

STRUCTURAL MECHANICS OF PACHYCEPHALOSAUR CRANIA PERMITTED HEAD-BUTTING BEHAVIOR

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ABSTRACT

Pachycephalosaurian dinosaurs have dorsally thickened crania and uniquely shaped frontoparietal domes in some genera, suggested as evidence for head- or flank-butting behavior. Trabeculae thought to have resisted impact compression are present as only one histological zone of some pachycephalosaur domes, and are surrounded superficially or replaced by thick compacta in adults. The capabilities of pachycephalosaurian crania for head-butting are testable by finite element analysis (FEA). FEA of 2- and 3-D dorsal skull shapes of adult *Homalocephale* and *Pachycephalosaurus* reveal that the domes could withstand considerable impact force at certain closing speeds, and that stress and strain would dissipate efficiently throughout the dorsal portion of the skull before reaching the brain. Greater vaulting of the dome permitted higher impact forces. An analysis restricted to the frontoparietal dome of a subadult pachycephalosaurine, with material properties corresponding to histological zones, shows higher compressive strain (not less) in the trabecular region. The trabecular zone, if present, would not have rigidly resisted compression but rather have allowed slight elastic compression and rebound. Modeled keratinous coverings of varying depth indicate reductions in force and energy transmission to underlying bone. FEA therefore leaves open the possibility of head-butting in both flat- and dome-headed pachycephalosaurs, especially at low collision speeds.

KEY WORDS: Pachycephalosauria, Dinosauria, behavior, finite element analysis, biomechanics, sexual selection

INTRODUCTION

Inference of behavior in extinct vertebrates often involves conflicting intuitions and

approaches, especially when the animals possessed novel structures without clear extant analogs. The functional capability of osseous structures is testable biomechanically, with each

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result contributing to a reasonable continuum of behavioral possibilities. We apply finite element analysis to circumscribe inferences of head-butting combat in pachycephalosaurian dinosaurs, by testing whether forces of such collisions would fall within the limits of bone strength for two representative taxa. This approach does not answer whether pachycephalosaurs engaged in such intraspecific combat, but does ground the debate within a quantitative biomechanical framework.

Dome-Based Combat in Pachycephalosaurs: Arguments from Analogy and Structure

Pachycephalosaurs have among the most distinctive head morphologies of any amniote clade, with a dorsally thickened cranium of comparatively solid bone, and uniquely shaped dome heads in some genera. The dome is suggestive that pachycephalosaurs exhibited head-butting behavior, analogous to that seen in mountain sheep and other ungulates, and hypothesized for dinocephalian synapsids (Barghusen 1975). Whereas we can only circumscribe possibilities of agonistic behavior in pachycephalosaurs, workers have considered copious evidence from dome functional morphology and extant analogs.

Precise structural analogs for pachycephalosaurs are elusive. Head-butting ovids such as mountain sheep and musk oxen have hollow horns, unlike the osseous expansion seen in pachycephalosaurs. Giraffes engage in side-butting with dome-like projections on the head (suggested for chalicotheres with similar domes: Munthe and Coombs 1979), but these are hollow structures and proportionally small compared with pachycephalosaur domes. Male marine iguanas engage in head-butting and shoving matches at low speeds (Carpenter 1967). Bakker et al. (2006) identified male giant forest hogs (*Hylochoerus meinertzhageni*) as analogs for combat more popularly envisioned for pachycephalosaurs. The hogs engage in high-energy head-to-head combat without regard to damaging their integument (Estes 1991), and even fracture and induce pseudarthroses of the frontals and parietals.

Such arguments from analogy elicit intriguing parallels and hypotheses, but will be unconvincing without specific tests derived from functional morphology. The primacy of biomechanics over analogy applies to function, evolution, and even ontogeny of agonistic behavior. Dome morphology within specific lineages of pachycephalosaurs, and their conformance or divergence with expectations of agonistic theory (Geist 1966), will be informative

about the evolution of combat between these dinosaurs.

Maryńska et al. (2004) and Fastovsky and Weishampel (2005) emphasize morphology in critical overviews of pachycephalosaur head-butting. In addition to the presence of a dome, evidence cited for intraspecific combat includes vertebral articulations providing spinal rigidity and the shape of the back of the skull indicative of strong neck musculature. Buckling through tongue-in-groove articulations between the presacral vertebrae (Maryńska and Osmólska 1974), and probable dense connective tissue within the endocranial cavity (Evans 2005), would have moderated deceleration on the brain (the most critical factor for surviving collisions). In an analysis of dome shape, Chapman et al. (1998) determined that neck-jarring “glancing blows” (Carpenter 1997) were unlikely even in highly-domed forms, indicating that self-correction (secondary, stabilizing impacts onto other parts of the skull: Barghusen 1975) was not essential for combat. As Sues (1978) noted, glancing blows are common in mountain sheep (Geist 1971), and their potential injurious effects are easily countered by the nuchal ligaments and neck muscles. Alexander (1997) determined that neck muscle with only a small percentage of head mass would absorb kinetic energy of a glancing blow in pachycephalosaurs, even under extreme conditions. Sues (1978) identified a long moment arm for the extensive insertion of dorsiflexor m. spinalis capitis (Maryńska and Osmólska 1974; m. transversospinalis capitis: Tsuihiji 2005), ideally sized and situated to counter and absorb such forces. Alexander (1989) further calculated instantaneous impact forces from head-on collisions, and concluded that axial musculature could absorb collision energy as the spinal column buckled behind the point of impact.

Nevertheless, the dome would have to absorb initial stresses of the collision. Galton (1971) and Sues (1978) noted column-like trabeculae in *Stegoceras* that are perpendicular to the dome’s external surface and potentially resisted compressive stresses. Plexiglas models (Sues 1978) supported this hypothesis, indicating that compressive stress trajectories would be coincident with the trabeculae.

However, morphological contraindications of head-butting behavior have arisen from multiple sources. The lack of air spaces within the dome (as seen in the horns of head-butting ovids), and absence of surface pathologies, which would presumably be linked to head-butting, have been prof-

ferred as contrary evidence that at best indicates flank-butting combat (Fastovsky and Weishampel 2005). The diversity of dome shapes, and their association with boss and spike ornamentation, suggests that the domes were important for species recognition (Goodwin and Horner 2004). The taxon with the most spectacular ornamentation, *Stygimoloch spinifer*, had a relatively narrow dome cited as incompatible with head-butting (Goodwin et al. 1998).

In a histological study of sectioned pachycephalosaur domes, Goodwin and Horner (2004) established that trabeculae hypothesized as resisting compression were only present in some specimens (see also Brown and Schlaikjer 1943: plate 43). The trabeculae constitute one zone (Zone II) of the dome, which diminished in thickness during ontogeny and was nearly obliterated by reworking in a large *Pachycephalosaurus wyomingensis*. Superficial to Zone II is a thick, nearly acellular cap of compact bone, which lacks traces of structures perpendicular to the dome's outer surface. This histology calls into question the facilities of the dome to resist compression, and for remodeling and repair after damaging collisions.

Biomechanical Tests of Head-Butting Capability in Pachycephalosaurs

Cranial structure has been the starting point for debates about pachycephalosaur behavior. We therefore tested the structural capacity of pachycephalosaur domes to withstand forces of putative intraspecific combat, using finite element analysis (FEA) of representative low- and dome-headed taxa. Our criteria for contradicting the domes' suitability for head-butting are that von Mises (yield) stress exceeds that of bone strength (approximately 300 MPa), and the presence of high stress in bone encompassing the endocranial cavity. We constructed finite element models of the skulls dorsal to the braincase in the flat-headed *Homalocephale colathoceros* (GI SPS 100/51: Maryńska and Osmólska 1974) and the largest dome-headed species, *Pachycephalosaurus wyomingensis* (AMNH 1696: Brown and Schlaikjer 1943).

Finite element modeling decomposes a continuous field into a mesh of multiple individual elements. In models of solid structures, the elements act analogously to a set of interconnected springs with collective physical properties of the original material. When calculated forces are applied to the finite element model, FEA yields distribution and magnitude of stress (force/area) and strain

(proportional deformation) that would have occurred within the mechanically loaded structure.

FEA of pachycephalosaur skulls requires modeling the shape and material properties of their thickened cranial dorsa and determining the impact forces of a simulated collision. Force would vary intertaxonomically and with the speed of an encounter, and material properties could vary histologically even within the skull of an individual. We therefore vary these parameters to encompass possible collision velocities and test for the effects of histological zonation within dome-headed forms.

Tissues of the integument that covered the dome would have been the first to absorb or transmit impact energy. The epidermis of pachycephalosaurs undoubtedly incorporated β -keratin, similar to their extant avian-crocodylian bracket. Although keratin is not as stiff as the mineralized component of bone (Bonser and Purslow 1995, Crenshaw 1980, Shah and Lee 2004), it is a strong and tough material (Bertram and Gosline 1986, Bonser et al. 2004) that can withstand a great deal of energy before experiencing permanent damage. Keratinization of scales analogous to the covering of crocodylian osteoderms (Vickaryous, personal commun., 2007) may have enabled transmission of collision forces to the dome without significant damage to the integument. Given its frontline role in potential impacts, we incorporate keratinous integument of varying thicknesses into FE simulations of pachycephalosaur head-butting.

Because putative combat behaviors would have been complex affairs, we term the magnitude of each collision velocity a "closing speed" that accommodates multiple combinations of approach velocities in the antagonists. The effects of a head-on closing speed of 5 m/s, for example, would be the same if both animals approached at 2.5 m/s, if one charged at 5 m/s as another held its ground, or if one approached even faster as the other retreated. (For simulations of head-on collisions, signs of velocity vectors would be opposite.) Additionally, by simulating forces of an impact to the side of a *Pachycephalosaurus* dome, we examined the possible effects on the dome if one animal collided obliquely with another.

Whether evidence ultimately favors combat or display functions of pachycephalosaur domes, their features can be traced phylogenetically to explore the structure's evolution through the clade. We therefore sought to complement the character optimization of Maryńska et al. (2004) by running a phylogenetic analysis of their included taxa. If the dome lacked a mechanical function and was pri-

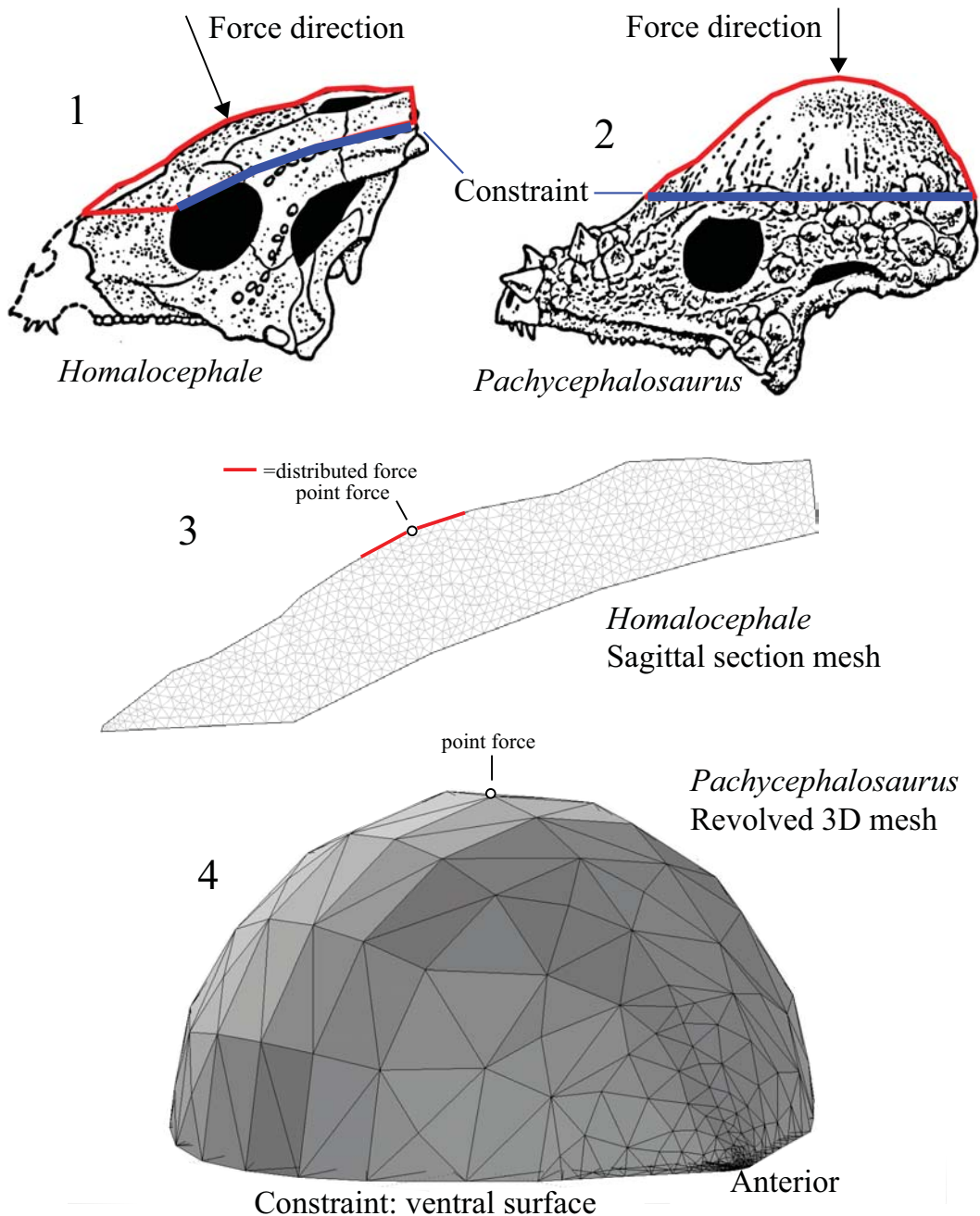


Figure 1. Construction of finite element models of cranial dorsal regions (red outlines) in (1) *Homalocephale colathoceros* and (2) adult *Pachycephalosaur wyomingensis*. Arrows represent the direction of collision forces applied to a sagittal-section finite element mesh for *Homalocephale* (3), and a 3D mesh (4) for *Pachycephalosaur*, shown in orthogonal view.

marily for species recognition, we might expect it to diminish in size as other, visually stimulating ornamentation accrued through pachycephalosaur evolution. To test this hypothesis, we mapped dome features and other “species recognition” characters from Maryńska et al. (2004) onto the results of our phylogenetic analysis.

MATERIALS AND METHODS

Finite Element Models

Figure 1 depicts templates for our models, force directions and constraints, and finite element meshes (at lower yet more intelligible resolutions than those ultimately used). Our primary source material for FEA models were lateral photographs

and reconstructions of the skulls of *Homalocephale* and *Pachycephalosaurius*. These were scanned on a flat-bed scanner and scaled to the actual linear sizes of the original specimens. The areas dorsal to the braincase were traced using the pen tool in Adobe Illustrator®. We exported coordinates of the traces as DXF computer-aided design files and imported these into the finite element program COMSOL Multiphysics® (using the “coerce to solid” drawing option to simulate a continuous structure).

We constructed several kinds of models for both pachycephalosaurs. As a control, to test whether stress distributions might differ simply because the animals varied greatly in size, we scaled the 2D sagittal sections to an identical length (see “forces” below). For a realistic model of the properly scaled *Homalocephale*, we used the extrude tool in Multiphysics® to expand its profile to the approximate width of the skull (about 6 cm). Two kinds of models were constructed for *Pachycephalosaurius*. We extruded the *Homalocephale*-length trace into a sagittal section the same width as the *Homalocephale* model. To construct a truly domed 3D model we rotated the trace about a line with identical y-coordinates near those of the trace’s ventral base (parallel to the x-axis) and with endpoints at their respective x-coordinates.

Another pachycephalosaurine model, based on a subadult (Museum of the Rockies MOR 453) sectioned by Goodwin and Horner (2004), was constructed as a materially realistic replication of Sues’s (1978) Plexiglas tests. This model allowed us to check the effects of a zone of trabecular bone on compressive stress and strain. We tested the hypothesis that if trabeculae resisted compression, a region of cancellous bone would exhibit low strain magnitude. In an essentially 2D model of a section of its dome (set to 1 mm thickness), we embedded a subdomain corresponding to the cancellous Zone II (Fig. 3A in Goodwin and Horner [2004]), and assigned appropriate material properties to all three zones. This model is based on a midsagittal histological section that did not extend completely through the dome. We restored the posterior portion as roughly symmetrical to the sectioned anterior portion, which may have resulted in an anteroposteriorly compressed model. A refined model would give more realistic results for stress distribution, but would not change the effects of varied material properties on relative strain magnitude.

At present we cannot characterize the morphology of keratinous integument covering the dome (Goodwin and Horner 2004; although in some specimens the pattern of vascular canals suggests supply to a mosaic of hexagonal scales). We therefore added keratinous zones of three different thicknesses to the model of the subadult pachycephalosaurine, to test the sensitivity of bone stress to inference of integumentary morphologies.

The models were meshed at varying resolutions in COMSOL Multiphysics®, using the mesh parameters and “remesh” options. Unusually large, small, or otherwise problematic meshes can result in stress artifacts or even solution failure. We ran analyses iteratively until we achieved results with the highest resolution mesh possible without a significant drop in solution time or performance. For example, our *Homalocephale* model had 20736 elements, and the *Pachycephalosaurius* dome mesh had 13732; the latter experienced errors at higher element numbers. Solutions at equivalent node positions converged in meshes of 5000 elements or more, and we have no reason to doubt the accuracy at other positions for larger meshes.

Material Properties

Measurements of bone material properties vary depending on the bone’s histology and the measurement protocol. We therefore assigned elastic modulus (stress-strain relationship $E=20$ GPa), Poisson’s ratio (transverse versus longitudinal strain $\nu=0.4$), and density ($\rho=2000$ kg/m³) that fall within the range commonly reported for compact bone.

For the subadult pachycephalosaurine model we assigned the above properties of compact bone in the deep and superficial histological zones I and III (Goodwin and Horner 2004). For the cancellous zone II, we assigned an appropriate elastic modulus of $E=8$ GPa, a density ρ of 0.5 that of compact bone, and the same Poisson’s ratio $\nu=0.4$. For models of the keratinous covering of this dome, we assigned material properties in the range calculated for β -keratin ($E=2.5$ GPa, $\rho=1300$ kg/m³, $\nu=0.4$: Bonser and Purslow 1995, Shah and Lee 2004).

Impact Forces and Displacement Boundary Conditions

During an impact, each pachycephalosaur’s kinetic energy would dissipate over a distance, yielding an impact force (Alexander 1989):

$$F = m \cdot v^2 / 2 \cdot d \quad (1)$$

where m is the mass of the animal, v is the closing speed, and d is the deceleration distance. We used one fast and one slower closing speed for both species: 6.7 and 3 m/s, respectively. The former was considered a reasonable “maximum” collective closing speed for the pachycephalosaurs, given their likely hip heights and limb proportions. (It is also the highest observed speed of collisions that inspired this study, between American football players coached by the second author.) The mass for *Homalocephale* was set to 36 kg (a volumetric model estimate courtesy Paul, personal commun., 2006) and that of *Pachycephalosaur* at 488 kg. For the latter mass, we scaled Gregory Paul’s volumetric estimate (personal commun., 2006) for a smaller specimen (Russell 1995) to the size of the modeled AMNH specimen, by cubing the ratio of their skull lengths. (The smaller specimen is on display as a pair of cast skeletons [NSM PV 20423, 20424] at the National Science Museum, Tokyo, Japan.)

Deceleration distances were more problematic to estimate. Flexion of the vertebral column would account for some of this distance, but the tongue-in-groove zygapophyseal articulations between the vertebrae would moderate the displacement. In preserved sequentially paired vertebrae of *Stegoceras validum* (UALVP 2), the “tongue” of the postzygapophysis can shift 0.3-0.5 cm until it hits a stop facet in the groove of the succeeding prezygapophyses. For the similarly-sized *Homalocephale colathoceros*, we considered 0.12 m to be a reasonable value for d , but also applied half and double this value to equation 1 to derive a sensitivity range of forces. The longer distance may be especially realistic if a combatant absorbed some of the collision force with its hind limbs. Based on comparisons of skull length, we set the base deceleration distance in *Pachycephalosaur* to 0.33 m and varied it around this value as with *Homalocephale*.

Calculated force magnitudes are listed Table 1. We applied these magnitudes to the modeled cranial elements perpendicular to the impacted surfaces. Two different force distributions were applied to the *Homalocephale* model. One was a point load and the other an edge load applied to a region just above the orbits, assuming a widely-spread impact. Because the *Homalocephale* model sloped downwards anteriorly, we applied x and y vector components of the estimated resultant force. For *Pachycephalosaur* we applied head-

on forces to a point at the apex of the dome using a point force application. The resulting stress seemed low, so we applied the force as if focused onto one square centimeter (multiplied by 10,000). This method is not strictly correct, but we wished to cover potential underestimates in our procedures. For the *Pachycephalosaur* side-impact test, we applied a high force (at 6.7 m/s and 0.33 m deceleration distance) perpendicular to a broad area of the dome’s lateral surface, simulating an impact to an opponent’s rib cage. The subadult pachycephalosaurine (MOR 453) model was based on a 2D sagittal section. Without a reliable mass estimate, we simply applied a compressive force of -1000 N (y -axis) to its dorsal-most edge. For all three specimens, we restricted the ventral boundaries of the models to an initial displacement of 0.

Phylogenetic Analysis and Character Optimization for Pachycephalosauria

To visualize optimization of characters associated with intraspecific behavior in pachycephalosaurs and obtain support values, we ran a Bayesian inference analysis on the matrix of Maryńska et al. (2004). (The matrix file is available as supplementary information and a command file from the first author.) Using MrBayes for Macintosh®, we ran the analysis on four parallel chains for two million Markov Chain-Monte Carlo generations, until standard deviations of split frequencies fell below 0.01. This analysis ensured thorough exploration of tree space and reliable assignment of posterior probability values to resulting nodes. We then imported the consensus tree into MacClade® and used the character trace function to visually map characters onto the tree. Probable “species recognition” character states include the dome, tubercles present on the cranium, tubercles on the mandible, and an extended posterior shelf on the cranium. The consensus tree file is available as supplementary information from the first author.

RESULTS

Control: Stress Distribution in Size-Normalized Dome Models

Figure 2 depicts results of an analysis with 2D models of cranial dorsa of *Homalocephale* and *Pachycephalosaur* scaled to the same length and with the same impact forces. In the *Homalocephale* simulation (Figure 2.1), high-magnitude von Mises stresses extend through the dome, reaching the brain cavity (Figure 2.1). In the *Pachycephalosaur*

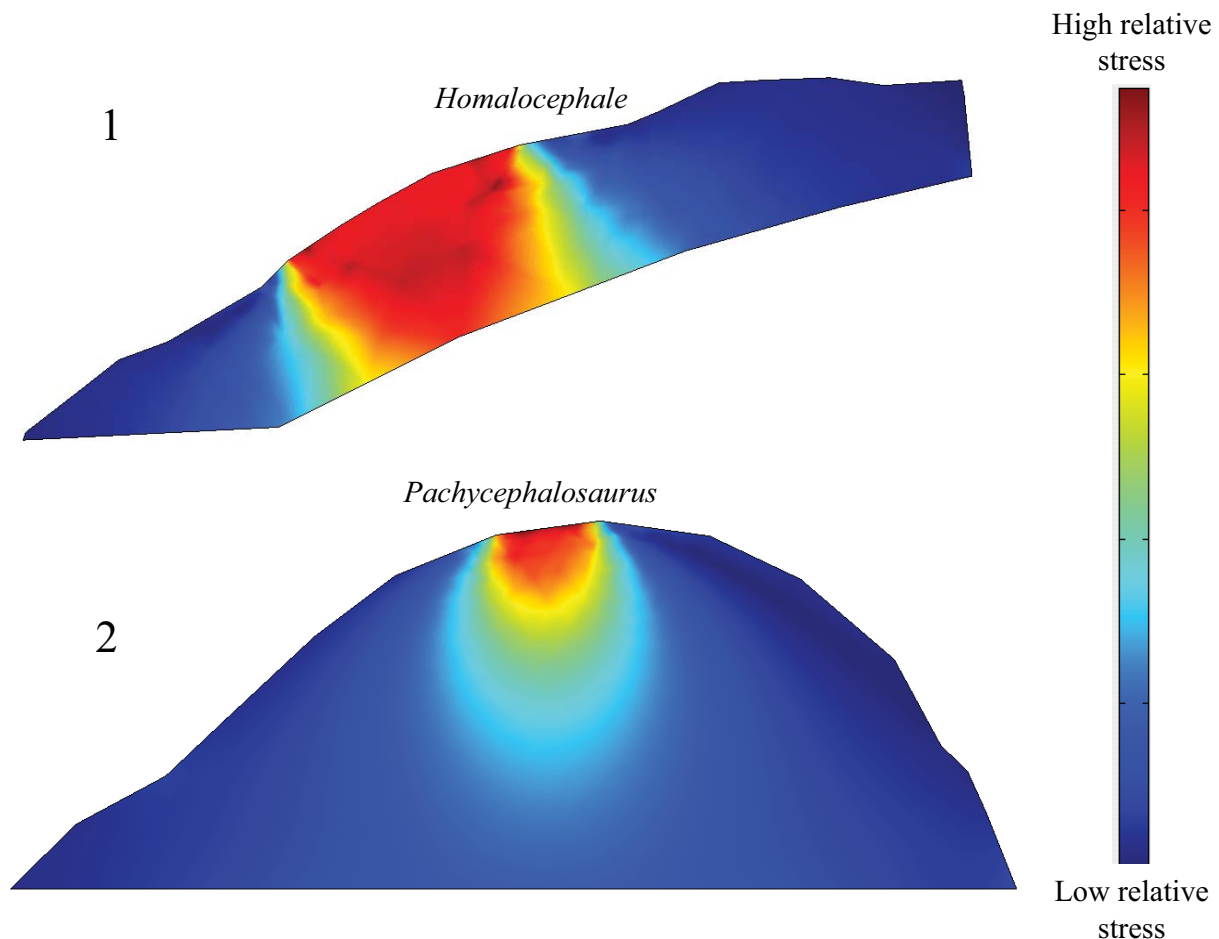


Figure 2. Results of control analysis, with midsagittal sections of *Homalocephale* and *Pachycephalosaurus* cranial dorsa scaled to the same length, and subjected to unit forces. In *Homalocephale* (1), high-stress propagates through the structure. In contrast, stress diminishes rapidly away from the point of contact in *Pachycephalosaurus* (2). The color scale (right) ranges from red for high stress to blue for low stress; absolute magnitudes are not given because stress patterns are the same regardless of the unit force applied. Differing results indicate that dome shape had a much greater influence on stress distribution than animal body size.

rus analysis, von Mises stresses diminish rapidly away from the point of impact (Figure 2.2), despite application of force to a smaller area than in the flatter-headed *Homalocephale*.

Stress Distribution in *Homalocephale*

Homalocephale results (Figure 3) reveal that the skull could unambiguously handle impact force at closing speeds of 6.7m/s to 3m/s. The one exception occurred at 6.7m/s with a deceleration distance of 0.06 m. Under these conditions, the skull model was not able to fully dissipate stress in the region dorsal to the brain, resulting in a well-defined area of high tensile stress adjacent to the endocranial cavity. Much higher peak stresses occurred at point impacts than at distributed impacts, but these are focused at the locus of impact and fall below the failure strength of bone.

Based on these results, it is reasonable to conclude that *Homalocephale* would have been able to handle head-butting behavior over most of the velocity and deceleration ranges tested, but that high speed impacts would have been more problematic.

Stress Distribution in 3D *Pachycephalosaurus* Models

Results for *Pachycephalosaurus wyomingensis* depict a skull that could withstand high impact forces. Stresses are low with a simple point application of the calculated impact force, and with much higher applied forces the stress still falls below the limits of bone strength. At 6.7 m/s (with maximum von Mises stress of 14660 Pa: Figure 4.1) and 3 m/s, stress would dissipate throughout the skull before it would reach the braincase (Fig-

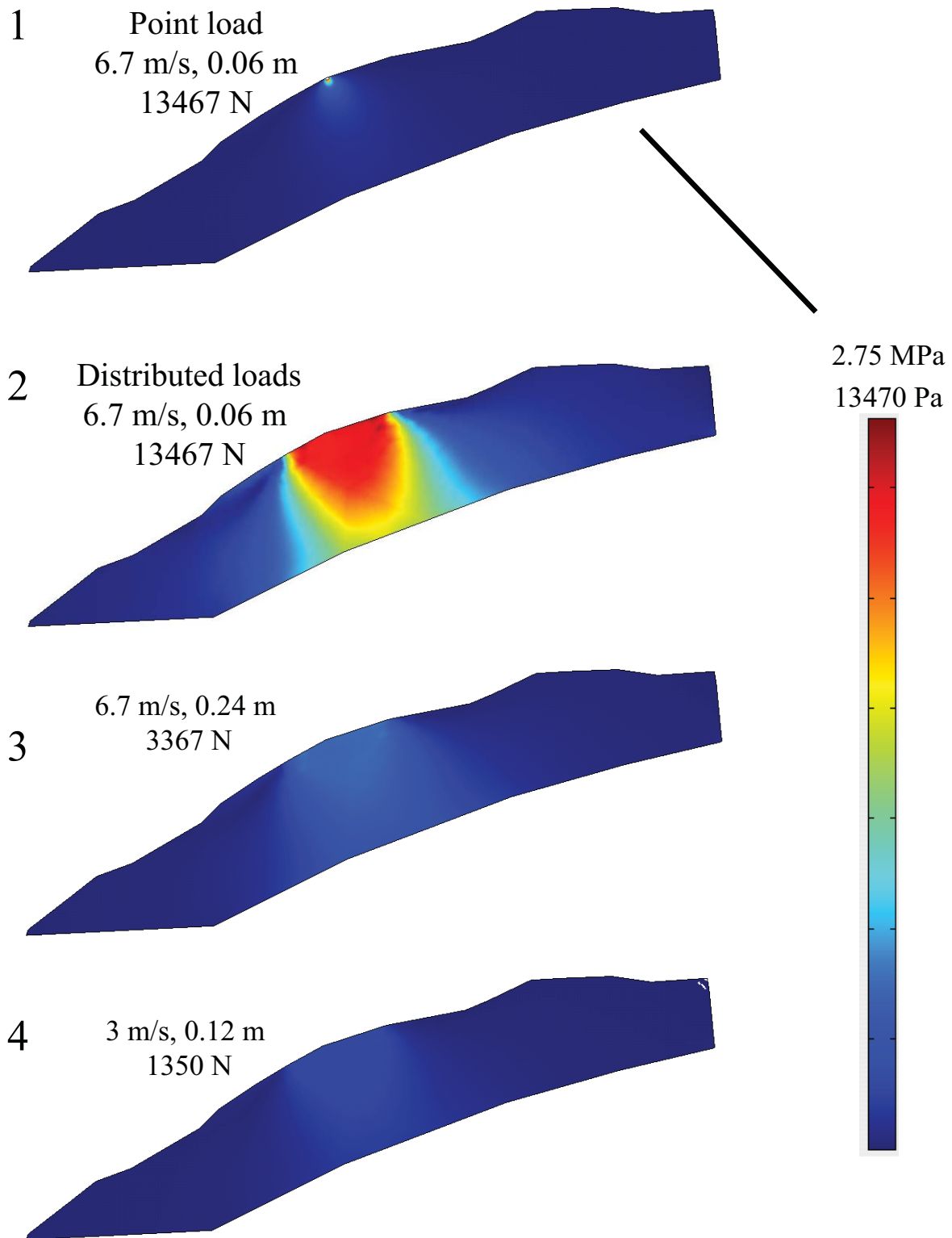


Figure 3. Distributions of von Mises stress in modeled sagittal sections of the dome of *Homalocephale colathoceros*. Stress is high immediately below point impacts (1), but well within the limits of bone strength (200-300 MPa). With high-energy distributed impacts, relatively high stress is evident adjacent to the endocranial cavity, (2), but in less strenuous collisions stress diminishes markedly before reaching the braincase (3, 4).

Multiphysics® point impact: 14660 Pa,
Force/area x area: 127.3 MPa

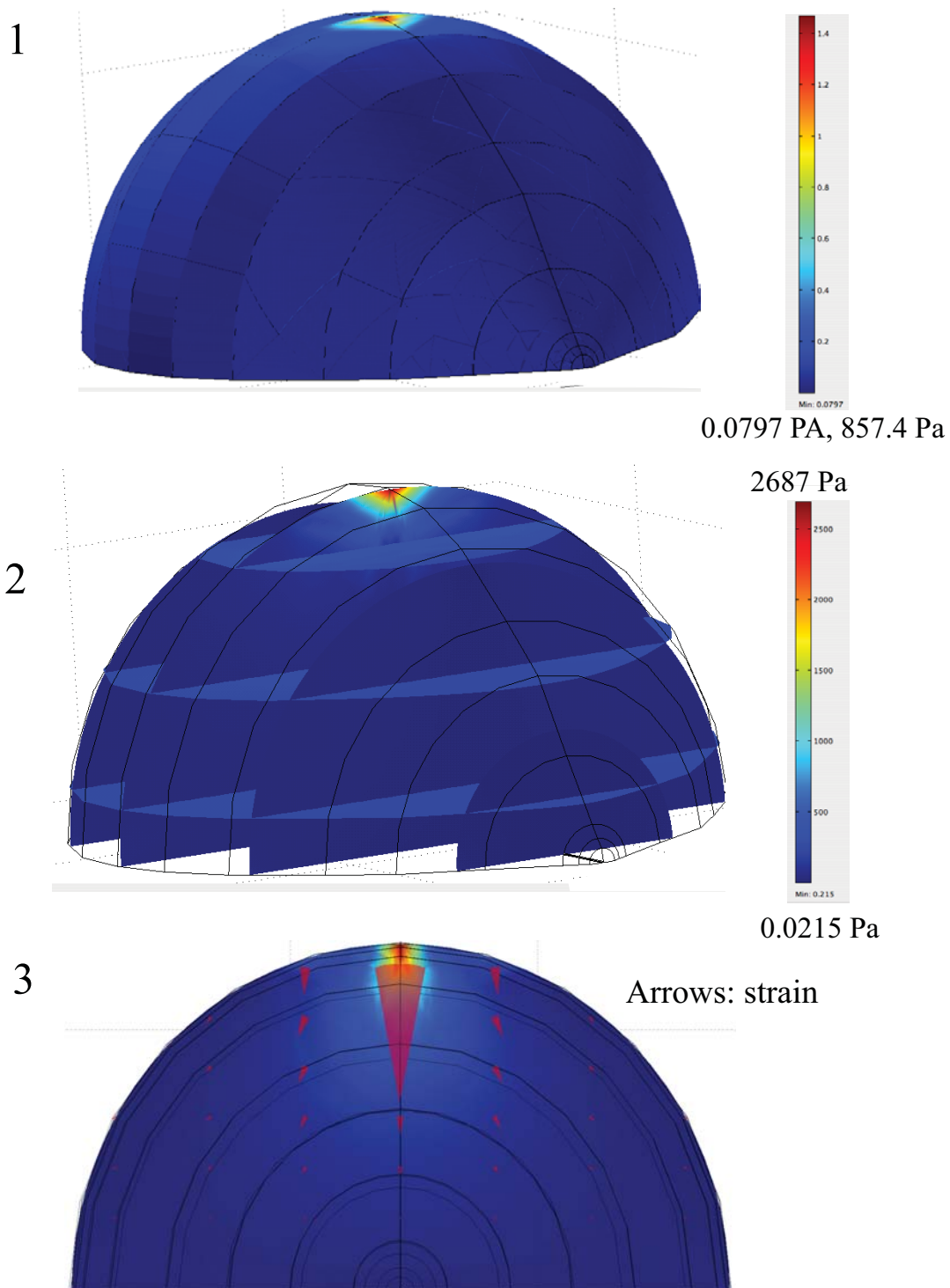


Figure 4. Distributions of von Mises stress in a finite element dome model of *Pachycephalosaurus wyomingensis*. Stress diminishes rapidly away from the point of impact and is very low near the endocranial cavity, in both high- (1) and low- (2) force impacts. Arrows superimposed over a transverse section (3) represent strain direction and relative magnitude through the structure. Strain magnitudes (arrow sizes) diminish markedly deep to the impact, and strain vectors diverge away from the brain.

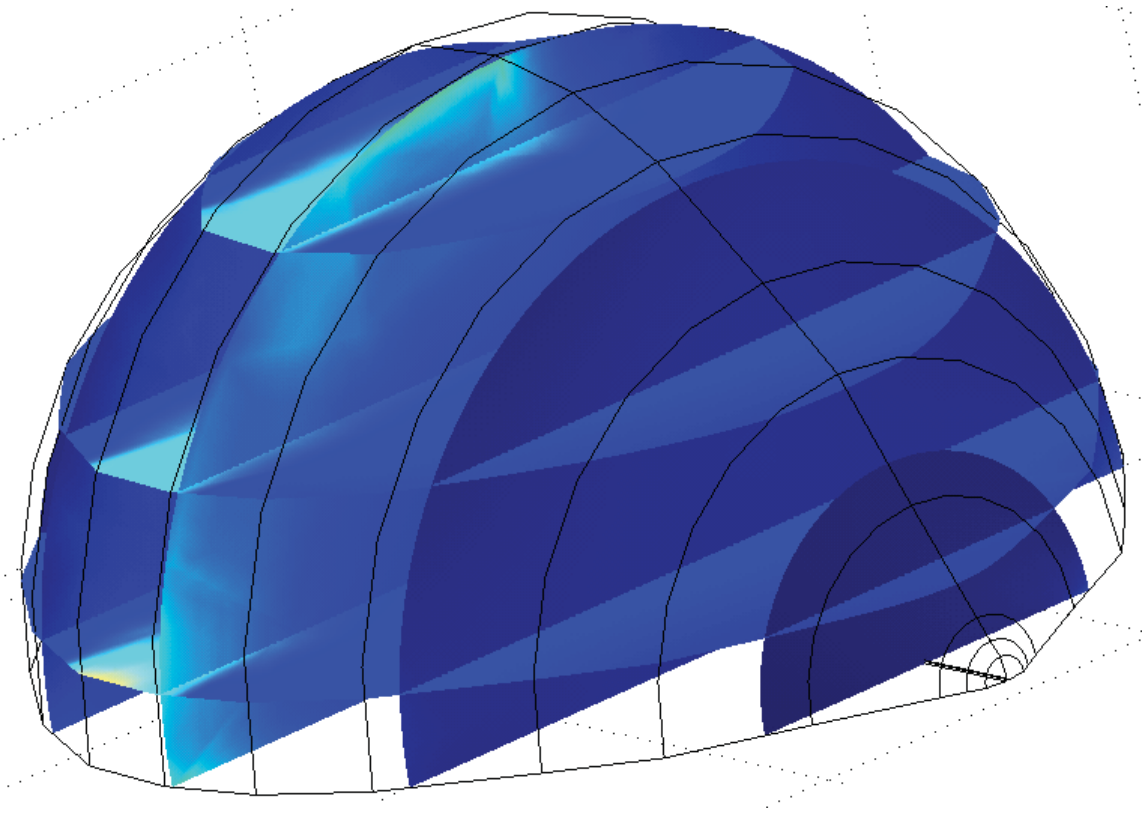


Figure 5. Computed von Mises stress distribution in *Pachycephalosaurus wyomingensis* dome under a broadly distributed, side-impact load. Transverse and frontal sections show that stress diminishes medially and anteroposteriorly; lighter blue correlates with higher stress.

ure 4.2). Strain decreased dramatically in magnitude as it was diverted laterally (Figure 4.3) and anteroposteriorly. If high stress was seen to reach the braincase, a high magnitude of stress would be prevalent throughout the images. A similar pattern of stress distribution occurs under the side-impact loading regime (Figure 5), with stress diminishing deep to the site of impact, and anterior and posterior to it.

Strain Results for the Subadult Pachycephalosaurine

Figures 6.1 and 6.2 depict the modeled specimen and sagittal section mesh, incorporating histological zones I, II, and III, of the subadult pachycephalosaurine. Figure 6.3 shows the distribution of compressive strain in the model. Cancellous zone II shows higher overall compressive strain than either of the contiguous zones of compact bone. Differences in strain magnitude between zones are especially evident in when the results are animated (Figure 7).

Greater strain in the cancellous zone also results in models with varying thicknesses of keratinous integument. However, strain within all three zones decreases when the load is applied to the integument (as would occur in life), and magnitudes of bone strain are inversely proportional to modeled thickness of the keratinous covering (Figures 6.4-6.6).

Phylogenetic Results and Character Optimization

Figure 8 depicts the 50% majority rule consensus tree from the phylogenetic analysis. The topology is similar to that presented by Maryánska et al. (2004), with a polytomy for *Goyocephale*, *Homalocephale*, *Ornatolithus*, and a clade consisting of more derived taxa. Relationships within this clade are similar to those reported in the consensus tree of Maryánska et al. (2004), but the seemingly high posterior probability values are low by molecular phylogenetics standards. The negligible 50% posterior probability support for a *Pachycephalosaurus-Prenocephale* grouping indi-

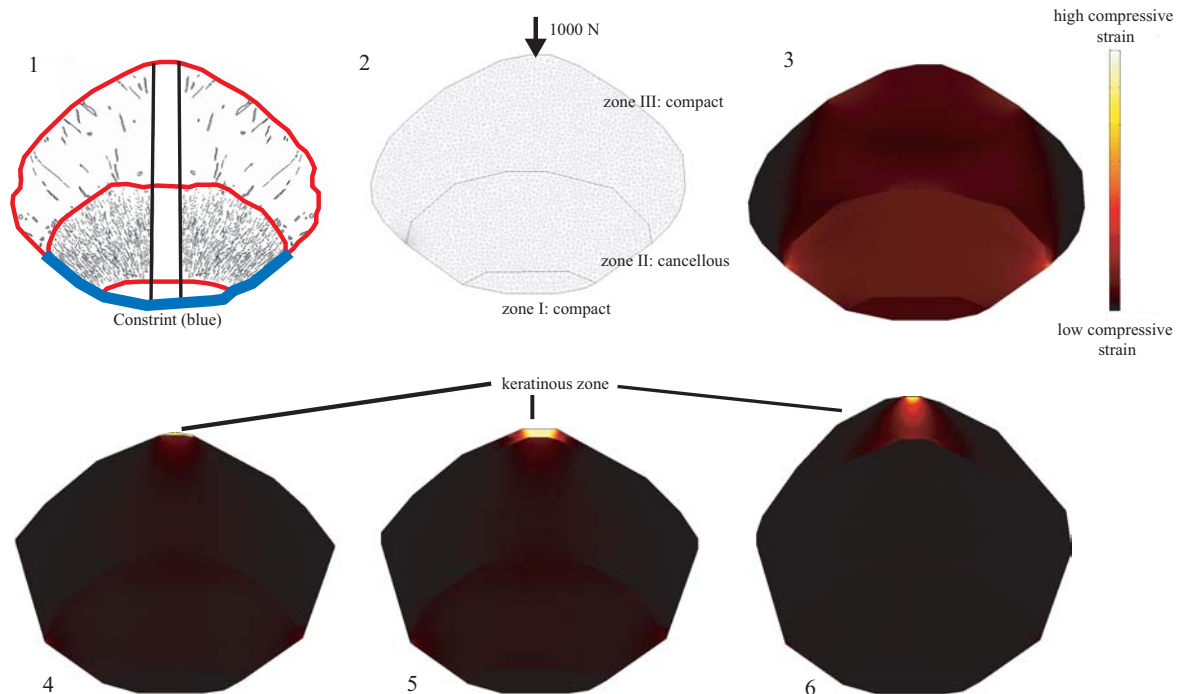


Figure 6. Finite element template (1; after Goodwin and Horner 2004), mesh (2), and compressive strain results (3) for a section through the dome of a subadult pachycephalosaurine. Material properties correspond to histological zones, and a unit impact force is applied. Strain is higher overall in cancellous Zone II than in superficial and deep zones of compacta. Bone strain diminishes successively with increasing thicknesses of keratin modeled as covering the domes (4-6).

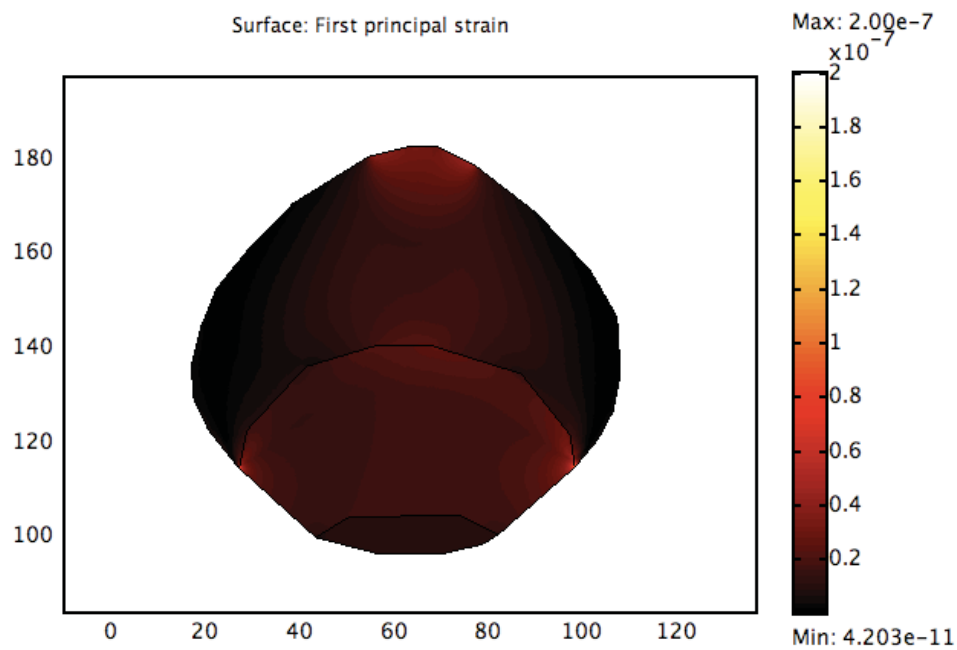


Figure 7. This animation depicts propagation of strain through a reconstructed mid-sagittal section of a pachycephalosaur, with applied forces and material properties as shown in Figure 6.2.

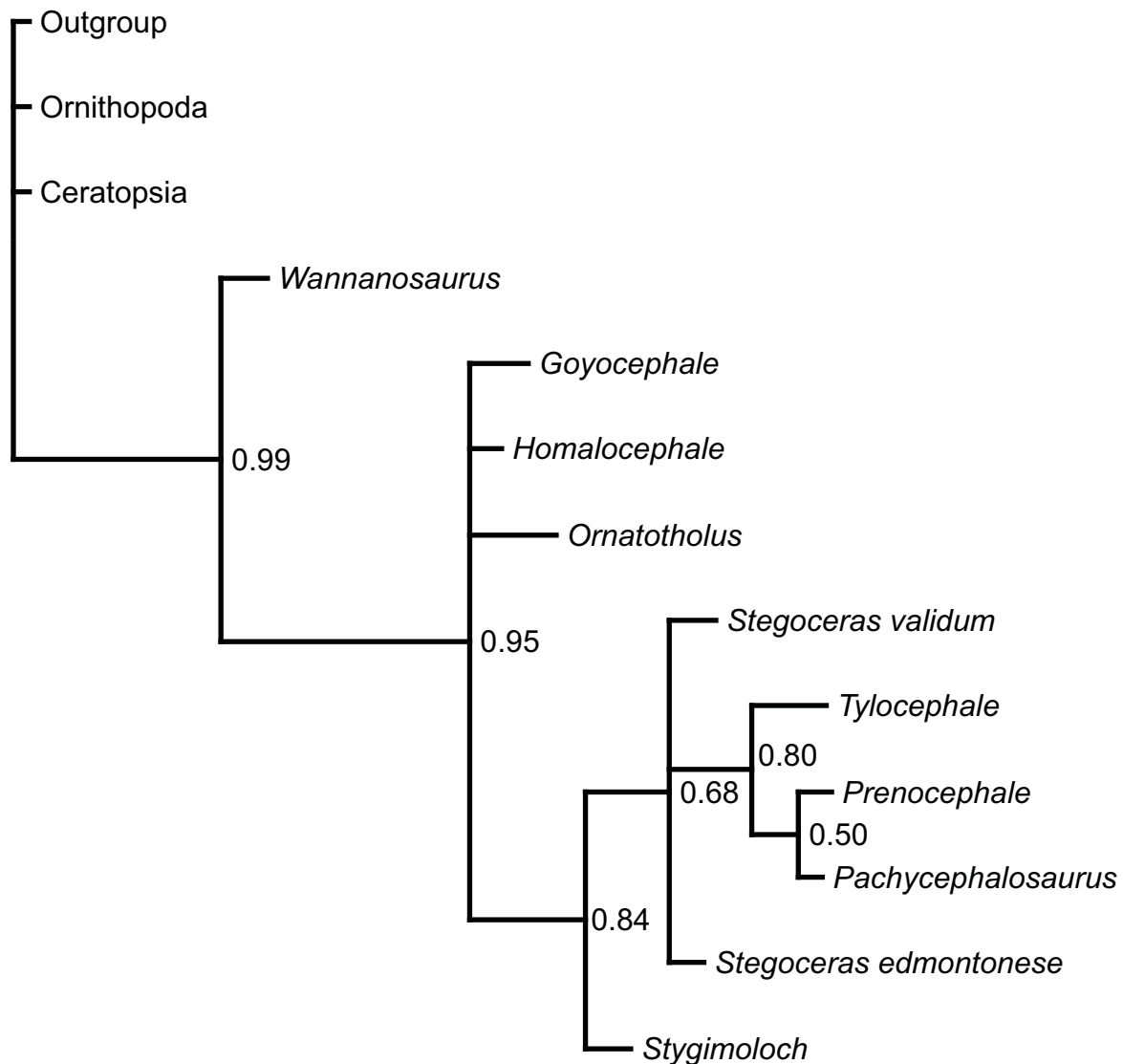


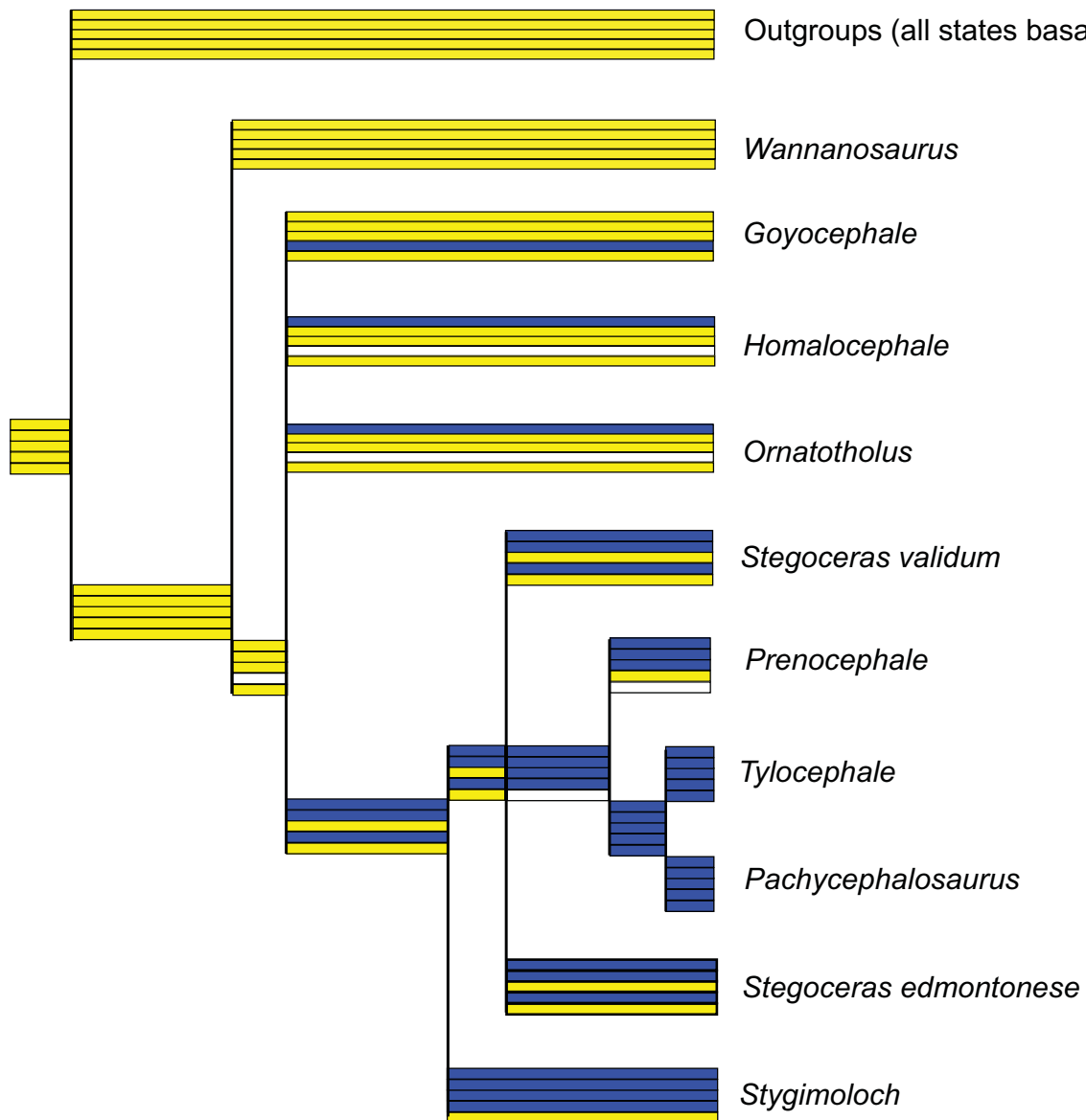
Figure 8. Bayesian inference phylogeny of pachycephalosaurs using the matrix of Maryńska et al. (2004). Posterior probability values to the right of nodes show strong support for most clades, but relatively weak support for a *Stegoceras*-bracketed group, and irresolution among taxa in a strongly supported *Tylocephale*+*Prenocephale*+*Pachycephalosaurus* clade.

cates a polytomy between these taxa and *Tylocephale*, as recovered by Maryńska et al. (2004).

Figure 9 maps characters related to dome mechanical and species recognition functions onto the consensus cladogram. Characters identifiable as for species recognition, such as an elaborate posterior cranial shelf and cranial and mandibular tubercles, generally increase in prominence in taxa with greater vaulting and addition of other bones to the frontoparietal dome. *Stygimoloch* is a notable exception to the trend. The pattern provides tentative evidence against the hypothesis that the dome became reduced as other species recognition features evolved, except in the case of *Stygimoloch*.

DISCUSSION

In both *Pachycephalosaurus* and *Homalocephale*, maximum von Mises and compressive stress fall below the 300 MPa yield stresses of bone (Table 1), even in high-force collisions. Based on this criterion for head-butting suitability, the high safety factors corroborate our hypothesis that the domes could withstand stresses of combat in these pachycephalosaurs. Notably, the highest rate of deceleration occurs in *Homalocephale* at the highest tested closing speed and shortest deceleration distance (approximately 76 g). This rate is within the range at which colliding American football play-

**Key:**





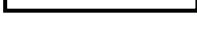
dome absent (0), present (1)		1: derived
sutures unfused (0), fused (1)		0: basal
expanded shelves absent (0), present (1)		?: unknown
mandible tubercles absent (0), present (1)		
nasal tubercles absent (0), present (1)		

Figure 9. Mechanically relevant and species recognition characters mapped onto pachycephalosaur phylogeny from Figure 8. The common ancestor of *Stegoceras* and *Stygimoloch* is interpreted as having a large dome and extra ornamentation, with additional display ornament evolving in subsequent lineages. Extra ornamentation in large-domed taxa, such as *Pachycephalosaurus* and *Tylocephale*, suggests that the dome was not solely for display and had a strong agonistic function such as head-butting. Enlarged ornamentation and a small dome (states not mapped) in *Stygimoloch* suggest greater emphasis on display and less on dome-to-dome combat.

Table 1. Values for calculation of impact forces using Equation 1, for 36 kg *Homalocephale colathoceros* and 488 kg *Pachycephalosaurus wyomingensis*, at closing speeds of 6.7 and 3 m/s for each. In *Pachycephalosaurus* the highest stress is for a focused point impact, and the alternate high stress is for the software's point force application. Peak stresses diminish indirect proportion with diminishing forces.

Homalocephale colathoceros 36 kg

Closing speed 6.7m/s

Deceleration distance	Force	Fx	Fy	Max. von Mises stress (point impact)
0.06 m	13467 N	5919	-12096	11.72 MPa
0.12 m	6734 N	2960	-6048	5.862 MPa
0.24 m	3367 N	1480	-3024	2.391 MPa

Closing speed 3m/s

0.06 m	2700 N	1175	-2402	2.328 MPa
0.12 m	1350 N	587.5	-1201	1.164 MPa
0.24 m	675 N	293.8	-600.5	0.582 MPa

Pachycephalosaurus wyomingensis 488 kg

Closing speed 6.7 m/s

Deceleration distance	Force (Fy)	Max. von Mises stress
		127.3 MPa
0.165 m	-66383 N	14660 MPa
0.33 m	-33191 N	
0.66 m	-16596 N	

Closing speed 3m/s

0.165 m	-14494 N
0.33 m	-7247 N
0.66 m	-3624 N

ers experience concussions (94 +/- 28 g: Viano et al. 2007) and suggests that the animals would have preferred lower collision speeds. We conclude that cranial mechanics of these animals permitted high-energy, head-to-head combat, and that ultimate collision speeds were constrained by other factors.

As with other analyses of complex behavior in fossil animals, we can test pachycephalosaurs' capability for head-butting and even characterize their potential performance. However, whereas biomechanics might support or contradict hypotheses of capability, our ability to test hypotheses of specific behaviors will remain asymptotic without trace evidence. Pathologies are common on the dorsal surfaces of pachycephalosaur domes (University of Alberta and Royal Tyrrell Museum specimens, P. Bell and E. Snively, unpublished data) and are conceivably the result of impact trauma, but may also

be age-related. Yet the domes of some pachycephalosaurs are an unusual case, in which a feature not seen in extant vertebrates is uniquely suitable for a postulated behavior (in this case cranial impacts against resistant structures). By cranial and post-cranial evidence (Galton 1971, Maryńska and Osmólska 1974, Sues 1978), our finite element results, and analogy with intraspecific combat in modern forms, we find inference of head-based combat in some pachycephalosaurs to be reasonable and compelling.

Whereas our conclusions about the possibility of pachycephalosaur head-butting differ from those of Goodwin and Horner (2004), our results parallel their caution about the compression resistance role of trabeculae. Stress would diminish greatly before it reached the cancellous zone II within some pachycephalosaur domes. However, a lower density and elastic modulus ensured that zone II would

experience higher compressive strain than surrounding zones, in which compact bone predominates. (This general result is predictable from material properties, but without FEA our deductive omniscience fails for postulating finer patterns of stress and strain.) These results indicate that trabeculae angled relative to the compressive force would experience some elastic deformation and recoil, as originally proposed by Alexander (1989) but at lower strain magnitudes.

Phylogenetic and Ontogenetic Scenarios for Pachycephalosaur Combat

Our phylogenetic analysis suggests escalating adaptation towards head-butting in some but not all lineages of pachycephalosaurs. The domes most suitable for head-butting co-occur with tubercular ornamentation in *Tylocephale*, *Prenocephale*, and *Pachycephalosaurus*. This association suggests that species differentiation was not dependent solely on the presence of a dome in these taxa, and that the dome had a function in addition to its species recognition role. FEA confirms the domes' suitability for hypothesized intraspecific combat. However, crania became less adept for high-energy head-butting in *Stygimoloch* (Goodwin et al. 1998) and *Dracorex*, taxa with the most outlandish tubercular ornamentation (Bakker et al. 2006). This evident decrease in performance conforms to suggestions of Goodwin et al. (1998) and Maryńska et al. (2004) that cranial thickenings and ornamentation in these animals evolved through flank- and head-butting adaptations to apomorphic display functions, in parallel with the evolution of horn and antler morphologies postulated for artiodactyls (Geist 1966). If the phylogeny here is correct, we suggest that head-butting increased in selective importance among high-domed forms, but that this function decreased in importance in at least one lineage of derived pachycephalosaurs.

Alternatively, strong evidence that low-domed specimens were subadults of contemporaneous high-domed taxa (Horner et al. 2007, Sullivan 2007) suggests an ontogeny of agonism for pachycephalosaurines. Such an ontogenetic scenario mirrors Geist's (1966) evolutionary scenario for artiodactyl agonism, and consolidates the current biomechanical results with the histological findings of Goodwin and Horner (2004). Flat-headed subadults of *Pachycephalosaurus* would have engaged in shoving and flank-butting matches, and display with enlarged cranial ornamentation. During a stage of rapid growth of the

dome, the resilient and easily remodeled trabecular zone would have facilitated head-butting as suggested by mechanical results in this study. Finally, large adults would rely on intimidation, display, and flank-butting, as the dome became massive and its acellular histology (Goodwin and Horner 2004) reduced its capacity for remodeling and repair.

Both evolutionary and ontogenetic scenarios are predictive and have contradictable components. For example, impact pathologies (if they can be so identified) are predicted as more commonly evident in high- than low-domed specimens, in individuals of moderate size. Further sensitivity analyses may reveal a range of soft-tissue morphologies that would enable or prohibit head-butting in large pachycephalosaurs, with keratin acting to protect the acellular osseous dome. Whereas we cannot envision reconstructing the integument with known accuracy, future workers may devise methods that surmount this obstacle and enable tests for head-butting at respective stages in each scenario.

Prospectus and Conclusions: Future Tests of Head-Butting

The current study analyzes mechanical response of simplified models of pachycephalosaur domes, at opposing poles of size and morphology for the clade. Refined models of *Homalocephale* and *Pachycephalosaurus* domes collisions (especially dynamic models) would better approximate in vivo stresses and strains under putative loadings, but are unlikely to shift the relative performance of their respective thickened crania. Yet our *Homalocephale* model in particular is greatly simplified, and results for it should be viewed with caution. Ideally, 3D finite element models of entire skulls (Rayfield 2007) of pachycephalosaurs, based on CT scans with material properties derived from X-ray attenuation data (Wroe et al. 2007), will be constructed across ontogenetic and phylogenetic spectra of these animals. Collision velocities based on quantitatively estimated speeds for pachycephalosaurs would improve upon the arbitrary velocities chosen here.

As noted above, the head-butting hypothesis is falsifiable if the keratinous covering of the dome can be established as precluding such combat. If surface vascularization suggests differential keratinous growth atop different regions of the dome surface, the resulting shapes may have prevented dome-dome contact.

Regardless of the shape of soft tissue covering the domes of pachycephalosaurs, species

recognition (Goodwin and Horner 2004) is compatible with combat behavior as a function of their thickened crania and must remain a primary hypothesis (without intraspecific recognition, such combat would be less likely). However, unless research on pachycephalosaurian integument and postcrania indicate otherwise, the present mechanical results uphold the possibility of head-butting behavior.

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