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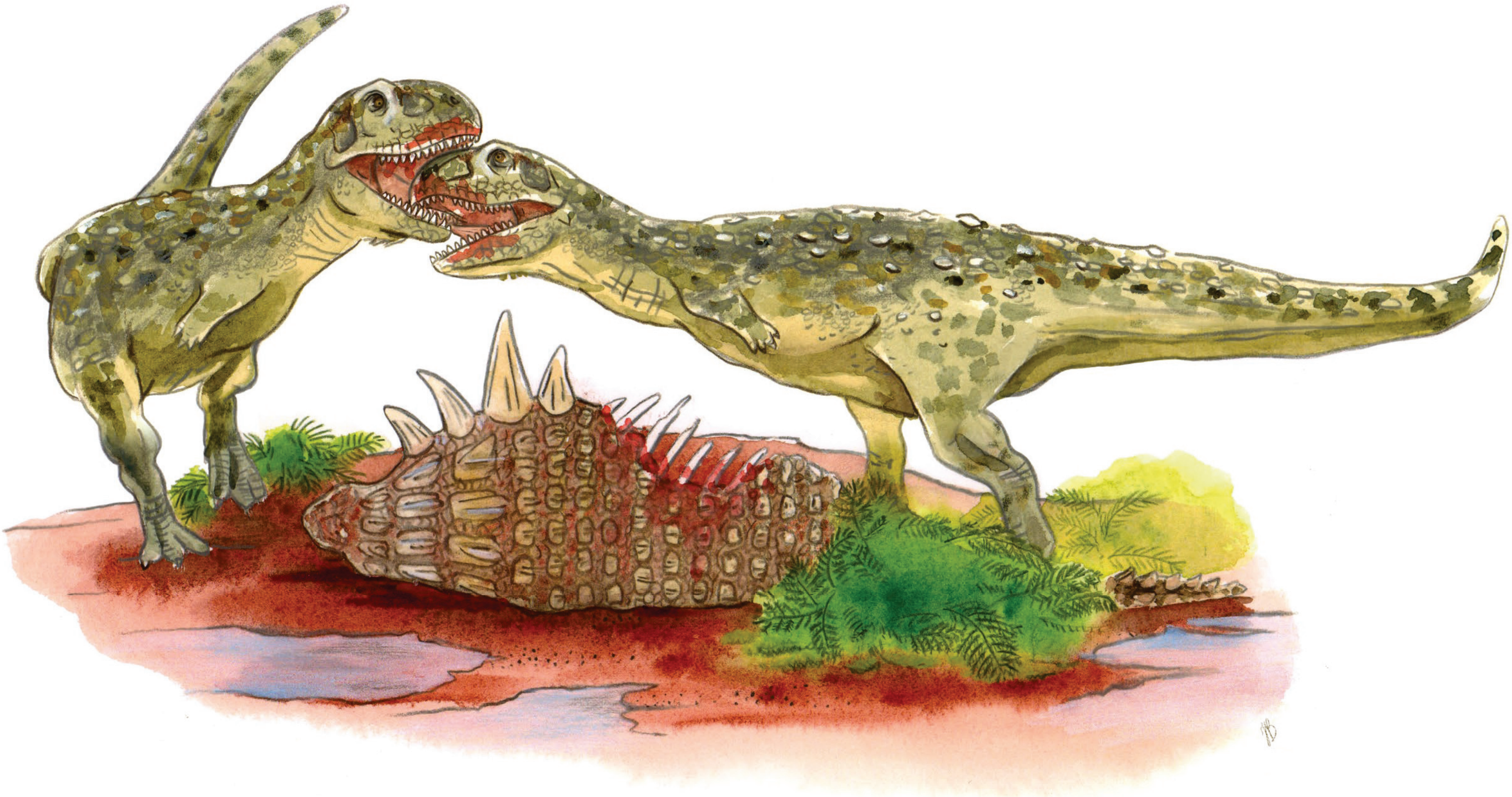

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Unusual Abelisauridae tooth mark on an Abelisauridae tooth from the Upper Cretaceous of Cruzy (Hérault, France): implications for feeding behaviours

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ABSTRACT

Bite marks in the fossil record provide information on trophic, behavioural and taphonomic interactions. Here we describe a bevelled bite mark with parallel striations on a denticulate tooth tentatively assigned to Abelisauridae indet. from the Upper Cretaceous (Campanian-Maastrichtian) deposit of Massecaps (municipality of Cruzy, Hérault), in southern France. Comparison of the bite mark with the different morphologies of serrated teeth found on the same deposit enables us to attribute it to the tooth morphotype that we tentatively refer to Abelisauridae indet. Although rarely described in the literature, similar confamilial bite marks have already been observed on Tyrannosauridae Osborn, 1906 teeth. The position and orientation of the bite mark rule out the possibility that it was made by one individual on another, during agonistic behaviour such as head-biting. The relatively large number (n = 44) of rootless teeth attributed to Abelisauridae indet. found at Massecaps locality, the scarcity of other Abelisauridae Bonaparte & Novas, 1985 skeletal remains, and the presence of non-theropod dinosaur skeletal remains marked by serrated teeth strongly suggest that these teeth were lost during the consumption of a carcasses and that tooth M5246 was marked on that occasion. The description of this previously undocumented mark among Abelisauridae expands our knowledge of large theropods feeding behaviour from the Campanian-Maastrichtian period.

KEY WORDS
Mesozoic,
paleoecology,
theropod,
taphonomy,
feeding behaviour.

RÉSUMÉ

Marque inhabituelle de dent d'Abelisauridae sur une dent d'Abelisauridae provenant des sédiments du Crétacé supérieur de Cruzy (Hérault, France) : implications pour les comportements alimentaires.

Les marques de morsure dans les archives fossiles fournissent des informations sur les interactions trophiques, comportementales et taphonomiques. Nous décrivons ici une marque de morsure biseautée avec des stries parallèles sur une dent crénelée provisoirement attribuée à un Abelisauridae indet. provenant du gisement du Crétacé supérieur (Campanien-Maastrichtien) de Massecaps (commune de Cruzy, Hérault), dans le sud de la France. La comparaison de la marque de morsure avec les différentes morphologies de dents crénelées trouvées sur le même gisement nous permet de l'attribuer au morphotype dentaire que nous attribuons provisoirement à un Abelisauridae indet. Bien que rarement figurées dans la littérature, des marques de morsures confamiliales similaires ont déjà été observées sur des dents de Tyrannosauridae Osborn, 1906. La position et l'orientation de la marque de morsure excluent la possibilité qu'elle ait été produite par un individu sur un autre, lors d'un comportement agonistique tel que les morsures faciales. Le nombre relativement important (n = 44) de dents sans racine attribuées à cet Abelisauridae indet. trouvées sur le site de Massecaps, la rareté d'autres restes squelettiques d'Abelisauridae Bonaparte & Novas, 1985, et la présence de restes squelettiques de dinosaures non théropodes marqués par des dents crénelées suggèrent fortement que ces dents ont été perdues lors de la consommation de carcasses et que la dent M5246 a été marquée à cette occasion. La description de cette marque jusqu'alors inconnue chez les Abelisauridae élargit nos connaissances sur le comportement alimentaire des grands théropodes de la période Campanien-Maastrichtien.

MOTS CLÉS
Mésozoïque,
paléoécologie,
théropode,
taphonomie,
comportement alimentaire.

INTRODUCTION

Bite marks, particularly on bones, are common in the fossil record and provide direct evidence of interactions between different organisms within ancient ecosystems (e.g., Everhart & Ewell 2006; Njau & Blumenschine 2006; Roberts *et al.* 2007; Pobiner 2008; Longrich & Ryan 2010; Vullo 2011; Collareta *et al.* 2017; Gônet *et al.* 2019; Drumheller *et al.* 2020; Perez *et al.* 2021; Lei *et al.* 2023). Their abundance can be attributed to two main factors. First, bones are closely associated with various organic tissues, such as muscle tissue, which is a valuable food resource for many carnivorous organisms. Bones themselves may be consumed by various organisms (e.g., Hutson *et al.* 2013; Gambín *et al.* 2017). Furthermore, they are composed of a mineralized part, apatite, which is resistant to physico-chemical alteration processes, favouring their preservation over time and explaining their abundance in the fossil record. Accordingly, they are particularly well suited to receiving and preserving bite marks in the fossil record, back to hundreds of millions of years ago (e.g., Lebedev *et al.* 2009). Bite marks left on bones by carnivores result from the application of force where the teeth (or the jawbone or beak in the case of toothless vertebrates) come into contact with the bone (Lei *et al.* 2023).

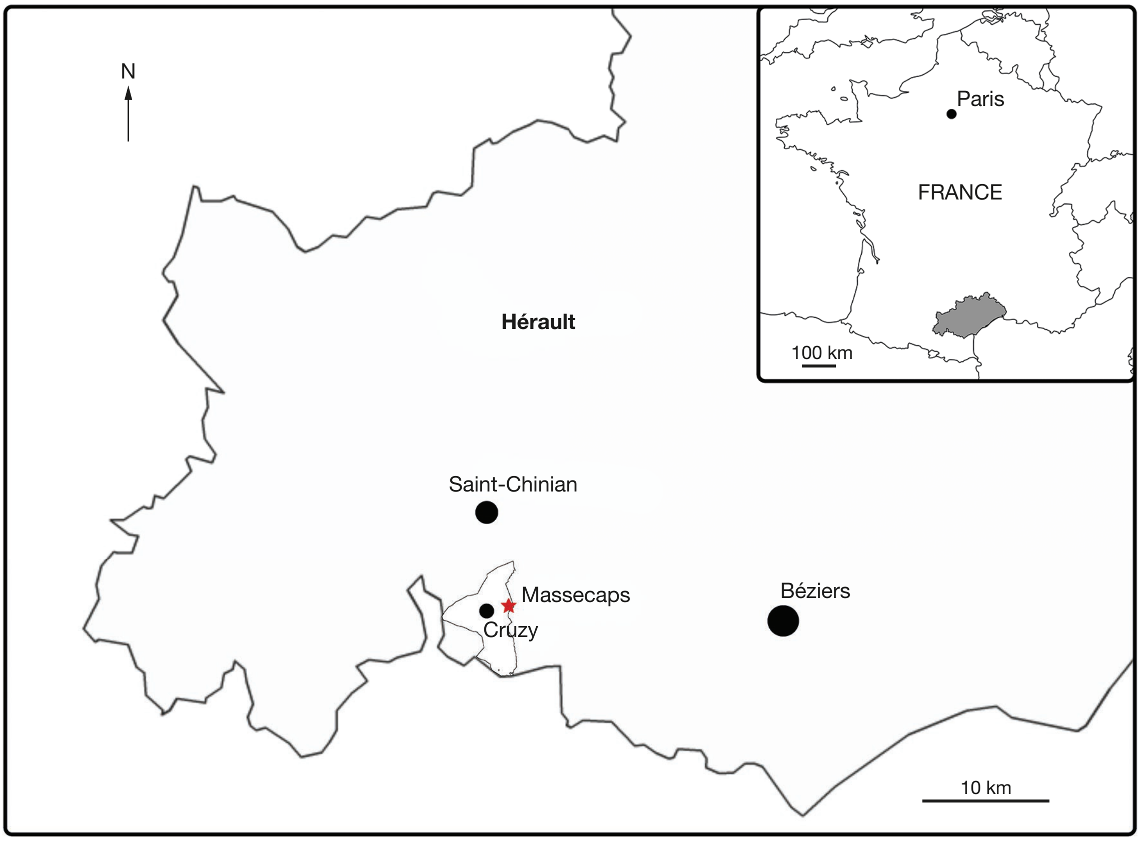


Fig. 1. — Geographical map showing the location Massecaps site (Campanian-Maastrichtian) in the municipality of Cruzy, Hérault, France.

Occurrences of theropod bite marks on fossilized vertebrate remains, although less frequent than those left by other contemporary groups (e.g., crocodiles; Hone & Rauhut 2010), are nevertheless well documented in the fossil record (e.g., Erickson & Olson 1996; Robinson *et al.* 2015; Hone & Tanke 2015; Hone & Chure 2018; Drumheller *et al.* 2020; Brown *et al.* 2021; Lei *et al.* 2023). These bite marks provide information about the trophic interactions and on their ecology, in particular by specifying feeding behaviour (e.g., Fiorillo 1991; Jacobsen 1998; Hone & Rauhut 2010; Paik *et al.* 2011; Robinson *et al.* 2015; Gônet *et al.* 2019; Brown *et al.* 2021).

Theropod bite marks on fossil remains identified as theropods are comparatively rarer (Jacobsen 1995, 1998; Bell & Currie 2010; Drumheller *et al.* 2020). They have sometimes been attributed to cannibalistic behaviour (Rogers *et al.* 2003; Longrich *et al.* 2010; Drumheller *et al.* 2020; Dalman & Lucas 2021), but also to intraspecific agonistic interactions, which are inferred from healed bite marks, mainly on the jawbones (Tanke & Currie 1998; Peterson *et al.* 2009; Brown *et al.* 2022). Abler (1992) mentions a Tyrannosauridae Osborn, 1906 tooth bearing a striated mark on the enamel, which they attribute to a Tyrannosauridae bite mark. However, this attribution is only mentioned and is neither discussed on the basis of its morphological description nor on the basis of the associated paleontological context. Jacobsen (1995) reports five teeth of Tyrannosauridae bearing bite marks with serrations attributed to Tyrannosauridae for four of them (TMP1990.082.0003 – fig. pD54; TMP1990.050.0111 – fig. pD52; TMP1989.050.0140 – fig. pD49; TMP1988.050.0145 – fig. pD45; TMP1988.050.0146 not figured). To our knowledge, these are the only references in the literature to theropod teeth bearing theropod bite marks. Although this type of mark seems uncommon in the fossil record, we think that it is mainly poorly documented and rarely featured in literature. Indeed, for example, 18 unreported specimens of tyrannosaur teeth from the Dinosaur Park Formation, housed in the Royal Tyrrell Museum collections, bear striations marks from other tyrannosaurid teeth (TMP2001.012.0193; TMP2000.012.0078; TMP1998.036.0160; TMP1979.011.0158; TMP2014.012.0052; TMP1997.012.0004; TMP1993.036.0056; TMP1995.012.0009; TMP2016.012.0062; TMP1992.036.1024; TMP2000.012.0080; TMP1992.036.0283; TMP1992.036.1065; TMP1997.012.0222; TMP1992.036.0078; TMP1996.012.0377; TMP1994.012.0299; TMP1997.012.0203; Caleb M. Brown pers. comm.). Therefore, despite the relatively well-documented head-biting behaviour, theropod tooth marks on theropod teeth appear underreported and seldom illustrated in the literature.

In this study, we describe a tooth that we tentatively attribute to an indeterminate Abelisauridae Bonaparte & Novas, 1985, which bears a bevelled and striated mark. We compare the striation spacing to the three morphotypes of denticulate teeth known from the same deposit. Based on these observations

Table 1. — Denticle length measurements for the 44 teeth attributed to Abelisauridae indet. found at the Massecaps locality. Total crown length is also reported (when possible) for each tooth. **n.a.**, means not applicable. For comparison, the width of the seven consecutive grooves visible on the mark worn by tooth M5246 was measured. Specimens housed in the Muséum of Cruzy by the Association culturelle archéologique et paléontologique.

Abelisauridae indet. tooth specimen (n = 44)	Length of 10 consecutive denticles (mm)		
	Mesial Carina-Mid Crown	Distal Carina-Mid Crown	Total crown length (mm)
M6	3.7	4.2	37
M7	3.7	4.1	46
M9	3.7	4	39
M11	3.1	3.5	33
M12	n.a.	n.a.	n.a.
M13	3.2	3.8	25
M14	3.1	3.7	32
M15	n.a.	3.4	36
M16	3.4	3.9	27
M17	n.a.	3.5	17
M147	n.a.	n.a.	n.a.
M213	2.8	3.4	37
M237	3.8	4.1	49
M257	n.a.	n.a.	n.a.
M468	n.a.	n.a.	n.a.
M519	n.a.	n.a.	n.a.
M674	2.9	3.5	38
M703	3.1	3.8	n.a.
M808	n.a.	n.a.	n.a.
M1010-3	3.1	3.9	43
M1103	n.a.	4.6	33
M1129	n.a.	n.a.	n.a.
M1174	3.6	4.3	39
M1203	3.7	4.0	34
M1482	n.a.	4.1	52
M1439 (Figs 4; 5)	4.0	4.4	47
M1509	n.a.	4.3	54
M1573	3.6	3.8	n.a.
M1778 (Fig. 5)	4.2	4.5	45
M1817	n.a.	n.a.	n.a.
M1854	n.a.	n.a.	n.a.
M1921	3.6	4.0	40
M1965	2.9	3.2	24
M2154	n.a.	3.5	28
M2402	3.2	3.7	27
M2600	3.8	n.a.	39
M3570	n.a.	n.a.	50
M4070	3.3	4.0	35
M4334	n.a.	3.5	24
M4803	3.3	4.0	n.a.
M5065-2	n.a.	4.2	55
M5246 (Figs 2; 3)	2.9	n.a.	n.a.
M5262	n.a.	4.0	n.a.
M5289	n.a.	n.a.	n.a.
Min	2.8	3.2	17
Max	4.2	4.6	55
Mean	3.4	3.9	t test
SD	0.4	0.4	p-value
Mean for the length of one denticule (mm)	0.3	0.4	0.0001845
M5246			
Width of 7 consecutives grooves (mm)			3.0
Mean for the width of one groove (mm)			0.4

and comparisons, we formulate a hypothesis explaining the formation of this mark, which we discuss in the context of agonistic interactions, cannibalism (or confamilial feeding) and feeding behaviour documented in non-avian theropods.

GEOGRAPHICAL, GEOLOGICAL AND FAUNAL SETTING

The paleontological locality of Massecaps is located in the municipality of Cruzy, Hérault, located to the west of Béziers and to the south of Saint-Chinian, in southern France (Fig. 1). The locality of Massecaps was discovered in 1996 in an abandoned vineyard to the east of the town of Cruzy (Buffetaut *et al.* 1999). It contains an accumulation of vertebrate fossil remains in sedimentary deposits dating from the Campanian-Maastrichtian period (Buffetaut *et al.* 1999). The sediments correspond to conglomerates, sands and clays, deposited during brief floods of a braided fluvial system, under a tropical climate alternating dry and wet seasons (Smektala *et al.* 2014). The most common remains on the site are, by far, the ones from the Bothremydidae Baur, 1891 *Foxemys mechinorum* Tong, Buffetaut & Claude, 1998. Some rare carapaces are articulated or in loose connection but the vast majority of the fossil remains found in Massecaps is disarticulated.

This site has yielded numerous fossilized remains representing a diverse fauna. Mollusks are represented by bivalves (possible Unionidae Rafinesque, 1820) and gastropods. Osteichthyans are represented by lepisosteids and mawsoniids (e.g., *Axelrodichthys megadromos* Cavin, Valentin & Garcia, 2016). Amphibians are represented by the albanerpetontids and discoglossids; Squamata Oppel, 1811 is also present (Buffetaut *et al.* 1999; Cavin *et al.* 2005, 2016, 2020) and notably represented by varanoids (recently referred to a freshwater mosasaur by Cavin *et al.* 2020). Chelonians are represented by the bothremydid *Foxemys mechinorum* Tong, Gaffney, & Buffetaut, 1998, the dortokids *Dortoka vasconica* Lapparent de Broin & Murelaga, 1996 and an helochelydrid identified as *Solemys* sp. (Buffetaut *et al.* 1999; Gaffney *et al.* 2006; Tong *et al.* 2022). Crocodylomorphs are represented by the allodaposuchid *Allodaposuchus precedens* Nopcsa, 1928, the hylaeochampsid *Acynodon iberoccitanicus* Buscalioni, Ortega & Vasse, 1997 (Martin & Buffetaut 2005; Martin 2007, 2010; Martin *et al.* 2016). Remains previously referred or potentially referred as *Ischyrochampsa* Vasse, 1995 (Buffetaut *et al.* 1999; Martin & Buffetaut 2005) have been reassigned to Allodaposuchidae Narváez, Brochu, Escaso, Pérez-García & Ortega, 2015 (cf. Martin *et al.* 2016). Pterosaurs are represented by an indeterminate azhdarchid (Buffetaut 2008). Remains of the zhelestid mammal *Labes garimondi* Pol *et al.*, 1992 have also been found in Massecaps (Martin *et al.* 2015).

Dinosaurs are represented by the rhabdodontid *Rhabdodon priscus* Matheron, 1869. Nonetheless, the type locality of *Obelignathus septimanicus* (Buffetaut & Le Loeuff, 1991) is situated in Montouliers, less than 10 km from Massecaps and the lack of appendicular diagnosis makes the two species undistinguishable from one to another on the postcranial elements (Chanthasit 2010). Dinosaurs are also represented by an indeterminate nodosaurid and an indeterminate titanosaur (Buffetaut *et al.* 1999; Buffetaut 2005; Chanthasit 2010; Klein *et al.* 2012; Díaz *et al.* 2013; Csiki-Sava *et al.* 2015). Theropods are represented by an indeterminate abelisaurid, an

Fig. 2. — Tooth of Abelisauridae indet., specimen M5246 from the locality of Massecaps in labial (**A**), mesial (**B**), distal (**C**), lingual (**D**), apical (**E**) and basal (**F**) views; **G**, enlarged view of the mark visible on the basal part of the labial surface. Scale bars: 10 mm. Photos from Lilian Cazes (CNRS/MNHN).

indeterminate dromaeosaurid (Buffetaut *et al.* 1999; Chanthasit & Buffetaut 2009) and the Enantiornithes Walker, 1981 *Martinavis cruzyensis* Walker, Buffetaut & Dyke, 2007 (Buffetaut 1998; 2005; Buffetaut *et al.* 1999; 2023; Walker *et al.* 2007; Chanthasit & Buffetaut 2009; Tortosa *et al.* 2014).

MATERIAL AND METHODS

Institutional abbreviations

ACAP Association culturelle archéologique et paléontologique, Cruzy; collection numbers Mxxxx correspond to specimens coming from the locality of Massecaps. The collection numbers cited in the results section comply with the editorial standards recommended by Chester *et al.* (2019) for semantic enhancement of specimen data in taxonomy literature.
CR2P Centre de Recherche en Paléontologie – Paris (MNHN, CNRS, SU);
MNHN Muséum national d'Histoire naturelle;
MHNAix.PV Muséum d'Histoire naturelle d'Aix-en-Provence;
TMP Royal Tyrrell Museum, Palaeontology collection.

Fossil material

The tooth that bears the mark is an incomplete theropod tooth (M5246) that we tentatively assigned to Abelisauridae indet. (see hereunder; Figs 2, 3). As a complement, we also describe and figure a complete theropod tooth (M1439) that we also attribute to Abelisauridae indet. (see hereunder; Fig. 4). We define this tooth to be the reference specimen. We also observed and figured five teeth of the three known morphotaxa with serrated teeth found at this site: one Ziphosuchia indet. tooth (M5085), two Dromaeosauridae indet. teeth (M561 and M324) and two Abelisauridae indet. teeth (M1439 and M1778) in order to measure the length of their denticles and compare them with the width of the striations observed on the bite mark (Fig. 5). Finally, we observed all theropod teeth that we tentatively assigned to Abelisauridae indet. found at this site (n = 44; Table 1). All this material is hosted at the Musée de Cruzy administered by the ACAP and is available to researchers upon request.

Preparation of theropod tooth M5246

The theropod tooth (M5246) was prepared by one of the authors (DB). It was cleaned of its clay gangue with use of soft brush and water only, ensuring that the surface of the fossil was not altered during the preparation process. This particular care taken during the preparation of the fossil guarantees the authenticity of the mark observed on the surface of the tooth.

Terminology used

The description of the theropod tooth follows the terminology published by Hendrickx *et al.* (2015) for theropod teeth. We use the term "denticles drag marks" introduced by Rogers *et al.* (2003, 2007) to characterize a mark due to the sliding of the denticles of a serrated tooth. We propose and define the new term – to our knowledge non-existent in the literature – "bevelled mark" to characterize the impact of a carina of a tooth on a rigid surface during biting, resulting in a mark defined by two faces well demarcated by a bevel.

Images and measurements

Observations were made using a Euromex EMZ-5TR binocular loupe and Euromex Iluminator EK-1 adjustable lights to enhance contrast. All photographs were taken by professional photographer Lilian Cazes at CR2P. We also acquired images using reflectance transformation imaging (RTI) technique in order to better observe the low relief of this bite mark (Hammer *et al.* 2002; Fig. 3).

To identify the potential taxa responsible for the bite mark, we measured the length of denticles of five denticulate teeth from the locality of Massecaps (crocodilian tooth M5085; Abelisauridae indet. teeth M1439 and M1778 and Dromaeosauridae indet. teeth M324 and M561) using a scale graduated to a tenth of a millimetre under a binocular loupe (Fig. 5).

Additionally, to determine the variability of denticles length for the morphotype identified as Abelisauridae indet. (see Discussion) as a function of overall tooth size and mesial or distal carina, we measured the length of ten successive denticles (when these were preserved) at mid-crown height on the mesial and distal carina for each tooth belonging to the morphotype identified as Abelisauridae indet. (n = 44; Table 1). Measurements were also taken using a scale graduated to a tenth of a millimetre under a binocular loupe.

Statistical test

We tested the normality of the two series of measurements of the length of the denticles (mesial and distal carinae) using a Shapiro test. We then tested for equality of variance using a Levene test. Since normality and homoscedasticity of the denticle length measurements are validated, the parametric t-test was used to compare mean values between the mesial and the distal carinae. Statistical tests were carried out using the statistical software R 4.4.3. The graphical representation (Fig. 6) of the average length of 10 denticles as a function of the corresponding total crown height, as well as the associated linear regression models, were also carried out using R 4.4.3 software. The level of statistical significance was set at p-value < 0.05.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
CERATOSAURIA Marsh, 1884
Superfamily Abelisauroidea Bonaparte, 1991
Family Abelisauridae Bonaparte & Novas, 1985

Abelisauridae indet.

Material examined. — **France** • 44 (fossil teeth); Hérault, Cruzy, Massecaps; 43°21'37.56"N, 2°57'17.46"E; "Valdo-Fuvélien", "Grès à reptiles" Formation; Campanian-Maastrichtian; 118 m a.s.l; ACAP leg; M6, M7, M9, M11, M12, M13, M14, M15, M16, M17, M213, M237, M257, M468, M519, M674, M703, M808, M1010-3, M147, M1103, M1129, M1174, M1203, M1439 (reference specimen, Fig. 4), M1482, M1509, M1573, M1778, M1817, M1854, M1921, M1965, M2154, M2402, M2600, M3570, M4070, M4334, M4803, M5065-2, M5246 (Figs 2, 3), M5262, M5289.

Locality. — Massecaps (43°21'37.56"N, 2°57'17.46"E); 1.3 km east of Cruzy, Hérault, France.

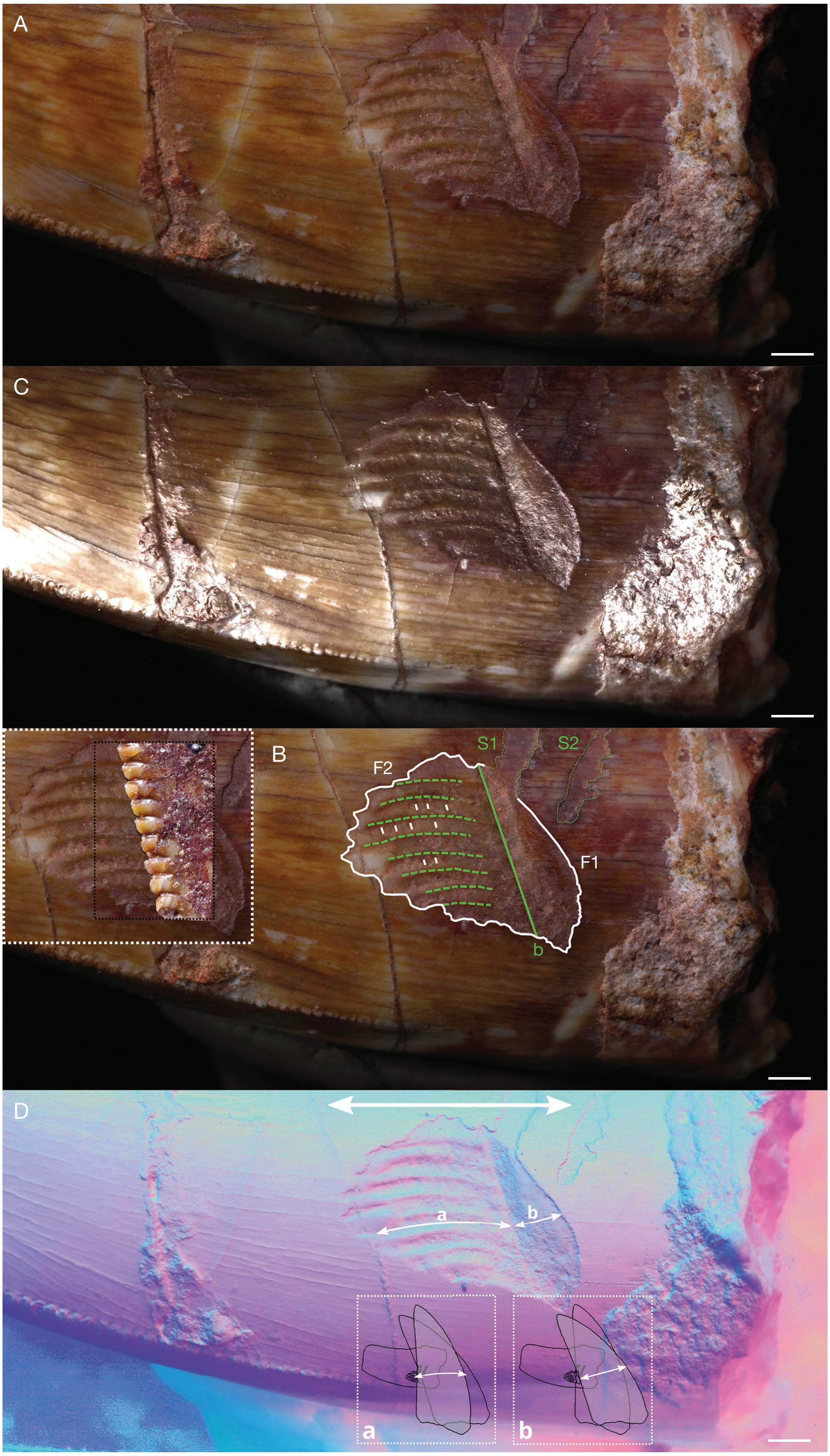
Stratigraphy. — "Valdo-Fuvélien", "Grès à reptiles" Formation.

Age. — Campanian-Maastrichtian (Buffetaut *et al.* 1999).

Reference specimen

M1439 (Fig. 4) has been chosen as the reference specimen of all this material because it has a complete crown and preserves almost all the denticles of the mesial and distal carinae, particularly the most apical ones (Fig. 4G).

Fig. 3. — Reflectance transforming imaging of M5246 tooth: **A**, RTI image in default mode; **B**, same image as A with interpretative drawing of the mark: surfaces **S1** and **S2** marked by thin green dotted lines represent the two enamel tears; note that **S1** is joined to the bevelled mark; **F1** (**white contours**), flat face of the mark separated by the axis of elongation of bevel **b** (**green line**) from the other face **F2** (**white contours**); the face **F2** features internal striations composed of eight ridged wrinkles (**broad green dotted lines**) and nine sub-parallel rounded grooves; the ridges show preserved enamel, while the grooves intersect the underlying dentine; some grooves show a succession of inner marks parallel to each other and perpendicular to the striations (white dashes); on the left, in the **white dotted frame**, we have duplicated the face bearing the striations (**F2**) and superimposed, on the same scale, the mid-crown denticles of the distal carina of tooth M1439 (Fig. 5I) to illustrate the excellent correspondence between the ridges and grooves that form the striations and which correspond respectively to the interdenticular spaces and denticle apices; **C**, RTI image in specular enhancement mode; **D**, RTI image in normal visualization; the thick white double arrow represents the first-order apicobasal (or basoapical) component of the relative movement of the tooth that left the mark; the other two thinner double arrows



represent the second-order labiolingual (or linguolabial) components changing at the position of the bevel. The white doted frames **a** and **b** illustrate the changing of the second order component. Scale bars: 1 mm. Photos from Léa De Brito.

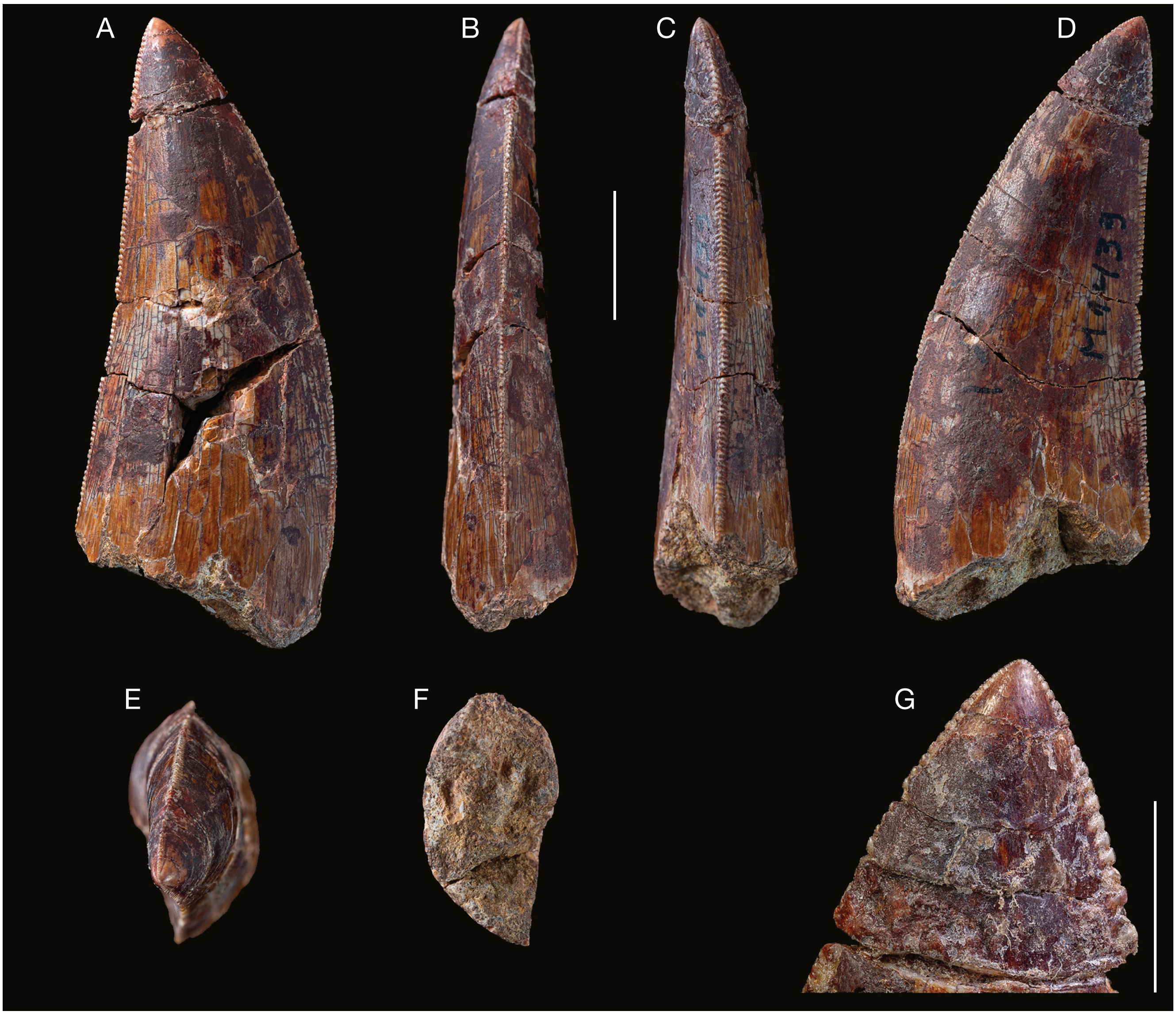


Fig. 4. — Tooth of Abelisauridae indet., specimen M1439 from the locality of Massecaps in labial (**A**), mesial (**B**), distal (**C**), lingual (**D**), apical (**E**), and basal (**F**) views; **G**, Enlarged view of the apex showing the most apical denticles whose length decreases rapidly towards the apex. Scale bar: A-F, 10 mm; G, 5 mm. Photos from Lilian Cazes (CNRS/MNHN).

Description

Tooth slightly elongated baso-apically and ziphodont in shape (*sensu* Hendrickx *et al.* (2020): "labiolingually compressed crown with serrated carinae and apically oriented apex"). Crown height ranges from 17 mm to 55 mm (average height = 37 mm ± 10 mm). The mesial margin of the crown is more recurved than the distal margin, which can be almost straight. In lateral view the mesial carina is convex and the distal carina is concave. The mesial carina ends in the region of the cervix for lateral tooth and more apically for more anterior teeth. Marginal undulations, flutes, longitudinal grooves, or ridges are absent. The enamel texture is irregular and smooth, and slightly oriented apico-basally (Fig. 2G). The distal carina has significantly wider denticles than the mesial carina (Table 1; Fig. 6). The average length of 10 denticles at mid-crown varies from 2.8 mm to 4.2 mm for the mesial carina and from 3.2 mm to 4.6 mm for the distal carina (3.4 ± 0.4 mm vs 3.9 ± 0.4 mm). Denticle length is fairly constant along the mesial and distal carina except for the apical-most and basal-most denticles. Denticles are inclined towards the tip of the crown and the major axis of the denticle is not perpendicular to the mesial margin of the crown. In lateral view denticles are parallelogram in shape. In mesial view, the denticles have a round to crescent-shaped contour; in distal view, the denticles are crescent-shaped. The interdenticular space is narrow. There is no interdenticular sulcus.

Tooth M5246

Although the apex is missing, the tooth appears to be slightly elongated baso-apically (30 mm without the apex) and ziphodont in shape (*sensu* Hendrickx *et al.* 2020: "labiolingually compressed crown with serrated carinae and apically oriented

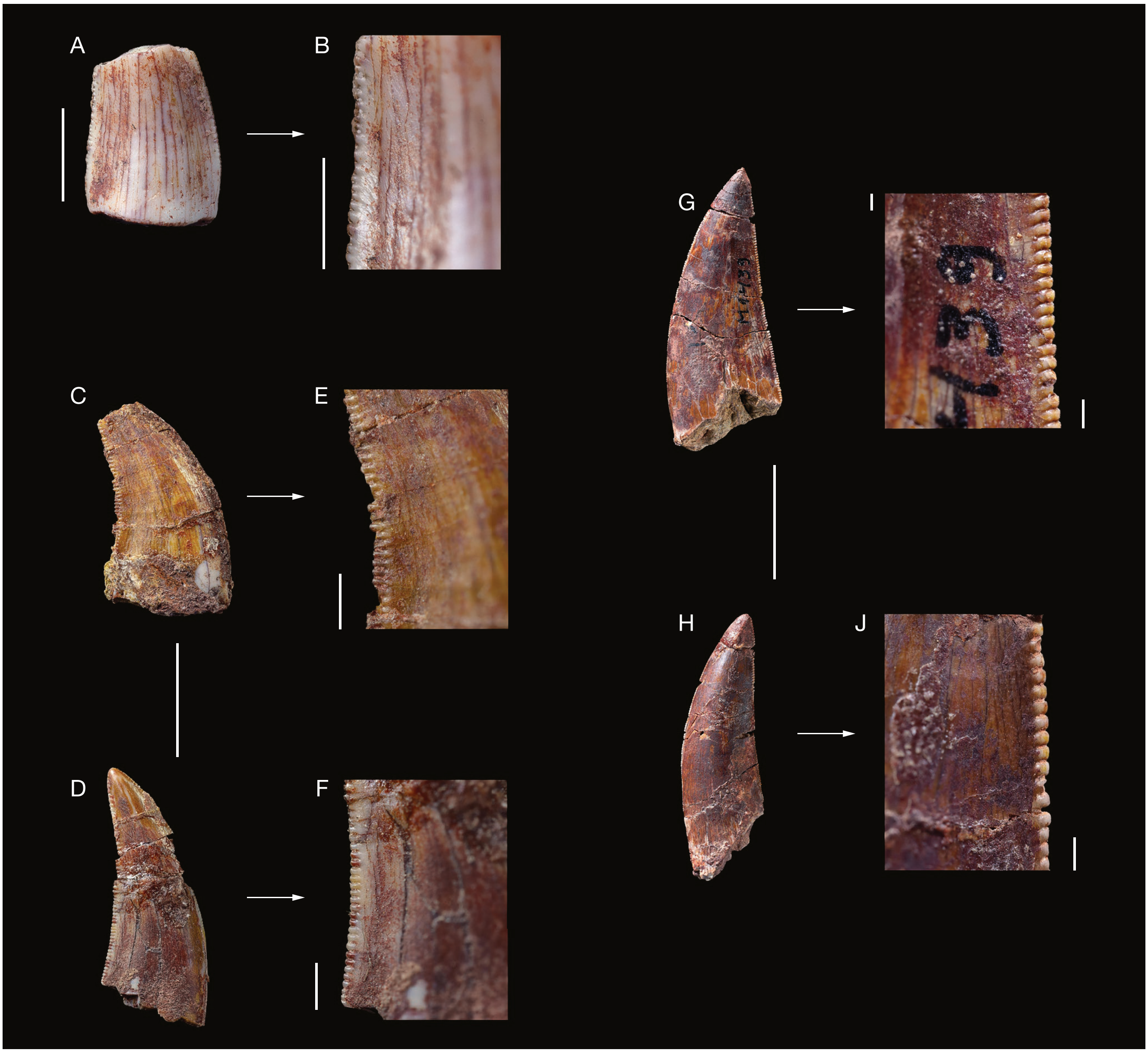


FIG. 5. — Ziphosuchia indet. tooth (**A**, **B**), Dromaeosauridae indet. teeth (**C**-**F**) and Abelisauridae indet. teeth (**G**-**J**) from the locality of Massecaps: **A**, Ziphosuchia indet., specimen M5085; **B**, detailed view of denticles from specimen M5085; **C**, **D**. Dromaeosauridae indet., specimens M561 and M324, respectively; **E**, **F**, detailed view of the denticles of specimens M561 and M324, respectively; **G**, **H**. Abelisauridae indet., specimens M1439 and M1778, respectively; **I**, **J**, detailed view of denticles of specimens M1439 and M1778, respectively. Scale bars: A, 2 mm; B, E, F, I, J, 1 mm; C, D, 5 mm; G, H, 20 mm. Photos from Lilian Cazes (CR2P, MNHN).

apex”). Comparison with other large theropod teeth from Massecaps, indicates that M5246, with its flat morphology as well as its rather straight and aligned carinae, is a lateral tooth. However, compared with M1439, M5246 has a more ovoid cross-section in basal view (Fig. 2F vs Fig. 4F), is less compressed laterally, has a mesial carina that ends more apically and mesial and distal carinae that appear straighter in mesial and distal views. This suggests a more anterior position in the jaw and that it is probably an antero-lateral tooth.

The denticles are poorly preserved in the mesial carina and completely broken on the distal carina, with the exception of the most basal part, where a few are preserved. The basal part of the tooth is damaged in the cervix region, and it is difficult to ascertain whether part of the root is preserved distally. The tooth bears a mark at the base of the lingual surface, close to the mesial edge (Figs 2D-G; 3).

The mesial carina bears 18 denticles per 5 mm and does not show density variations along the preserved section of the carina, except for its most distal part. The distal carina is not preserved, with the exception of the most basal part, making it impossible to count the density of denticles.

Mark

The mark is located on the lingual face of the tooth and has affected the enamel surface and extends into the underlying dentine. The mark has two faces that define a bevelled profile.

The face located most basally in the tooth is flat (Fig. 3B[F1]). The face located more apically bears slightly curved internal striations, parallel to each other and oriented perpendicular to the axis of elongation of the bevel (Fig. 3B[F2]). This basal face forms an angle with the tooth surface less important than the apical face. These striations are composed of a succession of nine grooves separated by eight wrinkles (Figs 2; 3). The mark has a well-marked V-shaped profile in cross-section. The complete mark measures 4 mm in the direction of bevel elongation. The width of seven consecutive grooves measures 3.0 mm and the mean width of one groove 0.4 mm (Table 1). Two enamel tears are visible (Fig. 3B[S1, S2]), one extending from the bevel termination located distally, the other parallel to the first just below (Figs 2; 3).

Denticle measurements

The mid-crown denticles of the crocodile tooth (M5085) are irregular in size, averaging less than 0.1 mm (Fig. 5A). For the teeth of Dromaeosauridae indet. (M324, M561), the average length of mid-crown denticle is 0.15 mm (Fig. 5E-F). For Abelisauridae indet. teeth (M1439, M1778), the mean length of mid-crown denticle is 0.4 mm (Fig. 5I-J; Table 1).

Furthermore, Abelisauridae indet. teeth have wider denticles on the distal carina than on the mesial carina (Mean denticles length calculated from all Abelisauridae indet. teeth equals 0.39 mm vs 0.34 mm; t test *p*-value = 0.0001845; Table 1). For instance, 10 denticles located on the mesial carina of M1439 measure 4 mm whereas ten denticles located on the distal carina measure 4.4 mm (Table 1). Denticle length is fairly constant along the mesial and distal carina except for the last *circa* ten most apical (and basal) denticles, whose respective lengths decrease significantly to 0.09 mm and 0.11 mm (Fig. 4G). The length of the denticles of the mesial and distal carinae is positively and significantly correlated with the total height of the crown (respective *p*-values = 0.0047 and 6e-04; Fig. 6).

DISCUSSION

Taxonomic assignment of tooth M5246

Abelisaurids are common in Campanian and Maastrichtian sediments of Europe. Their presence has been noticed in Spain from the Late Campanian of the Laño and Armuña localities (Astibia *et al.* 1990; Pérez-García *et al.* 2016; Isasmendi *et al.* 2021; 2022) from the Late Campanian - Early Maastrichtian locality of Poyos (Malafaia *et al.* 2023, 2025) and from the latest Maastrichtian Arén and Tremp formations in Ribagorza's country (Isasmendi *et al.* 2024). Their presence has also been reported multiple time in France. They are represented in the Early Campanian of Lambeau du Beausset with the species *Tarascosaurus salluvicus* Le Loeuff & Buffetaut, 1991 (Le Loeuff & Buffetaut 1991); but also in the Late Campanian in Velaux-Bastide Neuve and Fox-Amphoux (Tortosa *et al.* 2014), in Trets-La Boucharde, with the specimens known as "La Boucharde specimen" (Allain & Pereda-Superbiola 2003; Carrano & Sampson 2008), in Pourcieux (Buffetaut *et al.* 1988), and in the locality of Jas Neuf Sud, which yielded the species *Arcovenator escotae* Tortosa, Buffetaut, Vialle, Dutour, Turini & Cheylan, 2014 (Tortosa *et al.* 2014).

Finally, the presence of teeth, cranial and postcranial fragmentary elements referred to an Abelisauridae indet. have been documented multiple times in the area of Cruzy (Buffetaut 2005; Buffetaut *et al.* 1999; Ősi & Buffetaut 2011; Tortosa *et al.* 2014). Recently, Isasmendi *et al.* (2024) hypothesized that some teeth previously assigned to dromaeosaurids by Chanthasit & Buffetaut (2009) might belong to abelisaurids.

Abelisauridae dentition is well known from numerous taxa. However, *Arcovenator* Tortosa, Buffetaut, Vialle, Dutour, Turini & Cheylan, 2014 presents numerous unique features in its dentition such as a distal carina strongly deflected labially and a mesial carina gently curved mesio-lingually toward the base that ends well-above the cervix as well as an apex placed distal to the basalmost point of the distal margin of the crown (Hendrickx *et al.* 2020). M5246 has a broken and missing apex and a damaged distal carina. However, it shows a mesial carina that does not reach the cervix and a distal carina slightly convex similar to *Arcovenator escotae* teeth (Tortosa *et al.* 2014: fig. 4) and teeth referred to *Arcovenator* sp. from the Laño locality (Isasmendi *et al.* 2021; 2022). The tooth M5246 lacks some characteristics of *Arcovenator* such as a mesial carina gently curved mesio-lingually toward the base. The tooth M5246 and the 43 other teeth belonging to the same morphotype have mean denticle densities at mid-crown height of 12.8/5 mm and 14.7/5 mm for the mesial and distal carina, respectively, which are slightly lower than those reported for the three teeth attributed to *A. escotae* (MHNAix-PV.2011.12.15; MHNAix-PV.2011.12.20 and MHNAix-PV.2011.12.187). Contrarily to *A. escotae*, the denticles of the distal carina are longer than those of the mesial carina (Table 1 and Fig. 6). Apart from these morphological variations, we tentatively attribute M5246 tooth (as well as M1439 and M1778 teeth, that we selected and figured for comparison, and 41 other teeth [see Systematic palaeontology]) to Abelisauridae indet. due to their overall resemblance with the teeth of *A. escotae* and *Arcovenator* sp. from contemporaneous sediments of France and Spain, as well as the fact that Abelisauridae are, so far, the only medium to large size theropods known in Europe for this period.

Mark identification

The parallel striations of this mark correspond to the definition of the ichnospecies *Knethichnus parallelum* Jacobsen & Bromley, 2009 (Jacobsen & Bromley 2009). This mark is the product of serration traces, which originate when a theropod tooth, or other denticulate tooth, was dragged across a bone (or other hard surface such as tooth) at an angle at which only the denticles on the tooth meet the bone. We therefore interpret this mark as a bite mark produced by a denticulate tooth. The internal striations of the mark correspond to the marks left by the denticles of the tooth ("denticles drag marks"; Rogers *et al.* 2003, 2007; Jacobsen & Bromley 2009; Drumheller *et al.* 2020). The ridged shape of the wrinkles and the more rounded shape of the grooves (Figs 2; 3) cor-

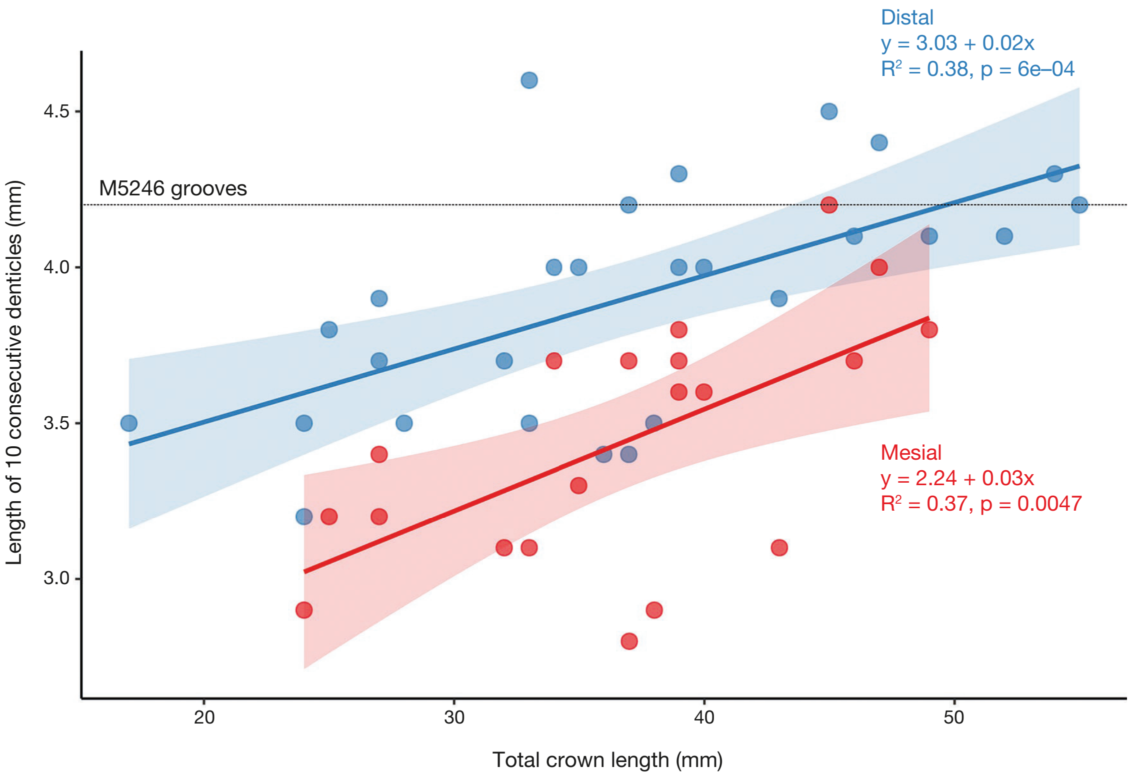


Fig. 6. — Graphical representation of the average length of ten denticles as a function of the corresponding total crown length. The light red dots correspond to the denticles of the mesial carina and the light blue dots to the denticles of the distal carina. The solid lines indicate the fitted linear regressions. The light-coloured bands around each regression line represent the 95% confidence intervals. The regression equations, coefficients of determination (R^2), and associated *p*-values are shown for each group. The black dotted line corresponds to the average width of the grooves (0.42 mm) measured on the mark worn by tooth M5246 and extrapolated to ten grooves (4.2 mm) to match the y-axis.

respond respectively to the interdenticular space between two consecutive denticles and to the apex of a denticle (Fig. 3B). This bite mark resembles certain bite marks on bones (cf. Rogers *et al.* [2003: fig. 3A, B]; Jacobsen & Bromley [2009: fig. 3A]; Drumheller *et al.* [2020: fig. 2A]). It also resembles the bite mark left by Tyrannosauridae on Tyrannosauridae teeth (cf. Abler [1992: fig. 10E] and Jacobsen [1995: fig. pD52]). However, illustrations in these studies are of poor quality and do not allow for a clear view of this type of mark, particularly for detailed comparison with the one shown in this study.

The relative movement of the tooth is complicated to determine and could either have a first order direction either apicobasally or basoapically (Fig. 3D). The bevel, sub-perpendicular to the shaft, is due to the mesial or distal carina of another tooth meeting the labial surface of tooth M5246 and probably marks a change in the relative second order labiolingual component (or conversely; Fig. 3D).

Producer assignment

Following the definition of the ichnospecies *Knethichnus parallelum* we compare this mark caused by the dragging of denticles to the different denticulate tooth morphotypes recovered in the locality of Massecaps, which belong to three taxa: small ziphosuchian teeth (cf. Company *et al.* 2005; Rabi & Sebők 2015; Fig. 5A, B), theropod teeth attributed to Dromaeosauridae indet. (Fig. 5C-F) and larger theropod teeth attributed to Abelisauridae indet. (Fig. 5G-J). In the case of the ziphosuchian tooth, the denticles are irregular in size, averaging less than 0.10 mm (Fig. 5A). For the teeth of Dromaeosauridae indet., the average width of a denticle is 0.15 mm (Fig. 5E, F). For Abelisauridae indet. teeth, the average width of a denticle is 0.40 mm (Fig. 5I, J; Table 1). The width of the grooves (0.4 mm) observed in the bite mark of the tooth M5246 therefore matches perfectly that of the denticles of Abelisauridae indet. teeth recovered from the same locality. We therefore assign its producer to an Abelisauridae indet. Furthermore, the regression models carried out for the mesial (n = 20) and distal (n = 27) carinae also clearly suggest that the average width of the grooves is compatible with the width of denticles located on the distal carina (Fig. 6). Taken together, this implies that the bite mark observed on the tooth M5246 was applied by the distal carina of another tooth of Abelisauridae indet.

Behavioural implications

This type of bite mark has been reported on several teeth of Tyrannosauridae (Abler 1992; Jacobsen 1995; and Caleb M. Brown pers. comm.) but remains poorly documented in the literature. To our knowledge, this is the first reported occurrence of this type of mark on an Abelisauridae tooth.

The fact that the bite mark affects both enamel and underlying dentine suggests that relatively high pressure has been applied to the tooth surface. This is possible provided that the tooth was immobile at the time the pressure was applied. A first hypothesis would be that the tooth was firmly anchored in the jaw when the mark was produced. The orientation of the bevel (sub-perpendicular to the shaft of the tooth) and the parallel striations indicate that the tooth that produced the mark was sub-perpendicular to the M5246 tooth that bears it. This implies that the mark could not have been left by an upper jaw tooth on a lower jaw tooth (or *vice versa*) of the same individual. The bite mark then could have been produced by one individual on another. This could have been produced on the occasion of agonistic behaviours involving head-biting, which is widely documented in present-day and fossil vertebrates (Tanke & Currie 1998 and reference therein; Chimento *et al.* 2019; Benoit *et al.* 2021; Iyoda & Yanagihara 2024) and in particular within non-avian theropods (Tanke & Currie 1998; Peterson *et al.* 2009; Brown *et al.* 2022). The definition of agonistic behaviour was initially proposed by Scott & Fredericson (1951) and clearly defined by Scott (1966) as "a behavioural system composed of behaviour patterns having the common function of adaptation to situations involving physical conflict between members of the same species". Even if access to food represents one of the most favourable theatres for the expression of these agonistic behaviours, we cannot exclude the hypothesis that this mark could have been produced during other types of social interaction involving agonistic behaviour (e.g., territorial occupation, sexual reproduction). Secondly, given that the taxonomic identification of these teeth in this study is limited to the family rank (Abelisauridae indet.), we cannot be absolutely certain that the bite mark involves two individuals of the same species. Thus, if we follow the definition *stricto sensu*, which circumscribes agonistic behaviour only to individuals of the same species, we can only hypothesize that this bite mark is evidence of confamilial social interaction.

However, the location of the striations on the lingual face of the tooth, their orientation, implying that the jaws of two individuals meet at a 90° angle and the fact that the striations probably correspond to the denticles of a distal carina make this first hypothesis mechanically unlikely. Alternatively, this bite mark may be the result of cannibalism, already documented in another Abelisauridae, *Majungasaurus crenatissimus* Depéret, 1896, from the Late Cretaceous of Madagascar (Rogers *et al.* 2003, 2007). Cannibalistic behaviour has also been documented in other theropods, such as *Utahraptor* Kirkland, Gaston & Burge, 1993 from the Early Cretaceous (Cedar Mountain Formation) of the United States (Britt *et al.* 2009), the Tyrannosauridae, including *Tyrannosaurus rex* Osborn, 1905, *Daspletosaurus* Russell, 1970 and *Albertosaurus sarcophagus* Osborn, 1905 (Longrich *et al.* 2010; Hone & Tanke 2015; McLain *et al.* 2018; Dalman & Lucas 2021; Coppock & Currie 2023). Possible cannibalistic behaviour in *Allosaurus* Marsh, 1877 is also hypothesized from an Upper Jurassic theropod bite mark assemblage coming from the Mygatt-Moore Quarry (Drumheller *et al.* 2020). A Tyrannosauridae tooth embedded in the dentary of another Tyrannosauridae has also been reported from the Maastrichtian, Alberta, Canada, and is either interpreted as confamilial or cannibalistic scavenging or fatal agonism (Bell & Currie 2010). Cannibalistic behaviour has also been reported in the theropod *Coelophysis bauri* Cope, 1889 (Nesbitt *et al.* 2006, and references therein), but Nesbitt *et al.* (2006) refute previous demonstration of cannibalistic behaviour for this species and question the commonality of such behaviour among non-avian dinosaurs. However, cannibalism has been documented in many current predatory species such as the Komodo dragon (*Varanus komodoensis* Ouwens, 1912) and in particular in taxa that bracket phylogenetically extinct non-avian theropods such as Crocodilia Owen, 1842 and Aves Linnaeus, 1758 (Roach & Brinkman 2007 and references therein). Furthermore, several studies published after Nesbitt *et al.* (2006) have documented cannibalism among theropods (Rogers *et al.* 2007; Britt *et al.* 2009; Longrich *et al.* 2010; Hone & Tanke 2015; McLain *et al.* 2018; Dalman & Lucas 2021; Coppock & Currie 2023). Both present and past data thus support the view of Roach & Brinkman (2007) that intraspecific predation was also a significant factor in the biology of non-avian theropods.

Interestingly, present-day scavenging on large mammal carcasses focuses mainly on the most nutritious and easily accessible body areas in the anus and rib cage (White & Diedrich 2012); although the taxa involved are not phylogenetically close to those discussed here. Skulls appear less targeted but may nevertheless bear bite marks (White & Diedrich 2012; Diedrich 2014). Hone & Watabe (2010) report a specimen of *Saurolophus* Brown, 1912 humerus bearing numerous bite marks left by a specimen of *Tarbosaurus* Maleev, 1955. The authors show that the arrangement and type of bite marks are indicative of scavenging behaviour. As mentioned above a Tyrannosauridae tooth embedded in the dentary of another Tyrannosauridae may be interpreted as confamilial or cannibalistic scavenging (Bell & Currie 2010).

However, the fact that tooth M5246 has no root suggests that it is probably a shed tooth, ruling out the possibility that the mark was caused by cannibalistic behaviour on a tooth still anchored in the jaw of a dead individual. Furthermore, at the locality of Massecaps, bones attributed to Abelisauridae indet. are relatively rare. They consist in one tibia and one maxilla out of more than 5000 vertebrate fossils inventoried (Authors pers. obs.). The 44 isolated teeth attributed to Abelisauridae indet. that have been recovered at the locality of Massecaps, including the tooth M5246, do not have the root preserved and therefore probably correspond for most of them to shed teeth (although it cannot be excluded that some teeth may have lost their roots during biostratinomic processes, prior to burial). The presence of relatively abundant rootless theropod teeth combined with the scarcity of other skeletal elements belonging to these same theropod taxa is a pattern frequently observed in Mesozoic bonebeds (e.g., Buffetaut & Suteethorn 1989; Lauters *et al.* 2008; Britt *et al.* 2009; Bell & Campione 2014; Eberth 2015; Evans *et al.* 2015; Fanti *et al.* 2015; Ullmann *et al.* 2017; Drumheller *et al.* 2020; Snyder *et al.* 2020; Allain *et al.* 2022). This is interpreted as the fact that, before they were buried, the carcasses attracted theropod dinosaurs that came to feed on them and lost teeth in the process. This is consistent with the presence of numerous fossilized bone

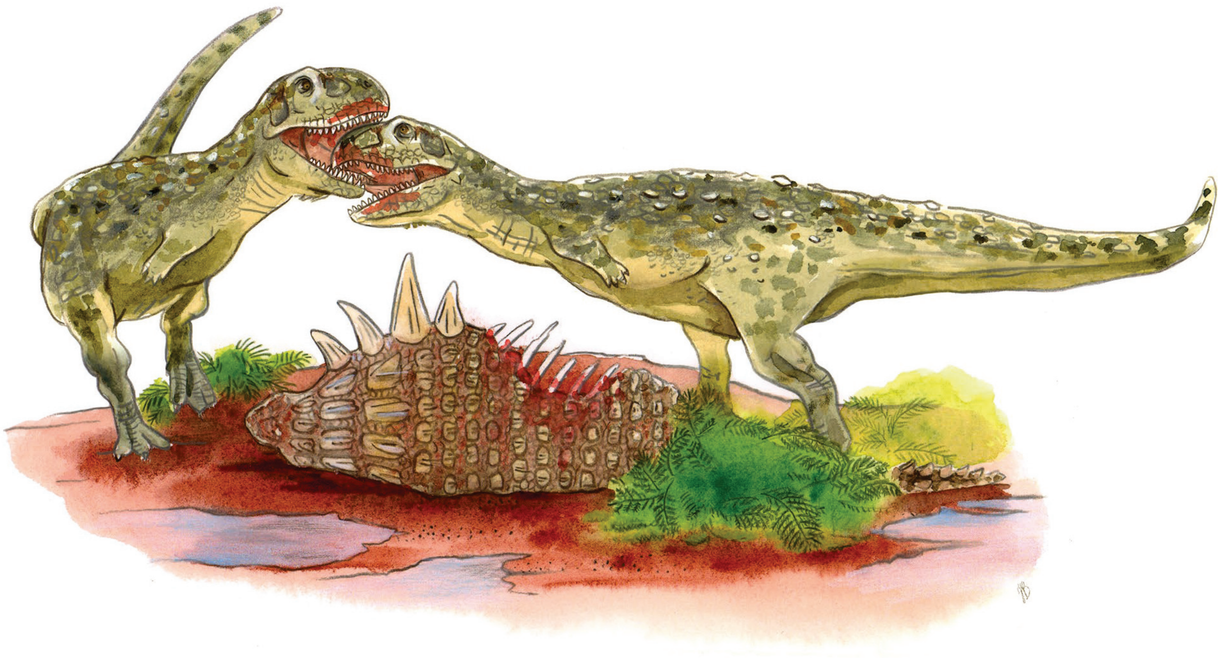


FIG. 7. — Reconstruction of the potential scene that led to the tooth mark observed on tooth M5246. Two Abelisauridae are depicted engaging at jaw level over an ankylosaur carcass. In theropods, a high tooth replacement rate, frequent tooth loss during feeding, and an exceptionally strong bite force occasionally resulted in shed teeth that could be bitten and marked when pressed against two occluding teeth or against hard elements, such as bones, during carcass consumption. Scientific illustration by Julie Borgese.

remains of herbivorous dinosaurs (Rhabdodontidae, Titanosauria and Nodosauridae) in the vertebrate fossil assemblage of the locality of Massecaps, some of which preserve bite marks that are currently being studied.

In view of these elements, it seems unlikely that the bite mark on this tooth is the product of cannibalistic (or at least confamilial) scavenging. Alternatively, in view of the paleontological and taphonomic context described in this study, the most parsimonious hypothesis is that this bite mark was inflicted by one individual of Abelisauridae indet. on one of its own shed teeth, which becomes stuck between two occluding teeth or between a tooth and a bone while the animal is feeding on a carcass. This is consistent with both published studies and numerous unpublished observations of tyrannosaurid teeth bearing tyrannosaurid bite marks (Abler 1992; Jacobsen 1995; Caleb M. Brown pers. comm.). These findings may be attributed to the high tooth replacement rate in theropods, combined with frequent tooth loss during feeding and an exceptionally strong bite force. As a result, shed teeth were occasionally bitten or crushed along with the prey, and could be pressed against hard part such as bones during the consumption of a carcass (Fig. 7).

CONCLUSION

Here we describe a bite mark on a tooth that we tentatively attribute to Abelisauridae indet. Measurements taken on this mark compared with those taken on the different denticulate teeth from the same deposit indicate that the bite mark was left by the distal carina of a tooth attributed to Abelisauridae indet. The orientation of the bite mark rules out the hypothesis that it could have been left by an upper or lower jaw tooth of the same individual. The orientation and position of the striations on the lingual surface of the tooth further suggest that they are unlikely to have been produced during head-biting agonistic behaviour, a phenomenon previously documented in non-avian theropods. Moreover, the fact that M5246 probably corresponds to a shed tooth, along with other taphonomic evidence from the locality of Massecaps and other Mesozoic bonebeds, allows us to rule out the hypothesis of a bite mark resulting from confamilial feeding. We therefore favour the interpretation that this mark was self-inflicted – left by the individual on its own tooth, likely during carcass consumption. This type of trace, previously known only in Tyrannosauridae, contributes to our understanding of Abelisauridae feeding behaviour and highlights notable ecological similarities between these two clades of large carnivorous dinosaurs.

Author contribution statement

Damien Boschetto: Excavation of the Massecaps deposit; preparation of fossil M5246; measurement acquisition; conceptualization; writing, editing and reviewing the manuscript.

Bruno Maggia: Excavation of the Massecaps deposit; conceptualization; writing, editing and reviewing the manuscript.

De Brito Léa: RTI image acquisition; writing, editing and reviewing the manuscript.

Julie Borgese: illustration; scientific reconstruction; writing, editing and reviewing the manuscript.

Didier Clavel: Excavation of the Massecaps deposit; writing, editing and reviewing the manuscript.

Jean-Pierre Chenet: Excavation of the Massecaps deposit; writing, editing and reviewing the manuscript.

Thomas Roques: Excavation of the Massecaps deposit; writing, editing and reviewing the manuscript.

Stéphane Sèbe: Excavation of the Massecaps deposit; writing, editing and reviewing the manuscript.

Jean-Marc Veyssières: Excavation of the Massecaps deposit; writing, editing and reviewing the manuscript.

Jean Goedert: Conceptualization; resources; writing, editing and reviewing the manuscript.

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