Bite and tooth marks on sauropod dinosaurs from the Morrison Formation (#85319)

First submission

Guidance from your Editor

Please submit by **12 May 2023** for the benefit of the authors (and your token reward) .

✓ **Structure and Criteria**
Please read the 'Structure and Criteria' page for general guidance.

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

If this article is published your review will be made public. You can choose whether to sign your review. If uploading a PDF please remove any identifiable information (if you want to remain anonymous).

Files

Download and review all files from the materials page.

8 Figure file(s)
1 Table file(s)
2 Raw data file(s)

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- ✓ Clear, unambiguous, professional English language used throughout.
- ✓ Intro & background to show context. Literature well referenced & relevant.
- ✓ Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- ✓ Figures are relevant, high quality, well labelled & described.
- ✓ Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- ✓ Original primary research within Scope of the journal.
- ✓ Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- ✓ Rigorous investigation performed to a high technical & ethical standard.
- ✓ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- ℹ Impact and novelty not assessed. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- ✓ All underlying data have been provided; they are robust, statistically sound, & controlled.
- ✓ Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Bite and tooth marks on sauropod dinosaurs from the Morrison Formation

Robert Lei [1] , **Emanuel Tschopp** [2] , **Christophe Hendrickx** [3] , **Mathew Wedel** [4] , **Mark Norell** [5] , **David W Hone** Corresp. [6]

[1] Università degli Studi di Modena e Reggio Emilia, Moderna, Italy

[2] Universität Hamburg, Hamburg, Germany

[3] Unidad Ejecutora Lillo, Tucumán, Argentina

[4] Western University of Health Sciences, Pomona, USA

[5] American Museum of Natural History, New York, USA

[6] School of Biological and Behavioural Sciences, Queen Mary University of London, London, United Kingdom

Corresponding Author: David W Hone
Email address: dwe_hone@yahoo.com

Tooth marked bones provide important evidence for feeding choices made by extinct carnivorous animals. In the case of the dinosaurs, most bite traces are attributed to the large and robust osteophagous tyrannosaurs, but those of other large carnivores remain underreported. Here we report on an extensive survey of the literature and some fossil collections cataloging a large number of sauropod bones (68) from the Upper Jurassic Morrison Formation of the USA that bear bite traces that can be attributed to theropods. We find that such bites on large sauropods, although less common than in tyrannosaur-dominated faunas, are known in large numbers from the Morrison Formation, and that none of the observed traces showed evidence of healing. The presence of tooth wear in non-tyrannosaur theropods further shows that they were biting into bone, but it remains difficult to assign individual bite traces to theropod taxa in the presence of multiple credible candidate biters. The widespread occurrence of bite traces without evidence of perimortem bites or healed bite traces, and of theropod tooth wear in Morrison Formation taxa suggests preferential feeding by theropods on juvenile sauropods, and likely scavenging of large-sized sauropod carcasses.

Bite and tooth marks on sauropod dinosaurs from the Morrison Formation

Roberto Lei[1], Emanuel Tschopp[2,3,4], Christophe Hendrickx[5], Mathew Wedel[6], Mark A. Norell[3], David William Elliott Hone*[7]

[1]Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Modena, Italy

[2]Department of Animal Biodiversity, Universität Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

[3]Division of Paleontology, American Museum of Natural History, New York, NY, USA

[4]GeoBioTec, Faculdade de Ciencias e Tecnologia, Universidade Nova de Lisboa, Caparica, Portugal

[5]Unidad Ejecutora Lillo, CONICET-Fundación Miguel Lillo, Miguel Lillo 251, San Miguel de Tucumán 4000, Tucumán, Argentina

[6]College of Osteopathic Medicine of the Pacific and College of Podiatric Medicine, Western University of Health Sciences, Pomona, California, USA

[7]School of Biological and Behavioural Sciences, Queen Mary University of London, Mile End Road, London, E1 4NS, UK

Corresponding Author:

David William Elliott Hone*

School of Biological and Behavioural Sciences, Queen Mary University of London, Mile End Road, London, E1 4NS, UK.

Email address: d.hone@qmul.ac.uk

Abstract

Tooth marked bones provide important evidence for feeding choices made by extinct carnivorous animals. In the case of the dinosaurs, most bite traces are attributed to the large and robust osteophagous tyrannosaurs, but those of other large carnivores remain underreported. Here we report on an extensive survey of the literature and some fossil collections cataloging a large number of sauropod bones (68) from the Upper Jurassic Morrison Formation of the USA that bear bite traces that can be attributed to theropods. We find that such bites on large sauropods, although less common than in tyrannosaur-dominated faunas, are known in large numbers from the Morrison Formation, and that none of the observed traces showed evidence of healing. The presence of tooth wear in non-tyrannosaur theropods further shows that they were biting into bone, but it remains difficult to assign individual bite traces to theropod taxa in the presence of multiple credible candidate ~~biters~~. The widespread occurrence of bite traces without evidence of perimortem bites or healed bite traces, and of theropod tooth wear in Morrison Formation taxa suggests preferential feeding by theropods on juvenile sauropods, and likely scavenging of large-sized sauropod carcasses.

Introduction

Tooth traces are a form of trace fossil produced by contact between a tooth and a bone, typically during feeding. They yield data regarding the biology and behavior of the bite-making animal and potentially about interactions between extinct species. Moreover, the analysis of multiple tooth traces may provide information about the ecological relationships existing between animals, such as non-avian dinosaurs (e.g., Fiorillo, 1991; Jacobsen, 1998; Hone & Chure, 2018).

Despite their potential importance, tooth traces from carnivorous theropods are generally poorly studied, with a handful of specimens described in detail and only two systematic surveys performed to date (see Jacobsen, 1998; Drumheller et al., 2020). This could be partly due to the rarity of such traces, which suggests that contact between bones and theropod teeth was often accidental (see Hone & Rauhut, 2010), and it was also hypothesized that the dentition of most taxa was not suited for processing such a hard tissue (Fiorillo, 1991). The only notable exception is the tyrannosaurids; numerous bite traces are known from formations where these are the dominant carnivorous clade (e.g., Fiorillo, 1991; Jacobsen, 1998; Hone & Rauhut, 2010). Of the few detailed descriptions of theropod tooth traces, many are those made by tyrannosaurs (e.g., Erickson & Olson, 1996; Hone & Watabe, 2010; De Palma et al., 2013), which leave traces more often than other theropods (Hone & Rauhut, 2010) such that these are perhaps the best understood clade in terms of their feeding patterns and ecology.

Tooth traces take different shapes depending on the behavior of the biting animal. For instance, elongated scars are produced by tooth dragging, whereas the collapse of the bone surface indicates particularly strong bites (D'Amore & Blumenschine, 2009). In some cases, it is also possible to infer information about the carnivore's size, which may be predicted from parallel traces, left by a single bite. Here, the distance separating them should reflect the spacing of the teeth, although several factors may bias the results and render it difficult to correctly assign a tracemaker (see Hone & Chure, 2018 and Brown et al., 2021).

Further information that may be inferred from tooth traces are about the ecological relationships between herbivores and carnivores. For example, prey preferences could be reflected by a majority of feeding traces associated with a particular taxon (Jacobsen, 2008) or potentially from the proportions of taxa with healed bites. However, it remains mostly impossible to distinguish between predation or scavenging events, restricting interpretations of interactions between living members of prey and predator species (e.g., see Currie & Jacobsen, 1995; Holtz, 2003; Bader et al., 2009; Hone & Chure, 2018). In some cases, failed hunting attempts were identified thanks to the presence of healing tissues in correspondence to the bites (De Palma et al., 2013). Otherwise, the location of the traces may favor one or the other interpretation (Hunt et al., 1994). One of the most interesting ecosystems to understand such carnivore-consumed (*sensu* Hone & Tanke, 2015) relationships is the terrestrial Upper Jurassic Morrison Formation in the western United States (Drumheller et al., 2020).

The Morrison Formation is an extremely large unit in the central to western part of North America (Turner & Peterson, 2004). It is mainly composed of continental sediments forming an alluvial plain, which is thought to have been covered in rivers and lakes (Foster, 2003; Turner & Peterson, 2004). The climate varied from semi-arid to more humid conditions depending on geography and time (Turner & Peterson, 2004; Maidment & Muxworthy 2019). The dinosaurian assemblage of the Morrison ecosystem comprises numerous taxa and is dominated by large sauropods such as *Camarasaurus, Diplodocus, Apatosaurus* and *Brachiosaurus* (Chure et al., 2006; Farlow et al., 2010; Whitlock et al., 2018; Foster, 2020; Mannion et al. 2021). There are also numerous large-bodied (>5m in body length) theropods including *Allosaurus*, *Ceratosaurus*, and *Torvosaurus* (Gilmore, 1920; Henderson, 1998; Bakker and Bir, 2004; Foster, 2020) which would have fed upon them, whether through hunting them as prey (as adult or juveniles) or scavenging from carcasses.

Several tooth marked bones belonging to sauropods from the Morrison Formation have been already described in detail (e.g., Hunt et al., 1994; Chure et al., 1998; Hone and Chure, 2018; Drumheller et al., 2020) but this remains an area of limited study given the huge numbers of bones that have been collected from this region. Such specimens represent a precious source of information to determine what may have eaten animals of this size given the discrepancy between most adult sauropods and contemporaneous theropods. Here we assess the interactions between theropods and sauropods in the Morrison Formation based on an examination of a total of 68 tooth marked elements from 40 individual sauropods. We find that wear on teeth of theropods was likely produced by feeding on sauropods and that tooth-on-bone contact was more frequent than previously thought. However, bites on large sauropods likely represent scavenging in most cases and that predation and consumption of juvenile sauropods was more common.

Materials and Methods

We surveyed sauropod specimens from the Morrison Formation looking for possible tooth traces. Data was acquired both from the literature and visits to collections by several authors. Whereas several of the noted occurrences derive from rather incidental observations during collection visits for reasons other than a survey of bite marks, we were able to systematically go through more than 600 single bones of Morrison Formation sauropods at the American Museum of Natural History (AMNH; an approximated 80% of the entire collection) with the aim of documenting any potential bite trace.

Two different classification methods, the first from Binford (1981) and D'Amore and Blumenschine (2009) and the second from Hone and Watabe (2010), were followed to describe tooth traces. Both approaches refer to four broad categories which mostly overlap. However, the first system aims at describing the trace's morphology, while the second one focuses on the behavior that led to the bite. We decided to primarily use the following terms defined by Hone & Watabe (2010):

1. Drag (caused by tooth dragging, intact cortex); some traces were classified as drags despite collapse of the bone cortex because they were interpreted as shallow scars left on already damaged tissue.

2. Bite and drag (caused by tooth dragging, damaged cortex)
3. Pit (no dragging, intact cortex)
4. Puncture (no dragging, damaged cortex).
5. To this we add a fifth category - ‘Removed’ - to indicate the complete removal of a portion of a bone. Note that this is effectively a subdivision of the Bite and Drag and / or Puncture categories since the teeth have penetrated the cortex in order to remove the piece of bone (Figure 1).

We determined the general shape of each scar, distinguishing between straight and curved scars. Each trace was measured in order to obtain the maximum value of length, width, and depth. In case of parallel traces (potentially produced by a single bite), we also determined the total dimension of the damaged area and the spacing separating the individual traces. Every measurement was performed three times to compensate for the measurement error and the final value was calculated from the arithmetic mean (Arnqvist & Martensson, 1998).

Most specimens were documented directly by the authors through either 3D scanning or photographs. Surface scans were acquired by means of an Artec 3D Spider scanner, whose micrometer precision allowed us to obtain high resolution digital reconstructions (see https://www.morphosource.org/projects/000518771/temporary_link/vv5ycCWyQ8bgNoLYPcumE1Zr?locale=en).

Due to the excessive size or irregular shape, several specimens had to be photographed instead, both because scanning them proved to be impractical (the software couldn’t produce a satisfactory reconstruction) and because moving them could have caused damage.

For many specimens, we provide measurements of length, width and depth of the bite traces. Moreover, in case of parallel traces (possibly left by the same bite), we also measured the spacing between one trace and the next one, along with the total length and width of the bite area (see Supplementary Information 1). Whenever possible, traces were measured with calipers on the original specimens. Where appropriate, measurements were taken from photographs. The photographed traces were measured through the morphometric software tpsDig. To do so, we created a tps file from the picture with tpsUtil. Then, we placed landmarks on the specimen and measured the distance separating them with the meter tool. Being a supra-specific analysis, the error associated with 2D data from 3D objects was considered acceptable (Cardini, 2014; Courtenay, 2018). The 3D-scanned specimens were measured with Meshlab. Landmarks were placed in correspondence to bite traces; the distance between them was calculated by means of the Pythagoras theorem =SQRT (POWER(X2 – X1;2)+POWER(Y2 + Y1;2)+POWER(Z2 – Z1;2)), where X; Y; Z are the values of the landmarks' coordinates.

We calculated the percentages of the following parameters: traces (from the same specimen) included within parallel clusters and at least partly affecting the articular surface, trace category, shape, and location (anatomical area). The latter was divided into i) low economy elements (less nutritive body parts) and ii) high economy elements (more nutritive body parts), generally following the classification proposed by Drumheller et al. (2020). We also determined the percentages of the taxa represented by the studied specimens at the 'clade' (Macronaria, Diplodocoidea), 'family' (Diplodocidae, Camarasauridae, Dicraeosauridae) and 'subfamily' (only within Diplodocidae: Apatosaurinae, Diplodocinae) equivalent rank levels.

To identify the potential bite makers on the sauropod bones, a survey of the dentition morphology of all carnivores from the Morrison Formation capable of leaving these tooth marks was done. Our dataset, which is mainly comprised of crown-based measurements published by Hendrickx et al. (2015a, 2020a, b), includes information on crown length, thickness, elongation as well as denticle density along the mesial and distal carinae in 293 in situ or isolated teeth belonging to four genus-level and six species-level (i.e., *Allosaurus fragilis*, *A. jimmadseni*, *Ceratosaurus nasicornis*, *Marshosaurus bicentesimus*, *Torvosaurus tanneri* and *T. gurneyi*) theropods from the Upper Jurassic of the United States and Portugal (see Supplementary Information 2). The mesial dentition morphology, premaxillary tooth orientation, position of the carinae in both mesial and distal teeth, as well as the pattern of spalled surfaces resulting from tooth-to-bone contact and degree of crown wear along the dentition was also explored in each of these taxa. Crown-based measurements as well as the dental nomenclature and orientation follow the recommendations of Smith et al. (2005), Smith and Dodson (2003), and Hendrickx et al. (2015b).

Results

In total, we identified 40 individual sauropods, collectively having 68 skeletal elements bearing bites, from literature and personal observations (Table 1). Among these, 8 elements (pelvis from *Camararaurus lewisi* BYU 9047; femur from diplodocinae CMC VP7747; humerus, sacrum, right femur, right foot phalanx from *Camarasaurus sp.* GMNH-PV 101; left scapula from *Galeamopus pabsti* NMZ 1000011; left metacarpal from *Galeamopus sp.* WDC GB) could not be completely analyzed and, therefore, are omitted from the analyses below. The remaining 60 bones, belonging to 37 individuals, are split across four anatomical regions: spine (18 elements), chest/abdomen (15 elements), upper limbs (4 elements), and lower limbs (24 elements), with one element (the apatosaurine caudal vertebra AMNH FARB 222 - 4) bearing bite traces on two different anatomical areas (both on the caudal neural arch and centra) and thus counted twice.

We found up to 48 tooth traces on a single bone and up to 12 traces within patches of parallel/sub-parallel scars (both on the ilium of the indeterminate eusauropod AMNH FARB 366), which were potentially produced by a single bite. Among the measured elements, the femur of the indeterminate apatosaurine AMNH FARB 222 bears both the largest bitten area (153 x 168 mm) and the largest single trace (128 x 28 mm, length x width), excluding removed traces. On the other hand, the smallest single trace (5.28 x 0.69 mm, length x width) was found on AMNH FARB 30066, a possible carpal bone of an indeterminate eusauropod.

As for tooth trace categories, we identified - among the 60 completely classified elements - a predominance of drags (174 – 50.0%) and bite and drags (158 – 45.4%) over pits (4 – 1.1%), punctures (3 – 0.9%) and removed traces (9 – 2.6%). These bite traces were also classified according to the parameters listed below and the results are plotted as bar charts.

1. Shape (Figure 2A):

   We divided the tooth traces in two categories based on their shape: straight and curved; this could give us information about the feeding style adopted by the carnivore.
2. Proximity to articular surfaces (Figure 2B):

   The amount of scars located on articular surfaces or on other parts of the bone away from the ends.
3. Trace type (Figure 2C):

   The category of the bite trace type.
4. Parallel clusters (Figure 2D):

The amount of scars included within parallel clusters which, according to D'Amore and Blumenschine (2009), are defined as groups of parallel traces close to each other and located on a similar area of the specimen.

5. Anatomical area (Figure 3):

   We provide two groups of charts, the first one is made by counting the bite traces associated to each anatomical region, while the second one by counting the individual bones bearing such traces. The latter one was made considering that an abundance of tooth traces on the same element may just be the result of a single feeding event.

   As we said, we analyzed 60 bones to produce these charts, however a fossil vertebra belonging to the apatosaurine AMNH FARB 222 was counted twice since it shows traces both on the neural arch and the centrum (which represents two different categories). For this reason, the total number of elements for the second group of charts is 61. Both groups of charts are divided between low and high economy elements, representing anatomical regions poor and rich in nutrients, respectively.

Based on these data, we inferred some information about the consumer's biology and feeding style, along with the nature of the event which caused the tooth traces.

Discussion

Identification of the trace maker

The best way to identify the trace maker are embedded teeth in the bone or those that were likely lost during biting (e.g., Buffetaut & Suteethorn, 1989; Currie & Jacobsen, 1995; Jennings & Hasiotis, 2006; De Palma et al., 2013; Alonso et al., 2017). Unfortunately, no such embedded crown was found in any of the sauropod specimens under study. Some authors such as Currie & Jacobsen (1995), Chure et al. (1998), Rogers et al. (2003), and Happ (2008) either identified the trace maker based on the morphology and dimensions of its tooth marks or proposed the best candidate based on body size and/or abundance. Hone and Chure (2018), however, pointed out that many coeval predators with relatively similar ziphodont dentition would likely leave comparable traces on bones. Accordingly, ontogenetic and intraspecific variation could easily bias the analysis, and bites applied with different angles and worn/broken teeth would also affect the results (Hone and Chure, 2018), although careful consideration of spacing can allow for some inferences to be made with confidence (Brown et al., 2021).

Based on the width, depth and spacing of the tooth marks, it can at least be confidently suggested that the tooth marks present on several specimens (AMNH FARB 92; AMNH FARB 222, 259, 264, 332, 392, 407, 582, 597, 642, 675, 5755, 5760, 5761, 6118, 30116, 30192; DINO 5119; TMP 1983.035.0003 [formerly UUVP 5309]) were left by large carnivore theropods. The largest predators from the Morrison Formation are non-maniraptoriform avetheropods and the tooth mark were most likely made by these theropods. Chure et al. (1998), Hone and Chure (2018), and Drumheller et al. (2020) also previously identified the bite marks found on sauropod specimens as belonging to large-bodied theropods. The extensive damage present on the indeterminate neosauropod AMNH FARB 264, on the two *Camarasaurus* specimens AMNH FARB 332 and AMNH FARB 582 (Figure 4), on the indeterminate diplodocoid AMNH FARB

392, and on the indeterminate diplodocine AMNH FARB 642 further supports large theropods as credible candidates preying on diverse sauropod taxa.

The high percentage of parallel drags (Figure 2D) suggests that the trace makers defleshed the carcass moving the head backwards, a pattern particularly common among large theropods based on their neck movements (Snively & Russell, 2007; Snively et al., 2013). Although teeth clearly came into contact with the bone surface, given the relative infrequency of tooth marks, such contact appears to be accidental (D'Amore & Blumenschine, 2009) rather than a systematic biting of the bone, as seen, by contrast, in tyrannosaurs (Hone & Rauhut, 2010). Although some theropods were capable of powerful bites (as suggested by the relatively high number of bite and drags and punctures), no evidence of bone gnawing (as defined by Capaldo & Blumenschine, 1994) was identified, and only six specimens (*Camarasaurus* AMNH FARB 332 and 582; Eusauropoda indet. AMNH FARB 366; Diplodocoidea indet. metapodial AMNH FARB 392 *Apatosaurus* AMNH FARB 550; Diplodocinae indet. AMNH FARB 642; *Galeamopus* WDC GB) bore extensive damage with parts of the bone removed.

Other terrestrial carnivores such as the small-bodied coelurosaurs *Ornitholestes* (Osborn, 1903), *Stokesosaurus* (Madsen, 1974), *Tanycolagreus* (Carpenter et al., 2005), *Coelurus* (Cope, 1887; Ostrom, 1980) and *Hesperornithoides* (Hartman et al., 2019) can be dismissed as possible candidates given that their crowns were not larger than 30 millimeters (C.H. pers. obs.; Figure 5) and could not have made such deep tooth marks on the sauropod bones because of limited jaw power. Likewise, the goniopholidid *Amphicotylus*, which is the largest terrestrial crocodylomorph from the Morrison Formation, does not have ziphodont crowns capable of making these large striations (Drumheller et al., 2020). Instead, goniopholidids have a conidont dentition suited for impaling and holding prey items (Hendrickx et al., 2019), and these predators probably fed mainly on fish and small-bodied reptiles, dinosaurs, and mammals (Foster, 2020).

The large theropods from the Morrison Formation are currently represented by five unequivocal avetheropods, namely, *Ceratosaurus nasicornis* (Gilmore, 1920; Madsen and Welles, 2000), *Marshosaurus bicentesimus* (Madsen, 1976a), *Torvosaurus tanneri* (Galton and Jensen, 1979; Britt, 1991), and two species of *Allosaurus*, *A. fragilis* (Madsen, 1976b) and *A. jimmadseni* (Chure and Loewen, 2020). *Saurophaganax maximus*, considered by Smith (1998) to be a junior synonym of *Allosaurus*, also most likely represents a different allosaurid taxon from a higher stratigraphic level of the Morrison Formation (Chure, 1995; Foster, 2020). Referring tooth marks to any of these taxa is particularly challenging given the similarity of their dentition and the fact that subtly different actions of feeding can result in very different spacing of bite marks, making matches to tooth patterns in the jaws of these large theropods very uncertain (Hone and Chure, 2018). Hone and Chure (2018) for instance tentatively ascribe the tooth marks found in the indeterminate diplodocoid DINO 5119 to *Allosaurus* sp. solely based on the much greater prevalence of this taxon on the fossil site. Likewise, Chure et al. (1998) inferred that *Torvosaurus* or *Ceratosaurus* were the most likely candidates for making the tooth mark seen on a pubic foot of *Allosaurus* (AMNH FARB 813) based on the size of the bite and known tooth size in the largest theropods from the Morrison Formation. Drumheller et al. (2020) finally postulated that the tooth marks with closely spaced striations were made by *Allosaurus* and/or *Ceratosaurus*, and those with the largest striations by *Torvosaurus*, a very large size *Allosaurus*, and/or *Saurophaganax* based on the average denticle width measured on the crowns of these theropods.

A thorough examination of the dentition of all large-bodied theropods from the Morrison Formation by one of us (C.H.) enables us to comment on these referrals and to provide additional information that may help identify the tracemaker among these theropods. As correctly pointed out by Drumheller et al. (2020), difference in denticle size occurred between the four largest theropods here, which can help identify the trace maker using the striation spacing left by the denticles. The teeth of *Ceratosaurus* (UMNH VP 5278) and *Allosaurus* (UMNH VP 6499, 6239; CM 21703; AMNH FARB 851) with coarser denticles have a denticle density of no fewer than 8 to 9 denticles per 5 mm (here abbreviated in d/5 mm) in the mesial and lateral dentitions and for both distal and mesial carinae. Conversely, the largest crowns of *Torvosaurus* (BYUVP 725-12817; ML 1100; SHN.067; SHN.268) have 5 to 6 mesial and distal d/5 mm in both the mesial and lateral dentition whereas the lowest denticle density measured in *Marshosaurus*' teeth (UMNH VP 6368; DMNS 3718) is 17-18 d/5 mm for the mesial carina and 14-15 for the distal carina (Supplementary Information 2). *Saurophaganax* and the largest specimens of *Allosaurus* possibly had a slightly lower denticle density than that measured in our theropod tooth sample. However, it is unlikely that the crowns of the largest allosaurids had a denticle density lower than 7 d/5 mm as in *Torvosaurus*, a number comparable to the largest tyrannosaurids (e.g., *Tyrannosaurus*, *Zhuchengtyrannus*), which have the coarsest denticles in all theropods with ziphodont teeth (C.H. pers. obs.). Based on this observation, striations spacing of more than 0.8 mm on the tooth mark were most likely made by the crowns of *Torvosaurus* whereas those between 0.6 and 0.8 mm such as the largest striations measured by Drumheller et al. (2020) and tentatively referred to *Torvosaurus* or a particularly large allosaurid, could be made by *Ceratosaurus*, *Torvosaurus*, *Allosaurus* or *Saurophaganax*.

Another aspect that requires attention is the robustness of the crowns of these large-bodied theropods. The mesial and lateral dentition of *Marshosaurus* are particularly labiolingually compressed (CBR<0.6), which contrasts with the thicker mesial crowns of *Ceratosaurus*

(CBR~0.6-0.85), *Torvosaurus* (CBR~0.65), and *Allosaurus* (CBR~0.8-1.16). The mesial dentition of these three last theropods, therefore, appear to be less liable to break when contacting bone than those of *Marshosaurus*. The lateral crowns of *Ceratosaurus* are, however, strongly laterally compressed (CBR~0.3-0.4) whereas those of *Torvosaurus* (CBR~0.48) and *Allosaurus* (CBR~0.65; Hendrickx et al., 2020) are thicker (Supplementary Information 2). The mesial and lateral teeth of *Allosaurus* are, in fact, particularly thick, to a point that this theropod is considered by Hendrickx et al. (2019, 2020b) to have a pachydont dentition similar to that of derived tyrannosaurids. The latter are well-known to have incrassate and robust teeth adapted to bone-biting involving high mechanical stresses (e.g., Holtz, 2003; Snively et al., 2006; Reichel, 2010; Hendrickx et al., 2019). Both mesial and lateral dentitions of allosaurids would, therefore, appear to be better able to withstand tooth-to-bone contact than any other carnivorous theropods from the Morrison Formation, and the deepest and numerous tooth marks seen on the largest sauropod bones such as those seen in AMNHH FARB 366 (a eurosauropod ilium) were probably made by *Allosaurus* and/or *Saurophaganax*. Particularly long traces (>5 cm) may also be the result of an allosaurid feeding style which, according to Snively et al. (2013), employed their powerful neck muscles to rapidly move the head downward.

A survey of spalled surfaces and the degree of crown wear in the four large-bodied theropods from the Morrison Formation, reveals that all of the large theropod taxa from the Morrison Formation probably engaged in some tooth-to-bone contact during feeding. Tooth wear nevertheless indicates that the tip of the snout with the mesial dentition in *Ceratosaurus*, *Marshosaurus* and *Torvosaurus* were more often in contact with bones, whereas both the mesial and mesio-lateral/transitional dentitions of *Allosaurus* engaged in tooth-to-bone contact.

Crown apices of fully erupted premaxillary and mesial maxillary and dentary teeth are indeed usually worn out (i.e. the enamel has fully worn away to expose the underlying dentine) in *Allosaurus fragilis* and *A. jimmadseni*. The apices of distal maxillary and dentary teeth can also be slightly worn, but are more often intact in this allosaurid, with the denticles often crossing the tip of the crown. Extremely worn out crowns with large spalled surfaces (differing from the wear facets due to tooth-to-tooth contact, which are common on the lingual surfaces of *Allosaurus* premaxillary teeth; C.H. pers. obs.) have also been observed in some premaxillary (rpm1 and 3 of UMNH VP 1251), mesial maxillary (lmx2 of NHFO 455 and rmx2 of USNM 8335) and mesial dentary teeth (Ldt2 and Rdt3 of NHFO 455; Ldt3 of UMNH VP 6475) of *Allosaurus* but, this is not common. In the three other large Morrison theropods, a fully worn out apex of the crowns has been observed in the mesialmost dentary tooth of *Ceratosaurus* (Ldt1 of UMNH VP 5278) and one premaxillary tooth of *Marshosaurus* (Lpmx2 of DMNS 3718), indicating that the mesialmost teeth of these two taxa were frequently in contact with bones. Worn out apices are mainly found in the first premaxillary and dentary teeth in *Ceratosaurus* whereas the apices of the more distal crowns are intact or slightly worn out. This also seems to be the case in *Marshosaurus* based on the small sample available. The lateral crowns of *Torvosaurus* either have the extremity of their apices worn out or intact apices. Fully worn out apices are rare in the lateral dentition of *Torvosaurus* and have only been observed in one dentary tooth (i.e., ldt6 of BYUVP 725-12817). Crowns with a strongly worn out apex have also been observed in two isolated *Torvosaurus* shed teeth from the Late Jurassic of Portugal (SHN.215 and SHN 364; Malafaia et al., 2017a, fig. 11e; C.H. pers. obs.). Based on their mesiodistal narrowness, elongation and/or thickness, these teeth most likely belong to the mesial dentition, suggesting that, unlike the lateral dentition, the mesial teeth of *Torvosaurus* were often in contact with bones.

Allosaurus also differs from the three basally-branching averostrans in its snout morphology, which is mediolaterally broad and bears five mesiodistally wide premaxillary teeth (Figure 6). The snouts of the megalosauroids *Marshosaurus* and *Torvosaurus* are comparatively narrower and anteroposteriorly longer, whereas that of *Ceratosaurus* is anteroposteriorly shorter and mediolaterally wider but not as wide as that of *Allosaurus*. *Ceratosaurus*, *Marshosaurus*, and *Torvosaurus* all bear three to four premaxillary crowns (Figure 6), which are particularly laterally compressed in the two megalosauroids. A small space also separates the first premaxillary alveoli/crown (pmx1) from the left and right side of the cranium in *Marshosaurus* and *Torvosaurus*, whereas this space is wider in *Ceratosaurus* and *Allosaurus*, and noticeably wide in some specimens of *Allosaurus*. These dental variations in the four apex theropods from the Morrison Formation are reflected in the spacing of bite marks, especially when the theropod head moves parallel to the long axis of the skull, leaving even spaces between the marks (Figure 6). We, however, agree with Hone and Chure (2018) that a head moving at a certain angle from its long axis during biting, as well as one or several misoriented crowns and unerupted, partially erupted, or missing teeth, directly affect the tooth mark pattern, making its identification particularly challenging (Figure 6). Partly erupted teeth were in fact revealed to be common in the premaxillae of *Ceratosaurus* and *Allosaurus* (Supplementary Information 2) and the fact that their apices are often perfectly intact shows that they did not participate in tooth-to-bone contact like the other fully erupted teeth. Therefore, only tooth marks showing a symmetrical pattern made of more than eight grooves with the two middle grooves being widely separated can be confidently assigned to allosaurids. Likewise, tooth marks with a symmetrical pattern of six grooves with the two middle grooves being particularly closely spaced are likely made by one of the two megalosauroids.

Conversely, asymmetrical tooth marks showing deep furrows could be made by any of the apex theropods from the Morrison Formation.

Although Hone and Chure (2018) interpret the dentition of *Allosaurus*, *Ceratosaurus* and *Torvosaurus* as homodont, sharing similar gross morphology, the mesial dentition of *Ceratosaurus*, *Allosaurus* and megalosauroids not only differ in the number of premaxillary teeth and the labiolingual thickness of the crown, but also in the orientation of their carinae. The mesial carina is facing mesially and is strongly lingually displaced in the mesial dentition of *Allosaurus* (Hendrickx et al., 2020b, 2020a). On the other hand, the mesial carina is facing anteriorly and is centrally positioned on the mesial side of mesial teeth in *Ceratosaurus*, *Marshosaurus*, and *Torvosaurus* (and indeed all megalosauroids; Hendrickx et al., 2015a). Likewise, the distal carinae of *Allosaurus* and *Ceratosaurus* are strongly labially displaced and face distally in mesial teeth whereas those of megalosauroids are centrally positioned or weakly labially displaced in the mesial (and lateral) dentition and face linguodistally in the first two premaxillary teeth (Hendrickx et al., 2015a; Figure 6). Consequently, the presence of striae on the lateral sides of multiple parallel tooth marks forming a symmetrical pattern likely results from the biting of an allosaurid. These striae would indeed be present in the tooth marks made by *Ceratosaurus*, *Marshosaurus* and *Torvosaurus* if the snout of the latter moved at a strong angle from the long axis of the head, so that the anteriorly and posteriorly positioned mesial and distal denticles, respectively, would contact the bone during biting. Because mesial denticles are significantly smaller than the distal ones (DSDI>1.2) in the mesial dentition of both *Ceratosaurus* and *Marshosaurus* (Hendrickx et al., 2019), a significant difference in the size in the striae from the two sides of a tooth mark would support these two taxa as the potential trackmakers.

Chure et al. (1998) discounted *Allosaurus* as a credible candidate of the large bite mark on a pubic foot of the same taxon (AMNH FARB 813) based on the fact that its crowns are significantly smaller than those of *Ceratosaurus* and *Torvosaurus*. With a crown height reaching up to 140 mm in some lateral teeth from Portugal (Malafaia et al., 2017b, 2017a), *Torvosaurus* bears among the largest crowns in all dinosaurs (Hendrickx et al., 2019; Figure 5). The largest *Ceratosaurus* crowns we measured are 75 mm in height and likely did not exceed 100 mm, whereas those of *Allosaurus* are indeed shorter, with a crown height of 58.4 mm measured in the largest (and best preserved) crown (CM 21703; n.b., with a CH of 68.85 mm, rmx6 of SMA 0005/02 is the tallest crown measured for *Allosaurus* [Hendrickx et al., 2015a] but the specimen is particularly badly preserved so that measurements on the dentition of SMA 0005/02 should be seen as tentative; Figure 5). As noted above, tooth wear suggests that the lateral teeth of *Ceratosaurus* and *Torvosaurus* probably rarely contacted bones whereas the mesial maxillary crowns of *Allosaurus* most likely did. Because the maxillary crowns from the largest allosaurid species probably exceeded 60 mm, we therefore consider *Allosaurus* and *Saurophaganax* as credible candidates of the tooth marks on AMNH FARB 813.

As for smaller traces, we did not observe any bisected or hook-shaped scores, which are typical for modern crocodiles (Njau & Blumenschine, 2006, and were likely produced by Morrison crocodyliforms, too; Hone et al., 2018; Hone & Chure, 2018). Similarly, the shape of the traces we recorded are different from what would be expected if they had been left by lizards (which usually produce curved scars, e.g. see D’Amore & Blumenschine, 2009) or mammals (e.g., West & Hasiotis, 2007; Longrich & Ryan, 2010). Early champsosaurs may be excluded too, considering they usually ate fish and that they possibly left traces similar to those of lizards and crocodyliforms (Foster, 2003, 2007; Hone et al., 2018). This suggests that the smaller traces were produced by small theropods, however we cannot tell if they were from small-sized taxa or juveniles of large theropods (since theropods were polyphyodont, Hendrickx et al., 2015b; Hone & Chure, 2018).

Collectively therefore, there is strong evidence that the various large bodied theropod taxa present in the Morrison formation were feeding on sauropods. In at least some cases it is possible to rule in, or out, various taxa as candidates for given bite traces based on their size and shape, though this remains difficult in most instances because of the lack of details available or the multiple possible bite makers.

Palaeoecological implications

The wear seen in various large theropod teeth listed above may seem at odds with the relatively low numbers of bite marks seen on sauropod bones (compared to tyrannosaur faunas at least) and the idea that non-tyrannosaurid theropods largely avoided tooth-on-bone contact when feeding. However, this is not necessarily the case. When scavenging or feeding upon the carcass of a large sauropod, there would be literally tons of meat available for carnivores (see also Pahl & Ruedas, 2021) and it should be possible even for a number of large-bodied theropods to feed extensively on this without biting into bones. As seen in Figure 3, there are numerous bites on both bones and parts of the skeleton that we term high economy (potentially considerable muscle or meat attached) and low economy (little meat available). With the exception of the pelvic girdles however, there tend to be similar percentages of bites on both sets of areas. In terms of the numbers of elements that were bitten, a number of high economy elements show very few bites (pectoral girdle, fibulae) and some low economy elements are more often bitten.

Collectively, this is difficult to interpret as, for example, ribs might be readily damaged or destroyed in feeding and small elements like distal caudals are rarely preserved so bites are not recorded even if present, and bones like the middle metatarsals might suffer few bites because they are covered by the lateral and medial ones. There are also far more low economy elements (e.g., there are five metatarsals for every fibula in the sauropod skeleton), the high economy ones are often considerably larger. The pelvic girdles at least show a high number of bitten elements and a high number of individual traces seen. Given the attachment of so many large muscles to this region this appears to have been an area of attention from large theropods.

Although the exact nature of the bite distribution here is confounded by potential taphonomic and behavioural biases, they do suggest that bite marks are actually not especially rare compared to tyrannosaur faunas. This has been found at up to 14 % of bones (Jacobsen, 1998) and here is approximately 9 % (71 bones out of over 800 viewed). The number here may well be inflated since one sauropod carcass may have multiple elements bearing traces, which is not a fair comparison to isolated elements, but this is still at least comparable to tyrannosaur faunas and does not represent a tiny fraction of the number of bites seen. The bites seen here are focussed neither on major areas of meat (e.g., proximal limbs and girdles) or late-stage scavenging of poor quality areas like metapodials.

However, if large theropods were predominantly predating and feeding upon juvenile animals, as suggested by Hone and Rauhut (2010) among others, then tooth-on-bone contact would have been much more common. Here, theropods would potentially be breaking up and consuming most of the animal (which would partly explain their rarity in the fossil record) and would therefore involve the tooth-on-bone contact that could wear down tooth crowns. Young animals would have generally smaller and weaker bones that a large theropod could bite through (compared to an adult sauropod) and these would also often be incompletely ossified and with incompletely closed sutures that would make them easier to process. In short, the relatively rare bites preserved on the bones of large sauropods were probably not causing the wear seen on large theropod teeth, these rather come from engagement with the destroyed (and so not preserved) bones of the more frequently consumed juvenile sauropods.

It is generally very difficult to determine whether tooth traces were the result of scavenging or predation events from bitten fossils (Holtz, 2003; Bader et al., 2009; Hone & Chure, 2018). The latter may be clearly identified by the presence of healing tissue surrounding the scar, indicating a failed hunting attempt (Bell et al., 2012; De Palma et al., 2013) though perimortem injuries that differ from feeding traces could in theory be identified. A number of specimens (*Camarasaurus* AMNH FARB 332 and AMNH FARB 582; Eusauropoda indet. AMNH FARB 366 (Area 1 and 8); Diplodocoidea indet. AMNH FARB 392 (metapodial I); *Apatosaurus* AMNH FARB 550; Diplodocinae indet. AMNH FARB 642; *Galeamopus* WDC GB) were clearly damaged by powerful bites. However, there is no reason to think that these were the result of predation attempts.

Predators typically aim at vital areas (like the hindquarters) to immobilize prey, so a manus or pes (as in *Camarasaurus* AMNH FARB 332 and the indeterminate diplodocoid AMNH FARB 392) would not represent an ideal target, being both hard and dangerous to bite on a fleeing or fighting animal. On the other hand, elements like the ilium of the indeterminate eusauropod AMNH FARB 366, the pubis of *Galeamopus* WDC GB or the dorsal vertebrae of *Apatosaurus* AMNH FARB 550 (Figure 7), all of which were relatively large sauropod individuals, were probably out of reach even for a large theropod. Instead, the fibula (as in *Camarasaurus* AMNH FARB 582) and femur (as in the indeterminate diplodocine AMNH FARB 642) could represent optimal targets to seriously wound and, possibly, immobilize the prey by damaging the knee or ankle joints (Hunt et al, 1994). However, the trace on the femur is located on the medial condyle of the distal end, an area which would probably have been out of reach in a living animal. On the other hand, the fibula was damaged on the posterior corner of the proximal end, a more easily accessible location. If this was indeed the result of predation, the absence of healing tissue would suggest that the sauropod died shortly after being attacked (c.f., Carpenter, 1998; Happ, 2008). In short, there is no convincing evidence here of any bites being attributed to predation attempts on large sauropods.

In the case of scavenging, more nutritious regions tend to be fed on first by carnivores or scavengers, such as the upper limbs, the chest and the abdomen and probably areas like the base of the tail. Not only do they represent attachment points for major muscle groups, but they may offer access to entrails too, also considering the location next to the anus/cloaca (Buffetaut & Suteethorn, 1989; Hunt et al., 1994; Jacobsen, 1998; Jennings & Hasiotis, 2006; Robinson et al., 2015). On the other hand, anatomical areas associated with low amounts of muscle, such as spinal elements and the lower limbs are generally the last to be consumed by carnivores (Hunt et al., 1994; Hone et al., 2010). In fact, less nutrient-bearing parts like the lower limbs may be preferably eaten only during times of low prey availability (Jacobsen, 1998). However, determining the difference between such late stage carcass consumption by a predator that made the kill, and a scavenger that has found a body may be impossible to determine without taphonomic evidence of transport, burial or decay of the bones prior to the infliction of bites, though this is possible in some cases (e.g. Hone & Watabe, 2010).

Among our samples, a number of bites are in positions and on elements that would neither be possible during a predation attempt or likely inflicted during early stages of carcass consumption and so might represent scavenging. For example, the indeterminate apatosaurine AMNH FARB 222, the preferred orientation of the scars on the tail vertebrae (oblique, posterodorsal to anteroventral) may indicate the employment of a specific defleshing technique (see Hunt et al., 1994) and, therefore, that they were the result of late stage consumption. This may also be true for the tooth traces on one rib of the indeterminate sauropod AMNH FARB 625 (aligned with the long axis) and the right scapula of *Camarasaurus supremus* AMNH FARB 5760 Sc-3 (showing a preferred orientation along the proximal margin, Figure 8). The latter specimen also displays a significant number of scars in the same area, which would be nearly impossible to produce on a living prey.

Similarly, the scars on the caudal vertebrae of *Camarasaurus supremus* AMNH FARB 5760 (Cd – y – 4) and *C. grandis* CM 11393 are located on their articular surface, an area accessible only after disarticulation, which can only really indicate late stage carcass consumption. Tooth traces located on the lower limbs (e.g. Diplodocoidea indet. AMNH FARB 597; *Camarasaurus* AMNH FARB 664 and also AMNH FARB 582, if not related to predation) and the spinal elements (e.g. *Camarasaurus supremus* AMNH FARB 5761) were also likely damaged during late stage feeding and may relate to scavenging, since they are associated with less nutritive areas. On the contrary, the bones from the upper limbs (e.g. Diplodocoidea indet. DINO 5119; Diplodocinae indet. AMNH FARB 660) and the chest/abdomen area (e.g. Macronaria indet. AMNH FARB 675) may have been bitten during early feeding, being located next to large muscles and entrails, although the general rarity of bites in these areas (Figure 3) suggests that such feeding did not normally reach the bone.

We found a total of 120 tooth traces associated with articular surfaces (on a total of 348 traces, distributed among 60 elements), especially on femora (17), metacarpals (26) and metatarsals (54). They may have been the result of carnivores feeding on the cartilage caps surrounding such regions, but may also represent attempts at disarticulating the carcass as previously seen in the tyrannosaurines (see Hone & Watabe, 2010). The latter hypothesis could be true for those specimens bearing bite and drag traces (e.g., the indeterminate diplodocoid metacarpal AMNH FARB 92), punctures and removed parts. These types of traces are typically associated with stronger bites (D'Amore & Blumenschine, 2009; Hone & Rauhut, 2010), which could be expected in case of disarticulation.

Most of the studied fossils were attributed to diplodoids and diplodocids (Table 1). Although this may indicate some sort of food preferences by Morrison theropods, it may just be due to taphonomic bias.

Conclusions

Although the survey here was not exhaustive, it reveals that there are numerous bite marks present on large sauropod bones and that these are generally underrepresented in the scientific literature. There is potentially a rich source of data present here to help better understand the feeding habits and ecology of the large Late Jurassic theropods both in the Morrison and likely other formations as well.

Interpreting the bite traces on sauropod bones remains difficult. Despite the extensive survey here, the presence of multiple candidate theropod trace makers and the variation in time, space, deposit and taxonomy of the sauropod faunas (as well as taphonomic and behavioural factors) means that drawing conclusions from this dataset as a whole is potentially problematic. However, it is clear that bite marks are more frequently produced on sauropods than previously realised and that there is wear to theropod teeth as the result of tooth-on-bone contact.

Ultimately this requires detailed study of individual specimens. The taphonomic history of the specimen and site is key to interpreting what the likely carnivore-consumed interaction was and information can be built up from here. Therefore, although this study points to the availability and importance of bite-traces on sauropods, the conclusions must remain tentative without considerable further study.

Acknowledgements

The authors thank Elisabete Malafaia for sharing photos of *Torvosaurus* teeth from Portugal. We thank Carl Mehling (AMNH) for assistance in collection access and specimen handling, Carolyn Merrill (AMNH) for training in and assistance with 3D scanning and model production, and Ayo Lewis for additional assistance in scanning. C.H. was funded by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Agencia Nacional de Promoción Científica y Tecnológica, Argentina to C.H. (Beca Pos-doctoral CONICET Legajo 181417). E.T. held a Theodore Roosevelt Memorial Fund and Division of Paleontology Postdoctoral Fellowship provided by Richard Gilder Graduate School at the American Museum of Natural History, New York, during the course of this work at AMNH, and currently holds a Alexander von Humboldt Fellowship for Experienced Researchers.

Institutional Abbreviations

AMNH FARB	American Museum of Natural History, Fossil Amphibians, Reptiles, and Birds Collections, New York, USA.
ANS	Academy of Natural Sciences, Philadelphia, USA.
BYUVP	Brigham Young University, Museum of Paleontology, Provo, USA.

CM	Carnegie Museum of Natural History, Pittsburgh, USA.
CMC	Cincinnati Museum Center, Cincinnati, USA.
DINO	Dinosaur National Monument, Jensen, USA.
DMNS	Denver Museum of Natural History, Denver, USA.
GMNH	Gunma Museum of Natural History, Gunma, Japan.
ML	Museu da Lourinha, Lourinha, Portugal.
MWC	Museum of Western Colorado, Grand Junction, USA.
NMZ	Natural History Museum Zurich, Switzerland.
SHN	Sociedade de Historia Natural, Torres Vedras, Portugal.
SMA	Sauriermuseum Aathal, Aathal, Switzerland.
TMP	Royal Tyrrell Museum, Drumheller, Canada.
UMNH VP	Utah Museum of Natural History, Salt Lake City, USA.
WDC	Wyoming Dinosaur Center, Thermopolis, USA.
YPM	Yale Peabody Museum, New Haven, USA.

References

Alonso A, Canudo JI, Torcida Fernández-Baldor F, Huerta P. 2017. Isolated theropod teeth associated with sauropod remains from El Oterillo II (Early Cretaceous) site of Salas de los Infantes (Burgos, Spain). *Journal of Iberian Geology*, 43:193-215.

Arnqvist G, Martensson T. 1998. Measurement error in geometric morphometrics: empirical strategies to assess and reduce its impact on measures of shape. *Acta Zoologica Academiae Scientiarum Hungaricae*, 44:73-96.

Bader KS, Hasiotis ST, Martin LD. 2009. Application of forensic science techniques to trace fossils on dinosaur bones from a quarry in the Upper Jurassic Morrison Formation, northeastern Wyoming. *Palaios*, 24:140-158.

Bakker RT, Bir G. 2004. Dinosaur crime scene investigations: theropod behavior at Como Bluff, Wyoming, and the evolution of birdness. In: Currie PJ, Koppelhus EB, Shugar MA, Wright JL, eds. *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*. Bloomington, Indiana: Indiana University Press. 301–342.

Bell PR, Currie PJ, Lee YN. 2012. Tyrannosaur feeding traces on Deinocheirus (Theropoda:? Ornithomimosauria) remains from the Nemegt Formation (Late Cretaceous), Mongolia. *Cretaceous Research*, 37:186-190.

Binford LR. 1981. Bones: Ancient Men and Modern Myths, Academic Press, New York. 320.

Britt BB. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young University Geology Studies,* 37:1–72.

Brown CM, Tanke DH, Hone DW. 2021. Rare evidence for ‘gnawing-like’ behavior in a small-bodied theropod dinosaur. *PeerJ*, 9:e11557.

Buffetaut E, Suteethorn V. 1989. A sauropod skeleton associated with theropod teeth in the Upper Jurassic of Thailand: remarks on the taphonomic and palaeoecological significance of such associations. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 73:77-83.

Capaldo SD, Blumenschine RJ. 1994. A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones. *American Antiquity,* 59:724-748.

Cardini, 2014. Missing the third dimension in geometric morphometrics: how to assess if 2D images really are a good proxy for 3D structures? *Hystrix, the Italian Journal of Mammalogy*, 25(2):73-81.

Carpenter K. 1998. Evidence of predatory behavior by carnivorous dinosaurs. *Gaia*, 15:135-144.

Carpenter K, Miles C, Ostrom JH, Cloward K. 2005. Redescription of the small maniraptoran theropods *Ornitholestes* and *Coelurus* from the Upper Jurassic Morrison Formation of Wyoming. In Carpenter K, ed. *The Carnivorous Dinosaurs*. Bloomington, Indiana: Indiana University Press. 49-71.

Chure DJ. 1995. A reassessment of the gigantic theropod *Saurophagus maximus* from the Morrison Formation (Upper Jurassic) of Oklahoma, USA. *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*, 103–106.

Chure DJ, Loewen MA. 2020. Cranial anatomy of *Allosaurus jimmadseni*, a new species from the lower part of the Morrison Formation (Upper Jurassic) of Western North America. *PeerJ,* 8:e7803.

Chure DJ, Fiorillo AR, Jacobsen A. 1998. Prey bone utilization by predatory dinosaurs in the Late Jurassic of North America, with comments on prey bone use by dinosaurs throughout the Mesozoic. *Gaia,* 15:227–232.

Chure DJ, Litwin R, Hasiotis ST, Evanoff E, Carpenter K. 2006. The fauna and flora of the Morrison Formation: 2006. *New Mexico Museum of Natural History and Science Bulletin,* 36:233–249.

Cope ED. 1887. The dinosaur genus *Coelurus*. *American Naturalist,* 21:367–369.

Courtenay LA, Maté-González MA, Aramendi J, Yravedra J, González-Aguilera D, Domínguez-Rodrigo M. 2018. Testing accuracy in 2D and 3D geometric morphometric methods for cut mark identification and classification. *PeerJ 6*, e5133:1-24.

Currie PJ, Jacobsen AR. 1995. An azhdarchid pterosaur eaten by a velociraptorine theropod. *Canadian Journal of Earth Sciences*, 32:922–925.

D'Amore DC, Blumenschine RJ. 2009. Komodo monitor (*Varanus komodoensis*) feeding behavior and dental function reflected through tooth marks on bone surfaces, and the application to ziphodont paleobiology. *Paleobiology,* 35:525–552.

DePalma RA, Burnham DA, Martin LD, Rothschild BM, Larson PL. 2013. Physical evidence of predatory behavior in *Tyrannosaurus rex*. *Proceedings of the National Academy of Sciences,* 110:12560-12564.

Drumheller SK, McHugh JB, Kane M, Riedel A, D'Amore DC. 2020. High frequencies of theropod bite marks provide evidence for feeding, scavenging, and possible cannibalism in a stressed Late Jurassic ecosystem. *PLOS ONE,* 15:e0233115.

Erickson GM, Olson KH. 1996. Bite marks attributable to *Tyrannosaurus rex*: preliminary description and implications. *Journal of Vertebrate Paleontology,* 16:175-178.

Farlow JO, Coroian ID, Foster JR. 2010. Giants on the landscape: modelling the abundance of megaherbivorous dinosaurs of the Morrison Formation (Late Jurassic, western USA). *Historical Biology,* 22:403–429.

Fiorillo AR. 1991. Prey bone utilization by predatory dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 88:157-166.

Foster JR. 2003. Paleoecological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain Region, U.S.A. New Mexico Museum of Natural History and Science Bulletin 23:2–100.

Foster JR. 2007. Jurassic West: The Dinosaurs of the Morrison Formation and Their World. Indiana University Press, Bloomington and Indianapolis, USA, pp.

Foster J. 2020. *Jurassic West: The Dinosaurs of the Morrison Formation and Their World*, Second edition. Indiana University Press, Bloomington, Indiana, 560 pp.

Galton PM, Jensen JA. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. *Brigham Young University Geology Studies,* 26:1–12.

Gilmore CW. 1920. Osteology of the carnivorous Dinosauria in the United State National museum: with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum,* 110:1–159.

Hammer WR, Hickerson WJ. 1993. evidence of a scavenging theropod. *Antarctic Journal of the United States*, 28:33.

Happ J. 2008. An analysis of predator-prey behavior in a head-to-head encounter between *Tyrannosaurus rex* and *Triceratops*. In: Larson P, Carpenter K, eds. *Tyrannosaurus rex the Tyrant king*. Indiana: Indiana University Press. 355-370.

Hartman S, Mortimer M, Wahl WR, Lomax DR, Lippincott J, Lovelace DM. 2019. A new paravian dinosaur from the Late Jurassic of North America supports a late acquisition of avian flight. *PeerJ,* 7:e7247.

Henderson DM. 1998. Skull and tooth morphology as indicators of niche partitioning in sympatric Morrison Formation theropods. *Gaia,* 15:219–226.

Hendrickx C, Mateus O, Araújo R. 2015a. The dentition of megalosaurid theropods. *Acta Palaeontologica Polonica,* 60:627–642.

Hendrickx C, Mateus O, Araújo R. 2015b. A proposed terminology of theropod teeth (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology,* 35:e982797.

Hendrickx C, Mateus O, Araújo R, Choiniere J. 2019. The distribution of dental features in non-avian theropod dinosaurs: Taxonomic potential, degree of homoplasy, and major evolutionary trends. *Palaeontologia Electronica,* 22:1–110.

Hendrickx C, Tschopp E, Ezcurra MD. 2020a. Taxonomic identification of isolated theropod teeth: The case of the shed tooth crown associated with *Aerosteon* (Theropoda: Megaraptora) and the dentition of Abelisauridae. *Cretaceous Research,* 108:104312.

Hendrickx C, Stiegler J, Currie PJ, Han F, Xu X, Choiniere JN, Wu X-C. 2020b. Dental anatomy of the apex predator *Sinraptor dongi* (Theropoda: Allosauroidea) from the Late Jurassic of China. *Canadian Journal of Earth Sciences,* 57:1127–1147.

Holtz TR Jnr. 2003. Dinosaur predation: evidence and ecomorphology. In Kelley PH, Kowalewski M, Hansen TA, eds. *Predator—Prey Interactions in the Fossil Record*. New York: Kluwer Press. 325–340

Hone DW, Rauhut OW. 2010. Feeding behaviour and bone utilization by theropod dinosaurs. *Lethaia,* 43:232-244.

Hone DW, Watabe M. 2010. New information on scavenging and selective feeding behaviour of tyrannosaurids. *Acta Palaeontologica Polonica*, 55:627-634.

Hone DWE, Tanke DH. 2015. Pre-and postmortem tyrannosaurid bite marks on the remains of Daspletosaurus (Tyrannosaurinae: Theropoda) from Dinosaur Provincial Park, Alberta, Canada. *PeerJ,* 3:e885.

Hone, DWE, Chure DJ. 2018. Difficulties in assigning trace makers from theropodan bite marks: an example from a young diplodocoid sauropod. *Lethaia,* 51:456–466.

Hone D, Choiniere J, Sullivan C, Xu X, Pittman M, Tan Q. 2010. New evidence for a trophic relationship between the dinosaurs Velociraptor and Protoceratops. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 291:488-492.

Hone DW, Tanke DH, Brown, CM. 2018. Bite marks on the frill of a juvenile Centrosaurus from the Late Cretaceous Dinosaur Provincial Park Formation, Alberta, Canada. *PeerJ*, 6:p.e5748.

Hunt AP, Meyer CA, Lockley MG, Lucas SG. 1994. Archaeology, toothmarks and sauropod dinosaur taphonomy. *Gaia,* 10:225–231.

Jacobsen AR, 1998. Feeding behaviour of carnivorous dinosaurs as determined by tooth marks on dinosaur bones. *Historical Biology*, 13:17-26.

Jennings DS, Hasiotis ST. 2006. Taphonomic analysis of a dinosaur feeding site using geographic information systems (GIS), Morrison Formation, southern Bighorn Basin, Wyoming, USA. *Palaios*, 21:480-492.

Longrich NR, Ryan MJ. 2010. Mammalian tooth marks on the bones of dinosaurs and other Late Cretaceous vertebrates. *Palaeontology,* 53:703-709.

Madsen JH. 1974. A new theropod dinosaur from the Upper Jurassic of Utah. *Journal of Paleontology*, 48:27–31.

Madsen JH. 1976a. A second new theropod dinosaur from the Late Jurassic of east central Utah. *Utah Geology,* 3:51–60.

Madsen JH. 1976b. *Allosaurus fragilis*: A Revised Osteology. *Utah Geological Survey Bulletin,* 109:1–177.

Madsen JH, Welles SP. 2000. *Ceratosaurus* (Dinosauria, Theropoda): a revised osteology. *Utah Geological Survey, Miscellaneous Publication,* 00–2:1–89.

Madsen, JH. 1974. A new theropod dinosaur from the Upper Jurassic of Utah. *Journal of Paleontology,* 48:27–31.

Maidment SCR, Muxworthy A. 2019. A chronostratigraphic framework for the Upper Jurassic Morrison Formation, western U.S.A. *Journal of Sedimentary Research,* 89:1017–1038.

Malafaia E, Mocho P, Escaso F, Ortega F. 2017a. New data on the anatomy of *Torvosaurus* and other remains of megalosauroid (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. *Journal of Iberian Geology,* 43:33–59.

Malafaia E, Escaso F, Mocho P, Serrano-Martínez A, Torices A, Cachão M, Ortega F. 2017b. Analysis of diversity, stratigraphic and geographical distribution of isolated theropod teeth from the Upper Jurassic of the Lusitanian Basin, Portugal. *Journal of Iberian Geology,* 43:257–291.

Mannion PD, Tschopp E, Whitlock JA. 2021. Anatomy and systematics of the diplodocoid *Amphicoelias altus* supports high sauropod dinosaur diversity in the Upper Jurassic Morrison Formation of the USA. *Royal Society Open Science,* 8:210377.

Njau JK, Blumenschine RJ. 2006. A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania. *Journal of Human Evolution,* 50:142-162.

Osborn HF. 1903. *Ornitholestes hermanni*, a new compsognathoid dinosaur from the Upper Jurassic. *Bulletin of the American Museum of Natural History,* 19:459–464.

Ostrom JH. 1980. *Coelurus* and *Ornitholestes*: are they the same? In: Jacobs LL, ed. *Aspects of Vertebrate History.* Flagstaff: Museum of Arizona Press. 245–56.

Pahl CC, Ruedas LA. 2021. Carnosaurs as Apex Scavengers: Agent-based simulations reveal possible vulture analogues in late Jurassic Dinosaurs. *Ecological Modelling*, 458:109706.

Reichel M. 2010. The heterodonty of *Albertosaurus sarcophagus* and *Tyrannosaurus rex*: biomechanical implications inferred through 3-D models. *Canadian Journal of Earth Sciences,* 47:1253–1261.

Robinson RF, Jasinski SE, Sullivan RM. 2015. Theropod Bite Marks on Dinosaur Bones: Indications of a Scavenger, Predator or both?; and their Taphonomic Implications. *Fossil Record* 4: *Bulletin* 67:275-282.

Rogers RR, Krause DW, Rogers KC. 2003. Cannibalism in the Madagascan dinosaur *Majungatholus atopus*. *Nature,* 422:515–518.

Smith DK. 1998. A morphometric analysis of *Allosaurus*. *Journal of Vertebrate Paleontology*, 18:126–142.

Smith JB, Dodson P. 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology,* 23:1–12.

Smith JB, Vann DR, Dodson P. 2005. Dental morphology and variation in theropod dinosaurs: Implications for the taxonomic identification of isolated teeth. *The Anatomical Record*, 285A:699–736.

Snively E, Russell AP. 2007. Functional variation of neck muscles and their relation to feeding style in Tyrannosauridae and other large theropod dinosaurs. *The Anatomical Record*, 290:934-957.

Snively E, Henderson DM, Phillips DS. 2006. Fused and vaulted nasals of tyrannosaurid dinosaurs: implications for cranial strength and feeding mechanics. *Acta Palaeontologica Polonica*, 51:435–454.

Snively E, Cotton JR, Ridgely R, Witmer LM. 2013. Multibody dynamics model of head and neck function in Allosaurus (Dinosauria, Theropoda). *Palaeontologia Electronica*, 16:1-29.

Turner CE, Peterson F. 2004. Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem–a synthesis. Sedimentary Geology 167:309–355.

West DL, Hasiotis ST. 2007. Trace Fossils in a Archaeological Context: Examples from Bison Skeletons, Texas, USA, Trace Fossils. 535-551.

Whitlock J, Trujillo K, Hanik G. 2018. Assemblage-level structure in Morrison Formation dinosaurs, Western Interior, USA. *Geology of the Intermountain West,* 5:9–22.

Figure and Table Captions

Figure 1. Examples of each tooth trace category used for this article. A) drag on pubis of AMNH FARB 675 (currently considered an indeterminate macronarian 3D model of the holotype of "*Apatosaurus*" *minimus,* © American Museum of Natural History); B) bite and drag on a phalanx of AMNH FARB 264 (3D model; an indeterminate neosauropod, © American Museum of Natural History); C) pit on a mid-caudal vertebra of AMNH FARB 5760 (part of the topotype material of *Camarasaurus supremus*); D) puncture on a metapodial of AMNH FARB 30116 (3D model; an indeterminate sauropod © American Museum of Natural History); E) removed on a fibula of AMNH FARB 582 (3D model; a *Camarasaurus* © American Museum of Natural History).

Figure 2. Charts of the bite traces on sauropod bones, in each case divided by the number of analysed bones. A) showing the number and percentage of analysed bite traces divided by their shape (straight or curved) and category (drag, bite and drag, pit, puncture, removed). B) Chart showing the number and percentages of bite traces found on articular ends of bones vs away from the articular ends. C) Chart of bite traces by type. D) Chart showing the number and percentages of bite traces seen in clusters vs isolated bones by bite type.

Figure 3. Charts of the bite traces on sauropod bones, in each case divided by the number of analysed bones. A) Chart showing the numbers and percentages of analysed bite traces found on low economy elements. B) Chart showing the numbers and percentages of analysed bones bearing bite traces found on low economy elements. C) Chart showing the numbers and percentages of analysed bite traces found on high economy elements. D) Chart showing the numbers and percentages of analysed bones bearing bite traces found on high economy elements.

Figure 4. A 3D model of the proximal end of a left fibula of *Camarasaurus* (AMNH FARB 582 © American Museum of Natural History) in posteromedial view, showing a removed part of a bone, presumably from a particularly strong bite (A).

Figure 5. Theropod diversity and largest lateral crowns of theropods from the Kimmeridgian-Tithonian Morrison Formation of North America. A. *Allosaurus* crown (UMNH VP 6105; CH=50 mm) extrapolated to a CH (crown height) of 70 mm, the largest crown probably bore by the

allosaurid *Saurophaganax maximus* (~10 m in body length); B. crown (BYUVP 725 12817; CH=105 mm) of the megalosaurid *Torvosaurus tanneri* (~9 m); C. crown (CM 21703; CH=58 mm) of the allosaurid *Allosaurus* sp. (~7 m); D. crown (ML 1828; CH=75 mm) of the ceratosaurid *Ceratosaurus* sp. (~6 m); E. crown (DMNS 3718, Rmx4; CH=41 mm) of the piatnitzkysaurid *Marshosaurus bicentessimus* (~ 4.5 m); F. crown (TPII 2000-09-29; CH~20 mm) of the tyrannosauroid *Tanycolagreus topwilsoni* (~4 m); G. crown (AMNH FARB 619; CH=6.6 mm) of the maniraptoriform *Ornitholestes hermanni* (2 m); H. crown (WDC-DML-001; CH=6.4 mm) of the troodontid *Hesperornithoides miessleri* (0.9 m).

Figure 6. Premaxilla and premaxillary dentition morphology and effect on the spacing between bite marks in the four apex predators from the Morrison Formation *Ceratosaurus*, *Marshosaurus*, *Torvosaurus* and *Allosaurus* (two specimens). A. Symmetrically duplicated premaxilla of *Ceratosaurus* (UMNH VP 5278), *Marshosaurus* (UMNH VP 7820), *Torvosaurus* (BYUVP 725 4882), and *Allosaurus* (*Allosaurus* specimen I: YPM PU 14554; *Allosaurus* specimen II: UMNH VP 20529) in ventral view; B. In situ or reconstructed premaxillary dentition of *Ceratosaurus*, *Marshosaurus*, *Torvosaurus* and *Allosaurus* in ventral view showing the orientation of the mesial (in red) and distal (in blue) carinae on the crowns; C-E, effect of tooth pattern and biting angle on the spacing between bite marks left by the premaxillary crowns of *Ceratosaurus*, *Marshosaurus*, *Torvosaurus* and *Allosaurus* when the head of the theropod moves C, parallel to the long axis of the skull; D, at an angle of 20 degrees from the long axis of the skull; and E, at an angle of 45 degrees from the long axis of the skull.

Figure 7. Neural spine summit of the dorsal vertebra of *Apatosaurus* sp. (AMNH FARB 550) showing extensive bite traces (in dorsolateral view). This region was unlikely to be the site of a predatory attack.

Figure 8. Scapula of *Camarasaurus supremus* (AMNH FARB 5760 sc-3) showing bite traces that follow the preferred orientation along the distal margin of the bone.

Figure 1

Examples of bite traces on Morrison Formation sauropod elements

Examples of each tooth trace category used for this article. A) drag on pubis of AMNH FARB 675 (currently considered an indeterminate macronarian 3D model of the holotype of "*Apatosaurus*" *minimus,* © American Museum ofNatural History); B) bite and drag on a phalanx of AMNH FARB 264 (3D model; an indeterminate neosauropod, © American Museum ofNatural History); C) pit on a mid-caudal vertebra of AMNH FARB 5760 (part of the topotype material of *Camarasaurus supremus*); D) puncture on a metapodial of AMNH FARB 30116 (3D model; an indeterminate sauropod © American Museum of Natural History); E) removed on a fibula of AMNH FARB 582 (3D model; a *Camarasaurus* © American Museum ofNatural History).

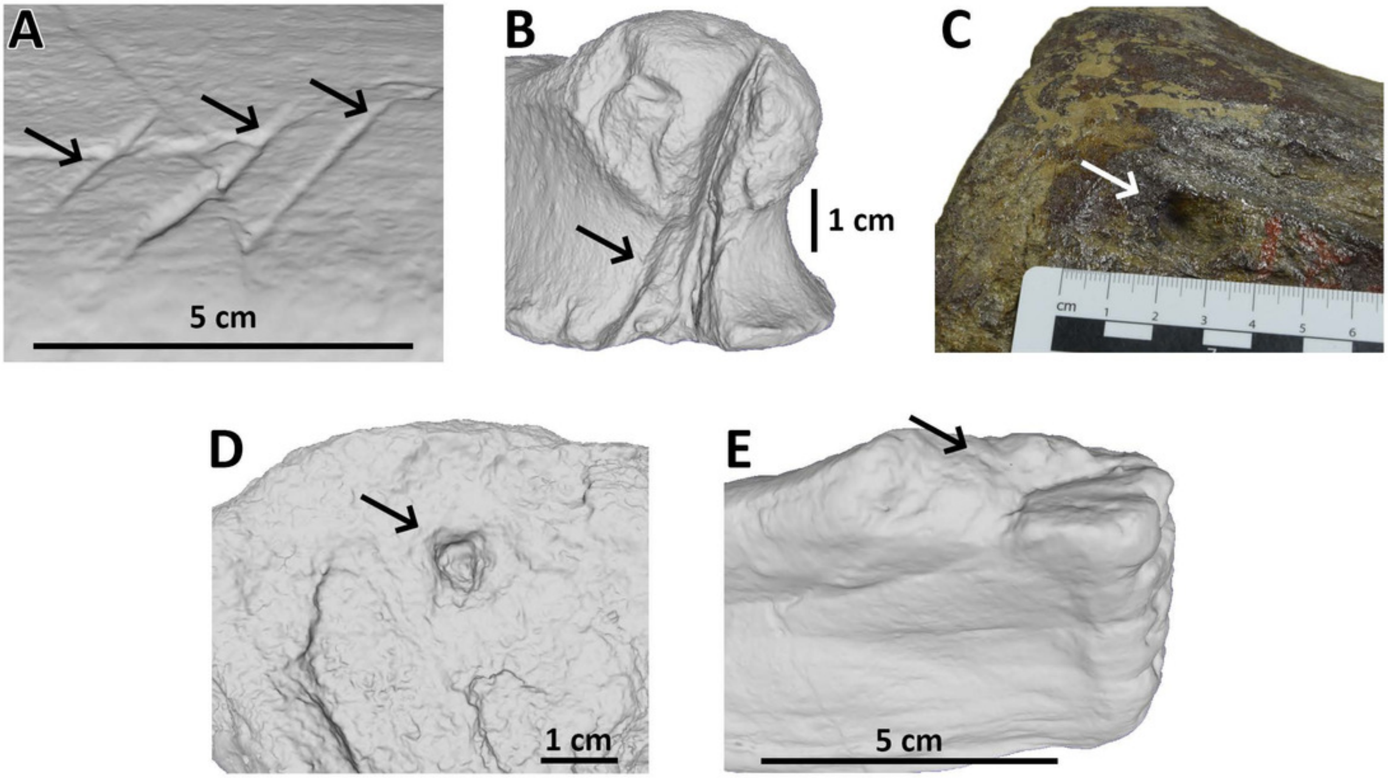

Figure 2

Charts of bite traces broken down by various categories

Charts of the bite traces on sauropod bones, in each case divided by the number of analysed bones. A) showing the number and percentage of analysed bite traces divided by their shape (straight or curved) and category (drag, bite and drag, pit, puncture, removed). B) Chart showing the number and percentages of bite traces found on articular ends of bones vs away from the articular ends. C) Chart of bite traces by type. D) Chart showing the number and percentages of bite traces seen in clusters vs isolated bones by bite type.

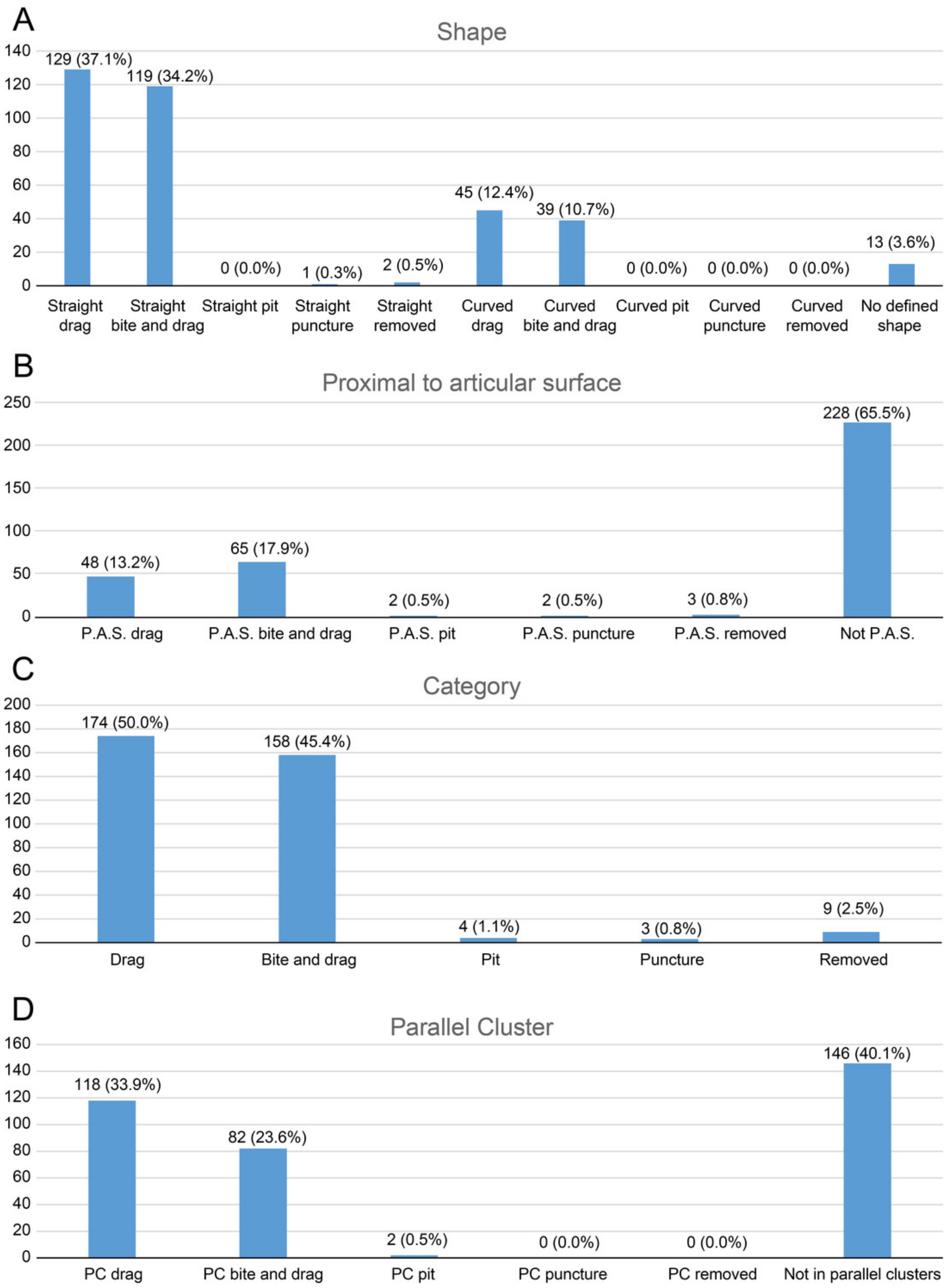
A
Shape
140
120
100
80
60
40
20
0
129 (37.1%)
119 (34.2%)
0 (0.0%)
1 (0.3%)
2 (0.5%)
45 (12.4%)
39 (10.7%)
0 (0.0%)
0 (0.0%)
0 (0.0%)
13 (3.6%)
Straight drag
Straight bite and drag
Straight pit
Straight puncture
Straight removed
Curved drag
Curved bite and drag
Curved pit
Curved puncture
Curved removed
No defined shape
B
Proximal to articular surface
250
200
150
100
50
0
48 (13.2%)
65 (17.9%)
2 (0.5%)
2 (0.5%)
3 (0.8%)
228 (65.5%)
P.A.S. drag
P.A.S. bite and drag
P.A.S. pit
P.A.S. puncture
P.A.S. removed
Not P.A.S.
C
Category
200
180
160
140
120
100
80
60
40
20
0
174 (50.0%)
158 (45.4%)
4 (1.1%)
3 (0.8%)
9 (2.5%)
Drag
Bite and drag
Pit
Puncture
Removed
D
Parallel Cluster
160
140
120
100
80
60
40
20
0
118 (33.9%)
82 (23.6%)
2 (0.5%)
0 (0.0%)
0 (0.0%)
146 (40.1%)
PC drag
PC bite and drag
PC pit
PC puncture
PC removed
Not in parallel clusters

Figure 3

Charts to show distributions of bite traces by anatomical region

Charts of the bite traces on sauropod bones, in each case divided by the number of analysed bones. A) Chart showing the numbers and percentages of analysed bite traces found on low economy elements. B) Chart showing the numbers and percentages of analysed bones bearing bite traces found on low economy elements. C) Chart showing the numbers and percentages of analysed bite traces found on high economy elements. D) Chart showing the numbers and percentages of analysed bones bearing bite traces found on high economy elements.

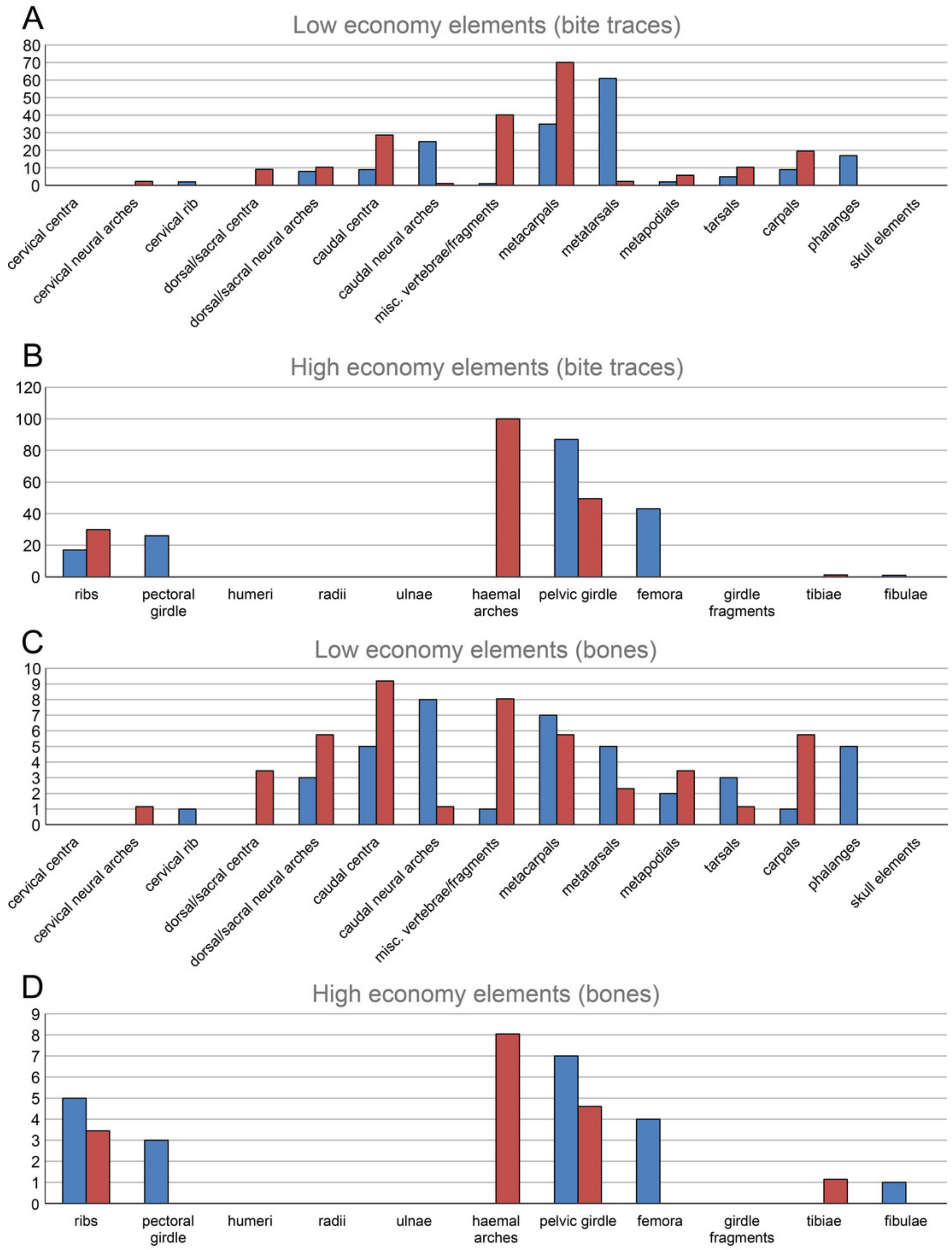
A
Low economy elements (bite traces)
0
10
20
30
40
50
60
70
80
cervical centra
cervical neural arches
cervical rib
dorsal/sacral centra
dorsal/sacral neural arches
caudal centra
caudal neural arches
misc. vertebrae/fragments
metacarpals
metatarsals
metapodials
tarsals
carpals
phalanges
skull elements
B
High economy elements (bite traces)
0
20
40
60
80
100
120
ribs
pectoral girdle
humeri
radii
ulnae
haemal arches
pelvic girdle
femora
girdle fragments
tibiae
fibulae
C
Low economy elements (bones)
0
1
2
3
4
5
6
7
8
9
10
cervical centra
cervical neural arches
cervical rib
dorsal/sacral centra
dorsal/sacral neural arches
caudal centra
caudal neural arches
misc. vertebrae/fragments
metacarpals
metatarsals
metapodials
tarsals
carpals
phalanges
skull elements
D
High economy elements (bones)
0
1
2
3
4
5
6
7
8
9
ribs
pectoral girdle
humeri
radii
ulnae
haemal arches
pelvic girdle
femora
girdle fragments
tibiae
fibulae

Figure 4

Bite trace on a sauropod fibula

A 3D model of the proximal end of a left fibula of *Camarasaurus* (AMNH FARB 582 © American Museum of Natural History) in posteromedial view, showing a removed part of a bone, presumably from a particularly strong bite (A).

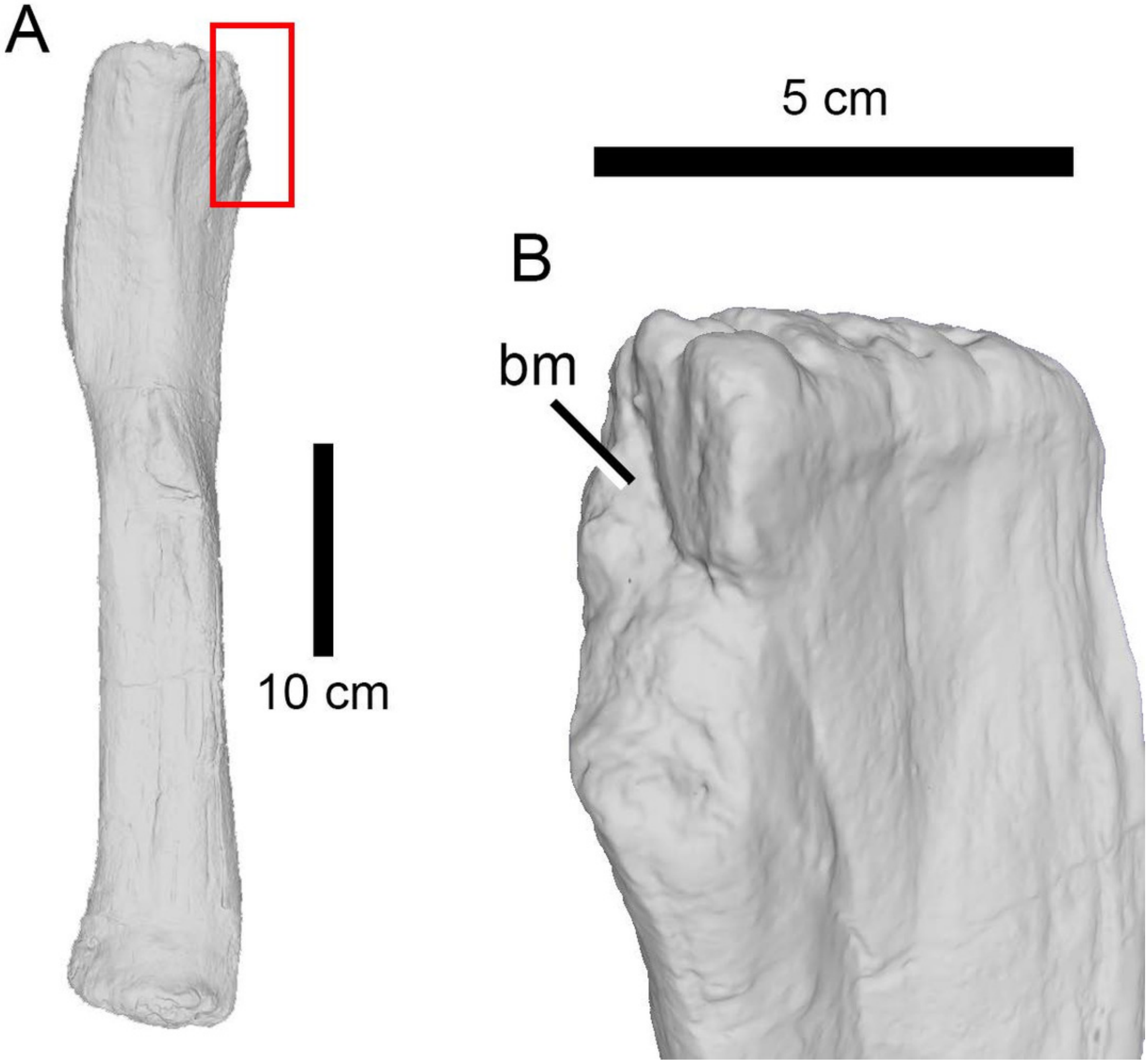

Figure 5

Morrison Formation theropods and their tooth crowns

Theropod diversity and largest lateral crowns of theropods from the Kimmeridgian-Tithonian Morrison Formation of North America. A. *Allosaurus* crown (UMNH VP 6105; CH=50 mm) extrapolated to a CH (crown height) of 70 mm, the largest crown probably bore by the allosaurid *Saurophaganax maximus* (~10 m in body length); B. crown (BYUVP 725 12817; CH=105 mm) of the megalosaurid *Torvosaurus tanneri* (~9 m); C. crown (CM 21703; CH=58 mm) of the allosaurid *Allosaurus* sp. (~7 m); D. crown (ML 1828; CH=75 mm) of the ceratosaurid *Ceratosaurus* sp. (~6 m); E. crown (DMNS 3718, Rmx4; CH=41 mm) of the piatnitzkysaurid *Marshosaurus bicentessimus* (~ 4.5 m); F. crown (TPII 2000-09-29; CH~20 mm) of the tyrannosauroid *Tanycolagreus topwilsoni* (~4 m); G. crown (AMNH FARB 619; CH=6.6 mm) of the maniraptoriform *Ornitholestes hermanni* (2 m); H. crown (WDC-DML-001; CH=6.4 mm) of the troodontid *Hesperornithoides miessleri* (0.9 m).

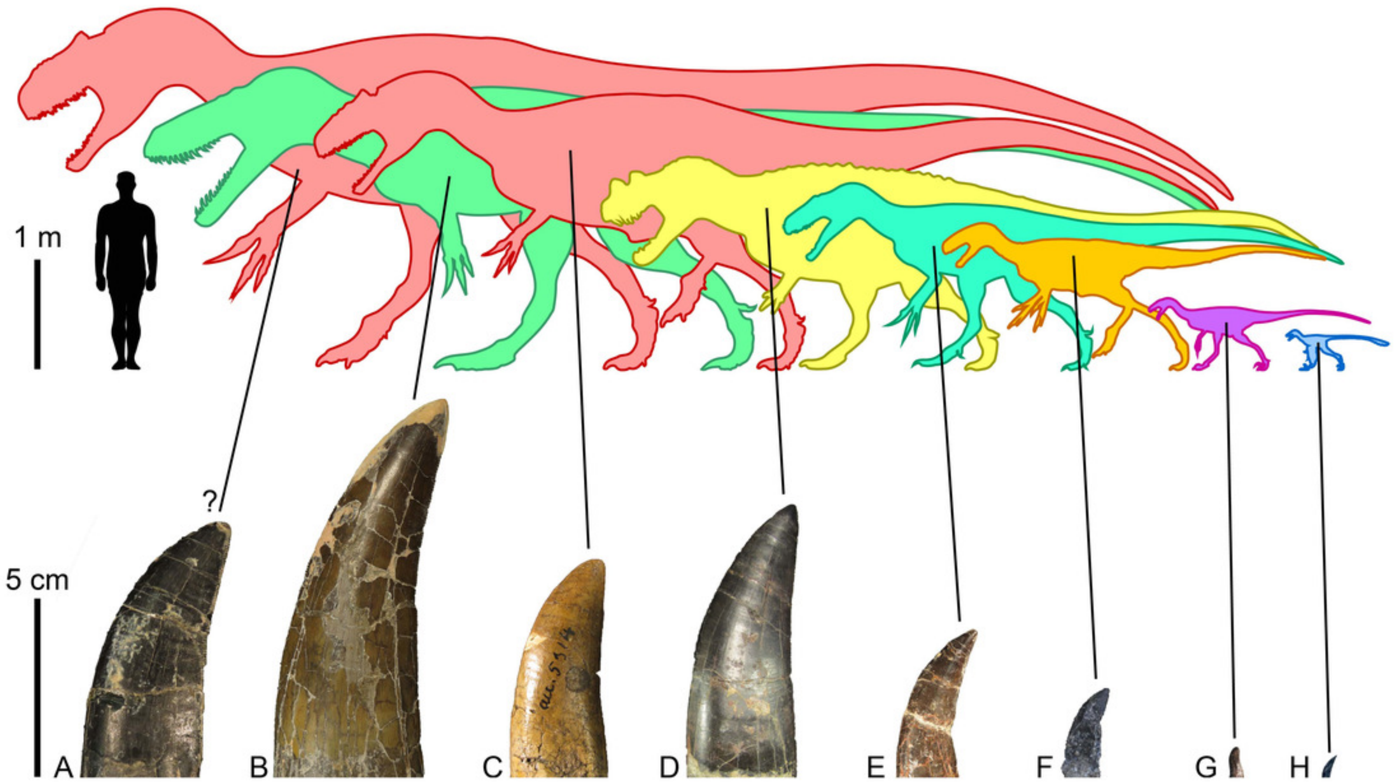
1 m
5 cm
?
A
B
C
D
E
F
G
H

Figure 6

Spacing of theropod teeth and the potential effects on bite traces

Premaxilla and premaxillary dentition morphology and effect on the spacing between bite marks in the four apex predators from the Morrison Formation *Ceratosaurus*, *Marshosaurus*, *Torvosaurus* and *Allosaurus* (two specimens). A. Symmetrically duplicated premaxilla of *Ceratosaurus* (UMNH VP 5278), *Marshosaurus* (UMNH VP 7820), *Torvosaurus* (BYUVP 725 4882), and *Allosaurus* (*Allosaurus* specimen I: YPM PU 14554; *Allosaurus* specimen II: UMNH VP 20529) in ventral view; B. In situ or reconstructed premaxillary dentition of *Ceratosaurus*, *Marshosaurus*, *Torvosaurus* and *Allosaurus* in ventral view showing the orientation of the mesial (in red) and distal (in blue) carinae on the crowns; C-E, effect of tooth pattern and biting angle on the spacing between bite marks left by the premaxillary crowns of *Ceratosaurus*, *Marshosaurus*, *Torvosaurus* and *Allosaurus* when the head of the theropod moves C, parallel to the long axis of the skull; D, at an angle of 20 degrees from the long axis of the skull; and E, at an angle of 45 degrees from the long axis of the skull.

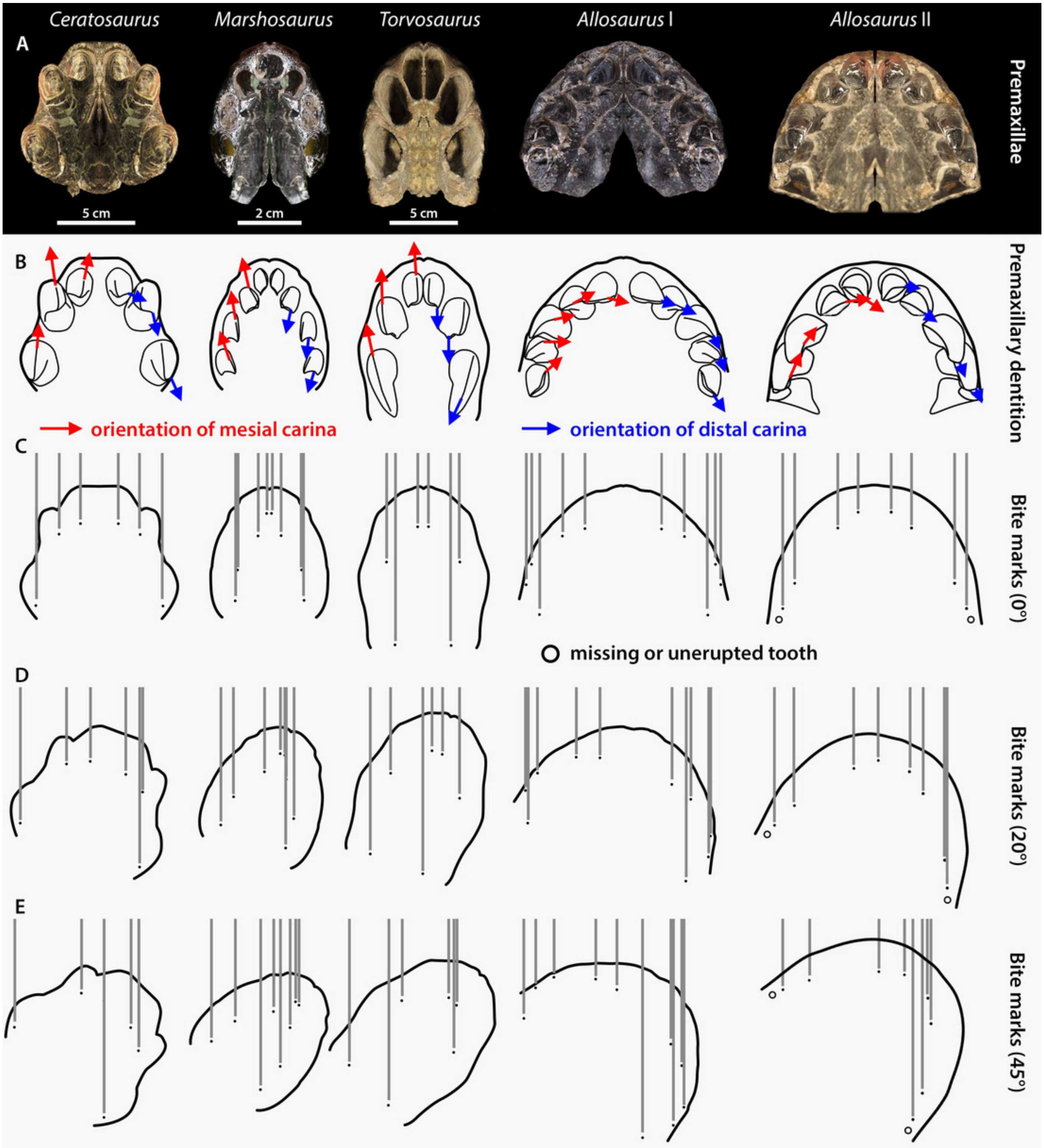
Ceratosaurus
Marshosaurus
Torvosaurus
Allosaurus I
Allosaurus II
A
5 cm
2 cm
5 cm
Premaxillae
B
Premaxillary dentition
orientation of mesial carina
orientation of distal carina
C
Bite marks (0°)
missing or unerupted tooth
D
Bite marks (20°)
E
Bite marks (45°)

Figure 7

Bite traces on a sauropod neural spine

Neural spine summit of the dorsal vertebra of *Apatosaurus* sp. (AMNH FARB 550) showing extensive bite traces (in dorsolateral view). This region was unlikely to be the site of a predatory attack.

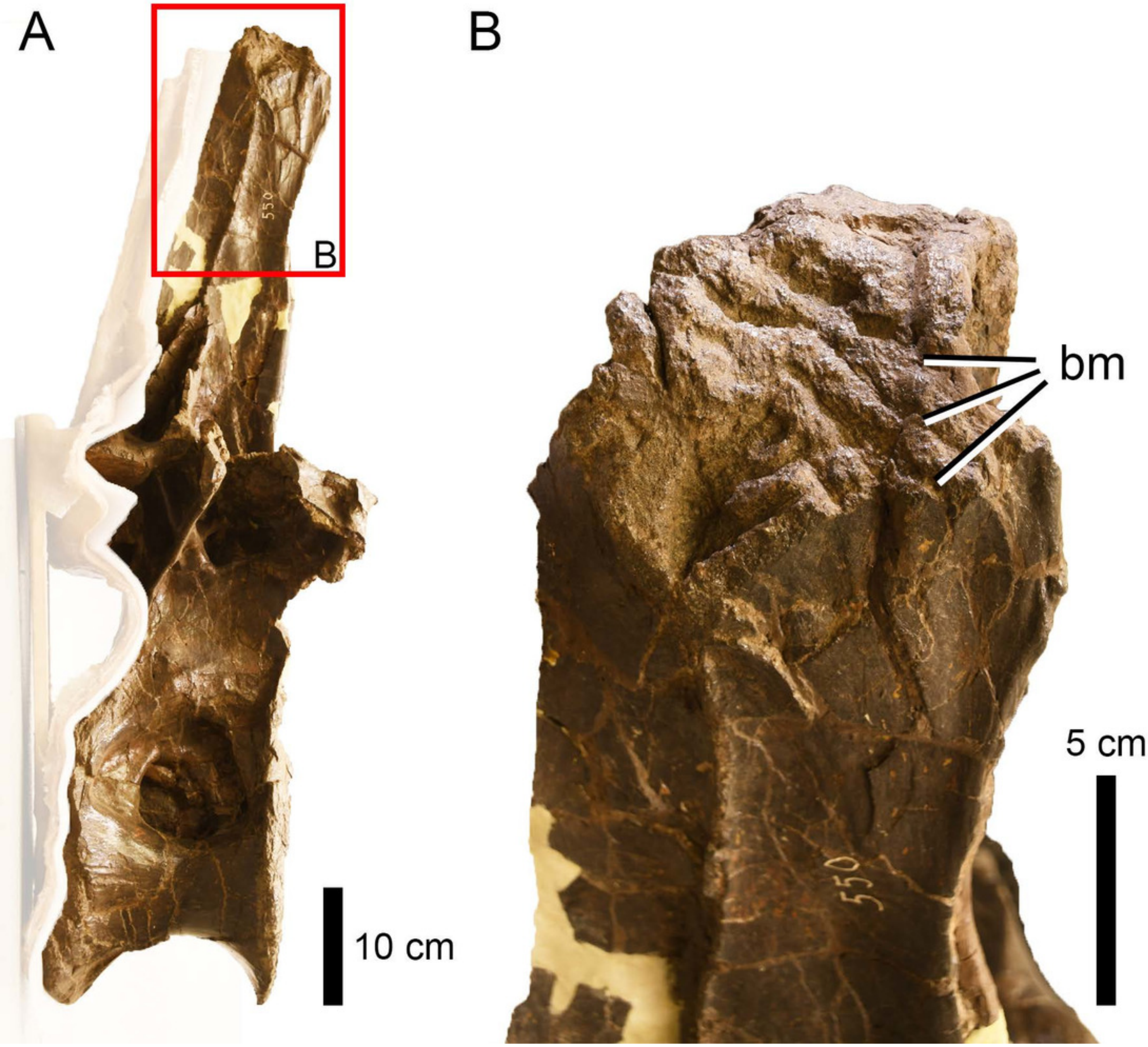

Figure 8

Sauropod scapula showing bite traces

Scapula of *Camarasaurus supremus* (AMNH FARB 5760 sc-3) showing bite traces that follow the preferred orientation along the distal margin of the bone.

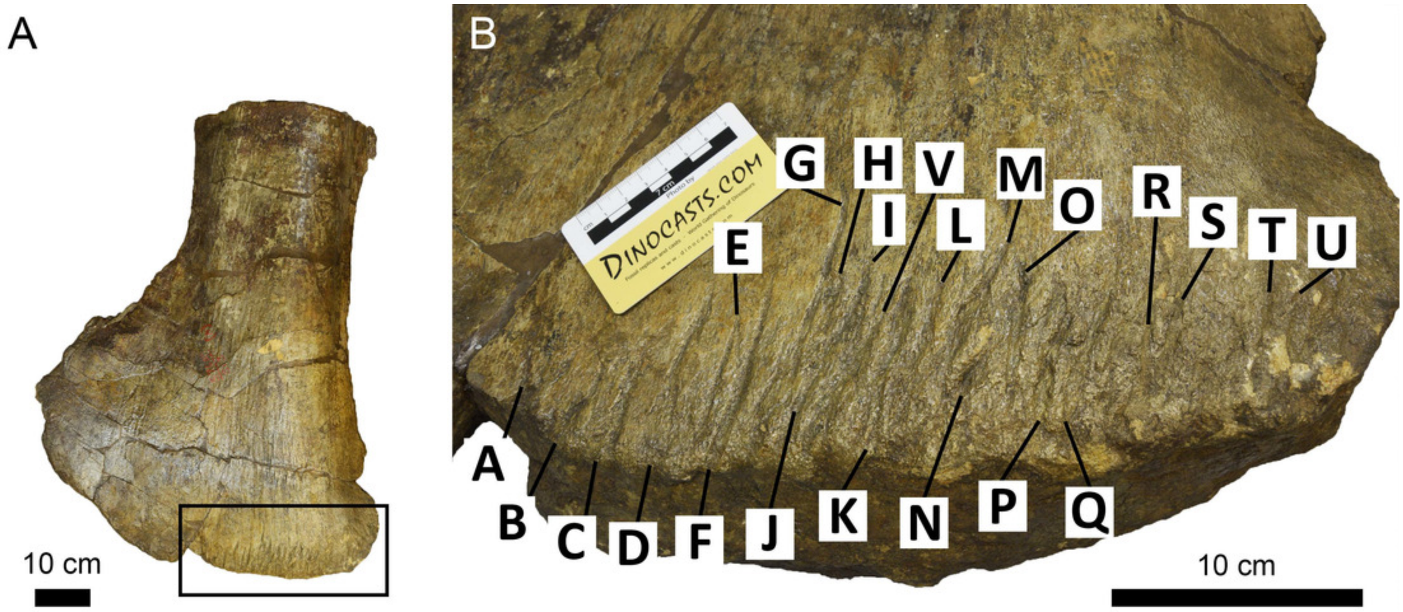

Table 1(on next page)

Taxonomic identity of sauropod specimens bearing bite traces

Number and percentages of tooth traces and sauropod individuals bearing them according to their taxonomy. At the clade-level, seven specimens, three classified as sauropod indet., one as neosauropod indet., and three as eusauropod indet., were referred as indeterminate (indet.). At the family-level, all diplodocoid and macronarian specimens that could not be assigned to a family-level clade are referred as indeterminate (indet.). At the subfamily-level, only diplodocid specimens, either assigned to Diplodocinae, Apatosaurinae, or an indeterminate sub-family level clade of Diplodocidae (indet.), are included. Note that within the analyzed specimens, diplodocids and diplodocoids are more represented than camarasaurids and macronarians, respetively. These may reflect various collection biases as well as potential genuine differences in population structure, but this should be considered when comparing the numbers of bite traces between various taxa here.

Table 1. Number and percentages of tooth traces and sauropod individuals bearing them according to their taxonomy. At the clade-level, seven specimens, three classified as sauropod indet., one as neosauropod indet., and three as eusauropod indet., were referred as indeterminate (indet.). At the family-level, all diplodocoid and macronarian specimens that could not be assigned to a family-level clade are referred as indeterminate (indet.). At the subfamily-level, only diplodocid specimens, either assigned to Diplodocinae, Apatosaurinae, or an indeterminate sub-family level clade of Diplodocidae (indet.), are included. Note that within the analyzed specimens, diplodocids and diplodocoids are more represented than camarasaurids and macronarians, respetively. These may reflect various collection biases as well as potential genuine differences in population structure, but this should be considered when comparing the numbers of bite traces between various taxa here.

CLADE	N° TOOTH TRACES	% TOOTH TRACES	N° INDIVIDUALS	% INDIVIDUALS
Clade-level				
Diplodocoidea	194	55.7	19	51.4%
Macronaria	82	23.6	11	29.7%
indet.	72	20.7	7	18.9%
Family-level				
Camarasauridae	65	18.7	9	24.3%

Dicraeosauridae	62	17.8	1	2.7%
Diplodocidae	96	27.6	13	35.1%
indet.	125	35.9	14	37.8%
Subfamily-level				
Apatosaurinae	75	78.1	6	46.2%
Diplodocinae	20	20.8	6	46.2%
Diplodocidae indet.	1	1	1	7.7%