Received: 20 December 2023 | Revised: 31 May 2024 | Accepted: 7 June 2024

DOI: 10.1002/ar.25526

RESEARCH ARTICLE

The Anatomical Record WILEY

Headbutting through time: A review of this hypothesized behavior in "dome-headed" fossil taxa

D. Cary Woodruff[1,2] | Nicole L. Ackermans[3]

[1]Phillip and Patricia Frost Museum of Science, Miami, Florida, USA

[2]Museum of the Rockies, Bozeman, Montana, USA

[3]College of Arts and Sciences, Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama, USA

Correspondence
D. Cary Woodruff, Phillip and Patricia Frost Museum of Science, 1101 Biscayne Blvd, Miami, FL 33132, USA.
Email: sauropod4@gmail.com

Abstract

Headbutting is a combative behavior most popularly portrayed and exemplified in the extant bighorn sheep (*Ovis canadensis*). When behaviorally proposed in extinct taxa, these organisms are oft depicted *Ovis*-like as having used modified cranial structures to combatively slam into one another. The combative behavioral hypothesis of headbutting has a long and rich history in the vertebrate fossil literature (not just within Dinosauria), but the core of this behavioral hypothesis in fossil terrestrial vertebrates is associated with an enlarged osseous cranial dome—an osteological structure with essentially no current counterpart. One confounding issue found in the literature is that while the term "headbutting" sounds simplistic enough, little terminology has been used to describe this hypothesized behavior. And pertinent to this special issue, potential brain trauma and the merits of such proposed pugilism have been assessed largely from the potential deformation of the overlying osseous structure; despite the fact that extant taxa readily show that brain damage can and does occur without osteological compromise. Additionally, the extant taxa serving as the behavioral counterpart for comparison are critical, not only because of the combative behaviors and morphologies they display, but also the way they engage in such behavior. Sheep (*Ovis*), warthogs (*Phacochoerus*), and bison (*Bison*) all engage in various forms of "headbutting", but the cranial morphologies and the way each engages in combat is markedly different. To hypothesize that an extinct organism engaged in headbutting like an extant counterpart in theory implies specific striking:contacting surfaces, speed, velocity, and overall how that action was executed. This review examines the history and usage of the headbutting behavioral hypothesis in these dome-headed fossil taxa, their respective extant behavioral counterparts, and proposes a protocol for specific behavioral terms relating to headbutting to stem future confusion. We also discuss the disparate morphology of combative cranial structures in the fossil record, and the implications of headbutting-induced brain injury in extinct taxa. Finally, we conclude with some potential implications for artistic reconstructions of fossil taxa regarding this behavioral repertoire.

KEYWORDS

bighorn sheep, brain injury, cranial combat, dome, fossil, pachycephalosaurid

1 | INTRODUCTION

Evidence of behavior in the fossil record is exceedingly sparse. In examining crown taxa, such as in cervids and bovids, comparisons to extant taxa can be more direct in reconstructing extinct behaviors (although by no means foolproof). For example, antlers in extinct cervids presumably served a similar behavioral and functional role as in extant taxa. However, reconstructing past behavior becomes especially problematic in clades lacking modern members. For example, while avian theropods (birds) are the most diverse group of extant terrestrial vertebrates today (>10,000 species; Cornell Lab of Ornithology; Center for Biological Diversity), their nonavian dinosaur kindred in many respects have no extant analogue.

With regards to, but not restricted entirely to, nonavian dinosaurs, indirect comparisons of osteological features between extinct and extant taxa are often made to infer hypothesized behaviors. For example, ceratopsian dinosaurs had cranial features including elaborate nasal and orbital horns that are popularly depicted as combative structures. In looking for extant analogs, bovids are large-bodied, quadrupedal, herbivorous, horned animals that readily exhibit agonistic (most often intraspecific) combat with said horns. Therefore, bovid-like cranial "wrestling" (Vander Linden & Dumont, 2019) has been a comparative behavior applied to ceratopsians artistically (such as the 1925 film *The Lost World*) and scientifically (see Farlow & Dodson, 1975; Farke, 2004; Figure 1).

One of the most popular portrayals of a pugilistic behavior in fossil taxa is headbutting. Famously exemplified in the extant bighorn sheep (*Ovis canadensis*), this agonistic behavior is popularly, and most often portrayed in the dinosaurian clade Pachycephalosauria. Bighorn sheep possess large, circumferentially curled keratinous covered horns on top of their head, while pachycephalosaurids generally had an enlarged spherical dome of hypermineralized bone atop their cranium (potentially also keratin covered). In a hypothesized behavioral scenario, two combatant pachycephalosaurids contact one another with high-velocity blows delivered with and to the domed mass of bone, akin to the headbutting behavior of bighorn sheep. The enlarged apical cranial structures of the bighorn sheep and pachycephalosaurids has been scientifically and artistically depicted as analogous, despite the fact that these two structures are morphologically nearly completely unalike. Headbutting behavior has even been hypothesized in nonmammalian therapsids and nonavian theropod dinosaurs that did not possess either bighorn sheep or pachycephalosaurid-like cranial structures (Bakker, 1986; Benoit et al., 2016; Cau et al., 2013; Delcourt, 2018; Mazzetta et al., 2009; Novas, 1989; Paul, 1988; Sampson & Witmer, 2007; Sereno & Brusatte, 2008; Snively et al., 2011).

This paper serves as a review of "headbutting" behavior within the terrestrial vertebrate fossil record, specifically in taxa with domed cranial structures. Additionally, we discuss the disconnect between a hypothesized shared behavior, despite nonoverlapping morphologies, as well as the potential implications towards artistic reconstructions in regards to combative styles in fossil taxa.

1.1 | What exactly is "headbutting"?

Throughout this review, there are demonstrable cases where the term "headbutting" (headbutting = head-butting = head butting) has caused cascading confusion

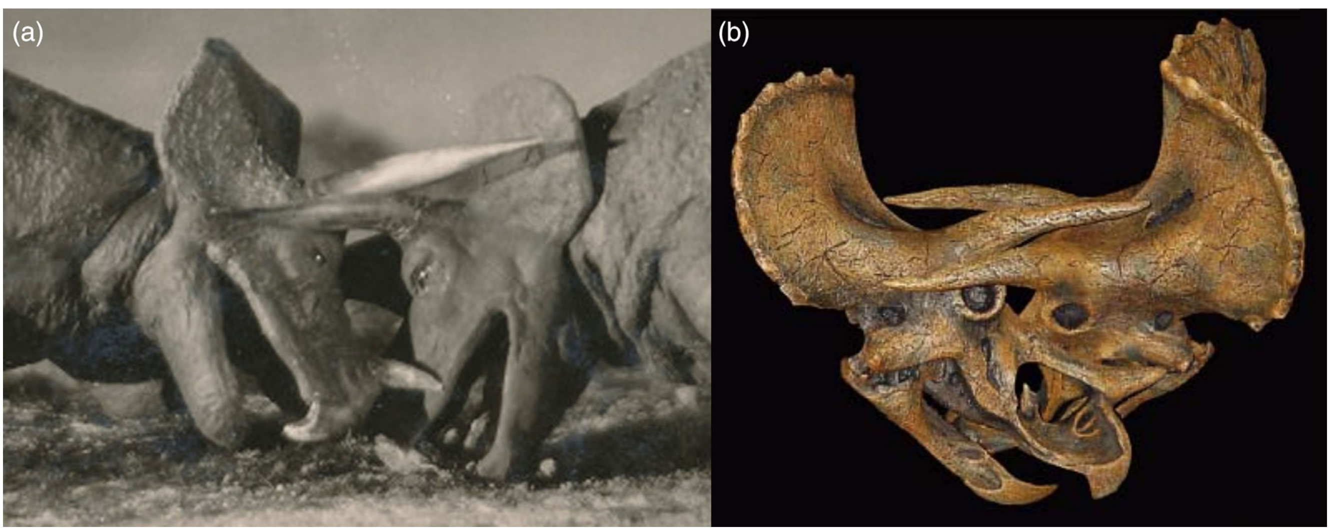

FIGURE 1 Bovid-like head-to-head "wrestling" portrayed in the ceratopsian *Triceratops*. (a) The first animated ceratopsian intraspecific combat shown via *Triceratops* in H. Hoyt's 1925 film *The Lost World*; (b) Study of how *Triceratops* horns could interlock for wrestling-style intraspecific combat (from Farke, 2004 Figure 2a reflected).

(see examples with Barghusen, 1975 and Geist, 1972). Unequivocally, the source of terminological confusion is that to date, "headbutting" (or other combative styles) have largely not been empirically defined. As is, one could say "headbutt" in the context that an organism uses its cranium combatively to strike or butt into any part of an opponent, or that two opponents butt crania together. Both are correct, but the engagement between opponents is very different, despite using the same term. As exemplified by studies such as Galton (1970), Carpenter (1997), Mazzetta et al. (2009), Snively et al. (2011), and Peterson et al. (2013) (discussed in detail in the text), an extant species behavior specifier qualitatively leaves less room for interpretation or confusion as to the specific behavior discussed. If a behavior for an extinct taxon is hypothesized, an extant analog should be specified. Sheep (*Ovis*), warthogs (*Phacochoerus*), and bison (*Bison bison*) all engage in various forms of cranial "butting" (Emlen, 2014), but the underlying morphologies and the way in which said behavior is expressed differs vastly (Figure 2).

When male bighorn sheep combatively engage in headbutting (they do also contact horns in noncombative ways [Hass & Jenni, 1993]), they run full-speed towards their opponent, and often lunge with their hind limbs, or launch, into one another, bringing the broad medial base region of the horns together (Schaffer, 1968). Thus, saying "bighorn sheep-like headbutting" implies specific actions, such as the exact striking and contacting surfaces (from here on referred to as striking:contacting). Additionally, although potentially redundant, we recommend including velocity specifiers as well, as studies such as Snively and Cox (2008) showed, even if it is the same striking:contacting surface (such as head-to-head or head-to-body) mechanically there is a considerable difference between high- and low-velocity impacts. We thus suggest in future work that if authors wish to specify the extant species comparison, they do so using up to date literature references and include the striking:contacting surfaces as well as the velocity, i.e., "warthog-like head-to-head high-velocity contact."

1.2 | The oddity of the cranial dome

There are many terrestrial vertebrate fossil clades—such as Dinocephalia, Therocephalia, Ceratopsia, Theropoda, Giraffidae, Cervidae, Antilocapridae, and Bovidae—that sported enlarged cranial ornamentation such as crests, horns, ossicones, antlers, and other protuberances that have been hypothesized to have served an agonistic combative role (Bakker, 1986; Barghusen, 1975; Barnosky, 1985; Benoit et al., 2016; Benton & Harper, 2020; Bubenik, 1990; Cau et al., 2013; Churcher, 1990; Delcourt, 2018; Farke, 2004; Mazzetta et al., 2009; Novas, 1989; Paul, 1988; Sampson & Witmer, 2007; Sereno & Brusatte, 2008; Snively et al., 2011; Solounias, 2007). But across both extant and extinct species, a domed cranial structure is fairly unique, thus far only recognized in dinocephalians, burnetiamorphs, pachycephalosaurids, chalicotheres, and possibly in some ceratopsians and artiodactyls (see Discussion; Figure 3). The osteological composition of such structures varies across these clades. For example, in *Moschops* spp., in lateral view, dorsal cranial elements are arched, as well as transversely widened and dorsoventrally thickened frontal bones contributing to their domed "forehead" (Benoit et al., 2017; Boonstra, 1957). Several burnetiamorphs have enlarged supratemporal, postfrontal, frontal, or nasal horns, crests, protuberances, and bosses (Day et al., 2018). And many had, dense, highly vascularized, dorsoventrally thickened and domed frontal and supraorbital bosses (Kulik & Sidor, 2019). In pachycephalosaurids, the frontal and parietal bones are spherically inflated and fused to create the frontoparietal dome (Maryánska et al., 2004). This dome, consisting of

FIGURE 2 Examples of cranial butting combative styles in extant mammals. (a) Head-to-head high-velocity striking in bighorn sheep (*Ovis canadensis*; from US Department of the Interior); (b) Head-to-head high-velocity "wrestling" in bison (*Bison bison*, Wikimedia CC BY-SA 4.0); (c) Head-to-head low-velocity pushing/shoving in warthogs (*Phacochoerus aethiopicus*, Wikimedia CC BY-SA 4.0).

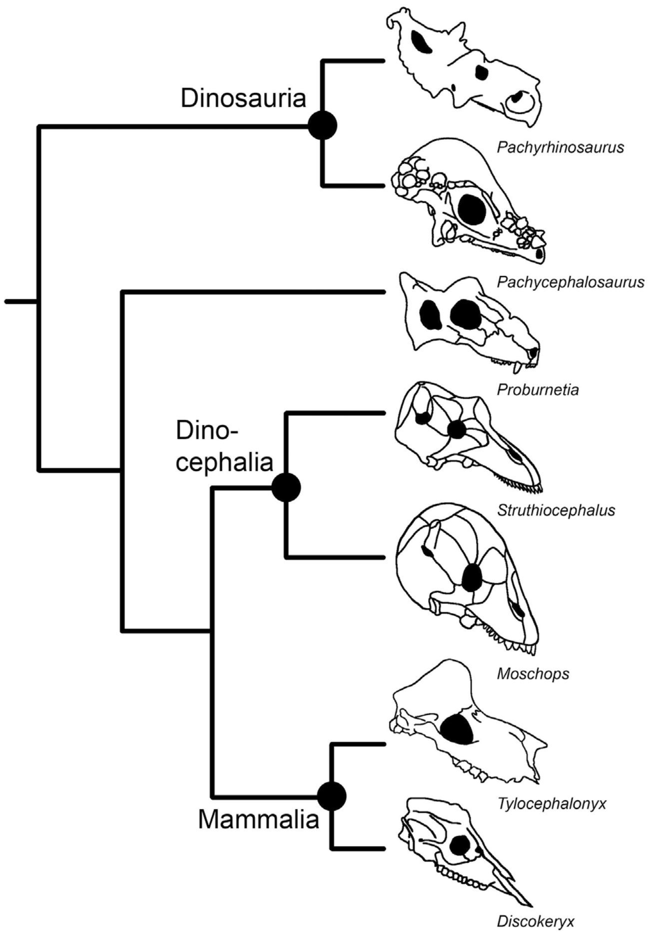

FIGURE 3 Phylogeny of some of the fossil taxa mentioned in this analysis that have been hypothesized to have engaged in headbutting. Silhouettes of skulls not to scale.

dense, hypermineralized bone could be upwards of 25 cm thick in the clade's eponym *Pachycephalosaurus wyomingensis* (Maryánska et al., 2004). Some ceratopsians, such as *Pachyrhinosaurus* had large, nasal and supraorbital bosses, likewise composed of dense bone in excess of 25 cm thick (Sternberg, 1950), covered in a large cornified pad, like the bosses of the African buffalo (*Syncerus* spp.) or muskox (*Ovibos moschatus*) (Hieronymus et al., 2009). In chalicotheres such as *Tylocephalonyx*, a dorsoventrally tall and vaulted dome was formed from the dorsal expansion of the frontal and parietal bones (Munthe & Coombs, 1979)—much like the dome of pachycephalosaurids. However, unlike the dense, hypermineralized dome of pachycephalosaurids, the dome of *Tylocephalonyx* was completely hollow (Munthe & Coombs, 1979).

While intra-/interspecific combat with cranial structures is observable in a plethora of extant taxa, today, the only terrestrial vertebrates with any comparable domed structures are the white-bellied duiker (*Cephalophus leucogaster*; Figure 4a,b) and the helmeted hornbill (*Rhinoplax vigil*; Figure 4e,f). Features, traits, and behaviors are convergently evolved, and the default should not be to assume that every structure or behavior is unique. For example, while ceratopsian orbital horns can morphologically be different from many bovids, both at least constitute a horn adjacent to the orbit that has an underlying osseous core and an overlying keratinous sheath. And as mentioned above, the hypothesis that such similar structures may have been used in like manner certainly is not implausible. But a domed cranial structure is incredibly rare today. Therefore, the comparisons to differing cranial structures, and their proposed extant behavioral analogs, can serve as a fascinating example of documenting the history, concept development, and rationale behind behavioral hypotheses in fossil taxa with no immediate extant counterparts.

2 | HISTORIC OVERVIEW OF HEADBUTTING IN THE DOMED-TAXA PALEONTOLOGICAL LITERATURE

2.1 | Nonmammalian therapsids

2.1.1 | Dinocephalia

Brink (1958) was the first to propose headbutting behavior in dinocephalians (within *Struthiocephalus kitchingi*; Figure 5a). Specifically, Brink (1958) cited that the horizontal occiput would produce a vertically oriented skull. With a ventrally directed snout, an enlarged and anteriorly directly frontonasal boss (which likely had a hornlike covering), and "not having the agility of a mammal", Brink (1958) saw this suite of morphologies as unlike those "expected" if they served an offensive, interspecific role, but instead, well-suited for bouts of intraspecific behavior.

In 1972, noting the, "…thick-boned skulls, and hornlike bumps on the head…" in many dinocephalians and dicynodontids, Geist (1972) said that these morphologies indicated that these animals engaged in combat, "by pushing each other in combat head-on, and wrestling…". Later on, making a prediction about the morphology of the occiput and cervical vertebrae from combative forces, Geist (1972) mentions, "…butting and head wrestling…".

However, in 1975, Barghusen challenged Brink's (1958) suggestion of headbutting in *Struthiocephalus*. Barghusen (1975) had no qualms with cranial combat, but alternatively proposed flank butting; "In head to head combat, the [horn] boss would serve to deflect the head to the side… In flank-butting, however, the boss would concentrate the force of the blow, thereby increasing its effectiveness in the manner… for primitive small-horned

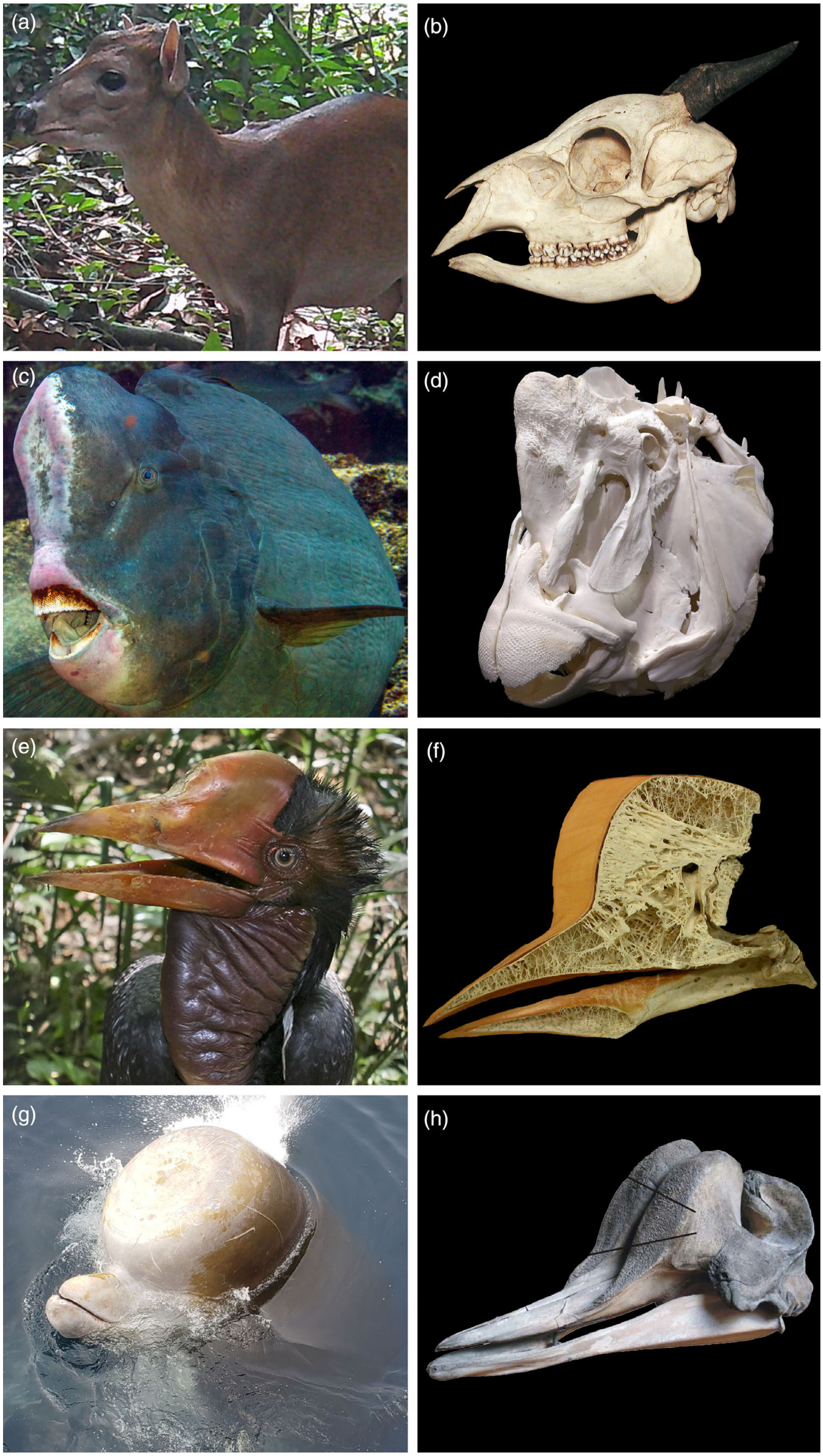

FIGURE 4 "Dome-headed" extant vertebrates. (a) White-bellied duiker (*Cephalophus leucogaster*; iNaturalist and X. Rufray); (b) White-bellied duiker skull (FMNH 27546; Field Museum of Natural History); (c) Green humphead parrotfish (*Bolbometopon muricatum*; iNaturalist and M. Rosenstein); (d) Green humphead parrotfish skull (skulls_steven); (e) Helmeted hornbill (*Rhinoplax vigil*; Wikimedia CC BY-SA 4.0); (f) Helmeted hornbill skull (Natural History Museum—London); (g) Northern bottlenose whale (*Hyperoodon ampullatus*, iNaturalist and J-F Rousseau); (h) Northern bottlenose whale skull (from Lambert et al., 2011).

mammals" (Barghusen, 1975 p. 306). Aside from *Struthiocephalus*, Barghusen (1975) also reviewed other hypothesized dinocephalian cranial combative adaptations, including the skulls of *Criocephalosaurus*, *Estemmenosuchus*, *Moschops*, and *Titanophoneus* (Figure 5b). Barghusen (1975) found support for structural modifications in

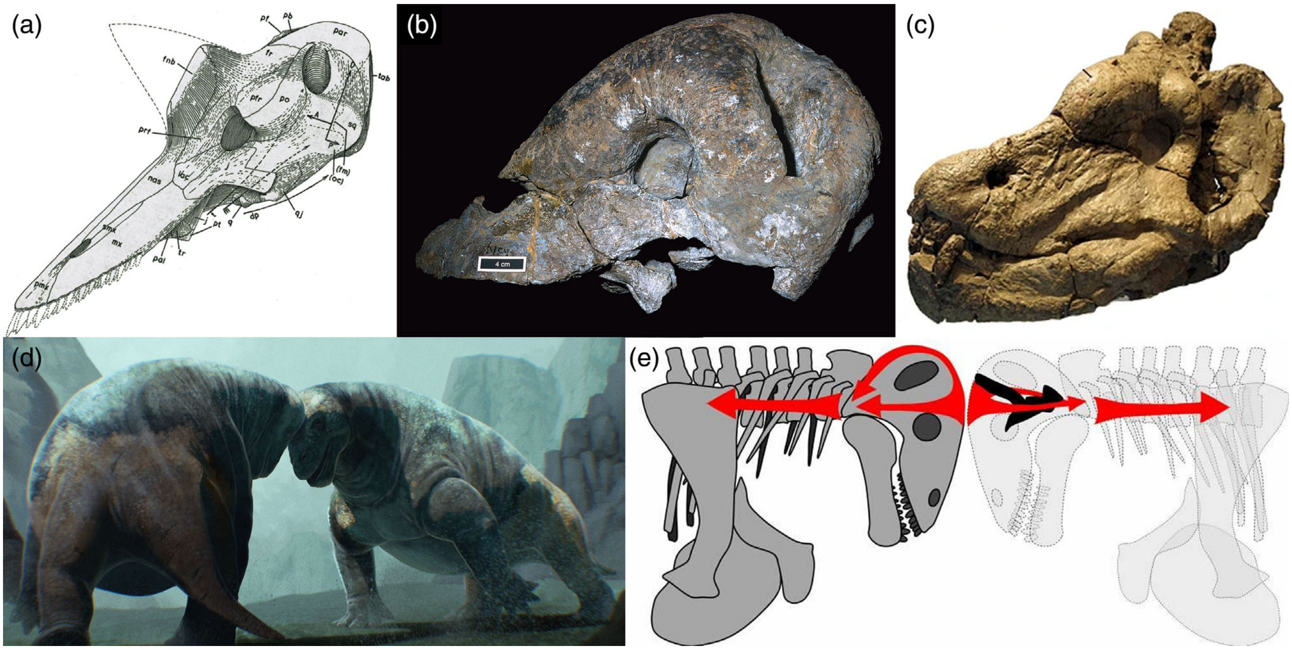

FIGURE 5 Cranial morphology in various therapsids hypothesized to be for intraspecific combat. (a) Illustrated skull of the tapinocephalid *Struthiocephalus kitchingi* (skull in right lateral view; from Brink, 1958); (b) Skull of the tapinocephalid *Criocephalosaurus* sp. (skull in left lateral view; Wikimedia CC BY-SA 4.0); (c) Skull of the anteosaurid *Anteosaurus magnificus* (skull in left lateral view; from Angielczyk, 2009); (d) Hypothesized headbutting between two *Moschops* © G. Ugueto; (e) Hypothesized dissipation of energy (red arrow = direction of energy transfer) during headbutting in *Moschops* (from Benoit et al., 2017). Skulls not to scale.

these other taxa that was consist with cranial combat (including the "dorsal head shield", the orientation of the occipital condyle and its role in reducing torque, and orientation of the head). Mechanically and behaviorally, opposed to *Ovis*-like high velocity cranial-to-cranial combat (see below), Barghusen (1975) proposed "frontal ramming" as in suids (such as the giant forest hog; D'Huart & Kingdon, 2013). In "frontal ramming", cranial-to-cranial contact can occur, but largely entails pushing or shoving matches between contestants.

Since Barghusen (1975), combative cranial morphology in dinocephalians is a favored hypothesis (Benoit et al., 2016, 2017; Benoit et al., 2021; Kulik & Sidor, 2019; Rubidge & Sidor, 2001), and one will find many supportive referrals, "…that the heavily thickened skulls of tapinocephalids [dinocephalians such as *Moschops*] were used for head butting" (Rubidge & Sidor, 2001 p. 462).With the utmost respect to Geist (1972) and Barghusen (1975), the referral to "headbutting" may be a somewhat misleading combative term. As mentioned previously, combative styles in animals are not universal, nor well defined. And unfortunately, Barghusen (1975) does not reference *Ovis* nor high-velocity cranial impacts directly, but "frontal pushing", "frontal ramming", and "frontal combat" are used throughout. Notably, for estemmenosuchids, Barghusen (1975) says, "The presence of bony bosses or horns in these animals strongly suggests the development of devices to control the head of an opponent during frontal combat." In the context of controlling the head of an opponent, specifically referencing suid combat, seems to indicate that Barghusen's (1975) use of "headbutting" seems to refer to "frontal pushing" or "frontal ramming"—not sensu stricto *Ovis*-like head-butting.

In the first synchrotron scans of a dinocephalian, the detailed study of Benoit et al. (2017) examined the paleoneurology of *Moschops capensis* to examine if the central nervous system expressed morphologies indicating its modification to withstand cranial blows. Compared to other nonmammalian therapsids, the lateral semicircular canal of *M. capensis*, when aligned to the horizon, oriented the head much more ventrally (Benoit et al., 2017). Brink (1958) had noted a similarly tilted braincase in *Struthiocephalus*, which aligned the fronto-parietal shield (the dorsoventrally thickened "forehead"), the foramen magnum, and the vertebrae. Such an alignment would, in theory, permit the transfer of energy to the "shock absorbing" vertebral column (Barghusen, 1975; Benoit et al., 2016, 2017). Benoit et al. (2017) noted that such a rotation of the braincase within the skull (cyptocephaly) was also observed in several other extinct therapsids, pachycephalosaurids, as well as several extant bovids, perissodactyls and proboscideans. While such a ventral orientation of the skull has been equally argued to support low browsing (Sereno et al., 2007), Benoit et al.

(2017) pointed out that not only had cranial combat been previously hypothesized in the other extinct examples, but that the extant taxa do actively engage in such combat.

Additionally, Benoit et al. (2017) observed that the endocast of *Moschops capensis* did not bear endocranial impressions of the nervous tissue. In consideration of potential brain trauma from headbutting, Benoit et al. (2017) hypothesized that the lack of impressions on the endocast indicated that a thick layer of various soft tissues—other than meninges—encased the brain, acting as a protective barrier for shock absorption (although see Ackermans & Reidenberg, 2024; this volume). Given the numerous morphologies, including: cyptocephaly, the ventral positioning of the foramen magnum, an inclined occiput, the enlarged and dorsoventrally thickened fronto-parietal shield, and that the fronto-parietal shield was structurally composed of dense outer bone and inner cancellous bone, Benoit et al. (2017) found this suite consistent with preventative adaptations for bone breakage under physical forces during headbutting. Notably, and much to this study's credit, Benoit et al. (2017) did not define or quantify their usage of headbutting. Likewise, velocity or force are not described in the publication, nor were there any proposed any extant analogs, or the specifics of such a hypothesized behavior. The only such term in the Benoit et al. (2017) study is "violent impacts", but only in reference that the suite of morphologies observed in *M. capensis* were consist with those seen in extant taxa that engaged in varied forms of headbutting behavior (Figure 5d,e).

2.1.2 | Burnetiamorpha

Combining osteohistology and computed tomography (CT) data, Kulik and Sidor (2019) compared the osteological makeup of the burnetiamorph skull roof to that of pachycephalosaurids. In pachycephalosaurids, the frontoparietal dome is created by the hypermineralized inflation of the frontals and parietals, while the dome of burnetiamorphs is comprised of a frontal boss (made from the inflated frontals) and a supraorbital boss (formed by the frontal and postfrontal; Kulik & Sidor, 2019).

Osteohistologically, Kulik and Sidor (2019) documented that the dome of burnetiamorphs exhibited a pattern of tissue zonation, superficially comparable to the tissue zones in pachycephalosaurid domes. However, in all but one of these zones Kulik and Sidor (2019) found differences in the compositions. Perhaps the most notable difference was that the external-most zone remained highly vascularized, unlike the corresponding zone in pachycephalosaurids which was the least vascularized (Goodwin & Horner, 2004; Kulik & Sidor, 2019). Comparatively, Kulik and Sidor (2019) also noted that even in immature pachycephalosaurid specimens, the ectocranial tissues were proportionally less vascularized and denser than in burnetiamorphs. Unlike the dense, hypermineralized frontoparietal dome of pachycephalosaurids that decreased in vascularity through ontogeny (Goodwin & Horner, 2004), that of burnetiamorphs was compositionally more comparable to immature pachycephalosaurids in that it maintained cancellous, vascularized bone throughout (Kulik & Sidor, 2019). As vascularity corresponds to tissue growth and maintenance (less vascular = slower growing; more vascular = faster growing), this indicates that burnetiamorph domes were composed of more responsive tissues throughout their lives than those of pachycephalosaurids.

2.2 | Dinosauria

2.2.1 | Pachycephalosauria

Unequivocally, the extinct clade most popularly portrayed as headbutting are the pachycephalosaurids. Not only forming the bulk of the scientific literature on dinosaurian headbutting, but also represented everywhere from toys to Hollywood cinema, pachycephalosaurid headbutting is perhaps one of the most iconic of dinosaurian behaviors (Figure 6). The history of headbutting behavior in Pachycephalosauria is fascinating, and we direct readers to Horner et al. (2022) for a concise history from the perspective of some of the authors involved in this behavioral debate.

The origins of headbutting behavior in Pachycephalosauria are unique, compared to other domed fossil taxa, in that the genesis of this hypothesis did not directly come from the scientific literature. In his popular natural history narrative *Evolution of the Vertebrates: A History of the Backboned Animals Through Time*, in discussing the frontoparietal dome of pachycephalosaurids, Colbert (1955 p.195) writes: "It is difficult if not impossible to guess that the adaptive significance of such a development [...] Perhaps (as a very wild surmise) the skull was used as a sort of battering ram." The following year, Colbert's "wild surmise" was popularized in L. Sprague de Camp's science fiction short story *A Gun for Dinosaur*. During a time-traveling big-game safari, the group spots a group of pachycephalosaurids, and that, "The males butt each other with these heads in fighting over the females" (de Camp, 1956).

It was not until 1970 that headbutting in pachycephalosaurids as a behavioral hypothesis formally entered the scientific literature. In a 1970 article entitled *Pachycephalosaurids—Dinosaurian Battering Rams*, P. Galton states, "...it can be said that two sheep butting behave in much

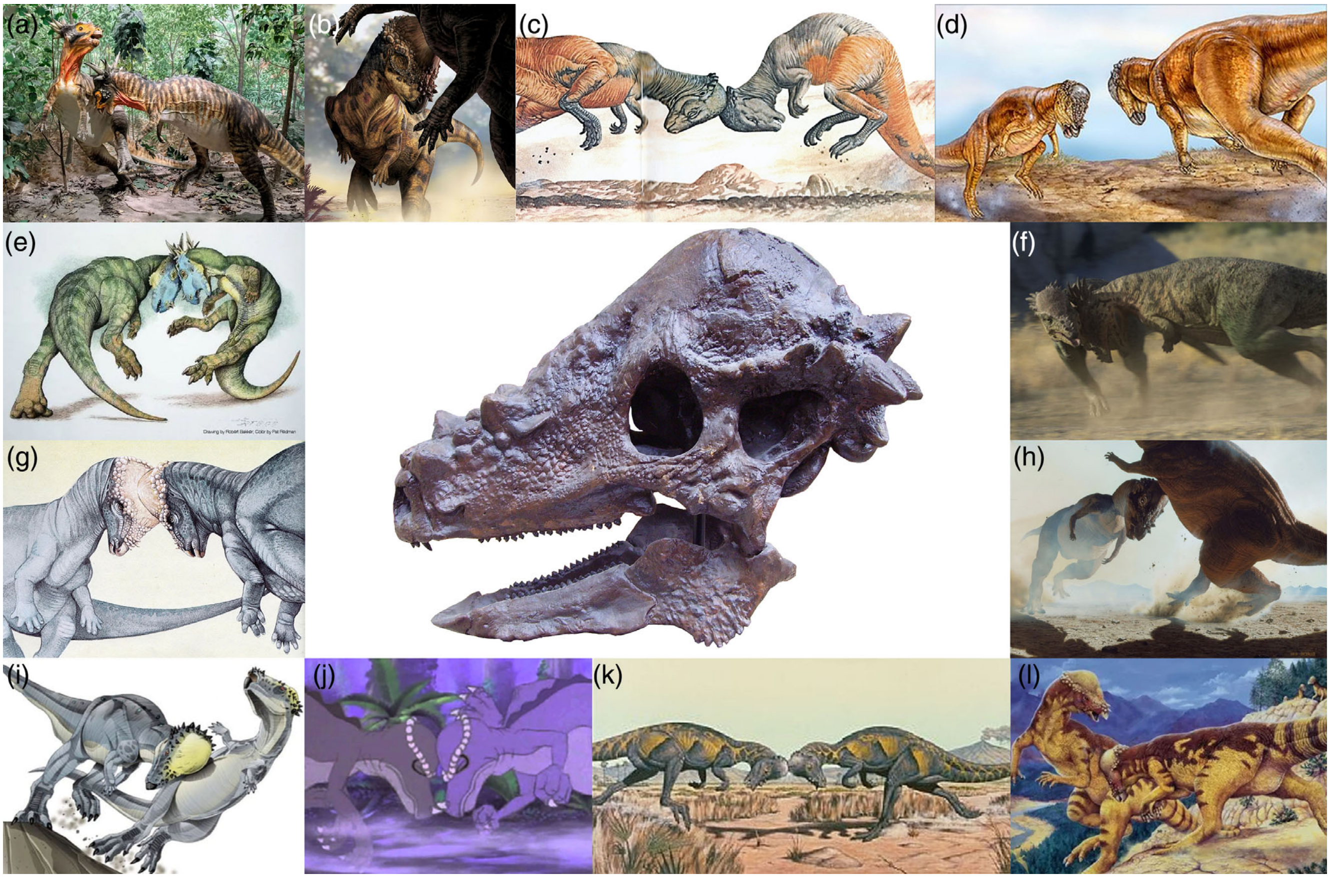

FIGURE 6 Skull of the pachycephalosaurid *Pachycephalosaurus wyomingensis* (skull in left lateral view; Wikimedia CC BY-SA 4.0) with intra- to interspecific combat depicted in pachycephalosaurids from scientific to pop cultural reconstructions. (a) "*Stygimoloch*" at the Denver Museum of Nature and Science created by G. Staab, d. McElvain, and T. Shankster; (b) *Pachycephalosaurus* by F. Tempesta; (c) *Pachycephalosaurus* by G. Caselli; (d) *Pachycephalosaurus* © L. O'Keefe; (e) "*Dracorex*" by B. Bakker (Bakker et al., 2006); (f) *Pachycephalosaurus* from Apple TV's *Prehistoric Planet*; (d) *Pachycephalosaurus* by C. Santoro; (h) *Pachycephalosaurus* © J. Gurche; (i) *Pachycephalosaurus* by T. Bradley; (j) *Pachycephalosaurus* from Universal Pictures' *The Land Before Time*; (k) *Pachycephalosaurus* by M. Hallett; (l) *Pachycephalosaurus* by P. Scott.

the same manner as did two pachycephalosaurids…" (Galton, 1970 p.27). In fact, in this article, Galton describes how he was inspired by *A Gun for Dinosaur*! Science fiction aside, Galton (1970) noted several aspects of pachycephalosaurid cranial morphology that he claimed supported such behavior, but the comparison to sheep appears first on page 31 when Galton states, "The various spikes and knobs are in an ineffective position on the peripheral part of the dome so it is unlikely that the dome was developed primarily for defense. It is more likely that the dome was used for intraspecific competition as in modern sheep and goats… Sheep and goats show certain specializations in the skull for head-on ramming that are duplicated by the pachycephalosaurids" (Galton, 1970 p.31). And relevant to this special volume, "However, the skull roof of sheep and goats differs in that it consists of a double layer of bone with extensive sinuses or air spaces between the layers. It has been suggested that this acts as a shock absorber and helps to prevent damage to the brain at impact.[1] The dome of pachycephalosaurids is solid bone so the protection supplied by air sinuses was apparently not needed" (Galton, 1970 p.31 and 32). Galton concludes the introduction of this behavioral hypothesis with (and a life reconstruction by B. Bakker), "Occasionally two individuals would have charged at each other with horizontal backbones, lowering their heads only a few moments before they collided head on with a resounding crash. Such head-on ramming would have occurred most commonly during the mating season" (Galton, 1970 p.31).

The year 1971 witnessed another paper on the function of pachycephalosaurid crania by P. Galton, stating "I consider that the thickened dome was used as a battering ram…". While readdressing many of the cranial morphologies of his 1970 paper, the 1971 study saw the first hypothesis on the functional role of the corrugated zygapophyses towards behavior. Galton (1971 p.46) concludes that, "…the thickened skull cap of pachycephalosaurids was used as a battering ram…In this respect the dome-headed dinosaurs of the Cretaceous were a functional analogue of the present day sheep…".

The ensuing decades post-Galton (1970, 1971) saw a flury of pchycephalosaurid research. Interestingly, these works were not in uniform agreement over the specifics of hypothesized pachycephalosaurid behaviors, and some, like Rigby Jr. et al. (1987), Landry (1995), and Reid (1996) advocated for the dome being a heat-exchange organ. While others, such as Maryańska and Osmólska (1974), favored the "battering ram" functional role of the dome. In examining the skull and postcrania of *Stegoceras validum*, Sues (1978) cited cyptocephaly, the ventral orientation of the occipital, the corrugated zygapophyseal facets of the dorsal vertebrae, and a novel photoelastic analysis as morphologies not only supportive of cranial combat, but specifically flank-butting, opposed to head-to-head high-velocity ramming, was likely the predominant mode of combat for pachycephalosaurids.

In his paradigm text *The Dinosaur Heresies*, Bakker (1986) delved into the function of the pachycephalosaurid dome. Positively referencing Galton (1970), Bakker (1986) was in favor of a combative functional role, but diverted comparisons to a human-based model. "Dome-headed dinosaurs can probably best be understood as wearing NFL-style football helmets over their minuscule braincase. Modern football helmets were not designed for merely passive protection; they were built so the wearer could ram his head into the unfortunate player opposite him.[2]" Despite being pro-cranial combat, Bakker (1986) challenged the bighorn sheep behavorial hyopthesis of Galton (1970) in favor of the flank-butting hypothesis of Sues (1978). Specifically, Bakker (1986 p.240) said, "A bighorn sheep's horns are wide and flat, so when two males clash, their horns meet across a wide surface […] But the rounded shape […] made a precise head-to-head blow nearly impossible […] Domed heads, therefore, like football helmets, were probably for butting an adversary in the body, not in the head."

While naming the dual domed and spiked squamosal pachycephalosaurine *Stygimoloch spinifer* now largely believed to be an ontogimorph and/or stratomorph of *Pachycephalosaurus* (Evans et al., 2021; Fowler, 2017; Goodwin & Evans, 2016; Horner & Goodwin, 2009; Longrich et al., 2010), Galton and Sues (1983) also reviewed proposed functional roles for flat-headed and domed pachycephalosaurids. Galton and Sues (1983) favored headbutting in domed taxa, and head-to-head shoving in flat-headed taxa. And just a few years later, this same duo subscribed to the flank-butting hypothesis.

Pachycephalosaurid behavioral hypotheses first entered the biomechanical realm via Alexander (1997). In a review chapter on dinosaur weaponry, Alexander (1997) compared Galton's (1970) hypothesis of bighorn sheep-like high-velocity ramming, to that of the alternative flank-butting hypothesis of Sues (1978). Alexander (1997) was interested in Sues's (1978) notion that if pachycephalosaurids had engaged in high-velocity head-to-head combat, then the spherical domes would be apt to deflect at potentially harmful angles and risked torsional damage to the cervical series. Alexander (1997) applied biomechanical data from bighorn sheep to apply a preliminary test of Sues' (1978) "cervical torsion" ideas. Citing previously gathered bighorn sheep data (from Kitchener, 1988), bighorns ram each other at speeds up to 6 m per second, resulting in kinetic energy of the ram's head at 18 J per kg of cranial mass[3] (Alexander, 1997). Given that 1 kg of muscle can absorb 170 J of energy, Alexander (1997) calculated that a *Pachycephalosaurus*' neck could safely absorb up to 11% of its cranial mass from an angled deflection. Noting that the more rapid a body is halted, the greater the force incurred, a spherical weapon for flank-butting seemed unusual; and given that no extant animals engage in such a behavior, Alexander (1997) seemed unsure of the flank-butting hypothesis.

Next, addressing Galton's (1970) hypothesis of high-velocity headbutting, Alexander (1997) seemed more in favor of this biomechanical behavioral hypothesis. Given the "spongy" nature of the frontoparietal dome, Alexander (1997) presumed that a certain degree of deformative cushioning from the dome upon impact would provide protective support. Deceleration of a bighorn sheep had been previously calculated to have been no greater than 34 m/s^2, equaling a force 3.4 times body mass, and that bending of the thoracic/lumbar vertebrae together with the back muscles absorb a great deal of this force (Alexander, 1997). And applying proportional calculations, Alexander (1997) found these values reasonable for a *Pachycephalosaurus*.

Biomechanically, Alexander (1997) supported Galton (1970) behavioral hypothesis, but with the utmost respect to the biomechanical doyen, we believe there may have been a slight confusion or misunderstanding on Alexander's (1997) part per the meaning of "spongy" in relation to the pachycephalosaurid frontoparietal dome. Alexander (1997) seems to follow Sues' (1978) usage of "spongy", but Sues (1978) specifically described the dome of *Stegoceras* "*validus*" (*validum*) as "dense bone" (Sues, 1978 p.464). Brown and Schlaikjer (1943), established that microanatomically, the frontoparietal dome is internally a highly vascularized tissue dominated with radial vascular canals. "Spongy" bone, i.e., cancellous bone, is indeed present in the interior of the dome, but the cortex and subperiosteal layers were composed of less vascularized, hypermineralized compact bone. Permineralization certainly makes the fossilized dome heavier, and those who have held a pachycephalosaurid dome know that given their weight, the living structure must have still been quite heavy (and several domes even exhibit conchoidal fractures, DCW pers. obs.). While a "spongy", impact deforming "balloon" certainly makes for a novel and entertaining reconstruction, this is not readily plausible given the osteostructural composition of the pachycephalosaurid dome.

Like Bakker (1986), Carpenter (1997) noted that the forehead and bases of the horns in sheep form a large and broad contact surface. Given the rarity of perfectly aligned contact in bighorn sheep, these broad impact surfaces still allow for successful, nontorsionally harmful contact (Carpenter, 1997). And with a spherical dome, unless perfectly centered on a small contact area, pachycephalosaurids would certainly have deflected off one another (Carpenter, 1997). Some pachycephalosaurids with pointed, peaked dome apices (such as "*Stenotholus*"; Giffin et al., 1988) would miss contact altogether (Carpenter, 1997). A similar sentiment was reached by Goodwin et al. (1998) for "*Stygimoloch*" *spinifer*, who additionally advocated for a primary display role. Sensu Sues (1978), Carpenter (1997) found flank-butting a much more likely behavioral hypothesis. Specifically, Carpenter (1997) envisioned two forms of flank-butting: 1) large spherical domes (like *Pachycephalosaurus*) were designed to increase the force for flank blows without causing much pain, and 2) those with large squamosal horns (like "*Stygimoloch*") were designed for causing "maximum" local pain.

In examining the ontogenetic development and the microstructure of the dome, Goodwin and Horner (2004) conducted the first osteohistological assessment of the pachycephalosaurid frontopariental dome. Previously, Galton (1970) had noted the microstructure of the dome and had commented on the radiating trabeculae and fibers which ran perpendicular to the external surface. Galton (1971) went further to claim that this structural arrangement was "ideal" for resisting apical forces. Conducting a photoelastic analysis involving a piece of plexiglass stressed into the shape of a pachycephalosaurid dome, Sues (1978) produced a radial pattern similar to the internal tissue of the dome, concluding it was favorable to resist compressional loads.

Throughout their ontogenetic assessment, Goodwin and Horner (2004) noted that the frontoparietal dome underwent rapid growth, and osteohistologically, they recognized three distinct compositional zones. "Zone I" remained fairly consistent through ontogeny and had a "ropey-looking" bone texture typical of endochondral bone (Goodwin & Horner, 2004). The thickness of "Zone II" decreased through ontogeny and was characterized by alternating radial vascular canals with long bony struts and radiating bundles of collagen fibers; and Goodwin and Horner (2004) noted that this produced the cancellous texture first observed by Brown and Schlaikjer (1943). The exteriormost zone, "Zone III", also thickened throughout ontogeny and consisted of dense, sparsely vascularized bone (Goodwin & Horner, 2004). Interestingly, the outermost surface of "Zone III" had abundant Sharpey's fibers, indicating to Goodwin and Horner (2004) that a nonkeratinous structure covered the dome in life. Thus, the quick growing, variably shaped and ornamented dome of pachycephalosaurids was theorized to serve a signaling role, much like the varied cranial ornamentation of African antelope. However, in these African bovids, while the horns can serve as signaling structures, they are also combative structures (Lundrigan, 1996). Snively & Cox, 2008 challenged the Goodwin and Horner (2004) study, marking the transition to more biomechanical-based investigations of the pachycephalosaurid dome. Using finite element analysis rendered from the skulls of *Homalocephale* and *Pachycephalosaurus*, Snively & Cox, 2008 concluded that impact forces could safely dissipate though the dome. Specifically, in *Homalocephale*, the dome was resistant to impact forces lower than 6.7 m/s, but the model was unable to dissipate stresses, while in *Pachycephalosaurus*, the dome was perfectly capable of distributing the stress well before reaching the brain Snively and Cox (2008). The authors reasoned that while mechanically, *Homalocephale* could have headbutted, high speed impacts would have been "problematic." And in regards to *Pachycephalosaurus*, Snively and Cox (2008) found that at 6.7 m/s (the "failure" speed for *Homalocephale*), the dome was perfectly capable of distributing the stress well before reaching the braincase. In both taxa, the maximum compression and von Mises stresses fell well below the 300 MPa yield limit of bone (Snively & Cox, 2008). In recognizing the multifaceted complexities in deciphering behaviors strictly form morphologic or mechanical observations, Snively and Cox (2008 p.14) concluded that, "... we find inference of head-based combat in some pachycephalosaurs to be reasonable and compelling"; and found that greater vaulting of the dome suggested a phylogenetic increase towards high-velocity headbutting, especially at lower collision impacts.

Despite being at odds with the osteohistologic and ontogenetic data, Snively and Theodor (2011) wanted to biomechanically compare pachycephalosaurid and artiodactyl crania. In comparison to the extant taxa, Snively and Theodor (2011) noted the closest similarities to *Stegoceras* was the white-bellied duiker (*Cephalophus leucogaster*). And Snively and Theodor (2011) noted that *Stegoceras*, white-bellied duiker, and bighorn sheep all possess a stratification of thickened cortical and cancellous cranial layers. Using CT-generated models from head-striking artiodactyls (duiker, muskox, and giraffe) and *Stegoceras validum*, Snively and Theodor (2011) examined bone density distribution and finite element analysis. For *Stegoceras*, stresses at the apex of the dome peaked at 46 MPa; approximately 200 MPa being the maximum compressional load for cortical bone (Snively & Theodor, 2011). Snively and Theodor (2011) concluded that mechanically, the spherical and dense dome of *Stegoceras* was structurally more effective in dissipating impact forces than the skull roofs of any extant headbutting artiodactyl.

From bighorn sheep, to muskoxen, and rhinoceros (even ceratopsian dinosaurs), many extant cranially combatting animals have extensive cranial sinuses. Located in the horn cores and in elements adjacent to the brain, one hypothesis is that these sinus complexes acted like natural shock absorbers to protect the brain (Geist, 1966; Schaffer & Reed, 1972). Testing this functional hypothesis in domestic goats, Farke (2008) found mixed support. Though models with cranial sinuses mechanically performed better at distributing stresses, Farke (2008) suggested that keratinous horn sheaths and cranial sutures were likely more important morphologies for absorbing cranial blows. Evaluating the combat in several ornithischian clades and outlining the "considerable discourse" on this topic to date, Farke (2014 p.246) commented that, "The collective data…suggest that pachycephalosaurs used their skulls for ramming."

Pathologies in pachycephalosaurid domes are commonplace and come in a variety of morphologies: they can be dish shaped, have raised margins, to even clean-edged, circular boring-shaped (Peterson & Bigalke, 2013 even investigated if these structures were artifacts of fluvial erosion). Out of 109 examined pachycephalosaurid domes, Peterson et al. (2013) found that 22% had pathologic structures on the dome, and of those, 63% had pathologies entirely restricted to the area of the dome apex. This zone of trauma seemed correlated when aligning two domed specimens together in the classic head-to-head striking position. However, noting not just the presence/absence of a dome, but also the degree of dome vaulting, as well as peripheral ornamentation, Peterson et al. (2013) stated that the high degree of variation likely indicated multiple combat styles. Specifically with extant qualifiers, the authors proposed four pachycephalosaurid cranial combat styles: 1) Bison-like head-shoving in taxa with large, broad domes (*Pachycephalosaurus*), 2) Bighorn sheep-like "clashing" in taxa with high-vaulted domes (*Prenocephale*), 3) goat-like broadside or flank butting in taxa with high domes and large squamosal horns ("*Stygimoloch*" and "*Dracorex*"), and 4) giraffe-style lateral "necking" involving the spikey peripheral elements ("*Stygimoloch*" and "*Dracorex*"; Figure 7).

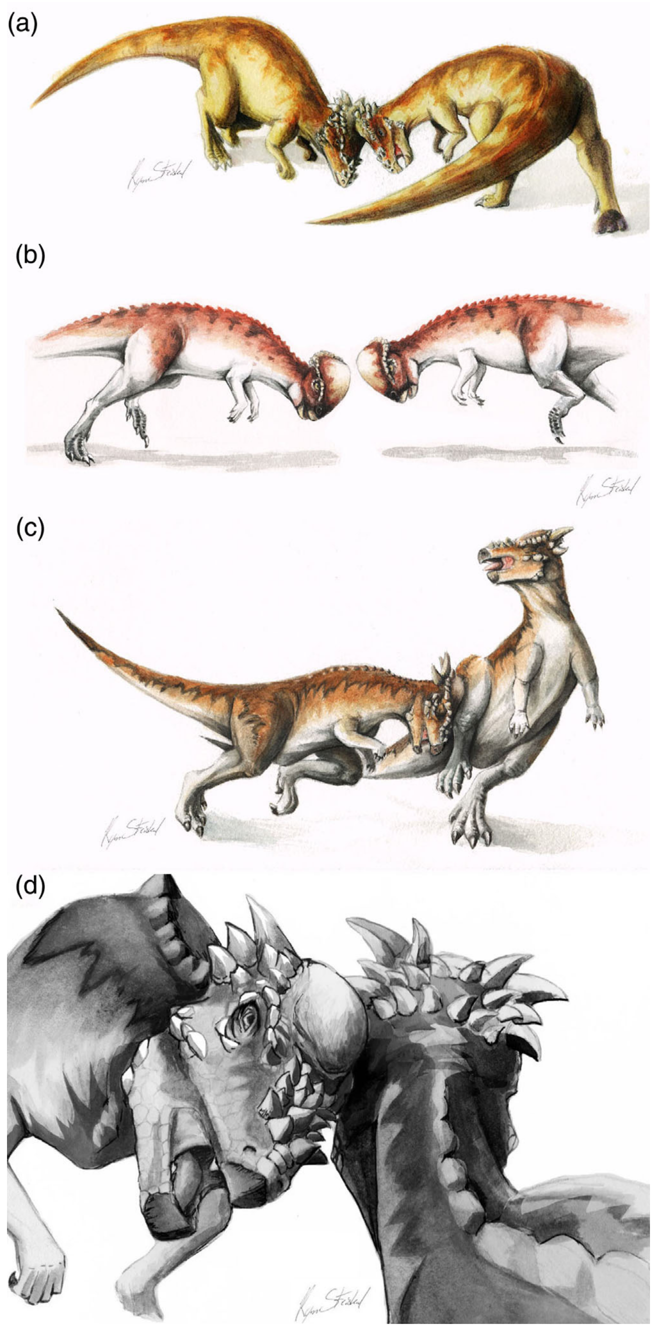

FIGURE 7 Hypothetical forms of cranial combat in Pachycephalosauria proposed by Peterson et al. (2013). (a) Bison-like head-to-head high-velocity shoving; (b) Bighorn sheep-like head-to-head high-velocity clashing; (c) Goat-like head-to-body high- to low-velocity clashing lateral butting; (d) Giraffe-like head-to-body high-velocity necking to lateral cranial clashing. Modified from figs 11 and 13 of Peterson et al. (2013).

Re-examining the osteohistology of the dome, Dyer et al. (2021) argued that shifting vascular canals not associated with growth vectors indicated that strain throughout the dome was neither constant through life, nor were said strains evenly distributed across the dome. They also interpreted these osteohistological attributes to demonstrate that the pachycephalosaurid dome underwent external loading from impacts associated with headbutting, *contra* Goodwin and Horner (2004).

In the first myological assessment of a pachycephalosaurid, Moore et al. (2022) found several morphologies indicating that *Stegoceras* had a muscular hip and hindlimb. Moore et al. (2022) found this posteriorly muscled *Stegoceras* in favor of headbutting, and noted several supportive morphologies including: the broad pelvis and stout hindlimbs would have, "...served to both broaden the stance and lower the centre of gravity of the body, which in turn would have provided added stability during headbutting contests"; the ossified myosepta in the caudal series would have, "...added significant rigidity to the base of the tail"; the enlarged medial tab would have braced and protected the pelvis from lateral impacts; the widening of the pelvis and base of the tail would have provided larger muscle attachment sites, which in turn would have provided greater, "...strength and stability to the hind limbs, pelvis, and tail"; and the more distal location of the fourth trochanter of the femur and associated musculature would have provided greater hindlimb thrust (Moore et al., 2022 p.37). Together, Moore et al. (2022) argued that these pelvic and caudal morphologies together all supported high-velocity, high-force cranial combat.

And the future of behavioral studies on the pachycephalosaurid frontoparietal dome has no indication of abating anytime soon. Kinematic modeling of the pachycephalosaurid vertebral column by Woodruff (2022; in prep) further challenges a high- velocity/impact function of the frontoparietal dome, and suggests that alternatively, kangaroos, not bighorn sheep may be a better extant behavioral analog.

2.2.2 | Ceratopsia

While a pachycephalosaurid-like spherical dome is not known from any ceratopsian, the pachyrostran pachyrhinosaurines *Achelousaurus horneri* and *Pachyrhinosaurus* spp., are notable ceratopsians in that opposed to the "classic" nasal and orbital horns, they possessed an incredibly rugose nasal and supraorbital boss. In *Pachyrhinosaurus* spp., the large, anteroposteriorly rectangular nasal boss could be *c*. 25 cm thick of dense, solid bone (Sternberg, 1950; Figure 8a). In a review of ceratopsian cranial morphology and potential behavioral significance, Farlow and Dodson (1975) hypothesized that unlike mountain goat (*Oreamnos americanus*)-like flank butting, cattle-like wrestling/shoving, and white rhinoceros (*Ceratotherium simum*)-like nasal ramming, as they proposed for various nasal/orbital horn-bearing taxa, the unique bosses of *Pachyrhinosaurus* may have been used in marine iguana (*Amblyrhynchus cristatus*)-like head-to-head shoving matches.

In their landmark and seminal study, Hieronymus et al. (2009) used centrosaurine ceratopsids, including *Achelousaurus horneri* and *Pachyrhinosaurus* spp., to test integument: osseous tissue correlates. Examining cornified sheaths and pads, scales, armor-like dermis, and projecting structures, Hieronymus et al. (2009) not only examined the morphology and textural structure of the bone underneath such features in extant taxa, but also their osteohistological composition as well. From all of the supportive evidence, Hieronymus et al. (2009) determined that thick cornified pads covered the rugose nasal and supraorbital bosses (Figure 8b). While the shape on the rugose boss does not 1:1 correspond to the shape of the overlying cornified pad, in extant analogs, the cornified structure could be arched. Behaviorally, Hieronymus et al. (2009) noted that thickened

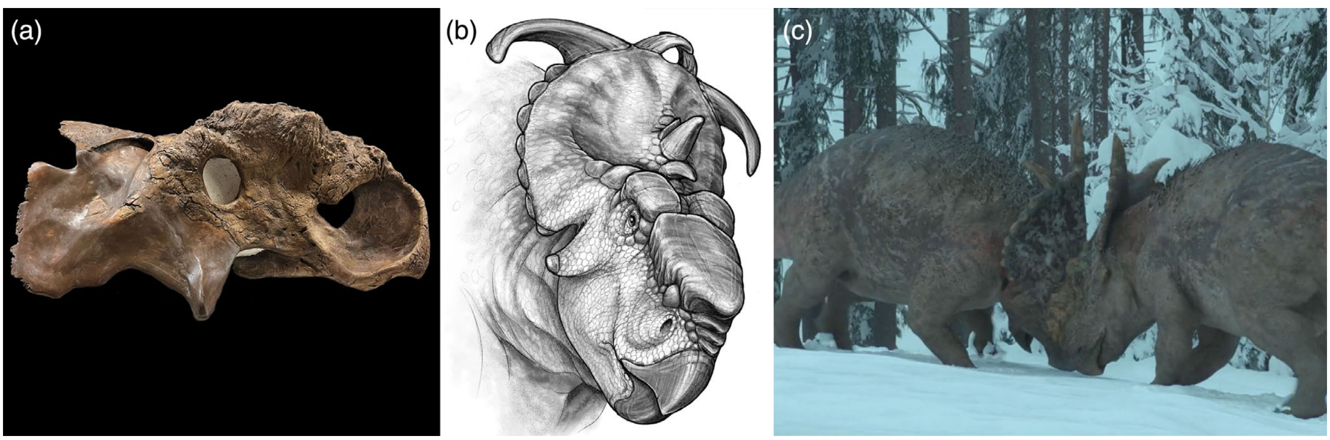

FIGURE 8 The hypothesized headbutting ceratopsian *Pachyrhinosaurus*. (a) *Pachyrhinosaurus* skull (TMP 1993.029.0004; Royal Tyrrell Museum of Palaeontology); (b) Life reconstruction by D. Dufault; (c) Hypothesized headbutting between two *Pachyrhinosaurus* from Apple TV's *Prehistoric Planet*.

cornified pads were also present in the headbutting African buffalo, banteng (*Bos javanicus*), and the helmeted hornbill, and based on the structural convergences, these bossed ceratopsians likewise engaged in headbutting (and echoed by Farke, 2014; Figure 8c).

2.3 | Mammalia

2.3.1 | Chalicotheriidae

If the "gorilla-goat"-like chalicotheres were not already weird enough, there are certain taxa, such as *Tylocephalonyx skinneri*, with domes that rivaled any pachycephalosaurid (Figure 9a). Reviewing the dome in chalicotheres, which most notably was hollow—compared to the hypermineralized dome of pachycephalosaurids, Munthe and Coombs (1979) examined every possible functional role. Munthe and Coombs (1979) examined if the dome was for an aquatic specialization, such as uses for buoyancy, to even a snorkel or oxygen tank-like reservoir; combat of any velocity; myological in origin, such as increased surface area for temporalis muscles, or an attachment site for a proboscis; signaling, be it acoustic or visual; to even water retention in desert environments. Many of these possibilities seem humorous, but Munthe and Coombs (1979) certainly left no stone unturned and ultimately favored the dome of chalicotheres as serving a combative role. Specifically citing giraffe-like flank-butting, they stated (p.88), "...the shape of the dome in chalicotheres is more appropriate to lateral than to frontal display" and "frontal wrestling or pushing remains a possible but less satisfying explanation for dome skulls in chalicotheres than lateral flank-butting."

2.3.2 | Artiodactyla

Another "domed" (albeit contentious) fossil mammal is the recently named and debated artiodactyl *Discokeryx xiezhi* (Wang et al., 2022). *Discokeryx* had a short neck with stout and robust cervical vertebrae, and most notably, a broad and thickened cranium that was claimed to be covered in a domed "keratinous helmet" like a pachycephalosaurid (Figure 9b). The finite element analysis of the cervical series conducted by Wang et al. (2022), as well as the overall vertebral morphology certainly supports the interpretation that the neck was mechanically designed for sustaining high-impact blows. However, we respectfully disagree with Wang et al.'s (2022) interpretation of the overlying keratinous sheath. In all of the *Discokeryx* specimens shown by Wang et al. (2022), the headgear is "flat" and "disklike." There is no doming of

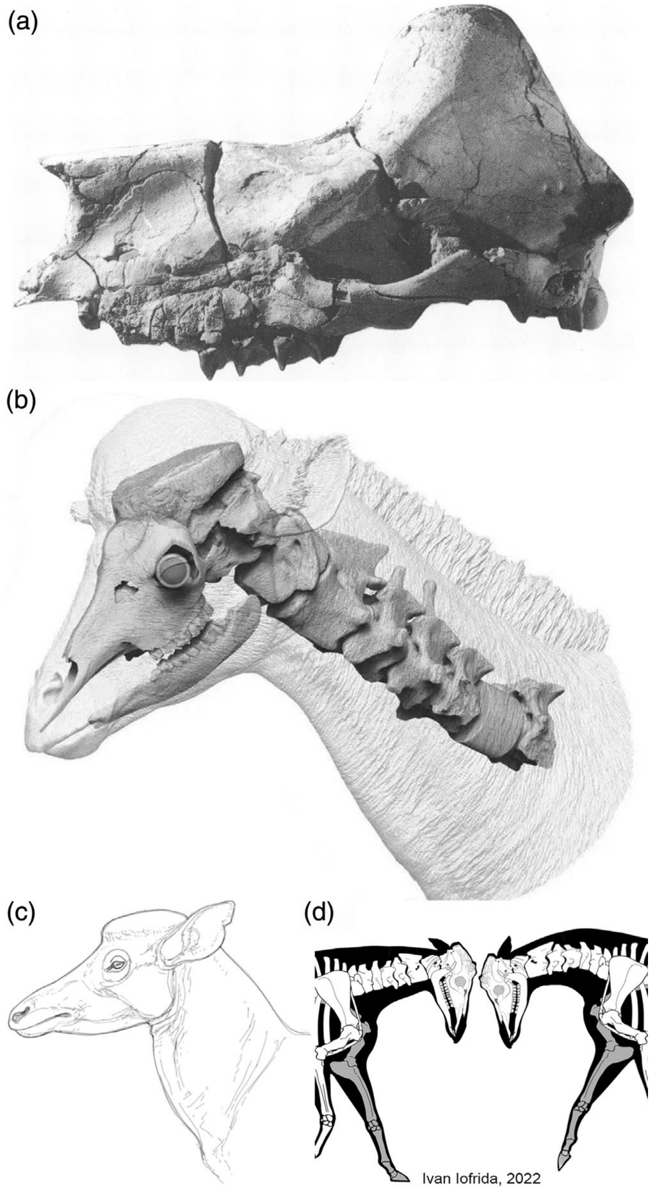

FIGURE 9 "Dome-headed" mammals. (a) Skull of the chalicothere *Tylocephalonyx skinneri* (skull in left lateral view; from Munthe & Coombs, 1979); (b) 3D reconstruction of the skull and cervical series of the artiodactyl *Discokeryx xiezhi* with an artistic soft-tissue overlay (from Wang et al., 2022). Note that in the soft-tissue overlay, the "dome" is flat, while the keratinous sheath has been reconstructed as being spherical and pachycephalosaurid-like; (c) Life reconstruction of *Discokeryx* with "flatter" keratinous covering (by V. Sinkkonen); (d) Skeletal reconstruction of "flat-headed" *Discokeryx* headbutting (by I. Iofrida). a and b not to scale.

the osseous core, nor any specimens that retain or preserve any indications of the overlying keratinous sheath. While the pachycephalosaurid dome represents an osseous structure with a likely domed epidermal covering, as Hieronymus et al. (2009) demonstrated for the aforementioned ceratopsid cranial integument, these highly rugose bosses possessed a cornified pad that does not have to uniformly follow the underlying bony core (sensu Hieronymus et al., 2009). However, a large, spherical keratinous covering overlying a "disklike" osseous core in *Discokeryx* is wholly conjectural. Contrarily, the "cranial disc" of *Discokeryx* bears a striking (no pun intended) resemblance to that of a muskox, in which the overlying keratinous sheaths certainly can have an arced contour, but the boss is still a relatively broad surface with a low degree of curvature. It is our conjecture, as illustrated by some likeminded paleoartists (such as I. Iofrida and V. Sinkkonen), that *Discokeryx* may alternatively have had a broad, low arced keratinous covering (Figure 9c,d).

3 | DISCUSSION

Headbutting, as hypothesized in extant species, is more extensive than perhaps previously thought. While not a plethora of examples, there is a similar history with regards to the repeated convergence of a domed cranial structure. In reviewing extant terrestrial vertebrates, numerous clades and taxa possess cranial morphologies that can additionally function in a combative role. While elongate teeth (tusks and fangs) and bony/cartilaginous protuberances ("warts" and ossicones) are commonplace, antlers and horns constitute one of the most common forms of cranial intraspecific "weaponry" in extant terrestrial vertebrates. Does the apparent "rarity" of agonistic domed structures indicate an evolutionary disadvantage?

While the number of domed compared to horned vertebrates is certainly skewed in extant vertebrates, terrestrial and even aerial combat with domed-headgear is present in the extant behavioral repertoire (and there are extant taxa, such as some whales, that headbutt even though they lack osseous/keratinous headgear; Ackermans et al., 2021). Similar to the domed "forehead" of *Moschops*, the white-bellied duiker possesses dorsoventrally thickened and rounded frontals, and various duiker species are described as engaging in "headbutting" behavior (Estes, 2012; Hart & Harl, 2001; Ralls, 1975). While the domed "forehead" of the white-bellied duiker has been reported to serve a combative role (Snively & Theodor, 2011), we cannot find any, and documentation of combat reported for this species is sparse. In the most in-depth study of duiker behavior (and the behavioral study referenced in both Hart & Harl, 2001 and Estes, 2012), Ralls (1975) described timed, play-by-play combat in Maxwell's duiker (*Cephalophus maxwelli*): "The first contact between the animals consisted of pressing their maxillary glands together […] with great intensity […] It was followed immediately by the first of ten head-to-head collisions. These collisions were violent; it seemed as if each male was attempting to throw his opponent off balance […] In addition to knocking each other into the air […] each of the males was flipped high into the air, with all four legs off the ground, once." (Ralls, 1975 p.242–243). And Lundrigan (1996) referred to this behavior in Maxwell's duiker as "ramming", defining this behavior as opponents charging at one another from a distance before colliding their crania together. Presumably, the domed "forehead" of the white-bellied duiker serves a similar functional role; but given that other species of duiker generally have a broad, flat "forehead", and the dorsoposteriorly oriented horns are locked and clashed during combat, it would be worthwhile to known what, if anything, behaviorally distinguishes the white-bellied duiker.

There are numerous birds today with casques—Bucerotidae, Cracinae, cassowary (*Casuarius* spp.), maleo (*Macrocephalon maleo*), horned guan (*Oreophasis derbianus*), helmeted guineafowl (*Numida meleagris*)—but none, quite like the helmeted hornbill. While in other birds, the keratinous covered casque is incredibly lightweight and composed of an elaborate network of trabecular bone (Green & Gignac, 2019, 2021, 2023), the helmeted hornbill casque has a *c.* 2 cm thick anterior margin of highly dense, ivory-like keratin (Stettenheim, 2000). In perhaps some of the most daring flight maneuvers, two combatants aerially joust with one another where they voraciously fly into one another, striking the broad, anterior surface of the casques (Kinnaird et al., 2003; Raman, 1998). These strikes can be so forceful that both birds are thrown backwards, and elaborate maneuvering is required to right themselves (Kinnaird et al., 2003). There are even marine taxa such as the green humphead parrotfish (*Bolbometopon muricatum*; Figure 4c,d) and the northern bottlenose whale (*Hyperoodon ampullatus*; Figure 4g,h) that use modified osseous structures to agonistically headbutt (Gowans & Rendell, 1999; Lambert et al., 2011; Munoz et al., 2012, 2014). The fact that rounded cranial structures that are used for delivering and receiving blows exists today "on land, air, and sea", shows that such structures are certainly not wholly disadvantageous.

4 | ALL DOMES ARE NOT CREATED EQUALLY

While the fronto-parietal shield of *Moschops*, the nasal boss of a *Pachyrhinosaurus*, and the frontoparietal dome of a *Pachycephalosaurus*, are certainly not identical structures, one can still abstractly hypothesize their use as headbutting cranial structures that possessed varying degrees of curvature. However, some structures in the aforementioned fossil taxa are much more structurally convergent. The frontal boss of a burnetiamorph, the pachycephalosaurid frontoparietal dome, and the fronto-parietal dome of *Tylocephalonyx* are specifically spherical cranial structures, yet they are not compositionally convergent. Aside from the likely differing integument covering, the burnetiamorph and pachycephalosaurid dome is composed of dense, zonated tissues, albeit with much disparity in their respective zones (Kulik & Sidor, 2019). Conversely, the frontoparietal dome of *Tylocephalonyx*, as reported by (Munthe & Coombs, 1979) was entirely hollow. Although it would require biomechanical testing to confirm, a hollow dome, while structurally being a strong shape, does not immediately instill confidence in an equally resilient combative structure. Additionally, as Benoit et al. (2017) noted, the headbutting structures of ungulates are not internally composed of dense bone, but instead, composed of an elaborate trabecular network (the same for many avian casques; Green & Gignac, 2019, 2023); whereas the fronto-parietal shield of *Moschops*, as well as the domes of burnetiamorphs and pachycephalosaurids had an outer surface of dense bone. Such headgear with a dense outer layer is also seen in the extant helmeted hornbill, the Northern bottlenose whale, and the white-bellied duiker (Gowans & Rendell, 1999; Green & Gignac, 2019; Green & Gignac, 2023; Lambert et al., 2011; Snively & Theodor, 2011). Therefore, we would counter the hypothesis of headbutting in *Tylocephalonyx* (Munthe & Coombs, 1979), and instead propose that an entirely hollow structure was primarily a signaling structure. And if correct, this would indicate that even such similarly shaped cranial structures were not functional correlates.

4.1 | Why a dome?

The fact that many fossil domes consist of variable layered osseous tissues, with most often an outer compact layer would appear to indicate that such features were not singularly signaling structures. As bovids and cervids readily demonstrate today, such cranial headgear serves as both a signaling and combative device (Geist, 1966). A pure signaling structure, such as a display feather, is much more efficient to grow and maintain compared to a multi-layered or dense osseous structure that requires active blood supply for health and maintenance (Buttemer et al., 2020; Hall, 1992). If these cranial domes served both a visual and combative role, how did they agonistically function?

In several of the studies discussed throughout this review, the authors noted the problems of two spherical objects colliding (though Barghusen, 1975 seems to suggest that contacting spheres are somehow self-correcting). Even in extant taxa that engage in high-velocity contact, such as bighorn sheep or muskoxen which have curved horns, the primary striking: contacting surfaces are broad and have a lesser degree of curvature (Geist, 1966; Kitchener, 1988). In this respect, given these contacting areas, headbutting could be seen as high-velocity, high-impact pushing matches. Many extant taxa today, such suids, even if forceful, use their combative cranial structures for head-to-head or head-to-body combat in more of a pushing or shoving motion (Ackermans et al., 2021). And in "shoving" taxa, such a suids and bovids, the contacting structures are more broad, not spherical. Even in the "dome-headed" helmeted hornbill and the green humphead parrotfish, the contact surface is broad with low curvature.

Perhaps broad foreheads and spheres are both equally sufficient in head-to-head shoving matches. Given the aforementioned issues with dual cranial strike deflection, we find head-to-body contact with a spherical structure to be more agreeable (the "flank-butting" hypotheses; Sues, 1978; Carpenter, 1997; Peterson et al., 2013). Contacting a body would reduce the chance of strike deflection, it increases the targeted surface area, and it means a significantly larger surface to push against. And as demonstrated in many of these ramming and headbutting taxa (from suids to the helmeted hornbill), a goal of these combative "pushes" is to off balance the opponent. Deflection may even be a purposeful design of domed such structures. While the apex of a dome likely represents a potentially injurious point of impact (regardless of velocity), a sphere pushing into the broad side of an opponent could represent not only a forceful impact, but attempts to brace/counter against a sphere could cause one to lose balance. We humans can comparably visualize this is in sumo wrestlers—not only do they forcefully clash with opponents, but many *kimarite* (winning techniques) of this sport specifically rely on the size and shape of the attacker in order to make their opponent lose their balance (Japan Sumo Association). And as extant cranial combatants demonstrate, not one single combative style is ever used—cervids can exhibit gentle touching with barely interlocking antlers, to full-blown lethal combat (although incredibly rare; Emlen, 2014). Of course, we cannot say that extinct taxa with domes never engaged in any form or variety of head-to-head combat, but we find domes more parsimoniously explainable from the primary context of head-to-body contact.

4.2 | Brain injury in the fossil record?

Disease and trauma in the fossil record are fleeting glimpses and snapshots in time into the life of an animal eons ago. For a malady to be recorded in the fossil record, it must leave some trace or indicator, primarily in the osseous record—leaving documentation of such disorders exceedingly sparse. As noted previously, the pathologies along the apices of pachycephalosaurid domes suggest that at least some pathologies are indicators of force above the brain cavity that was strong enough to damage and reshape the adjacent bone in extreme cases (Peterson et al., 2013; Peterson & Vittore, 2012). Whether brain tissue was affected in more routine combat remains difficult to interpret.

In extant species, broken bones are one of the most obvious indications of injury, but many other indicators are only visible in soft tissue, as is the case for brain injury. In humans and other species, brain injury can often be caused by one or multiple blows to the head without cranial bone damage. Brain injury is multifactorial, and its severity depends heavily on force and frequency of impacts, angle of attack, skull thickness, presence of skull ornamentation, amount of cerebrospinal fluid, shape and smoothness of the braincase (see Ackermans et al. (2024) in this special issue), brain size, meningeal thickness, neck musculature, and vertebral anatomy. Even more yet-unknown factors likely contribute, but this injury is understudied in species other than humans and common laboratory species. The variability of injury factors and the complete lack of any data pertaining to brain injury in the reptilian brain, let alone the sparsity of the fossil record and its lack of soft tissue preservation, all make it extremely difficult to speculate on whether headbutting (or flank-butting) dinosaurs sustained brain injury. Nevertheless, we will make a crude assumption based on comparisons of anatomy, predicted behavior, and pathology in extant species.

There is a misconstrued evolutionary adage that nature is the perfect engineer, and along the theme of cranial combat, there is a popular notion that headbutting taxa must be "bioengineered" to be impervious to neurological injury from cranial trauma (Ackermans, 2023). However, as recently demonstrated by Ackermans et al. (2022), some charismatic headbutting taxa—bighorn sheep and muskoxen—do in fact show cellular evidence of brain injury caused by headbutting (albeit in a small sample size). The effects of this type of injury on behavioral changes are still under investigation.

While extinct animals suspected of headbutting have been compared to bovids in behavior, they likely differed drastically in brain anatomy. Among the potential headbutters discussed in this text, the extinct artiodactyl *Discokeryx*, has one of the closest analogs to extant species in bovids. Bovids tend to have a large, folded brains that rest snugly within a rough braincase. As only a partial caudal specimen of a *Discokeryx* braincase was recovered, no endocast exists to date and we infer a similar brain anatomy to modern bovids. Thus, if *Discokeryx* fought using their heads, they may have sustained some brain damage, based on their cranial and vertebral anatomy in comparison with that of extant giraffids or bovids. The skull and postcranial elements of *Discokeryx* were relatively massive and adorned with a vascularized disc which suggests selection to endure strong impacts, similarly to bovids. In line with the pathologies on the pachycephalosaurid dome being recognized as possible "side effects" of hypothesized high-velocity combat, we should likewise infer that any kind of cranially combating fossil taxa was potentially susceptible to some form of brain injury as well.

Within mammals, brain: braincase ratio can impact a species susceptibility to brain injury. The human brain, for example, is particularly susceptible to the mechanical forces sustained during head impacts due to the large size of the surrounded by a large amount of cerebrospinal fluid within a globular, smooth braincase (Risling et al., 2019). Human cranial anatomy is optimized for a large brain and bipedalism but is susceptible to coup-contrecoup injury when the head is impacted (the brain hits one skull wall, then bounces off, and hits again on the opposite side, doubling the injury; Bayly et al., 2005). Conversely, sheep have a very tight interface between brain and braincase, to the point that the walls of the neurocranium appear molded to the gyri and sulci of the brain, which in turn would provide some stabilization and support against impact injury (Ackermans, 2023, in this special issue). Stretching this analysis further to non-avian dinosaurs, pachycephalosaurids especially, is challenging. Endocranial casts of pachycephalosaurids have been described (Bourke et al., 2014; Giffin, 1989a, 1989b; Stocker et al., 2016) but an endocast can only provide information on the shape braincase and does not always equate a 1:1 representation of the brain. Specifically, in animals like reptiles (and presumably derived archosauromorphs), there is a small amount of interstitial space between the brain and the braincase (Watanabe et al., 2019). We might therefore assufvme that pachycephalosaurids (and perhaps other dinosaurs that practiced any variation of cranial combat), sustained impact forces to the head that could have traveled to the brain and created some cellular pathology. While the extremely thickened pachycephalosaurid dome may have certainly dispersed impact shock, it is possible that, as in musk-oxen and bighorn sheep, repetitive head impacts may have still reached, and damaged the brain. The minimum amount of accumulated brain damage necessary to cause behavioral sequelae—and thus evolutionary pressure—of any kind, has yet to be defined in humans or other extant species, let alone extinct ones. Indeed, if there is no

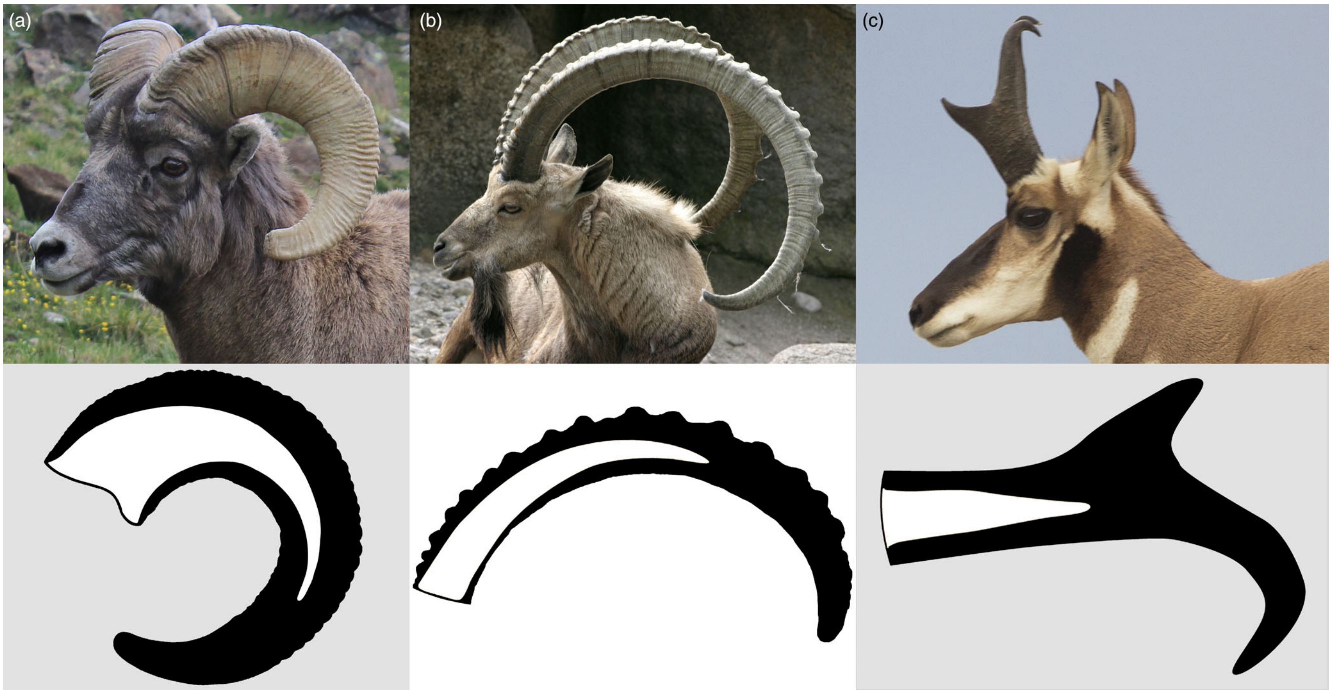

FIGURE 10 Bone core to keratinous sheath ratio and morphology in extant artiodactyls. (a) Bighorn sheep (*Ovis canadensis*); (b) Nubian ibex (*Capra nubiana*); (c) Pronghorn antelope (*Antilocapra americana*). Horns below each taxa show the osseous ratio (bone = white) and the morphology of the keratinous sheath (keratin = black). Taxa and horns not to scale. Modified from Goss (2012) and Brown (2017).

negative consequence of fighting, then there is no evolutionary advantage to winning a fight (Ackermans, 2023).

4.3 | Potential considerations for paleoreconstructions

Since the time of C. Knight's ceratopsians, the keratinous sheaths over the bony cores are largely reconstructed as "cow-like"; that is, a smooth texture to the sheath. Countless museum displays and paleoeducators even describe ceratopsian horns and the overlying sheath in life as "cow-like". Members of Bovinae certainly do have smooth keratinous sheaths, but as Vander Linden and Dumont (2019) showed, many nonheadbutting Bovinae "wrestle" with curved horns. In this combat style, while opponents can and do "ram" into one another, the curves in the horns are designed to interlock, when real test of strength begins.

The combative styles and subsequent definitions of Vander Linden and Dumont (2019) are ruminant specific—and nonmammalian fossil taxa could have completely morphologically varied—but in other ruminant combat styles, there is vast morphological variation of the keratin sheath among ruminants. To select a few striking examples, the "prongs" of the pronghorn antelope, and the notches and ridges in ibex or bighorn sheep horns do not have corresponding osteological correlates (Figure 10). Surprisingly, we were unable to locate any mechanical study testing the functional roles of these keratinous modifications specifically, but in observed intraspecific combat in ruminants with "ridged"/"pronged"/"notched"/etc. keratinous sheaths, those features appear to either interlock or "grip" the horns from slipping or deflecting past one another. If these keratinous morphologies in ruminants are convergent with combat styles, then a "bighorn sheep-like pachycephalosaurid" could be reconstructed with a transversely ridged keratinous sheath over the dome, which would reduce deflections, and "fencing-like ceratopsian horns" could have variable forms of ridged or notched sheaths as well (sensu Witton, 2018).

5 | CONCLUSIONS

When viewing the skeleton of a fossil organism, two of our most basic human questions are, "What did it look like?", and "How did it behave?". Studying the anatomy of extant organisms and osteological correlates can aide in reconstructing and better understanding the internal and external anatomy of fossil taxa. And likewise, studying not only the behavior of phylogenetically related organisms, but also the behaviors associated with particular anatomical traits can help generate hypothesized behavioral comparisons. But such challenges become exponentially greater when extant analogs are lacking, or in certain respects, insufficient.

Headbutting is one behavior that has been hypothesized in several fossil taxa—especially for taxa with domed cranial structures. While this behavior is today most often associated with the bighorn sheep, stating that a fossil taxon engaged in "bighorn sheep-like headbutting" implies specific actions. Therefore, it is not just the contact between the two combatants, but also how this contact is delivered that is inherent when such a comparison is made. And often in the literature, a behavior has been given, but no extant analog is referenced. As mentioned throughout this work, headbutting may sound inherently simple, but which part of the body delivers the strike, receives the blow, or the velocity of the contact, are incredibly diverse and varied even within extant headbutting taxa.

If a study does not wish to define or quantify proposed cranial combat in a fossil taxon, we advocate following Benoit et al. (2017); velocity and force is not mentioned, no extant analogs are proposed, nor are any specific combative behaviors. And simply stating that the morphology(−ies) under examination is functionally consistent with "violent impacts" is a much more agreeable way of stating that such a structure could possibly be combative in nature without introducing preconceived behavioral notions. However, if future studies wish to address combative function, in an attempt to circumvent such previous issues, we suggest following such a workflow: 1) a close understanding of the comparative osteological structures. Just because two features appear similar, they may be structurally quite different from one another (i.e., the frontoparietal domes of pachycephalosaurids and *Tylocephalonyx*). 2) explicitly state the extant organism(s) that the fossil taxon is being compared to. 3) state the striking:contacting surfaces, and 4) the velocity of the blow, ex. "bighorn sheep-like, head-to-head, high-velocity impact". This is where biomechanical analyses, such as finite element analyses, could enhance our understandings of the mechanical properties of cranial combat even more. And even if seemingly redundant, such a workflow will explicitly document (1) the makeup of the structure in question, (2) the taxon being behaviorally compared to, (3) the parts of the body giving and receiving the impact, and (4) the speed of the contact—which will give no room for misunderstanding or misinterpretation. As the shape of a combative structure can indicate how it interacted with an opposing surface, these contacting surfaces, and the velocity of these blows would affect not just the morphology of the structures in question, but much of the skeleton. And an extant analog (if available) helps to compare and explain the observed morphologies and their hypothesized usage. Therefore, these specific details are imperative to understanding the biomechanical nature of such hypothesized combat.

AUTHOR CONTRIBUTIONS

D. Cary Woodruff: Conceptualization; investigation; writing – original draft; methodology; writing – review and editing. **Nicole L. Ackermans:** Conceptualization; investigation; writing – original draft; methodology; writing – review and editing.

ACKNOWLEDGMENTS

Both of us wish to thank A. Ward and her amazing podcast *Ologies*. DCW first learned about NLA's research from an interview on the show, and that sparked an introductory email which has led all the way to this paper. Exceptional science communication does not just engage with a nonscientific audience, it also informs and brings other scientists together—so thanks again "Dad Ward." For an informative review of headbutting in theropods and reconstructing horn sheathes in ceratopsians, we encourage readers to check out M. Winton's blogs *Theropod dinosaurs were a bunch of buttheads: the evidence for and development of ideas around theropod cranial combat* and *Can we predict the horn shapes of fossil animals? A thought experiment starring Triceratops*. Thanks to all of the amazing artists who allowed us to include there works, and to N. Cochran, M. Dempsey, J. Lewis, and S. Myers for helping to identify artists. Thanks to handling editor J. Reidenberg, and reviewers A. Hartstone-Rose and D. Hone for editorial feedback in earlier iterations. From DCW to D. Evans, J. Horner, and M. Goodwin: for going on 15 years, I've gotten to learn so much about pachycephalosaurids from the best. We may have "butted" our own heads time-to-time, but I'm grateful for the time and what I got to learn from each of you. Sauropods are still better.

FUNDING INFORMATION

DCW nor NLA used specific funding for this publication.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

AUTHOR PRONOUNS

DCW: he/him, NLA: she/her.

ORCID

D. Cary Woodruff https://orcid.org/0000-0002-3728-134X

Nicole L. Ackermans https://orcid.org/0000-0001-8336-1888

ENDNOTES

[1] This notion has since been disproven and is discussed later in the text. Indeed, using sinuses as a "crumple-zone" would ensure a quick way to infection and death. Additionally, bighorn sheep frontal bone is no different in strength or composition than any other cortical bone (Fuller & Donahue, 2021).

[2] The idea that American football helmets are perfectly designed to protect from injury is somewhat counterintuitive given the high rate of brain injury sustained by players.

[3] Kitchener's (1988) calculations were estimated from a film analysis.

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How to cite this article: Woodruff, D. C., & Ackermans, N. L. (2024). Headbutting through time: A review of this hypothesized behavior in "dome-headed" fossil taxa. *The Anatomical Record*, 1–22. https://doi.org/10.1002/ar.25526