

## **“Bizarre Structures” Point to Dromaeosaurs as Parasites and a New Theory for the Origin of Avian Flight.**

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### **Abstract**

Ceratopsian neck frills, lambeosaurine crests, hadrosaur scales, stegosaur plates, cranial dome horns of *Pachycephalosaurus* (= *Stygomoloch*), diplodocid “whip” tails, sauropod dermal spikes, elaborate osteoderms, and elongated neural spines are considered bizarre dinosaur structures. Species identification, thermoregulation, sexual selection and display functions are theorized to explain these structures, not mechanically suitable for defense against large theropods. I propose that bizarre structures may have served to defend against parasitic dorsal attacks from riding dromaeosaurs. Removal of soft tissues by dromaeosaurs may have caused desiccation necrosis, callus formation and osteomyelitis, consistent with deformities in fossilized bone. Frequent dismounts from large living dinosaurs may explain the origin of feathers, gliding and avian flight. Plausibility of dorsal dromaeosaur riding is theorized from extant models including: the accipitrids (eagles), *Geospiza difficilis septentrionalis* (vampire finch), *Gulo gulo* (wolverine), *Isistius* sp. (cookie cutter shark), and vampire bat. Geologist Davidson-Arnott questions the “lethal sandslide” burial of the Mongolian “fighting pair,” a *Velociraptor* and *Protoceratops*, found locked in battle. Re-evaluation of their deposition favors a solitary approach to feeding in dromaeosaurs.

*Keywords:* lambeosaurine crest, neck frill, stegosaur plate, neural spine, whip tail

### **Introduction**

Birds most likely evolved from an animal closely related to dromaeosaurs (Chatterjee & Templin, 2004). Small feathered dinosaurs of the Late Jurassic, *Archaeopteryx*, *Aurornis*, *Anchiornis*, *Xiaotingia* and *Eosinopteryx* share many features with birds and basal dromaeosaurs (Godefroit et al., 2013a; Godefroit et al., 2013b; Xu et al., 2011; Hu et al., 2009; Feducia, 1993). Bird and dromaeosaur lineages probably diverged and diversified in the Jurassic (Godefroit et al., 2013a; Hu et al., 2009). Flight did not come out of nowhere; it most likely evolved from gliding (Longrich et al., 2012), which presumably offered some selective advantage (Chatterjee & Templin, 2004). The cursorial (ground up) theory maintains that flight evolved in running

bipeds as they leaped into the air after prey (Padian, 1998). The arboreal theory explains the benefit of gliding as an adaptation to life in the trees with animals jumping from branch to branch, parachuting, and ultimately flying down from heights (Chatterjee & Templin, 2004).

Dromaeosaurs had curved claws on four limbs with a particularly large (sickle) claw on the second digit of each hind foot. The sickle claw was proposed by Ostrom (1969) as a slashing tool for disemboweling prey, an idea opposed by Carpenter (1998) who argued that it was a puncturing weapon. In nature, claws are used for gripping and fighting, but seldom for killing of prey. Cassowaries and ostriches have been known to attack dogs and humans, causing death, but not for purposes of predation. Cassowaries have caused serious injuries by kicking or jumping on victims, with the majority of attacks motivated by defense or resulting from conditioning to human food (Kofron, 1999).



**Figure 1. Dromaeosaur Foot.** (Tyrrell Museum)

In 2006, Manning et al. used a hydraulic replica of a dromaeosaur leg to attack a fresh pig carcass to show that the sickle claw of the second pedal digit could not have been used for cutting or slashing, functioning instead like a giant meat hook. With dimensions and shape based on dromaeosaurs *Velociraptor* and *Deinonychus*, the model claw created small punctures of 3-4cm depth, but was not able to cut or slash the pig carcass (Manning et al., 2006). If comparable to claws of modern birds and reptiles, the underside of the dromaeosaur claw was probably not sharp (Manning et al., 2006). Manning et al. (2006) suggested that dromaeosaurid claws were designed like climbing crampons to grip prey many times larger.

Fowler et al. (2011) agreed with Manning that birds evolved from something like a dromaeosaur, and that curved claws suggest a gripping function. Fowler et al. (2011) pointed to quill knobs indicating firmly-attached flight feathers on the arms of *Rahonavis* (Forster et al., 1998) and *Velociraptor* (Turner et al., 2007), which were clearly too large for life in the trees or flight. Elongated rigid feathers have been demonstrated without quill knobs on the forelimbs of *Ornithomimus* (Zelenitsky et al., 2012), demonstrating that quill knobs are not merely coincidental to the existence of large feathers in dinosaurs. Acknowledging that large feathered dromaeosaurs may have evolved from small feathered fliers, Fowler et al. (2011) argued instead that flapping was first used to stabilize theropods as they clung to large live prey, prior to the divergence of *Avialae* (birds). They compared deinonychosaurians with large birds of prey, such as accipitrids, capable of eating live prey that have been weakened through exhaustion and blood loss.

Multiple incomplete skeletons of *Deinonychus antirrhopus*, in association with the large herbivore *Tenontosaurus tilletti*, were interpreted as evidence for pack hunting (Maxwell et al., 1995). As reinterpreted by Roach and Brinkman (2007), four unassociated dromaeosaurs may have been independently attracted to the carcass of *Tenontosaurus* and subsequently killed each other. The site of a kill can be a dangerous place, especially for competitive carnivores not organized into a cooperative hierarchy. The remaining evidence for pack-hunting in dromaeosaurs consists mainly of parallel theropod trackways, for which multiple explanations are possible (Roach & Brinkman, 2007).

Skeletons of *Velociraptor* and *Protoceratops* in the Djadochta Formation of the Gobi Desert have become known as the “fighting pair” because the articulated skeletons were found locked in battle (Carpenter, 1998). The right forearm of the *Velociraptor* is clenched in the beak of the *Protoceratops*, and the right leg appears trapped under the crouched body of the *Protoceratops* (Carpenter, 1998). Carpenter suggests that the forelimbs and left hind limb of the *Protoceratops* were removed by scavengers. In contrast, the lack of scavenging of the *Velociraptor* is explained by burial due to drifting sand (Carpenter, 1998).

Ignoring the missing pieces of *Protoceratops*, at a time when pack-hunting was a popular assumption, Loope et al. (1999) suggested that the “fighting pair” were buried instantly by a “Lethal Sandslide,” resulting from an intense rainstorm causing a perched water table to build up on top of a calcite layer. Loope et al. theorized that evaporation of rainwater may have caused the calcite layer to form about a half meter below the surface of the lee slope of the sand dune.

Without a source of calcium from the groundwater table, the plausibility of an impermeable calcite layer forming on the dune slope is questionable (R. Davidson-Arnott, personal communication, November 30, 2011). Calcite layers in sand are usually formed through evaporation from the water table, which could be expected at the base of a dune. On the slope of the dune, it would take thousands of years for that much calcium to accumulate from atmospheric sources. Without the stabilizing effect of vegetation, a dune would likely move over thousands of years, thus preventing calcium accumulation. Furthermore, an impermeable calcite layer would not form in the presence of enough rainfall to support vegetation. Windblown sand is a more likely explanation for structureless deposits at the bottoms of lee slopes, exactly where Loope identified “alluvial fans” from lethal sandslides (R. Davidson-Arnott, personal communication, November 30, 2011). Loope et al. (1999) acknowledged the theoretical sandslide to be a, “Heretofore unknown geological phenomenon” (p. 707).

If Carpenter’s original analysis is correct and the “fighting pair” was covered by drifting sand, they might still have been buried before the arrival of numerous distant scavengers (Carpenter, 1998). If a *Velociraptor* pack was on the scene during the struggle, it would be difficult to explain how drifting sand could have prevented the large-scale disarticulation of both carcasses (Carpenter, 1998). If one member of a *Velociraptor* pack was locked in battle with a slightly

larger *Protoceratops*, the pair would most-likely have been separated by a continued attack from other pack members. It requires no tenuous assumptions or unknown phenomenon to imagine a solitary *Velociraptor*, pinned under its victim and covered by drifting sand.

## **Extant Models Supporting the Dismount Theory**

Large birds of prey may serve as appropriate models to explain the function of the “sickle claw” in dromaeosaurids (Fowler et al., 2011; Manning et al., 2006). Golden eagles have been filmed attacking reindeer calves (Walker, 2009) and using their claws to ride the backs of the calves. Episodes of riding were separated by disengagement followed by ongoing attack.

Bald eagles have been known to overcome adult deer by striking repeatedly and disengaging between attacks (Fredrickson, 1972, pp. 153-157). In the Chugach Range eagles account for 30% of predation on Dall’s sheep lambs (Lohuis, 2013a,b).

When extracting blood from seabirds, the vampire finch (*Geospiza difficilis septentrionalis*) also rides the back of a large victim. The long beak of the vampire finch may be an adaptation to feeding on blood (Schluter & Grant, 1984). The elongated beak may help to gain access to vascular tissues beneath a layer of feathers. By analogy, elongation of the rostrum may have helped the dromaeosaurs and their ancestors to reach between spikes, plates and scutes, or to reach muscle tissue exposed under narrow breaches of thick skin.

Extant crocodiles and birds are of limited use in extant phylogenetic bracketing (EPB) to explain bizarre structures in dinosaurs because they lack such structures (Padian & Horner, 2011). We can look to extant (living) animals outside the EPB, not for traces of inheritance, but for demonstration of plausibility. Nature sometimes re-invents a useful strategy when an unrelated animal faces a similar challenge. The need to derive nutrition from a large animal has challenged many unrelated creatures.

The cookiecutter shark (*Isistius* sp.) shares the parasitic lifestyle of the vampire finch and vampire bat. Measuring up to 54cm, it feeds on a wide variety of large sharks, fish (Papastamatiou et al., 2010), dolphins and whales (Dwyer & Visser, 2011). The cookiecutter shark uses the suction of its mouth and hook-like upper teeth for attachment. It then engages saw-like lower teeth, and a rotating motion to gouge out a plug of flesh (Motta & Wilga, 2001).

For small animals feeding on large victims, it may be necessary to disengage in response to intense resistance or after feeding from an animal that remains vigorous. Flight is a common exit strategy, employed by birds and the vampire bat (Greenhall, 1971). Bioluminescent camouflage and a nocturnal habit may help the cookiecutter shark to escape after feeding on dangerous victims. The wolverine jumps into deep snow, between repeated attacks on a large animal.

During engagement, an attachment strategy is common, often involving hook-like teeth or claws. The eagle, fish and wolverine tend to engage the backs of large victims, suggesting that the back may present a point of vulnerability on large terrestrial vertebrates.

### **Wolverine Predation on Large Ungulates**

Known for claws and valor, the average adult male wolverine (*Gulo gulo*) weighs only 13.5 kg, with females averaging 9.5kg (Lofroth, 2001; Rausch & Pearson, 1972). Once considered a predator of small prey, the wolverine is increasingly recognized as a solitary predator of large ungulates. Kozhechkin (1990) documented 19 cases of moose killed by wolverines in Siberia. Wolverines have been known to prey on adult moose in Sweden (Haglund, 1974). In Scandinavia reindeer provide the most important winter food source for wolverine (Mattisson et al., 2011; Landa et al., 1997; Skogland, 1989; Pulliainen, 1988).

Wolverines apparently attack by climbing onto the backs of the prey floundering in deep snow, sometimes mounting and dismounting repeatedly (J. Persson, personal communication, August 15, 2013).

A wolverine is reported to have eaten from the back and severed the spinal cord of a live cow elk (Grinnell, 1926). Grinnell (1920) reports other instances of wolverine attacks on large prey. In one instance, a live moose was found with a large hole in its back that exposed the spine. Tracks in snow indicated a prolonged struggle, estimated to have taken two or three days.

A wolverine was observed riding the back of a caribou, mounting and dismounting repeatedly until the caribou collapsed (Burkholder, 1962).

Wolverines account for about 7% of adult Dall's sheep mortality in the Chugach Range of Alaska (Lohuis, 2013a,b). A wolverine was sighted on the carcass of one ewe that had been seen alive just 48 hours prior. The ewe was found upright in deep snow with most of the meat removed from the neck and the back above the shoulders (R. Schwanke & T. Lohuis, personal communication, June 12-20, 2013).



**Figure 2. Dall's Sheep Killed by Wolverine.** Dr. Tom Lohuis is removing the radio collar (photo by Rebecca Schwanke, April 3<sup>rd</sup> 2009)

Lofroth et al. (2007) documented eight instances of wolverines killing adult caribou. A female wolverine was seen jumping on the back of a mature bull caribou, mounting and dismounting repeatedly between visual observations from the air (F. Corbould, personal communication, December 6, 2013). Snow tracking revealed a struggle of 1-2 days, over a distance of 250m, leading to the site of Corbould's observations (Lofroth, 1997). The caribou broke numerous tree branches in an effort to dislodge the wolverine, bedding down three times to rest between attacks (E. Lofroth, personal communication, July 2013).

Lofroth (2007) analyzed hair in scat (feces) to show that large ungulate mammals comprised the bulk of most winter wolverine diets, and that small animals became the primary prey only when larger food items were unavailable. Bone fragments made up a small part of the scat. Fragments from large animals were found occasionally, but were typically not identifiable to any one group or species (E. Lofroth, personal communication, January 13, 2014). Morphologically identifiable bones were found from birds and small mammals (Lofroth, 2007), presumably because those animals could be swallowed whole or in large sections.

The wolverine example suggests that ingested bones of birds and small animals may not indicate the normal diet of the carnivore. Bird bones in the stomach of *Microraptor* (O'Connor et al., 2011) may not necessarily indicate the usual diet in dromaeosaurs or their ancestors. Small animal bones have not been reported in stomach contents of dromaeosaurs other than *Microraptor*. Ingested bones have been found in the stomach regions of other large and small theropods (Varricchio, 2001; Ostrom, 1978). A thin-walled bone fragment from a large pterosaur was found between the ribs of *Velociraptor* (Hone et al., 2012). Bone crushing behavior has seldom been attributed to theropods other than large tyrannosaurids (Roach & Brinkman, 2007, p. 118). It may be that dromaeosaurs were capable of crushing and eating thin-walled pterosaur bones, but otherwise limited to the soft tissues when feeding on large dinosaurs.

## **Dismount Hypothesis for the Origin of Avian Flight**

A tooth of *Saurornitholestes* was found embedded in a thin-walled bone of *Quetzalcoatlus*, and assumed to be the result of scavenging because the dromaeosaur would not likely have been able to kill the very large pterosaur (Currie & Jacobsen, 1995). Dromaeosaurs probably were opportunistic predators and scavengers, but a parasitic feeding strategy should also be considered.

Wolverines demonstrate the plausibility of back-riding with frequent dismounts, but they normally kill their prey and cache the meat in snow for later consumption. In the warmer Jurassic climate, meat would have spoiled quickly, so killing a large dinosaur might not have provided a long-term food supply for a small Jurassic carnivore. Parasites like the hook worm avoid killing their host, so as to maintain the opportunity to feed repeatedly. As a hypothetical parasite, the dromaeosaur would need only to climb onto the back of a large victim, hold on tight, fill its stomach and then dismount.

## **Feather Development**

To dismount after eating from a large living victim, the dromaeosaur would have faced a dangerous jump to the ground. Every incremental stage of wing and feather development would have reduced the risk of injury from such a dismount. Besides the insulating effect, simple fuzzy feathers on limbs and body would have provided air resistance and cushioning, especially for a small animal. The wood duck chick demonstrates the use of down to help it survive the fall from the nest. Admittedly larger than a duckling, the common ancestor between dromaeosaurs and birds may have been small in size (Chatterjee & Templin, 2004). *Anchiornis* weighed about 110 grams (Xu et al., 2009). Possible feathers have been identified in a 0.75 meter specimen of *Juravenator starki*, which resembles *Compsognathus* (Chiappe & Göhlich, 2010). Loft and glide may have improved with incrementally larger and stiffer feathers, perhaps allowing the common ancestor to land farther from the large living victim. The evolution of larger dromaeosaurs may have followed the development of more complex gliding feathers and the divergence of *Avialae*.



The primary wing feathers separate during the upstroke in modern birds to allow air to pass between feathers (Tobalske et al., 2003), which is important for low-speed flapping flight, hovering, and wing-assisted incline running (Longrich et al., 2012). Longrich et al. (2012) have shown that overlapping feathers of *Anchiornis* and *Archaeopteryx* were not able to separate which would have made it difficult to take off from the ground, without hindering the ability to glide from an elevated position. Limb mobility and modeling suggest that *Microraptor* and *Anchiornis* were both four-winged gliders (Alexander et al., 2010).

The skeletal structure of *Anchiornis* is almost identical to *Eosinopteryx*, both found in the Middle-Late Jurassic Tiaojishan Formation (Godefroit et al., 2013a). *Eosinopteryx* had short uncurved pedal claws and shorter feathers on long limbs, likely adaptations for unimpeded running on land (Godefroit et al. 2013a). Long stiff feathers on the hindlimbs of *Anchiornis* may have impeded running on land and are considered arboreal adaptations, yet the extreme elongation of the lower legs in *Anchiornis* suggests strong cursorial capability (Godefroit et al., 2013a; Hu et al, 2009), which would not seem necessary for life in the trees. Similar body plans but different claws and plumage suggest different niches and a complexity to the origin of flight (Godefroit et al., 2013a; Hu et al, 2009), not fully explained by arboreal adaptation. Dorsal riding parasitic behavior would explain the long legs of *Anchiornis* for running, jumping and climbing over plates and spikes. The need for a gliding dismount would explain long feathers on those long legs.

## Claws and Limbs

If Manning et al. (2006) are correct that the sickle claw worked as a climbing crampon, it would have been well-adapted for climbing a flank and then riding the back. The sickle claw was on the second digit of the dromaeosaur hind foot, the inner-most (medial) digit of the three large toes. If a dromaeosaur straddled a large dinosaur, the enlarged medial second claw would have been well positioned to grip the victim. Three functional but smaller curved claws on each of the elongated front limbs, and two other functional claws on each hind foot, may have offset lateral forces to the two large sickle claws.

The second pes (pedal) digits in dromaeosaurs were highly extensible, which allowed the sickle claws to be carried above the ground during ambulation. The second pes digits in *Anchiornis*, *Archaeopteryx* and *Xiaotingia* were also highly extensible but the sickle-shaped second claws were only slightly larger than the claws of the third digits (Xu et al., 2011). The sickle claws of the second pes digits were more-noticeably enlarged in dromaeosaurs (Xu et al., 2011). In *Anchiornis*, *Archaeopteryx* and *Xiaotingia*, the length of the second phalanx of the second digit was not reduced and lacked the prominent proximoventral heel of the dromaeosaurs (Xu et al., 2011). The shortened second phalanx in dromaeosaurs may have been necessary to carry the weight of larger animals while using the sickle claw for rapid climbing maneuvers. The prominent proximoventral heel may have allowed dromaeosaurs to support some of their weight on the second digit, while holding the enlarged claw above the ground during ambulation.



It may be that dromaeosaurs diverged from *Avialae* on the basis of size. Small avialans may have developing flight from gliding, diverging from basal dromaeosaurs that maintained some ability to glide while enlarging the second claw and shortening the second phalanx to support larger size. Slender jaws of small avialans may have improved access to soft tissues in established ulcers or narrow gaps between osteoderms, while larger size may have allowed dromaeosaurs to chew through thickened layers of skin, occupying a different parasitic niche.

Chatterjee and Templin (2004) point to a powerful shoulder girdle, biceps tubercle, elongated and laterally facing coracoid, ossification of the sternum and furcula, elongated forelimbs, swivel wrist joint and opisthopubic pelvis as features of dromaeosaurs that would have helped their ancestors to climb trees. Parachuting and gliding as adaptations to jumping from trees (Chatterjee & Templin, 2004). The dismount theory is essentially the same as the arboreal theory except for the substitution of the large herbivore as the object to climb, and from which to jump. The benefit of climbing trees is explained as a means to escape predators and exploit new habitats, whereas the benefit of climbing a large herbivore would have been nutritional.

The two theories are not mutually exclusive, in that protobirds and small early dromaeosaurs may have climbed trees and herbivores. The wolverine is a proficient climber of trees and prey (Grinnell, 1926). It may be that hooked claws are useful for riding prey and climbing trees, and that those two behaviors are complementary. While arboreal benefits may have contributed to the origin of flight, the arboreal theory does not explain the persistence of quill knobs for the attachment of flight feathers in *Rahonavis* (Forster et al., 1998) and *Velociraptor* (Turner et al., 2007), which were too large for life in the trees.

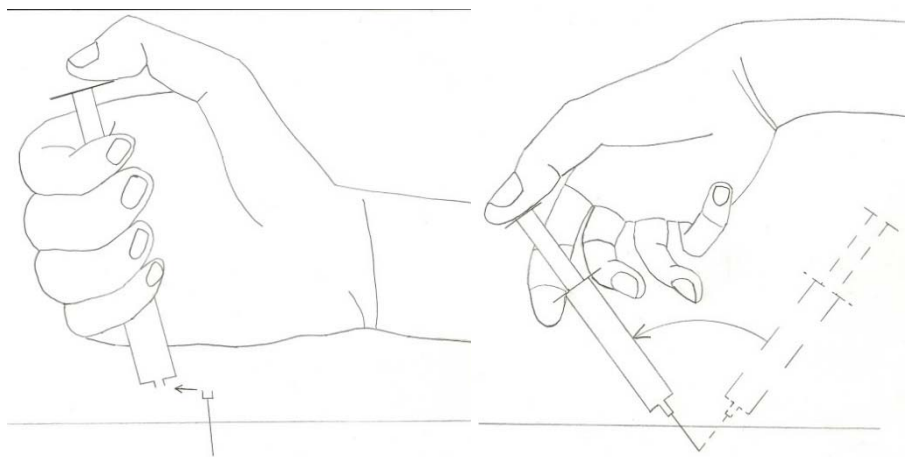
In comparison to other theropods the pubis was opisthopubic (strongly retroverted) in dromaeosaurs (Chatterjee & Templin, 2004; Norell & Makovicky, 2004). In most other non-avian theropods, the pubis projected more anteroventrally between the hind legs. A pubis that hung down between legs might have limited the hypothetical ability to straddle the back of another dinosaur or to step over obstacles such as plates or spikes. The pubis may have been retroverted (opisthopubic) in dromaeosaurs to increase clearance under the pelvis and thereby facilitate riding behavior. (See figure 9)

Ultimately facilitating flight, the elongated forelimbs in avialans and dromaeosaurs (Hu et al., 2009) may also have improved clearance under the body, to ride over the top of plates and spikes. Longer forelimbs may also have provided more travel with flexion and extension, by which to absorb the shocks from a moving victim or from jumping off to the ground. Longer forelimbs may also have improved the ability to reach past osteoderms and find skin that would allow claws to penetrate. The abductive range of motion of a laterally facing coracoid may have augmented riding capabilities, as would a powerful shoulder girdle, even before the use of the forelimb for gliding and flapping.

## Muzzle Elongation

Elongation of a narrow muzzle may have allowed dromaeosaurs and protobirds to reach vascular tissue under thick skin and between scutes, plates, and spikes. The elongated dromaeosaur muzzle may have reduced shearing forces on teeth while gripping a large moving animal. Ostrom (1969, p. 14) described the skull of *Deinonychus antirrhopus* as, “Very loosely bound together and probably highly kinetic.”

Breakage of dromaeosaur teeth may be analogous to the breakage of needles in the moving body of a combative animal or patient. To decrease shearing forces at the needle hub and allow the syringe to pivot, a technique is employed by which fingertips are used to hold the syringe at the proximal end (opposite from the needle). It is important to maintain some distance between the weight of the hand and the point of connection with the moving animal. When the distal end of the syringe is held in a fist, needle breakage is much more common (Dave Merz, personal communication, 1997-2013). The author broke many needles in cattle before learning this technique.



**Figure 3. Injection of Moving Animal.** Needle shears when held in fist (left). Syringe rotates when weight of hand is held away from point of contact (right).

The long slender dromaeosaur muzzle may have created the necessary distance from front teeth to the heavier parts of the dromaeosaur head (Norell & Makovicky, 2004, p. 200). With teeth hooked in moving flesh, the elongated rostrum may have allowed the dromaeosaur head to pivot in response to movements of its victim, minimizing shearing forces to teeth, head and neck.

## Bizarre Structures

### Stegosaur Plates

Scientists have struggled to explain the plates of *Stegosaurus* and many of the other “bizarre structures” in dinosaurs (Padian & Horner, 2011). Many of the bizarre structures could have evolved to defend against riding dromaeosaurs.

Defensive explanations for bizarre structures were often refuted due to the assumption of a large theropod as the predator. Stegosaur plates consist of a thin layer of compact bone surrounding a core of spongy trabecular bone that would be crushed easily by the teeth of any large theropod (Padian & Horner, 2011; Main et al., 2005; Buffrenil et al., 1986). As obstacles to get in the way of a dromaeosaur, plates would have required little strength and offered no temptation for biting. For a riding dromaeosaur, the dorsal midline would have provided the optimal position of stability, just as it does for a human rider on a horse. As barriers to riding dromaeosaurs, the stegosaur plates would have occupied that strategic location. The diamond shape maximized height and length so the plates would have been difficult to go around and hard to jump over.



**Figure 4. *Stegosaurus*.** (Tyrrell Museum)

Any external structure, scent or color, could have identified a species or provided a sexual display. For nature to select one form of display over another still requires an explanation. Nature seldom selects heavy structures for display alone. When heavy structures are used for display, it is uncommon for both genders to be taxed equally with the metabolic costs of producing and carrying such structures. In cervids, antlers are used not only for display, but also for sexual testing of strength and sometimes for defense against predators. Antlers are normally minimized or absent in females. There is significant sexual dimorphism in antelope horns, and elephant tusks, with larger structures typical of the male gender. The horns of female antelope tend to be specialized as stabbing weapons, as compared to the horns of male antelope which tend to be better adapted for clashing and pushing (Packer, 1983). Horns and tusks are often used for physical tests of strength and sometimes for interspecific conflict. Elephants, for example have been known to use tusks to kill rhinos (BBC, 2000; Slotow, 2000). Stegosaur plates demonstrate no sexual dimorphism (Padian & Horner, 2011) and no apparent utility for sexual competitions of strength.

Plates may have discouraged attack by making *Stegosaurus* look larger (Carpenter, 1997), but structures that serve only to create the illusion of a threat do not tend to enjoy long-term success unless the promised threat can be fulfilled (Padian & Horner, 2011).

Vascular plates would have increased the animal's profile to the sun, making it harder to cool off when shade was scarce and cooling was most important. Increasing surface area also makes it harder to retain heat in cold weather. African elephants flap their ears to move air over their bodies, not merely to increase surface area but also to fan themselves to create air flow and cool off (Buss, 1971). To stay warm, they hold the ears close to their bodies, minimizing surface area exposed for heat loss and sheltering the body. The key to any regulatory mechanism is the ability to turn it on or off as needed to promote balance. Without the ability to move, rigid structures protruding from the body would probably not have been useful for regulating temperature. It is unlikely that stegosaurs used muscle attachments to change the angle of the plates, and very unlikely that the plates flapped like the ears of an elephant. It seems unlikely that flat rigid plates could have wrapped around the curved body of a stegosaur, so they would have done little to shelter the animal from cold.

Farlow, Hayashai & Tattersall (2010) argue that crocodylian osteoderms allow blood to flow to the body surface during times of heat exposure, but many animals adjust blood flow to the surface to regulate temperature, which can be done with or without osteoderms or plates (Kellog, 2006). Farlow et al. (2010) admit that the large openings at the base of the stegosaur plate may have accommodated blood vessels to nourish the plate. Main et al. (2005) argue against a thermoregulatory function based on the lack of large vascular connections between internal and surfaces of stegosaur plates. Without significant blood flow to the surface of the plates, conduction may have allowed heat to cross the cortical bone (Farlow et al., 2010), compromising efficiency of heat exchange. Stegosaur plates evolved from Thyreophoran osteoderms, which did not initially protrude far from the skin and probably served a primary defensive function (Main et al., 2005)

Given the shorter posture, and relatively wide flat back of the earlier thyreophorans, their backs may have offered accessible platforms for the earliest back-riding coelurosaurs. For example, a small agile compsognathid might have been able to jump and then scramble onto the back of a basal thyreophoran dinosaur. Small jaws and teeth may have been able to remove soft tissues between osteoderms in sufficient quantity to nourish a small coelurosaur. The evolution of plates from thyreophoran osteoderms might have been a response to dorsal riding.

Dromaeosaur teeth have been identified after the middle of the Jurassic (van der Lubbe et al., 2009; Zinke, 1998; Metcalf et al., 1992). The temporal association between the early evolution of dromaeosaurs, and the enlargement of stegosaur plates over the latter half of the Jurassic, may be more than coincidental. Improved capability for dorsal attack, by dromaeosaurs and their predecessors, may have driven the elevation of plates and body stature that define stegosaurs. Early dromaeosaurs may have responded to bigger plates, by increasing their own size and riding adaptations, secondarily allowing them to exploit other groups of dinosaurs. It is possible that advances in dromaeosaur riding capability may have caused the extinction of stegosaurs near the end of the Jurassic.

## Ceratopsian Neck Frills

It has been theorized that brow horns were used by ceratopsians for intraspecific fighting and that the neck frills functioned as shields against the horns of competitors (Farke et al., 2009). Neck frills evolved before horns in ceratopsians (Krauss et al., 2010), so their original purpose was not to shield against horns. Prior to the evolution of front-facing ceratopsian horns, it is difficult to explain how the frill would have provided an advantage in a head pushing contest (Krauss et al., 2010).

Many ceratopsian frills were fenestrated, which seems inconsistent with a shield-like function, however modelling of chasmosaurine intraspecific combat has shown that the fenestrae in neck frills may have been positioned outside the range of impact from brow horns (Krauss et al., 2010). Some ceratopsians like *Torosaurus* had relatively thin fenestrated frills (Scannella & Horner, 2010).

Whether or not, fenestrae are consistent with intraspecific head pushing contests, holes would have allowed the frill to extend farther over the neck while minimizing weight. Just as an engineer might “skeletonize” a beam, nature may have built fenestrae into the ceratopsian frill to minimize weight without compromising length.

If the dromaeosaur tried to bite the neck, it might have risked a crushing injury from the pinch between the rim of the frill and the ceratopsian spine. Even the small early frills would have come to rest against some part of the spine with the neck in full extension. Progressively longer frills would have protected more of the spine. Longer fenestrated frills may have transmitted the required force from head to rim, without any direct impact to the fenestrae.

Many ceratopsian frills included rear-facing spikes along the rim, which might have added to the utility of these structures for protecting necks from dorsally-riding dromaeosaurs. If a running ceratopsian were to come to a sudden stop, the inertia of a riding dromaeosaur might sometimes have caused it to be impaled on such rear-facing spikes. Laterally oriented hooks on neck frills may have swung side to side with lateral movements of the head, catching the unwary dromaeosaur and throwing it to the ground.

It may be that a ceratopsian could withstand a parasitic attack on the back, but not on the relatively vulnerable neck, as will be discussed for sauropods, hadrosaurs and *Pachycephalosaurus*. Efforts have been made to explain neck frills for thermoregulation, display, and species recognition, as previously discussed for Stegosaur plates. Ceratopsian neck frills also lacked significant sexual dimorphism (Padian & Horner, 2011).



**Figure 5. *Chasmosaurus*.** (Tyrrell Museum)

## **Hadrosaur**

### **Dorsal Scales**

Hadrosaur skin impressions show tubercles that may have made the skin more resistant to puncturing and tearing (Anderson et al., 1998). On a mosaic of background scales the skin of *Saurolophus* included domed shields up to 30mm in diameter, and 25mm star-shaped scales with tapered points fitting between edges of adjacent hexagonal scales (Bell, 2012).

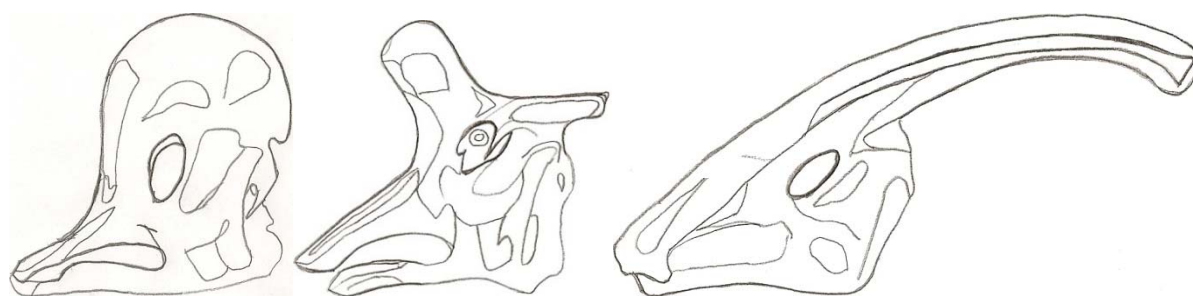
In *Kritosaurus*, a series of skin traces project 60mm vertically above the neural spines of the back (Parks, 1920, pp. 73-74, plate II). In contrast, the cervical skin trace was folded with an average of three small tubercles fitting into a span of 10mm (Parks, 1920, p. 73). Horner (1984) described a skin frill above the neural spines in the tail of a hadrosaur, with thin segments 50mm long and 45mm tall, separated by 10mm gaps. Bell (2012) observed similar midline dorsal scales up to 80mm long and 40mm high on tails of *Saurolophus*. Murphy et al. (2006, pp. 125-126) describe a series of triangular dorsal midline skin traces extending from the tail to the base of the neck in a hadrosaur, with no large tubercles on the neck.

The scales of the midline frill are marked by dorsoventrally oriented ridges (Bell, 2012; Horner, 1984), which may have added lateral rigidity to the thin vertical structures. If the scales were sharp at the superior margin, then grooves and ridges may also have created a serrated edge.

Large vertically oriented scales on the dorsal midline resemble the teeth in the blade of a saw, and may have served a similar purpose if brought into contact with riding dromaeosaurs during violent bucking or deceleration maneuvers on the part of the hadrosaur. Large skin tubercles and a frill of midline scales would probably have limited skin flexibility, which may explain the apparent absence of such features on the neck, where a large range of motion would have been required. The neck may have been left vulnerable without such large tubercles and scales.

## Hadrosaur Crests

To compensate for vulnerability in the neck, running hadrosaur may have reared their heads back in conjunction with a sudden stop, using the momentum of the riding dromaeosaur to cause an impact with the top of the large hadrosaur head. A crest on the top of the head may have improved this hypothetical maneuver by extending the reach of the head with the neck in extension, perhaps also separating the point of impact from important facial structures such as the eyes and mouth. *Tsintaosaurus* had a vertically-oriented “unicorn” crest (Prieto-Márquez & Wagner; 2013), which would have pointed posteriorly with the neck in extension. Posterior evolution of the crest in *Parasaurolophus* may have allowed the crest to swing like a club with lateral movements of the neck. Extreme posterior extension of the crest in *Parasaurolophus* might have protected both neck and withers from small parasitic attackers, without any need for extension of the neck.



**Figure 6. Lambeosaurine Skulls with Crests.** *Corynthosaurus*, *Lambeosaurus* and *Parasaurolophus* (from left to right)

Assuming a large theropod predator, the bones in lambeosaurine crests were too thin to serve a defensive purpose (Padian & Horner, 2011; Weishampel, 1981). Here again, sexual display and competition hypotheses are weakened by the lack of evidence for sexual dimorphism (Padian & Horner, 2011). An olfactory function for the crest is unlikely, due to the lack of any particular enlargement of the lambeosaurine olfactory lobe (Padian & Horner, 2011; Evans et al., 2009). The tubular structure of the lambeosaurine crests may have favored strength with a minimum of bony mass (Prieto-Márquez & Wagner; 2013). The solid posterior crests in *Saurolophus*, and other crested hadrosaurines (Bell, 2011), may have provided a similar neck-protecting advantage, but would not likely have served any acoustic or olfactory function.

## Pachycephalosaur Domes and Spikes

Goodwin and Horner (2004) argue against a frontal head-butting behavior for *Pachycephalosaurius*, due to the radial arrangement of bone in the cranial dome, which would have done little to buffer the brain from the impact of sexual combat (Padian & Horner, 2011; Goodwin & Horner, 2004). Rear-facing head spikes in *Stygimoloch* and *Pachycephalosaurius*



would not have been involved in frontal combat (Padian & Horner, 2011; Goodwin et al., 1998). The weight, resilience and vaulted surface of the dome, may have helped *Pachycephalosaurus* to fend off riding attackers using the maneuver hypothesized above for hadrosaurs. *Stygmoloch* may be the sub-adult form of *Pachycephalosaurus* (Padian & Horner, 2011; Horner & Goodwin, 2009). Rear facing spikes may have allowed young individuals to use the hypothesized head-rearing defense, augmented by the mass and bulk of a cranial dome in mature individuals.

## Sauropod Dorsal Spikes

Four types of dorsal spikes will be discussed on four very different sauropods, each with a different internal structure, but all creating a similar external appearance. Different internal structure and histology suggest separate evolutionary origins. If species recognition was a problem for sauropods, then nature probably would have selected something besides another dorsal spike to tell them apart.

*Amargasaurus* has elongated neural spines projecting from the back of its relatively short neck. Each of these neural spines branch into two long spikes to create a double row of bony projections from the back of the neck. Each spike is circular in cross-section and tapered towards a pointed tip (Novas, 2009). The tallest spines are found on the middle part of the neck, where they reached 60 cm in length (Novas, 2009). The bony spikes are bowed backward as if to repel an attack from behind. The neck spines of *Amargasaurus* are even longer than the “Y” shaped spines protruding from the back of the neck vertebrae in *Dicraeosaurus* (Palmer, 1999). Considered too delicate for defense against a large theropod, the function of these long slender rods is unknown (Updike, 2007).



**Figure 7. *Amargasaurus*.** (Ernesto Bachmann Museum, El ChocArgentina)

Like ceratopsian neck frills, lambeosaurine crests, and pachycephalosaur headgear, it is hypothesized that neck spikes of

*Amargasaurus* may have prevented dromaeosaurs from gaining access to the neck. Some degree of parasitic attack may have been acceptable on the back but perhaps not on the neck where spinal musculature would have been thinner. Osteoderms in ankylosaurs and sauropods are sometimes arranged in mosaics, with flexibility maintained by narrow gaps of fibrous tissue between scutes (Cerde & Powell, 2010). Hardened by calcium or thickened by layers of keratin, it may be that hard nodules reinforced and stiffened the skin on the backs of many dinosaurs. Larger volumes of keratin or calcium, including mosaics of large scutes, would have hindered flexibility. The requirement for flexibility in the neck may have limited the thickening of the

dermis in that area. Like the rear-facing headgear of the ceratopsians, lambeosaurs, and *Stygimoloch*, the elongated neural spines of *Amargasaurus* may have compensated for vulnerability in the neck.

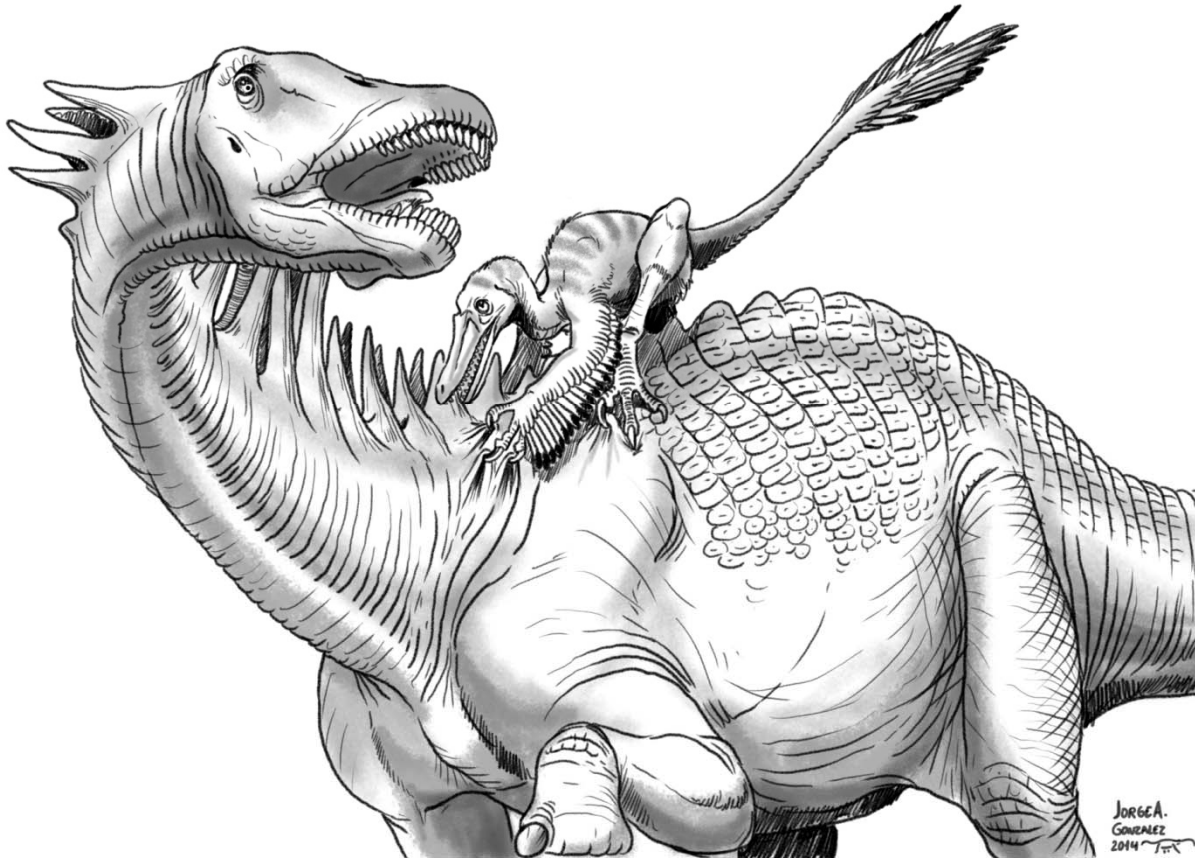
*Agustinia* had plates and spikes attached to the vertebral bones (Bonaparte, 1999). In *Agustinia*, the plates and spikes were not part of the vertebral bones, but attached to them (Bonaparte, 1999). The Cretaceous sauropod, *Agustinia*, displays diplodocid and titanosaurian characteristics.

Czerkas (1993) documented fossilized skin (keratin) from the tip of the tail in a Late Jurassic diplodocid with a sequence of conical spines. Larger spines were found next to large vertebrae. The spines appeared to be oriented in a single row along the mid-line of the tail. Czerkas (1993) speculated that this row of spikes may have followed the crest of the back and neck.

The Cretaceous titanosaur *Ampelosaurus atacis*, had osteoderms that were not restricted to the dorsal midline, but did include large spines (Le Loeuff et al., 1994).

For the three types of sauropod spikes that apparently were positioned on the dorsal midline, defense against attack from the ground would seem an unlikely explanation. The midline spikes would have protected the part of the sauropod least accessible to a large theropod. A large theropod might have been able to bring its jaws down onto the back of a juvenile sauropod or one of the smaller species, but it seems unlikely that a large theropod would have been able to reach, let alone bite the back of the larger sauropods. Spikes on the back would have done nothing to deter attack from the side. If the purpose was to fend off attack from the ground, spikes on the belly or flanks might have been more strategic.

Dorsal attacks from dromaeosaurs would explain the four structurally distinct types of spikes on the backs of four very different sauropods, *Amargasaurus* (Novas, 2009), *Agustinia* (Bonaparte, 1999), *Ampelosaurus atacis* (Le Loeuff et al., 1994), and the diplodocid described by Czerkas (1993). Given the diversity of large sauropods prior to the appearance of dromaeosaurs, it seems plausible that diverse mechanisms would evolve to produce spikes on the backs of each group. The appearance of bony spikes on sauropods of the Cretaceous may suggest that Cretaceous dromaeosaurs had developed enough size to step over or chew through the dermal spines encountered in the Late Jurassic.



**Figure 8.** *Velociraptor* on *Amargasaurus*. (illustration by Jorge Gonzalez)

### Sauropod “Whip” Tails

It has been suggested long whip-like diplodocid tails may have served as weapons to fend off predators (Bakker, 1994), but there is much doubt that those thin tails could have generated enough force to deter a large theropod (Myhrvold & Currie, 1997; Christiansen, 1996). Some diplodocid tails have spikes at the end (Czerkas, 1993). *Shunosaurus* had spikes and a club at the end of its tail (Dong et al., 1989), so a defensive function seems likely. Diplodocids did not have tail musculature powerful enough to swing the tail in a whip-like fashion (Christiansen, 1996). The thin bones at the end of the tail were probably not strong enough to fend off a large theropod (Christiansen, 1996). The fusion of bones sometimes seen in the diplodocid tail does not fit with a whip-like function (Christiansen, 1996).

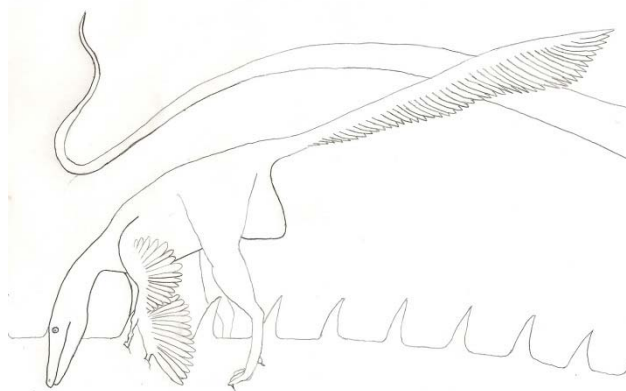
Myhrvold and Currie (1997) agreed that the diplodocid tail was not well adapted as a direct-impact weapon against a large predator, but their computer model suggested that the tail-tip could be moved at 540 m/s, fast enough to generate a loud supersonic noise. There are several problems with their suggestion that the loud crack of the whip tail might have frightened large

predators. Rapid deceleration of living tissues from supersonic speeds would be incredibly traumatic. The tip or popper in a whip breaks down quickly when used to generate a cracking sound. Even the smallest club or spike attached to the end of a whip would hinder the generation of a “crack” and break away quickly.

As with plates increasing the appearance of size for a stegosaur, a loud noise would create only the illusion of threat, which is seldom successful over evolutionary time (Padian & Horner, 2011).

Even over short periods of exposure, bears learn quickly to ignore the harmless noise of bear bangers, when exposed frequently without injury. It is a different story when bears are hunted. The bear that ignores the sounds of hunting rifles, tends to lose its place in the gene pool. Where regulations prevent hunters from shooting grizzly bears, “dinner-bell bears” have learned to go to the sound of gunfire to take over hunter’s kills (Mueller, 2005; McMillion, 1998). Experience is much the same with loud noises used to scare birds, which soon learn to ignore loud noises, unless the noise is associated with injury to some member of the flock ( Bishop, 2003; Mott & Boyd, 1995; Moerbeek et al., 1987; Spanier, 1980).

Insufficiently heavy at the tip to have been effective against a large theropod, the tail of *Diplodocus* may not have needed to reach supersonic speed to be effective against a dromaeosaur or an avialan like *Anchiornis*. Functioning not like a whip but more like a fly swat, the long tail may have provided a perimeter of defense to resist small attackers in an open environment. The long thin tail may have been able to reach attackers on parts of the back, perhaps also ejecting small attackers from the backs of young and other members of a herd.



**Figure 9. Dromaeosaur on *Diplodocus*.**  
(illustration by Aimee Fraser)

## **Elongated Neural Spines of *Spinosaurus***

The sail of *Spinosaurus* should be considered along with other bizarre structures for which a functional consensus has been elusive (Bailey, 1997). The distal morphology of spines suggests that the dorsal margin of the sail was located well proximal to the tips of the elongate neural spines (Rega et al., 2012). If the elongate spines supported a sail for thermoregulation or fat storage, then it would seem unnecessary for the bones to extend beyond the edge of the soft tissue sail. Unnecessarily robust for the repulsion of dromaeosaurs, the sail might have protected the back from other large carnivores. For an animal feeding on a carcass, the sail might have provided a barrier to surprise attacks from competitors.

## Skeletal Deformities

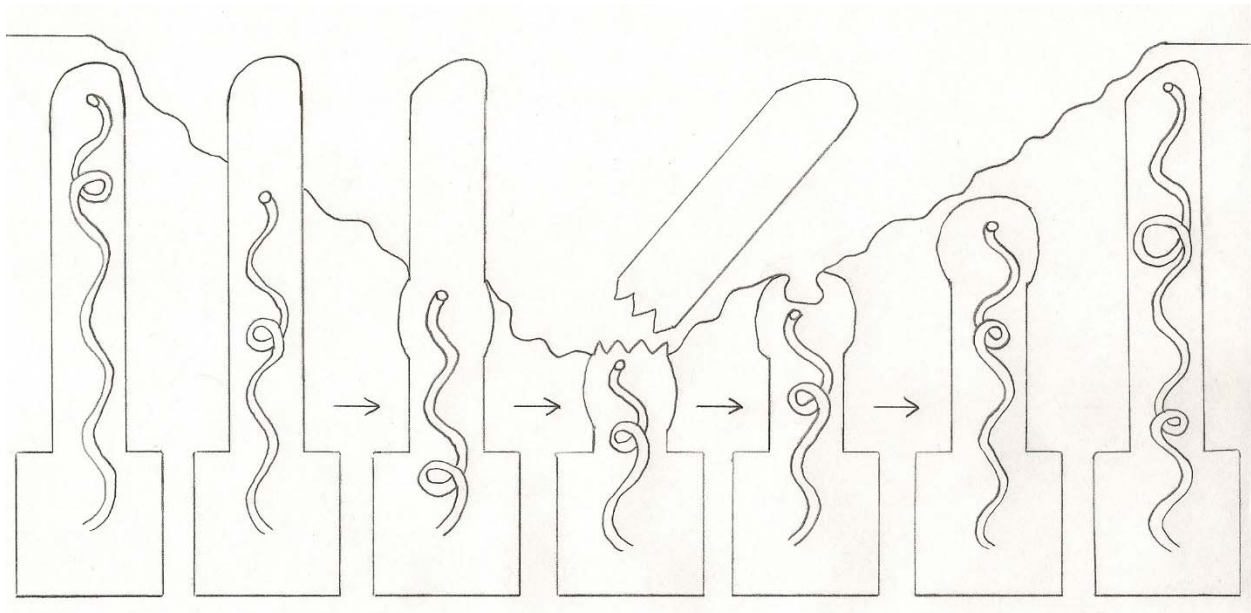
Dromaeosaurs seldom crushed the thick-walled bones of terrestrial dinosaurs (Roach & Brinkman, 2007, p. 118). Dromaeosaur dorsal parasitic feeding may have occasionally have caused deep ulceration, stripping bones of the surrounding soft tissue. Exposed bone can be changed by osteomyelitis and desiccation necrosis (McCulloch & Kloth, 2010).

Infectious periostitis is documented in the scapula of a ceratopsian, and an abscess was noted in the ilium of *Camptosaurus* (Rothschild, 1997). Osteomyelitis occasionally affects hadrosaur caudal vertebrae, including neural spines (Tanke & Rothschild, In press; Carpenter, 1998).

The proximal hadrosaur tail would have been accessible from the back and may have been vulnerable to biting, perhaps due to greater surface convexity in the cross-section of the tail as compared to the back. Flat surfaces may be more difficult to bite. Partially-healed injuries are common in the vertebral spines (spinous processes) of hadrosaur tails, suggesting periods of post-injury survival long enough for significant but not complete healing (Tanke & Rothschild, In press). Injuries are common at the distal (superior) tips of the spinous processes, which are often swollen by the formation of callus (Tanke & Rothschild, In press). Tanke and Rothschild (In press) argue against mating trauma and tyrannosaur biting as the cause of these injuries, instead hypothesizing injury from conspecifics stepping over tails in a herd. Some hadrosaur tail injuries were caused by tyrannosaurs, as proven by the tooth crown found in the partially healed centrum of a hadrosaur from the Hell Creek Formation (DePalma et al., 2013). Tanke and Rothschild (In press) argue that blood vessel openings have sometimes been incorrectly identified as tyrannosaur “toothmarks.” In Alberta, they have found no evidence of Tyrannosaur bites on a large number of healing hadrosaur specimens.

If dromaeosaurs removed soft tissues overlying hadrosaur caudal neural spines, desiccation necrosis might lead to sloughing of exposed bone that protruded beyond the base of the ulcer (Pavletic, 2010; McCulloch & Kloth, 2010). The natural history of protruding bone is theoretical, due to the widespread modern use of skin grafts, debridement and amputation to cover exposed bone. Sloughing would occur gradually due to oxidation and microbial effects on collagen. Osteoclasts would likely digest dead bone adjacent to viable perfused bone. Repeated dromaeosaur attacks might break off devitalized bone. In the interim before sloughing of the devitalized bone, a callus might be expected adjacent to the necrotic bone, which might resemble the callus that forms around a fracture. Granulation tissue is not able to cover protruding bone (Pavletic, 2010), but it does maintain periosteum that is kept moist by nearby vascular soft tissue (McCulloch & Kloth, 2010). Granulation tissue would maintain periosteum and cortical bone at the base of the ulcer. Periosteum nourishes cortical bone and causes it to thicken at the site of injury.

After sloughing of necrotic bone, the inner (trabecular) bone would desiccate easily and would not granulate over (McCulloch & Kloth, 2010), so it would likely ulcerate when exposed to air. In the *Edmontosaurus* on display at the Denver Museum of Natural History (DMNH 1943) (Carpenter, 1998), and many similar specimens at the Tyrrell Museum (Tanke & Rothschild, In press), a group of spinous processes are shortened, terminating in thickened cortical bone, sometimes surrounding a depressed core of trabecular bone. Groups of shortened spinous processes may reflect the shape of a tyrannosaur muzzle (Carpenter, 1998), the foot of a conspecific (Tanke & Rothschild, In press) or the contour of an ulcer caused by removal of soft tissues.



**Figure 10. Neural Spines at Various Stages of Response to Exposure.** Desiccation necrosis leads to sloughing of devitalized bone with callus formation in remaining bone. The wavy line indicates the soft-tissue surface in an ulcer. Stylized blood vessels indicate viable bone.

## Conclusion

The pack-hunting doctrine can be questioned by a return to Carpenter's original interpretation of the "fighting pair" (Carpenter, 1998). Extant parasitic and predatory approaches to large animals involve riding and disengagement, often from the backs of living victims. Literally and figuratively, the bizarre dinosaur structures point to dromaeosaurs riding large herbivores. The dismount may have played a role in the origin of flight and the persistence of large feathers in *Velociraptor*. Future mechanical studies may help to test the functional hypotheses for specialized dromaeosaur structures and bizarre structures in other dinosaurs. Removal of soft tissue requires further investigation as a cause of bony deformity.



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## References

- Alexander DE, Gong E, Martin L, Burnham D, Falk AR (2010) Reply to Brougham and Brusatte: Overall anatomy confirms posture and flight model offers insight into the evolution of bird flight. *PNAS* 107(40).
- Anderson BG, Lucas SG, Barrick RE, Heckert AB, Basabivazo GT (1998) Dinosaur skin impressions and associated skeletal remain from the upper Campanian of Southwestern New Mexico: new data on the integument morphology of hadrosaurs. *Journal of Vertebrate Paleontology* 18(4): 739-745.
- BBC News (2000, Feb 14) Elephants kill endangered rhino. Retrieved from <http://news.bbc.co.uk/2/hi/642731.stm>
- Bailey J (1997) Neural spine elongation in dinosaurs; Sailbacks or buffalo-backs? *Journal of Paleontology* 71: 1124-1146.
- Bakker R (1994) The bite of the bronto. *Earth* 3(6): 26-35.
- Bell PR (2011) Description of the skull *Saurolophus osborni* Brown 1912 (Ornithischia: Hadrosauridae) *Cretaceous Research* 32(1): 30-44.
- Bell PR (2012) Standardized terminology and potential taxonomic utility for hadrosaurid skin impressions: A case study for *Saurolophus* from Canada and Mongolia. *Plos One* 7(2) Retrieved from: <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0031295> Accessed 14 March 2014.
- Bishop J (2003) Review of international research literature regarding the effectiveness of auditory bird scaring techniques and potential alternatives. Available: <http://archive.defra.gov.uk/environment/quality/noise/research/birdscaring/birdscaring.pdf> Accessed 12 December 2013.
- Bonaparte J (1999) An armoured sauropod from the Aptian of Northern Patagonia, Argentina. In: Y Tomida, T Rich & P Vickers-Rich (eds), *Proceedings of the Second Gondwanan Dinosaur Symposium*. Tokyo: National Science Museum Monographs 15: 1–12.
- Buffrenil V, de Farlow J, de Ricqlès A (1986). Growth and function in *Stegosaurus* plates: evidence from bone histology. *Paleobiology* 12: 459–473.
- Burkholder (1962) Observations concerning wolverine. *Journal of Mammalogy* 43: 263-264.
- Buss IO (1971) The functional significance of movements and positions of the pinnae of the African elephant, *Loxodonta Africana*. *Journal of Mammalogy* 52(1): 21-27.
- Carpenter K (1997) Ankylosauria. In: O Farlow & K Brett-Surman (eds), *The Complete Dinosaur*. Bloomington: Indiana University Press: 307-316.
- Carpenter K (1998) Evidence of predatory behavior by carnivorous dinosaurs. *Gaia* 15: 135-



- Cerda I, Powell J (2010) Dermal armor histology of *Saltasaurus loricatus*, an Upper Cretaceous sauropod dinosaur from Northwest Argentina. *Acta Palaeontologica Polonica* 55(3): 389-398.
- Chatterjee S, Templin R (2004) Feathered coelurosaurs from China: new light on the arboreal origin of avian flight. In: P Currie, E Koppelhus, M Shugar & J Wright (eds), *Feathered Dragons*. Bloomington: Indiana University Press: 251-181.
- Chiappe LM, Göhlich UB (2010) Anatomy of *Juravenator starki* (Theropoda: Coelurosauria) from the Late Jurassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 258(3): 257-296.
- Christiansen P (1996) The “whiplash” tail of diplodocid sauropods: Was it really a weapon? In: Morales M (ed), *The Continental Jurassic*. Museum of Northern Arizona Bulletin 60: 51-58.
- Currie PJ & Jacobsen AR (1995) An azhdarchid pterosaur eaten by a velociraptorine theropod. *Can. J. Earth Sci.* 32: 992-925.
- Czerkas S (1993) Discovery of dermal spines reveals a new look for sauropod dinosaurs. *Geology* 20: 1068-1070.
- DePalma RA, Bunham DA, Martin LD, Rothschild BM, Larson PL (2013) Physical evidence of predatory behavior in *Tyrannosaurus rex*. *PNAS* 110(31): 12560-12564.
- Dong Z, Peng G, Huang D (1989). The discovery of the bony tail club of sauropods. *Vertebrata Palasiatica* 27: 219–224
- Dwyer S, Visser I (2011) Cookie cutter shark (*Isistius* sp.) bites on cetaceans, with particular reference to killer whales (Orca) (*Orcinus orca*). *Aquatic Mammals* 37(2): 111-138.
- Evans DC, Ridgely R, Witmer LM (2009) Endocranial anatomy of lambeosaurine hadrosaurids (Dinosauria: Ornithischia): A sensorineural perspective on cranial crest function. *Anatomical Record* 292: 1315-1337.
- Farke A, Wolff E, Tanke D (2009) Evidence of combat in *Triceratops*. *PLoS One* 4, e4252. (Online DOI: DOI:[10.1371/journal.pone.0004252](https://doi.org/10.1371/journal.pone.0004252)).
- Farlow JO, Hayashai S, Tattersall GJ (2010) Internal vascularity of the dermal plates of *Stegosaurus* (Ornithischia, Thyreophora). *Swiss J. Geosci* 103: 173-185.
- Feducia A (1993) Evidence from claw geometry indicating arboreal habits of Archaeopteryx. *Science* 259: 790-793.
- Forster A, Sampson D, Chiappe M, Krause W (1998) The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* 279: 1915-1919.
- Fowler D, Freedman E, Scannella J, Kambic R (2011) The Predatory Ecology of Deinonychus and the Origin of Flapping in Birds. *PLoS ONE* 6(12): 1-12. Available: <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0028964> Accessed 12 December 2013.
- Fredrickson O (1972) *The silence of the North*. New York. Warner Books: 153-157.

- Godefroit P, Demuynck H, Dyke G, Hu D, Escuillié F, Claeys P (2013a) Reduced plumage and flight ability of a new Jurassic paravian theropod from China. *Nature Communications* 4(1394): 1-6.
- Godefroit P, Cau A, Dong-Yu H, Escuillié F, Wenhao W, Dyke G (2013b) A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. *Nature* 498: 359-361.
- Goodwin MB, Buchholz EA, Johnson RE (1998) Cranial anatomy and diagnosis of *Stygmoloch spinifer* (Ornithischia: Pachycephalosauria) with comments on cranial display structures in agonistic behavior. *Journal of Vertebrate Paleontology* 18: 363-375.
- Goodwin MB, Horner JR (2004) Cranial histology of pachycephalosaurs (Ornithischia: Marginocephalia) reveals transitory structures inconsistent with head-butting behavior. *Paleobiology* 30(2): 253-267.
- Greenhall AM (1971) Attacking behavior of the vampire bat, *Desmodus rotundus*, under field conditions in Mexico. *Biotropica* 3(2): 136-141.
- Grinnell G (1920) As to the wolverine. *Journal of Mammalogy* 1(4): 182-184.
- Grinnell G (1926) Some habits of the wolverine. *Journal of Mammalogy* 7(1): 30-34.
- Haglund B (1974) Moose relations with predators in Sweden, with special reference to bear and wolverine. *Le Naturaliste Canadien* 101: 457-466.
- Hone D, Tsuihiji T, Watabe M, Tsogtbaatr K (2012) Pterosaurs as a food source for small dromaeosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 331-332: 27-30.
- Horner JR (1984) A “segmented” epidermal tail frill in a species of hadrosaurian dinosaur. *Journal of Paleontology* 58: 270-271.
- Horner JR, Goodwin MB (2009) Extreme cranial ontogeny in the Upper Cretaceous dinosaur *Pachycephalosaurius*. *PLoS One* 4. Retrieved from: <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0007626#pone-0007626-g010> Accessed 15 March 2014.
- Hu D, Hou L, Zhang L, Xu X (2009) A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* 461: 640-643.
- Kellogg DL (2006) In vivo mechanisms of cutaneous vasodilation and vasoconstriction in humans during thermoregulatory challenges. *Journal of applied physiology* 100(5): 1709-1718.
- Kofron C (1999) Attacks to humans and domestic animals by the southern cassowary (*Casuarius casuarius johnsonii*) in Queensland, Australia. *Journal of Zoology* 249: 375-381.
- Kozhechkin V (1990) On cases of wolverine hunting the moose in eastern Siberia. Abstracts of Papers and Posters from the Third International Moose Symposium: Syktyvkar, USSR.
- Krauss D, Pezon A, Nguyen P, Salame I, Rywkin S (2010) Evolutionary interactions between horn and frill morphology in Chasmosaurine ceratopsians. In: M Ryan, B Chinnery-Allgeier & D Eberth (eds), *New perspectives on horned dinosaurs*. The Royal Tyrrell Museum Ceratopsian Symposium. Bloomington: Indiana University Press: 282-292.
- Landa A, Strand O, Swenson J, Skogland T (1997) Wolverines and their prey in Southern Norway. *Canadian Journal of Zoology* 75(8): 1292-1299.
- Le Loeuff J, Buffetaut E, Cavin L, Matin M, Martin V, Tong H (1994) An armoured titanosaurid sauropod from the Late Cretaceous of Southern France and the occurrence of osteoderms in the Titanosauridae. *Gaia* 10: 155-159.
- Lofroth E (1997) Northern Wolverine Project: Wolverine ecology in logged and unlogged plateau and foothill landscapes. Unpub. Prog. Rep. Ministry of Environment, Victoria, BC, Canada.

- Lofroth E (2001) Northern wolverine project: 2000/01 Year End Report: Wolverine Ecology in Plateau and Foothill Landscapes 1996-2001. Available: [http://www.env.gov.bc.ca/wildlife/wsi/reports/769\\_WSI\\_769\\_RPT.PDF](http://www.env.gov.bc.ca/wildlife/wsi/reports/769_WSI_769_RPT.PDF) Accessed 12 December 2013.
- Lofroth E, Krebs J, Harrower W, Lewis D (2007) Food habits of wolverine *Gulo gulo* in montane ecosystems of British Columbia, Canada. *Wildlife Biology* 13(2): 31-37.
- Lohuis TD (2013a) Dall's sheep research in the Chugach Range, GMUs 13D and 14C. Retrieved from: [http://www.adfg.alaska.gov/static/speciesinfo/dallsheep/pdfs/chugach\\_range\\_dalls\\_sheep\\_research.pdf/](http://www.adfg.alaska.gov/static/speciesinfo/dallsheep/pdfs/chugach_range_dalls_sheep_research.pdf/) Accessed 17 January 2004.
- Lohuis TD (2013b) Ewe Dall's sheep survival, pregnancy and parturition rates, and lamb recruitment in GMU 13D, Chugach Mountains, Alaska. (work in progress) Federal Aid Progress report, Project #6.16, Alaska Department of Fish and Game, Juneau AK: 4-7.
- Longrich NR, Vinther J, Meng Q, Li Q, Russell A (2012) Primitive wing feather arrangements in *Archaeopteryx lithographica* and *Anchiornis huxleyi*. *Current Biology* 22(23): 2262-2267.
- Loope D, Mason J, Dingus L (1999) Lethal sandslides from eolian dunes. *The Journal of Geology* 107: 707-713.
- Main R, Ricqlès A, Horner J, Padian K (2005) The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs. *Paleobiology* 31(2): 291-314.
- Manning P, Payne D, Pennicott J, Barrett P, Ennos R (2006) Dinosaur killer claws or climbing crampons? *Biology Letters* 2(1): 110-112.
- Mattisson J, Andrén H, Persson J, Segerström P (2011) Influence of intraguild interactions on resources and Eurasian lynx. *Journal of Mammalogy* 92(6): 1321-1330. Available: [http://www.wolverineproject.se/uploads/1/3/9/2/13929225/j\\_mammal\\_2011\\_mattissoninfluence\\_of\\_intraguild\\_interactions\\_on\\_resource\\_use\\_by\\_wolverines\\_and\\_eurasian\\_lynx921321-13306.pdf](http://www.wolverineproject.se/uploads/1/3/9/2/13929225/j_mammal_2011_mattissoninfluence_of_intraguild_interactions_on_resource_use_by_wolverines_and_eurasian_lynx921321-13306.pdf) Accessed 12 December 2013.
- Maxwell W, Ostrom J (1995) Taphonomy and paleobiological implications of *Tenontosaurus-Deinonychus* associations. *Journal of Vertebrate Paleontology* 15: 707-712.
- McCulloch J, Kloth L (2010) *Wound Healing: Evidence-based Management 4<sup>th</sup> ed.* USA: FA Davis. p. 159.
- McMillion S (1998) Mark of the Grizzly: True stories of recent bear attacks and the hard lessons learned. US: Falcon Publishers: 169-178.
- Metcalf SJ, Vaughan RF, Benton MJ, Cole J, Simms MJ, Dartnall DL (1992) A new Bathonian (Middle Jurassic) microvertebrate site, within the Chipping Norton Limestone Formation at Hornsleaslow Quarry, Gloucestershire. *Proceedings of the Geologists' Association* 103 (4): 321-342.
- Moerbeek D, van Dobben W, Osieck E, Boere G, Bungenberg de Jong C (1987) Cormorant damage prevention at a fish farm in the Netherlands. *Biological Conservation* 39(1): 23-38.
- Mott D, Boyd F (1995) A review of techniques for preventing cormorant depredations at aquaculture facilities in Southeastern United States. *Colonial Waterbirds* 18: 176-180.
- Motta P, Wilga C (2001) Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks. *Environmental Biology of Fishes* 60: 130-156.
- Mueller L (2005) *Bear Attacks of the Century: True Stories of Courage and Survival.* US: Globe Pequot: 69-80.

- Murphy NL, Trexler D, Thompson M (2006) “Leonardo”, a mummified *Brachylophosaurus* from the Judith River Formation. In K Carpenter (ed.), *Horns and beaks: Ceratopsian and ornithopod dinosaurs*. Bloomington: Indiana University Press: 117-133.
- Myhrvold N, Currie P (1997) Supersonic sauropods? Tail dynamics in the diplodocids. *Paleobiology* 23: 393-409.
- Norell M, Makovicky P (2004) *Dromaeosauridae*. In: D Weishampel, P Dodson and H Osmolska (eds), *The Dinosauria*, Second Edition. University of California Press, Berkeley: 196-209.
- Novas F (2009) *The age of dinosaurs in South America*. Bloomington: Indiana University Press: 172-175.
- O’Connor J, Zhou Z, Xu X (2011) Additional specimen of *Microraptor* provides unique evidence of dinosaurs preying on birds. *PNAS* 108(49): 19662–19665.
- Ostrom JH (1969) Osteology of *Deinonychus antirrhopus*, an unusual theropod from the lower Cretaceous of Montana. *Peabody Museum Nat. Hist. Bull.* 30: 1-165.
- Ostrom JH (1978) The osteology of *Compsognathus longipes* Wagner. *Zitteliana* 4: 73–118.
- Packer C (1983) Sexual dimorphism: the horns of African antelopes. *Science* 221(4616): 1191-1193.
- Padian K (1998) The origin of birds and their flight. *Scientific American* 278 (2): 38-47.
- Padian K, Horner J (2011) The evolution of ‘bizarre structures’ in dinosaurs: biomechanics, sexual selection, social selection or species recognition? *Journal of Zoology* 283(1): 3-17.
- Palmer D (1999) *The Marshall Illustrated Encyclopedia of Dinosaur and Prehistoric Animals*. London: Marshall Editions: 132.
- Papastamatiou Y, Wetherbee B, O’Sullivan J, Goodmanlowe G, Lowe C (2010) Foraging ecology of cookiecutter sharks (*Isistius brasiliensis*) on pelagic fishes in Hawaii, inferred from prey bite wounds. *Environ Biol Fish* 88(4): 361-368.
- Parks WA (1920) [1868-1936] Osteology of the trachodont dinosaur *Kritosaurus incurvimanus*. University of Toronto Studies, Geological Series #11: 1-74. Retrieved from: <https://archive.org/stream/cu31924004594895#page/n1/mode/2up> Accessed 14 March 2014.
- Pavletic M (2010) *Atlas of small animal wound management and reconstructive surgery 3<sup>rd</sup> ed.*. Iowa, USA: Wiley-Blackwell. p. 153.
- Prieto-Márquez A, Wagner JR (2013) The ‘unicorn’ dinosaur that wasn’t: A new reconstruction of the crest of *Tsintaosaurus* and the early evolution of the lambeosaurine crest and rostrum. *PLoS One* 8(11). Retrieved from: <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0082268> Accessed 15 March 2014.
- Pullianen E (1988) Ecology, Status and management of the Finnish wolverine *Gulo gulo* populations. *Lustra* 31: 21-28.
- Rausch R, Pearson A (1972) Notes on the wolverine in Alaska and the Yukon Territory. *Journal of Wildlife Management* 36(2): 249-268.
- Rega E, Noriega K, Sumida S, Huttenlocker A, Lee A, Kennedy B (2012) Healed Fractures in the Neural Spines of an Associated Skeleton of *Dimetrodon*: Implications for Dorsal Sail Morphology and Function. *Fieldiana Life and Earth Sciences* 5: 104-111.

- Roach B, Brinkman D (2007) A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs. *Peabody Museum of Nat Hist Bull* 48(1): 103-138.
- Rothschild MB (1997) Dinosaurian paleopathology. In: JO Farlow & MK Brett-Surman (eds.) *The Complete Dinosaur*. University of Indiana Press: 426-448.
- Scannella J, Horner J (2010) *Torosaurus* Marsh, 1891 is *Triceratops* Marsh, 1889 (Ceratopsidae: Chasmosaurinae): synonymy through ontogeny. *J. Vertebr. Paleontol.* 30(4): 1157-1168.
- Schluter D, Grant P (1984) Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis*. *Evolution* 38(4): 856-869.
- Skogland T (1989) Comparative social organization of wild reindeer in relation to food, mates, and predation avoidance. *Advances in Ethology* 29: 74.
- Slotow R, van Dyk G, Poole J, Page B, Kocke A (2000) Older bull elephants control young males. *Nature* 408: 425-426.
- Spanier E (1980) The use of distress calls to repel night herons from fish ponds. *Journal of Applied Ecology* 17: 287-293.
- Tanke DH, Rothschild BM (In press) Paleopathology in Late Cretaceous Hadrosauridae from Alberta, Canada. In: DA Eberth & DC Evans (eds.), *Hadrosaurs*. Bloomington, Indiana: Indiana University Press.
- Tobalske BW, Hedrick TL, Biewener AA (2003) Wing kinematics of avian flight across speeds. *Journal of Avian Biology* 34:177-184.
- Turner A, Makovicky P, Norell M (2007) Feather quill knobs in the dinosaur *Velociraptor*. *Science*. 317: 1721.
- Updike J (2007) Extreme dinosaurs. *National Geographic Magazine* 212(6): 32-57.
- van der Lubbe T, Richter U, Knötschke N (2009) Velociraptorine dromaeosaurid teeth from the Kimmeridgian (Late Jurassic) of Germany. *Acta Palaeontologica Polonica* 54: 401-408.
- Varricchio DJ (2001) Gut contents from a Cretaceous tyrannosaurid: implications for theropod dinosaur digestive tracts. *Journal of Paleontology* 75(2): 401-406.
- Walker M (2009) Eagles filmed hunting reindeer. BBC News. Available: [http://news.bbc.co.uk/earth/hi/earth\\_news/newsid\\_8314000/8314558.stm](http://news.bbc.co.uk/earth/hi/earth_news/newsid_8314000/8314558.stm). Accessed 12 December 2013.
- Weishampel B (1981) Acoustic analyses of potential vocalization in lambeosaurine dinosaurs (Reptilia: Ornithischia). *Paleobiology* 7(2):252-261.
- Xu X, Zhao Q, Norell M, Sullivan C, Hone D, Erickson G, Wang X, Han F, Gou Y (2009) A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. *Chinese Science Bulletin* 54(3): 430-435.
- Xu X, You H, Du K, Han F (2011) An *Archaeopteryx*-like theropod from China and the origin of Avialae. *Nature* 475: 465-470.
- Zinke J (1998) Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). *Paläontologische Zeitschrift* 72: 179-189.
- Zelenitsky et al. (2012) Feathered non-avian dinosaurs from North America provide insight into wing origins. *Science* 338: 510-514.