quad (1)$$

where F is the force loaded on a horn during a fight to dislodge an opponent off the substrate, hereafter called fighting force (N), L is the length of the horn (mm), R is the radius of the horn (mm), and I is the second moment of area of the horn (mm⁴). The second moment of area is a fourth-dimensional shape factor that describes the distribution of mass in the cross-section of a structure about the neutral bending axis (where there is no net compressive or tensile bending stress). For structures of the same total mass, a higher second moment of area indicates that mass is distributed farther from the bending axis (e.g. steel I-beams used in construction). Beam theory (Gordon, 1976) also predicts that the amount of bending, or the deflection of the horn during a fight, is:

$$\delta = \frac{FL^3}{3EI} \quad (2)$$

where F is the fighting force (N), L is the length of the horn (mm), I is the second moment of area of the horn (mm⁴), and E is the stiffness of the horn cuticle (MPa). These equations indicate that both horn length and second moment of area are important variables in determining the stress and deflection of a horn during fights, and thus how well the weapon is likely to perform in combat. While several studies have examined variation in horn length (Eberhard, 1987; Morón, 1995; Christiansen, 2006; Kawano, 2006; Hongo, 2007), no study to date has explored how second moment of area differs within and among species.

Winning a fight requires a male to successfully dislodge his opponent from the contested resource site, so the force a horn experiences in a fight depends on the strength with which the opponent clings to the substrate. In the Asian rhinoceros beetle, *Trypoxylus dichotomus*, males only escalate to intense fights with size-matched rivals (Hongo, 2007; E.L. McCullough, personal observation). Fighting forces are therefore expected to increase with body size because larger males fight larger, and presumably also stronger, individuals (Lailvaux *et al.*, 2005). We found that the force a male must transmit through his horn to dislodge a typical rival increases linearly with male size, so larger males (and thus also their correspondingly longer horns) do in fact experience higher forces during fights (McCullough, 2014). Based on these observations, an optimal horn should be able both to withstand the high stresses imposed during fights without breaking, and to be stiff enough to resist deflection in response to these

loads. Indeed, only a small percentage (4%) of males actually have broken horns in wild populations (McCullough, 2014), which suggests that horns are structurally adapted to perform well in fights. However, little information is known about how horn structure varies across horns of different lengths to withstand these different fighting loads.

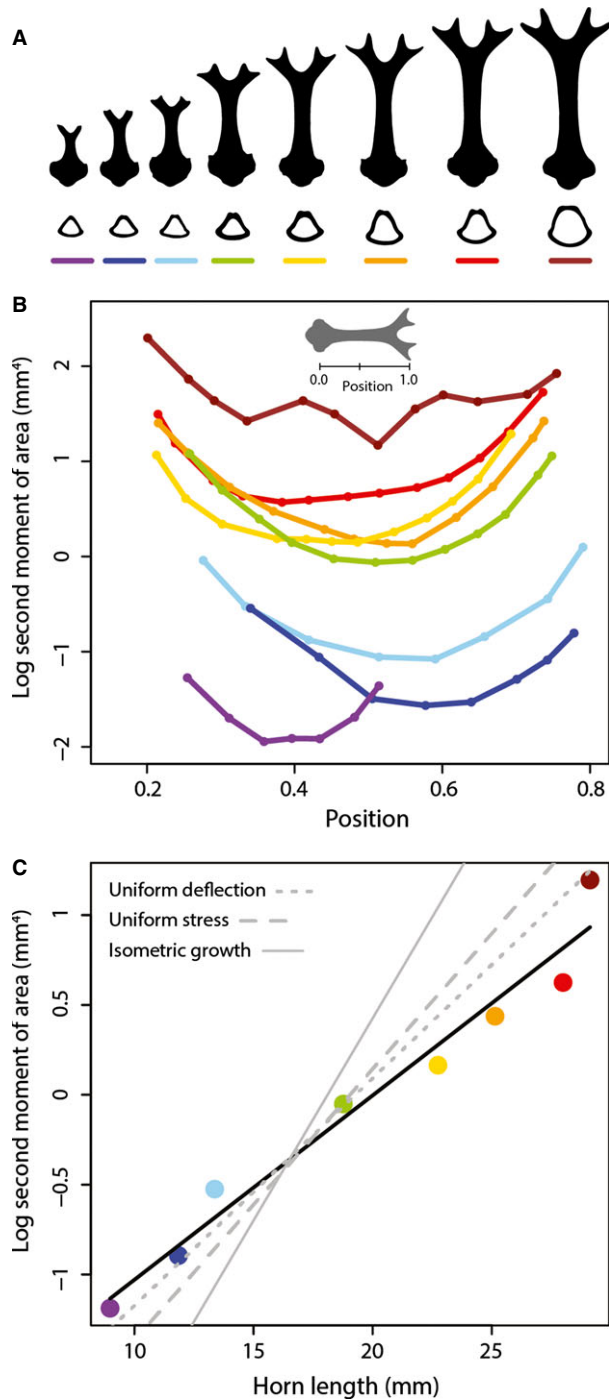
Because the stress and deflection of horns during fights increase with fighting forces, but decrease with second moment of area of the horn cross-section (Gordon, 1976; Wainwright *et al.*, 1976), the stress and deflection of horns in fights may stay relatively constant across individuals of different body sizes if there is a commensurate increase in second moment of area with increasing horn length (Kitchener, 1985). In support of this hypothesis, previous studies have shown that the second moment of area of ungulate horns increases with body size, suggesting that the maximum stress and deflection in the horn during fights remains the same (Kitchener, 1985). Whether these relationships are also found in the weapons of other taxa, and whether weapons have been selected to resist deflection, maintain constant bending stresses, or both, has never been explored.

Here, we examine the cross-sectional shape and second moment of area of horns within and among rhinoceros beetle species to assess whether changes in cross-sectional morphology accompany changes in body size to maintain structural performance across horn lengths (Kitchener, 1985). We predict that horns are structurally adapted to be strong and stiff fighting structures, such that the bending stresses and deflections of horns during fights are kept to a minimum. We use beam theory to predict how the second moment of area of horns should scale with horn length if horns have been selected to maintain constant stress or constant deflection, and compare our observations against these predictions to test whether horns are structurally adapted for combat.

MATERIAL AND METHODS

WITHIN-SPECIES VARIATION IN HORN LENGTH

Eight *Trypoxylus dichotomus* horns spanning the natural range of horn length (9–29 mm) were chosen to evaluate intra-specific variation in cross-sectional horn morphology. Specimens were selected from a large sample of beetles that were purchased as final instar larvae from a commercial insect vendor (Yasaka Kabuto Kuwagata World, Hamada City, Japan) and reared to adulthood in the laboratory. Horns were dissected from the body, and horn length was measured to the nearest 0.01 mm with dial calipers from the clypeus to the tip of the right tine.



Specimens were mounted in floral foam for micro-computed tomography (micro-CT) scanning. The specimens were scanned with a SkyScan 1173 micro-CT scanner (Bruker microCT, Kontich, Belgium) at 70 kV and 110 μ A, and the section images were reconstructed with the reconstruction program NRecon. Eight to 12 transverse cross-sectional images, depending on horn length, spaced approximately

Figure 1. (A) Variation in horn length among the eight micro-CT scanned horns used in the intra-specific comparisons and transverse slices from the middle of the horn shaft. (B) Relationship between slice position along the length of the horn shaft and second moment of area. Warm colours indicate larger horns; cool colours indicate shorter horns. The length of the curve is shorter for smaller horns because the horn shaft comprises a smaller proportion of total horn length. (C) Relationship between horn length and log second moment of area in the middle of the horn shaft ($R^2 = 0.96$, $F_{1,6} = 159.9$, $P < 0.001$; $\log \text{second moment of area} = 0.10 * \text{horn length} - 2.05$). Dashed grey line shows relationship if stress remains uniform across horn lengths (assuming a constant stress of 72 MPa). Dotted grey line shows relationship if deflection remains uniform across horn length (assuming a constant deflection of 2% horn length). Solid grey line shows relationship if horns exhibit isometric growth.

every 0.8 mm along the length of the horn shaft were chosen for cross-sectional horn shape analysis. We define the horn shaft as the constricted, middle section of the horn between the head and the branched tip. The location of each slice was measured as a fractional position along the antero-posterior axis of the horn between the clypeus (position = 0) and the horn tip (position = 1; Fig. 1). The second moment of area of each horn cross-section was measured in ImageJ using the BoneJ plugin (Doube *et al.*, 2010).

To test whether cross-sectional horn shape reflects a history of selection to maintain constant bending stresses or constant deflections during fights across the intra-specific range of horn lengths, we compared our second moment of area measurements to predicted values under assumptions of both constant stress and constant deflection (Supporting Information, Appendix S1). Specifically, we used Equation 1 to predict the second moment of area of horns assuming a constant stress of 72 MPa (based on the ultimate bending stress of locust hind legs; Dirks & Taylor, 2012), and used Equation 2 to predict the second moment of area of horns assuming a constant, small deflection of 2% horn length (Combes & Daniel, 2003). For these calculations, we estimated the fighting force of a horn of a given length based on field estimates of the forces exerted on *T. dichotomus* horns during fights ($\text{fighting force} = 0.12 * \text{horn length} + 0.94$; McCullough, 2014). We used our actual measurements of horn length and radius (maximum chord length perpendicular to the neutral bending axis), and assumed a Young's modulus of 15.98 GPa (based on the material properties of dung beetle clypeus cuticle; Sun, Tong & Ma, 2008). We also compared our second moment of area

measurements to predicted values under a null assumption of isometric horn growth (see Supporting Information, Appendix S1, for details).

AMONG-SPECIES VARIATION IN HORN LENGTH

One large male from 14 different Dynastinae species was selected to compare cross-sectional horn morphology among species (Table 1). Dried specimens were purchased from a commercial insect vendor (Insect Sale, Taiwan). Body size and horn length were measured to the nearest 0.01 mm with dial calipers. Prothorax width was used as a linear measure of body size (see Emlen, 1997, for justification), and horn length was measured as the straight-line distance from the clypeus to the horn tip. Specimens were micro-CT scanned as described above, and the section images were reconstructed with NRecon. For each of the 14 different species, one transverse slice from the midpoint of the horn shaft was selected for cross-sectional horn shape analysis using BoneJ. We also used this cross-sectional image to measure cuticle thickness in ImageJ, and report the average thickness of measurements taken from each of the four cardinal directions around the centre of the horn (Table 1).

STATISTICAL ANALYSES

Visual inspection of the data suggested that the relationship between second moment of area and horn

Table 1. Horn length, body size, and cuticle thickness for the 14 rhinoceros beetle species used in the inter-specific comparisons. All measurements are in millimetres

Species	Horn length	Body size	Cuticle thickness
<i>Brachysiderus quadrimaculatus</i>	9.85	16.61	0.36
<i>Diloboderus abderus</i>	12.54	11.71	0.23
<i>Allomyrina davides</i>	14.60	19.54	0.36
<i>Scapenes australis</i>	15.31	20.32	0.44
<i>Megaceras morpheus</i>	17.45	19.19	0.31
<i>Xylotrupes gideon</i>	25.63	22.54	0.44
<i>Golofa claviger</i>	25.64	20.78	0.36
<i>Golofa porteri</i>	27.67	23.80	0.23
<i>Eupatorus birmanicus</i>	28.41	23.13	0.48
<i>Trypoxylus dichotomus</i>	29.12	24.65	0.25
<i>Eupatorus gracilicornis</i>	33.69	25.75	0.44
<i>Megasoma elephas</i>	42.75	20.78	0.46
<i>Chalcosoma caucasus</i>	43.78	29.32	0.48
<i>Dynastes hercules</i>	51.68	36.59	0.57

length was non-linear. We compared the goodness of fit [based on Akaike's information criterion (AIC)] of linear, quadratic, and exponential models, and found that the exponential model described the relationship between second moment of area and horn length best for both the intra-specific (AIC for exponential model = 9.1; quadratic model = 12.4; linear model = 15.1) and inter-specific comparisons (AIC for exponential model = 59.7; quadratic model = 59.9; linear model = 63.6). We therefore log transformed the second moment of area data, and used simple linear regression to analyze the relationship between horn length and log second moment of area within and among species. The results are qualitatively the same if we used body size instead of horn length because horn length and body size are strongly correlated ($R^2 = 0.91$ within *T. dichotomus*; $R^2 = 0.72$ among the 14 species). We could not control for evolutionary structure using methods of phylogenetic independent contrasts or linear mixed effects models due to the lack of a complete phylogeny for the Dynastinae.

RESULTS

WITHIN-SPECIES VARIATION IN HORN LENGTH

Trypoxylus dichotomus males have a long, forked head horn that has a triangular-shaped cross-section (Fig. 1A). In general, there was a U-shaped relationship between the log second moment of area and the cross-sectional slice location for all eight horns (Fig. 1B). Specifically, the log second moment of area increased towards both the proximal base and the distal tip of the horn, and was lowest in the middle of the horn shaft. Previous studies have shown that horns are also the most likely to break in the middle of the horn shaft (McCullough, 2014), where the second moment of area is at its minimum. Intriguingly, the largest horn did not exhibit a simple U-shaped relationship, although the minimum second moment of area still occurred in the middle of the horn shaft. We did not see any obvious differences in horn morphology that could explain the irregular pattern exhibited by the largest horn, so additional measurements from more large specimens are needed to determine how consistent this relationship is for the largest size class of horns.

Horn length explained 96% of the variation in the log second moment of area for the eight *T. dichotomus* horns (Fig. 1C; $R^2 = 0.96$, $F_{1,6} = 159.9$, $P < 0.001$). The slope of this line was 0.10 ± 0.008 (estimate \pm SE), which closely matched the predicted slopes assuming both constant deflection (0.13 ± 0.009 , $R^2 = 0.98$) and constant stress (0.15 ± 0.008 , $R^2 = 0.97$). The observed

slope was significantly different from the predicted slope assuming isometric horn growth (0.23 ± 0.013 , $R^2 = 0.98$, $T_6 = -15.1$, $P < 0.001$).

AMONG-SPECIES VARIATION IN HORN LENGTH

Horn length explained 54% of the variation in the log of second moment of area among the 14 different rhinoceros beetle species (Fig. 2; $R^2 = 0.54$, $F_{1,12} = 13.85$, $P < 0.001$). The slope of this line was 0.08 ± 0.02 , which is not significantly different from the slope observed within-species ($T_{12} = -1.05$, $P = 0.32$).

DISCUSSION

We found that changes in body size and horn length were accompanied by changes in the cross-sectional morphology of rhinoceros beetle horns. Specifically, the second moment of area of horns increased exponentially with horn length both within and among species. We also found that the intra-specific relationship between horn length and second moment for *T. dichotomus* was significantly different from the relationship predicted under simple isometric horn growth, but was a close fit to the predicted relationships of how second moment of area should scale if horns have been selected to maintain both uniform stress and deflection. These results support the

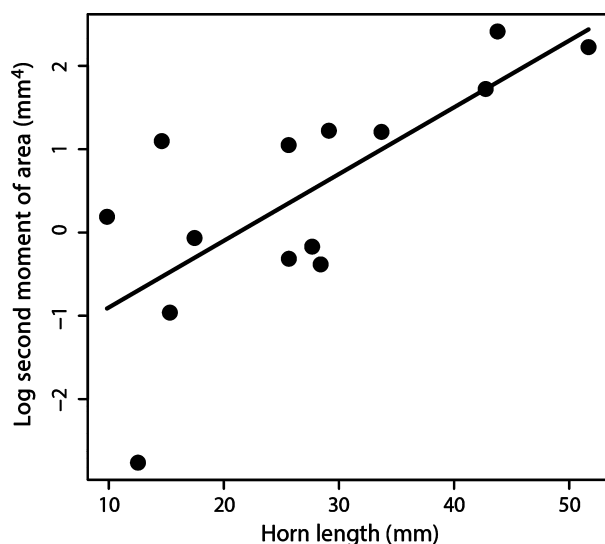


Figure 2. Relationship between horn length and log second moment of area at the middle of the horn shaft for each of the 14 different species ($R^2 = 0.54$, $F_{1,12} = 13.85$, $P < 0.001$; $\log \text{ second moment of area} = 0.08 * \text{horn length} - 1.70$).

hypothesis that rhinoceros beetle horns are structurally adapted to be strong and stiff fighting structures, such that the deflections and stresses experienced during fights remain constant regardless of horn length.

We were unable to make *a priori* predictions about how second moment of area should scale with horn length among species because the fighting forces experienced by horns are still unknown for most species. We therefore could not test whether the inter-specific relationship between horn length and second moment of area fit the general predictions for how second moment of area should scale assuming constant stress or constant deflection. This relationship is also based on measurements from just one large male of each of the 14 different species, so future studies are needed to test whether the pattern also holds for species averages based on measurements from multiple individuals across the full range of body and horn sizes. However, despite our relatively small sample size, the fact that the relationship between horn length and log second moment of area was similar within and among species suggests that evolutionary changes in horn length among species have been accompanied by changes in second moment of area to preserve structural performance across the inter-specific range of horn length (Kitchener, 1985, 1991).

We note that our predictions about the relationship between horn length and second moment of area are based on the assumptions that: (1) fighting forces; (2) cross-sectional horn morphology; and (3) physical properties of the horn cuticle are similar among species (Kitchener, 1985). We expect that all three of these simplifying assumptions are at least partially violated, and discuss the effect of each of these factors in turn.

First, head horns are expected to always experience vertical bending during fights because in all species studied to date, males insert their head horns underneath an opponent to pry him off contested resource sites (Beebe, 1947; Eberhard, 1977, 1980; Siva-Jothy, 1987; Hongo, 2003; McCullough *et al.*, 2014). Horns can therefore be modelled as a simple cantilever beam that is fixed at the base and loaded at the tip with fighting forces. However, horns are also likely to experience other types of fighting loads, because species fight on a variety of different substrates (e.g. on broad tree trunks and narrow shoots, or inside tunnels) and use slightly different manoeuvres to dislodge their opponents. For example, *Trypoxylus dichotomus* males use their long, forked head horn to pry and twist opponents off the trunks and branches of trees, such that their horns are both bent vertically and twisted during fights (Siva-Jothy, 1987; Hongo, 2003). In contrast, *Golofa porteri* males use their slender horns like a fencing sword to lift

opponents off narrow shoots and push them sideways off balance, which generates both vertical and lateral bending loads (Eberhard, 1977). Different fighting styles may favour different horn morphologies (McCullough *et al.*, 2014), which may explain some of the scatter in the observed relationship between horn length and second moment of area. This relationship may also differ between groups of species that fight more or less forcefully. In ungulates, for example, the second moment of area of horns increases linearly with body size in all species, but the slopes of these relationships are steeper among species with more forceful fighting styles (Kitchener, 1985, 1991). Unfortunately, very few rhinoceros beetle species have been rigorously studied in the field, so the specific fighting behaviours of most species are still unknown. Future work is needed to test if and how the relationships between horn length and cross-sectional horn morphology vary among species with different fighting styles.

Second, the equations used to predict how second moment of area should scale with horn length apply only for uniform, straight beams, so the taper and curvature of horns undoubtedly introduce error into our predictions. The slight taper of horns should cause maximum stress to be overestimated by less than 5% (Young & Budynas, 2002), but we do not know how horn curvature will affect these estimates. Additionally, species vary substantially in cross-sectional horn shape (Fig. 3), with species exhibiting circular or semi-circular cross-sections (e.g. *Eupatorus gracilicornis* and *Golofa porteri*; Fig. 3(K, H)), elliptical cross-sections (e.g. *Scapanes australis*, *Chalcosoma caucasus*, and *Dynastes hercules*; Fig. 3D, M, N), triangular cross-sections (e.g. *Diloboderus abderus* and *Trypoxylus dichotomus*; Fig. 3B, J), as well as highly irregularly shaped cross-sections (e.g. *Brachysiderus quadrimaculatus* and *Allomyrina davides*; Fig. 3A, C). Such differences in cross-sectional horn shape are likely to affect how the second moment of area should scale with horn length, and therefore may contribute to the scatter in the relationship observed here. For example, the horns and antlers of ungulates also vary in cross-sectional shape, and much of this variation is attributed to differences in the intensity of fights and the degree of fight ritualization (Kitchener, 1991). Specifically, species with unpredictable fighting styles typically have circular cross-sections that are ideal at resisting bending forces from all possible bending axes, while species that fight more forcefully and ritualistically have elliptical cross-sections that are better at resisting bending forces from the predictable fighting axes (Wainwright *et al.*, 1976; Kitchener, 1991). We recently found evidence that the cross-sectional horn shapes of three rhinoceros beetle species (*Trypoxylus dichotomus*, *Dynastes hercules*, and

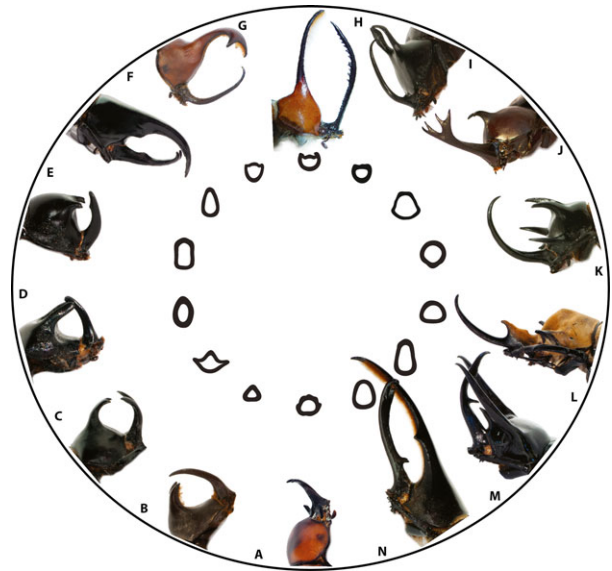


Figure 3. Photographs and transverse slices from the middle of the horn shaft for each of the 14 different species used in the inter-specific comparisons. Species are ordered clockwise from shortest horn (A) to longest horn (N). Photographs and cross-sections are not to scale.

Golofa porteri) are adapted to resist deflection in response to species-specific fighting forces (McCullough *et al.*, 2014), so we expect that the variation in cross-sectional horn morphology of other rhinoceros beetles also reflects different fighting styles.

Third, our predictions of how second moment of area should scale with horn length are also based on the assumption that the physical properties of horn cuticle are similar among species. The physical properties (e.g. Young's modulus) of insect cuticle are influenced by numerous factors, including thickness, degree of hydration, relative amounts of chitin and protein, and number, orientation, and cross-linking of the chitin layers (Andersen, Peter & Roepstorff, 1996; Vincent & Wegst, 2004). Differences in any of these factors can therefore change the material properties of the cuticle. We found that the thickness of the horn cuticle differs among rhinoceros beetle species (Table 1), which suggests that the physical properties of horns are at least somewhat different among species. Little is known about the specific properties of rhinoceros beetle horn cuticle, so future work is needed to determine how much the physical properties differ within and among species, and whether individuals can adjust these properties to maintain the structural integrity of their horns (Smith *et al.*, 2000; Barbakadze *et al.*, 2006). However, previous studies using biomechanical modelling to predict the stresses and strains of complex

structures (e.g. skulls) have found that the stress distributions and strain magnitudes predicted by finite-element models are more sensitive to variation in the structure's shape than to variation in material properties (Ross *et al.*, 2005; Strait *et al.*, 2005). These observations suggest that differences in the shape of rhinoceros beetle horns will be more important in determining horn performance than differences in their material properties (Dumont, Grosse & Slater, 2009).

In summary, our results suggest that increases in horn length and thus fighting forces, both intra-specifically and inter-specifically, are balanced by commensurate changes in cross-sectional horn shape to maintain both high stiffness and strength during fights (Kitchener, 1985). Our research therefore supports the idea that rhinoceros beetle horns are functional weapons that are structurally adapted to meet the mechanical demands of fighting (McCullough *et al.*, 2014). Future studies are now needed that test these predictions by experimentally measuring the stress and deflection of different horn types in response to their typical fighting loads.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Calculations for our predicted values of second moment of area under assumptions of constant stress, constant deflection, and isometric growth.