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Evaluating Combat in Ornithischian Dinosaurs

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ABSTRACT

Ornithischia, a diverse clade of herbivorous dinosaurs, has numerous members with structures hypothesized to function in combat. These include the horned ceratopsids, dome-headed pachycephalosaurs, spike-thumbed iguanodonts, tail-clubbed ankylosaurs, and spiked stegosaurs, among others. Three main lines of evidence support such inferences: 1) analogy with modern animals; 2) biomechanical analysis and simulation; and 3) paleopathology. The most solid inferences utilize multiple pieces of evidence, although this is hampered by a limited understanding of combat in modern animals.

Keywords: Ornithischia, Dinosauria, functional morphology, combat, modeling, paleopathology

INTRODUCTION

Ornithischians are a remarkably morphologically disparate group of non-avian dinosaurs, displaying a panoply of body shapes, sizes, and bony ornaments (Figures 1, 2). This clade includes the three-horned *Triceratops*, the plated *Stegosaurus*, the bone-headed *Pachycephalosaurius*, the tail-clubbed *Ankylosaurus*, and the crested *Corythosaurus*, to name just a few. Through the years, many of the unusual structures among ornithischians have been ascribed roles in intraspecific and interspecific combat (Table 1). Non-antagonistic functional explanations have also entered the mix, with the general consensus on the function of various “odd” structures in dinosaurs changing in light of new evidence and new interpretations. Here, I review combat across Ornithischia and propose standards of inquiry to resolve remaining questions.

Definitions. For the purposes of this paper, “combat” refers to physical intra- and interspecific antagonistic interactions. Examples include horn locking, biting, use of tail clubs or spikes, and ramming. Purposes include, but are not limited to, defense against predators, contests for social dominance, mating competitions, or any other number of behaviors.

EVIDENCE FOR COMBAT

Combat intuitively was common across ornithischian dinosaurs, as in extant animals, but nonetheless is frustratingly difficult to demonstrate in any convincing fashion. Previous evidence for combat falls into three categories.

Analogy. Combat behavior can be observed directly in modern animals, establishing solid links between morphology and function. For instance, antelopes lock their horns in intraspecific combat. Perhaps, then, horned dinosaurs used their horns similarly (Farlow & Dodson, 1975). Analogy is effective for generating hypotheses about combat behavior in extinct animals, but it does not demonstrate that such behavior actually happened. Furthermore, analogy with modern animals suggests that many structures that are not primarily weapons (e.g., beaks, claws, and tails) could be used as weapons under certain circumstances. This is difficult to test and thus is not considered further here.

An additional weakness of analogy is that function is often not adequately understood in extant organisms, creating overconfidence in behavioral reconstructions for extinct animals. For

instance, the cranial sinuses of some bovids were purported to function as shock absorbers during head ramming (Schaffer & Reed, 1972), and analogous sinuses in ceratopsid dinosaurs were thus highlighted as adaptations for combat (Molnar, 1977; Forster, 1996). However, the function of sinuses in bovids was poorly understood, and detailed work using multiple lines of evidence suggested that the sinuses had little relation to combat (Farke, 2008, 2010a). Thus, a potential piece of support for ceratopsian combat was discredited (Farke, 2010b). In other cases, similarities between extinct and extant taxa are overstated. For instance, the horns of ceratopsids and bovids project in vastly different orientations, hampering functional comparison (Farke, 2004).

Biomechanical studies. Physical and digital simulations of varying complexity inform the understanding of combat in ornithischian dinosaurs (e.g., Sues, 1978; Farke, 2004; Carpenter et al., 2005; Arbour, 2009; Farke, Chapman & Andersen, 2010; Mallison, 2011; Snively & Theodor, 2011). These analyses are useful in demonstrating the biological feasibility of certain behaviors, but are *not* proof that the behavior actually happened. Another potential problem is that many modeling approaches have not been validated even in extant taxa, so the biological realism of a particular analysis cannot be evaluated. Necessary simplifications in the models further constrain their realism (e.g., static models of dynamic processes). Nonetheless, these sorts of biomechanical studies are useful for constraining and understanding the physical capabilities of ornithischian morphology.

Paleopathology. Evidence of disease processes is relatively common in dinosaur fossils (recently summarized by Rega, 2012), but reliably identifying trauma caused by combat is quite difficult. Any number of processes can mar the skeleton, and even when trauma is established its ultimate origin usually cannot be known (see examples below). As a result, isolated case reports, while interesting in their own right, should not be used to infer patterns of combat behavior. For instance, a broken and healed *Triceratops* horn (Gilmore, 1919) could be cited as an example of combat. Perhaps the animal broke off its horn in a fight with another *Triceratops*, as happens with extant antelope (Packer, 1983), or perhaps it was damaged in a battle with *Tyrannosaurus*. However, these are nothing more than “just-so” stories. Perhaps the horn was broken during a bad encounter with underbrush. Perhaps a developmental accident *in ovum* prevented full development of the horn, or a random infection created an abscess that weakened the horn to the point that it fell off. Many scenarios are possible, and we often cannot evaluate which is correct from the fossil record. Thus, case studies of pathology are not particularly informative for inferring combat behavior.

By contrast, overall patterns of paleopathology within taxa may be more informative, although a simple tally of specimens is only a start. For instance, a ~10% rate of spike pathology in *Stegosaurus* is intriguing (Carpenter et al., 2005), but its meaning is unclear, other than to show that the tail spikes were sometimes injured. Multi-taxon or multi-element surveys are most useful for reconstructing behavioral patterns. For example, study of cranial pathologies in across the skulls of *Triceratops* and *Centrosaurus* showed clear differences in the rate of pathology between the two, suggesting in turn behavioral differences between them (Farke, Wolff & Tanke, 2009). Rigorous statistical tests, as well as a comprehensive listing of all examined specimens, are necessary to ensure validity and reproducibility of the results.

OVERVIEW OF COMBAT BY CLADE

Heterodontosauridae

Some heterodontosaurids, but not all, have caniniform teeth in the upper and lower jaws.

These are superficially similar to structures in musk deer and peccaries, inviting speculation that heterodontosaurids used their teeth for combat and that these teeth were sexually dimorphic (Thulborn, 1974; Molnar, 1977). Even juvenile heterodontosaurids have prominent caniniform teeth, and their presence or absence seems to be phylogenetic rather than sexually dimorphic (Butler, Porro & Norman, 2008). The most recent functional assessment posited that the teeth were most likely involved in prey capture as part of an omnivorous diet, rather than having a major role in combat (Norman et al., 2011). Although this does not entirely exclude the possibility that heterodontosaurids (or other ornithischians with prominent premaxillary teeth) used their teeth as weapons, the evidence at this point is quite weak.

Iguanodontia

“Thumb spikes”—an enlarged and conical modification of the ungual on manual digit I—characterize some basal iguanodontians (e.g., *Iguanodon* and *Ouranosaurus*; Figure 2a). This structure was highly mobile and massive in some species (Norman, 1980), prompting speculation of its use as a mating aid, defensive weapon against predators, or weapon for intraspecific combat (Owen, 1872; Lydekker, 1890; Norman, 1980). The size of the spike shows clear interspecific variation, but intraspecific variation and pathology have not yet been studied in any detail. The use of the iguanodont “thumb spike” as a combat weapon seems quite likely on morphological grounds, although a role in food processing (Norman, 1980) is also possible.

The elaborate cranial crests and enlarged narial arches of some hadrosaurid iguanodontians, such as *Parasaurolophus* and *Gryposaurus* respectively, have invited casual speculation of a function as a weapon (Abel, 1924; Molnar, 1977). However, general patterns of growth, intimate integration with the respiratory system, and the delicate structure of many crests suggests a role in sound production and display rather than a major role in combat (Ostrom, 1962; Weishampel, 1981).

Stegosauria

Stegosaurs display a series of thin, bony plates along the midline of their back as well as robust spikes variably placed on the tail, pectoral, or pelvic regions (Figure 2c). These highly modified osteoderms have been the subject of considerable speculation virtually since their discovery, initially hypothesized as defensive weapons (Marsh, 1880). However, the plates of many stegosaurs are extremely thin and presumably poorly constructed to withstand heavy forces. Thus, their offensive and defensive values were questioned (Gilmore, 1914), a concern that continues to this day. Thermoregulation has received considerable attention as a function for the plates (Farlow, Thompson & Rosner, 1976; Farlow, Hayashi & Tattersall, 2010; Buffrénil, Farlow & Ricqlès, 1986), but extensive variability in plate size and shape across stegosaurs as well as the arrangement of the internal vascular features argues against a universal role for the plates in thermoregulation (Main et al., 2005). Instead, the role of the plates in visual display is more likely (Carpenter, 1998; Main et al., 2005).

By contrast, the spikes of stegosaurs (usually on the tail) are more commonly accepted as combat weapons. Beyond their general shape, biomechanical calculations show that the tail spikes of *Kentrosaurus* and *Stegosaurus* could inflict considerable force when swung with the tail, potentially even piercing bone (Carpenter et al., 2005; Mallison, 2011; Arbour, 2009, suggested the force may have been insufficient to break bone). A caudal vertebra from the theropod *Allosaurus* was purported to show a puncture wound inflicted by a *Stegosaurus* tail spike (Carpenter et al., 2005). Other disease processes can create perforations in bone (see Rega,

2012 for a recent summary), and thus this example should be considered provisional. In a survey of *Stegosaurus* spikes, five out of 51 (~10%) displayed pathology, and this overall pattern was used to argue for the use of the spikes as weapons (McWhinney, Rothschild & Carpenter, 2001). Although this seems quite plausible, it is not possible to identify any individual pathology as definitively resulting from combat, and it is unknown if this rate of pathology differs from that expected by chance. Examination of other postcranial bones may be informative.

Ankylosauria

Two major clades of ankylosaurs, Nodosauridae and Ankylosauridae, have inferred combat behavior in association with their dermal armor. Prominent, laterally projecting shoulder spikes occur in many nodosaurids, variously posited to function as anti-predator weapons or for intraspecific wrestling contests (Bakker, 1986; Blows, 2001; Carpenter, 2012). Although this certainly seems plausible, there is no evidence to test the scenario.

Ankylosaurids are well-known for their bony distal tail clubs with an inferred function as weapons (Figure 2b; Maleev, 1952; Coombs, 1979, 1995). Speculation of the tail acting as a decoy to draw predators away from the head (Thulborn, 1993) is difficult to test and largely unaccepted because the tail club shape so poorly matches head shape (Carpenter, 2004). Tail clubs show strong interspecific variation and are absent in the ontogenetically youngest ankylosaurids (Currie, 1991; Coombs, 1995; Arbour & Currie, 2013). Some of the major hindlimb muscles probably had an important role in tail club movement (Coombs, 1979; Arbour, 2009). Biomechanical analysis evaluated the potential impact force for a variety of club morphologies; the smallest known clubs were not capable of breaking bone whereas the largest were (Arbour, 2009). Arbour concluded that the clubs were not primarily anti-predator weapons, because they were not functional until late in ontogeny (or not at all in taxa with small clubs). An assumption here is that bone-breaking force is required for function as a weapon; however, any degree of pain inflicted by the club may have been an effective deterrent. Nonetheless, the great interspecific and ontogenetic variation in the clubs indicates they probably were not exclusively for defense. Use in visual display is possible, although mostly untestable. Intraspecific combat is another possibility, with “clubbing contests” between individuals. This potentially could be manifested in paleopathologies; ankylosaurids would be expected to have a greater frequency of rib trauma than nodosaurids, for instance (Arbour, 2009). Derived ankylosaurids may show a greater frequency of pathology in the pelvis and caudal vertebrae than other ankylosaurians, although non-traumatic causes are probable for many of these instances (Arbour and Currie, 2011). Pathologies in ankylosaurid tail clubs (e.g., Arbour and Currie, 2011; Carpenter et al., 2011) may be the result of tail club use, but this cannot be demonstrated irrefutably,

Pachycephalosauria

The massive fronto-parietal domes of some pachycephalosaurs (Figure 2d) invite considerable discourse on cranial function (e.g., Colbert, 1955; Davitashvili, 1961; Galton, 1971; Sues, 1978; Carpenter, 1997). The massive horns of sheep and goats were used as an analogy to infer that the domes of pachycephalosaurs functioned as battering rams in head-to-head combat (e.g., Galton, 1971). Later work showed numerous functional correlates (dome-like skull, enlarged cervical musculature, dense cortical bone, etc.) shared between pachycephalosaurs and modern ramming taxa (Snively & Theodor, 2011). Both physical modeling and finite element analysis present visualizations of stress transmission through the skull during hypothetical impacts (Sues, 1978; Snively & Cox, 2008; Snively & Theodor, 2011). Trabecular bone patterns

in a sectioned skull of *Stegoceras* corresponded closely to stress patterns in a plastic dome under load (Sues, 1978). A broader sample of pachycephalosaur domes later showed that radiating bone architecture was lost as the animals reached full size, and the presumed adaptation was simply a consequence of rapid growth (Goodwin & Horner, 2004). This was used to suggest in turn that pachycephalosaurs didn't use their skulls for ramming, although an alternative hypothesis is that the solid bone of adults was quite adequate for ramming behavior (see Longrich, Sankey & Tanke, 2010 for additional critique). Individuals inferred as the oldest in the sample still retain two distinct zones of bone (Goodwin & Horner, 2004), and similar zonation is seen in modern mammals that ram heads (Snively & Theodor, 2011). Finite element models suggest that the domes of pachycephalosaurs could adequately dissipate impact forces (Snively & Cox, 2008; Snively & Theodor, 2011).

Lesions marring the otherwise smooth dome of pachycephalosaurs have been interpreted variously as taphonomic artifacts (Sullivan, 2003), nontraumatic bone resorption (Tanke & Farke, 2006), or the result of cranial trauma or osteomyelitis following dermal abrasion (Peterson & Vittore, 2012). Over 20 percent of sampled pachycephalosaur domes have such lesions, mostly on the frontal region (Peterson, Dischler & Longrich, 2013). Surface anatomy and radiology exclude taphonomic processes (feeding traces or abrasion) as the cause of these features, instead demonstrating that they formed during the life of the animal. Interpretation of the lesions as the result of cranial trauma or osteomyelitis following minor epidermal abrasion (Peterson et al., 2013; Peterson & Vittore, 2012), perhaps during ramming behavior, seems plausible. Histological data could provide additional tests of this interpretation.

The domes of pachycephalosaurs transformed radically during ontogeny, and some previously identified “flat-headed” taxa probably represent younger ontogenetic stages of “full-domed” taxa (e.g., *Ornatolithus browni* and *Dracorex hogwartsia* are probably juveniles of *Stegoceras validum* and *Pachycephalosaurus wyomingensis*, respectively; Horner & Goodwin, 2009; Schott et al., 2011). This is consistent with domes being used visually to indicate status within a population (Padian & Horner, 2011a), but does not preclude the possibility of other functions. Indeed, the horns of bighorn sheep establish social dominance as well as serve in ramming (Geist, 1966).

The collective data—comparative, histological, and pathological—strongly suggest that pachycephalosaurs used their skulls for ramming. Head-to-head combat has been most popularized, based on analogy with sheep and goats as well as presumed skeletal adaptations in pachycephalosaurs (Peterson et al., 2013; Galton, 1971; Sues, 1978; Snively & Theodor, 2011). Examples of the latter include orientation of the vertebral series and positioning of the foramen magnum relative to the occipital condyle (Sues, 1978). Carpenter (1997) disputed the efficacy of these features, noting that the small contact areas of the domes and the curve of the vertebral series were not well configured for the safe dissipation of forces from head-to-head ramming. An inferred keratinous covering on the dome may have altered the skull shape drastically (Goodwin & Horner, 2004), perhaps allowing a broader contact. The issue of vertebral orientation is a critical one, although it requires a more thorough analysis of vertebral anatomy in modern ramming animals. Carpenter (1997) suggested flank-butting as an alternative, and this certainly seems plausible given the behavior's prevalence today. Peterson and colleagues (2013) proposed that the patterns they observed in lesions on the dome were most consistent with head-to-head combat, although a survey of postcranial pathologies in pachycephalosaurs would be most useful in resolving this issue. Unfortunately, few verifiable postcrania are known for pachycephalosaurs, and the question remains open. Brown and Russell (2013) tentatively

suggested that myorhabdoi (ossified myoseptal tendons) in the tail were associated with a tripod stance during ramming behavior, but this too is difficult to test. The role of the myorhabdoi as defensive structures against flank butting was dismissed for lack of evidence.

Ceratopsia

The fearsome appearance of the horns and frills of ceratopsians virtually mandates an explanation as structures for combat against conspecifics and predators, and this topic has a long history in the literature (e.g., Lull, 1933; Farlow & Dodson, 1975). The earliest ceratopsians had small, comparatively unornamented skulls, and the successive evolution of frills and horns has been tied to changes in the type of combat (Farlow & Dodson, 1975; Molnar, 1977). Some psittacosaur, early ceratopsians with relatively simple morphology, have prominent jugal horns speculated to enable flank butting (Molnar, 1977). This assertion is untested, but could be validated with documentation of relevant paleopathologies. Incipient nasal horns in basal neoceratopsians (e.g., *Protoceratops*) have similarly been suggested to have a combat role (Farlow & Dodson, 1975; Molnar, 1977), but again this is untested via other lines of evidence.

Large ceratopsids such as *Triceratops* (Figure 2e) have received the most attention in studies of potential combat. The horns are frequently analogized with those in bovids or chameleons, both of which engage in intraspecific combat (Farlow & Dodson, 1975). Furthermore, the evolutionary transformation in pachyrhinosaurin ceratopsians, from horncores to massive and blunt bosses, parallels transformations in modern taxa with ramming behavior (Hieronymus et al., 2009). This phylogenetic test addresses one critique of such structures functioning as weapons (Padian & Horner, 2011b). Anatomical features, such as bony buttresses for the horns, fusion of the anterior cervical vertebrae to support the skull, and enlarged sinuses to absorb shocks, have all been cited as adaptations for combat (e.g., Molnar, 1977; Forster, 1996). However, some of these features occur in early, unhorned ceratopsians (e.g., fused vertebrae), and others (sinuses) are unrelated to combat in modern animals and better explained as a byproduct of skull growth in ceratopsids (Farke, 2010b). Scale models demonstrated that *Triceratops* was physically capable of locking horns, but could not conclusively demonstrate that such behavior actually occurred (Farke, 2004). Computer modeling of the frill in *Triceratops* showed that it had the potential to act as a defense against horn thrusts, but the thin and strut-like nature of the frill in most ceratopsians precludes this as a general function (Farke et al., 2010).

Cranial pathologies are frequently attributed to intraspecific combat in ceratopsids (e.g., Gilmore, 1919; Lull, 1933; Farke, 2004). But, some presumed puncture wounds are best explained as the result of non-traumatic bone resorption (Tanke & Farke, 2006). Nonetheless, other types of lesions on the skull are consistent with a traumatic origin. A survey of *Centrosaurus* and *Triceratops* fossils showed differences in the patterns of cranial pathology between the two; this was tentatively interpreted as evidence of differing combat styles (Farke et al., 2009). In all, the bulk of the evidence strongly suggests that intraspecific combat was at least one function of the horns in most ceratopsids.

Defense against predators is a commonly invoked combat function for ceratopsid horns, but little evidence is available beyond analogy with modern horned animals. Purported healed bite marks on a *Triceratops* are intriguing (Happ, 2008), although at least some are potentially explainable as non-traumatic resorption.

DISCUSSION

Combat and species recognition. The primary function of “bizarre” structures in

dinosaurs is the topic of heated debate, particularly over whether they were primarily for “species recognition” (Knell & Sampson, 2011; Padian & Horner, 2011a, 2011b, 2013; Hone, Naish & Cuthill, 2012; Hone & Naish, 2013; Knell et al., 2013). A full recounting of this issue is beyond the scope of this article, other than to note that the bulk of evidence indicates that combat almost certainly *did* happen in ornithischians (Table 1). Whether or not this was the ultimate origin of horns, spikes, and domes is a separate question, but one that also seems likely (Hone & Naish, 2013).

Future directions. In reality, multiple lines of evidence are required to confidently infer combat in any particular group of ornithischian dinosaurs. Furthermore, significant conceptual gaps prevent a rigorous test of many hypotheses. Thus, I propose three recommendations for future investigators:

1) Utilize a multi-faceted approach to infer behavior in extinct animals. Analogy, modeling, or paleopathology alone are not sufficient.

2) The functional morphology of proposed modern analogs for extinct taxa *must* be evaluated in more detail. Is the evidence circumstantial, or have multiple lines of evidence indeed supported function in the modern organisms? How frequently do modern animals engage in combat? Recursive partition analysis and ancestral character state reconstruction show considerable promise for correlating behavior and morphology in extinct and extant animals alike (Hieronymus et al., 2009; Snively & Theodor, 2011).

3) Patterns of pathology in modern animals are a worthy topic of study. Some data suggest a connection between behavior and pathology (Peterson et al., 2013; Packer, 1983), but a great deal more study is needed. Furthermore, pathology in dinosaurs must be interpreted with appropriate caution (Rega, 2012).

Multiple lines of evidence suggest that many ornithischian clades engaged in combat behavior (Table 1). Undoubtedly, further testing will allow a clearer picture of its mode, prevalence, and evolution.

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Table 1. Structures in ornithischian dinosaurs with previously hypothesized roles as combat weapons as well as lines of evidence. See text for relevant discussion and citations.

Taxon	Structure	Evidence			Assessment
		Analogy	Modeling	Paleopathology	
Heterodontosauridae	Caniniform teeth	X			Unlikely
Basal Iguanodontia	“Thumb spike”				Plausible
Hadrosauridae	Crest				Unlikely
Stegosauria	Plates				Unlikely
Stegosauria	Spikes		X	X	Plausible
Ankylosauria	Spikes, tail club		X	X	Plausible
Pachycephalosauria	Cranial dome	X	X	X	Plausible
Psittacosauridae	Jugal horns	X			Plausible
Basal Neoceratopsia	Nasal boss	X			Plausible
Ceratopsidae	Horns	X	X	X	Plausible

FIGURES

Figure 1. A generalized phylogeny of Ornithischia, illustrating major groups with hypothesized combat. Silhouettes are not to scale. Images are all CC-BY, by Jaime Headden (*Iguanodon*, and *Psittacosaurus*), Andrew Farke (*Centrosaurus*, *Euoplocephalus*, and *Stegosaurus*), and Gareth Monger (*Acrocephale* and *Protoceratops*), from www.phylopic.org.

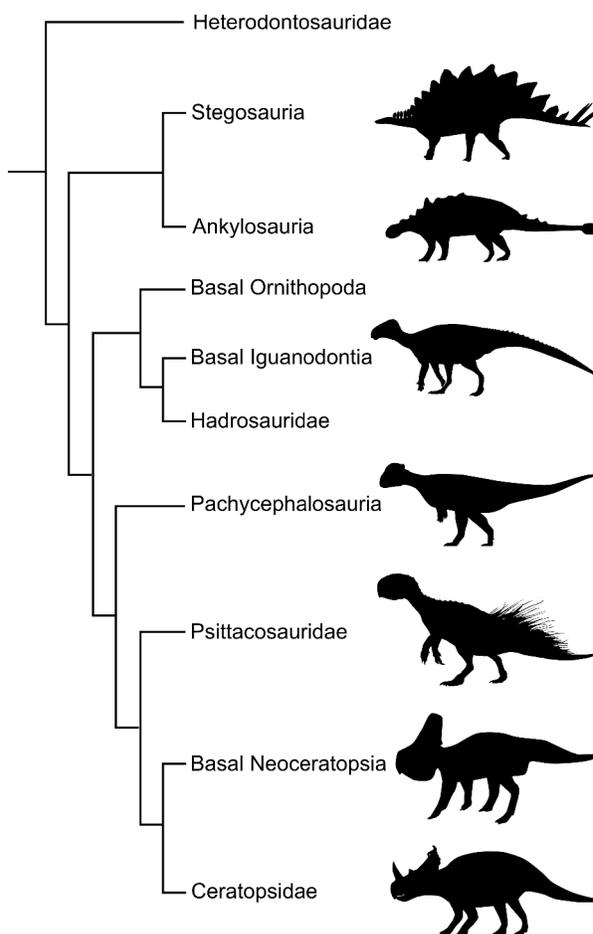


Figure 2. Representative structures from ornithischian dinosaurs with inferred combat function. (a) thumb spike of *Iguanodon* (modified after Owen, 1872); (b) tail club of the ankylosaur *Anodontosaurus* (modified after Arbour & Currie, 2013); (c) tail spike of *Stegosaurus* (cast, courtesy of Raymond M. Alf Museum of Paleontology, Claremont, California, USA); (d) skull of *Pachycephalosaurus* showing dome (modified after Horner & Goodwin, 2009); (e) skull of *Triceratops* showing horns (courtesy of Burpee Museum of Natural History, Rockford, Illinois, USA). Scale bars equal 10 cm.

