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DUE TO PREDATOR BITES AND GROUND IMPACT**

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TURTLE SHELL AND MAMMAL SKULL RESISTANCE TO FRACTURE DUE TO PREDATOR BITES AND GROUND IMPACT

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We investigate the relation between the thickness and diameter of naturally occurring shells, such as the carapaces of turtles and the skulls of mammals. We hypothesize that shells used for different protective functions (for example, protection against headbutting or falling on the ground) will exhibit different power-law trends for shell thickness and diameter. To test this hypothesis, we examine over 600 shells from museum collections with diameters between 1 and 100 cm. Our measurements indicate that eggs, turtle shells, and mammalian skulls exhibit clear and distinct allometric trends. We use a theoretical scaling analysis based on elastic thin shell theory to show that the trends observed are consistent with the corresponding protective functions hypothesized. We thus provide theoretical evidence that shells can be classified by their protective function.

1. Introduction

While the study of safety factors of leg bones during locomotion has a long history [McMahon and Bonner 1985; Currey 1988; Biewener 1990; Biewener 2003; Vogel 2003], less work has been done on shells and armor. Over millions of years, shell-based armor has evolved in a variety of organisms, and has manifested in diverse forms such as eggshells, mollusk shells, skulls, nuts, fingernails, and gourds. Some of these champion protectors, such as the abalone shell, have inspired material science advances such as new forms of bullet-proof armor [Jackson et al. 1988; Menig et al. 2000]. Others, such as the Macadamia nut shell, still require ingenious methods (for example, lasers [Jennings and Macmillan 1986]) to fracture without crushing their fragile contents. One significant obstacle in predicting the strength of natural shells is understanding their complex material properties [Currey 2002]. As a result, existing mechanical shell theories must be applied exceedingly carefully.

The study of man-made shells is a well-developed subject in architectural and mechanical engineering. A physical description of shells used in architecture is provided by [Heyman 1995]; mathematical treatments of shells are provided by [Flügge 1973; Heyman 1977; Steele 1989]. In this study, we consider a spherical shell with a thickness t much less than its diameter L , as in the inset of Figure 1. If its material properties are homogeneous and isotropic, we may apply a relation from linear elastic shell theory [Steele 1989] to determine the shell's strength. As shown in the Appendix, the maximum force F that a shell can resist, when loaded between two plates, is

$$F = A\sigma_f t^2, \quad (1)$$

where t is the shell thickness, σ_f is the ultimate tensile stress of the material, and $A = \pi$. This relation shows that for spherical shells, breaking force depends exclusively on shell thickness. It is noteworthy

Keywords: strength, function, protection, shells, allometry.

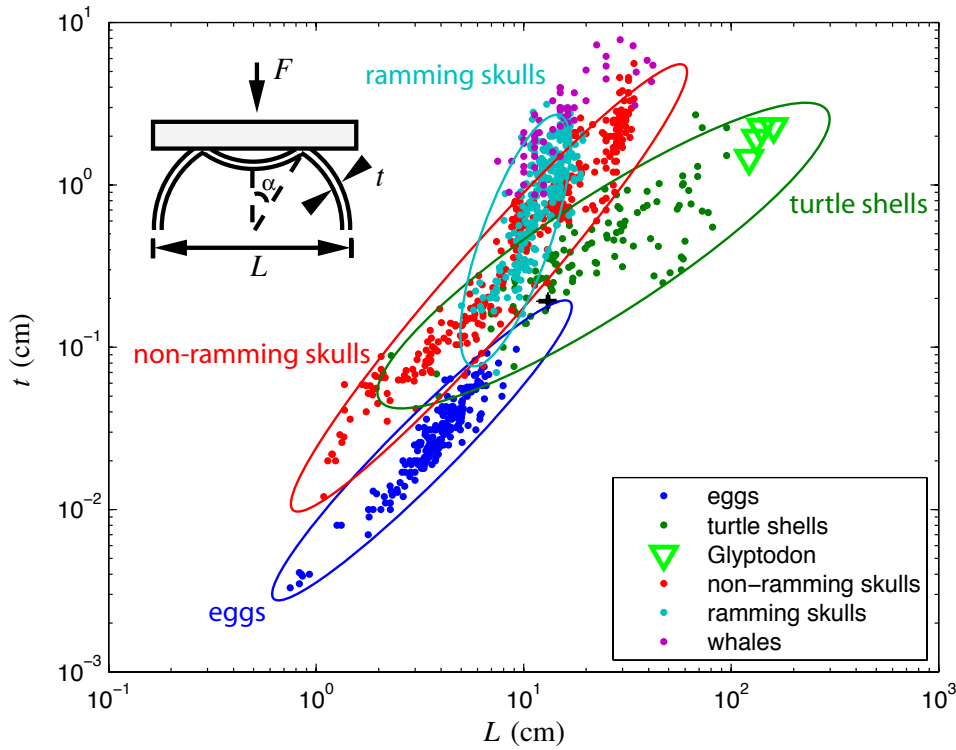


Figure 1. Relation between diameter L and thickness t for turtles, skulls, and eggshells (reprinted from [Schönwetter 1960]). The ovals indicate the range of thicknesses found for each shell type. Inset: schematic of a spherical shell of thickness t and diameter L subject to an applied force F by a flat plate. The load dimples the shell, inducing high stresses at points along a circular region at an angle α to the vertical.

that the derivation (in the Appendix) relies upon the elastic energy of the shell and so implicitly takes into account the work *to* fracture. Consideration of the work *of* fracture is beyond the scope of this study.

While the assumptions surrounding the derivation of (1) are numerous, extensive experiments by Ar et al. [1979] have shown that (1) provides excellent predictions for egg-breaking. They tested the following hypothesis:

H0. *Birds evolved eggs of sufficient thickness to support the mother's weight during incubation.*

To test this hypothesis, the authors measured the force to break hundreds of eggs, ranging in mass between 0.86 and 1460 g, collecting the data summarized in Figure 2. They found that (1) provides an excellent estimate of breaking strength over a large range of egg sizes and shapes. Specifically, their measurements of breaking force show that $F = 1.7t^{2.0}$ (Figure 1, with $r = 0.98$, t in cm, and F in kgf). Using (1) to infer the value of σ_f yields that the tensile strength of eggshells is $\sigma_f \approx 53.6$ MPa, a value that is within the range given for mollusk and eggshells [Biggs et al. 1976]. Next, [Ar et al. 1979; Pritchard 1993] use scaling arguments involving (1) to make a biologically meaningful statement about constraints on eggshells. They showed that in order for eggs to support the weight of their mother during incubation, the egg thickness must scale with egg diameter L according to $t \sim L^{3/2}$. The work on eggshells represents

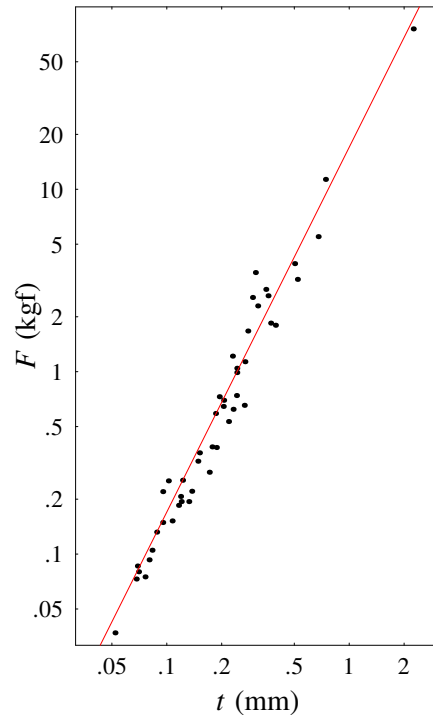


Figure 2. The relation between breaking force F and egg thickness t . The best fit (red line) is given by (1). Adapted from [Ar et al. 1979].

the most precise work on natural shells performed thus far. As we review here, there is much evidence that other kinds of shells have also evolved to resist specific types of loads.

Currey [1988] extensively studied the strength of mollusk shells, giving compelling evidence that they evolved to resist the attacks of predators. He examined the stomachs of fishes, finding that only fish above a certain size had the remains of mollusk shells in their stomachs; this evidence suggests that fish must grow to a critical size before mustering sufficient jaw strength to break mollusk shells. By examining populations of dog whelks exposed to crab predation, Currey found that in areas of intense predation, shells were stronger, weight for weight, than in areas with less predation. Currey also found that the maximum load of a shell varies according to thickness to the 1.7 power, in rough accordance with the trend found for eggs by Ar et al. Zuschin and Stanton [2001] also confirmed that mollusk shells increase in strength primarily by thickening rather than changing their material properties.

Substantial work has been done on the allometry of skulls and is summarized by Emerson and Bramble [1993]. The skull is divided into two parts: the cerebral skull, consisting of the braincase and the eye and ear capsules, and the facial skull, consisting of the jaw and associated musculature. Of particular interest to previous investigators has been the scaling of braincase size to body size. Another topic receiving attention has been how the scaling of predator jaws affects prey consumption [Radinsky 1981]. One example reviewed by Emerson and Bramble shows the importance of jaw size: an examination of the stomach contents of Southeast Asian frogs finds that only frogs above a certain size can eat crabs, presumably because of their jaw strength. It is noteworthy that among these studies, braincase thickness

has not been systematically measured. As we will show here, thickness is the most important variable governing the strength of the cerebral skull.

Ramming animals such as those of the family Bovidae have skulls that must resist the impact forces of head-to-head strikes. Generally, such skulls are covered by one of a variety of horns, whose utility for wrestling, fencing and ramming are discussed by Lundrigan [1996]. Schaffer [1968] estimates the impact forces resulting from ramming goats and sheep. He shows that the neck musculature of sheep is sufficient to prevent the neck from excessive skull rotation upon impact. Other authors, such as Alvarez [1990], have investigated the design of the horns, showing in particular that the horn's wide base of attachment with the skull helps minimize stress during impact. Very few of these authors have examined the skull thickness of ramming animals.

Zangerl [1969] gives a comprehensive overview of turtle shell anatomy and development. It has been suggested that the success of the turtle family is owed to the strength of the turtle's shell; however, biomechanical evidence for this has yet to be found. The shell mass of a turtle is reported to be a significant fraction (25–30%) of body mass [Bramble 1974; Iverson 1984]. This fraction remains constant across a range of turtles sizes: specifically, shell mass scales with the 1.2 power of body mass, or nearly isometrically. In contrast, the plastron is not isometric with body mass, but scales with body mass to the 0.5 power, indicating that larger turtles have thicker plastron than suggested by isometry. The mechanical rationale for these trends remains unknown.

In this study, we will test three hypotheses:

H1. *Turtles evolved shells to resist the bites of predators.*

H2. *Nonramming mammals evolved skulls to resist impact in accidental falls.*

H3. *Ramming mammals evolved skulls to resist headbutting impacts.*

Studies on ramming impacts [Jaslow and Biewener 1995] have used destructive testing and high-speed imagery to make quantitative measurements of stress and strain in shells under impact. In this study, we will use an approach based on nondestructive measurements and scaling. Central to our approach is the assumption that animals evolved shells of the minimum thickness necessary to satisfy their functionality [Alexander 1996].

Our approach is to compare the thickness of shells across a broad range of species. Such measurements do not provide a complete description of shell strength, but provide at least a first-order description, and a simple metric by which to compare different shells. Our methods and results on shell measurements are presented in Sections 2 and 3, respectively. In Section 4, we present scaling arguments intended to provide physical insight into the geometric trends observed. In Section 5, we discuss the implications of our work and future avenues for research.

2. Methods

We measured the geometries of 111 turtle carapaces, 341 hornless mammalian skulls, 264 horned mammalian skulls, and 4 glyptodon fossils, courtesy of the Smithsonian and American Museums of Natural History. Rulers, calipers, and ball-micrometers were used to take these measurements in the same relative position for each type of shell. Turtle carapace thickness was measured at the intersection of the first pleural scute and its adjoining marginal scute. glyptodon shell thicknesses were measured at their anterior

edge. Skulls were measured at the pharyngeal tubercle, accessed at the brainstem opening. An ordinary least squares (OLS) regression, implemented in MATLAB, was used to find the best fits to the data, standard errors of fitting, and closeness of fit (R^2). Best fits are given using one significant digit.

In our study, we assume shells are spherical. The shell “diameter” L reported is defined as twice the shell’s maximum radius of curvature. In turtle shells, the maximum radius of curvature was measured directly with rulers placed inside the open half of the shell. Animal skulls were generally not available in cross section. Thus, the diameter was measured by placing measuring tools inside the skull through the brainstem opening.

Before presenting our results, we briefly comment on our assumption of sphericity. Firstly, we observed that many shells (especially brain cases) were indeed nearly spherical, in part because spheres minimize the material required to grow the shell. To demonstrate this statement quantitatively, cross-sections of the shells would have to be measured, by either destructive methods or by using an X-ray machine, all of which is beyond the scope of this study. Examples of clearly nonspherical shells include aquatic shells (turtles, mollusks) that appeared hydrodynamically streamlined. Secondly, we speculate that deviations from sphericity will have a second-order effect on strength compared to changes in thickness. For example, in egg-breaking studies [Ar et al. 1979], no effort was made to choose specimens that were spherical; however, the authors found that the main relation used in this work, (1), was still an excellent predictor of strength for eggs of nearly all shapes and sizes. Based on the success of the methods employed in [Ar et al. 1979], we continue with our study, assuming the shells are generally spherical.

3. Results

Figure 1 shows the relation between shell thickness t and diameter L for the shells studied; tabulated values are given in the Electronic Supplement. Clearly, each shell type (turtles, ramming skulls, and non-ramming skulls) exhibits a different power-law trend, as shown by the ellipses in Figure 1. Best power-law fits for the data were found using the method of least squares and are presented in Table 1. In the next section, we propose scaling arguments to account for the scaling exponents observed.

	OLS		Lower 95%		Upper 95%		R^2	N	L (cm) range	Rationale
	a	b	a	b	a	b				
Eggs	0.004	1.4	0.004	1.3	0.005	1.5	0.90	201	0.7–13	incubation
Turtle shells	0.03	0.8	0.03	0.7	0.05	0.9	0.71	111	2.3–95	bite resistance
Hornless skulls	0.02	1.5	0.01	1.4	0.02	1.5	0.93	341	10–16	falling
Horned skulls	0.0026	2.3	0.0015	2.1	0.0044	2.6	0.64	264	10–20	ramming
Whales	1.3	0.2	0.7	0.1	2.3	0.2	0.61	60	10–40	NA

Table 1. Best fits for shell thickness as a function of shell length, given in terms of coefficients a and b , where the shell thickness t and length L vary according to $t = bL^a$. Fitting coefficients are given using the OLS method, which provides the best fit coefficients and closeness of fit R^2 . The upper and lower bounds for the 95th-percentile confidence interval estimates for a and b are given. N shells were measured by ourselves and by previous workers [Ar et al. 1979].

4. Model

We propose simple models to account for the shell geometry trends observed in Section 3.

4.1. Turtles. The armored shell of the turtle has long been assumed to protect turtles from predation [Zangerl 1969; Gibbons 1987]. The shell protects the legs and head, which, for many species, can be retracted into the shell. However, a few animals use their teeth to nibble at the edges of the shell, or poke into soft or thin parts of the shell or carapace. This includes ravens, raccoons, and coyotes [Gibbons 1987; Boarman 2003]. Other very large predators dispatch turtles by biting through their shells with great force. Alligators and crocodiles have been observed eating turtles by biting through their shells [Carpenter and Lindsey 1980; Pérez-Higareda et al. 1989]. Sharks, especially tiger sharks, are known to bite through sea turtle shells of all sizes [Stancyk 1981]. Given this biological evidence, we hypothesize that turtle shells evolved to resist the bites of predators.

To test this hypothesis, we determine whether our measurements of turtle shells (Figure 3a) are consistent with resisting the attacks of predators. For a turtle shell to resist the bite force F_{pred} of a predator, we require the breaking force of the shell F to satisfy

$$F > F_{\text{pred}}. \quad (2)$$

The scaling of F_{pred} in (2) is estimated using measurements [Meers 2003; Wroe et al. 2005] of predator bite force and weight W_{pred} , for which

$$F_{\text{pred}} \sim W_{\text{pred}}^{0.6}, \quad (3)$$

where $R^2 = 0.76$. This relation is consistent with the view that the maximum force exerted by animals scales as the cross-sectional area of the animal's muscles [Alexander 1985; McMahon and Bonner 1985]. The measurements by Wroe et al. [2005] also provide a relation between the weight of the predators and the weight W of their largest prey

$$W_{\text{pred}} = 1.5W^{0.9}, \quad (4)$$

where weights are expressed in newtons and $R^2 = 0.82$. The weight W of turtle shells is modeled as a hemisphere with the density ρ of water: $W = \frac{1}{12}\pi\rho gL^3$, where g is the acceleration of gravity. Combining relations (1)–(4) yields the result that turtle shells should be nearly isometric to resist predation equally among all turtle sizes: $t \sim L^{0.8}$. Our predictions are close to the trends given by our measurements, as shown by the points in Figure 3b, whose best fit gives $t \sim L^{0.8}$ with $R^2 = 0.68$. Comparing turtle shells from over two orders of magnitude in length scale, as in Figure 3a, one finds little visible difference in their thickness-length aspect ratios, as predicted by our model.

Figure 3c shows two relations: filled symbols relate the breaking force and weight W of turtle shells (whose best fit is $F \sim W^{0.5}$); open symbols relate the bite force of predators to the weight of their largest prey (whose best fit is $F_{\text{pred}} \sim W^{0.6}$). It is noteworthy that while trends for shell strength F and bite force F_{pred} were found using three independent sources (our study, [Meers 2003], and [Wroe et al. 2005]), nevertheless F and F_{pred} are found to have similar power-law exponents (a values of 0.5 and 0.6). This similarity suggests that shell thickness and bite force evolved in parallel. Using a t -test, we find that there is only a 0.05% probability that the power-law exponents are identical [Zar 2007].

In this section, we hypothesized that predators are capable of breaking turtle shells. We now examine the reasonableness of this assumption by examining which animals in Figure 3c can successfully bite

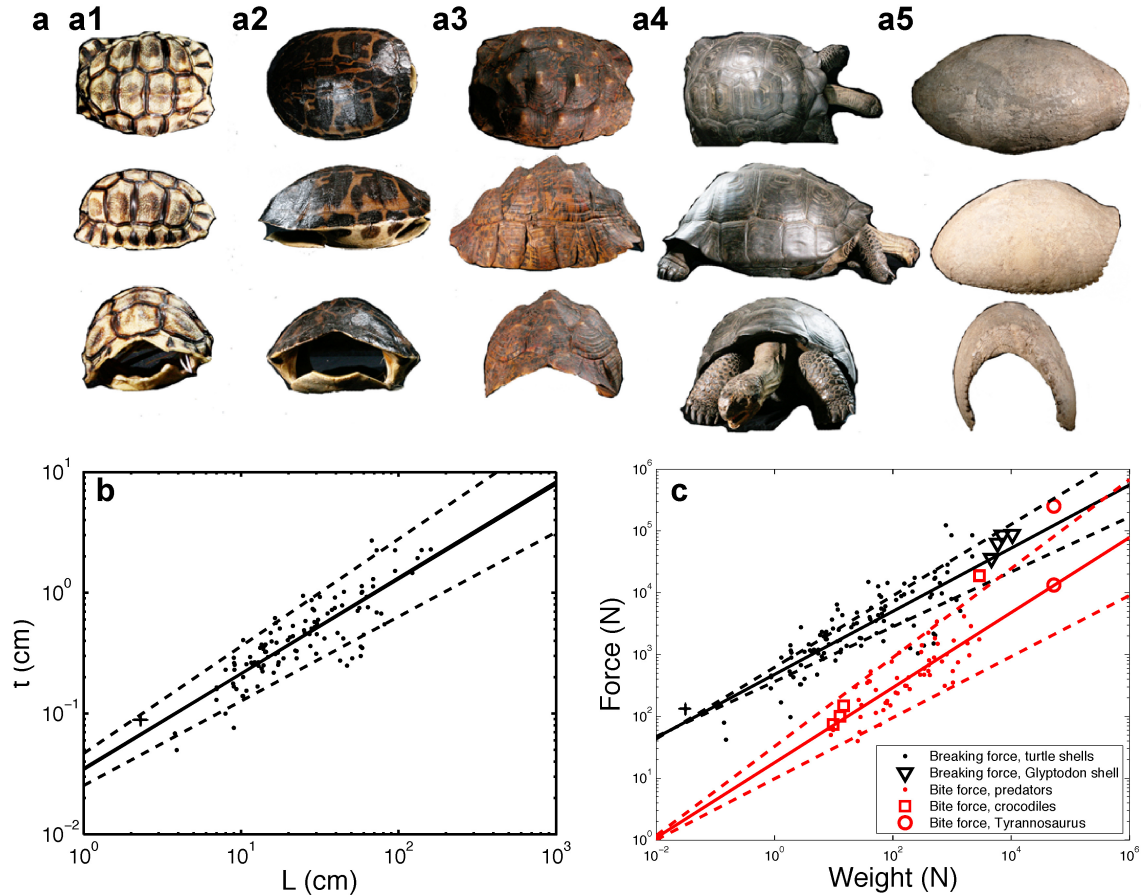


Figure 3. (a) Turtle shells from 3–100 cm in diameter, here magnified to the same size, highlighting the similarity of their proportions. (a1) Angulate tortoise (*Chersina angulata*), $L = 3.9$ cm. (a2) Florida redbelly turtle (*Pseudemys nelsoni*), $L = 28.5$ cm. (a3) Leopard tortoise (*Geochelone pardalis*), $L = 29.1$ cm. (a4) Galapagos giant tortoise (*Geochelone nigra*), $L = 58.8$ cm. (a5) Shell of glyptodon, a prehistoric armored mammal, $L = 130$ cm. (b) The relation between turtle shell thickness t and length L . Solid lines indicate the best fit ($t = 0.04L^{0.8}$); dashed lines indicate the 95% confidence intervals for this fit. Characteristic errors of measurement are shown. (c) Bite force F_{pred} of predators (red) and bite resistance F of turtle shells (black) as a function of their body weights W . Solid lines indicate the best fits: $F_{\text{pred}} = 20W^{0.6}$, $F = 470W^{0.5}$; dashed lines indicate the 95% confidence intervals for this fit.

through a turtle shell. Suppose that predators would like to prey on animals of their same weight. Then the vertical distance between the curves in Figure 3c shows that the average breaking force of turtle shells is approximately 40 times the average bite force of same-weight predators: specifically $F_b \approx SF_p$ with a constant safety factor $S = 40$. Clearly, turtles can resist the bite force of predators of the same weight.

Conversely, by drawing horizontal lines in Figure 3c, we predict that predators 200 times the weight of turtles can succeed in their attack. Thus, juvenile turtles (or turtles with masses on the order of grams)

may be eaten by numerous predators. Moreover, we predict that a 360 kg adult alligator is sufficiently strong to bite through the shell of a 2 kg turtle. Weaknesses such as thinner areas in the shell will allow predators to attack even larger turtles. As turtles grow larger, they will have fewer predators. The so-called “size refuge” of turtles, the size at which they have grown too large to have their shells broken by any predators, is $M^* = 100$ kg, which corresponds to the weights of the Galapagos turtles. Our predictions seem physically reasonable, and give credibility to our scaling argument.

We also include in Figure 3c the predicted shell strength of the armadillo-like glyptodon (Figure 3a5) and the bite force of the predator *Tyrannosaurus rex* [Erickson et al. 2003; Meers 2003]. While the glyptodon has little shared genetics with the turtles, its shell length and thickness follow the trends predicted for turtles (Figure 1), suggesting a universality in shell thickness trends among mammals and reptiles.

In this part of our investigation, our goal was to rationalize the measured scaling for turtle shell thickness. Using previously collected predator bite force data, we found that the scaling exponents for shell thickness are consistent with turtles resisting predator bites. A future approach might take into consideration the measured breaking force of the shell and the energetics of the turtle’s bearing of their shell.

4.2. Nonramming skulls. Creatures that are taller and faster than turtles must survive the impacts of accidental falls. We hypothesize that mammalian skulls (Figure 4a) are designed to survive impacts from either falling from a stand or from head-to-head ramming. We consider the mechanics of each of these impacts in turn.

One design requirement for a skull is that it should resist breaking due to impact with the ground during locomotion. For the animal to survive such a fall, the breaking force F of the skull must be in excess of this impact force F_{impact} :

$$F > F_{\text{impact}}. \quad (5)$$

The impact force F_{impact} results entirely from the transfer of gravitational energy into kinetic and finally into elastic deformation energy of the skull. At the moment of impact, the speed U of a skull of mass M falling from a height H is $U = \sqrt{2gH}$, where H is the maximum height of the skull during locomotion. The impact force is simply the momentum of this impact divided by the impact time τ :

$$F_{\text{impact}} = MU/\tau = M\sqrt{2gH}/\tau. \quad (6)$$

We simplify (6) by making some further assumptions. First, since we have assumed the shell is spherical, we can write the weight of the shell as $M \sim \rho L^3$. Second, we must make an assumption about the contact duration τ during impact with the ground. Impact mechanics is a complex subject [Chaudhri et al. 1981; Stronge and Stronge 2000; Goldsmith 2001]. For an elastic sphere of diameter L striking a rigid plane surface, the contact time is given by

$$\tau = \frac{\pi}{2} \sqrt{\frac{M}{\pi H_d L}}, \quad (7)$$

where H_d is the dynamic hardness of the sphere, a material property. Assuming H_d is a constant yields that $\tau \sim L$. Thus, $F_{\text{impact}} \sim H^{1/2} L^2$. Combining (6) with (1) yields

$$t \sim H^{1/4} L. \quad (8)$$

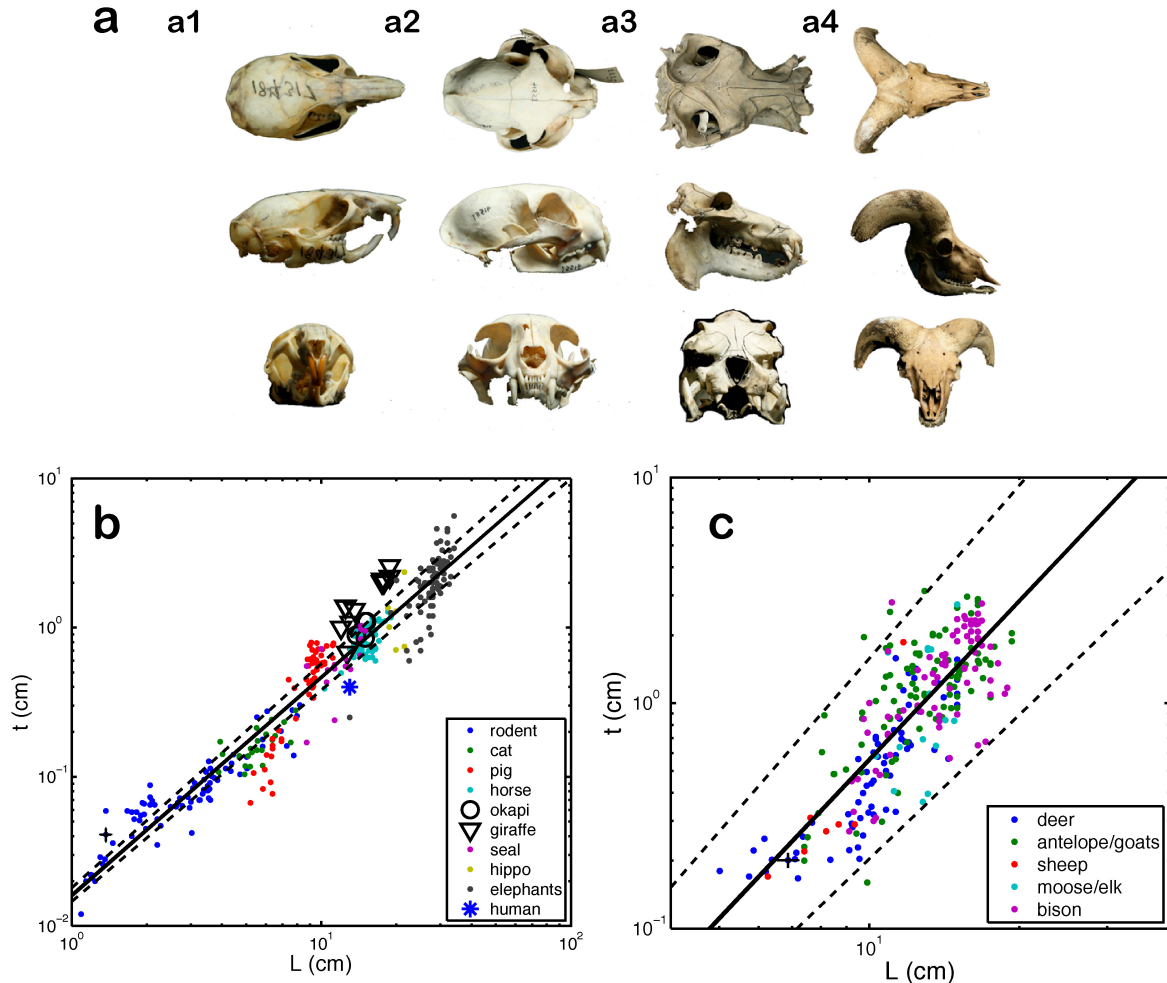


Figure 4. (a) Some mammalian skulls measured in this study. Measurements of characteristic skull thickness were performed at the skull’s opening to the brainstem. (a1) Rat (*Rattus rattus*). (a2) Cat (*Felis catus*). (a3) Hippopotamus (*Hippopotamus amphibius*). (a4) Bighorn sheep (*Ovis ammon*). (b) The relation between diameter L and shell thickness t for hornless mammalian skulls. The solid line indicates best fit $t = 0.02L^{1.5}$, dashed lines the 95% confidence intervals for this fit. (c) Relation between diameter L and shell thickness t for horned mammalian skulls. The inset shows the relation between diameter and thickness of mountain goat skulls, which display less scatter than the data for other horned mammalian skulls. The solid line indicates best fit $t = 0.0026L^{2.3}$ for all horned skulls and $t = 0.0019L^{2.6}$ for mountain goat skulls; dashed lines the 95% confidence intervals for this fit. Characteristic errors of measurement are shown.

Equation (8) successfully predicts the change of skull thickness with head height (see open symbols in Figure 4b). Juvenile giraffes have comparable heights (2 m) and skull dimensions (thickness 0.8–1.1 cm and length 12–15 cm) to their evolutionary predecessors, the okapi. As giraffes grow to their adult heights

of 5 m, their skulls broaden to $L \approx 17\text{--}19$ cm and thicken to $t \approx 2\text{--}2.6$ cm. According to (8), increasing an animal's height by a factor n and skull length by a factor m results in the skull thickening by a factor $p = n^{1/4}m$. Since giraffes increase in height by a factor of $n = 2.5$ and in skull length by a factor of $m = 1.1\text{--}1.6$, we predict that their skulls should thicken by a factor of $p = 1.4\text{--}2.0$. This predicted thickening is less than (but comparable to) the measured value $p = 1.8\text{--}3.2$. Thus, our model provides one reason for why giraffes have thicker skulls than okapi: the giraffe skull must grow thicker as the animal ages in order to absorb the shock of falling from a greater height.

Assuming that animals must at least survive falls from a stand yields that $H \sim L$. Therefore, (8) simplifies to $t \sim L^{1.25}$, which has an exponent close (1.25 versus 1.4) to the trend observed, $t = 0.018L^{1.4}$ with $R^2 = 0.93$ (Figure 4b). Thus, our model works well to predict skull thickness scaling exponents for non-ramming mammals.

4.3. Ramming skulls. Some creatures must endure the impacts due to headbutting during mating rituals and self-defense, as is common in the family Bovidae (cows, sheep, rams, and bulls [Schaffer 1968; Lundrigan 1996]) as well as other mammals that are purported to ram underwater such as beaked and sperm whales [Carrier et al. 2002]. The skulls of such creatures must be able to survive the impact of a headbutt: the breaking force F must exceed the impact force F_{impact} : $F > F_{\text{impact}}$. The impact force results from the two skulls striking each other at relative speed $2U$. Since both animals are at a standstill after the headbutt, the total impact force is given by $F_{\text{impact}} = 2MU/\tau$, where M and U are the mass and speed of the animal. Kitchener [1988] claims that much of this impact energy is absorbed by the neck muscles of the animal. As a worst case scenario, we assume that all the kinetic energy of the running animals is transferred entirely into elastic deformation energy of the skull.

We now make a series of assumptions to simplify our relation for impact force. First, since (7) also holds for the impact of two identical spheres [Goldsmith 2001], we assume that the impact time again scales as L . Next, we can make some assumptions for running speed from the biology literature. The maximum speed of swimming animals is nearly constant at 1–2 m/s [Sato et al. 2007]. The maximum speed U of large terrestrial mammals [Iriarte-Díaz 2002] has been shown to scale as $U \sim L^{-0.5}$ where L is the skull size (assuming that animal skull size scales with body size). These assumptions yield that $F_{\text{impact}} \sim L^{1.5\text{--}2.0}$.

Proceeding similarly to the analysis in Sections 4.1 and 4.2, we predict that land-based and aquatic mammals should have a trend of $t \sim L^{0.75\text{--}1.0}$ in order to resist fracture by headbutting. However, for land-based mammals, we observed a trend of $t = 0.0026L^{2.3}$ with $R^2 = 0.65$, which exhibits a power exponent a more than double our predictions. Our model thus works rather poorly to predict the thickness of ramming animals. The R^2 coefficient indicates the high variability in skull thickness for this class of animals. We note that less variability is present among certain individual species, such as mountain goats, for which $t = 0.0019L^{2.6}$ with $R^2 = 0.96$.

Finally, while our model cannot account for the observed trends of ramming skull thicknesses, it is useful to investigate its predictive ability for an individual case. We consider the ramming of bighorn sheep. According to high-speed measurements [Schaffer 1968; Kitchener 1988], two bighorn sheep, each of mass $M = 100$ kg can run towards each other at a relative speed of $2U = 50$ mph = 20 m/s, striking with an impact time τ of 0.3 seconds. This yields an impact force of $2MU/\tau \approx 3000\text{--}6000$ N [Kitchener 1988]. Given a maximum tensile stress of $\sigma_f = 100$ MPa (given for bone in [Vogel 2003]), our

model predicts that a skull thickness of $t \sim (2MU/(\tau\sigma_f))^{0.5} = 0.5\text{--}0.7$ cm is needed to avoid fracture, which is less than (but of the same order of magnitude as) the skull thickness of 1.9 cm for bighorn sheep (Figure 4c). One reason for this discrepancy is that our model relies on an assumption of uniform shell thickness, whereas in our observations, sheep skulls had walls that were honeycombed; thus, while it worked well for other types of shells, it performs poorly here. We are unable to validate Hypothesis 3, that ramming skulls have thicknesses in order to absorb impact force by plastic deformation. Instead, it is likely that much of the energy of impact is absorbed by neck muscles [Kitchener 1988]. It is worthwhile to note, however, that the skulls of ramming animals must be stronger than those of non-rammers of the same size, as shown by the trends in thicknesses in Figure 1. While some portion of the impact energy may be absorbed by musculature, ramming animals still require skulls thicker than their non-ramming counterparts.

We apply our results to two other classes of animals, speculated to use ramming. Shown in Figure 1 are measurements of whale skull thickness, which are fitted by the trend $t = 0.12L^{1.1}$ with $R^2 = 0.66$ (see Table 1). Since this power-law exponent of 1.1 is much smaller than 2.4, the observed power law for ramming creatures, we conclude that whale skulls were not designed for ramming. Another animal once postulated to use ramming is the thick-headed dinosaur *Pachycephalosaurus* [Goodwin and Horner 2004]. Trends from previous measurements of 7 dinosaurs ($t = 0.3L^{1.2}$ with $R^2 = 0.94$) exhibit a power exponent much less than that of the rammers in this study, suggesting that *Pachycephalosaurus*' skull was also not designed for ramming.

5. Summary and conclusions

In this study, we used measurements of shell thickness to describe quantitatively how shell strength varied across turtles and mammals. The key results of this study include (1) clarifying the biomechanical rationale for why shell strength depends exclusively on thickness rather than on diameter and (2) using this result to conduct a structural classification of shells. Our scaling arguments were able to account for the geometries measured for turtle shells and hornless skulls, but not for horned skulls.

Our measurements indicate that eggs, turtle shells, and mammal skulls each exhibit distinct geometric trends. We showed this quantitatively by monitoring changes in thickness t according to shell size L . Specifically, we modeled change in shell shape using power laws, $t \sim bL^a$, where b is a scaling prefactor and the scaling exponent a indicates how the shell must change in thickness-to-length aspect ratio as the shell grows. For example, values of $a \approx 1$ indicate isometry, in which the organism's proportions are independent of size. Values of $a < 1$ indicate negative allometry, in which thickness-to-length ratio decreases with shell length. Conversely, values of $a > 1$ indicate positive allometry, in which thickness-to-length ratio increases with shell length; such organisms must devote relatively more resources into building up their shell thickness as they grow.

The exponent a can be used to compare how much energy it costs to bear the shell as the animal increases in size, a topic considered in [Zani and Claussen 1995; Miller and Birchard 2005]. The maximum force that animals can produce scales as their length squared [Alexander 1985]. The weight of the shells scales as $L^2t \sim L^{2+a}$. Since all of the observed exponents a are greater than zero, larger animals will use a larger portion of their maximum load-bearing capacity than smaller animals. This means that larger animals will also use more energy to bear the shell during locomotion.

Eggshells exhibit a power law of $a \approx 1.5$ in order for eggs to support the gravitational loads of their mothers [Ar et al. 1979]. Our measurements indicated that $a \approx 0.8$ for turtles, $a \approx 1.4$ for non-ramming skulls, and $a \approx 2.4$ for ramming skulls. We hypothesized that turtle shells evolved to resist predator bites and mammal skulls evolved to resist the impact of accidental falls to the ground. Using simple scaling arguments for destructive force, we predicted scaling exponents consistent with those measured for turtles and non-ramming skulls, providing theoretical evidence for the validity of our hypotheses 1 and 2. We were unable to account for the scaling of ramming skulls. To further validate our hypotheses would require one to also predict the prefactors b and the factors of safety.

We now make a few comments on the measured prefactors b in our study (see Table 1). Predicting such prefactors is beyond the scope of this study, as it would require quantitative fracture experiments. However, such prefactors are important in developing factors of safety. A safety factor for a shell may be defined as the ratio of the maximum force to the typical force that may be resisted by the shell. The concept of safety factor is an important factor in device design and manufacturing. For instance, to design portable and safe helmets for use in sports and the military, one must first choose a particular function for the helmet, such as deflecting a bullet or resisting a fall, and then a factor of safety [Newman 2001]. With regards to natural shells, future workers may gain some insight on safety factors by conducting free-fall experiments. For example, reports by the CDC state that nearly 100% of human falls from six stories or higher are fatal, mainly due to head trauma, followed by abdominal hemorrhage [Stevens 2005]. In our theoretical section, we show that breaking force scales as falling height to the one-half power. Thus, if each story is approximately 2–3 human body lengths, and the skull is designed to survive falling from a single body length, the safety factor for the human skull (asterisk in Figure 3b) should be approximately $\sqrt{12}-\sqrt{18} \sim 3.5-4.2$. It would be interesting to examine safety factors for skulls among arboreal animals, in which the height fallen can greatly exceed body length.

In this study, we have focused on strength trends among adult animals. This was because juvenile skulls and shells were generally not readily available in museums. Some juvenile skulls were available for pigs and elephants as shown by the trends in Figure 4b. During growth, pig skulls increased in length by a factor of five, and elephant skulls by a factor of two. Trends in thickness among these two species indicates growth within these species at higher allometric rates ($a > 4$) than for hornless skulls in general. Our methods could not account for this large increase in thickness. Perhaps the thickening helps to offset decreases in bone density with age. For instance, falls by humans are the leading cause of death and injury for those over 65 years of age [Stevens 2005]. Other factors that may affect shell strength are the effect of environmental contaminants such as DDT in reducing shell density or thickness [Green 1998].

While here we examined how structural strength affects skull shape, the effect of hydrodynamic and aerodynamic forces remains unknown. For example, aquatic turtle shells have recently been found to be flattened compared to the land-dwelling turtles studied (Tristan Stayton, personal communication). Other superficial adaptations to the shell may also affect strength without accruing substantial weight; thus, for example, spines and ribs [Strathmann 1981] may deter predators or break a fall.

Appendix: Supplementary information

We describe the mechanics of a spherical shell loaded by a point or an area of pressure, as discussed by Steele [1989]. Consider a vertical point load F acting on a spherical dome of uniform thickness t ,

diameter L composed of an isotropic, homogeneous material (see Figure 1). If the shell is sufficiently stiff, loading causes the cap to invert at an edge which lies at an angle $\alpha < 0.3$ with respect to the vertical. This observation has been confirmed qualitatively by Ar et al. [1979], who observed apex flattening of eggshells when loaded. The shells' greatest stresses lie at the edge of this shallow spherical cap, and will be estimated here. The elastic potential energy associated with this dimpled deformation, found using a linear expansion, is

$$U(\alpha) = -FL\frac{\alpha^2}{4} + 2\pi Etc^2\sqrt{\frac{L}{c}}\alpha^3, \quad (\text{A.1})$$

where E is the Young's modulus of the material and c is the reduced thickness, $c = t/\sqrt{12(1-\nu^2)}$. For a given force, the dimple forms at a position such that the potential energy is a minimum; this occurs at the angle

$$\alpha^* = \frac{FL}{12\pi Etc^2\sqrt{L/c}}. \quad (\text{A.2})$$

As shown in [Steele 1989, Equations 5 and 7b], the bending moment per radius of the shell, M_s , and bending stress σ_b at the edge of this dimple can be expressed as

$$M_s = Etc\sqrt{\frac{4c}{L}}\alpha^*, \quad \sigma_b = \frac{6M_s}{t^2} = \frac{F}{\pi t^2}. \quad (\text{A.3})$$

Thus, the shell breaks when the stress at the edge exceeds the fracture stress σ_f ; this occurs when the applied force exceeds the breaking force, $F = \pi\sigma_f t^2$.

Supplementary information

A table of lengths and thicknesses of skulls and turtle shells is available in the Electronic Supplement.

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