

Let them fight: using finite element analysis to determine combative evolutionary drivers of ceratopsian (Dinosauria: Ornithischia) horns

Eric Austin Ames¹, Andre J. Rowe¹ and David John Button^{1,2}

¹ School of Earth Sciences, University of Bristol, Bristol, United Kingdom

² Dinosaur Isle Museum, Sandown, Isle of Wight, United Kingdom

ABSTRACT

The intensely-researched fossil record of ceratopsian dinosaurs makes them an ideal clade to test hypotheses of morphological evolutionary drivers. These dinosaurs are best known for their extravagant headgear, including an assortment of cranial horns and often elaborate frills. While the frills have been suggested as display structures, their horns have been hypothesized as intraspecific combat weapons with various fighting styles from modern analogs providing ample baselines for testing. However, while direct fossil evidence of intraspecific combat does exist, an absence of biomechanical data makes determining whether different ceratopsid taxa were best suited to specific combat styles very difficult. Here we used 3D finite element analysis to model differences in biomechanical performance in simulated combat behaviors of five ceratopsian taxa (*Psittacosaurus*, *Protoceratops*, *Centrosaurus*, *Spiclypeus*, and *Triceratops*). Size-corrected results indicate that *Psittacosaurus* and *Protoceratops* skulls, which lack elaborate horns, exhibit high and low stress cranial stress magnitudes respectively. The nasal horn of *Centrosaurus* was well-suited for accommodating vertical and longitudinal stresses but much less so for mediolateral ones. The supraorbital horns of *Spiclypeus* and *Triceratops* demonstrate consistently low-to-moderate stresses across most tests, correlating with various fighting behaviors. These results suggest that differing intraspecific combat behaviors may be an evolutionary driver of ceratopsian cranial weaponry, with strong skulls being a result of phylogenetic inertia from earlier members of the clade. This study helps ascertain the effectiveness of cranial weaponry in ceratopsids for intraspecific combat and fills a notable knowledge gap in our understanding of these dinosaurs.

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Corresponding author
Eric Austin Ames,
zv24043@alumni.bristol.ac.uk

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INTRODUCTION

The emergence of cranial weaponry in the animal kingdom, as well as their precise function, has been an extensively studied phenomenon throughout the decades (Emlen, 2008). They have independently evolved in various tetrapod clades, both extant and extinct. These include the bony horns and antlers, covered in hollow keratinous sheaths, seen in modern ungulates (Geist, 1966; Lundrigan, 1996; Zhang et al., 2018), the purely

keratinous horns seen in rhinos ([Geist, 1966](#); [Emlen, 2008](#); [Sims & Yates, 2010](#)), the ossicones of giraffes ([Churcher, 1990](#)), the horns of Jackson's chameleons ([Cottingham, 2020](#)), and the horns exhibited by ceratosaurian theropods such as *Ceratosaurus* and *Carnotaurus* ([Rowe & Gauthier, 1990](#); [Mazzetta et al., 2009](#)), among others.

Cranial weaponry have been historically associated with intraspecific competition, as sexual selection has generally been considered their most likely evolutionary driver ([Darwin, 1871](#); [Andersson, 1994](#); [Hongo, 2007](#); [Hone, Wood & Knell, 2016](#)), even in species where females also exhibit such weaponry ([Kiltie, 1985](#); [Roberts, 1996](#); [Stankowich & Caro, 2009](#)). Cranial weaponry in males of many ([Packer, 1983](#); [Bro-Jørgensen, 2007](#)), but not all ([Espmark, 1964](#); [Maiorino et al., 2015](#); [Mallon, 2017](#); [Knapp, Knell & Hone, 2021](#)) species tend to be larger and more robust than females, with reproductive success being strongly correlated with their size ([Clutton-Brock, Guinness & Albon, 1982](#); [Metz et al., 2018](#)). Additionally, for ungulates in particular, the adaptive radiation out into open spaces from closed forested habitats, and the subsequent grouping and herding behavior that came with it, resulted in larger, more complex horns ([Estes, 1974](#); [Emlen, 2008](#); [Cabrera & Stankowich, 2020](#)). The primary use for such cranial weaponry is intraspecific combat ([Clutton-Brock, 1982](#)), although the behavioural context differs greatly among horned taxa ([Geist, 1966](#); [Geist, 1977](#); [Janis, 1982](#); [Packer, 1983](#); [Estes, 1991](#); [Roberts, 1996](#); [Stankowich & Caro, 2009](#); [Vander Linden & Dumont, 2019](#)). Regardless of motivation, the range of combat styles exhibited in animals with cranial weaponry is quite considerable, with horn morphology being strongly correlated with combat styles such as “stabbers”, “fencers”, “rammers”, and “wrestlers” ([Lundrigan, 1996](#); [McCullough, Ledger & Moore, 2015](#); [Vander Linden & Dumont, 2019](#); [Kitchener, 2000](#)).

“Stabbers” like mountain goats (*Oreamnos americanus*), dik-diks (*Madoqua kirkii*), and klipspringers (*Oreotragus oreotragus*) are characterized by horns that exhibit very weak curves, little-to-no catching arch, and can be described as extended stab zones ([Lundrigan, 1996](#)). They typically aim at the opponent's head and body without any interlocking and can be described as fighting with an “air cushion” between them ([Walther, 1974](#); [Zhang et al., 2018](#); [Vander Linden & Dumont, 2019](#)). “Fencers” like gemsbok oryx (*Oryx gazella*), blackbucks (*Antilope cervicapra*), Thomsons gazelle (*Eudorcas thomsonii*), Spanish ibex (*Capra pyrenaica*), and markhor (*Capra falconeri*) typically have longer horns and slightly more pronounced catching arches. They typically clash horns with downwards nods of the head, bows of the neck, or even rearing up to bring them down. They briefly contact horns rather than interlocking them for extended periods ([Walther, 1980](#); [Alvarez, 1990](#); [Vander Linden & Dumont, 2019](#)). “Rammers” like bighorn sheep (*Ovis canadensis*), bison (*Bison bison*), musk oxen (*Ovibos moschatus*) and takin (*Budorcas taxicolor*) are distinguished by extremely large horn stems and very strong curvature. They fight by building up momentum and charging before crashing their horns together at speed and disengaging ([Lundrigan, 1996](#); [Drake et al., 2016](#); [Vander Linden & Dumont, 2019](#); [Lee et al., 2024](#)). “Wrestlers” like red and white-tailed deer (*Cervus elaphus*; *Odocoileus virginianus*), elk (*Cervus canadensis*), moose (*Alces alces*), African buffalo (*Syncerus caffer*), addax (*Addax nasomaculatus*), and saiga antelope (*Saiga tatarica*) are the most complex and common. They have horns and antlers with long reaches and very pronounced

catching arches with features to help them twist, push, and shove for extended periods ([Clutton-Brock, Guinness & Albon, 1982](#); [Klinkhamer et al., 2019](#); [Vander Linden & Dumont, 2019](#)). It is worth noting that these are not set in stone. For instance, African buffalo were originally described as rammers ([Lundrigan, 1996](#)) before being relabeled as wrestlers ([Vander Linden & Dumont, 2019](#)). Furthermore, fights can have multiple parts, with bison starting with ramming and transitioning into a combination of wrestling and fencing ([Lott, 1974](#)). Additionally, any animal with a sufficient stab point may choose to gore enemies with them ([Lundrigan, 1996](#)).

Overview of ceratopsia and their horns

Among the various clades of tetrapods with cranial weaponry, the ceratopsian dinosaurs are some of the most visually recognizable. Initially described during the Bone Wars ([Marsh, 1890](#); [Marsh, 1891a](#)), ceratopsians are a group of marginocephalian ornithischian dinosaurs diagnosable by skull features such as a pronounced naris, a rostral “beak” bone, a very large premaxilla, a bony frill made from the parietal and squamosal bones, and a variety of supraorbital and nasal horns ([Hailu & Dodson, 2012](#); [Dodson, Forster & Sampson, 2012](#)) that exhibit considerable ontogenetic change ([Goodwin et al., 2006](#); [Horner & Goodwin, 2006](#)). They originated in the Late Jurassic ([Xu et al., 2006](#); [Hailu & Dodson, 2012](#)) but eventually reached the peak of their diversity in the Campanian and Maastrichtian stages of the Late Cretaceous, becoming a staple of Late Cretaceous North American ecosystems ([Dodson, Forster & Sampson, 2012](#); [Mallon et al., 2013](#); [Stein, 2019](#)). In earlier ceratopsians such as *Psittacosaurus* ([Osborn, 1923](#)) and *Yinlong* ([Xu et al., 2006](#)), the parieto-squamosal frills are either simple or absent and they lack supraorbital horns. However, some like *Protoceratops* and *Montanaceratops* ([Granger, Gregory & Berkey, 1923](#); [Brown & Schlaikjer, 1942](#); [Chinnery & Weishampel, 1998](#)) possess larger frills and the enlarged naris where later-derived ceratopsians possess a nasal horn ([Hailu & Dodson, 2012](#)). Members of the later Ceratopsoidea clade, such as *Zuniceratops* ([Wolfe & Kirkland, 1998](#)) exhibit notable supraorbital horns.

The later-diverging clade Ceratopsidae is typically divided into two clades: Centrosaurinae and Chasmosaurinae ([Lambe, 1915](#); [Dodson, Forster & Sampson, 2012](#)). The older members of the centrosaurine clade exhibited larger supraorbital horns and a pronounced naris ([Kirkland & Deblieux, 2010](#); [Sampson et al., 2013](#); [Lund, Sampson & Loewen, 2016](#); [Dalman et al., 2020](#)) exhibiting larger supraorbital horns and a pronounced naris. However, later centrosaurines had reduced supraorbital horns and possessed shorter but more elaborate parieto-squamosal frills with a wide variety of spikes and horns, as well as large nasal horns and bosses ([Sampson, Ryan & Tanke, 1997](#); [Ryan & Russell, 2005](#); [Hieronymus et al., 2009](#); [Fiorillo & Tykoski, 2012](#)). By contrast, chasmosaurines are characterized by generally taller frills with less elaborate epoccipitals and larger supraorbital horns in comparison to their nasal horns ([Dodson, Forster & Sampson, 2012](#)), but exceptions to these do exist ([Sampson et al., 2010](#); [Brown & Henderson, 2015](#); [Mallon et al., 2016](#)).

The function and evolutionary drivers of ceratopsian horns and frills have long been a matter of debate. Historical theories include antipredator defense ([Bakker, 1986](#);

Happ, 2008) and anchorage for additional jaw musculature attached to the frill (*Haas, 1955*). However, since the 1970s, their horns and frills have been hypothesized as sexually selected traits like modern horned animals (*Farlow & Dodson, 1975*), with more recently debated hypotheses including interspecific recognition (*Padian & Horner, 2011; Knell & Sampson, 2011; Hone & Naish, 2013*), socio-sexual display (*Hone, Naish & Cuthill, 2011; Knapp, Knell & Hone, 2021*), and intraspecific combat (*Farke, 2004; Farke, Wolff & Tanke, 2009; Hieronymus et al., 2009*). The latter hypothesis has fossil evidence in the form of bone lesions and traumatic fenestrae on the squamosal of *Triceratops* (*Farke, Wolff & Tanke, 2009; D'Anastasio et al., 2022*), indicating that at least some ceratopsian taxa regularly used their horns for intraspecific combat. The ready preservation of ceratopsian skulls make them an ideal clade to test the theory of intraspecific competition and varying combat styles being a powerful evolutionary driver of their diverse cranial weaponry like those of modern analogous animals (*Geist, 1966; Bro-Jørgensen, 2007; Metz et al., 2018; Vander Linden & Dumont, 2019*).

Hypotheses

Despite fossil evidence of intraspecific combat in certain ceratopsian taxa, there have been no biomechanical studies to ascertain the effectiveness of specific combat styles for this clade. While analogies to modern animals have been made (*Farlow & Dodson, 1975; Hieronymus et al., 2009*), such hypotheses do not confirm that the structures of extinct animals would perform the same function as extant ones (*Farke, 2014*). As such, there is a notable knowledge gap in which the biomechanics of ceratopsian cranial weaponry is not well understood.

Finite element analysis (FEA) is a computational method of calculating the patterns of stress and strain placed on structural components under loading (*Richmond et al., 2005; Ross, 2005*). Since its inception, it has become a popular means of investigating biomechanics, with various studies investigating the mechanical function of anatomical features in both extinct (*Rayfield, 2005; Klinkhamer et al., 2019; Ballell & Ferrón, 2021; Qin et al., 2023; Rowe & Rayfield, 2025*) and extant (*McCullough, Tobalske & Emlen, 2014; Nganvongpanit et al., 2017; Mitchell et al., 2025*) animals, making this an ideal means of analyzing ceratopsian horn function. In this study, we used 3D FEA to quantify the biomechanical performance of ceratopsian horns and test the following hypotheses:

1. The skulls of late-diverging, horned ceratopsid taxa are stronger under simulated combat stress loads than hornless, early-diverging outgroups. This will evaluate if the overall shapes of ceratopsid skulls evolved to accommodate intraspecific combat behaviors.
2. The skulls and horn morphotypes of different ceratopsids are better suited for accommodating stresses correlating with different combat styles, with centrosaurines being stronger under stabbing-related loads and chasmosaurines under wrestling-related ones. This will test whether the differing skull and horn morphologies between these two clades may represent adaptations towards accommodating the loads imposed by different combat behaviors.

Table 1 List of specimens included in this study. Table includes specimen numbers, mass estimates, estimated “realistic” forces in newtons based on the method of *Klinkhamer et al. (2019)*, size-corrected force values based on surface areas and cross multiplying with the force and surface of the CosmoCaxia *Triceratops*, and element count for each tetrahedral mesh.

Species	Specimen number	Mass estimate (kg)	Estimated “In-Life” forces (Newtons)	“Size-Corrected” forces (Newtons)	Element count
<i>Psittacosaurus lujiatunensis</i>	IVPP V12617	20	600	3,426	4,612,961
<i>Protoceratops andrewsi</i>	NHMW-GEO 2015/0404/0001	83	2,490	12,782	1,702,174
<i>Centrosaurus apertus</i>	USNM 8897	2,500	75,000	40,254	2,005,008
<i>Spiclypeus shipporum</i>	NHMW-GEO-2021/0006/0001 (Based on CMN 57081)	3,500	105,000	99,593	1,958,602
<i>Triceratops horridus</i>	USNM V2100	5,216	156,480	123,631	3,635,581
	USNM V2124 (Composite: USNM V2580)				
<i>Triceratops horridus</i>	MCFO-0506	8,000	240,000	240,000	2,035,076

Consideration of the results, and how they differ between taxa across ceratopsian phylogeny, will be used to evaluate the hypothesis that adaptations to different combat styles was an evolutionary driver of the morphological variance seen in horned dinosaurs.

MATERIALS AND METHODS

Specimen acquisition

Surface scans from six specimens of ceratopsian skulls belonging to five taxa (Table 1; Table S1) were chosen based on availability, model quality, and experimental repeatability. Two specimens belong to *Triceratops horridus* (Marsh, 1889), with one from a scan on Sketchfab of a skull currently in CosmoCaxa (Sketchfab, <https://sketchfab.com/3d-models/triceratops-2e8eacd4bf4943c7bddbd61abdd02f56>), and another based on surface scan data on the specimens Smithsonian National Museum of Natural History, Washington D.C., United States (USNM) 2100 and 2124 provided by the USNM (Smithsonian Institution, <http://n2t.net/ark:/65665/33a0d8fbe-d3d6-4c5e-9817-99a45cf5bc07>). Additionally, surface scans of the complete *Centrosaurus apertus* (Lambe, 1904) skull specimen USNM 8897 were acquired with permission from the USNM (Smithsonian Institution, <http://n2t.net/ark:/65665/3815f2a37-bffb-4053-92aa-1f732db93a5d>), which presents an ideal representation for most centrosaurines that exhibit similarly large nasal horns (Dodson, Forster & Sampson, 2012). A surface scan of *Spiclypeus shipporum* based on the cast NHMW-GEO-2021/0006/0001, which in turn is based on the specimen CMN 57081, was acquired from Sketchfab (Sketchfab, <https://sketchfab.com/3d-models/spiclypeus-fossil-fcf4e769772743518a160b8274a9bfc8>), which consists of a complete skull with a notable extra fenestra on the left squamosal which may be a pathology acquired from combat or disease (Mallon et al., 2016). This specimen makes for an ideal representative of another branch of chasmosaurines that include *Spiclypeus* and *Kosmoceras* (Sampson et al., 2010), which are distinguished for their outward curving supraorbital horns compared to the straighter horns of *Triceratops*, and a chance to investigate how diverse fighting styles were in chasmosaurines. For earlier ceratopsians, a model based on surface scans of *Protoceratops andrewsi* (Granger, Gregory & Berkey, 1923) specimen NHMW-GEO

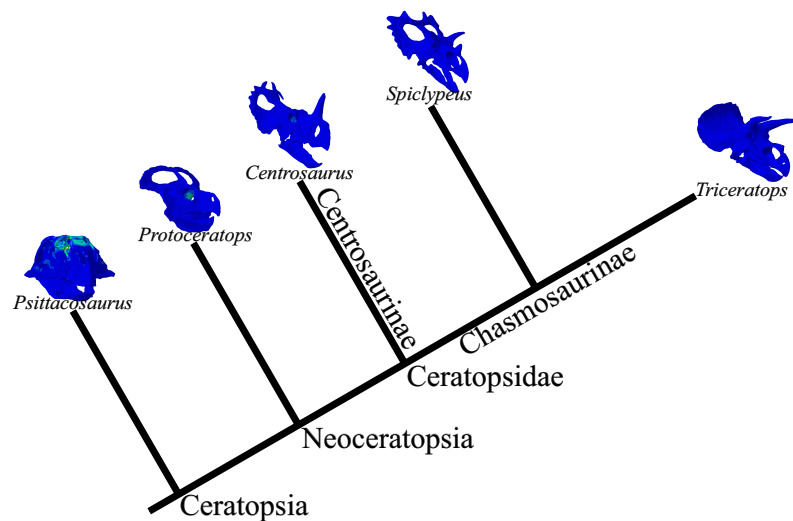


Figure 1 Simple cladogram showing the phylogenetic position of the five ceratopsians used in this study. Each of the five ceratopsian skulls is positioned in a very simplified family tree to demonstrate their general phylogenetic relationship. *Psittacosaurus* is the most early-derived, *Protoceratops* is within Neoceratopsia, *Centrosaurus* is within Centrosaurinae, and *Spiclypeus* and *Triceratops* are within Chasmosaurinae. 3D model credits: *Psittacosaurus* (David Button, Laura Porro, Stephan Lautenschlager, Marc Jones, Paul Barrett; <https://creativecommons.org/licenses/by/4.0/>), *Protoceratops* (Clara and Viola Winkler; <https://creativecommons.org/licenses/by-nc/4.0/>), *Centrosaurus* (Courtesy of the Smithsonian Institution), *Spiclypeus* (Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>), USNM *Triceratops* (Courtesy of the Smithsonian Institution). Copyright: Smithsonian Institution.

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2015/0404/0001 in Vienna (Printables, <https://www.printables.com/model/973084-protoceratops-andrewsi-nhmw-geo-201504040001>) was acquired and a 3D model of a *Psittacosaurus lujiatunensis* skull based on the specimen IVPP V12617 (Taylor et al., 2017) and modified (Button et al., 2023) was provided by Dr. David Button (https://figshare.com/articles/dataset/Supplementary_data_for_Button_et_al_Multiple_pathways_to_herbivory_underpinned_deep_divergences_in_ornithischian_evolution/21750494?file=38593874). All five taxa present solid baselines for different portions of the ceratopsian family tree (Fig. 1) and an opportunity to investigate if and how combat styles varied throughout their evolution. While the use of surface scans rather than CT scans has its share of pros and cons (Fahlke & Autenrieth, 2016; Lautenschlager, 2016; Rowe & Rayfield, 2022), their more ready availability (Rowe & Rayfield, 2024) and the difficulty of CT scanning ceratopsid skulls due to their size (Dodson, Forster & Sampson, 2012) makes this the most viable option.

Retrodeformation

While all six skulls were reasonably complete, each of them exhibited some degree of taphonomic deformation, pathologies, or general unrefined patches in the model itself, as was the case with the CosmoCaxia *Triceratops*. Because of this, each skull required some degree of retrodeformation to repair these deformations and restore their original anatomical condition (Figs. S1, S2A) (Herbst et al., 2022; Clark, Jenkins & Brodersen, 2023).

NHMW-GEO 2015/0404/0001 and IVPP V12617 only required a simple run through the symmetrize tool in Blender 3.2.1 to repair taphonomic deformation. By contrast, the scan of NHMW-GEO-2021/0006/0001 (Based on CMN 57081) required the sculpting of a basic sphere and the Boolean Union modifier in Blender 3.2.1 to fill in the pathology on its squamosal ([Herbst et al., 2022](#)) and the removal of the support stands on the model. The CosmoCaxia *Triceratops* scan required the “symmetrize” tool as well as the smooth and scrape tools, dissolving vertices that resulted in jagged edges on the back of the frill. The USNM V 2100 and USNM V 2124 scans required the combination of the former (the upper portion of the skull) and the latter (the lower jaw), and the opening of the orbital bones as the original scan had them filled in. Finally, the scan of USNM 8897 required a similar combination of the skull and lower jaw and removal of the support stands. After initial retrodeformation in Blender, each model was placed in Geomagic 2021 (Oqton, Ghent, Belgium) and went through the “Mesh Doctor” tool, which fixed any remaining flaws ([Fig. S1](#)).

Tetrahedral mesh creation and material properties

Each skull model was imported into Hypermesh (2022 version, Altair Engineering, Troy, MI, USA) to create tetrahedral meshes for FEA ([Fig. S2B](#)). The polygon count for each mesh ranges from 1,702,174 for the *Protoceratops* to 4,612,961 for the *Psittacosaurus*, with a conscious effort made to find a suitable balance between anatomical fidelity of the skull and an element count that results in reasonable FEA computational time. Each skull model and their elements were given the material properties of the mandibular bone of *Alligator mississippiensis* ([Zapata et al., 2010](#)) as a close approximation for dinosaur bone properties, with a Young’s Modulus of 20.49 Gigapascals (GPa) and a Poisson’s Ratio of 0.4.

In addition, horn-only models for *Triceratops*, *Centrosaurus*, and *Spiclypeus* were created using the separation tool in Blender 3.2.1 to compare the effects of keratin sheaths on stresses experienced on the horns, which has been noted in modern analogs ([Li et al., 2010](#); [Zhang et al., 2018](#); [Yang et al., 2022](#)). The horns were removed from the skull models using Blender’s separation tool, which created a hollow shape for all of them. The shapes were put into Geomagic Wrap 2021, where they were duplicated. Although cattle horn keratin has a width of 2.5 mm ([Li et al., 2010](#)), this was doubled to 5 mm to consider the larger mass of the horned ceratopsids. The shape was duplicated again for the bone core. The normals were flipped to properly combine the bone core and keratin sheath and bridge the gap between them. The bottom of the bone core was then filled. After completing the horn-only models in Geomagic 2021, the same tetrahedral process was used, with separate tetrameshes for the bone core and keratin sheaths. While the bone cores retained the same material properties as the complete skulls, the keratinous sheaths were given the properties of those of cattle horns due to them being the closest analog to ceratopsian horns anatomically, with a Young’s Modulus of 2.3 GPa and a Poisson’s Ratio of 0.38 ([Li et al., 2010](#)). While rhinos are typically compared to ceratopsians as a modern analog, their horns are primarily composed of keratin with no bone core ([Hieronymus, Witmer & Ridgely, 2006](#)) and therefore does not make a viable template for FEA.

Table 2 Checklist of what specimens were tested for general anatomical axes stress simulations. Green check marks indicate they were tested, while red X's indicate they were not.

Species	Specimen #	Mediolateral	Longitudinal	Vertical
<i>Psittacosaurus lujiatunensis</i>	IVPP V12617	✓	✓	✓
<i>Protoceratops andrewsi</i>	NHMW-GEO 2015/0404/0001	✓	✓	✓
<i>Centrosaurus apertus</i>	USNM 8897	✓	✓	✓
<i>Spiclypeus shipporum</i>	NHMW-GEO-2021/0006/0001 (Based on CMN 57081)	✓	✓	✓
<i>Triceratops horridus</i>	USNM V2100 USNM V2124 (Composite: USNM V2580)	✓	✓	✓
<i>Triceratops horridus</i>	MCFO-0506	✓	✓	✓

Force calculations

We calculated forces to be applied as loads to the models in HyperMesh. The CosmoCaxia *Triceratops* was done first, with the force being calculated by multiplying mass by acceleration based on analogous studies on cervids (Klinkhamer *et al.*, 2019). A mass of 8,000 kg was used for an average sized *Triceratops* (Table 1) (Stein, 2019). Because no velocity or acceleration estimates for ceratopsian top speed were found, the deceleration provided in Klinkhamer of 30 ms^{-2} was used for the acceleration (Klinkhamer *et al.*, 2019), resulting in a force of 240,000 newtons for both horns. Tests with single horns utilized 120,000 newtons. While these forces may be imprecise, these are meant to compare the relative performance between models of different skulls, rather than drawing conclusions from absolute stress magnitudes. Consequently, these results should be robust to uncertainties in material properties and applied forces.

For the other five models, two calculation methods were used for forces (Table 1). The same $F = M \times A$ calculation was used for the other five models using the most recent and consistent average adult mass estimates for each taxon (Benson *et al.*, 2014; Stein, 2019; Campione & Evans, 2020) to give an unscaled, “in-life” force for each as a best guess of performance when the animal was alive. Some of these estimates, including the one used for the CosmoCaxia *Triceratops*, used the median of a wide range of estimates. The USNM *Triceratops* mass estimate was acquired by cross multiplying the mass estimate used for the CosmoCaxia specimen and the sizes of their respective skulls. Given that these specific individuals do not have exact mass estimates attached to them, these serve as baselines for further studies. The second scaled for differences in size among taxa by loading all models so that the ratio between total applied force: model surface area remained consistent between them (equal to that calculated for the CosmoCaxia *Triceratops*). By scaling applied forces in this way, comparison of FE results among these ‘size-corrected’ models will indicate differences in performance purely due to variance in shape, rather than size (Dumont, Grosse & Slater, 2009).

FEA test categories

Loads were placed on the skulls and horns of each model in accordance with a variety of combat situations, with constraints placed on 15 selected nodes around the foramen

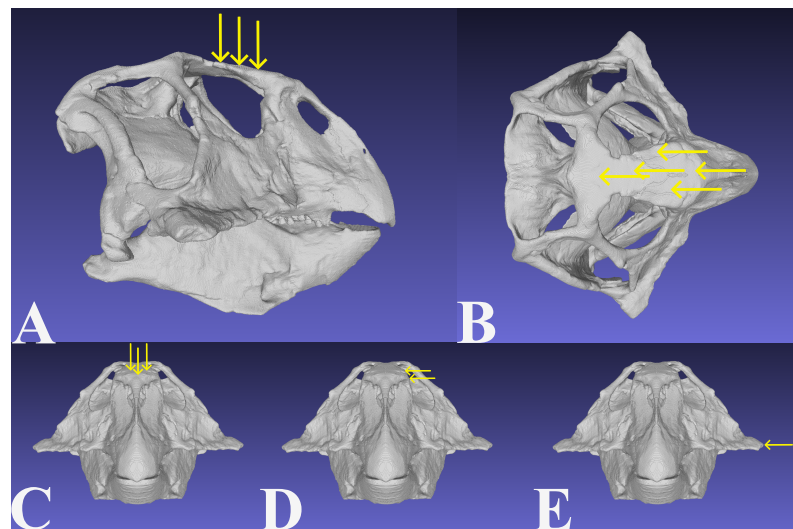


Figure 2 Visual graph of stress load directions and positions for *Psittacosaurus* combat behavior tests. Stress load directions and positions on the skull are represented by yellow arrows. The panels represent simulations for (A) vertical and (B) longitudinal axes, (C) ramming, (D) mediolateral axis, (E) and jugal horn stabbing. Certain simulations can also be translated for *Protoceratops*. 3D model credits: David Button, Laura Porro, Stephan Lautenschlager, Marc Jones, Paul Barrett; <https://creativecommons.org/licenses/by/4.0/>. Full-size DOI: 10.7717/peerj.21728/fig-2

magnum and three degrees of freedom. The first group of tests consisted of each model being loaded with a uniform load applied on the mediolateral, longitudinal, and vertical anatomical axes (Table 2, Figs. 2, 3). For *Psittacosaurus* and *Protoceratops*, their lack of horns meant those loads were placed on the roof of the skull and jugal horns. The CosmoCaxia *Triceratops* also had loads placed on the jugal horns to test if jugal horns became less relevant for combat in later ceratopsians. For the horn-only models, loads were distributed on the specific side of the horn, depending on the chosen axis, to compare stress results between bare bone cores and ones covered in keratinous sheaths. These analyses are not meant to simulate specific behaviors, but rather to compare the strength of different horn morphotypes against long-axis compression, mediolateral bending, and dorsal-ventral bending. This will help in understanding how differences in shape translate to differences in stress accommodation.

Regarding combat simulations, each complete skull model was run through various tests corresponding with general combat styles based on those from ruminants and suggested for ceratopsians (Farlow & Dodson, 1975; Molnar, 1977; Lundrigan, 1996; Farke, Wolff & Tanke, 2009; Vander Linden & Dumont, 2019) (Table 3, Figs. 2, 3). Stabbing and ramming simulations had loads distributed on the stabbing points of the horns and roof of the skull—frontal, prefrontal, and maxilla—respectively. *Psittacosaurus* specifically had one simulation testing the viability of using their pronounced jugal horns for stabbing (Molnar, 1977), which was also done for *Protoceratops* and *Triceratops* to test the viability on more derived ceratopsians. Wrestling loads were categorized as “static” wrestling, with all the loads distributed on the frontal bone between the supraorbital horns and “dynamic”

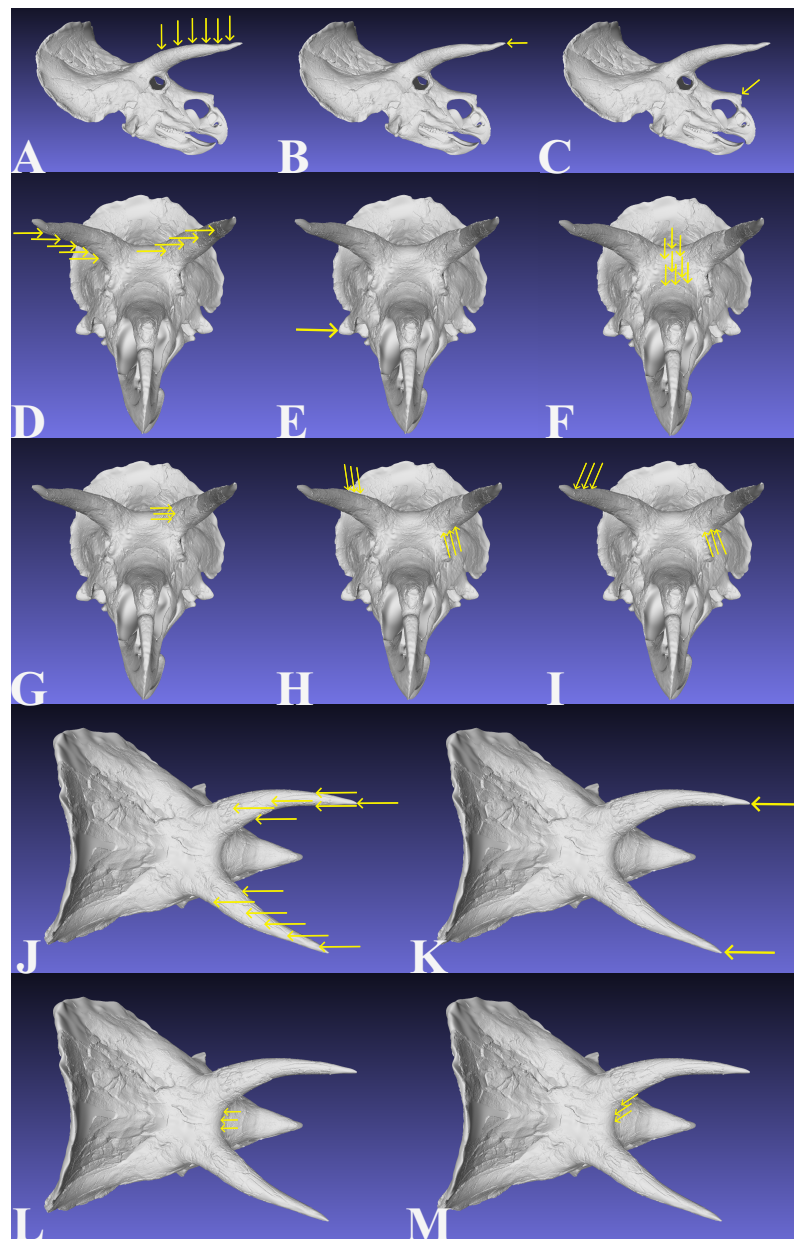


Figure 3 Visual graph of stress load directions and positions for *Triceratops* combat behavior tests. Stress load directions and positions on the skull are represented by yellow arrows. The panels represent simulations for (A) vertical axis, (B) single horn stabbing, (C) nasal stabbing, (D) mediolateral axis, (E) jugal horn stabbing, (F) ramming, (G) single horn contact, (H) full horn locking, (I) oblique horn locking, (J) longitudinal axis, (K) supraorbital horn stabbing, (L) “static” wrestling and (M) “dynamic” wrestling. Certain simulations can also be translated for *Centrosaurus* and *Spiclypeus*. 3D Model credit: Courtesy of the Smithsonian Institution. Copyright: Smithsonian Institution.

Full-size  DOI: [10.7717/peerj.21728/fig-3](https://doi.org/10.7717/peerj.21728/fig-3)

wrestling with the forces parallel to the length of the supraorbital horn. These were to quantify performances under each specific fighting style to test if different horn morphologies performed better than others under certain styles.

Table 3 Checklist of what specimens were tested for basic combat style stress simulations. Green check marks indicate they were tested, while red X's indicate they were not.

Species	Specimen #	Stabbing (jugal)	Stabbing (nasal)	Stabbing (supraorbital)	Ramming	Wrestling (static)	Wrestling (dynamic)
<i>Psittacosaurus lujiatunensis</i>	IVPP V12617	✓	✗	✗	✓	✗	✗
<i>Protoceratops andrewsi</i>	NHMW-GEO 2015/0404/0001	✓	✓	✗	✓	✗	✗
<i>Centrosaurus apertus</i>	USNM 8897	✗	✓	✗	✓	✗	✗
<i>Spiclypeus shipporum</i>	NHMW-GEO-2021/0006/0001 (Based on CMN 57081)	✗	✓	✓	✓	✓	✓
<i>Triceratops horridus</i>	USNM V2100 USNM V2124 (Composite: USNM V2580)	✗	✓	✓	✓	✓	✓
<i>Triceratops horridus</i>	MCFO-0506	✓	✗	✓	✓	✓	✓

Table 4 Checklist of what specimens were tested for stress simulations based on Farke's (2004) horn locking positions. Green check marks indicate they were tested, while red X's indicate they were not.

Species	Specimen #	Single horn contact	Full horn locking	Oblique horn locking
<i>Psittacosaurus lujiatunensis</i>	IVPP V12617	✗	✗	✗
<i>Protoceratops andrewsi</i>	NHMW-GEO 2015/0404/0001	✗	✗	✗
<i>Centrosaurus apertus</i>	USNM 8897	✓	✗	✗
<i>Spiclypeus shipporum</i>	NHMW-GEO-2021/0006/0001 (Based on CMN 57081)	✓	✓	✓
<i>Triceratops horridus</i>	USNM V2100 USNM V2124 (Composite: USNM V2580)	✓	✓	✓
<i>Triceratops horridus</i>	MCFO-0506	✓	✓	✓

Finally, horned taxa in this study had loads placed on their horns and skulls corresponding with potential horn locking positions proposed for ceratopsians (Table 4, Figs. 3, S3): single horn contact with one horn on each combatant making contact at the stem, full horn locking with contact on both horns roughly a quarter of the way up their length, and oblique horn locking with contact on the stem of one horn and near the stabbing point of the other (Farke, 2004). These were to compare performances between horn morphotypes in pre-determined types of horn locking. All tests were operated under the assumption that the skulls will perform better in “species typical” loads (Lundrigan, 1996; McCullough, 2014; McCullough, Tobalske & Emlen, 2014; Emberts, Hwang & Wiens, 2021).

Model solving and results comparison

All these simulations were exported as INP files and run through Abaqus (2022 and 2024 versions, Dassault), with von Mises stresses plotted as colored contour maps to visualize stress distribution. Field reports were written for von Mises stress results and element volumes. The top 10% of the stress values were removed to account for common FEA artifacts, as the highest stresses are typically on the constraint points and are

methodological artifacts that require exclusion ([Walmsley et al., 2013](#)). The mesh-weighted arithmetic mean (MWAM) was then calculated using a modified R code from [Ballell & Ferrón \(2021\)](#) to account for differences in element size within and among this study's models. While small elements may concentrate high stresses, re-standardizing them with this method minimizes these artifacts and allows for comparisons between different models that have different distributions of element sizes ([Marcé Nogué et al., 2016](#); [Ballell & Ferrón, 2021](#)). Furthermore, scaled element stresses were calculated using a modified R code from [Tseng \(2009\)](#), although scaling by mean values, rather than the median, for better comparisons with the MWAM results. These were then used to create bar plots in R to demonstrate stress values across the six specimens for the same simulations.

RESULTS

Anatomical axis stress tests

Results across these taxa showed notable differences in stress magnitudes between the “in-life” and “size-corrected” runs, which demonstrate the necessity of standardizing for size when comparing performance differences due to morphology across a clade.

Psittacosaurus

The forces on the frontal bone—where the supraorbital horns of more derived chasmosaurines would be—resulted in stresses primarily distributed across the interior of the frontal, nasal, and orbital bones when the forces were facing in the mediolateral, longitudinal, and vertical axes. The highest values were concentrated in the parietal and interior of the frontal. The frontal experienced the highest amount of stress in the vertical axis test whereas the nasal held that distinction in the mediolateral test. The MWAM and scaled elemental stress values provide interesting trends as well. The longitudinal axis test resulted in lower stresses and a lower MWAM value overall than the other two axes ([Fig. 4](#)).

Protoceratops

The *Protoceratops* skull had similar visual trends on the contour plots to *Psittacosaurus*, with stress distribution for this taxon being concentrated almost exclusively to the frontal and parietal region regardless of what anatomical axis the forces were facing. The MWAM and scaled elemental stress values exhibited a similar trend, with the three axes showing very low stress values. However, the longitudinal axis had slightly lower values than the other two ([Fig. 5](#)).

Centrosaurus

All three axes demonstrated stress distributions across the skull, with the longitudinal and vertical tests having moderate stresses at the top of the prefrontal and nasal bones as well as the maxilla, premaxilla, naris, and base of the nasal horn. However, the mediolateral stress test experienced higher magnitudes, with the highest values concentrated on the lacrimal, nasal, and base of the nasal horn. This was corroborated by the MWAM and scaled elemental stress plots, with the mediolateral axis having considerably higher values in both plots ([Fig. 6](#)).

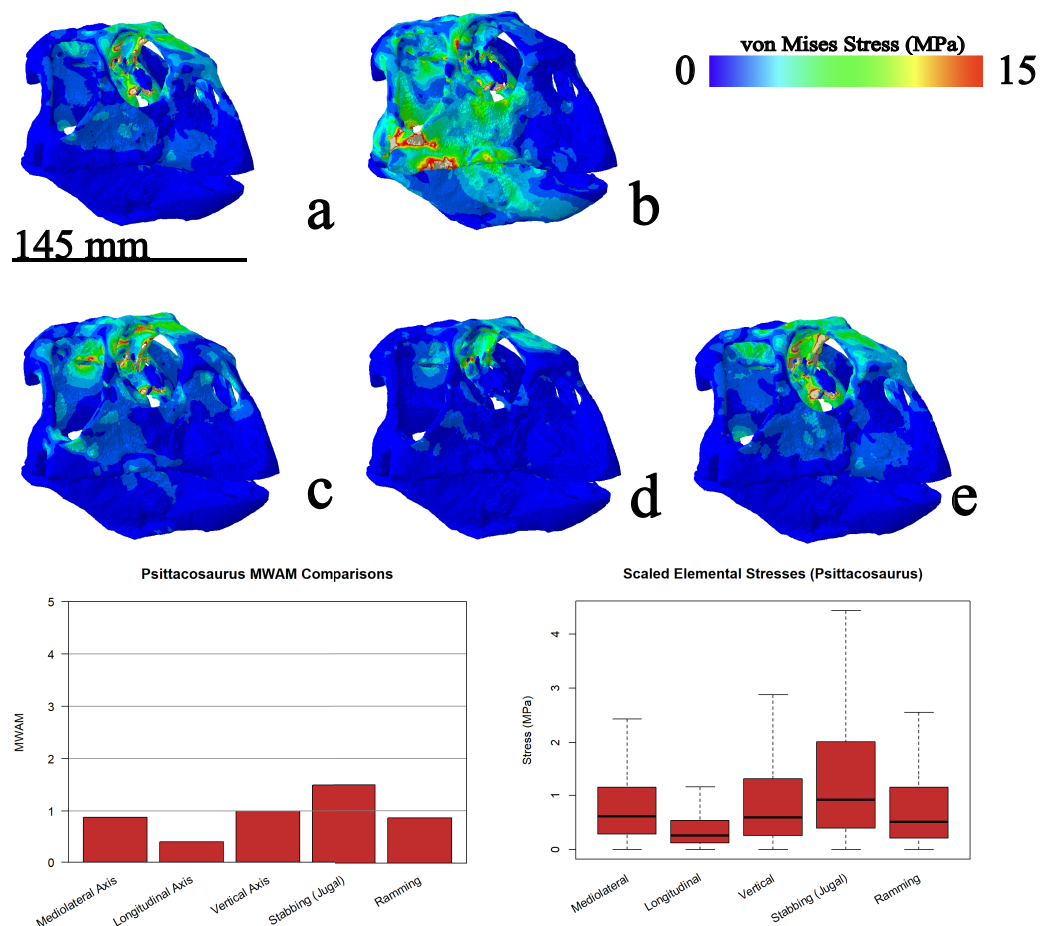


Figure 4 Von Mises stress distributions on the cranium of *Psittacosaurus lujiatunensis*, mesh-weighted arithmetic mean bar plots, and scaled elemental stress boxplots for various combat simulations. von Mises stress distribution on the cranium of *Psittacosaurus lujiatunensis* (IVPP V12617) for (A) ramming and (B) jugal horn stabbing simulations, as well as (C) mediolateral (D) longitudinal, and (E) vertical axes. Gray areas represent von Mises levels exceeding 15 MPa. 3D model credits: David Button, Laura Porro, Stephan Lautenschlager, Marc Jones, Paul Barrett; <https://creativecommons.org/licenses/by/4.0/>. Full-size DOI: 10.7717/peerj.21728/fig-4

Spiclypeus

In all three anatomical axes, the stress was distributed across the entire length of the supraorbital horns and the rim of the orbital bones, with the highest concentrations being on the stems. The mediolateral and vertical tests had stress hotspots on the top of the stem, while the longitudinal test had hotspots on the front facing side. The MWAM and scaled elemental stress plots showed similar values for all three axes, with the longitudinal axis being slightly lower (Fig. 7).

Triceratops

Both skulls showed similar trends when comparing anatomical axis stress values. They demonstrated moderate stress values distributed across the entire length of the horn in the mediolateral and vertical axis tests, and lower values along the horns in the longitudinal

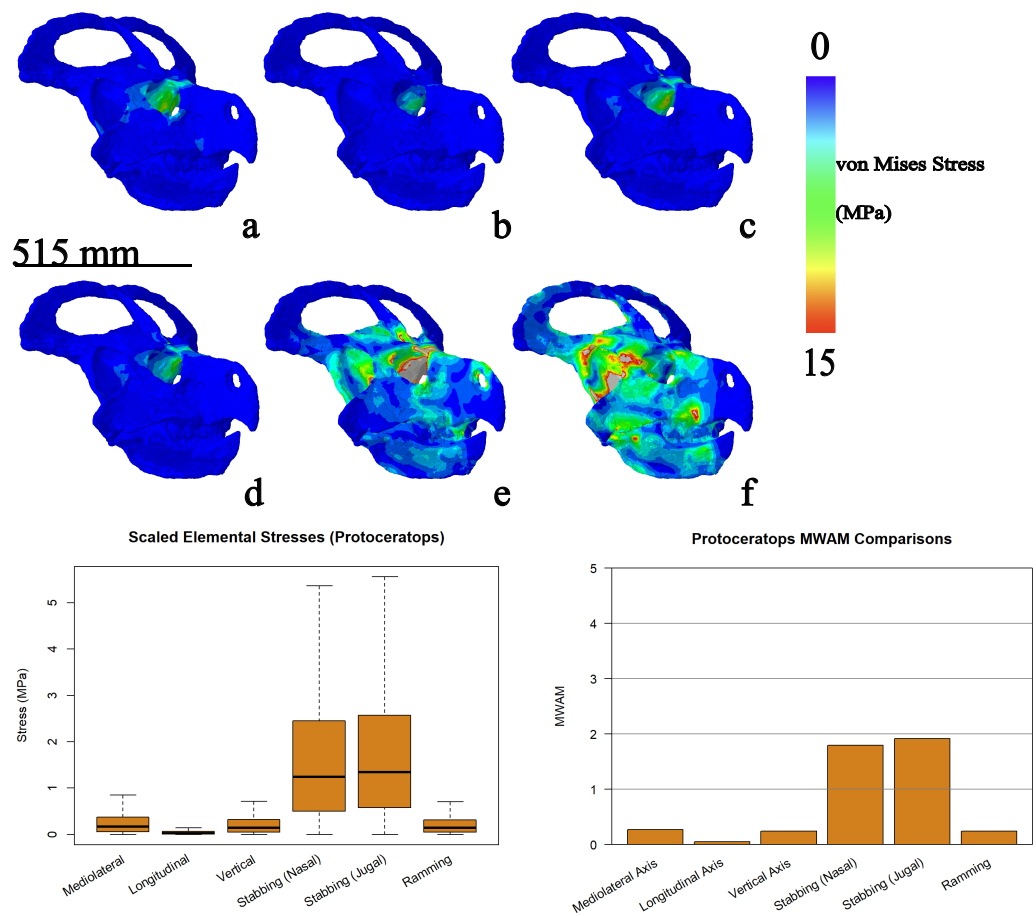


Figure 5 Von Mises stress distributions on the cranium of *Protoceratops andrewsi*, mesh-Weighted arithmetic mean bar plots, and scaled elemental stress boxplots for various combat simulations. von Mises stress distribution on the cranium of *Protoceratops andrewsi* (NHMW-GEO 2015/0404/0001) for (A) the mediolateral, (B) longitudinal and (C) vertical stresses, as well as (D) ramming, (E) nasal stabbing, (F) and jugal horn stabbing behaviors. Gray areas represent von Mises levels exceeding 15 MPa. 3D model credits: Clara and Viola Winkler; <https://creativecommons.org/licenses/by-nc/4.0/>.

Full-size DOI: 10.7717/peerj.21728/fig-5

test. This trend remained consistent in both MWAM and scaled element stress plots, with the longitudinal axis showing notably lower values in both plots than the other two (Figs. 8, 9).

Size-corrected comparison

The stress magnitudes for size corrected comparisons resulted in an increase in magnitude for *Psittacosaurus* and *Protoceratops*, and a decrease for the *Centrosaurus*, *Spiclypeus*, and USNM *Triceratops* (Table 1; Fig. 10). When all six specimens were corrected for size, the MWAM and scaled element stress plots demonstrated interesting trends between the taxa (Fig. 11). The *Psittacosaurus* and *Centrosaurus* had consistently higher values in both plots for each axis. *Psittacosaurus* had higher values than the *Centrosaurus* in the vertical axis test. Additionally, the *Centrosaurus* had considerably higher values for the mediolateral axis than the other two. The *Protoceratops*, *Spiclypeus*,

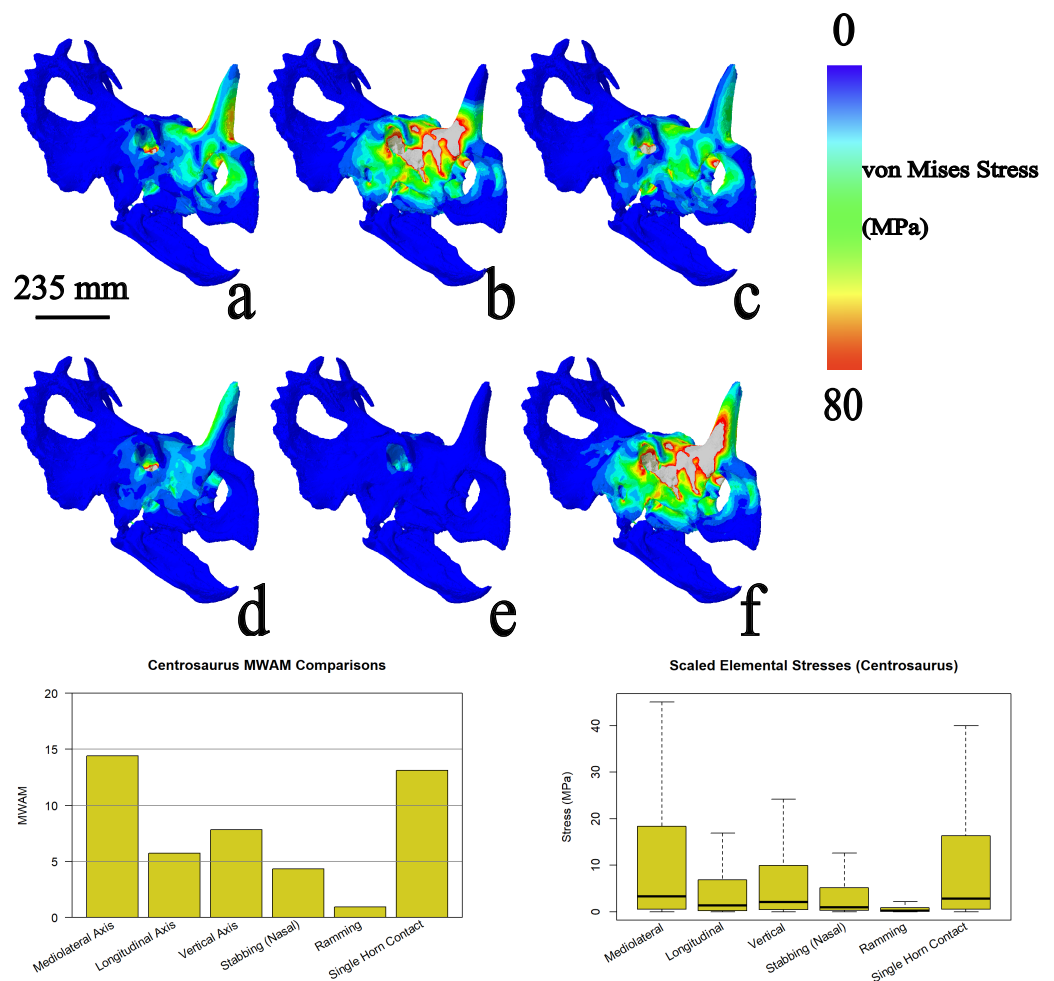


Figure 6 Von Mises stress distributions on the cranium of *Centrosaurus apertus*, mesh-weighted arithmetic mean bar plots, and scaled elemental stress boxplots for various combat simulations. von Mises stress distribution on the cranium of *Centrosaurus apertus* (USNM 8897) for (A) the longitudinal, (B) mediolateral and (C) vertical stresses, as well as (D) nasal stabbing and (E) ramming behaviors, (F) and the single horn contact position. Gray areas represent von Mises levels exceeding 80 MPa. 3D model credits: Courtesy of the Smithsonian Institution. Copyright: Smithsonian Institution for panels A–F. [Full-size DOI: 10.7717/peerj.21728/fig-6](https://doi.org/10.7717/peerj.21728/fig-6)

and both *Triceratops* had lower values across the three axes. All five taxa show the lowest values in the longitudinal tests.

Basic combat tests

Psittacosaurus

The *Psittacosaurus* ramming simulation demonstrated stress distributions very similar to those of the vertical axis test, with moderate values concentrated across the frontal, nasal, and orbital bones and the highest values on the interior of the parietal and frontal bones. The jugal stabbing simulation demonstrated very high values across the stem of the jugal horn. In the MWAM and scaled element plots, the ramming values demonstrated very

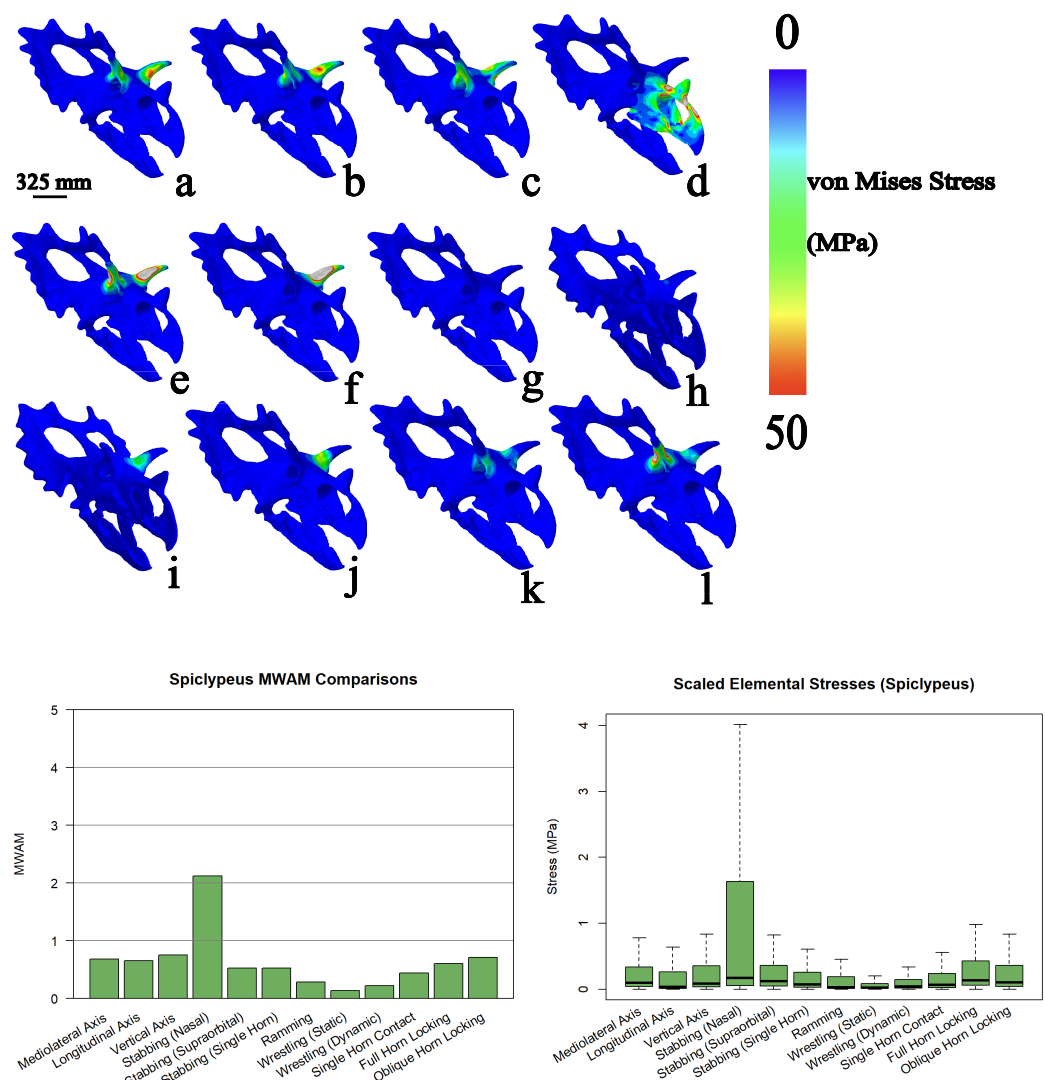


Figure 7 Von Mises stress distributions on the cranium of *Spiclypeus shipporum*, mesh-weighted arithmetic mean bar plots, and scaled elemental stress boxplots for various combat simulations. von Mises stress distribution on the cranium of *Spiclypeus shipporum* NHMW-GEO-2021/0006/0001 (Based on CMN 57081) for (A) the longitudinal, (B) mediolateral and (C) vertical stresses, (D) the nasal and (E, F) supraorbital stabbing, (G) ramming, (H) “static” and (I) “dynamic” wrestling behaviors, (J) the single horn contact, (K) full horn locking and (L) oblique horn locking positions. Gray areas represent von Mises levels exceeding 50 MPa. 3D model credits: Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>. Full-size DOI: 10.7717/peerj.21728/fig-7

similar values to those of the mediolateral and vertical axis test while the jugal stab resulted in considerably higher values in both plots (Fig. 4).

Protoceratops

For *Protoceratops*, the ramming simulation also demonstrated similarities to the vertical axis test, with moderate values on the frontal and parietal bones. However, when the force was concentrated on the naris, moderate stress values were demonstrated throughout the

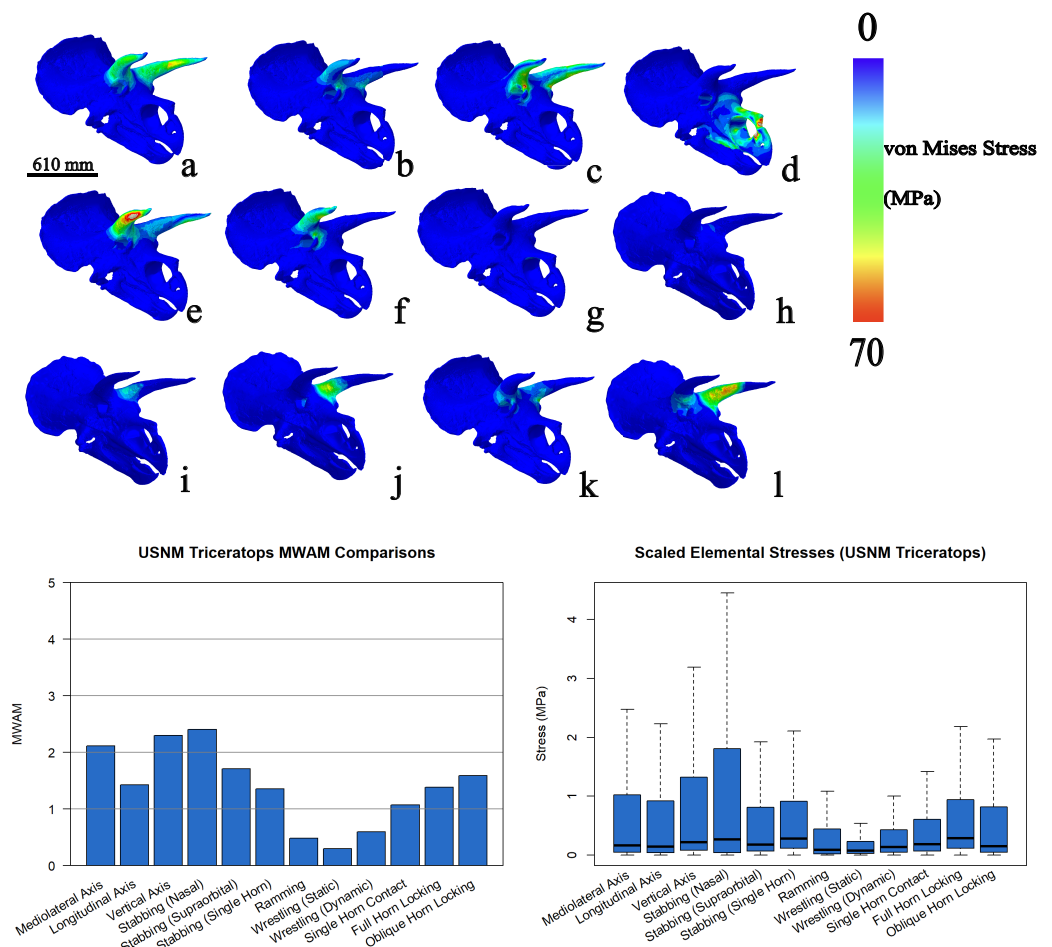


Figure 8 Von Mises stress distributions on the cranium of the USNM *Triceratops horridus*, mesh-weighted arithmetic mean bar plots, and scaled elemental stress boxplots for various combat simulations. von Mises stress distribution on the cranium of *Triceratops horridus* (USNM V2100 and USNM V2124) for (A) the mediolateral, (B) longitudinal and (C) vertical axes, (D) nasal, (E, F) and supraorbital stabbing, (G) ramming, (H) “static” and (I) “dynamic” wrestling behaviors, and (J) the single horn contact, (K) full horn locking and (L) oblique horn locking positions. Gray areas represent von Mises levels exceeding 70 MPa. 3D model credits: Courtesy of the Smithsonian Institution. Copyright: Smithsonian Institution for panels A–L.

Full-size [DOI: 10.7717/peerj.21728/fig-8](https://doi.org/10.7717/peerj.21728/fig-8)

skull with the frontal and parietal having much higher magnitudes. When the jugal horns were tested, high stress values were concentrated on the quadrate and squamosal. The MWAM and scaled elemental stress plots demonstrated higher values in both stabbing simulations compared to ramming, correlating with the contour plots (Fig. 5).

Centrosaurus

Centrosaurus demonstrated moderate stress values across the length of the nasal horn in the nasal stabbing simulation, with lower values across the maxilla, nasal and prefrontal bones. Meanwhile, exceptionally low stresses were seen on the interior of the orbital bones in the ramming test. In both MWAM and scaled element stress plots, the nasal stabbing test accordingly showed comparatively higher values than the ramming test (Fig. 6).

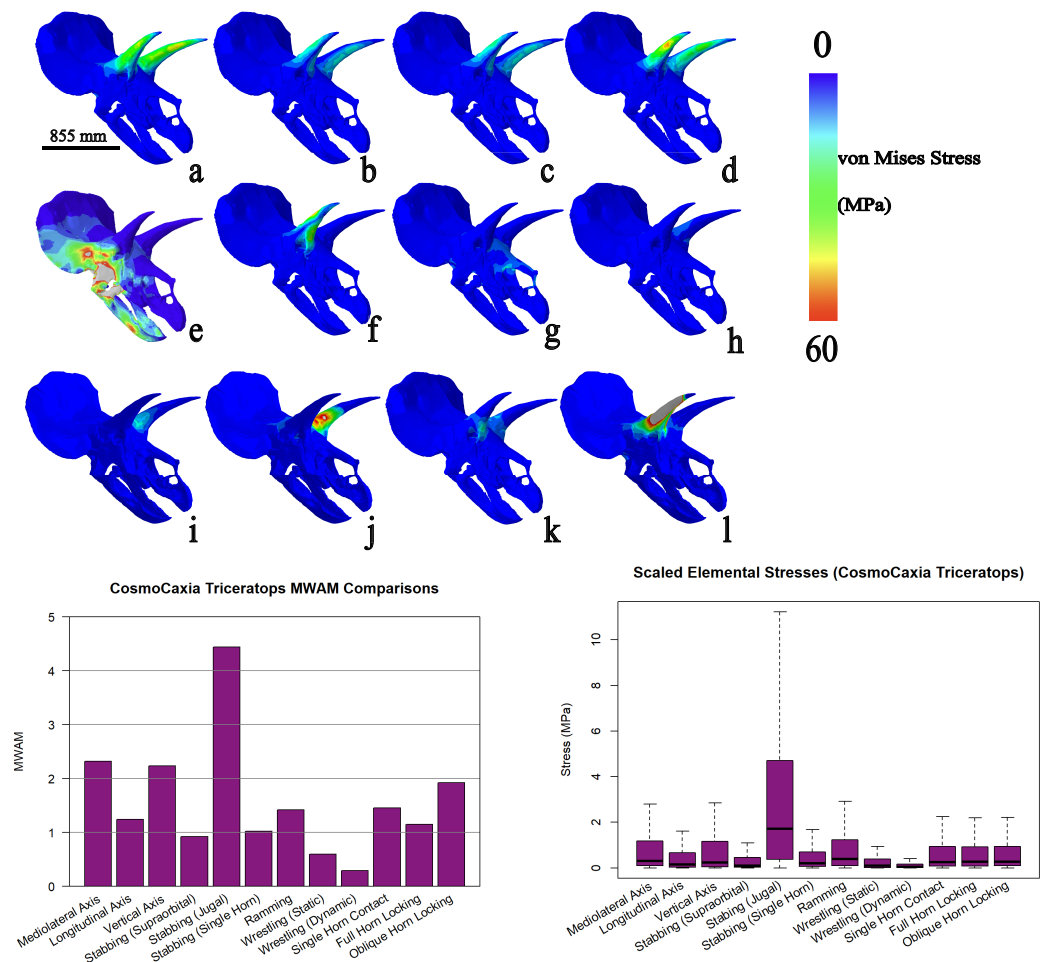


Figure 9 Von Mises stress distributions on the cranium of the *Cosmocaxia Triceratops horridus*, mesh-weighted arithmetic mean bar plots, and scaled elemental stress boxplots for various combat simulations. von Mises stress distribution on the cranium of *Triceratops horridus* (MCFO-0506) for (A) the medirolateral, (B) longitudinal and (C) vertical stresses, the (D) supraorbital, (E) jugal, (F) and single horn stabbing, (G) ramming, (H) “static” and (I) “dynamic” wrestling behaviors, (J) and the single horn contact, (K) full horn locking and (L) oblique horn locking positions. Gray areas represent von Mises levels exceeding 60 MPa. 3D model credits: Tavernier Amaury; <https://creativecommons.org/licenses/by-nc-sa/4.0/>. Full-size DOI: 10.7717/peerj.21728/fig-9

Spiclypeus

The nasal stabbing test for *Spiclypeus* demonstrated moderate stress values on the naris, with the highest values concentrated at the stem of the nasal horn and the naris. For supraorbital horn stabbing tests, high stress values were concentrated across the catching arch of the horns. Ramming simulations showed similarly low stresses to the *Centrosaurus* while wrestling tests showed moderate stresses on the stem of the horns. In the MWAM and scaled element stress tests, the nasal stab test had considerably higher values than the supraorbital tests, while ramming and wrestling showed very low values (Fig. 7).

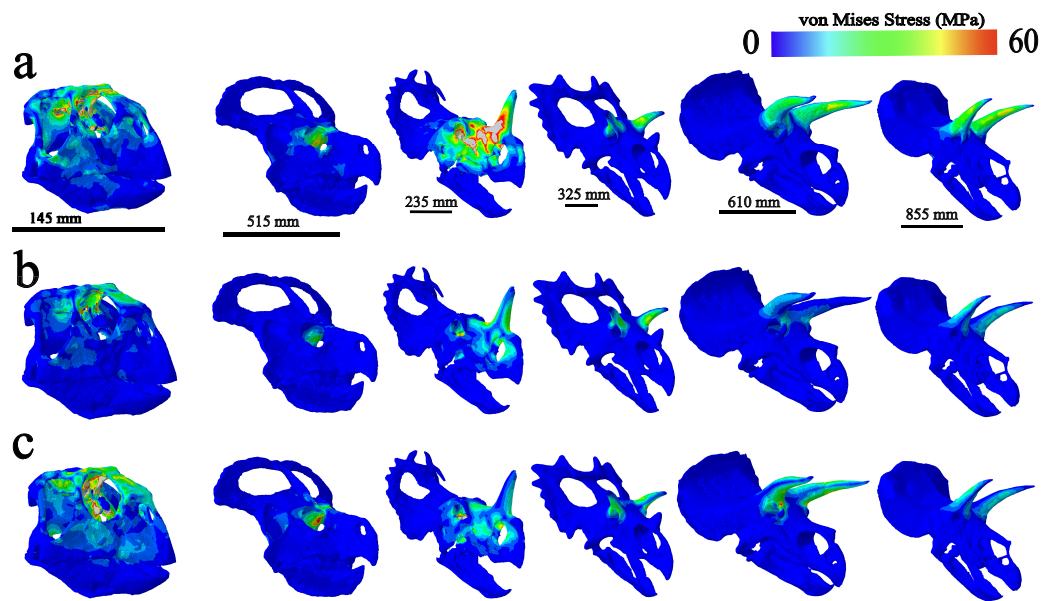


Figure 10 Von Mises stress contour plots for all six ceratopsian skull specimens after correcting force magnitudes for size and comparing stress distributions in different anatomical axis tests. Skull images are organized by axes, with (A) the top row for mediolateral, (B) the middle for longitudinal, (C) and the bottom for vertical. Gray areas represent von Mises levels exceeding 60 MPa. 3D model credits: *Psittacosaurus* (David Button, Laura Porro, Stephan Lautenschlager, Marc Jones, Paul Barrett; <https://creativecommons.org/licenses/by/4.0/>), *Protoceratops* (Clara and Viola Winkler; <https://creativecommons.org/licenses/by-nc/4.0/>), *Centrosaurus* (Courtesy of the Smithsonian Institution), *Spiclypeus* (Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>), USNM *Triceratops* (Courtesy of the Smithsonian Institution). *Cosmocaxia Triceratops* (Tavernier Amaury; <https://creativecommons.org/licenses/by-nc-sa/4.0/>). Copyright: Smithsonian Institution.

Full-size DOI: 10.7717/peerj.21728/fig-10

Triceratops

The USNM *Triceratops* was tested for nasal horn stabbing while the CosmoCaxia specimen was tested for jugal horn stabbing. The former showed moderate magnitudes across the naris with the highest values concentrated on the stem of the nasal horn. The latter demonstrated very high stress magnitudes across the entire jugal. Both specimens showed mainly moderate values on the supraorbital stabbing tests, with the highest magnitudes concentrated at the middle of the catching arch. The ramming test showed very low magnitudes on the rim of the nasal, while the wrestling tests had similarly low magnitudes on the stem of the horns. Supraorbital stabbing showed low values on the MWAM and scaled elemental stresses, as did ramming and wrestling tests. While the nasal and jugal horn stabbing tests had the highest values on both plots, the latter was the highest by a larger margin (Figs. 8, 9).

Size-corrected comparison

Size-corrected comparisons demonstrated interesting trends. For nasal stabbing, the *Protoceratops* demonstrated the highest values in both MWAM and scaled element stresses

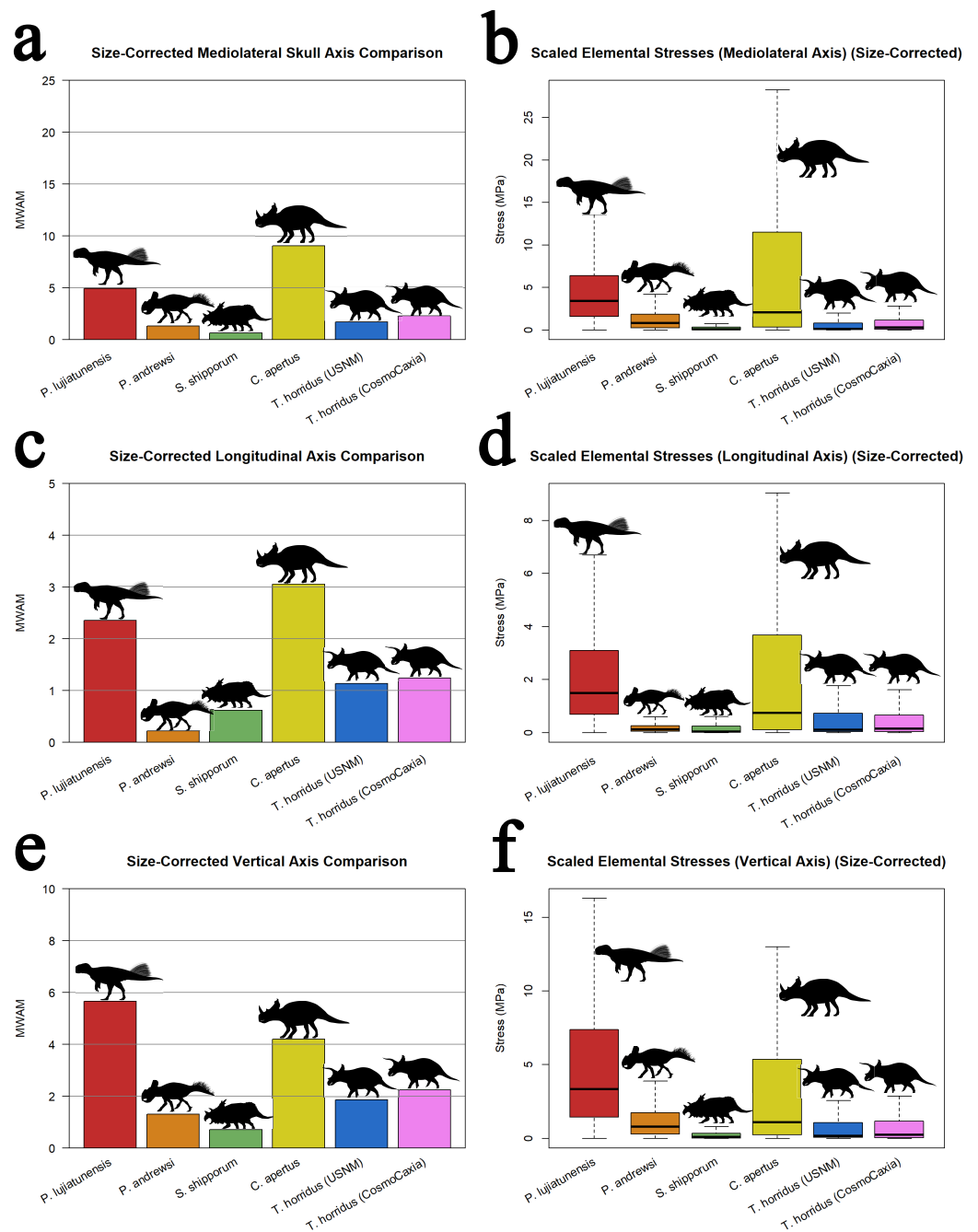


Figure 11 Mesh-weighted arithmetic mean (MWAM) bar plots and scaled element stress boxplots comparing the six ceratopsian specimens in size-corrected anatomical stress tests. (A, B) medio-lateral, (C, D) longitudinal, (E, F) vertical anatomical axes. Phylogenic credits go to Jagged Fang Designs (<https://creativecommons.org/licenses/by/4.0/>), Scott Hartman (<https://creativecommons.org/licenses/by/3.0/>), Andrew Farke (<https://creativecommons.org/licenses/by/3.0/>), Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>), and Matt Dempsey (<https://creativecommons.org/licenses/by/3.0/>). Full-size DOI: 10.7717/peerj.21728/fig-11

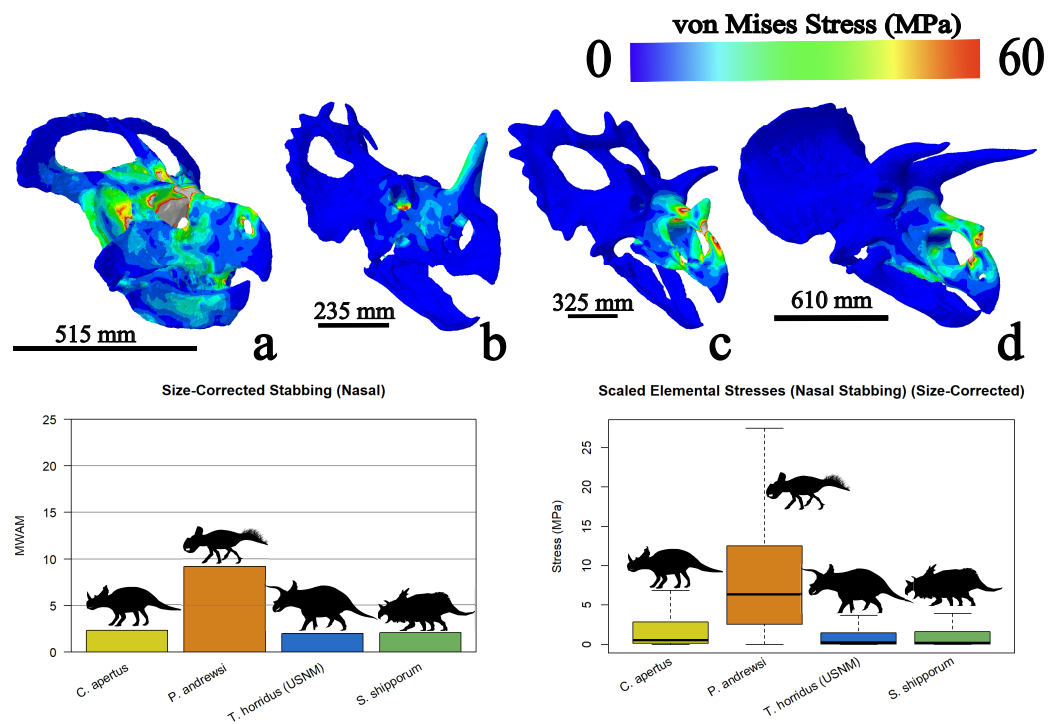


Figure 12 Comparisons of selected ceratopsian skulls in size-corrected nasal horn stabbing simulations, mesh-weighted arithmetic mean bar plots, and scaled elemental stress boxplots. Size-corrected von Mises stress distributions on the skulls of (A) *Protoceratops*, (B) *Centrosaurus*, (C) *Spiclypeus*, and (D) the USNM *Triceratops* from simulating stabbing behaviors with the nasal horn. Gray areas indicate von Mises levels exceeding 60 MPa. Phylopic credits go to Scott Hartman (<https://creativecommons.org/licenses/by/3.0/>), Andrew Farke (<https://creativecommons.org/licenses/by/3.0/>), Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>), and Matt Dempsey (<https://creativecommons.org/licenses/by/3.0/>). 3D model credits: *Protoceratops* (Clara and Viola Winkler; <https://creativecommons.org/licenses/by-nc/4.0/>), *Centrosaurus* (Courtesy of the Smithsonian Institution), *Spiclypeus* (Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>), USNM *Triceratops* (Courtesy of the Smithsonian Institution). Copyright: Smithsonian Institution for panels B and D.

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compared to its counterparts (Fig. 12), while it and *Psittacosaurus* had a comparatively small increase in jugal stabbing tests compared to *Triceratops* (Fig. 13). Conversely, while *Spiclypeus* had the highest stress concentrations in the contour plots, it demonstrated slightly lower values than *Triceratops* on the supraorbital stabbing plots (Fig. 14). In ramming simulations, the *Psittacosaurus* had much higher values on both plots than the other taxa (Fig. 15). Finally, in wrestling tests, the *Spiclypeus* and *Triceratops* skulls all had very low values, with the CosmoCaxia *Triceratops* having the highest values for static wrestling and the USNM *Triceratops* for dynamic wrestling (Fig. 16).

Farke horn locking positions

Centrosaurus

Due to the lack of supraorbital horns, *Centrosaurus* was only tested for single horn contact. Stress distributions were nearly identical to the mediolateral axis test, with the highest

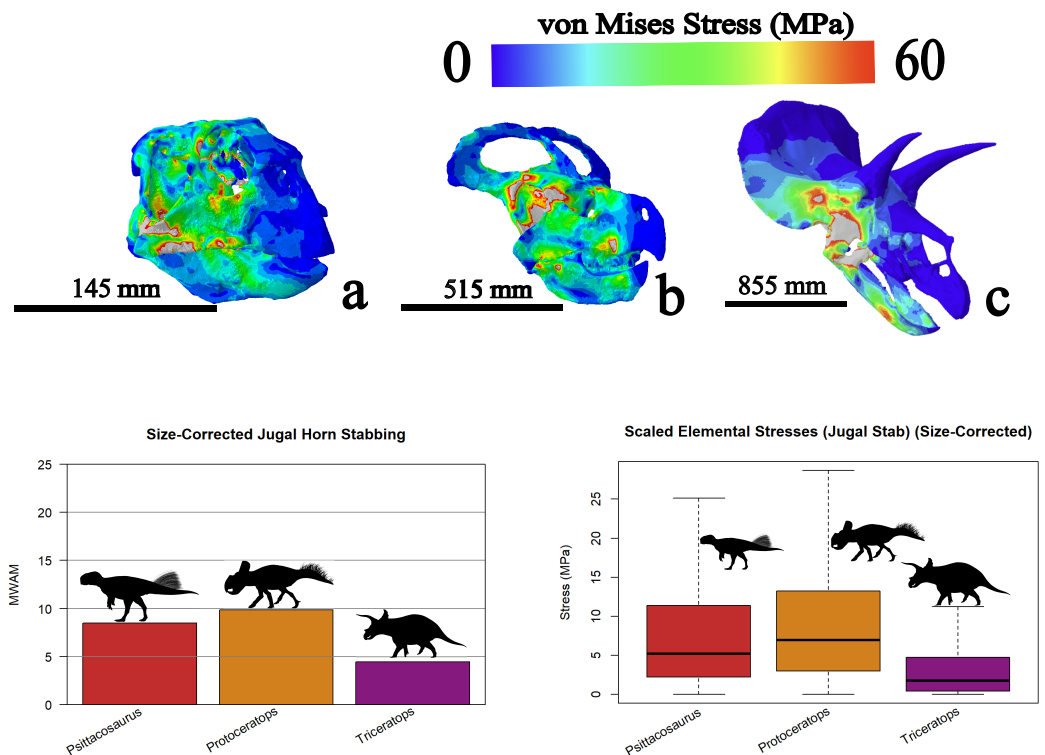


Figure 13 Comparisons of selected ceratopsian skulls in size-corrected jugal horn stabbing simulations, mesh-weighted arithmetic mean bar plots, and scaled elemental stress boxplots. Size-corrected von Mises stress distributions on the skulls of (A) *Psittacosaurus*, (B) *Protoceratops*, and (C) *Cosmocoxia Triceratops* from simulating stabbing behaviors with the jugal horn. Gray areas indicate von Mises levels exceeding 60 MPa. Phylogenic credits go to Jagged Fang Designs (<https://creativecommons.org/licenses/by/4.0/>), Scott Hartman (<https://creativecommons.org/licenses/by/3.0/>), and Matt Dempsey (<https://creativecommons.org/licenses/by/3.0/>). 3D model credits: *Psittacosaurus* (David Button, Laura Porro, Stephan Lautenschlager, Marc Jones, Paul Barrett; <https://creativecommons.org/licenses/by/4.0/>), *Protoceratops* (Clara and Viola Winkler; <https://creativecommons.org/licenses/by-nc/4.0/>), *Cosmocoxia Triceratops* (Tavernier Amaury; <https://creativecommons.org/licenses/by-nc-sa/4.0/>).

Full-size DOI: 10.7717/peerj.21728/fig-13

magnitudes concentrated on the lacrimal, maxilla, nasal, and base of the nasal horn. Accordingly, this horn locking position had similar values to the mediolateral axis test in both MWAM and scaled element stress plots (Fig. 6).

Spiclypeus

The single horn contact test resulted in moderate stress magnitudes on the supraorbital horn stem like the wrestling tests, while full horn locking resulted in lower magnitudes on the stems and on the rims of the orbital bones. Conversely, the oblique horn locking test resulted in high stresses on the stem and catching arch of one of the horns and low magnitudes on the stem of the other. On the MWAM and scaled element stress test, all three had low values with oblique horn locking being the highest in the former, and full horn locking in the latter (Fig. 7).

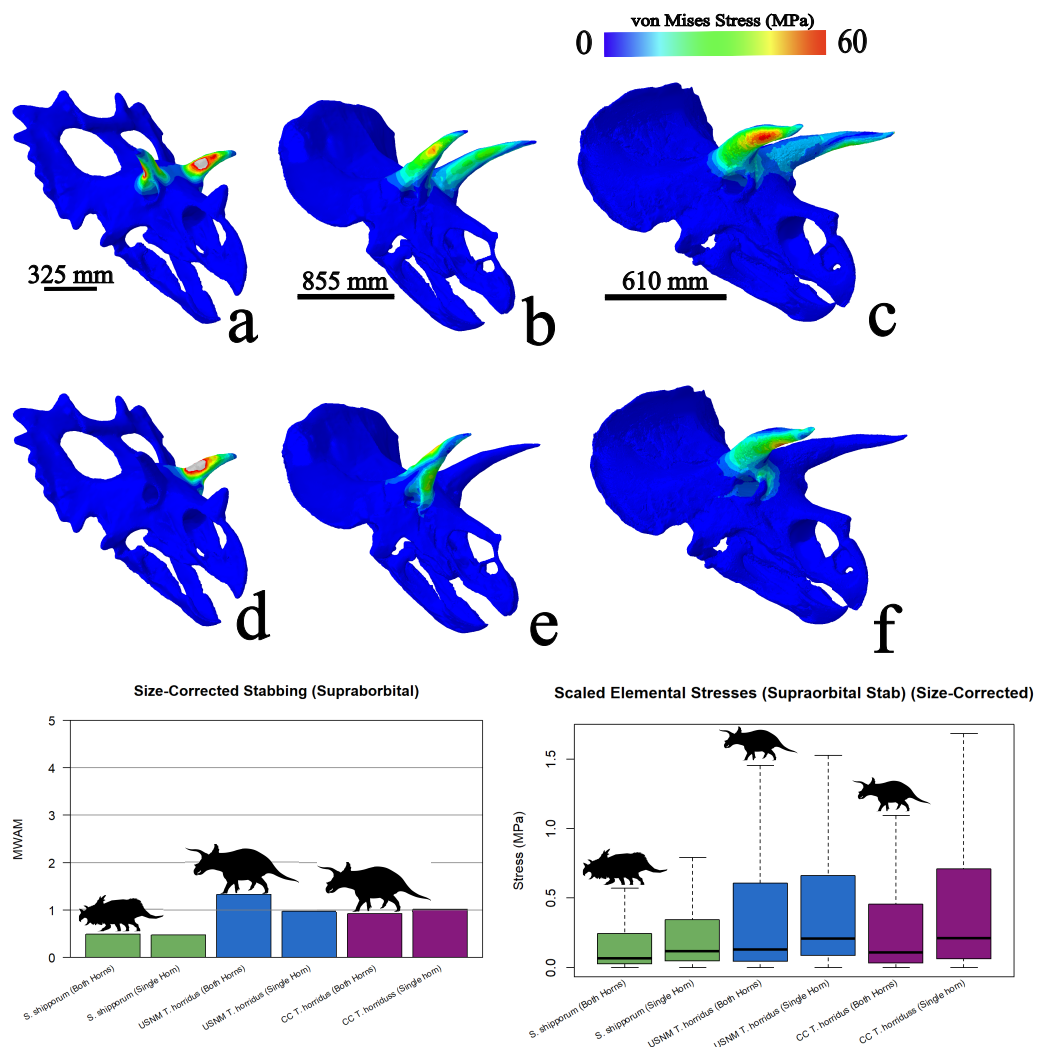


Figure 14 Comparisons of selected ceratopsian skulls in size-corrected supraorbital horn stabbing simulations, mesh-weighted arithmetic mean bar plots, and scaled elemental stress boxplots. Size-corrected von Mises stress distributions on the skulls of (A) *Spiclypeus*, (B) the USNM *Triceratops*, and (C) the CosmoCaxia *Triceratops* from simulating stabbing behaviors with (A–C) both supraorbital horns and (D–F) a single horn. Gray areas indicate von Mises levels exceeding 60 MPa. Phylogenic credits go to Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>) and Matt Dempsey (<https://creativecommons.org/licenses/by/3.0/>). 3D model credits: *Spiclypeus* (Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>), USNM *Triceratops* (Courtesy of the Smithsonian Institution). Cosmocaxia *Triceratops* (Tavernier Amaury; <https://creativecommons.org/licenses/by-nc-sa/4.0/>). Copyright: Smithsonian Institution for panels C and F. Full-size [DOI: 10.7717/peerj.21728/fig-14](https://doi.org/10.7717/peerj.21728/fig-14)

Triceratops

Both *Triceratops* skulls demonstrated the most stress on the stem of the supraorbital horn in single horn contact tests, with the CosmoCaxia specimen showing higher stress magnitudes due to the greater loads placed on it. However, both had extremely low magnitudes on the horn stems and orbital bones in the full horn locking test. The oblique

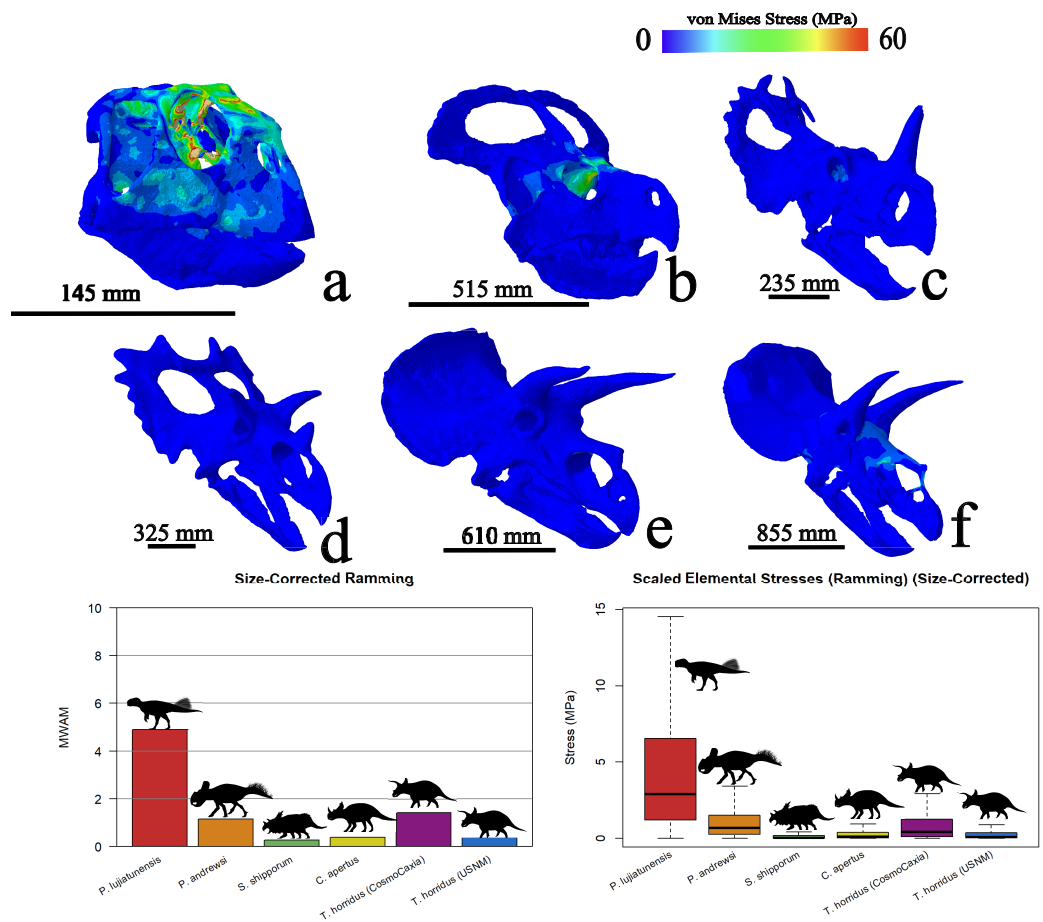


Figure 15 Comparisons of selected ceratopsian skulls in size-corrected ramming simulations, mesh-weighted arithmetic mean bar plots, and scaled elemental stress boxplots. Size-corrected von Mises stress distributions on the skulls of (A) *Psittacosaurus*, (B) *Protoceratops*, (C) *Centrosaurus*, (D) *Spiclypeus*, (E) the USNM *Triceratops*, and (F) the CosmoCaxia *Triceratops* from simulating ramming behaviors. Gray areas indicate von Mises levels exceeding 60 MPa. Phylopic credits go to Jagged Fang Designs (<https://creativecommons.org/licenses/by/4.0/>), Scott Hartman (<https://creativecommons.org/licenses/by/3.0/>), Andrew Farke (<https://creativecommons.org/licenses/by/3.0/>), Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>), and Matt Dempsey (<https://creativecommons.org/licenses/by/3.0/>). 3D model credits: *Psittacosaurus* (David Button, Laura Porro, Stephan Lautenschlager, Marc Jones, Paul Barrett; <https://creativecommons.org/licenses/by/4.0/>), *Protoceratops* (Clara and Viola Winkler; <https://creativecommons.org/licenses/by-nc/4.0/>), *Centrosaurus* (Courtesy of the Smithsonian Institution), *Spiclypeus* (Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>), USNM *Triceratops* (Courtesy of the Smithsonian Institution). Cosmocaxia *Triceratops* (Tavernier Amaury; <https://creativecommons.org/licenses/by-nc-sa/4.0/>). Copyright: Smithsonian Institution for panels C and E.

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horn locking test demonstrated a noted difference, with the USNM specimen experiencing moderate stress magnitudes on the catching arch while the CosmoCaxia skull showed much higher magnitudes across most of the horn's length. However, while the USNM *Triceratops* had the same value trends in the plots as the *Spiclypeus*, the CosmoCaxia *Triceratops* had full horn locking with the lowest value in the MWAM plot, and all three positions had identical values in the scaled elemental stress plot (Figs. 8, 9).

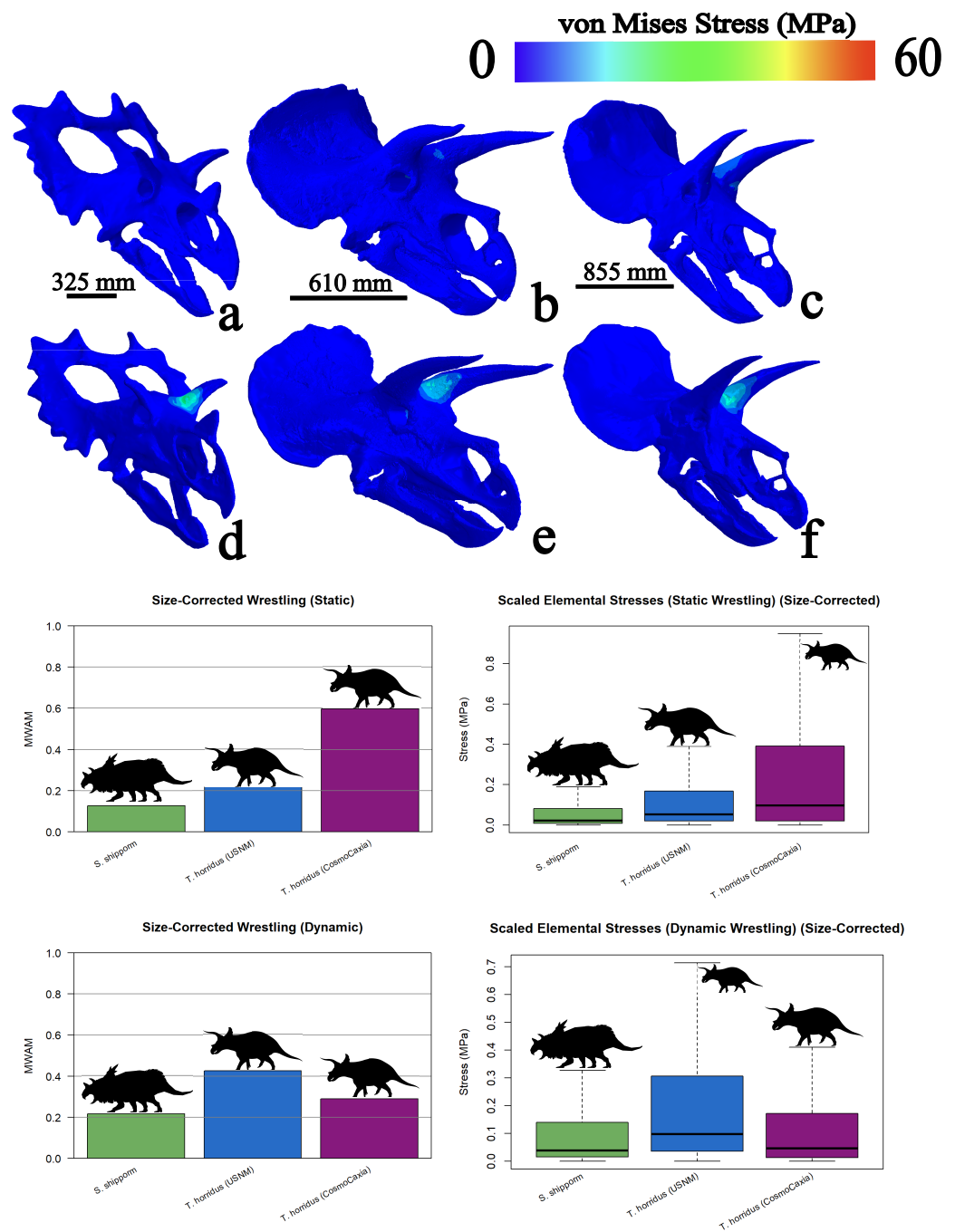


Figure 16 Comparisons of selected ceratopsian skulls in size-corrected wrestling simulations. (A) Size-corrected von Mises stress distributions on the skulls of *Spiclypeus*, the USNM *Triceratops*, and the CosmoCaxia *Triceratops* from simulating (A–C) “static” and (D–F) “dynamic” wrestling behaviors. Gray areas indicate von Mises levels exceeding 60 MPa. (B–E) Mesh-weighted arithmetic mean (MWAM) bar plots and scaled element stress boxplots comparing the ceratopsians in size-corrected (B, C) “static” wrestling and (D, E) “dynamic” wrestling behaviors. Phylopic credits go to Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>) and Matt Dempsey (<https://creativecommons.org/licenses/by/3.0/>). 3D model credits: *Spiclypeus* (Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>), USNM *Triceratops* (Courtesy of the Smithsonian Institution). Cosmocaxia *Triceratops* (Tavernier Amaury; <https://creativecommons.org/licenses/by-nc-sa/4.0/>). Copyright: Smithsonian Institution for panels B and E. Full-size DOI: 10.7717/peerj.21728/fig-16

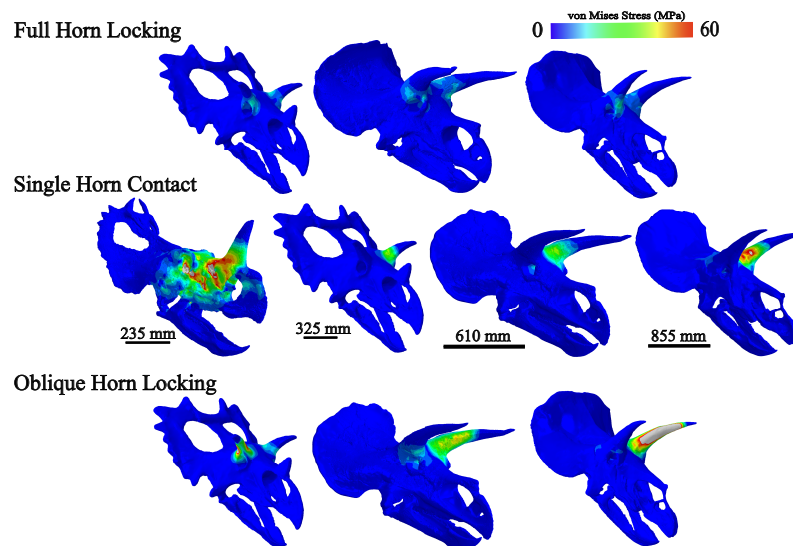


Figure 17 Comparisons of selected ceratopsian skulls in size-corrected horn-locking simulations based on Farke (2004). Size-corrected von Mises stress distributions on the skulls of (A) *Centrosaurus*, *Spiclypeus*, the USNM *Triceratops*, and the CosmoCaxia *Triceratops* from simulating different horn locking positions. Gray areas indicate von Mises levels exceeding 60 MPa. The top row represents full horn locking (FHL), the middle row represents single horn contact (SHC), and the bottom row represents oblique horn locking (OHL). 3D model credits: *Centrosaurus* (Courtesy of the Smithsonian Institution), *Spiclypeus* (Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>), USNM *Triceratops* (Courtesy of the Smithsonian Institution). Cosmocaxia *Triceratops* (Tavernier Amaury; <https://creativecommons.org/licenses/by-nc-sa/4.0/>). Copyright: Smithsonian Institution.

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Size-corrected comparison

When corrected for size (Fig. 17), *Centrosaurus* had much higher values in both MWAM and scaled elemental stress plots for single horn contact. The *Spiclypeus* and *Triceratops* all demonstrated low values in both plots for full horn locking, with the former being slightly lower and the two skulls of the latter showing slim differences. This difference was increased in oblique horn locking, with the CosmoCaxia *Triceratops* demonstrating much higher values than the *Spiclypeus* and the USNM *Triceratops* (Fig. 18).

Horn only tests and effects of keratin sheaths

Horn-only models demonstrated varying levels of stress depending on the taxon and anatomical axis (Figs. 19, 20), but a general trend can be seen in which the keratin sheath resulted in a decrease in MWAM and scaled elemental stress values (Figs. 21–24). The *Centrosaurus* and *Spiclypeus* nasal horns and the latter's supraorbital horns demonstrated very high stress values on the stem of the horn on the mediolateral axis compared to the longitudinal and vertical tests, but the magnitude was diminished when all were given their keratin sheaths (Figs. 21, 22). By contrast, the supraorbital horns of the *Triceratops* specimens experienced the highest stress values on the longitudinal axis compared to the

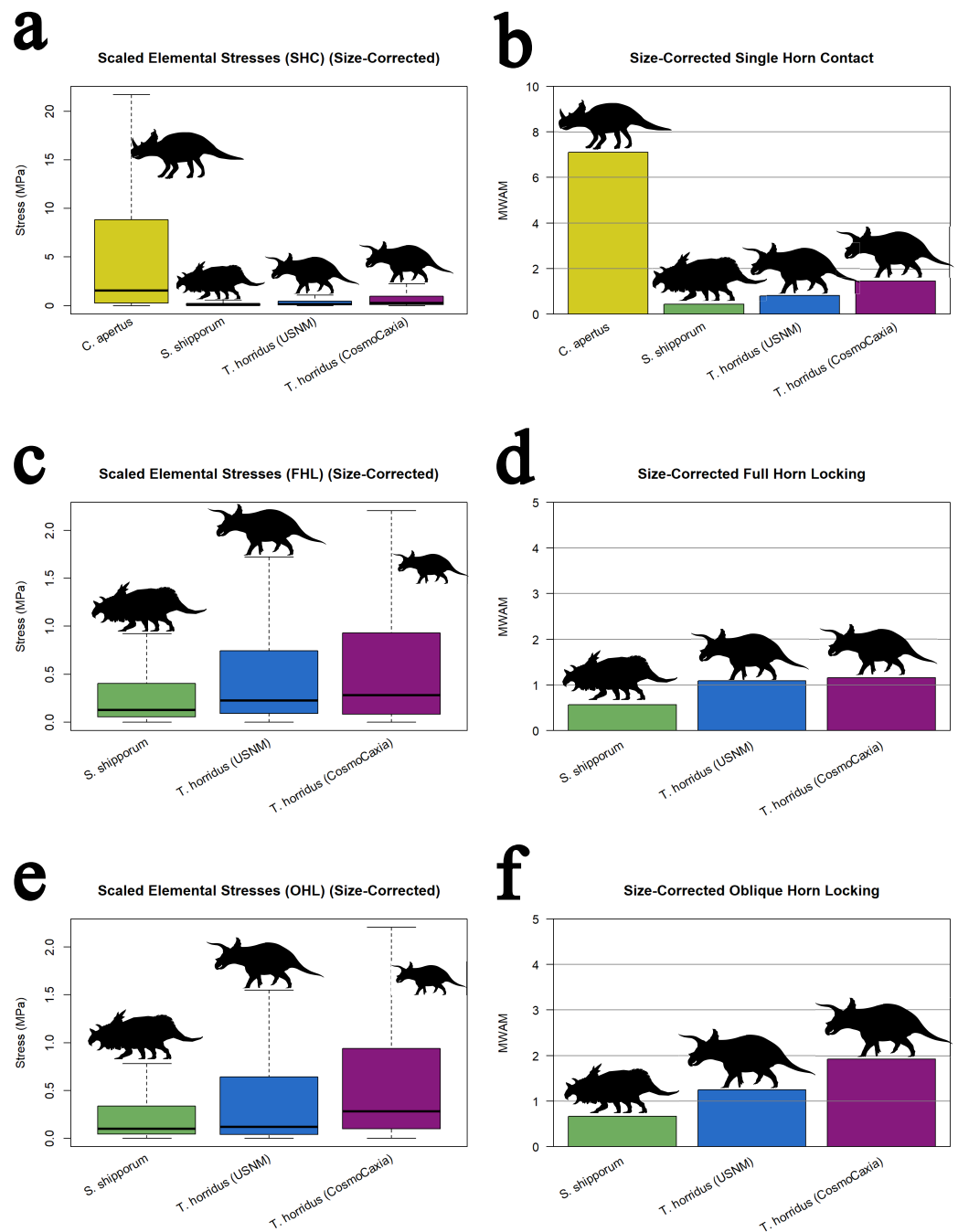


Figure 18 Mesh-weighted arithmetic mean (MWAM) bar plots and scaled element stress boxplots comparing selected ceratopsian specimens in size-corrected horn locking position tests based on Farke (2004). (A, B) Single horn contact, (C, D) full horn locking, (E, F) and oblique horn locking. Phylopic credits go to Andrew Farke (<https://creativecommons.org/licenses/by/3.0/>), Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>), and Matt Dempsey (<https://creativecommons.org/licenses/by/3.0/>). Full-size DOI: 10.7717/peerj.21728/fig-18

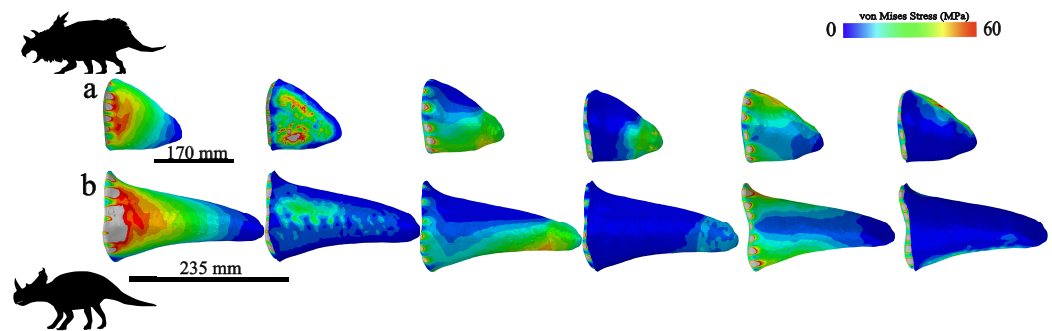


Figure 19 Comparisons of von Mises stress distributions on the nasal horns of *Centrosaurus* and *Spiclypeus* for each anatomical axis. (A) *Centrosaurus* and (B) *Spiclypeus*, with the following anatomical axes from left to right: Mediolateral, longitudinal, and vertical. Comparisons were made on bare bone cores and those with keratinous coverings to compare stress magnitude and distribution. Gray areas indicate von Mises levels exceeding 60 MPa. Phylopic credits go to Andrew Farke (<https://creativecommons.org/licenses/by/3.0/>) and Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>). 3D model credits: *Centrosaurus* (Courtesy of the Smithsonian Institution), *Spiclypeus* (Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>), Copyright: Smithsonian Institution for panel B.

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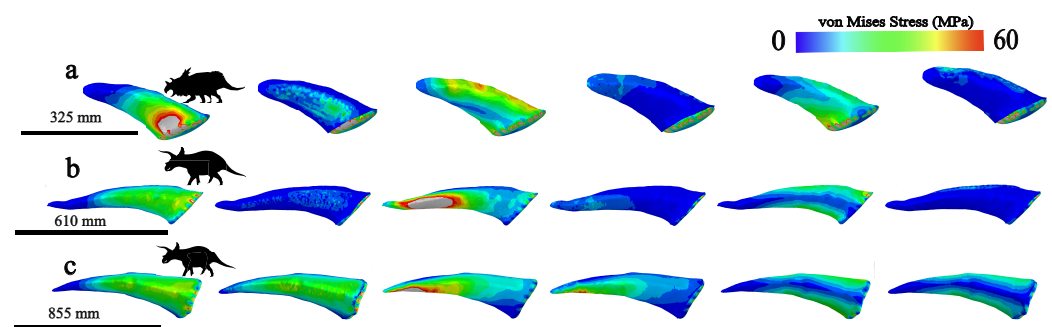


Figure 20 Comparisons of the von Mises stress distributions on the supraorbital horns of *Spiclypeus*, the USNM *Triceratops*, and the CosmoCaxia *Triceratops*. (A) *Spiclypeus*, (B) USNM *Triceratops*, (C) and CosmoCaxia *Triceratops* with the following anatomical axes from left to right: Mediolateral, longitudinal, and vertical. Comparisons were made on bare bone cores and those with keratinous coverings to compare stress magnitude and distribution. Gray areas indicate von Mises levels exceeding 60 MPa. Phylopic credits go to Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>) and Matt Dempsey (<https://creativecommons.org/licenses/by/3.0/>). 3D model credits: *Spiclypeus* (Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>), USNM *Triceratops* (Courtesy of the Smithsonian Institution). CosmoCaxia *Triceratops* (Tavernier Amaury; <https://creativecommons.org/licenses/by-nc-sa/4.0/>). Copyright: Smithsonian Institution for panel B.

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mediolateral and vertical axes, but the trend of the keratin sheath causing a notable decrease in MWAM and scaled elemental stress values remained consistent (Figs. 23, 24). When compared to the complete skull models, the mediolateral and vertical tests on the horn-only models were generally consistent in stress distributions. Meanwhile, the longitudinal tests are largely consistent with stabbing behavior tests. These results helped disentangle horn shape from influences of the skull itself and demonstrated accommodations for different stresses in a vacuum.

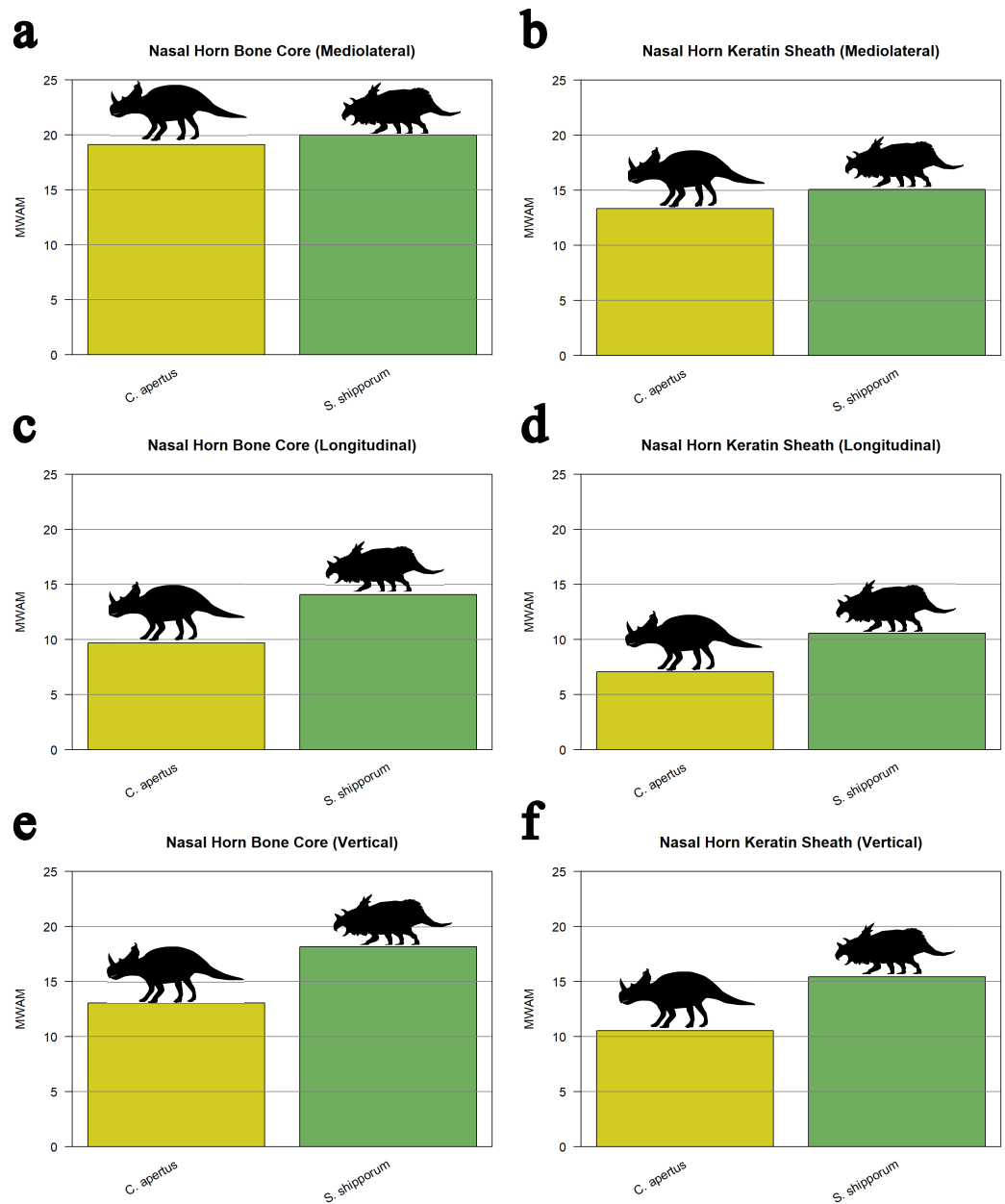


Figure 21 MWAM bar plots comparing the effects of keratin sheaths on the nasal horns of *Centrosaurus* and *Spiclypeus*. (A–F) Mesh-weighted arithmetic mean (MWAM) bar plots. Tests were made on stresses placed on mediolateral, longitudinal, and vertical axes. Phylopic credits go to Andrew Farke (<https://creativecommons.org/licenses/by/3.0/>) and Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>). Full-size DOI: 10.7717/peerj.21728/fig-21

DISCUSSION

Viability of combat behaviors in ceratopsians

With the assumption that horns will accommodate stresses that most resemble real fighting behaviors in nature (McCullough, Tobalske & Emlen, 2014), the results demonstrate that ceratopsians exhibit a wide spectrum of feasibility for different fighting

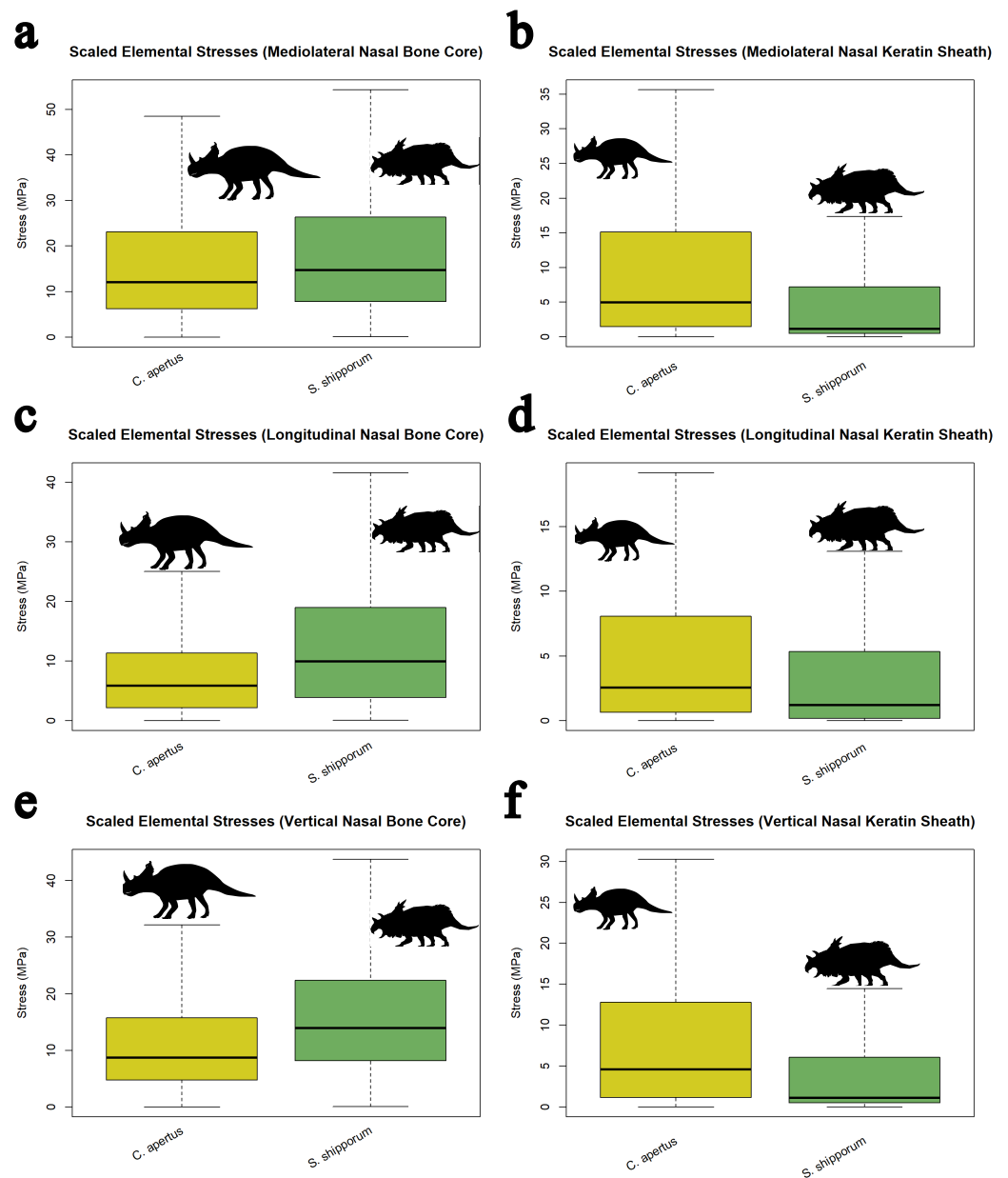


Figure 22 Scaled elemental stress boxplots comparing the effects of keratin sheaths on the nasal horns of *Centrosaurus* and *Spiclypeus*. (A–F) Scaled element stress boxplots. Tests were made on stresses placed on mediolateral, longitudinal, and vertical axes. Phylopic credits go to Andrew Farke (<https://creativecommons.org/licenses/by/3.0/>) and Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>). Full-size  DOI: 10.7717/peerj.21728/fig-22

styles. *Psittacosaurus*, as an early-diverging member of the clade (Hailu & Dodson, 2012), provides a baseline in testing the viability of intraspecific combat for ceratopsian skulls early in their evolutionary history. Although they do not exhibit the nasal or supraorbital horns of their later-diverging cousins, they do possess very enlarged jugal protrusions (Hailu & Dodson, 2012) that could provide the means for a unique form of stabbing

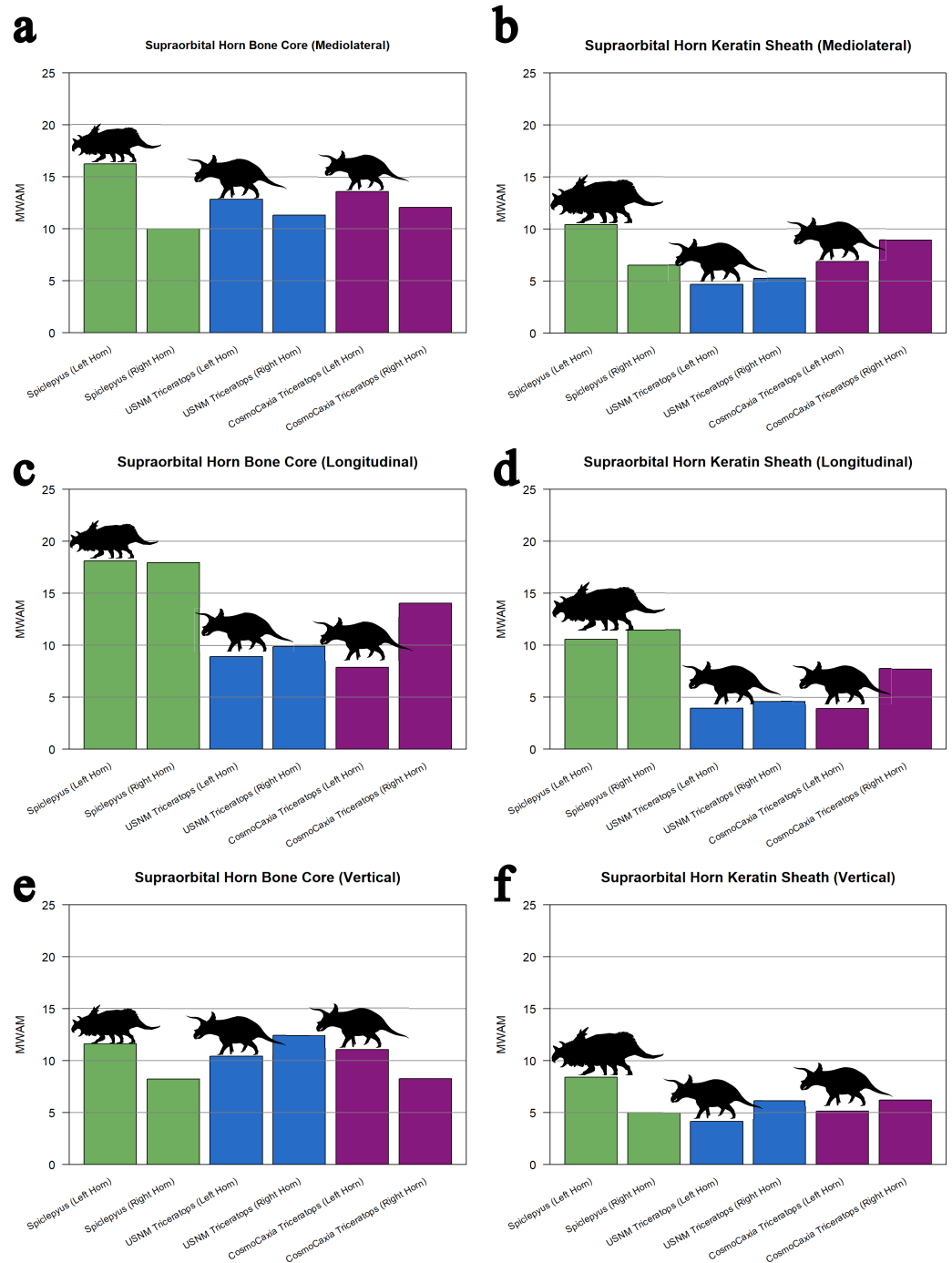


Figure 23 MWAM bar plots comparing the effects of keratin sheaths on the supraorbital horns of *Spiclypeus* and the two *Triceratops* specimens. (A–F) Mesh-weighted arithmetic mean (MWAM) bar plots. Tests were made on stresses placed on mediolateral, longitudinal, and vertical axes. Phylopic credits go to Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>) and Matt Dempsey (<https://creativecommons.org/licenses/by/3.0/>). Full-size DOI: 10.7717/peerj.21728/fig-23

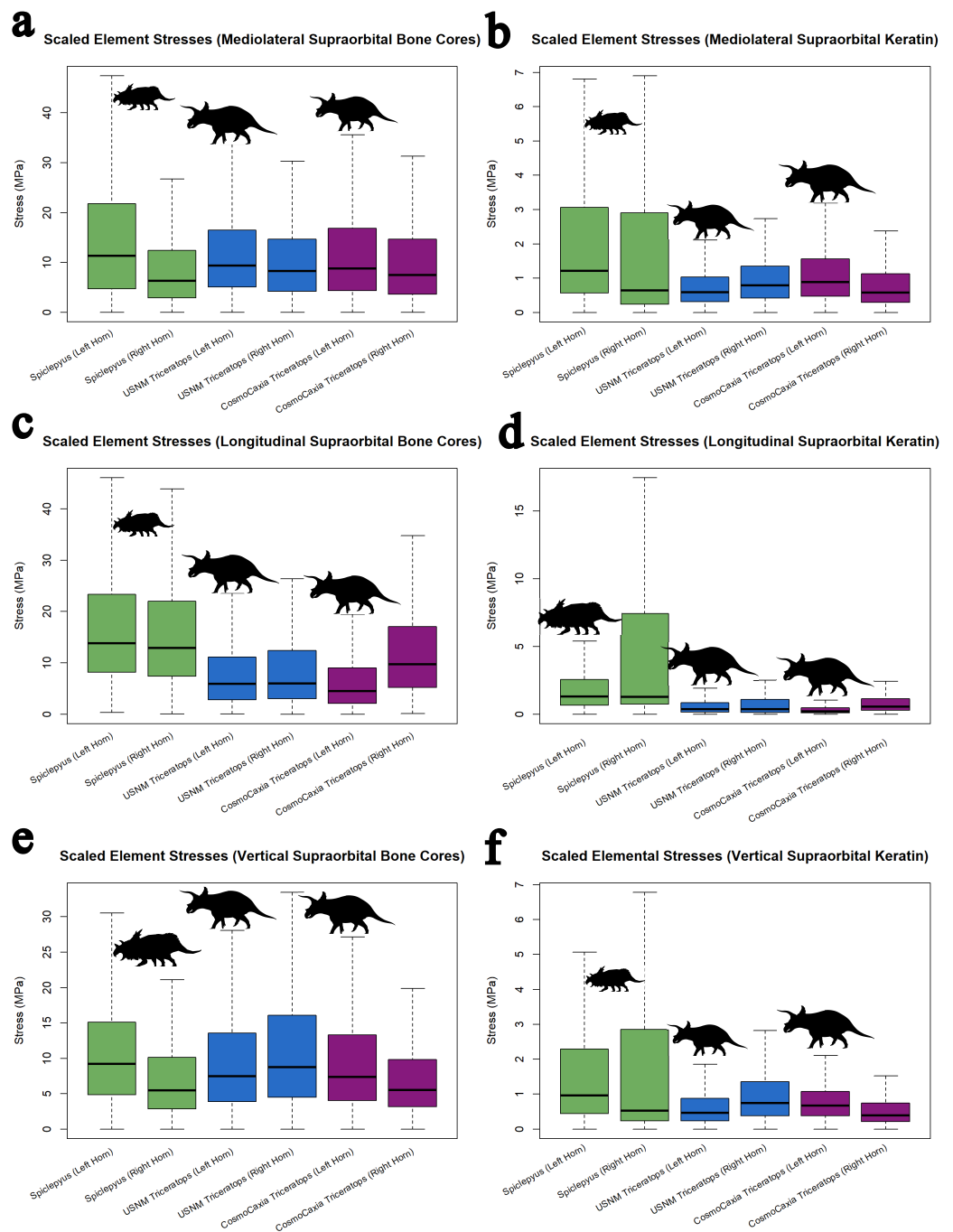


Figure 24 Scaled element stress boxplots comparing the effects of keratin sheaths on the supraorbital horns of *Spiclypeus* and the two *Triceratops* specimens. (A–F) Scaled element stress boxplots. Tests were made on stresses placed on mediolateral, longitudinal, and vertical axes. Phylopic credits go to Tasman Dixon (<https://creativecommons.org/publicdomain/zero/1.0/>) and Matt Dempsey (<https://creativecommons.org/licenses/by/3.0/>). Full-size DOI: 10.7717/peerj.21728/fig-24

([Molnar, 1977](#)) assisted by a very flexible atlas-axis complex ([Podlesnov, 2018](#)).

Additionally, they possess flat frontal bones that have been proposed as a means for basic ramming behaviors ([Zhou et al., 2006](#)). This study's biomechanical tests indicate that while the skull is relatively strong, the jugal horns were not well-suited for stabbing behaviors, which calls this type of combat into question. In addition, size-corrected force load tests indicate that *Psittacosaurus* had a skull much less suited for ramming than later-diverging ceratopsians. However, given the high amount of morphological variation in *Psittacosaurus* skulls depending on the species ([Hedrick & Dodson, 2013](#)), this comes with the caveat that the results of one species in this genus might not be precisely the same as others.

Protoceratops occupies an intermediate phylogenetic position between the earlier *Psittacosaurus* and later-diverging coronosaurid ceratopsids. After correcting for size, its robust skull appears to be better adapted for intraspecific combat than *Psittacosaurus*, with a greater resistance to longitudinal stresses compared to mediolateral and vertical ones. Biomechanical tests indicate that ramming with the frontal and nasal portion of the skull may have been viable given the low MWAM and scaled elemental stress values in our ramming simulations. However, the size-corrected forces indicate basic stabbing concentrated at the pronounced naris may not have been viable compared to its later-diverging cousins, albeit with the caveat that *Protoceratops* exhibits considerable individual variation across the entire skull ([Lambert et al., 2001](#); [Knapp, Knell & Hone, 2021](#)). Furthermore, biomechanical tests indicate that the jugal horns were similarly unviable for combat as the ones of *Psittacosaurus*. It seems most likely that basic ramming with the frontal and nasal portions of the skull was the most viable combat style.

For *Centrosaurus*, previous studies have suggested that this taxon would have primarily used its large nasal horn for stabbing behaviors ([Farlow & Dodson, 1975](#); [Farke, 2004](#)). Results indicate that *Centrosaurus* may have been specialized as a stabber, with a much greater resistance to longitudinal and vertical stresses than mediolateral ones. In addition, when the force loads were size-corrected, stabbing with the nasal horn showed to be more viable compared to the more early-diverging *Protoceratops*. Along with the lack of supraorbital horns, evidence suggests that stabbing behaviors may have been the most viable.

The chasmosaurines *Spiclypeus* and *Triceratops* have very similar stress values across most major combat tests. Size-corrected comparisons indicate that their horns were generally strong and well-suited to accommodating a wide range of forces, which would be necessary for wrestling or other high-energy behaviors that would result in unpredictable combinations of forces being put on them. Along with wrestling, size-corrected tests indicate that *Triceratops* may have also been well suited for using their supraorbital horns as stabbing weapons as well as their nasal horns exhibiting surprisingly low stress values in ramming simulations. However, the presence of such large supraorbital horns makes ramming behaviors with the roof of the skull like in bighorn sheep or bison ([Vander Linden & Dumont, 2019](#); [Woodruff & Ackermans, 2026](#)) less viable and potentially even hazardous ([Farke, 2004](#)). The high stress magnitudes and outward curved supraorbital horns of *Spiclypeus* make direct stabbing behaviors unlikely, but such

behaviors may be more viable with its pronounced nasal horn. These differences may provide a signal about the functional significance of variance in horn morphology (McCullough, Tobalske & Emlen, 2014). Overall, wrestling appears to be the most viable combat style for *Spiclypeus* and especially *Triceratops*, with the latter also being a capable stabber. It should be noted, however, that the unique morphology of these animals means that such combat behaviors would not be completely one-to-one with modern analogs (Farke, 2004), so such comparisons should be treated with caution (Knell et al., 2013).

Behavioral implications of results

The lack of weaponry on the top of the skull of *Psittacosaurus* (Hailu & Dodson, 2012) indicates that they did not exhibit fighting behaviors like those known from later-deriving ceratopsids, which is corroborated by its relatively weak performance in size-corrected ramming comparisons. Additionally, the massive jugal horns may seem like viable intraspecific weapons (Molnar, 1977), but this study's biomechanical evidence suggests otherwise. This does open the doors for testing various other hypotheses for these jugal horns, however, including socio-sexual display (mutual or otherwise) (Hone, Naish & Cuthill, 2011). This extends to *Protoceratops*, with its pronounced jugal horns (Brown & Schlaikjer, 1940; Lambert et al., 2001) resulting in similarly weak performances. *Protoceratops* also lacked supraorbital or prominent nasal horns (Brown & Schlaikjer, 1940), but its skull did have a pronounced naris that would support a nasal horn in more derived taxa (Farke, 2014). This has been historically proposed to have been used for ramming a conspecific's flanks in a similar manner to mountain goats (*Oreamnos americanus*) and chamois (*Rupicapra rupicapra*) (Farlow & Dodson, 1975; Molnar, 1977; Farke, 2004; Vander Linden & Dumont, 2019). Given our biomechanical tests, the proposed flank-ramming is certainly possible, but such combat behaviors have a caveat in that ramming with the entire roof of the skull would have been more viable than what can be described as a stabbing analog by striking with the naris alone, and the potential fragility of the frill is another factor that requires further research.

The biomechanical results and fossil evidence presents an interesting case of possible specialization for a specific combat style for *Centrosaurus*. Centrosaurines have often been compared to rhinos and mountain goats such as *Oreamnos americanus*, with their large nasal horns being used to stab and gore each other's flanks (Molnar, 1977; Farke, 2004; Farke, Wolff & Tanke, 2009). This is further corroborated by a comparative lack of bone lesions on their skulls when compared to *Triceratops* (Farke, Wolff & Tanke, 2009), which further vindicates the notion that the head was not the primary target of *Centrosaurus* in potential intraspecific fights. Along with the considerable disparity in stress levels in the mediolateral axis compared to the longitudinal and vertical axes, it is possible that *Centrosaurus* was specialized as a stabber at the expense of most other potential fighting styles.

Spiclypeus and *Triceratops* serve as an interesting dichotomy to the *Centrosaurus*. While *Centrosaurus* is possibly specialized as a stabber, the two chasmosaurines might be well-suited for a myriad of combat styles with horns capable of accommodating forces correlating with wrestling. With the presence of an extraordinary fenestra on the

squamosal of the former (Mallon *et al.*, 2016) and evidence of frequent lesions and even traumatic injuries on the squamosal of the latter (Farke, Wolff & Tanke, 2009; D’Anastasio *et al.*, 2022), there is particularly strong evidence of at least certain chasmosaurines using their horns for intraspecific combat. It has been suggested that *Triceratops* locked their supraorbital horns in a variety of potential positions (Farke, 2004) and would have primarily wrestled with one another (Farlow & Dodson, 1975; Molnar, 1977) in a similar manner to many cervids and bovids (Geist, 1966; Clutton-Brock, Guinness & Albon, 1982; Lundrigan, 1996; Vander Linden & Dumont, 2019). The biomechanical tests support most of these notions, with wrestling potentially being the primary fighting style for these taxa. However, this is also a good example of fighting styles not being mutually exclusive, with stabbing also being viable with *Triceratops* and *Spiclypeus* with their supraorbital and nasal horns respectively. The angles of movement in which these taxa could stab with their horns requires further study. Fencing behaviors are very difficult to interpret due to the lack of cervical vertebrae in this study (Lundrigan, 1996; Vander Linden & Dumont, 2019), but single horn contact positions, which can serve as a suitable analog, are viable for both taxa. While all three chasmosaurine skulls show low size-corrected results for full horn locking, oblique horn locking seems less likely for these two taxa. Due to the different oblique horn locking results between the USNM and CosmoCaxia *Triceratops*, individual variation may also factor into stress accommodation (Bonenfant *et al.*, 2009; McCullough, Ledger & Moore, 2015).

Correlations between these different combat styles and possible ceratopsian social structure and habitats can also be cautiously inferred. *Psittacosaurus* is known for residing in closed forested habitats (Vinther *et al.*, 2016), which are generally associated with much smaller weaponry, if any at all (Cabrerá & Stankowich, 2020). Combined with its basal position on the ceratopsian family tree and small physical size, this coincides with the lack of obvious weaponry and comparatively basic display structures in their jugal horns. In addition, while *Psittacosaurus* have been found in age segregated groups (Meng *et al.*, 2004; Qi, Barrett & Eberth, 2007), these have been exclusively juvenile specimens with no evidence to suggest gregariousness in adults (Zhao *et al.*, 2013). By contrast, there are multiple instances of *Protoceratops* and *Centrosaurus* death assemblages with individuals of multiple ages (Jerzykiewicz *et al.*, 1993; Sampson, 2001; Erberth & Getty, 2005; Hone *et al.*, 2014), along with more apparent cranial structures (Brown & Schlaikjer, 1940; Hailu & Dodson, 2012; Ryan & Russell, 2005; Farke, 2014) that correlate with their residence in more open habitats as well as their larger physical size and more derived phylogenetic positions (Jerzykiewicz, 1997; Erberth, 2005; Dingus *et al.*, 2008), something that is largely consistent with modern herbivores with cranial ornaments (Cabrerá & Stankowich, 2020). *Spiclypeus* and *Triceratops* are interesting in that while they both inhabited coastal plains (Brinkman, 1990; de Rooij *et al.*, 2022), there is little evidence of gregariousness outside of a possible age-segregated group for *Triceratops* (Mathews *et al.*, 2009). It is possible that these two taxa were similarly able to develop their weaponry in comparatively open environments and were gregarious to a certain degree given the early development of their horns and frills (Goodwin *et al.*, 2006) but were not quite as social as *Centrosaurus*. That being said, some studies call the correlation between

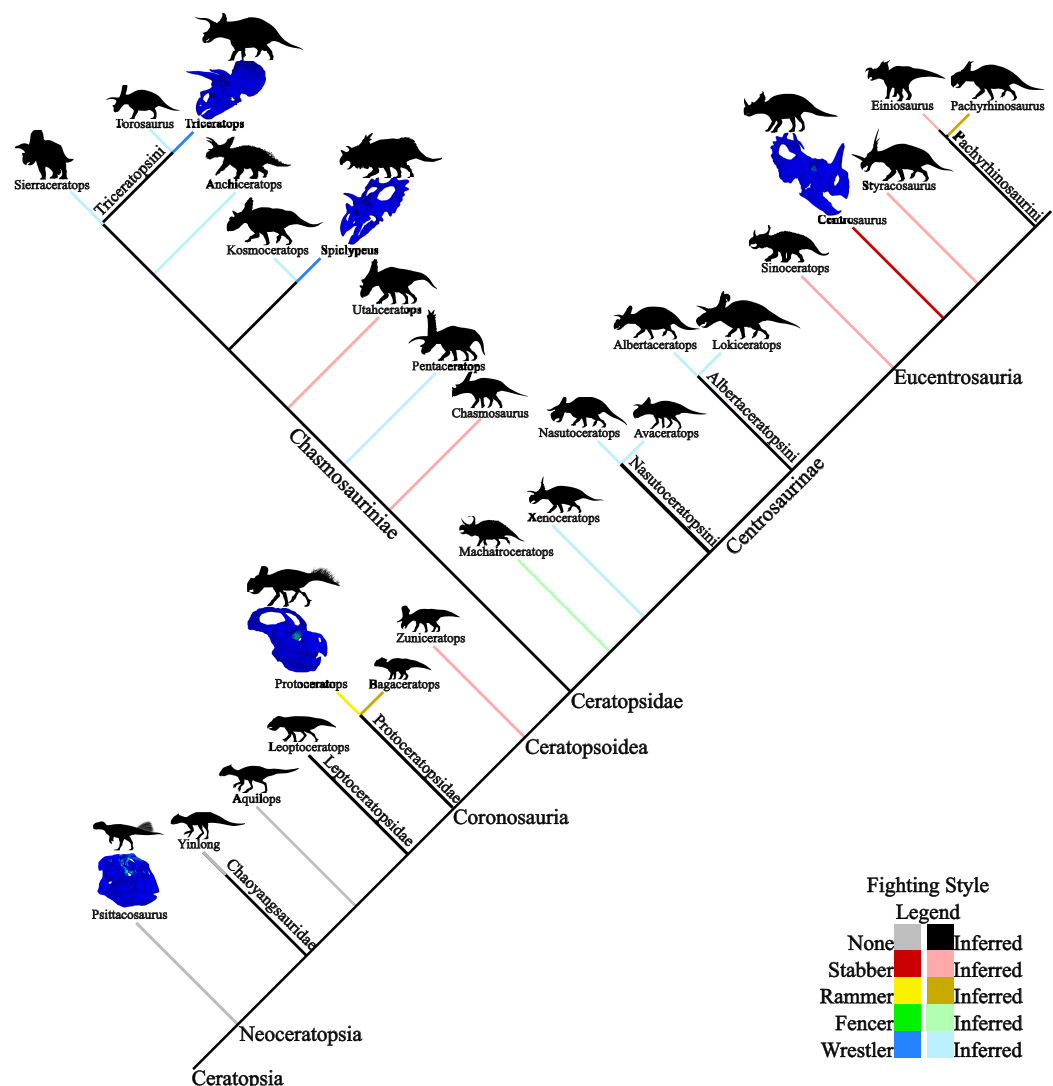


Figure 25 Simplified cladogram of ceratopsia based on *Morschhauser et al. (2018)*, *Dalman et al. (2022)*, and *Loewen et al. (2024)*. Nodes labeled with cranial weapon morphological trends of each clade and branch tips color coded into inferred primary fighting styles for each selected taxon. Brighter colors signify taxa used for this study and their inferred primary fighting style; more faded colors represent cautious inferences based on similar horn morphology. Skulls are placed on top of nodes of species that were tested in this study to demonstrate different morphotypes. Phylogenic credits can be found in [Table S2](#). 3D model credits: *Psittacosaurus* (David Button, Laura Porro, Stephan Lautenschlager, Marc Jones, Paul Barrett; <https://creativecommons.org/licenses/by/4.0/>), *Protoceratops* (Clara and Viola Winkler; <https://creativecommons.org/licenses/by-nc/4.0/>), *Centrosaurus* (Courtesy of the Smithsonian Institution), *Spiclypeus* (Mikesira; <https://creativecommons.org/licenses/by-nc-sa/4.0/>), USNM *Triceratops* (Courtesy of the Smithsonian Institution). *Cosmocaxia Triceratops* (Tavernier Amaury; <https://creativecommons.org/licenses/by-nc-sa/4.0/>). Copyright: Smithsonian Institution.

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horn size and habitat into question (*Caro et al., 2003*) and the broad range of habitats that ceratopsians likely lived in (*Sampson, 2001*) means that these inferences are to be treated with caution until a larger sample size is acquired.

Anti-predator defense is a more difficult behavior to infer for ceratopsians and their cranial weaponry. Horns and antlers primarily evolve for sexual selection rather than anti-predator defense (Geist, 1966; Bro-Jørgensen, 2007; Knell et al., 2013); certain morphotypes in modern horned animals serve no real defensive purpose in such situations (Estes, 1991; Roberts, 1996; Peterson & Ciucci, 2003; Ruth, 2004), and dehorning has no effect on predation susceptibility in large herbivores like rhinos (Chimes et al., 2022). Additionally, one of the most famous fossils of all time shows a *Protoceratops* defending itself against a *Velociraptor* with its jaws rather than its enlarged naris (Kielan-Jaworowska & Barsbold, 1972), which is admittedly only a single instance but still worth mentioning. However, there is circumstantial evidence of *Triceratops* surviving an attack from a *Tyrannosaurus* with healed bite marks on its supraorbital horn and squamosal (Happ, 2008), and several modern herbivores have co-opted their horns for successful predator deterrence. Gemsbok (*Oryx gazella*) (Mills, 1990), black rhinoceros (*Diceros bicornis*) (Schaller, 1972; Morinte & Keter, 2000), and African buffalo (*Syncerus caffer*) (Mloszewski, 1983) have records of using their horns to deter and kill lions (*Panthera leo*) and hyenas (*Crocuta crocuta*). The same is true for elk (*Cervus canadensis*) (Metz et al., 2018) and musk oxen (*Ovibos moschatus*) (Reynolds, Reynolds & Shideler, 2002) against wolves (*Canis lupus*) and bears (*Ursus arctos*). Similarly, female ungulate horns, which tend to be shorter and of the stabbing variety, have been suggested as anti-predator tools rather than similar direct competition like in males (Stankowich & Caro, 2009). As such, while ceratopsid horns may primarily be for intraspecific combat, predator deterrence might be a viable behavior for at least some taxa. In the provided taxa for this study, the relatively straight horns of *Triceratops* and *Centrosaurus* could provide optimal antipredator defense, while the outwardly splayed horns of *Spiclypeus* would be less optimal for such behaviors, as demonstrated by the stabbing tests (Figs. 12, 14).

Phylogenetic trends of ceratopsian combat styles

Due to the small sample size of this study, making a comprehensive correlation between trends of cranial weapon morphology and phylogeny within the ceratopsian clade is difficult. However, as each specimen represents a distinct morphotype from different phylogenetic positions, some broad evolutionary inferences can be made (Fig. 25). *Psittacosaurus*, an early diverging ceratopsian, retains the ancestral condition of lacking obvious specializations to combat with no supraorbital or nasal horns (Hailu & Dodson, 2012; Podlesnov, 2018) and biomechanical evidence suggests their skulls were not viable for intraspecific combat at this point in their evolutionary history, with their jugal horns evolving as display structures. While other early-diverging ceratopsians like chaoyangsaurids (Xijin, Zhengwu & Xing, 1999) and *Aquilops* (Farke et al., 2014) also lack such specializations, the larger, quadrupedal leptoceratopsids (Nopcsa, 1923; Makovicky, 2001) require more biomechanical data.

Early-diverging coronosaurian (Madzia et al., 2021) ceratopsids, such as *Protoceratops* and *Bagaceratops* (Maryanska & Osmolska, 1975) exhibit early adaptations for combat, with our biomechanical tests on the former demonstrating an ability to accommodate higher stresses on the roof of the skull. This correlates with several anatomical adaptations

including an enlargement of the skull, fusion of cervical vertebrae to create the syncervical ([Hailu & Dodson, 2012](#)) to support such a large head, and the development of a pronounced naris to the extent of possessing a small nasal horn ([Maiorino et al., 2015](#)). Such increases in skull strength and robustness may be a result of phylogenetic inertia ([Blomberg & Garland, 2002](#); [Shanahan, 2011](#)), with ceratopsians inheriting this as an independent adaptation, be it to accommodate for stronger bite forces allowing for the consumption of tougher vegetation ([Maiorino et al., 2018](#); [Button & Zanno, 2020](#); [Button et al., 2023](#)) or compensating for larger skull size and loads put on the head by the cranial ornaments ([Farke, 2010](#)), that was later co-opted for intraspecific combat. However, the higher stresses experienced when the force loads were concentrated on the naris present a caveat for the limits in skull strength within early-diverging coronosaurid ceratopsids.

Early ceratopsoids such as *Zuniceratops* ([Wolfe & Kirkland, 1998](#)) and *Turanoceratops* ([Nessov, Kaznyshkina & Cherepanov, 1989](#); [Sues & Averianov, 2009](#)) possess supraorbital horns with similar morphotypes to those of *Triceratops*, with biomechanical tests on the latter allowing us to infer that these taxa may have been similarly capable of stabbing as late-diverging chasmosaurines. However, the horns on these taxa are less pronounced and have a narrow gap between them on the frontal bone, indicating that they may be less suited for wrestling behaviors. Within Ceratopsidae, wrestling styles may have independently evolved multiple times across their evolutionary history. Such large supraorbital horns remain generally consistent within chasmosaurines, with *Spiclypeus* providing a morphotype that can be used to infer behaviors for taxa like *Chasmosaurus* ([Lambe, 1914](#); [Maidment & Barrett, 2011](#)), *Utahceratops* and *Kosmoceratops* ([Sampson et al., 2010](#)). Biomechanical studies indicate that this group of chasmosaurines may have been able to stab with their nasal horns. However, while *Spiclypeus* and *Kosmoceratops* have essentially identical outward-curving horns that are more viable for wrestling than stabbing or fencing, the reduced supraorbital horns of *Chasmosaurus* and *Utahceratops* may constrain them to stabbing behaviors.

Agujaceratops ([Lehman, 1989](#)), *Pentaceratops* ([Osborn & Sternberg, 1923](#); [Rowe et al., 1981](#)) and later-diverging chasmosaurines like *Anchiceratops* ([Brown, 1914](#)), *Sierraceratops* ([Dalman et al., 2022](#)), *Triceratops* itself and other triceratopsins like *Torosaurus* ([Marsh, 1891b](#); [Longrich, 2011](#); [Longrich & Field, 2012](#); [Maiorino et al., 2013](#); [Mallon et al., 2022](#)) generally have more pronounced, forward facing supraorbital horns and reduced nasal horns. The main exception is *Regaliceratops*, which possesses a more pronounced nasal horn compared to the supraorbital horns ([Brown & Henderson, 2015](#)). This specific genus provides a rare example of a violation in this pattern of phylogenetic inertia and how novel arrangements still occurred on occasion even later into the ceratopsians' evolutionary history. Outside of this taxon, this largely consistent horn morphotype can be compared to our *Triceratops* specimens, which are generally well-suited for accommodating a variety of forces. Therefore, this can be inferred as later-diverging chasmosaurines possibly stabilizing for wrestling behaviors. However, their clear stabbing points and the wider gap between their horns on the frontal bone indicate that fencing and stabbing behaviors may have been similarly viable.

Centrosaurines provide interesting trends in horn morphology. Early-diverging centrosaurines like *Diabloceratops* (Kirkland & Deblieux, 2010), *Machairoceratops* (Lund, Sampson & Loewen, 2016), *Avaceratops* (Dodson, 1986; Penkalski & Dodson, 1999), *Nasutoceratops* (Sampson et al., 2013), *Xenoceratops* (Ryan, Evans & Shepherd, 2012), *Albertaceratops* (Ryan, 2007), and *Lokiceratops* (Dalman et al., 2022) exhibit more pronounced, diversely shaped supraorbital horns and very diminished nasal horns like chasmosaurines. *Diabloceratops* and *Machairoceratops* have longer supraorbital horns than earlier ceratopsoids and a wider gap between them but only a slight increase in curvature, indicating that they may have primarily been fencers and stabbers. By contrast, the curved horns of *Nasutoceratops*, which vaguely resemble the curve seen in the USNM *Triceratops* skull, and the horn morphology of *Avaceratops*, *Xenoceratops*, and members of the *Albertaceratopsini* (Dalman et al., 2022) resembling those of late-diverging chasmosaurines, lead to the inference of them being primarily wrestlers. Later-diverging centrosaurines like *Centrosaurus* (Lambe, 1904; Ryan & Russell, 2005), *Sinoceratops* (Xu et al., 2010), and *Styracosaurus* (Lambe, 1913; Holmes et al., 2020) evolved much more pronounced nasal horns and bosses (Hieronymus, 2009), with our biomechanical results marking a possible transition to more specialized stabbing behaviors. While *Einiosaurus* (Sampson, 1995) and *Pachyrhinosaurus* (Sternberg, 1950) present a possible transition to dedicated ramming behaviors with potential correlating injuries (Farke, Wolff & Tanke, 2009; Hieronymus, 2009), a lack of biomechanical results for these taxa and no similar nasal bosses in relatives in this sample set make such assumptions difficult to ascertain. It must be noted that these inferences may change with larger sample sizes and more biomechanical tests across more taxa.

Differing combat styles as an evolutionary driver?

The evolutionary drivers of ceratopsian cranial weapon diversity have been one of the most widely explored aspects of this clade, with various hypotheses having been tested. Species recognition (Padian & Horner, 2011) has not held up under scrutiny (Knell & Sampson, 2011; Knapp et al., 2018) while socio-sexual selection has (Hone, Naish & Cuthill, 2011; Hone, Wood & Knell, 2016; Knapp, Knell & Hone, 2021). The biomechanical evidence in this study supports the idea that differing combat styles may have also been a driver of different horn morphologies (Emlen, 2008) in addition to socio-sexual selection. Animal weaponry has been shown to be stronger under species-typical loads that correlate with their preferred fighting styles and weaker in atypical ones (McCullough, Tobalske & Emlen, 2014). This study's biomechanical tests remain consistent to this pattern. Ceratopsian horns appear to exhibit lower stresses under loading regimes corresponding with certain fighting styles, with the larger nasal horn of *Centrosaurus* demonstrating resistance to stresses correlating with stabbing behaviors (Figs. 6, 12) and the chasmosaurines showing notable resistance towards generalized horn-locking wrestling behaviors (Figs. 7–9, 16) (Caro et al., 2003). As such, intraspecific combat might be a very important proponent in the lifestyles of these dinosaurs with selective pressures to evolve horns that can better accommodate stresses correlating with specific styles (McCullough, Tobalske & Emlen, 2014). These pressures may not have been present until later in the evolution of these two

clades, however, with early-diverging taxa of chasmosaurines like *Agujaceratops* and *Pentaceratops* (Dalman et al., 2022) and centrosaurines like *Diabloceratops* and *Nasutoceratops* evolving pronounced supraorbital horns relatively quickly in their evolutionary history (Kirkland & Deblieux, 2010; Sampson et al., 2013; Loewen et al., 2024) with very similar morphotypes. The lack of evidence of sexual dimorphism in ceratopsids (Maiorino et al., 2015; Mallon, 2017) calls into question the possibility of such horns being a selected trait in males like in many modern herbivores (Clutton-Brock, Guinness & Albon, 1982; Metz et al., 2018), but mutual mate choice is a possibility (Knapp, Knell & Hone, 2021) and cryptic dimorphism (Murphy, 2007; Rice et al., 2017) with less obvious features requires further research. Furthermore, future studies can be made to determine if certain combat styles can inflict differing levels of damage (Embets, Hwang & Wiens, 2021), and future biomechanical tests on other taxa can help strengthen or question the notion of combat styles being such a major evolutionary driver.

Keratin sheaths

While the bone cores of the ceratopsid horns in this study showed varying levels of stress magnitudes depending on their shape and what anatomical axis was being tested, one common trend is that the presence of a keratinous sheath decreases both the MWAM and scaled elemental stress values. This is in line with modern herbivores that have similar keratinous coverings on their horns, which can be incredibly tough (Wegst & Ashby, 2004) and help in dissipating particularly large amounts of stress (Drake et al., 2016; Zhang et al., 2018; Yang et al., 2022; Lee et al., 2024). With cattle, which possess the most visually analogous keratinous sheaths to ceratopsids with a hollow sheath surrounding the bone core (Huang & Yu, 1997), a high fracture toughness and ability to shield the core from damage (Li et al., 2010; Li, Zhao & Feng, 2011) lends to credence of the idea that ceratopsid keratin sheaths may have provided similar benefits.

However, there are some limitations for the keratin sheath tests for this study that must be addressed. While such coverings have been assumed for horned ceratopsians (Dodson, Forster & Sampson, 2012), such biopolymers degrade quickly (Mahan et al., 2023) and do not fossilize very well outside of feathers (Moyer, Zheng & Schweitzer, 2016). In addition, the only instance of evidence of keratin sheaths on ceratopsians is *Psittacosaurus* (Bell et al., 2022), which are primarily on the jugal horns. The idea of ceratopsid keratinous sheaths changing shape across their ontogeny like the bone cores (Horner & Goodwin, 2006) of some modern herbivores (Goss, 2012), while not without merit, lacks solid evidence and is difficult to recreate. Finally, the microstructure of ceratopsid keratinous sheaths is difficult to ascertain due to the wide variety in modern animal horns (Zhang et al., 2018) and the effects of hydration in keratin (Li et al., 2010) are yet to be investigated.

CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

This FEA study represents the first examination of the viability of intraspecific combat styles in ceratopsians and determining if differing styles were a major evolutionary driver

for the diversity of their cranial weaponry. After size-correction, the skull and jugal horns of *Psittacosaurus* performed relatively poorly compared to other ceratopsians in ramming and stabbing behaviors, making combat behaviors unlikely for this taxon. *Protoceratops* accommodated a fair amount of stress in basic ramming behaviors but performs more poorly in stabbing with the nasal bone. Results for the *Centrosaurus* correlated with a specialization towards stabbing behaviors, being better suited to accommodating for longitudinal and vertical axis stresses than mediolateral stress ones. By contrast, the chasmosaurines *Spiclypeus* and *Triceratops* demonstrated moderate stress magnitudes across most anatomical, combat, and horn locking tests with some outliers, with the lowest being found in tests that may indicate more generalized wrestling behaviors. The enlargement and increased robustness of their skulls was likely a result of phylogenetic inertia, with these traits being co-opted for more dedicated and diverse forms of intraspecific combat. This diversity in potential fighting styles was possibly a major evolutionary driver that contributed to the wide range of morphologies seen in ceratopsian cranial weaponry.

Due to the time-consuming nature of finite element analysis and the relatively small sample size (five taxa, six specimens), it is essential to expand this study and consider other factors. The first is to include more taxa to strengthen or question the conclusions made in this study and to determine if the inferred phylogenetic trends between ceratopsian combat styles hold up to scrutiny. The second is to include cervical vertebrae and determine if similar adaptations for strength and flexibility occur to those found in modern herbivores with similarly diverse fighting styles, as they could either support the conclusions of this study or call them into question if they do not line up with proposed combat styles. The third is to determine if morphological trends using geometric morphometrics can reinforce any trends between certain ceratopsian skull shapes and the viability of certain combat styles. The fourth is simulating the effects of hydration of keratin sheaths and seeing what effects they have on stress reduction on the horns. The fifth is to analyze the effects of shearing and torsion forces on the horns of ceratopsians as they slide past one another, as this could possibly affect the simulated stresses on each combat style employed by ceratopsians. The sixth and final one is to better determine the effects of individual variation across many other ceratopsid taxa, as this study only has one species with two individuals to compare to one another. This can help ascertain if certain intraspecific horn shapes could be more desirable in combat situations. All these factors in future work can help expand our understanding and further fill the knowledge gap of just how these dinosaurs utilized some of the most iconic examples of cranial weaponry in the natural world.

INSTITUTIONAL ABBREVIATIONS

CMN	Canadian Museum of Nature, Ontario, Canada
CosmoCaxia	CosmoCaxia Barcelona, Barcelona, Spain
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China

NHMW Natural History Museum Vienna, Vienna, Austria
USNM Smithsonian National Museum of Natural History, Washington D.C., United States

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Author Contributions

- Eric Austin Ames conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Andre J. Rowe conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- David John Button conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The data is available at Zenodo and MorphoSource:

Zenodo:

- Eric Austin Ames Jr, David J. Button & Andre J. Rowe. (2026). Finite Element Dataset for "Let them fight: Using finite element analysis to determine combative evolutionary drivers of ceratopsian horns": Psittacosaurus [Dataset]. Zenodo. <https://doi.org/10.5281/zenodo.19475481>.

- Eric Austin Ames Jr, David J. Button & Andre J. Rowe. (2026). Finite Element Dataset for “Let them fight: Using finite element analysis to determine combative evolutionary drivers of ceratopsian horns”: USNM Specimens [Dataset]. Zenodo. <https://doi.org/10.5281/zenodo.18775165>.
- Eric Austin Ames Jr, David J. Button & Andre J. Rowe. (2026). Finite Element Dataset for “Let them fight: Using finite element analysis to determine combative evolutionary drivers of ceratopsian horns”: Triceratops and Spiclypeus [Dataset]. Zenodo. <https://doi.org/10.5281/zenodo.19475552>.
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- Eric Austin Ames Jr, David J. Button & Andre J. Rowe. (2026). R Code Dataset for “Let them fight: Using finite element analysis to determine combative evolutionary drivers of ceratopsian horns” (Version 1.0) [Dataset]. Zenodo. <https://doi.org/10.5281/zenodo.19454129>.

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Supplemental Information

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