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HORN USE IN *TRICERATOPS* (DINOSAURIA: CERATOPSIDAE): TESTING BEHAVIORAL HYPOTHESES USING SCALE MODELS

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ABSTRACT

Triceratops, a common chasmosaurine ceratopsid dinosaur from the Late Cretaceous of North America, is known for its cranial ornamentation, including a single nasal horn and large, paired supraorbital horns. It is commonly surmised that *Triceratops* used its horns in intraspecific combat, but this hypothesis has not been rigorously tested. Scale models of *Triceratops* skulls were used to determine if it could physically lock horns as has been suggested. Three hypothetical horn locking positions were found, involving varying orientations of the combatants' skulls. Based on these positions, it was hypothesized that injuries caused by horns were especially likely in certain portions of the frill, jugals, and postorbital horncore tips. This corresponds to some previously reported pathologies in chasmosaurine specimens. Uncertainties in this modeling exercise center around variations in horn orientation, size, shape, and the possible existence of a keratinous supraorbital horncore sheath. *Triceratops* differs from modern horned mammals in its horn orientation, which suggests that if it engaged in intraspecific combat, its fighting style was quite different from these modern animals. During hypothetical horn locking in *Triceratops*, most of the force was directed against the medial and lateral surfaces of the horn cores. This has implications for future studies of ceratopsid cranial functional morphology, especially as related to horn architecture and the development of the frontal sinus complex.

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INTRODUCTION

The ceratopsid dinosaurs, a group of large herbivorous dinosaurs from the Late Cretaceous of western North America, are known for their unusual cranial ornamentation. Ceratopsid skulls are typically characterized by a caudally projecting bony frill composed of the parietal and squamosal bones, as well as a combination of dorsally projecting horns above the eyes and external nares. The supraorbital horns are derived from the postorbital bones, and the horn over the nares is an outgrowth

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of the nasal bones, augmented by a separate ossification in chasmosaurine ceratopsids (a clade including *Chasmosaurus*, *Triceratops*, and others). Horn size varies both within and between taxa. For instance, *Centrosaurus* possesses an elongate nasal horn, and brow horns are small or absent. *Triceratops* has two elongate brow horns, whereas the nasal horn is reduced in size relative to that of *Centrosaurus*. These varied horn morphologies have invited a tremendous body of speculation over horn use.

Proposed uses for ceratopsid horns include intraspecific display and combat (Farlow and Dodson 1975; Lull 1933; Sampson et al. 1997), defense against predators (Hatcher et al. 1907; Lull 1933), thermoregulation (Barrick et al. 1998), and as aids in knocking down vegetation (Tait and Brown 1928). Images of two male *Triceratops* with horns locked in struggle over a group of females are particularly compelling, but largely speculative. The use of horns in intraspecific combat has received special attention in both the popular press and the scientific literature (e.g., Farlow and Dodson 1975; Lull 1933). Most cranial abnormalities, such as anomalous fenestrae in the frill, have been attributed to wounds received from intraspecific agonistic behavior (Lull 1933).

Previous workers have reviewed ceratopsian adaptations for combat as well as their similarities to modern horned animals (Farlow and Dodson 1975; Molnar 1977), but none have tested the physical possibility of combat in these animals. Farlow and Dodson (1975) divided ceratopsian combat into three categories, following a model for ungulate horn evolution proposed by Geist (1966). In brief, animals with type 1 combat behavior stood parallel and delivered blows against each other's flanks. Farlow and Dodson (1975) considered the small hornless neoceratopsian *Protoceratops* and the American mountain goat to exemplify this behavior. In type 2 combat behavior, individuals locked horns and wrestled; *Triceratops*, some chameleons, and domestic cattle were thought to share this behavior pattern. Animals using type 3 combat behavior, inferred in *Centrosaurus* and the modern rhinoceros, may also clash horns or use them to inflict injury. All three of these categories included the possible use of horns and frills as display organs. Molnar (1977) summarized cranial structures expected in animals engaging in horn locking behavior. These include firm support for the horncores; projection of the horns beyond the snout; protection of the jaw muscles, ears, and eyes; stiffening of the cervical vertebral series; and evidence of cranial puncture wounds. Because all of these features occur in ceratopsids, Molnar concluded that horn locking behavior was possible in *Triceratops* and many of its close relatives.

Alexander (1989) illustrated two *Triceratops* models locking horns; he concluded that their horns could interlock, but they may not have been strong enough for intraspecific combat (based on comparisons of horn cross-sectional area versus body mass in *Triceratops* and a variety of horned mammals). Farlow (1990) disputed Alexander's (1989) claim about *Triceratops* horn strength, using comparisons of horn cross-sectional area versus horn reach for *Triceratops* and horned mammals. He also briefly commented on orientation differences between antelope horns and ceratopsid horns. Yet, neither Alexander (1989) nor Farlow (1990) fully investigated all possible horn locking configurations and their behavioral implications.

The present study uses scale models to test the assumption that the horned dinosaur *Triceratops* could lock horns with its conspecifics. I seek to test the *feasibility* of horn locking behavior in this animal, not to prove that such behavior actually occurred. Additionally, this study does not consider or test other possible uses for the horns (such as predator defense or intraspecific recognition).

Triceratops was chosen as a study subject for three reasons. First, it is one of the best-known horned dinosaurs, with a number of well-preserved, uncrushed skulls in museum collections. Second, its horn morphology is representative of many other chasmosaurine ceratopsids. Finally, accurate scale models of *Triceratops* skulls were readily available for use in this project.

Abbreviations

Abbreviations used in the text are as follows: AMNH: American Museum of Natural History, New York, New York. MPM: Milwaukee Public Museum, Wisconsin. ROM: Royal Ontario Museum, Toronto, Ontario. SDSM: South Dakota School of Mines and Technology Museum of Geology, Rapid City. SMM: Science Museum of Minnesota, St. Paul. SMNH: Saskatchewan Museum of Natural History, Regina. TMP: Royal Tyrrell Museum of Paleontology, Drumheller, Alberta. USNM: National Museum of Natural History, Washington, D.C. YPM: Yale Peabody Museum of Natural History, New Haven, Connecticut.

MATERIALS AND METHODS

Scale models of *Triceratops prorsus* skulls (primarily based upon the holotype specimen YPM 1822) were used to test horn locking positions. The models were produced as part of the "Favorite Collection" skull models line, sculpted by Takashi Oda for Kinto and Company. The models were cast in poly-resin, and the skull and lower jaws were integrated into a single unit.

The models were sculpted at approximately 15% natural size. In order to verify their accuracy, they were compared with photographs, drawings, and measurements of YPM 1822. No major differences were noted between the scale model and the original specimen (see Appendix). Models were used in this study rather than full-size casts because the small models were easier to manipulate; it is presumed that this would achieve results similar to those found using full-size replicas. Also, models are appropriate here because scale-dependent factors (such as intracranial stress and strain) were not tested.

It was assumed that skull morphology accurately represents the shape of the head in life. However, a keratinous sheath may have increased horn length by a variable amount (Hatcher et al. 1907). Thus, the methodology presented here tested "horncore locking" rather than "horn locking," but the latter term will be used for simplicity. For the purposes of this study, it was assumed that the length of the horncores approximated the length of the horns (i.e., horncore plus horn sheath). Deviations from this assumption are addressed in the discussion.

Two identical skull models were used concurrently to determine positions in which the horns could interlock. Multiple positions were tried, with two constraints. First, the horns could not intersect with cranial fenestrae or foramina, such as the external nares or supratemporal fenestrae. In life, such action would have been harmful or fatal to the animals and not conducive to sustained horn locking. Thus, it is presumed that they would have avoided this behavior during wrestling matches (however, this assumption does not consider the possibility of a well-placed horn thrust used to disable an opponent and end the wrestling match). Second, the skull was constrained to rotate down 90 degrees or less from horizontal (as defined by the maxillary tooth row), reflecting limits in neck movement. This degree of movement is somewhat arbitrary, as the mechanics of ceratopsid neck motion are largely unexplored. Ultimately, this last constraint proved inconsequential, as it was found that most horn locking positions took place when the skulls were at an angle of 45 degrees or less from horizontal.

The skull models were photographed in all possible horn locking positions, and the relative skull positions were noted for later analysis and interpretation.

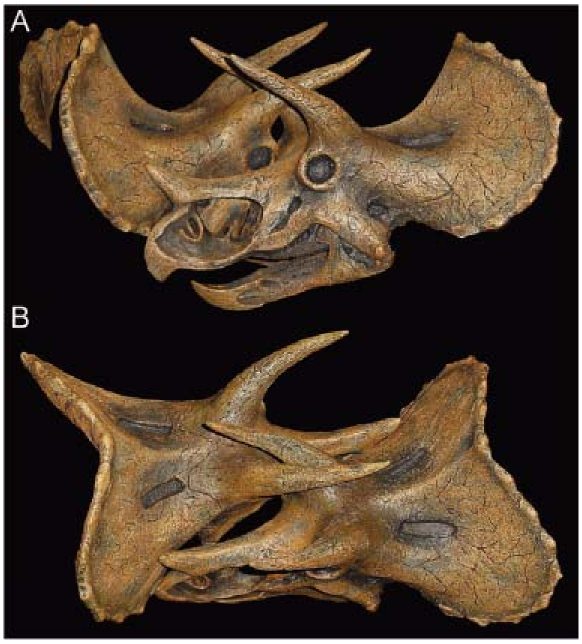

Figure 1. *Triceratops prorsus* skull models in the single horn contact (SHC) position, in A) lateral view, and B) dorsal view.

RESULTS

Three possible horn locking positions were found for the *Triceratops prorsus* skull models (Figures 1-3).

The first position (Figure 1), termed "single horn contact," or SHC, involved contact between only one postorbital horn of each combatant. The skulls were held roughly parallel to each other and subhorizontal, and the postorbital horns contacted each other near their bases.

The second position (Figure 2), termed "full horn locking," or FHL, involved contact between both postorbital horns of both combatants. The skulls were held roughly parallel to each other, at approximately 45 degrees below horizontal, and the snouts were nearly touching along their entire length. The postorbital horns contacted each other approximately one-fourth of the way up their length.

The third position (Figure 3), termed "oblique horn locking," or OHL, also involved contact between both postorbital horns of both combatants. The skulls were held subhorizontal and roughly parallel to each other, although they were also inclined toward each other along the sagittal plane. Horn contact was near the base of one postorbital horn for one animal and near the tip of one horn for the other, and vice versa for the other postorbital horns.

These positions do not include other possible modes of horn interaction, such as positions in

Figure 2. *Triceratops prorsus* skull models in the full horn locking (FHL) position, in A) lateral view, and B) dorsal view.

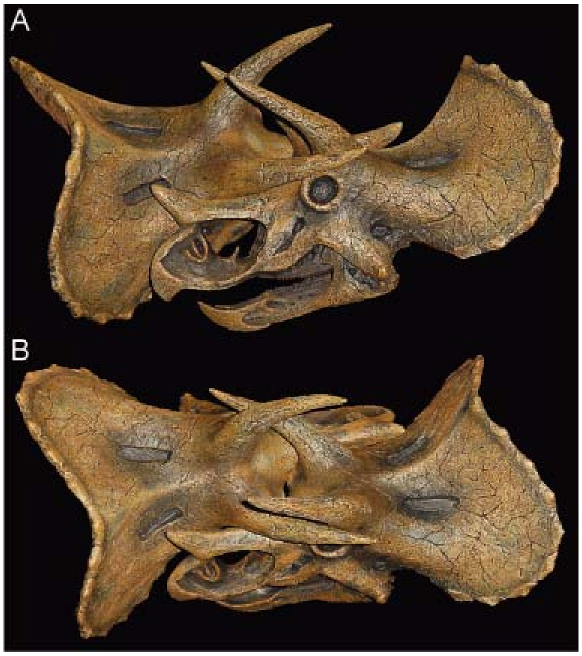

Figure 3. *Triceratops prorsus* skull models in the oblique horn locking (OHL) position, in A) lateral view, and B) dorsal view.

which the animals may have stood with skulls parallel, striking the horns together but not interlocking. Additionally, the positions cited here only reflect end members on a whole spectrum of intermediate positions.

DISCUSSION

In all of the horn locking positions, horn contact was made on the lateral and medial surfaces of the postorbital horncores. Thus, it appears that most of the force was applied to the horncores on their lateral and medial surfaces, rather than the rostral or caudal surfaces. Chasmosaurine ceratopsid postorbital horncores, particularly those of *Triceratops*, are often slightly mediolaterally compressed rather than perfectly round in cross section. This would have allowed a greater surface area on the medio-lateral surfaces of the horns, and hence a greater area of contact when the horns were locked.

Horn Locking and Paleopathologies

Based on the horn locking positions explored in this study, specific predictions can be made for sites on the skull where horn-induced trauma should occur (Figure 4). In the single horn contact position, there was little danger of injury from the postorbital horns (unless the skulls were tilted down to a great degree rostrally). The nasal horn was placed against the rostromedial portion of the squamosal bone of the frill, and the horn could possibly inflict injury here.

In the full horn locking position, both the nasal horn and the postorbital horns were possible sources of injury. The nasal horn was positioned very near the opponent's jugal, and the tips of the postorbital horns of both animals were quite near the rival's parietal portion of the frill, in the upper temporal fenestra region.

In the oblique horn locking position, the nasal horns once again were the major possible cause of injury. Here, injuries are predicted in the rostral portions of both the squamosals and the parietals.

Some known pathologies in *Triceratops* skulls correspond to injuries predicted by these models (Figure 5). Hatcher et al. (1907) noted a series of abnormal foramina along the medial border of the left squamosal of the specimen USNM 1201, which they interpreted as a traumatic injury. This corresponds to possible injury positions predicted by the FHL and OHL models. Additionally, Erickson (1966) noted an anomalous foramen in the jugal of specimen SMM P62/1/1. This corresponds to the placement of the nasal horn against the jugal in the FHL model. The skull SMNH P1163.4 lacks a major portion of the right squamosal, which

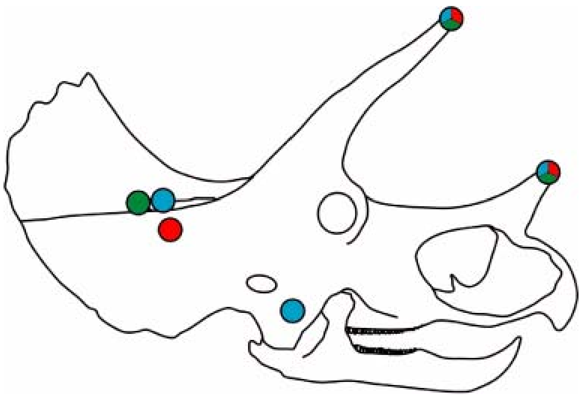

Figure 4. Schematic of *Triceratops prorsus* skull, showing areas where cranial pathologies are predicted by the SHC (red dots), FHL (blue dots), and OHL (green dots) models of horn locking.

occurred pre mortem based upon bone texture; the parietal bar of this specimen may display a healed fracture (Tanke and Rothschild 2002). These injury locations correspond to those predicted by all three of the horn locking positions shown here**.**

Injuries to the horncores themselves are also possible. Gilmore (1919) documented a pair of chasmosaurine (probably *Triceratops*) horncores, USNM 4708, in which the distal end of the right horncore is missing. Some evidence of healing is visible on the tip of this horn. Additionally, Rothschild and Tanke (1992) figured a cf. *Anchiceratops* (a chasmosaurine closely related to *Triceratops*) horncore, TMP 89.12.8, with pseudoarthrosis on its distal tip. This too may be due to trauma (Tanke, personal commun., 2003), whether from combat or other causes (e.g., a collision with a tree). Possibly such breaks occurred when stresses within horncore became too great for the bone to withstand. This could happen in any of the modeled horn positions, but horn injury would be particularly likely in those cases where the very tip of the horn was subjected to especially great stress, as in the OHL position (or if the SHC position were adopted with horn contact placed more distally). Injuries to the nasal horn are also possible in all three of the positions. However, this horn is typically much shorter and robust and thus less likely to break than the postorbital horns.

Some *Triceratops* specimens exhibit possible traumatic injuries not predicted by any of the models. For instance, the right frontal of the skull YPM 1823 preserves an anomalous foramen. None of the horn locking positions infer horn contact in this area. If this pathology is horn induced, it may have been caused by a slip of an opponent's horn.

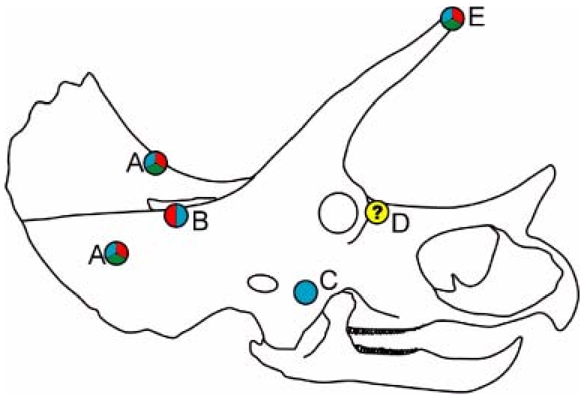

Figure 5. Schematic of *Triceratops prorsus* skull, showing the approximate locations of cranial lesions observed in actual *Triceratops* specimens. A) SMNH P1163.4, B) USNM 1201, C) SMM P62/1/1, D) YPM 1823, E) USNM 4708. Locations of lesions from the left side of the skull are mirrored to that of the right side. The colors of the dots, following the convention of Figure 4, indicate horn locking models with which the lesions are consistent. A yellow dot indicates a lesion which does not correspond to the horn locking positions inferred here.

It is tempting to suggest that the pathological specimens described here illustrate a stereotypy in lesion placement consistent with horn-induced injury, but the sample size simply isn't large enough to make this suggestion. Additionally, reports of pathology may be biased toward the horns and frill. Further work is needed to accurately map and define the occurrence of lesions in ceratopsian skulls.

Many of the reported lesions are consistent with horn-thrust injuries, but it is extremely important to note that traumatic injury has not been conclusively demonstrated in many of these specimens. Careful examination, perhaps coupled with bone histology work, is necessary to support the claims that these cranial anomalies are due to trauma and not other factors (as in the case of many squamosal fenestrae, long attributed to horn injuries but now reinterpreted as a disease or other bone remodeling process possibly analogous to that seen in some modern turtle carapaces; Tanke and Farke 2002). Bone fractures (as seen in SMNH P1163.4) are the only truly unambiguous indication of trauma. Indications of osteomyelitis or other conditions are less reliable, as they may be associated with non-traumatic disease processes. Even if the pathologies can be shown to result from trauma, it is difficult to conclusively demonstrate that these injuries resulted from horn locking behavior and not environmental obstacles (e.g. rocks, trees) or predator encounters.

Difficulties in Modeling Behavior

Horn shape, size, and orientation are variable in *Triceratops* (well illustrated in Lehman 1990), complicating interpretation and application of this study's results. The nasal horn is a particularly important variable. This horn is relatively long in YPM 1822, and there was some danger of the horn piercing a rival animal's skull during horn locking. This may have limited the range of movement for fighting animals. The nasal horn is reduced in size in many other *Triceratops* specimens (e.g., SDSM 2670), so these animals may have had a greater range of movement during combat. In fact, the nasal horn was so blunt in some specimens (e.g., USNM 1201) that it could have been used to butt against opponents' flanks without risk of major injury to either animal. Additionally, a blunt nasal horn would presumably reduce the risk of injury to the frill in any of the hypothesized positions.

Postorbital horn length and orientation also vary in *Triceratops*. Forster (1996) noted that YPM 1822 has comparatively short horns relative to its basal skull length, contrasting with the relatively longer horns seen in other specimens (e.g., USNM 1201). Additionally, the horns of YPM 1822 are at a smaller angle relative to horizontal than in some other *Triceratops* specimens (e.g., USNM 4928). This variation could affect horn locking in several ways. If the horns were relatively longer, but at the same orientation as in the models used here, horn locking positions would remain much the same. However, in cases of extreme elongation, horn contact would have to occur more distally on the horn core to reduce risk of injury to the frill. If the horns were at a greater angle to vertical, the relative orientation of the combatants' skulls would also have to be at a greater angle to allow effective horn locking in some positions. If the horns were at a greater angle to each other in the sagittal plane, the horns would contact each other quite proximally in the SHC position, but the horns would contact each other more distally in the OHL or FHL positions. Based upon experiments with simple clay models, all of the same horn locking positions were repeatable with these different horn orientations. However, much more experimentation is needed to determine how the full spectrum of *Triceratops* horn variation would have affected horn locking positions. If *Triceratops* wrestled in life, it likely employed any number of variations upon the positions found here.

The inferred presence of a keratinous sheath on the outside of the horns also complicates modeling, particularly if the sheath significantly lengthened the horn or altered horn shape. Anecdotally, Hatcher et al. (1907, p. 32) reported that when the *Triceratops* specimen YPM 1821 was discovered, "a portion of the investing horny material was still in place about the left horn core, though in such a decomposed condition that it was impossible to preserve it." Happ and Morrow (2000) also reported possible remnants of the horn sheath in a *Triceratops* specimen from the Hell Creek Formation of Montana, but this specimen has not been fully described. However, none of these fossils reveal the length or shape of the sheath, or if it was indeed a keratinous sheath and not just a layer of skin. Any speculation upon sheath morphology is difficult. But, it is highly unlikely that *Triceratops* had complicated, curled horns such as seen in the mountain sheep, *Ovis canadensis*. In this and other sheep and goats with curled horns, the horncore itself is also curled, although not to the degree of the sheath (Schaffer and Reed 1972). This contrasts with the relatively straight horncores seen in *Triceratops*. The curled horn morphology is also apparently related to head-butting behavior (Lundrigan 1996), a behavior that was clearly difficult if not impossible in *Triceratops*. In any case, the addition of horn length by a sheath would affect horn locking behavior in the manner discussed above for variations in horncore length. Horn locking positions would remain much the same, regardless of sheath length.

A major simplification of this study is the use of two identical cranial models. In actuality, it is highly unlikely that any two interacting *Triceratops* had identical cranial morphology. Horn locking would still be possible, but variations in skull morphology must be investigated with further modeling.

Triceratops Horn Locking Compared with Bovid Mammal Horn Locking

The supraorbital horns of *Triceratops* and many of its close relatives are frequently compared to those of bovid mammals such as bison, goats, and African antelope (e.g., Farlow and Dodson 1975). Indeed, the gross horn morphology of both groups is quite similar, in that the horns are paired, placed posteriorly on the skull, and unbranched. However, horn orientation is quite different between the two groups (Farlow 1990). In *Triceratops* and other known chasmosaurines, the postorbital horns are directed rostro-dorsally relative to the rest of the skull, with only a small lateral component in most taxa. The horns of bovid mammals may point laterally (as in the American bison or the African buffalo), caudally (as in gazelle and oryx), or laterally and rostrally (e.g., some domesticated cattle). Also, the horns of bovids may be "curled" (as in bighorn sheep) or twisted (as in kudu).

Logically, horn morphology should be correlated to fighting style (e.g., Geist 1966). But, few morphometric studies have investigated the relationship (if any) between horn orientation, horn shape, and horn use in bovid mammals. Lundrigan (1996) studied this problem for 21 bovid species representing 11 of the 12 bovid tribes. Interestingly, she found that neither the vertical angle of the horns nor their angle with the sagittal plane was significantly correlated to any fighting mode. This would suggest that horn orientation has little bearing on the behavior for which these horns are used. Instead, Lundrigan (1996) found that the overall horn shape and length (e.g., the degree of curvature and the greatest straight-line length of the horn) were significantly correlated to fighting mode.

Bovids with very short horns and short catching arches (the recurved region between the base and the tip of the horn) tended to engage in stabbing behavior (e.g., mountain goats). Neither of these qualities applies to *Triceratops*, but it may apply to other ceratopsid dinosaurs (see next section).

Lundrigan (1996) determined that bovids employing ramming behavior (e.g., bighorn sheep) tended to have "curled" horns with a large basal circumference. Such behavior clearly was not possible in *Triceratops*, due to the near-vertical horn orientation that prevented any frontal contact. Also, this horn orientation would have made a high-speed head-to-head charge quite hazardous.

According to Lundrigan's (1996) analysis, bovids that employ "fencing" behavior (in which the horns are clashed against each other, without sustained locking) usually possess a long horn "reach" (greatest "straight" length of horn, exclusive of curves). Such behavior would have been physically possible in *Triceratops*.

Bovids engaging in sustained wrestling (horn locking) behavior generally have a large "catching arch," (Lundrigan 1996). In many of these animals, the dorsal surface of the skull is held nearly against the ground during horn locking. This specific position could not have occurred in *Triceratops*, due to limitations in mobility imposed by its vastly different horn orientation, probably more limited neck mobility, and the large bony frill. If *Triceratops* locked horns, it would have done so in a manner different from that seen in bovids, as illustrated by the models in this study (Figures 1-3). The complex motions required to interlock the horns of *Triceratops* suggest that the individual combatants had to carefully and deliberately orchestrate horn locking.

Caro et al. (2003) also discussed the relationship between horn shape and behavior. However, their study primarily focused upon qualitative variables such as horn tip orientation or horn sheath morphology, and information such as absolute horn size and orientation was not considered. Thus, their results are not directly comparable to Lundrigan's (1996) results. Nonetheless, Caro et al. (2003) also found significant correlations between horn morphology and fighting style, most of which broadly match Lundrigan's results.

It is quite probable that relationships between horn morphology and behavior existed in ceratopsid dinosaurs, as discussed by other workers (e.g., Farlow and Dodson 1975). But ultimately, ceratopsid behavior cannot be directly inferred from that of bovids due to the disparate phylogenetic origin, unique horn orientation, and other unusual cranial features (such as nasal horns and frills) found in ceratopsids.

Some extant chameleons (e.g., *Chamaeleo jacksoni*) superficially resemble *Triceratops* in horn number (up to three horns), position (one nasal and two supraorbital), and orientation (directed rostrally). Most importantly, three-horned chameleons are known to lock horns in intraspecific combat. During these confrontations, male Jackson's chameleons will face off and then rush forward to interlock horns. Then, they may twist their heads back and forth in an effort to throw each other off balance. The combatants may also attempt to stab each other in the body or limbs (Carpenter and Ferguson 1977). Some illustrated chameleon horn locking positions even resemble those modeled for *Triceratops* (e.g., Farlow 2001). Unfortunately, the analogy is not perfect. For instance, the horns are directed almost horizontally in chameleons, contrasting with the more vertical orientation of ceratopsids, and chameleons are much smaller than ceratopsids. Nonetheless, chameleons provide an extant precedent for wrestling with three horns.

Horn Use in Other Chasmosaurines

The observations made for *Triceratops* likely apply to most other chasmosaurines, particularly those with elongated postorbital horns (including *Anchiceratops, Arrhinoceratops*, *Diceratops*, *Pentaceratops*, and *Torosaurus*). The only major difference occurs in some individuals of the genus *Chasmosaurus*; many specimens of this taxon (e.g., ROM 843) have very small or non-existent postorbital horns. Clearly, horn locking did not occur here (barring the presence of extremely elongated horn sheaths which have not been preserved in the fossil record). If intraspecific fighting did occur in these individuals without postorbital horns, it was probably quite different relative to *Triceratops*, perhaps with head or flank butting or stabbing behavior. Further work on *Chasmosaurus* cranial models may elucidate this.

Few cranial pathologies have been described in chasmosaurines outside of *Triceratops* (excluding squamosal fenestrae, of dubious origin as mentioned above), but those that have been are consistent with horn locking models discussed above. For instance, *Torosaurus* specimen MPM VP8149 displays a lesion on the medio-rostral margin of the left squamosal (Marshall and Barretto 2001), a location consistent with all three of the hypothetical horn locking positions. *Diceratops* specimen USNM 2412 displays an area of calloused bone on the left squamosal, also suggesting horn-induced injury. Careful study of other chasmosaurine specimens may show additional evidence of cranial pathology.

The results of this study are not applicable to any described centrosaurine taxa, because most of these taxa do not possess elongated postorbital horns.

CONCLUSIONS

The implications of this exploratory study for the current understanding of chasmosaurine biology are quite broad. First, it shows that horn locking behavior was physically possible in *Triceratops,* although it does not prove that it actually happened. Second, this work places limits upon the fighting techniques of these animals. Only a limited range of horn locking positions was feasible for the models used in this study. Presumably the positions vary slightly between individuals, depending on horn size, orientation, and the length of a hypothetical keratinous sheath. Additional work with models possessing other horn configurations could further elucidate this hypothesis. This study also posits pathologic “hot zones,” the cranial areas where traumatic injuries could be expected. Traditionally, nearly all ceratopsid cranial abnormalities are attributed to injuries incurred during fighting. A careful analysis of all “pathological” specimens is needed to confirm or refute this paradigm.

Finally, this study lays groundwork for future biomechanical studies of the ceratopsid skull, by suggesting the orientation and location of forces acting upon the horncores. These forces may have had a great influence on ceratopsid skull evolution, particularly the development of the frontal sinus complex overlying the braincase and underlying the horns. However, the horns are only one part of the ceratopsid skull, and any future work must consider the skull as a functional whole.

Clearly, the scientific understanding of ceratopsid skull function and evolution is in its earliest stages. With both new and old modeling techniques, our understanding of ceratopsid biology may move from the realm of informed speculation to rigorous hypothesis testing.

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REFERENCES

Alexander, R.M. 1989. *Dynamics of Dinosaurs and Other Extinct Giants.* Columbia University Press: New York.

Barrick, R.E., Stoskopf, M.K., Marcot, J.D., Russell, D.A., and Showers, W.J. 1998. The thermoregulatory functions of the *Triceratops* frill and horns: Heat flow measured with oxygen isotopes. *Journal of Vertebrate Paleontology*, 18:746-750.

Carpenter, C.C., and Ferguson, G.W. 1977. Variation and evolution of stereotyped behavior in reptiles, p. 335-554. In Gans, C., and Tinkle, D.W. (eds.), *Biology of the Reptilia.* Academic Press, London.

Caro, T.M., Graham, C.M., Stoner, C.J., and Flores, M.M. 2003. Correlates of horn and antler shape in bovids and cervids. *Behavioral Ecology and Sociobiology,* 55:32-41.

Erickson, B.R. 1966. Mounted skeleton of *Triceratops prorsus* in the Science Museum. *Scientific Publications of the Science Museum of Minnesota*, 1:1-15.

Farlow, J.O. 1990. Dynamic dinosaurs. *Paleobiology*, 16:234-241.

Farlow, J.O. 2001. *Bringing Dinosaur Bones to Life*. Franklin Watts, New York.

Farlow, J.O., and Dodson, P. 1975. The behavioral significance of frill and horn morphology in ceratopsian dinosaurs. *Evolution*, 29:353-361.

Forster, C.A. 1996. Species resolution in *Triceratops:* cladistic and morphometric approaches. *Journal of Vertebrate Paleontology*, 16:259-270.

Geist, V. 1966. The evolution of horn-like organs. *Behaviour*, 27:175-214.

Gilmore, C.W. 1919. New restoration of *Triceratops,* with notes on the osteology of the genus. *Proceedings of the United States National Museum*, 55:97-112.

Happ, J.W., and Morrow, C.M. 2000. Evidence of soft tissue associated with nasal and supraorbital horn cores, rostral and exoccipital of *Triceratops*. *Journal of Vertebrate Paleontology*, 20 (supplement to number 3):47A.

Hatcher, J.B., Marsh, O.C., and Lull, R.S. 1907. *The Ceratopsia. United States Geological Survey Monograph*, 49:1-300.

Lehman, T.M. 1990. The ceratopsian subfamily Chasmosaurinae: sexual dimorphism and systematics, p. 211-229. In Carpenter, K., and Currie, P.J. (eds.), *Dinosaur Systematics: Approaches and Perspectives*. Cambridge University Press, Cambridge.

Lull, R.S. 1933. A revision of the Ceratopsia, or horned dinosaurs. *Memoirs of the Peabody Museum of Natural History*, 3:1-175.

Lundrigan, B. 1996. Morphology of horns and fighting behavior in the family Bovidae. *Journal of Mammalogy*, 77:462-475.

Marshall, C., and Barretto, C. 2001. A healed *Torosaurus* skull injury and the implications for developmental morphology of the ceratopsian frill. *Journal of Morphology*, 248:259.

Molnar, R.E. 1977. Analogies in the evolution of combat and display structures in ornithopods and ungulates. *Evolutionary Theory*, 3:165-190.

Rothschild, B.M., and Tanke, D.H. 1992. Paleopathology: insights to lifestyle and health in the geological record. *GeoScience Canada*, 19:73-82.

Sampson, S.D., Ryan, M.J., and Tanke, D.H. 1997. Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia: Ceratopsidae): taxonomic and behavioural implications. *Zoological Journal of the Linnean Society*, 121:293-337.

Schaffer, W.M., and Reed, C.A. 1972. The co-evolution of social behavior and cranial morphology in sheep and goats (Bovidae, Caprini). *Fieldiana Zoology*, 61:1-88.

Tait, J., and Brown, B. 1928 . How the Ceratopsia carried and used their head. *Transactions of the Royal Society of Canada, Series 3*, 22:13-23.

Tanke, D.H., and Farke, A.A. 2002. Bone resorption, bone lesions, and extra fenestrae in ceratopsid dinosaurs. *Journal of Vertebrate Paleontology*, 22 (supplement to number 3):113A.

Tanke, D.H., and Rothschild, B.M. 2002. DINOSORES: An Annotated Bibliography of Dinosaur Palaeopathology and Related Topics–1838-2001. *New Mexico Museum of Natural History and Science Bulletin*, 20:1-96+iv.

APPENDIX

Dimensions of the models used in this study were compared with dimensions of the original specimen, to evaluate the models' accuracy. The measurements for the original specimen, YPM 1822, are taken from Hatcher et al. (1907), and the measurements of the model were made using sliding calipers. The model's dimensions range from 12.1% to 22.4% of the dimensions given by Hatcher, with an average value of 14.8%. The measurements for the model and the original specimen have a correlation coefficient of .977, with an R^2 value of .955, $p<.005$. All measurements are in millimeters. A slight difference in nasal horn orientation exists between the model and the original specimen. Given the variation in cranial form within *Triceratops* (see Discussion), this difference was not considered to be of great importance.

Measurement	Original Specimen	Model	Percent
Length of skull from distal tip of nasal horn core to caudal border of parietal	1383	202	14.6%
Greatest width of frill	944	165	17.5%
Width across squamosal rostro-ventral borders	556	67	12.1%
Width across distal ends of epijugals	532	89	16.7%
Distance from rostral border of orbit to apex of rostral	712	102	14.3%
Distance from orbit to tip of nasal horn core	660	89	13.5%
Distance between orbits	245	55	22.4%
Distance from ventral border of orbit to distal tip of jugal	340	50	14.7%
Rostro-caudal orbit diameter	128	16	12.5%
Dorso-ventral orbit diameter	122	16	13.1%
Distance from dorsal border of orbit to tip of postorbital horncore	550	84	15.3%
Distance from tip of postorbital horncore to tip of nasal horncore	650	86	13.2%
Distance from rostral border of orbit to caudal border of external naris	250	32	12.8%