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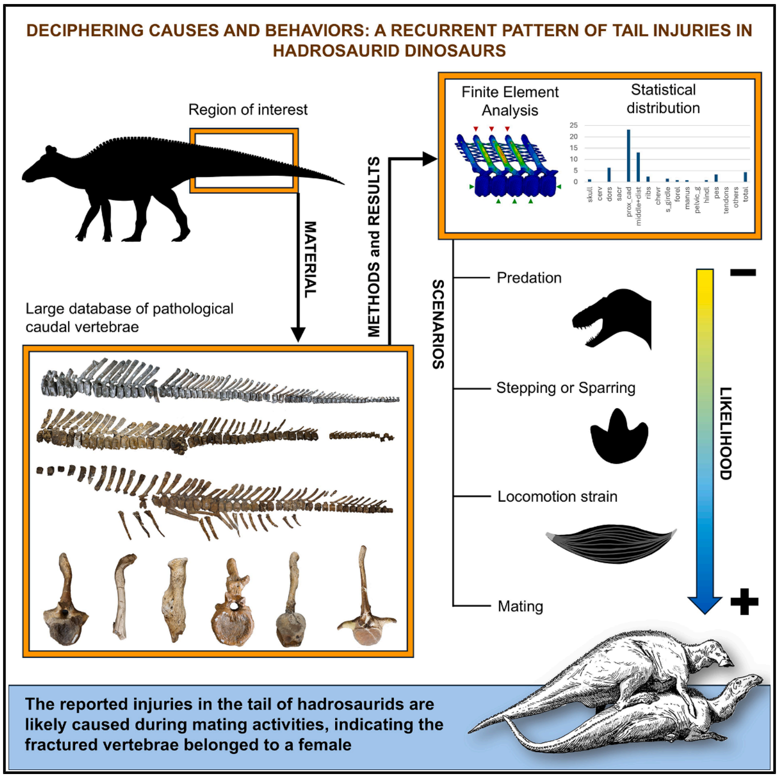
Deciphering causes and behaviors: A recurrent pattern of tail injuries in hadrosaurid dinosaurs

Graphical abstract



Highlights

- A traumatic pattern is found in the proximo-middle part of many hadrosaur tails
- FEA shows how caudal spines are similarly broken by a diagonal pressing force
- After evaluating different hypotheses, mating traumas are the most likely cause
- The injured specimens might represent female individuals

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In brief

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Deciphering causes and behaviors: A recurrent pattern of tail injuries in hadrosaurid dinosaurs

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SUMMARY

Elevated frequencies of repeated injuries are identified in the proximo-middle caudal region of hadrosaurid dinosaur tails. The affected vertebrae show healing injuries in the distal region of the vertebral neural spines, but the causes are yet indeterminate. A finite element analysis was performed on a modeled caudal vertebral series to test if such injuries were caused by loading weight. Our results indicate that the deforming stress resulted from the same dorsal force pressing upon a large area of the tail. We scrutinized all possible biological scenarios that could cause the pathological deformation of the bones. The affected area corresponds to the putative position of the cloacal opening, indicating the possibility that the dorsal force might correspond to the action of a mounting male. As such, these potential mating injuries may represent the first indirect evidence of sexual behavior in non-avian dinosaurs, and a novel approach to recognize female individuals.

INTRODUCTION

Reconstructing the lifestyle, social interactions, and behaviors of extinct animals based solely on fossilized remains is challenging, especially when the studied taxa do not have any modern analogs. However, paleopathology—the study of fossilized injuries and lesions[1]—provides tools that can be used to help decipher dinosaur behaviors.[2] Injuries caused by prey-predator interactions,[3] intraspecific fighting,[2,4] and social activity[5] may be evident in the form of healing trauma in fossils of individuals that initially survived such events. In particular, hadrosaurids display an elevated number of injuries[5] compared with other dinosaur groups, especially in the neural spines of the proximo-middle caudal vertebrae.[6] A number of causes have been hypothesized for these injuries including that they are due to conspecifics accidentally stepping on the tails of their peers, perhaps when the herd was resting,[6] they result from intraspecific fights,[6,7] or from muscular strain during locomotion or other habitual activities such as feeding and walking.[8] Importantly, Tanke[9] suggested another intriguing cause, namely that the fractured neural spines of these proximo-middle caudal vertebrae could occur secondary to mating: the male mounts the female by pressing on the dorsal part of the proximal portion of the tail, resulting in a series of injuries to the associated caudal neural spines. However, this explanation was challenged, with side strikes or trampling considered as more plausible interpretations.[5] Critics of the "mating hypothesis" focused on the limited number of specimens displaying the trauma and observed that morphologically similar injuries can have different etiologies.[10] It was highlighted that reproductive behavior involving injury to a female would be maladaptive with negative implications for fitness not conducive to natural selection. In the current study, we analyze the pathological characteristics of the injured tails and their distribution in different species from various localities and eras, in an effort to identify the possible cause(s) for this pathological pattern. A finite element analysis (FEA) was undertaken on a digitally modeled series of caudal vertebrae based on *Edmontosaurus*, to simulate a loading mass on a hadrosaur tail to understand the distribution of the stressing entity on the body, the effect of different angular forces on the spine and

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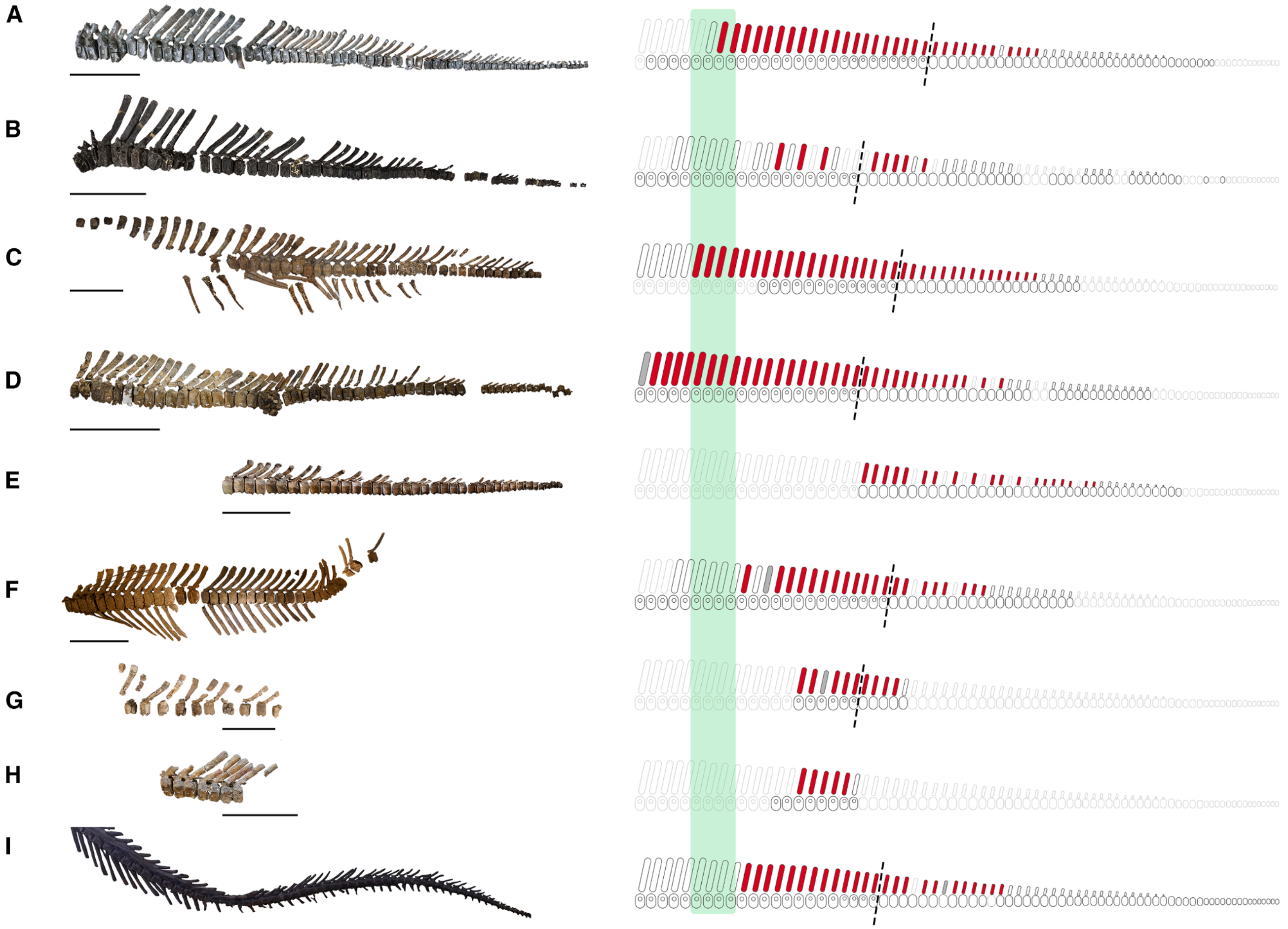

Figure 1. Hadrosaurid tails and location of pathologies in relation to the cloacal region
Olorotitan arharensis AEHM 2/845 (A), *Hypacrosaurus stebingeri* MOR 549 (B), cf. *Edmontosaurus* MOR 3003 (C), cf. *Edmontosaurus* TMP 1970.018.0001 (D), Hadrosauridae indet. AMNH FARB 5426 (E), *Edmontosaurus* sp. RAM 7150 (F), cf. *Brachylophosaurus* BDM 003 (G), *Amurosaurus riabinini* AEHM 1/304–310 (H), and *Edmontosaurus annectens* AMNH FARB 5886 (I). B and G are mirrored. Red bars indicate pathological neural spines. Dotted black lines mark the transition from proximal to middle caudals, indicated by loss of transverse processes. The green column highlights the possible location site of the cloaca. Scale bars, 50 cm.

structure of the vertebra, and which deformation angle of the spine corresponded best to the data observed in the surveyed museum collections. Finally, the analytical and statistical results are assessed against the aforementioned etiologies to determine the most plausible explanation for the injuries.

RESULTS

Hadrosaur collections in Canada (Royal Ontorio Museum, TMP [Royal Tyrrell Museum of Palaeontology], and CMN [Canadian Museum of Nature]), the USA (AMNH [American Museum of Natural History], BDM [Badlands Dinosaur Museum], LACM [Los Angeles County Museum], MOR [Museum of the Rockies], RAM [Raymond Alf Museum of Paleontology], and Smithsonian National Museum of Natural History), the UK (NHMUK [Natural History Museum]), and Russia (AEHM [Amur Natural History Museum]) were examined, and 551 pathological neural spines in individual hadrosaurid caudal vertebrae were recorded, mainly located in the proximo-middle region of the tail (see Tables S1 and S2). Seven complete tails and two associated vertebral sequences, belonging to five different genera (*Olorotitan*, *Amurosaurus*, *Edmontosaurus*, *Hypacrosaurus*, and cf. *Brachylophosaurus*), showed a similar pattern (Figure 1). The pathological deformation of the proximo-middle caudal spines appears to have been caused by direct trauma. We analyzed the bodily distribution of paleopathological lesions in hadrosaurids from the AEHM collection using the population approach for the fossil record proposed by Siviero et al.[5] to identify if statistical differences in frequencies were evident in the different regions of the body. For the purpose of this study, the AEHM collection was considered as a single population, because the bonebeds of Blagoveschensk and Kundur (far eastern Russia) are coeval in time, and geographically close. A total of 118 pathological bones were identified from a sum of 2,717 specimens. The ratio “pathological/entire collection” is 4.3% (Table S3). When considered as a whole, the body areas with the highest

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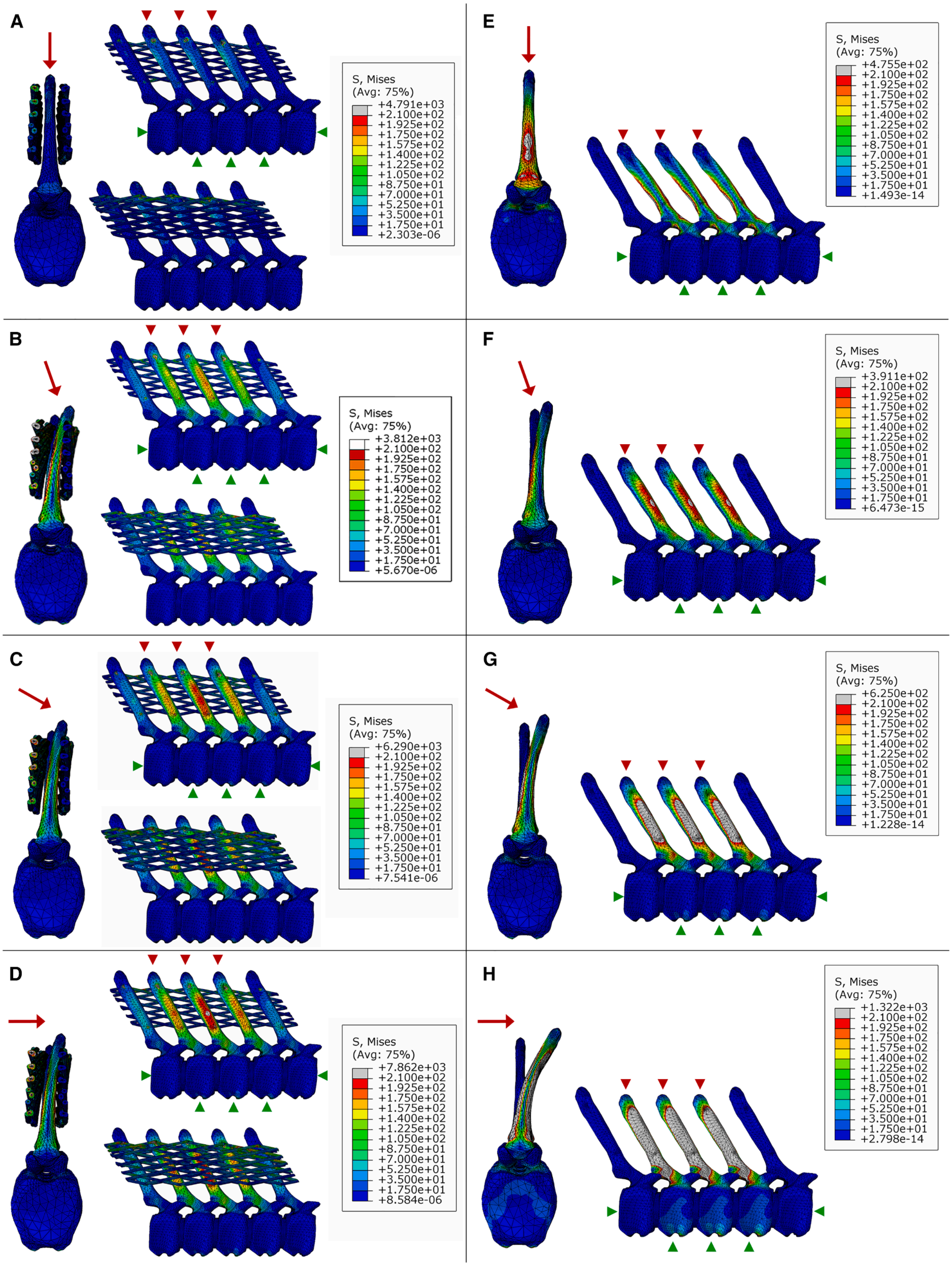

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frequency of paleopathological lesions are the vertebral series (n = 93; 10.3%) and pedal phalanges (n = 263; 3.4%) This prevalence also reflects the fact that, in museum collections, vertebrae (especially caudals) and pedal phalanges are the most commonly preserved bones in hadrosaurid localities (FB, pers. obs.). In the tail, the proximal caudals show the highest prevalence (n = 28; 23.7%), followed by the middle (n = 39; 12.0%), and the distals (n = 12; 10.2%). Additional lesions are also represented, but to a lesser extent, in the skull (n = 6; 1.2%), ribs (n = 4; 2.4%), shoulder girdle (n = 1; 1.5%), forelimb (n = 2; 0.9%), and manus (n = 1; 0.8%). The tail is predominantly the body region with the greatest amount of fossilized paleopathological lesions, as previously reported for an *Edmontosaurus* population.[5] Combining proximal, middle, and distal caudals together, a total number of 79 paleopathological elements from a total of 512 vertebrae are counted (15.4%). These predominantly comprise examples of trauma (n = 61; 51.7% of the total number of lesions), with minor developmental defects (n = 16; 13.5% of the total amount of lesions), infection (n = 1), and a lesion of unknown etiology represented to a lesser extent.

Statistical analysis

A Pearson chi-squared analysis indicated an association between pathologies and body regions (X^2 = 117.98, df = 8, p value <2.2e-16). These values are associated with all pathologies recorded in the collection, not just trauma. A second analysis was run which only included traumatic injuries, but the results were similar (X^2 = 114.42, df = 8, p value <2.2e-16). Low p values were also found in the relationship between pathologies and the different areas of the axial skeletons (X^2= 23.628, df = 2, p value = 7.399e-06) and in the tail region (X^2= 6.4951, df = 2, p value = 0.03887). As reported by Siviero et al.,[5] the distribution of pathological lesions shows a compelling association with body regions, particularly the tail, an association that was also detected with the binary logistic regression (Table S3). As such, the concentration of pathologies in the tail was probably linked to analogous causes between the different species. In fact, the similarity of the lesions between these hadrosaurid specimens is remarkable, especially considering that the species lived at different times (Campanian to Maastrichtian) and in a variety of geographical areas (North America to Asia).

FEA

FEAs were performed on the *Edmontosaurus* modeled vertebral series by applying loadings along four directions to test different angles of force (Figure 2). A range of scenarios were simulated, including the animal standing or lying on the ground and the presence or absence of associated ossified tendons, because of their reinforcing role.[11] To understand the nature of the lesions, it was important to consider the action of ossified tendons, arranged in a lattice on the lateral sides of the neural spines, and providing a mechanism for alleviating and redistributing the stresses that act upon them. In fact, simulations conducted without the tendon lattice resulted in an accumulation of stresses in the middle of the neural spine and not on the distal end as observed in the reported fossilized neural spines. The application of a straight vertical load at 0° to the dorsoventral axis generated a caudal bending of the spine that is not observed in the fossil record. This was also the case for application of a load at 90°. The most noteworthy results were instead obtained with the load directed at an angle of between 30° and 60° to the dorsoventral axis. These loadings generated bending of the neural spines, countered by the arrangement of the tendon lattice, along with a concentration of stress toward the middle region of the neural spines (Video S1). However, the tendon lattice shifts the accumulation of stress toward the point of its contact with the neural spines, i.e., their distal extremities (Video S1). This position is consistent with the pathologies observed in the fossil record (Tables S1 and S2). The presence of the tendon lattice is believed to have evolved to increase the stability and locomotor efficiency of these animals.[11] Increased stiffness at the anterior-most region of the tail due to the presence of the tendon lattice reduces displacement during vertebral rotation when subjected to loads, thereby leading to a local concentration of mechanical stress and resulting in injury.

DISCUSSION

In general, wherever there is a substantial fossil record for hadrosaurids, the same demonstrable injury pattern affecting this particular region of the tail is evident.[5,7] The distal ends of the neural spines of the proximal and middle caudal vertebrae are the areas most affected, with the lower section of the spines, near the vertebral centra, impacted to a lesser extent. The apical portion of the neural spine in affected vertebrae was typically covered in newly formed bone, sometimes exhibiting mild-to-severe grades of infection (osteomyelitis), with low to marked frequencies of draining sinuses and randomly distributed patches of reactive bone. It is possible that the infection was caused by open wounds secondary to the initial trauma. When reactive bone occurred, it projected inferiorly along the margins of the spine, covering it with a candlewax-like bony formation. Furthermore, fracture of the spinous process sometimes corresponded to the formation of calluses, usually projecting from one or both of its lateral sides. The callus originated from the fracture line, the focal point of stress on the bone surface. Occasionally, enthesophytes were also observed near fracture lines, representing a secondary reaction to the healing process. In some instances, vertebrae at the end of the tail can also show pathological deformations, but these differ from those reported in the proximo-middle caudal vertebrae and comprise hypertrophied neural spines and lack evidence of fractures. These might indicate the

Figure 2. FEA results on the modeled vertebral series

Forces are applied to the set of vertebrae and the tendons (A–D), and the same analyses were run for the vertebral model without tendons (E and F). The angle of the loading force is shown by the red arrow, whereas the applied forces in the model are represented by the three small red triangles: 0° (vertical load; A and E), 30° (B and F), 60° (C and G), and 90° (horizontal load; D and H). The small green triangles indicate the location of the *a priori* restrains, mimicking the effect of the anterior and posterior caudal vertebrae along the tail, and the caudofemoralis muscle. For further details check supplemental information and the extensive data video.

body's efforts to support the injured local musculature by expanding the attachment surface of tendons and muscles on sections of injured bone. This pathological deformation occurred in the area distal to the complex spinal tendon lattice, indicating that these structures helped to bear pressure and limit mechanical strain on the spines. In our survey (see Table S1), we showed that this pathological pattern is present in different hadrosaurid taxa, living in different ecological regions and spanning from the Campanian to the Maastrichtian. Hence, this recurrent pattern suggests a shared cause, presumably linked to the ecology of the species, most likely a so-far untested behavior, and common among hadrosaurids. As such, different ecological scenarios can explain the pathological pattern of broken caudal neural spines.

Hypothetical scenarios to explain the pathological pattern

Hypothesis 1: Predation

In general, predation attempts have a higher failure than success rate, leaving the prey to survive, uninjured. For example, the successful rate of killing prey in modern predators is reported to not be above 25% in raptorial birds, and usually less than 50% in predatory mammals.[12] Post-traumatic lesions from failed predation can be recognized by bite marks on the bones. However, the nature of bite marks in the fossil record is ambiguous, because they usually show clear and smooth margins,[13] suggesting the predator fed on a carcass given the absence of evidence of active healing. Peri- and postmortem bite-marks are very common in hadrosaurid bones,[14–16] although they seem to be focused on limb elements.[16] Surveys of bite-mark patterns indicate that carcasses were usually dismembered.[16] As such, the expected low level of successful predation, combined with the high rate of prey survival, is a feasible candidate to explain the high frequency of pathologies on the hadrosaurid caudal neural spines.

However, failed predation attempts might result in a plethora of different body modifications, such as truncation of the tail,[17] healing/healed bite-marks,[18] or the occurrence of embedded teeth in bone.[19] Truncations are so far reported only in two saurischian taxa, cf. *Massospondylus* sp.[20] and *Majungasaurus*,[17] characterized by fusion of distal elements, extensive reactive bone growth, and absence of more distal elements. On the other hand, healing processes usually obliterate any clear predatory indications, such as bite or claw marks,[19] resulting in an external appearance resembling trauma of different etiologies. Carpenter[10] described DMNH 1,493, a near-complete skeleton of *Edmontosaurus annectens* from the Hell Creek Formation of Montana. The tail of the specimen, specifically between caudals 13–17, shows a pathological deformation of the tip of the spines, with an "oblique, saddle-shaped groove that shows exostotic regrowth of bone at its terminus."[10] The anterior and posterior spines show lateral traumas, resulting in an arc-like pattern of damage. Carpenter[10] hypothesized a failed predation because of the restriction of the injury to five vertebrae, the overall morphology of the truncated neural spines, the presence of a pit interpreted as a tooth puncture, and a mangled section in the injured spines that resembled the shape of a theropod mouth. The pathological pattern is similar to those reported in this research, although limited to a much narrower portion of the tail. The focused nature of the injury is the most reliable indicator for a predatory attempt, as the sigmoid neural spines might have different etiologies, and the pit could be a draining sinus due to osteomyelitis.

Another specimen shows a clearer failed predation scenario. DePalma et al.[19] report two middle caudals belonging to a hadrosaurid with an embedded tooth from South Dakota (USA). A tooth of a large theropod (most likely *Tyrannosaurus rex*) perforates the ventrolateral side, between the two vertebral centra, inducing severe infective bone proliferation. The orientation of the puncture suggests the theropod attacked from the rear, biting on the lateral side of the tail and apparently not from above, since the neural spines show no deformation. Adult hadrosaurids were about 2.9 m tall at the hip,[10] and only a few predators could attack the dorsal region of the tail of a running hadrosaurid (i.e., *Tyrannosaurus, Gorgosaurus,* and *Albertosaurus*), whereas smaller predators could aim for the legs. A non-fatal vertical bite, as in the one hypothesized for DMNH 1,493, would have resulted in a single pathological "location." Smaller animals, such as the dromaeosaurids, could have used their claws for puncturing the flesh of the prey,[10,21] or to capture them by climbing and holding onto them.[22,23] These actions, however, are again more likely to have resulted in smaller focused areas of pathology, probably located on the legs and sides of the prey. Bites from large theropods would have covered no more than five caudal vertebrae in an adult hadrosaurid (Figures 4A and 4B), a narrower range than reported in this analysis (Figure 1), resulting in a particular pattern of pathological changes as seen in other hadrosaurid specimens, such as *Edmontosaurus* DMNS 1,493 (FB, pers. obs.) and *Brachylophosaurus* JRF.102 (DF and EFF, pers. obs.). Furthermore, no healing tooth marks and/or embedded teeth were recognized in any of the pathological neural spines examined in this study.

In conclusion, these observations suggest that the "predation" hypothesis does not satisfactorily explain the pathological caudal pattern evident in hadrosaurids.

Hypothesis 2: Muscular stress induced by rotational displacement

The position of the pathological spines corresponds to the attachment site for the *Musculus transversospinalis*. This long and thin muscular fascia runs along the entire length of the axial skeleton, lying on the lateral sides of the neural spines. The *m. transversospinalis* is laterally covered by the *m. longissimus*, forming the epaxial musculature of the tail of hadrosaurids.[24] This set of muscles have an important role in the stabilization of the entire vertebral column and lateral contraction of the tail,[25] which is likely more pronounced than dorsal bending. It can be hypothesized that the stress caused by rotational displacement, especially during locomotion, from the action of the *m. caudifemoralis* might explain the pathological pattern affecting the hadrosaurids. However, the presence of a stiff and complex lattice of ossified tendons extending from the dorsosacral region to the middle caudal region provides stability to the tail, thereby preventing dorsoventral movement of the vertebrae and limiting lateral bending stress, especially in the portion of the tail showing the pathological deformation of the tip of the neural spines.

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Unfortunately, gait biomechanics in hadrosaurids is poorly understood, and there is insufficient data to demonstrate that the reported pathological patterns derive from locomotion-related muscular stress. However, the recurrent location of the trauma in addition to the absence of such injuries in other non-hadrosaurid hadrosauroids with a similar body plan (see later) casts doubt on this scenario.

Hypothesis 3: Herding and trampling

Tanke and Rothschild[9] interpreted the high frequencies of trauma in the centra of caudal vertebrae as a result of herding behavior in which individuals trampled over the tails of their peers.[9] This scenario is suggested based on the appearance (horizontal to oblique fracture) and location (endplate of the centrum) of the lesions in the injured vertebrae. A high concentration of trampling injuries is found in distal vertebrae rather than in proximal and middle caudals, elements that usually do not preserve the thinner and therefore more fragile neural spines. Because of this, the relationship between fractured centra and spine morphology is difficult to report given the usual absence of the latter in isolated material (FB, pers. obs). When the neural spines are preserved along with the vertebral centra in distal vertebrae, in our survey the more distal vertebrae do not show breakage of their spines, in contrast with the established pathological pattern of proximal and anterior middle caudals. Indeed, some of the distal vertebrae display hypertrophy of the distal most tip of the spine, with this hypothesized to be due to the actions of tendons as opposed to direct trauma.

Trampling would occur when the affected animal was resting, with the tail lying on the ground,[9] and the peer stepping on the posterior area of the tail. The hip and proximal regions of the tail can extend up to 1.5 m from the ventral surface of the belly in a resting position, and the likelihood of an individual randomly stepping on the dorsal, sacral or proximal caudal regions of a resting animal is quite low. The odds increase when considering the distal region of the tail, as it is dorsoventrally narrower and more exposed to external injury. However, such an injury could originate from a localized trauma. The foot of a peer could crush no more than three to four sequential vertebrae, and not an extensive, articulated series in a single traumatic event.

Trampling might be considered a possibility to explain the single fractures evident on the articular surfaces of vertebral centra and smaller overgrowths over the neural arch, but this scenario does not satisfactorily explain the pattern of pathological proximo-middle caudal neural spines that involve sequences of 5+ vertebrae.

Hypothesis 4: Intraspecific sparring

Caudal injuries could originate from the swinging of the tail as a defense mechanism against other dinosaurs. However, this scenario cannot adequately account for the high frequencies of the reported lesions. The hadrosaurid tail is extremely wide in cross-section, approximately twice or three times the width of the vertebral centrum, tapering dorsally on the neural spines.[24] The lateral side of the vertebral centra is covered directly by *m. caudifemoralis*, and dorsally the *m. ilioischiocaudalis* covers the basal portion of the neural spines. Persons and Currie[24] propose an enlarged tail musculature, with substantial hypaxial musculature, but moderately sized epaxial musculature, based on the chevron length and length of the neural spines. The lateral side of the tail is much wider than the apical side and, during a lateral-to-oblique impact, the point of contact on the two tails is located on the hypaxial musculature of the lateral side of the centra, not on the spine.[24] Therefore, a swinging action might explain the presence of injuries at the base of a neural spine, but it is unlikely that a lateral impact could have localized trauma to the extreme distal area along a sequence of more than five neural spines. This pattern of injuries would have required an elongated, strong, and dorsally oriented impact that hadrosaurid tails were not morphologically capable of performing.[24] The same use of the tail during hypothetical intraspecific fighting also fails to explain the pathological pattern because the point of contact between two hadrosaurid tails would be located on the hypaxial musculature—therefore on the lateral side of the vertebral centrum and again not on the neural spine.

Hypothesis 5: Atypical behaviors

Another alternative explanation for the pathological deformations can be related to other physical competitions, such as social mounting between males, but this behavior is very rare in nature.[26] Some animals (e.g., elephants) engage in behavior that involves rolling on the back, such as wallowing in mud,[27,28] but there are no reports of injuries caused by this behavior in modern animals. During wallowing, the entire back of the animal rolls, possibly causing stress throughout the axial skeleton. It is possible that hadrosaurids might have fractured their caudal neural spines when wallowing, with them collapsing beneath their own body weight. Considering the comparable height of the neural spines in dorsal, sacral, and proximal caudal vertebrae, however, similar pathological patterns of injuries would be expected in these areas. As such, the much lower occurrence of lesions in those spines enables this hypothesis to be rejected.

Hypothesis 6: Mating

The cloaca is the only opening of the urogenital and digestive systems in certain animals, including archosaurs (birds and crocodiles), and in dinosaurs it is hypothesized to be positioned caudally to the distal end of the ischium.[29] The pathological neural spines are localized to the proximo-middle caudals, particularly in the area above the supposed location of the cloacal opening, and typically affected more than five consecutive neural spines, sometimes discontinuously (Figure 1). The high frequency of trauma in the proximo-middle caudal neural spines, seemingly induced by vertical loading, can be related to the force caused by a mounting male pressing on the caudal dorsal midline of the female tail, inadvertently causing injury and thereby leaving pathological markers that potentially signify fossilized female dinosaurs.

The instinct for mating surges when individuals reach sexual maturity, and the vast majority of vertebral specimens (99.5%; 548/551) described here belonged to sexually mature adults, based on the state of fusion of the neurocentral suture. In fact, in this survey, only three pathological elements are recognized as possible juveniles (MOR 355 7-14-2, TMP 1980.016.0448, and TMP 1986.077.0031; based on unfused ventral surfaces of the pedicles of the neural arch) despite many hundreds of juvenile specimens being checked for pathologies. Juvenile hadrosaurid bones are much more common in the fossil record than those of adults (possibly because of the typically higher mortality rate observed in herd herbivores and because of the

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r-type reproductive strategies of hadrosaurids—characterized by abundant juveniles with high growth rates).[30,31] Thus, these limited cases of pathological juvenile neural spines are anomalous when compared to the abundance of caudal lesions in adults. Although hadrosaurids are hypothesized to reach sexual maturity at 2–3 years (at ~50% adult body size),[32,33] the relative absence of injured neural spines in juveniles (except for the aforementioned three elements), perhaps not yet sexually mature, is another line of evidence supporting the mating hypothesis. The rare fractures in these three juveniles might represent non-mature females that were subject to aggression from males of the same species, during the reproductive season, caused by a possible marked size difference, or perhaps were injuries caused by chance events, such as an impact from an external object or a fall. The disparity in size between sexually mature young females and older males is very pronounced,[33] making it likely that the young were injured during mating. In the case of *Edmontosaurus*, an early sexually mature female of about 3 years old is estimated to be around 2 tons, while late adult individuals can weigh more than 7 tons.[33] This imposed great pressure on the proximodorsal region of the tail, likely causing fractures.

Another line of evidence is suggested in the tail of *Edmontosaurus* sp. AMNH FARB 5,886, in which two vertebrae show spherical overgrowths on the distal ends of the neural spines (Figures S3A–S3F). Although the nature of these anomalies is yet to be determined, it has been suggested that they are fossilized benign tumors, and possibly button or osteoid osteoma.[34,35] Many cancers develop in response to chronic tissue injury and inflammation, in which the resulting cell death increases the tumorigenic potential of the neighboring cells.[36] Repetitive stress provoked by periodic activities—such as mating—results in continuous tissue damage and inflammation connected to the repair mechanism and visible in some tails where more than two traumatic events can be recognized based on the presence of injuries in different states of healing (e.g., MOR 3003), thereby potentially increasing the risk of development of neoplasia.

After considering these other scenarios, we argue that mating is the most likely scenario to have caused the recurrent pattern of injuries. However, this hypothesis has some issues that need to be thoroughly addressed.

The problems with statistical assumptions and mating-related biases

Number of individuals

The difficulty in testing a certain behavior from a paleopathological pattern is the reliance on the assumption that the surveyed elements represent a single population. Unfortunately, most of the time this is not possible, because fossils can be re-arranged by taphonomy, overlapping with other remains from different localities and times, and/or represent only a fraction of a population. Bonebeds, like the hadrosaurid localities in Canada or the USA, and mass-death deposits as in Bernissart (Belgium), can provide more reliable information about the presence of a certain condition in a dinosaur population. However, the archived specimens in a museum collection might not represent the entirety of a bonebed due to sampling biases. Siviero et al.[5] proposed a statistical approach to describe paleopathologies in an *Edmontosaurus* population from a bonebed dug in the Lance Formation of Wyoming (USA). The authors surveyed all the specimens recovered from the locality, diagnosing conditions and distributions across individuals. While it is easier to determine the number of individuals by matching appendicular elements, it is more difficult to discern one individual from another solely from the vertebrae. Therefore, under these premises, we propose that in the absence of articulated series, each vertebra represents a different individual. This assumption poses a strong bias in the prevalence of pathologies in our survey, but Siviero et al.[5] demonstrated that this approach can help in further understanding of the general health of a fossilized population. This assumption must be considered carefully, however, because collections can be composed of different populations in time. A museum collection considered for a general pathological overview of a large clade (e.g., Hadrosauridae) must present specimens of coeval species living in close proximity to each other (e.g., Blagovenschensk and Kundur localities).

Juvenile individuals

The pathological specimens here reported belonged to mature and adult individuals. Generally, adult hadrosaurids present an obliteration of the neurocentral suture (the contact surface between the vertebral centrum and the neural arch), indicative for somatic adulthood.[37] Furthermore, adult hadrosaurids show stouter and heavier caudal elements compared with those of juveniles (FB, pers. obs.), especially thicker neural spines in the proximo-middle transition. In the database, only a few elements are recognized as juveniles, perhaps subadults (MOR 355 7-14-2, TMP 1980.016.0448, and TMP 1986.077.0031), since the ventral surface of the pedicles of the neural arch show the typical articular pattern of unfused elements. As discussed earlier, juvenile hadrosaurid bones are much commoner in the fossil record that those of adults because of their higher mortality rate as herd herbivores,[30] and because of their r-type reproductive strategies.[31,38] We observed other articulated vertebral series from juvenile hadrosaurids (CMN 8784, RAM 14000, and LACM 23504), but none show the reported pathological conditions. Thus, these rare cases of traumatic juvenile neural spines are anomalous when compared to the main pattern of caudal pathologies in adults. As such, they can likely be ascribed to the other scenarios considered.

Distal vertebrae

The lesions in the caudal neural spines in hadrosaurids are found in the proximo-middle transition, but unusually-shaped, swollen, and jagged neural spines can also be found in some distal caudals. However, these deformations do not show the typical bending deformities evident in the more proximal vertebrae. Rather, they suggest an over-ossification of the bone surface caused by stress distribution from the ossified tendons. In fact, ossified tendons could redistribute internal forces across the elements of the tail, thereby acting in a similar way to the ropes of a cantilever bridge.[11] In a caudal series with elongated neural spines, as in hadrosaurids, a great development of the spines leads to the transmission of greater compressive forces by the tendons, reducing bending moments within the neural arch. The lattice also greatly reduces bending and stress on the axial skeleton that could cause major structural failures in the scenarios described earlier. Ossified tendons store elastic energy, reduce tensile stress on the vertebral column more than bending stress, and have higher ultimate tensile strength than cartilage tendon or bone. Thus, ossified tendons can withstand larger tensile stress.[11] During the traumatic event, the ruptured balance of the spines and the related tendons that connected them in a continuous "beam" could have had a "domino" effect as in a cantilever bridge (DF, pers. obs.), passing the tensile force from tendon to tendon to pull and withstand the force of impaction. The spines located far from the origin site of the injury (as in the distal and extreme distals) could have dissipated this prolonged tensile force by increasing the attachment surface for the non-ossified tendons of *m. longissimus* and *m. transversospinalis* and reinforced the *ligamentum apicum dorsalis* (a small ligament connecting the apical regions of two consecutive neural spines), thereby resulting in a deformed neural spine. As such, it is possible that the pathological distal neural spines represent a severe secondary ossification from the distribution of the impact stress on the proximal region of the tail, distributed through the tendon lattice.

Sexual distribution of injuries

If the paleopathological pattern of traumatic caudal neural spines is linked to mating, hence the suggestion that female hadrosaurids can be recognized by such, it can be hypothesized that the distribution between pathological and non-pathological caudal neural spines should be bimodal in the fossil record. However, when considering a fossilized population (either a bonebed or a museum collection from a single locality), this 50-50 distribution is not detected, a result that might challenge the mating scenario.

In modern animal taxa, the ratio of adult males to females in a social group or population (ASR, adult sex ratio) varies significantly among species. In many birds, for example, males are more numerous than females,[39] but this is not always the case.[40] In some mammal species (e.g., elephants, sperm whales, and bats), individual group sex ratios do not reflect that of the overall population, because societies are matrilineal, and males are either solitary or they form all-male groups.[41] ASR are still the subject of many studies and analyses of modern taxa, and it comes as no surprise that defining ASR for fossil species is almost impossible, given the nature of the fossil record itself. Finding a 50-50 distribution of pathological proximo-middle caudal spines in a given bonebed or museum collection of hadrosaurids is extremely unlikely, considering not only the unknown social structure of these species, but also the numerous biases: physiological (trauma can have different timing in healing between individuals), preservation (not all individuals of a populations fossilize), taphonomy (not all fossilized individuals are preserved during the geological ages), and collection biases (not all fossilized individuals are preserved and found). In conclusion, the undetected 50-50 ASR in our survey of pathological and non-pathological caudal vertebrae does not disprove the mating scenario.

Sexual dimorphisms in the dinosaurian fossil record

Sexual dimorphism is problematic to identify in extinct taxa, especially for those animals that do not have a direct living relative today, such as the non-avian dinosaurs. The different sexes mostly show sexual variation of different degrees,[42] for example in body size and mass. The evolution of ostentatious structures for mate attraction or intrasexual competition is led mainly by sexual selection, as a variant of natural selection.[43] These novel features—anatomical, physiological, or behavioral—would increase the reproductive possibility of a species at the expense of the survival of the individual, female or male.[44] Because of the intrinsic nature of the fossil record, it is nearly impossible to determine if a specific dinosaur individual was male or female or, more generally, to assess features of sexual dimorphism.[45] In the past, researchers suggested that the different patterns, forms, and sizes of dinosaurian head structures could imply sex-based differences, such as the elongated tubular crest of *Parasaurolophus walkeri*, compared with the shorter and curved one of *P. cyrtocristatus*,[46] the ceratopsian configuration of horns and frills, or the head crests of some theropods.[47] Although the assumption that exaggerated features might represent sexual dimorphism may be correct in some cases, it is unlikely for others.[47] Verdú et al.[48] described the intraspecific bone variations in the Bernissart *Iguanodon* at the Royal Belgian Institute of Natural Sciences, looking for possible sexual dimorphism within the large quantity of complete skeletons, corresponding to at least two or three different groups of individuals. The authors detected a bimodal distribution limited to the pollex, with "large" versus "short" morphologies, suggesting that evolution of this structure could have been led by both natural selection (as a weapon against predators) and sexual selection (for intraspecific combat between males). However, a defined sexual identification of individuals is impossible from simple, morphological traits. The best scenario for recognition of a specific sex, namely female, is the recovery of a complete skeleton with preserved eggs (or the embryo in the case of oviparous species) within the oviduct. Given the paucity of such discoveries, however, the recognition of medullary bone (MB) in dinosaurian long bones can be indicative of female individuals.

Medullary bone

MB is a histological feature that can indicate the sex in a fossilized species. In non-avian dinosaurs, it has been found in long bones of *Tyrannosaurus rex*,[49,50] *Allosaurus fragilis*,[51] *Tenontosaurus tilletti*,[51] *Dysalotosaurus lettowvorbecki*,[52] *Confuciusornis sanctus*,[53] *Pinguinus*,[54] and *Mirusavis parvus*.[55] During the pre-ovulation stage of the egg-laying cycle of female birds, MB is deposited within the medullary cavity of long bones (e.g., humerus, radius-ulna, and tibiotarsus-fibula) in wood thrush[56] to act as a calcium deposit, and it develops a short time before the first egg is laid. In chickens (*Gallus gallus*), it is formed around one-two weeks before the first egg is laid, and it is resorbed approximately three weeks after the last egg is laid.[57] Timing of formation and subsequent resorption of MB differs between species,[57] as well as the incubation period of their eggs. In chickens, the formation of the egg inside the shell gland takes around 20 h, and the spermatozoa inseminated into the infundibulum following oviposition can fertilize an ovulated egg within around 15 min.[58] The average number of days for avian incubation is 44.4, while a duration of 107.3 days is required for reptiles.[59] A period of 74 days of incubation was suggested for the theropod *Troodon*,[59] while 83.16 days for *Protoceratops andrewsi*, and 171.47 days for *Hypacrosaurus stebingeri* have

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also been advanced.[60] If the fertilization and timing of formation/resorption of the MB in non-avian dinosaurs followed a similar timing to birds, then an individual with evidence of MB likely died in a time range of about five weeks (two weeks before first egg laid to three weeks after the last one) during the reproduction period. The extensive remodeling due to callus formation or infection in the hadrosaurid injured neural spines suggests the putative females were mounted several months before, and that the ovulatory time was already over at the time of death. One can assume that an individual showing this specific pattern of pathologies would not present MB within long bones, since it had already been reabsorbed after the ovulation/incubation period. Medullary-like endosteal tissues might still be discovered in these specimens, but caution should be considered when claiming that such tissue is the pre-ovulatory MB since the former has been observed in specimens suffering from osteopetrosis[57,61,62] and traumatic lesions.[63] It was not possible to test the co-presence of (1) MB in long bones, (2) pathological proximo-middle neural spines, and (3) possible presence of MB-like tissue in a single individual, therefore we urge future histological analysis when long bones are found associated with a pathological tail.

Cranial ornamentation

Hadrosaurids generally have a conservative post-cranial skeleton, especially for the axis, with phylogenetic signals located mainly in the pelvic and shoulder elements.[64] Instead, they were extremely specialized in the head. In the recent hadrosaurid phylogeny by Prieto-Márquez and Wagner,[65] hadrosaurid skull characters account for 68.7% of the total (233 characters out of 339), and such differentiation is evident in the wide range of different crests that adorned the heads of these animals. These comprised hollow, tubular, or helmet structures (*Parasaurolophus, Lambeosaurus, Corythosaurus*, and *Tsintaosaurus*); short and bony rods (*Saurolophus*); enlarged nasal axe-like crests (*Gryposaurus, Kritosaurus*, and *Rhinorex*); flat and spatula-like plates (*Brachylophosaurus* and *Probrachylophosaurus*); fleshy comb-like structures (*E. regalis*); or no crest at all (*E. annectens* and *Kundurosaurus*). In the past, the idea that different crest morphologies represented different sexes (e.g., *P. walkeri* and *P. cyrtocristatus*)[66] or different species (*L. lambei* and "*Procheneosaurus*"/*Tetragonosaurus*[67]) was generally accepted, but studies have since proven that the different morphotypes were indeed separate species.[46,68] The cranial variations within Hadrosauridae might have had multiple functions that encompassed both sexual and natural selections, as in the case of modern deer antlers. A fragile equilibrium may have existed between the development of a novel structure that was attractive to potential mates but could also aid in intraspecific competition against a possible risk for the individual's survival in an ecological context.[69] The evidence of injured neural spines in the proximo-mid caudal region, associated with a complete post-cranial skeleton and a skull, could serve as a "Rosetta Stone" for the interpretation of sexual dimorphism in dinosaurs. A preserved skull with a broken tail could potentially reveal a series of osteological features and measurements attributed to the female sex within a species or a population that could then be compared with isolated or disarticulated material from the same fossil deposit, layer, or formation.

Sexual organs and hypothetical mating position

Unfortunately, no reproductive organs have been found in the non-avian dinosaur fossil record to date. Ovarian follicles have been reported in the basal bird *Jeholornis* and two enantiornithines,[70] and an impression of a cloaca was identified in *Psittacosaurus*.[29] The *Psittacosaurus* specimen indicates that the cloaca is located just caudal to the distal end of the ischium, a position likely also shared by other ornithischians such as the hadrosaurids. To hypothesize the shape and mechanism of the copulatory male organ, one can look at modern archosaurs. Crocodiles possess an intromittent phallus that everts without changing size.[71] In the American alligator (*Alligator mississippiensis*), "the phallus is a curved, rigid, collagenous shaft anchored on the ventral wall of the cloacal protodeum by paired crurae."[72] Some species of paleognathans, such as ostriches and emus, also show an intromittent phallus in the form of short and wide club-like organs.[73,74] During bird evolution, the intromittent phallus was reduced or lost in multiple lineages, as in Galliformes (with the exception of cracids) and in the common ancestor of Neoaves.[75] These birds reproduce via the "cloacal kiss," transferring sperm by pressing the cloaca against that of the female. The only clade of neognathan birds with a proper extending phallus is Anseriformes, which possess specific and unique long, twisted, and convoluted organs that co-evolved with the intricate internal vaginal duct of the females.[76] Based on phylogenetical bracketing,[77] it seems reasonable to assume that hadrosaurids had an intromittent phallus similar to that of crocodiles or palaeognathans. Combining our observations and analyses, we evaluated previously portrayed mating postures (Figures 3A–3D). However, considering how mating positions are still too speculative (varying based on mass, limb biomechanics, and morphology of sexual organs), we decided to reconstruct the two *Olorotitan* (Figure 3E) in the moment after the copula, with the injuries already present in the female's tail (Figure 3F).

The absence of pathological caudal spines in non-hadrosaurid ornithopods

In our survey, it was noted that the reported pattern of injury is not present in non-hadrosaurid ornithopods. In the numerous skeletons of *Iguanodon bernissartensis* from Bernissart (Belgium) and from the British iguanodontian material at NHMUK, no pathological caudal spines have been recognized (Figure 4C). In particular, the "Bernissart Sinkhole" is helpful for comparing the pathological caudal pattern of hadrosaurids, given the presence of about 25 complete specimens and a large quantity of disarticulated and isolated material, from at least three to four groups of individuals.[78] The material belongs mainly to *I. bernissartensis,* and a complete skeleton with few other specimens of "*Mantellisaurus*" *atherfieldensis*.[79,80] Verdú et al.[48] recognized two morphotypes within the population of *I. bernissartensis*, based on the shape and size of the spike-like pollex, suggesting it may be a secondary sexual characteristic. While the articulated skeletons preserve most of the tails, in our survey we observed the complete absence of pathological neural spines in these tails. The presence of two morphotypes within the populations contradicts the idea that the *Iguanodon* groups were formed by a single sex (although further body-mass-related analyses are required to confirm the occurrence

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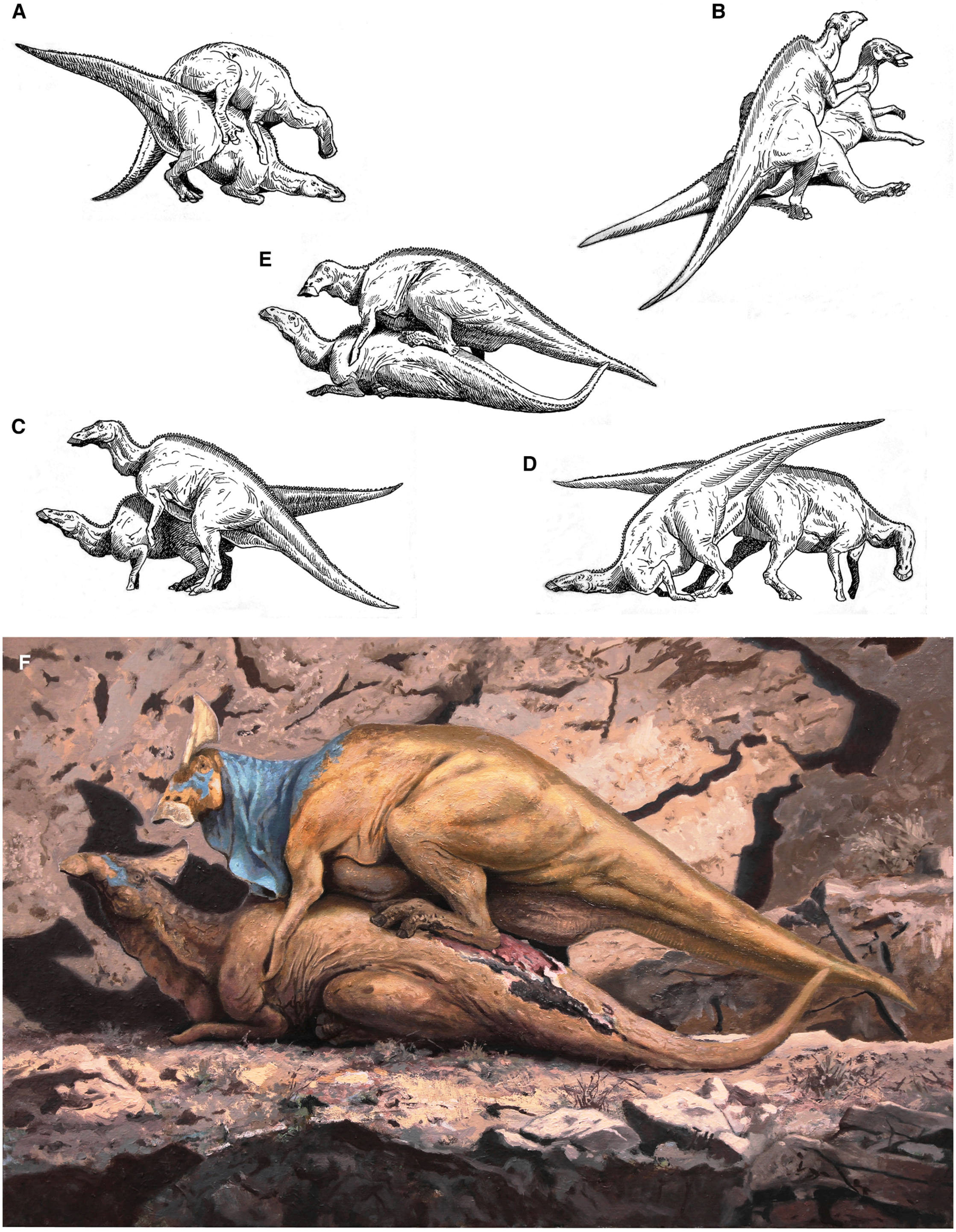

Figure 3. Paleoartistic restoration of hadrosaurid mating postures

The different diagrams show the mating postures of two generic hadrosaurids that have been hypothesized in recent years in academia and in the media (A–E). Using Figure 1 as a reference, we portrayed the posture we hypothesized in this research, showing the injured zone in the proximal and anterior middle section of the female tail (F). The female shows fresh and older traumas, as suggested by MOR 3003. Because we do not have any fossilized reproductive organs, we cannot define a specific mating position; hence, the illustration shows the moment directly after the copulation. Artworks by the paleoartist Troco.

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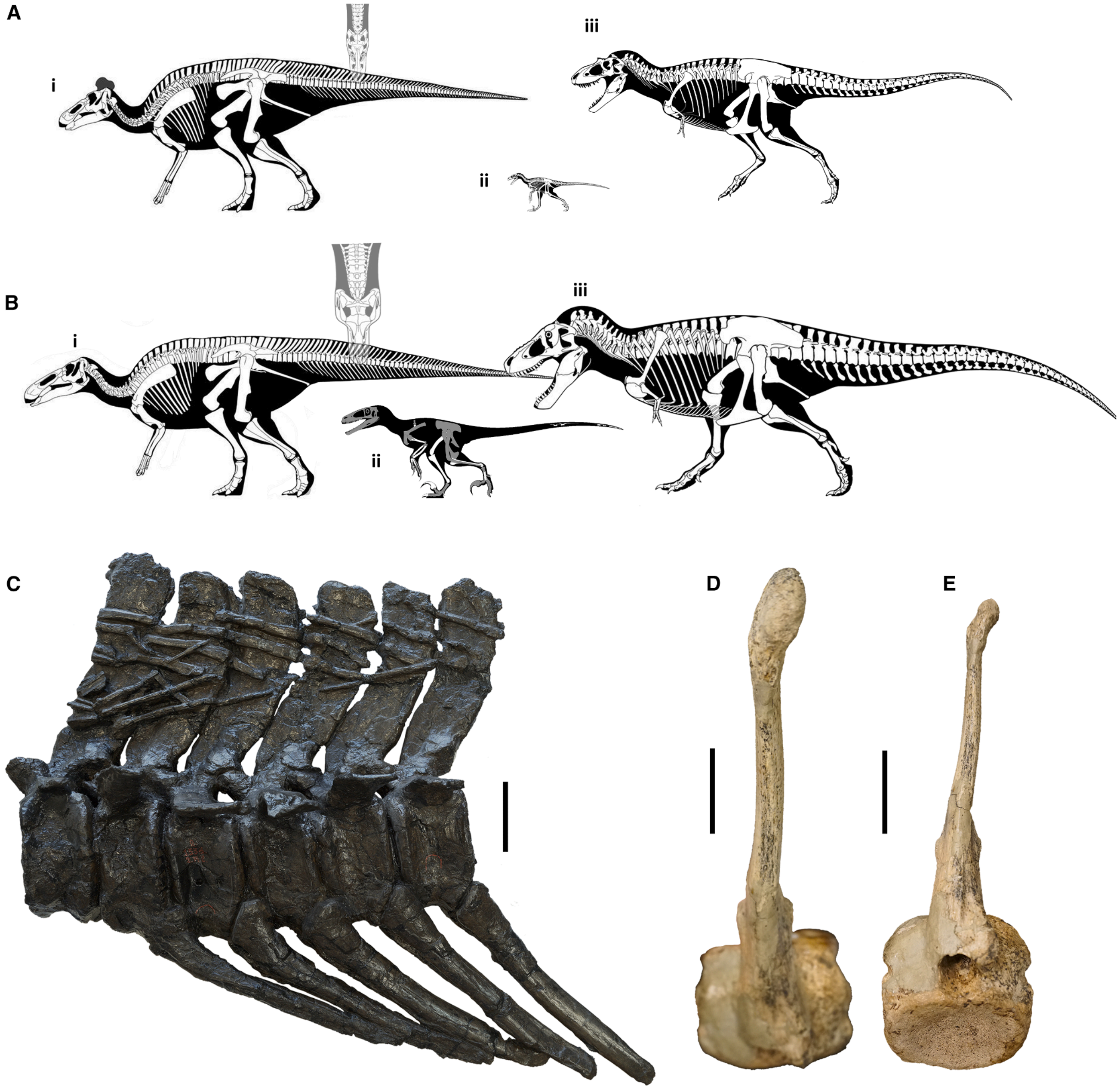

Figure 4. Predation hypothesis and cases in non-hadrosaurid ornithopods

Faunistical relationships between hadrosaurids and their predators.

(A) Horseshoe Canyon Formation: *Edmontosaurus regalis* (i), *Atrociraptor mashalli* (ii), and *Albertosaurus sarcophagus* (iii); (B) Hell Creek Formation: *Edmontosaurus annectens* (i), *Dakotaraptor steini* (ii), and *Tyrannosaurus rex* (iii). Pictures by Scott Hartman (Aii, Biii), PaleoNeolitic from Wikipedia (Bii), and Genya Masukawa (Ai, Aiii, Bi). The shaded tyrannosaurid head profiles highlight the biting area on the hadrosaur tails, showing that it would have affected only a short portion of the neural spines.

(C) The anteriormost section of the tail of the holotype RBINS R51 of *Iguanodon bernissartensis*, showing no pathological deformation. AMNH FARB 30696, a proximal caudal vertebra of *Gilmoreosaurus mongoliensis* in dorsal view (D) and cranial view (E). Scale bars, 10 cm.

of possible sexual dimorphism). *Iguanodon* has a similar size to hadrosaurids, but they bear important anatomical differences in the shape of the head, limb proportion, morphology of the pelvic girdle, and especially the configuration of the tail. The proximal neural spines are generally shorter than those of hadrosaurids, but the ossified tendons derived from *m. transversospinalis* are thicker and longer than in hadrosaurids. The frequency of injured neural spines in hadrosaurids is high, and it does not seem to correlate with taphonomical or preservation bias. In the *Iguanodon* groups from Bernissart, the presence

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of a large population prevents any biological biases. Furthermore, the *Iguanodon* individuals are adults and fully mature, both sexually and osteologically (Stein, pers. obs. to FB). Hence, the question about the absence of any caudal injuries in these *Iguanodon* groups remains open, suggesting that a further biomechanical examination of the Bernissart herds is necessary.

Another non-hadrosaurid exception is observed in a proximal caudal vertebra of the Mongolian hadrosauroid *Gilmoreosaurus mongoliensis* AMNH FARB 30696 (Figures 4D and 4E). Unfortunately, the other neural spines associated with the specimen do not show pathological features, either in the centrum or neural arches. As such, this single isolated case cannot at present be used to assume similar mating behavior in non-hadrosaurid ornithopods.

Caudal pathologies in other non-ornithopod dinosaurs

It does need to be appreciated that other dinosaurs also exhibit tail pathologies. In particular, Cruzado-Caballero et al.[81] suggest that titanosaurs are the sauropods with the highest percentage of diagnosed pathologies. Other examples are found in ceratopsians[82] and theropods.[83] A total of 26 caudal pathologies has been found in sauropod dinosaurs, identified as a fracture, a less defined traumatic condition, four infections, two tumors, eight cases of diffuse idiopathic skeletal hyperostosis (DISH), four spondyloarthropathies, a congenital malformation, and two cystic lesions.[81] In theropods, 40 caudal pathologies have been reported in the literature, comprising two fractures, six cases of osteomyelitis, an amputation, three congenital malformations, eight spondyloarthropathies, two examples of osteoarthritis, a case of DISH in addition to several lesions of uncertain etiology. The total quantity represents 11.8% of the total pathologies surveyed in theropods, but this result is conditioned by a certain degree of collection bias, typical of museum collections.[82] Other limited pathologies are found in ankylosaurids[84] and stegosaurids.[85] Three fractured and healed caudal neural spines have been described in *Pachyrhinosaurus*, along with fusion of middle and distal caudals, endplate perforation and fractures, and fusion between vertebrae and chevrons (spondyloarthropathy) in other ceratopsians.[82,86]

Hadrosaurids show a clear pathological pattern of fractured proximal and anterior middle caudal neural spines, supported by an extensive database. The reported fractured proximal spines in *Pachyrhinosaurus*[82] might suggest a similar etiology (i.e., mating), but more paleoepidemiological analyses of large collections and populations are needed. The wide pelvic girdle and short, curved tail in the horned dinosaurs, however, suggests that dorsolateral pressure caused by a mating partner may have had a different distribution of forces compared to hadrosaurids, hence likely inducing different aspect and ratio of tail pathologies in the horned dinosaurs. The cases of DISH reported in *Diplodocus, Apatosaurus*, and *Camarasaurus* was initially suggested to be a consequence of mating.[87] However, these conditions are found in the middle caudal region (ranging from 18 to 23), and sauropod tails are not as stiffed as that of hadrosaurids, given the lack of the lattice of ossified tendons. Based on these observations, it is unlikely that the reported sauropod tail pathologies can have the similar etiology from mating trauma. However, this does not rule the mating scenario entirely. Indeed, sauropods represent the most likely clade of dinosaurs to attain mating injuries due to their colossal size which might be expected to put notable pressure on the female body.

Our assertion that hadrosaurids are the dinosaurs with the highest prevalence of caudal pathologies is based on the fact that the published surveys in non-ornithopod dinosaurs are based on surveys of literature. As such, they represent neither the pathological ratio of a collection nor a population. We strongly recommend that future researchers undertake detailed pathological studies of museum collections for other dinosaur clades to either confirm or refute our findings, thereby augmenting our ability to link pathological patterns to different behaviors.

Analogs: Aggressive mating behaviors in modern animals

Injuries to females during reproduction are not uncommon in nature today. Competition between males to access a mating partner often results in violent contests,[88] that can carry over to aggression that poses a threat to the female.[89] Examples of aggressive mating behaviors that result in injury or even the death of the female can be found in extant animals, including turtles,[90,91] primates, artiodactyls, felids,[92] and seals.[92,93] Although this violence is maladaptive for the female, such conflict between sexes can evolve due to the benefits gained by males, who behave in ways consistent with maximizing their own inclusive fitness.[94] From the female perspective, sexually aggressive tactics increase the cost of mating by decreasing the probability of survival and reproduction.[92] In other words, severe mounting injuries increase female mortality and thus impede potential population growth.[93] Therefore, sexual selection causes a tradeoff among partners between aggression and survival. If aggressive courtship leads to fertilization and is not too costly in terms of the survival of the individual, such behavior can endure,[92] as we hypothesize here for hadrosaurids. At the time of death, the fractures in the studied vertebrae displayed differing stages of healing suggesting that the purported female hadrosaurids survived for a period of time after the initial injury. However, we cannot currently ascertain that the proposed mating injuries were the main cause of death of these animals. Perhaps, the trauma could have resulted in the animal being more vulnerable to death by predation or ill health secondary to the mating injuries.

In conclusion, this analysis of hadrosaurid paleopathology reveals that most of the pathological bones are concentrated in the proximo-middle caudal region of the tail. This location is approximately dorsal to the putative location of the cloacal opening, thereby suggesting a likely connection to mating activities. FEA demonstrated that a straight and vertical load would result in a posterior shift of the neural spine, while a load directed laterally would cause lateral bending of the neural spine, with the location of the critical limit positioned proximally on the neural spine, conformations not detected in the samples observed. Instead, the pathological deformation of the fossilized neural spines best matches the virtual model when the same force is applied following a more oblique direction, with the strongest correlation obtained with loads oriented at 30°–60°. The final FEA results suggest that the male mounted the female from the side, the latter probably lying on the side, with the male pressing on the apical portion of the proximal and middle caudal neural spines causing the female to sustain a series of accidental fractures. Other scenarios—failed predation, locomotion stress, and herding behaviors—are considered less likely to explain the results obtained in our survey and analyses, but they cannot be ruled out completely. As of now, it is impossible to clearly identify the exact reason for the reported pathological pattern. However, the presence of these injured tails in adult hadrosaurids, throughout their geographic and stratigraphic ranges (from the Campanian to the Maastrichtian), with similar pathological lesions in the same anatomical position plausibly may have been linked to copulation, with the injured individuals likely to be female. Different species may have engaged in different behaviors, but all needed to eat, drink, move, avoid predators and reproduce. Based on the current state of knowledge, the only one of these activities that could feasibly result in potentially recurrent and survivable injuries is mating. As such, the identification of these injuries provides an important potential new way of inferring sex in dinosaurs, while also furthering our understanding of the dinosaur mating process.

Limitations of the study

The limitations of the study are mainly 2-fold, related to the number of individuals considered in the analysis and the computational skills for FEA. The first one is explained under the section number of individuals, and it involves the uncertainty of associating one or more disarticulated and/or disassociated materials to one or more individuals, especially in a bonebed. In that paragraph, we provided an approach to reduce the impact of uncertainty on our study.

In the FEA, we analyzed the stress of the applied forces in a vertebral series formed by five vertebrae with a tendon lattice. However, to obtain a more reliable and realistic result, it would have been necessary to add more vertebral elements and differed the orientation of the tendon and the musculature of the proximal region of the tail (comprising the *m. caudofemoralis*, the *m. ilioischiocaudalis*, the *m. transversospinalis*, and the *m. longissimus*).[24] However, the application of all these anatomical factors exceeded the computational skill of the working station available and, as such, we limited the analyses to the elements reported.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Filippo Bertozzo (filippo.bertozzo@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Original datasets are included in the supplemental information.
- Paleopathological dataset of the Wyoming *Edmontosaurus* is taken from Siviero et al.[5]
- Paleopathological description of hadrosaurid tail injuries is included in Method S1 in the supplemental information.
- This paper does not report original code.

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AUTHOR CONTRIBUTIONS

Conceptualization, F.B., D.H.T., S.C., F.M., G.A., and E.M.; survey and data collection, F.B. and D.H.T.; methodology, F.B., S.C., D.H.T., and E.M.; investigation, F.B., D.H.T., S.C., F.M., G.A., and E.M.; visualization, F.B., S.C., and F.M.; supervision, E.M., P.G., and A.R.; writing – original draft, F.B., S.C., and E.M.; writing – review & editing, all the authors.

DECLARATION OF INTERESTS

Authors declare that they have no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
- METHOD DETAILS
  - ○ Specimens
  - ○ Finite element analysis (FEA)
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
ImageJ	https://imagej.nih.gov/ij/	ImageJ 1.53c
ABAQUS	https://www.technia.com/en/advanced-simulation/software/abaqus/	Abaqus CAE 2022
Pixologic zBrush	https://www.maxon.net/it/zbrush	Pixologic zBrush 2022
3D Studio Max	https://www.autodesk.com/products/3ds-max/overview	3D Studio Max 2021
Adobe Photoshop	https://www.adobe.com/be_en/products/photoshop/	Adobe Photoshop 2025 26.3.0
RStudio	RStudio Team https://www.rstudio.com/	Rstudio 4.4.1
SPSS	https://www.ibm.com/products/spss-statistics	SPSS 2020 27.0

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

The data analyzed in this study were collected both from the literature and firsthand examination of fossils housed in public repositories. The following abbreviations denote museum collections where fossil material in this supplement is accessed.

AEHM - Amur Natural History Museum of the Institute of Geology and Natural Management of Far Eastern Branch of the Russian Academy of Sciences (IGNM FEB RAS), Blagoveschensk, Russia.

AMNH FARB - American Museum of Natural History, Fossil Amphibians, Reptiles, and Birds Collection, New York, USA.

BDM - Badlands Dinosaur Museum, Dickinson, North Dakota, USA.

CMN - Canadian Museum of Nature, Ottawa, Canada.

DMNS - Denver Museum of Nature and Science, Denver, US.

LACM - Los Angeles County Museum, Los Angeles, California, USA.

MOR - Museum of the Rockies, Bozeman, Montana, USA.

NHMUK - Natural History Museum, London, UK.

RBINS - Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

RAM - Raymond Alf Museum of Paleontology, Claremont, California, USA.

ROM - Royal Ontario Museum, Toronto, Ontario, Canada.

TMP - Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

USNM - Smithsonian National Museum of Natural History, Washington DC, USA.

METHOD DETAILS

Specimens

The reported fossilized injuries were recognized, when present, as healing fractures, evidenced by the presence of callus, reactive bone surfaces, draining sinuses, sigmoidal or bent deformities, asymmetries, and pseudoarthroses. The affected bones were measured using a 1mm caliper or a 1m string and photographed with a Sony a5100 camera following standard directions (cranial, caudal, lateral (both sides), dorsal, and ventral). Measurements of angular distortion, callus deformation, or vertical splitting were taken using the free software, ImageJ®.

Articulated/associated tails studied in this work are assigned to *Edmontosaurus* (RAM 7150; AMNH FARB 5245; RTMP 1970.018.0001), *Hypacrosaurus stebingeri* (MOR 549), *Olorotitan arharensis* (AEHM 2/845), *Amurosaurus riabinini* (AEHM 1/304-310), c.f. *Brachylophosaurus* (BDM 003), and an Hadrosauridae indet. (AMNH FARB 5426). Similar pathologies were also recognized in the tails of USNM 2414 *Edmontosaurus annectens* (Carrano, in prep.), and MOR 3003 (“Warwick’s Duck”; Fowler et al., in prep). The tails were photographed, and the images were manually merged in Adobe Photoshop and scaled down with matching dimensions. It was not possible to photograph AMNH FARB 5245 because the specimen could not be removed from its drawer, but it is visible in the mounted cast observable in the Ornithischian Hall of the AMNH.

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Finite element analysis (FEA)

The FEA were performed using the ABAQUS CAE 2022 software (Dassault Systèmes Simulia Comp.). To quantify the load force applied on the female tail, a 3D model of Edmontosaurus proximal and middle caudal vertebrae was sculpted, in Pixologic zBrush 2022 based on a skeletal model of the same taxon. The model was retopologized to reduce polygon density. Finally, it was imported into the software 3D Studio Max to calculate the total surface area and the volume. A total mass of 5.88 tons was estimated for *Edmontosaurus* following Romano et al.,[95] assuming a maximum size for the hadrosaurid. However, during mating, only the posterior area of the male would have pressed on the female body, thus the section comprising the pelvic region and the tail was cropped from the main body volume. The final mass of the adult male individual was estimated to be 2.88 tons, following the procedure presented by Romano and Manucci[96] and Dumont et al.,[97] generating a force of 314 N acting on each of the 30 vertices belonging to the distal portion of the neural spines. The total load of the male individual is hypothesized to be equally distributed among the vertebrae above the cloacal opening where the two bodies enter into contact. The section of the tail of interest was simulated as having a total length of $\sim$0.5 m, thus the model of said section comprises a total of no more than five caudal vertebrae. This amount is based on the minimum contiguous succession of pathological caudals in this survey, and it was imposed by the computational limitation of our working system. Three vertebrae on which the loadings are applied and two additional vertebrae at each extremity to simulate the attachment to the rest of the body. Each group of modeled caudal vertebrae have a mesh composed of 28278 tetrahedra. Each vertebra is connected to the others by intervertebral disks, modeled as cylinders with articular facets matching those of the vertebrae. Each intervertebral disk was modeled to have a mesh of 18056 tetrahedra. In addition to the five tail vertebrae and the four intervertebral disks, models of the ossified tendons are included. The tendons have been organized in two series of fused elements and connected to the lateral faces of the neural spines in two areas per neural spine, as observed in the articulated specimens. The two models of the tendon lattice were mirrored, and each is composed of 63756 tetrahedra. The loadings were tested with a direction of 0°, 30°, 60° and 90° with respect to the dorsoventral axis of the neural spine. The constraints were applied to the articular facets of the vertebrae at the two ends; at the facets of articulation with the chevrons, to simulate the reaction of the ground; and at the extremities of the ossified tendons, to simulate its anchorage with the rest of the structure. The positions of the constraints have been chosen in accordance with the De Saint-Venant principle,[98] to avoid the influence of constraints on the results of the simulation. The simulations were performed with different sets of constraints and directions of the applied loadings. The constraints at the chevron articular facets were applied to simulate the lying of the animal on the ground, while they were switched off to simulate the animal standing. The action of the ossified tendons was tested by adding the tendon lattice to the simulation and evaluating the contribution to the stress distribution. Bones were considered a homogenous material[99] with an elastic modulus of 17 GPa, a Poisson's ratio of 0.3, and a maximum tensile strength of 210 MPa31.[99] These data correspond to the material properties of ostrich limb bones, adopted due to the close phylogenetic relationship between dinosaurs and birds.[99] Ossified tendons were considered to have the same material properties as bones. The intervertebral disks were modeled to have the same material properties as articular cartilage, with an elastic modulus of 25 MPa and a Poisson's ratio of 0.3.[100]

The simulations performed without the constraints at the chevron articular facets showed a great displacement without a significative increment of stress values, proving that the articular disks may have accommodated the stresses allowing the tail to bend and preventing the occurrence of localized stress points. Adding the constraints to the chevron articular facets and without the tendon lattice, the stresses concentrate near the mid portion of the neural spine, with greater intensity as the lateral component of the loading increases. The presence of the ossified tendon lattice greatly increases the stiffness of the system. The tendons do not prevent the rupture of the neural spines but redistribute the stresses from a position near the middle region of the neural spine towards its distal portion, coincident with the fusion between the tendon lattice and the vertebrae. The forces acting on the distal extremities of the neural spines and the counter-reaction of the vertebral body opposing them create a flexural moment that generate stresses concentrated on the lateral surfaces of the neural spines. The concentration of forces in small areas can generate cracks that may lead to fracture lines and later to the breaking of the bone, as observed in the fossil record. The action of the tendon lattice is even more noticeable with the loadings having a preponderant lateral component, with a significant reduction of the lateral displacement of the neural spines. The loadings directed straight dorsoventrally show a posterior shift of the vertebrae, a conformation not detected in the pathological fossil record.

QUANTIFICATION AND STATISTICAL ANALYSIS

Each vertebra was considered as a single individual, both from isolated and associated material because i) in a complete tail, a series of non consecutive neural spines can show pathological conditions, but gaps might be present between some of them, with apparently "healthy" spines lying between those with evidence of trauma; ii) isolated caudal vertebrae from bonebeds could belong to the same individual, but because of their fossilized condition, this cannot be proven in the absence of clear associations; iii) several pathological spines described in the literature[5,9] are isolated or belong to associated elements, but the descriptions omit a complete, exhaustive list of such elements; iv) when considering the published literature, previous authors usually did not mention the total number of preserved vertebrae in the skeleton(s) analyzed, imposing a certain bias in detecting the real frequency of pathological and non-pathological bones. Given the nature of this study, results comprise primarily descriptive statistics. We followed a previous methodology used to analyze the statistical distribution of paleopathologies in a population of *Edmontosaurus*.[5] This involved using two-way Pearson chi-squared tests to evaluate associations between pathology/body regions and trauma/body regions

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(specifically, focusing on the axial and tail regions) in our database. P values < 0.05 were considered significant. The analysis was conducted in RStudio (R Core Team, 2021), with "Pathological Numbers" corresponding to the pathological specimens, and "total" corresponding to the whole referred collection.

To compare the palaeopathological frequencies between the Wyoming database[5] and the AEHM collection defined among the body regions, a binary logistic regression was used with the statistical software SPSS (IBM, 2020). The binomial analysis compared the dependent "Pathology" considering value 1 as "present" and value 0 as "absent" with the independent variables (covariates) represented by the body regions and the museum collections (nominal entries). The working spreadsheet was modified by keeping body areas from[5] and by merging manual phalanges and forelimbs within one category ("forelimbs"), as well as pedal phalanges with forelimbs ("hindlimbs"), to avoid too many variables.