A predation attempt in a Late Cretaceous pleurodire turtle from Patagonia

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ABSTRACT

In the present contribution, we report the evidence of a predation attempt against a semi-aquatic pleurodire turtle who survived the attack. The almost complete shell of this adult turtle, the holotype of *Rionegrochelys caldieroi*, was found in the Upper Cretaceous Plottier Formation, El Anfiteatro area, Río Negro province, Patagonia. The shell displays two distinct but synchronously produced trace fossils in the anterior right portion of the plastron. One of the trace fossils is semicircular and indicates where the bone has been broken during the attack, as a consequence of a bite. The other one reflects the predator's teeth morphology, and suggests a crocodyliform as the best candidate. Computed tomography analysis reveals regenerated tissue associated with both trace fossils, indicating healing of the wound. No vital organ was seriously injured during the attack, and the turtle survived, lacking a fragment of the shell. Taking into account the evidence in the fossil record, the unambiguous predator-prey relationship between crocodyliforms and turtles is present from at least the Late Jurassic, and the *Rionegrochelys caldieroi* holotype and their trace fossils is a new evidence of this interaction.

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1. Introduction

The paleoecology and paleobiology of a vertebrate paleo-community, including interactions between organisms, can be studied based on the ichnological evidence especially when the trace fossils provide complementary information to the body fossil record. These biological interactions between vertebrates can reflect different aspects of a community, such as the structure of the trophic net and the energy transfer, nesting behavior, or stages in an ecological succession (e.g. Cariglino and Gutiérrez, 2011; Danise et al., 2014; Gianechini and de Valais, 2016). One of these ecological interactions is predation (i.e. consumption of one organism -the prey- by another organism -the predator- in which the prey is alive when the predator first attacks it; sensu Begon et al., 2006).

However, even the most direct lines of evidence of alleged predation (e.g. teeth bite traces, stomach contents, coprolites) rarely provide unambiguous means to distinguish predators from scavengers or even parasites (Kowalewski, 2002).

Among the diverse vertebrate fossil record from the El Anfiteatro area, Río Negro province, northwestern Patagonia, Argentina (Canudo et al., 2004; Salgado et al., 2009), an almost complete shell of an adult pleurodire turtle, named *Rionegrochelys caldieroi* de la Fuente, Maniel and Jannello 2017 *in* de la Fuente et al. (2017) (Fig.1), was recovered from the upper Coniacian–lower Santonian Plottier Formation (Río Neuquén Subgroup). Its holotype is distinctive by having: i) a prominent and discontinuous mid-carapace crest; ii) peripheral bones 2–11 with strongly guttered ends; iii) three lobe shaped posterior margin of the vertebral bone number 5 in the carapace; and iv) the plastron longer than the carapace (sensu de la Fuente et al., 2017). Of particular interest to this study, the specimen lacks a portion of the anterior, right part of the plastron, which has been previously suggested to be a wound made during the animal's lifetime by Salgado et al. (2009: 775) (Fig. 1B-D).

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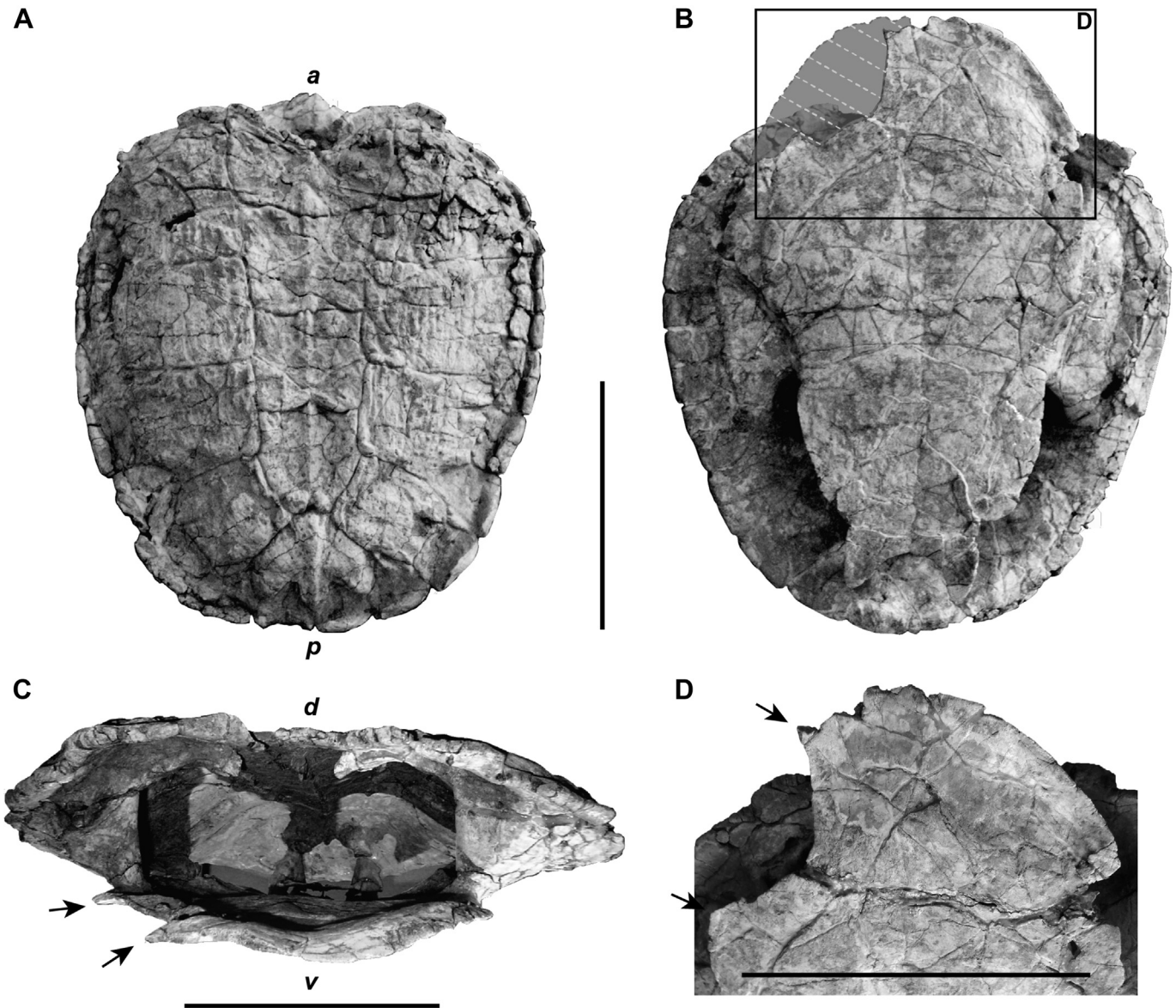
Fig. 1. The holotype of *Rionegrochelys caldieroi*, MPCA-AT 258, from the Plottier Formation, El Anfiteatro Area, Río Negro province, Argentina, displaying a predation attempt. **A**, carapace in dorsal view. **B**, plastron in ventral view, the grey zone represents the bone area lost due to the bite. **C**, shell in anterior view. **D**, close-up of the proximal portion of the plastron, in ventral view. Black arrows indicate the wounded area. Abbreviations: *a*, anterior view of the carapace, *p*, posterior view, *d*, dorsal view, and *v*, ventral view. Scale bars: 20 cm.

We hypothesize that the missing portion was caused by an attempt of predation by a large vertebrate predator. In order to corroborate or reject the predation hypothesis, we describe and discuss the affected area on the plastron of *Rionegrochelys caldieroi* in an ichnological and osteological point of view. Besides, we interpret the paleoecological, paleobiological and ichnological significance of this putative injured area.

2. Geological and paleontological context

2.1. Geological setting

The studied shell MPCA-AT 258 came from the northern flank of the Parrita fossiliferous site (El Anfiteatro area), north of the Meseta de Rentería, Río Negro province, Argentina (39° 18′ 13″S; 68° 24′ 35″ W; Fig. 2A).

In the area, a continental succession belonging to the Neuquén Group is exposed and is characterized by mainly fluvial deposits and, to a lesser degree, aeolian and lacustrine deposits (Cazau and Uliana, 1973; Hugo and Leanza, 2001; Leanza et al., 2008; Stipanicic et al., 1968). The entire succession was laid down during part of the Late Cretaceous (Cenomanian to middle Campanian), when the Neuquén Basin participates in a retro-arc foreland phase triggered by the Andean compressional tectonics (Franzese et al., 2003).

The El Anfiteatro area comprises five lithostratigraphic units, namely the Huincul Formation (upper Cenomanian–Turonian), the Cerro Lisandro Formation (lower Turonian), the Portezuelo Formation (upper Turonian–Coniacian p.p.), the Plottier Formation (upper Coniacian–lower Santonian) and the Bajo de la Carpa Formation (Santonian) (Salgado et al., 2009; see Garrido, 2010 for an alternate interpretation). The vertebrate fossil-bearing levels have been found in deposits of the Cerro Lisandro, Portezuelo and Plottier formations; in the last unit, abundant remains of turtles,
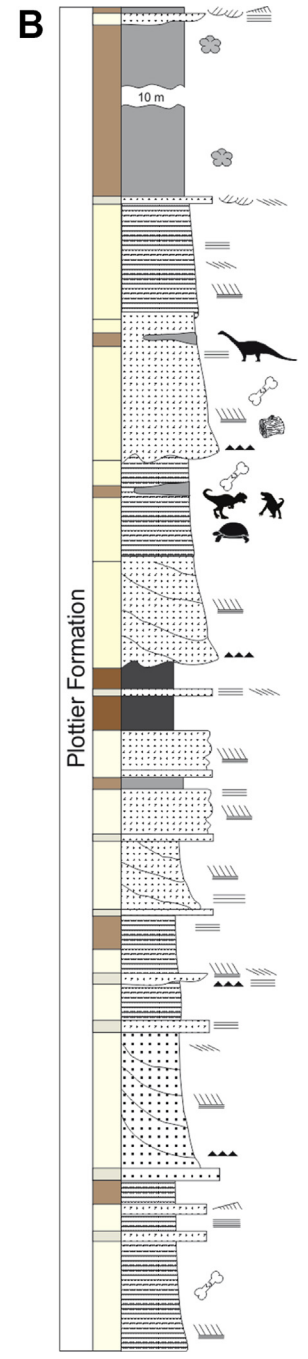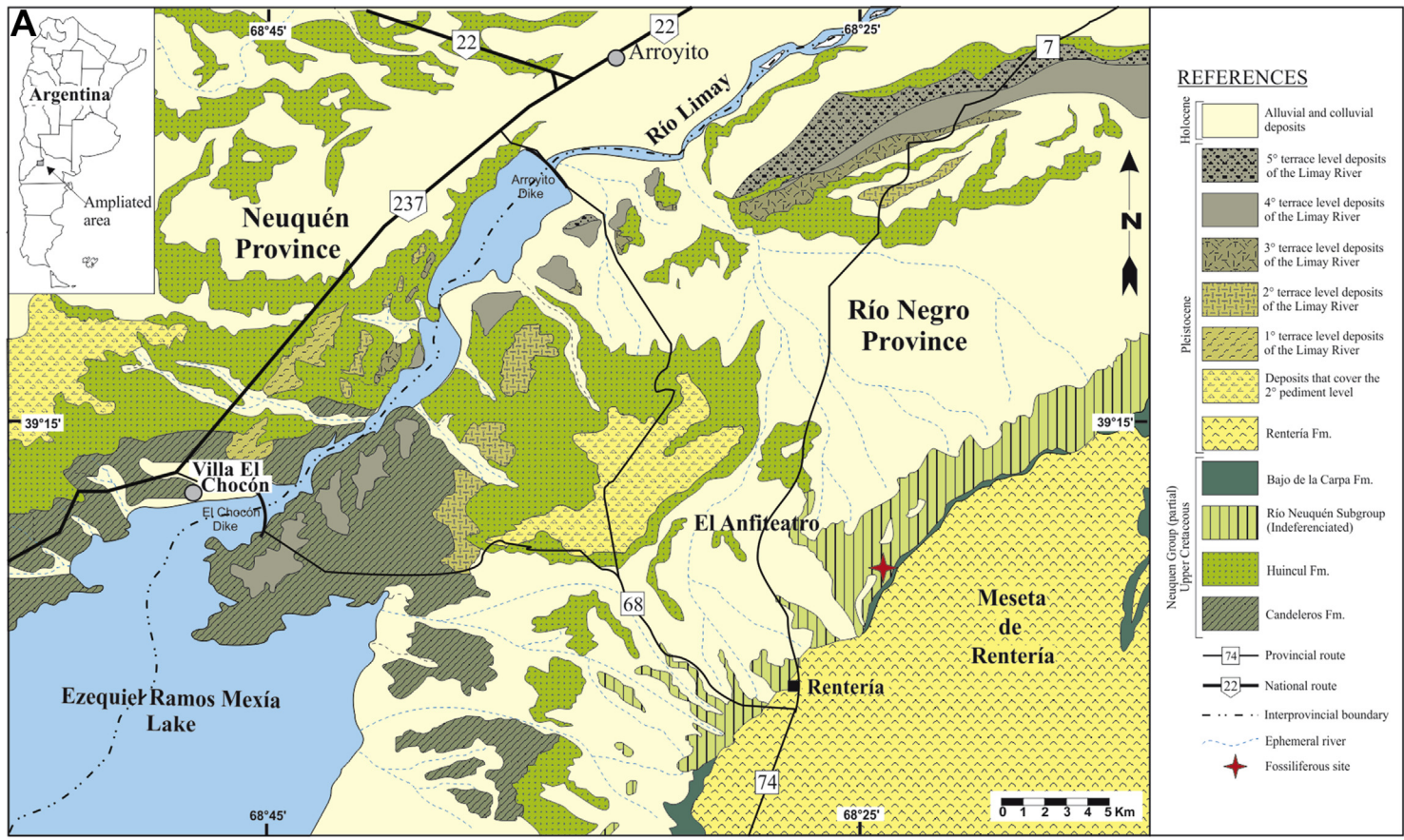
Fig. 2. Geologic data of the El Anfiteatro area, Río Negro province, Argentina. **A**, geologic map of the fossiliferous area, in the Río Negro province, Argentina, near the Villa El Chocón. The red star indicates the ichnological quarry, called Parrita site. **B**, stratigraphy section of the fossiliferous outcrop, from the Plottier Formation. Colors of deposits are indicated according Rock-Color Chart Committe (1991). Modified from de la Fuente et al. (2017).

crocodiles and dinosaurs have been discovered (Salgado et al., 2009; see next section 2.2). The Plottier Formation is the uppermost lithostratigraphic unit of the Río Neuquén Subgroup, underlying the Bajo de la Carpa Formation (Santonian) of the Río Colorado Subgroup (Garrido, 2010). Depending on the adopted lithostratigraphic scheme (see Garrido, 2010: fig. 3, p. 125), the Plottier Formation either lies above the Portezuelo Formation (upper Turonian−Coniacian p.p.) or the Sierra Barrosa Formation (middle−upper Coniacian).

The deposits within the Plottier Formation represent a distal flood plain environment characterized by an ephemeral meandering fluvial system (Salgado et al., 2009), controlled by different paleoclimatic regimes (Garrido, 2010).

The specimen of *Rionegrochelys caldieroi* MPCA AT-258 was extracted from about 31 m from the base of the stratigraphic section at the Parrita site, within a four meters thick, well-sorted, yellow silty-sandstone body, where no other specimens were found (de la Fuente et al., 2017) (Fig. 2B). This deposit has been interpreted as a crevasse splay deposit produced during a flooding event (de la Fuente et al., 2017).

2.2. Vertebrate paleofauna from the Plottier Formation

The associated vertebrate fossil record from the Plottier Formation, in the El Anfiteatro area, is composed of abundant and diverse remains of bones, osteoderms, tooth and plastral plates (Canudo et al., 2004; Salgado et al., 2009; de la Fuente et al., 2017). Among the components of the vertebrate paleofauna, the dinosaurs are quite diverse. A partial dorsal vertebra and other fragmentary specimen of an indeterminate titanosaurian sauropod and a pedal ungual phalanx assigned to Ornithopoda indet. represent the herbivorous elements of the paleocommunity (Salgado et al., 2009). Theropod taxa are represented by isolated teeth belong to cf. Carcharodontosauridae, Coelurosauria indet. and a maniraptoriform cf. Unenlagiinaean, and an incomplete caudal vertebra with uncertain assignment (Salgado et al., 2009). Besides the specimens belonging to *Rionegrochelys caldieroi*, there are plastral plates related to the long necked chelid group *Hydromedusa-Yaminuechelys* (sensu Salgado et al., 2009). Both extant long necked *Hydromedusa* and *Chelodina* are carnivourous, preferentially feeding on tadpoles, frogs, small fishes and snails (Pritchard, 1979; Ernst and Barbour, 1989). Other carnivorous taxa from the El Anfiteatro area are members of Crocodyliformes indet., represented by seven osteoderms and isolated bones (Salgado et al., 2009).

A Neuquenian tetrapod assemblage is recognized in the Plottier Formation (Leanza et al., 2004), composed of large and robust titanosaurid sauropods, alvarezsaurid theropods (shared with Coloradoan assemblage), large basal coelurosaurian theropods, small South-Gondwanan pleurodiran panchelids (shared with Lohancuran and Limayan tetrapod assemblages), and North-Gondwanan podocnemidoid pleurodirans. In the last years, new discoveries, which have been referred to Mesoeucrocodylia indet. (Arcucci et al., 2011), peirosaurid notosuchians (Filippi et al., 2013a), titanosaur sauropods such as *Petrobrasaurus puestohernandezi*, an aelosaurini (Filippi et al., 2011, 2013b), cf. Carcharodontosauridae, and indeterminated maniraptora theropod dinosaurs (Canudo et al., 2009), have enriched the diversity of Neuquenian assemblage.

3. Material and methods

The wound-bearing shell fossil is housed in the paleontological collection of the Museo Provincial "Carlos Ameghino" (MPCA), Cipolletti, Río Negro province, Argentina. The trace fossils, cataloged as MPCA-AT 700-1 and MPCA-AT 700-2, are preserved in the right epiplastron and the anterior portion of the hyoplastron of MPCA-AT 258, holotype of *Rionegrochelys caldieroi*. To evaluate the association between the trace fossils and the possible producer, paleobiological aspects (e.g. anatomy, ethology) of the vertebrate fossil record from the Plottier Formation (Filippi et al., 2011; Canudo et al., 2009; Novas, 2009, and references therein), were considered.

3.1. Digital photogrammetry

High-resolution digital photogrammetry was undertaken to get three dimensional views of the morphology of the injured area. This method is based on Structure from Motion (SfM) (Ullman, 1979) and Multi View Stereo (MVS) (Seitz et al., 2006) algorithms and produces high quality dense point clouds. The software package Agisoft PhotoScan Professional Edition (Educational License, version 1.4.1) was used to model the studied specimen, creating three-dimensional (3D) textured meshes by means of semi-automatic processing of images (Mallison and Wings, 2014). A 3D model of the holotype of *Rionegrochelys caldieroi* was reconstructed from 399 images taken with a reflex digital camera (35 mm focal length, resolution 6000 × 4000 and pixel size of 3.84 × 3.84 μm). In order to correctly scale the calculated model, a metric reference marker was applied on the surface; after scaling, the maximum scale bar error is less than 1 mm. The three-dimensional model of the wounded area was converted in a color topographic profile and contour map using the software Paraview (version 5.4.1). The 3D model of *Rionegrochelys caldieroi* is available as supplementary material in the online repository Figshare (10.6084/m9.figshare.6852827).

3.2. Computed tomography

The microstructure of the bone tissue was analyzed through a computed tomography (CT) scan. The CT scan was performed with a Philips MX 8000 QuadCT scanner (120 Kv peak voltage, 300 mAs, 344 mA and 873 ms exposure time). Cross-section slices were obtained every 0.75 mm. The CT data are interpreted as grayscales that reflect the differences in the X-ray attenuation as they pass through the sample (see Rowe et al., 2016), expressed in Hounsfield units (HU), a quantitative scale for describing radiodensity. The HU is a dimensionless unit used to express CT numbers in a standardized and convenient form, obtained from a linear transformation of the X-ray attenuation coefficients. This transformation is based on the definitions of the distilled water at standard pressure and temperature, defined as zero HU units, and the air, whose HU is −1.000 (Spoor et al., 2000). Bone tissues range from 700 HU for cancellous (spongy) to about 3000 HU for highly compact (cortical) or tissue with cellular bone regeneration (callus) (Gilbert et al., 2016). The Hounsfield scale was created for medical uses, and it is not suitable for the wide range of fossil materials (Rowe et al., 2016), especially if highly mineralised or matrix-filled. Nevertheless, the HU represents an absolute, objective and comparative radiodensity scale, so it can be used regardless of the relationship of the obtained value with the data of extant animal tissues (see Spoor et al., 2000). The specimen MPCA-AT 258 is poorly mineralised and it is not matrix-filled, so the radiodensity values can be considered reliable in this case and CT scan can be used to evaluate healed bone growth (DePalma et al., 2013; Drumheller et al., 2014). HU values were obtained from nine slices (see Fig. 4B) of the plastron and measured with the software ImageJ. Eight slices (i.e. 188, 197, 244, 254, 264, 302, 319 and 334 *in* Fig. 4B) pass through the injured area, while the ninth one (i.e. 357 *in* Fig. 4B) was selected outside the putative injured area, in order to check radiodensity values in an unaffected area. For each slices, six (in slices 188, 197, 244, 254, 264 and 357) and seven (in slices 302, 319 and 334) measurement points around the injured area, were chosen to take the measures. For further details see Figure 4 caption and the supplementary data.
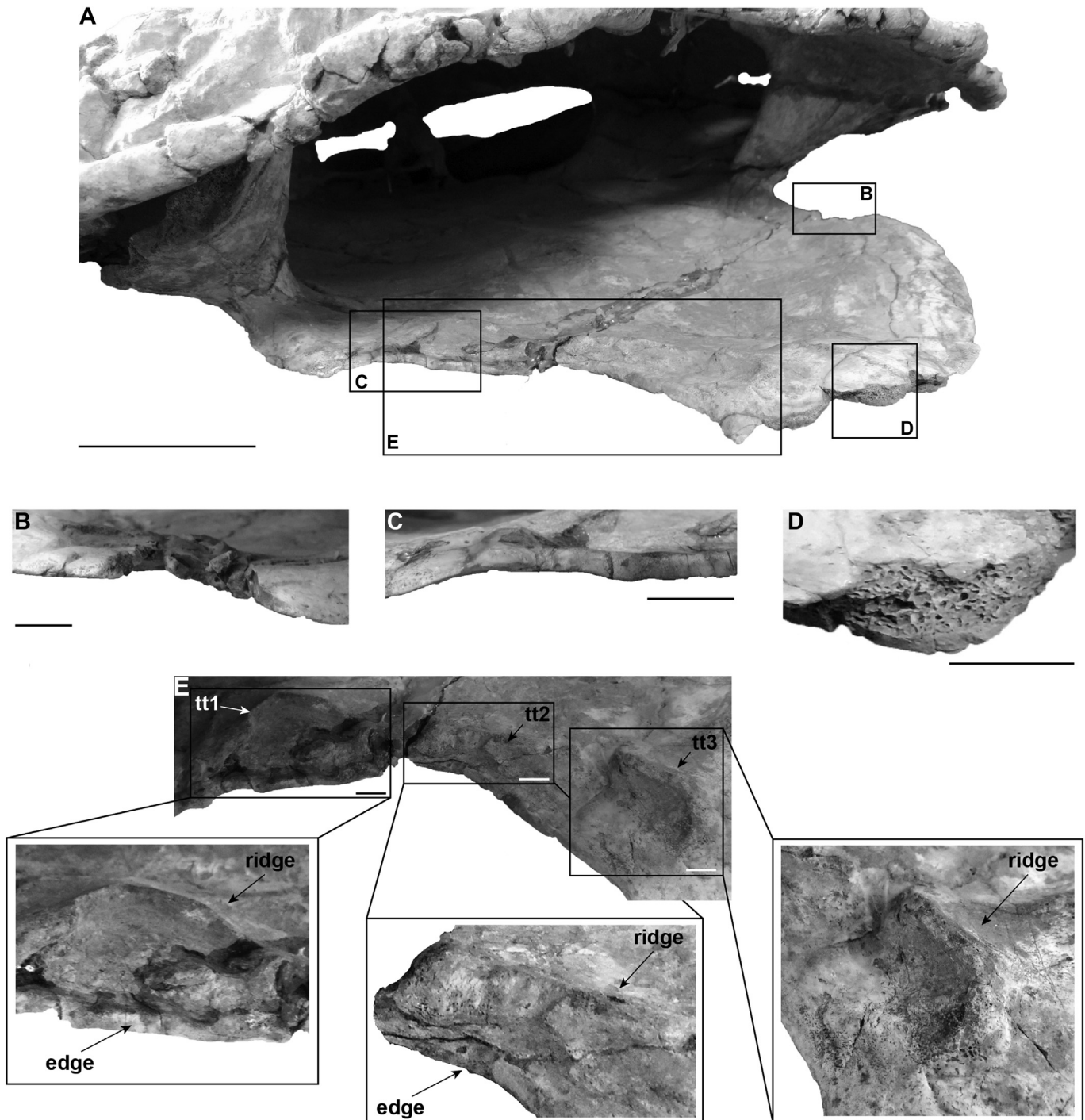
Fig. 3. Overview of the plastron of the holotype of *Rionegrochelys caldieroi*, MPCA-AT 258. **A**, the plastron of *Rionegrochelys caldieroi* in visceral, lateral view. **B**, current fracture affecting the left margin of the plastron of *Rionegrochelys caldieroi*, produced during field and laboratory operations. **C**, portion of the edge in the wounded area of the plastron; note in the close-up the smooth surface of the edge. **D**, current fracture, exposing the internal structure of the bone, affecting the central margin of the plastron just outside the wounded area; this fracture was produced during field and laboratory operations. **E**, close-ups of the three tooth traces associated to the undulating ridge in the wounded area of the plastron. In the close-ups, the smooth edge can be also observed. tt1, tt2, tt3 and associated arrows indicate tooth traces preserved along the undulating ridge. Scale bars: 5 cm (A) and 1 cm (B–E).

4. Results

The plastron of the holotype of *Rionegrochelys caldieroi* is 450 mm in overall length, while the carapace is 430 mm in overall length (de la Fuente et al., 2017). This difference in the maximum length results in a slight, anteriorly directed protrusion of the plastron from the anterior margin of the carapace. Both in visceral and ventral views, the plastron shows a pronounced bilateral symmetry of the different plastral bones making up the epi-, ento-, hyo-, meso-, hypo- and xiphiplastron (de la Fuente et al., 2017). Some portions of the right epi- and
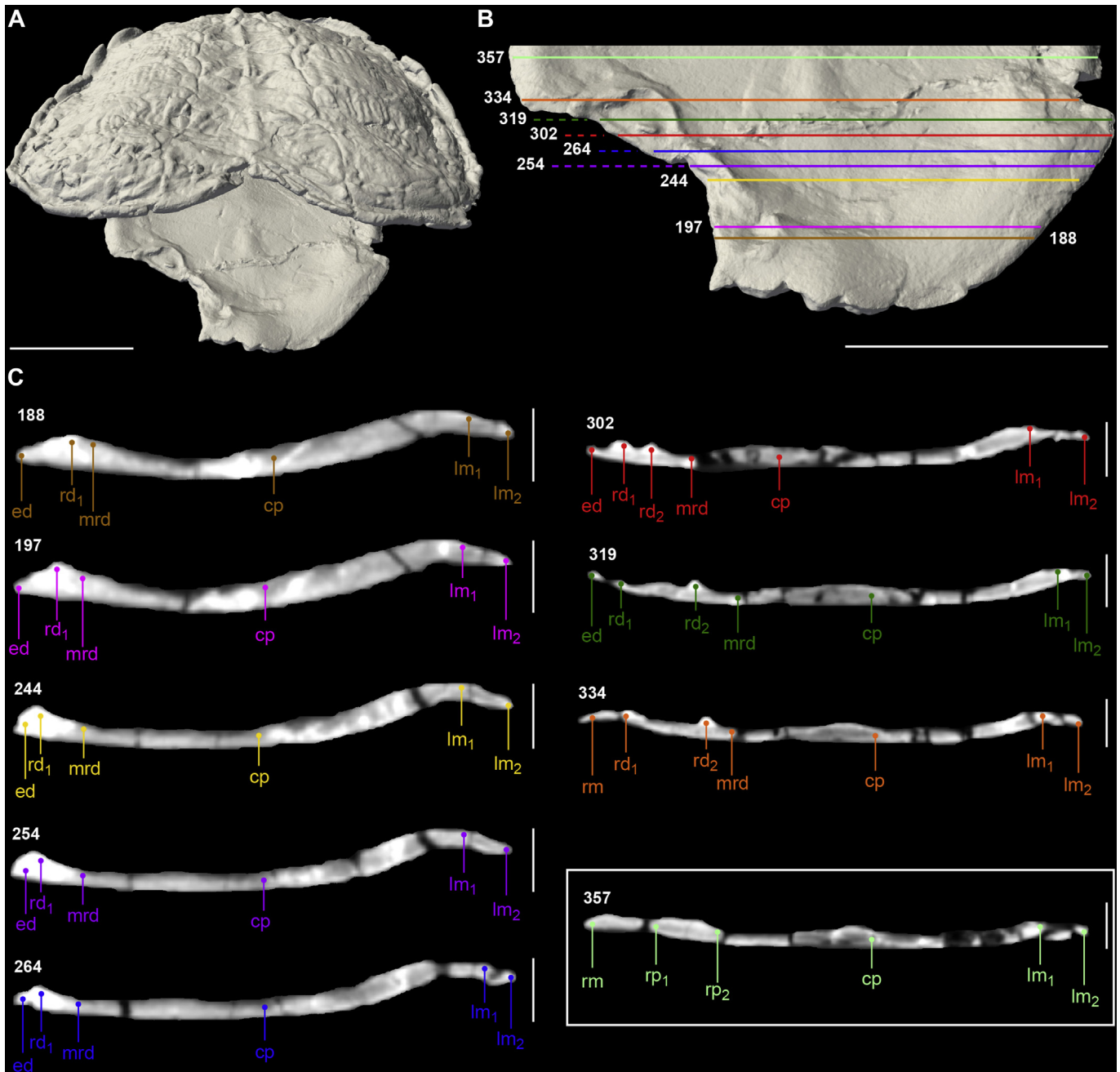
Fig. 4. Images by computed tomography scan of the wounded area in the carapace of the holotype of *Rionegrochelys caldieroi*, MPCA-AT 258. **A**, 3D reconstruction of the carapace obtained with high-resolution digital photogrammetry. **B**, close-up of the proximal portion of the plastron preserving the wounded area. The colored lines indicate the location of the cross-section slices (identified by numbers) shown in C. **C**, cross-section slices obtained from the computed tomography and edited with ImageJ software. The colored lines and associated circles indicate the areas where the HUs have been measured and are named by considering their relative position along the cross-section: cp, central portion of the plastron; ed, edge; lm, left margin of the plastron; mrd, medial to the ridge, rd, ridge; rm, right margin of the plastron; rp, right portion of the plastron. White rectangle enclose the slice 357 selected outside the wounded area. Scale bars: 10 cm (A,B) and 1 cm (C).

hyoplastron, namely the anterior portion of the extragular scute and the central and lateral portions of the humeral scute, are lacking.

In the right half plastron, the area exposed after the ablation of part of the plastron is characterized by a semicircular edge (MPCA-AT 700-1; see Section 3) and a surrounding bone ridge (Figs. 3 and 5). The semicircle displays a slight irregular line and measures 155 mm of arc length and 132.7 mm from end to end or chord length. The edge of the bone is smooth, composed of cortical tissue, with a variable thickness from 2.8 mm to 4.7 mm.

Other areas along the margin of the plastron are affected by sharp fractures exposing the internal structure of the bone (Fig. 3B,D).

The external surface of the plastron of the studied area is smooth, with no scratches, burrows or deformations, and lacks evidence of scarring or extra injuries (Figs. 1B,D). Unlike the external surface, the visceral surface of the plastron displays a strong sigmoidal or undulating ridge ranging between 7.5 mm and 13.6 mm in height (Fig. 3). This undulating ridge displays three concave curves (MPCA-AT 700-2, see Section 3; Figs. 3A,B and 5C-E)
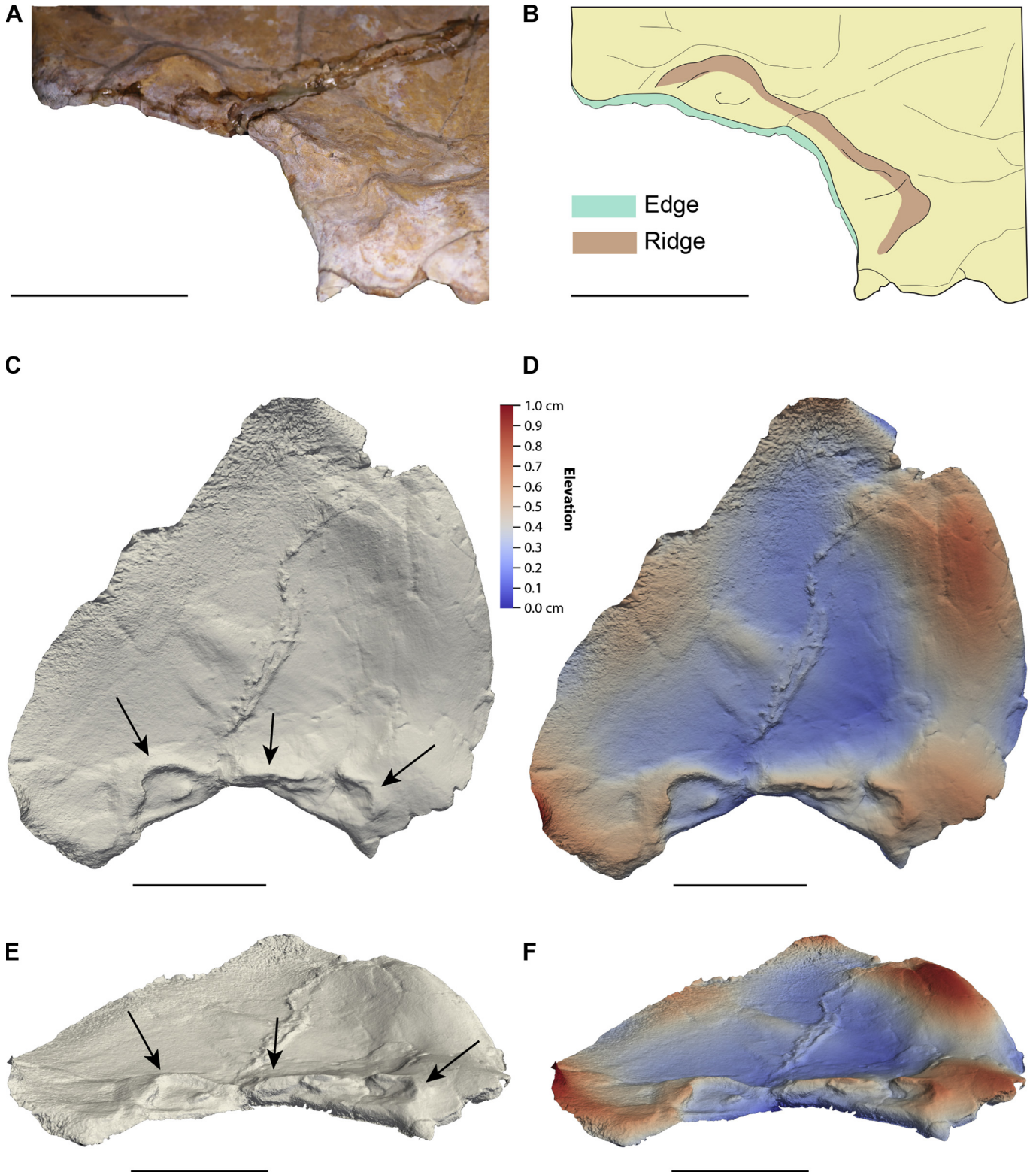
Fig. 5. Predation attempt on the holotype of *Rionegrochelys caldieroi*, MPCA-AT 258. **A**, detail of the wounded area on the visceral surface of the plastron. **B**, interpretative drawing of a; in yellow is the surface not affected; in green, the edge or trace fossil representing where the bone has broken because of the bite during the attempt of predation, MPCA-AT 700-1; in brown, the ridge or scar on the bone (a pathological structure), whose morphology reflects the predator's teeth attack, MPCA-AT 700-2 (the trace fossil). **C**, solid three-dimensional model of the wounded area on the visceral surface of the plastron, in normal view. **D**, color topographic profile of the wounded area, in normal view (the bony ridge is highlighted in light red and red tones). **E**, solid three-dimensional model of the wounded area on the visceral surface of the plastron, in inclined view. **F**, color topographic profile of the wounded area, in inclined view. Black arrows in C and E indicate the alleged position of predator's tooth in the bony ridge. Scale bars: 5 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

arranged as semicircles laterally aligned. The first and third curves (tt1 and tt3 respectively in Figs. 3E and 5C,E) have a strong sinuosity, while the middle one (tt2 in Figs. 3E and 5C,E) is less pronounced. The average length at the base of the edge of these semicircles is 29.2 mm.

The visceral surface bone between the semicircular edge and the undulating ridge displays no deformations or scratches and has a relative constant thickness of 2.5 mm. The ridge sector with the less pronounced curve or tt2 is almost in contact with the semicircular edge. Medially to the bone ridge, the bone surface is also smooth and with no extramorphological deformation associated to the studied area.

HU total average values, obtained from different cross-sections slices passing through the putative injured area (Fig. 4A,B; see caption figure 4 for abbreviations), were as follows: 2414.4 HU for ed, 2723.4 HU for rd1 and 2716.2 for rd2 (slices188, 197, 244, 254, 264, 302, 319 and 334; Fig. 4C); 1710.6 for mrd (slices 188, 197, 244, 254, 264, 302, 319 and 334; Fig. 4C); 1925.5 HU for rm (slices 334 and 357; Fig. 4C); 1678.5 HU and 1692.4 HU for rp1 and rp2, respectively (slice 357); 1194.8 HU for cp (all the slices; Fig. 4C); 1717.5 and 1788.1 HU for lm1 and lm2, respectively (all the slices; Fig. 4C). The overall results and a scatterplot obtained from the HU values measured are reported in the supplementary data. Table 1 summarizes the HU values obtained.

5. Discussion

5.1. Paleobiological and paleoecological significance

The holotype of *Rionegrochelys caldieroi* has a missing portion of the anterior right part of the plastron. In both extant and extinct turtle, it is common to find pits, holes and scratches in the shells. Many times, these traces are interpreted as feeding traces made by diverse organisms, such as invertebrates or tiny mammals using mouthparts and/or teeth, which result in regular and particular traces (e.g. Meyer, 2011; Mikuláš et al., 2006; Reolid et al., 2015; Zonneveld et al., 2015), or as pathological modifications due to diseases by fungi, bacteria or algae (Lovich et al., 1996; Garner et al., 1997; Pereda-Suberbiola et al., 2000; Hernández-Divers et al., 2009), which usually present irregular surfaces (see Garner et al., 1997:1). Moreover, the macroscopic appearance of wounds produced by diseases has an irregular shape and spreads over a large part of the shell (Garner et al., 1997; Pereda-Suberbiola et al., 2000; Adkesson et al., 2007; Hernández-Divers et al., 2009). Sometimes, shell deformations can be also attributed to congenital phenomena (e.g. absence of bone element, conjoined or parasitic twin, see Rothschild et al., 2013).

In the present case, the studied area in the right plastron of *Rionegrochelys caldieroi* does not fit exactly with any of the explanation above mentioned and cannot be related to any of those causes.

According to the CT information, both edge and ridge bone have the highest HU values, while the rest of the bony tissue of the plastron shows lower values (see Table 1 and supplementary data). Given that both densely compact bone and tissue with disorder cells display high HU values (e.g. Villa and Lynnerup, 2012; Gilbert et al., 2016), it is here interpreted that the undulating ridge and the edge have regenerated cells. The ridge is consistent with bone regeneration associated to the production of a scar and tissue thickening, while the edge of the wounded zone is most likely characterized by bone regeneration without tissue thickening (Figs. 3E, 5). The formation of a callus is incompatible with the development of an infective process, which in turn favored its healing (Canale, 2010). Lower HU values instead indicate much less dense, not regenerated, compact bone (Gilbert et al., 2016).

There are some other broken sectors in the carapace and the plastron with low HU values, with no cell regeneration in those areas (Figs. 3B,D and 4, and supplementary data), supporting that those damages are the result of postmortem alteration. Some of them have cracked surfaces related with taphonomic processes (weathering), while others have sharp fractures showing the external and internal bone structures, produced by recent processes during field and lab operations (Figs. 1 and 3).

The morphology of the thickened bone displaying the bony ridge on the visceral surface is interpreted herein as the effect of the scar generated by the teeth of a vertebrate biting the plastron trying to prey the turtle. Each one of the three negative concave curves —with the bone edge wounded as reference point— corresponds to the effect of the action of a tooth (Figs. 3E and 5). The thickened bone in the area is the result of the process of cellular regeneration and healing, reaction that has been documented in similar cases in extant Testudines (Danini, 1946; Rothschild et al., 2013).

The bone tissue regeneration, as evidenced by the CT scan, is considered as a proof that, after the attack, the individual, although wounded, continued to live. Therefore, we propose this is a case of failed predation and not of scavenging (i.e. feeding on decaying corpses, sensu Begon et al., 2006).

Although the turtle died when it was an adult, there is not enough data about its ontogenetic stage at the time of the attack, which occurred at least long enough for the wound to heal, the cortical and epithelial tissues to regenerate and the scars to form. Studies on reptilian skin wounds have shown that they heal similarly to mammalian injuries, but relatively slower (Smith and Barker, 1988; Bennett, 1989; Frye, 1991; Ballard and Cheek, 2003; Mitchell and Díaz-Figueroa, 2004). Though little information is available, the healing process of reptilian bone is usually slower than in birds and mammals (Mader, 1996; Mitchell, 2002). Some studies made in fractured shells of extant terrestrial turtles have suggested a healing period of seven to eighteen weeks, although worse defects may require a substantially longer time (Boon et al., 2017; DiGeronimo and Brandão, 2019).

The survival of the individual indicates that the attack did not harm any vital organ or arteries in the neck, skull, or shoulder girdle. More significant injury or death may have been averted based on some characters of the post cranial skeleton of *Rionegrochelys caldieroi*. The turtle cervical column has eight vertebrae (e.g. Williams, 1950; Müller et al., 2010), with morphological

Table 1
Summary of the HU (Hounsfield units) values obtained from the cross-section slices and used to describe radiodensity in the plastron of the holotype of *Rionegrochelys caldieroi*. For each cross-section slice, the mean value (mean HU), the minimum value (Min HU) and the maximum value (Max HU) are reported with respect to the area (in square millimeters) where the measurement was taken. The measuring points are sensu Figure 4C.

Slices	Parameters	Measurement points									
		ed	rd1	rd2	mrd	rm	rp1	rp2	cp	lm1	lm2
Total	Mean HU	2414.4	2723.4	2716.2	1710.6	1925.5	1678.537	1692.375	1194.8	1717.5	1788.1
	Min HU (mean)	2014.4	2470.7	2510.7	1214.4	1718.5	1585	1130	995.1	1187.2	1185.7
	Max HU (mean)	2563.6	2856	2821.7	2040.1	2047.5	1759	1873	1352	2006.9	2050.4

variation that allows several types of movements (Werneburg et al., 2014). Pleurodires can fold their head and neck sideward in a horizontal plane, anterior to the rib cage and inside the shell (e.g. Vallois, 1922; Shah, 1963; Herrel et al., 2008). These characteristics would have protected them against predators (Werneburg et al., 2014). Moreover, the shell of *Rionegrochelys caldieroi* displays an anterior plastral expansion that could probably protect the vital organs from a predator attack.

Previous paleohistology studies made in the microstructure of the shell of *Rionegrochelys caldieroi* have indicated that this taxon had a semi-aquatic to terrestrial life habits, with a massive structure and a higher degree of compactness than other panchelids (de la Fuente et al., 2017). This could suggest that this species had walking habits, such as the extant *Chelus fimbriatus* (Schneider, 1783), who exhibits a walking bottom habits, or the extant *Platemys platycephala* (Schneider, 1792), who had ambulatory walking habits, but it was not essentially terrestrial as the Testudinidae are today. This means that *Rionegrochelys caldieroi* would have lived mostly in small lakes or ephemeral ponds, living partially on dry land, maybe looking for new ponds nearby. Thereby, this is the first case of an evidence of failed predation, represented by trace fossils of a healed wound in a specimen belong to Testudines of semi-aquatic habits. It is important to mention that the extant terrestrial turtle species regenerate their tissues better and faster than aquatic species (Hunt, 1957).

As already mentioned, an entire sector of bone has been removed from the rest of the shell by a predator (tracemaker, in this case), leaving an empty area. It has been observed in current turtles that during the hibernation period, small mammals can get to nibble the limbs of the turtles, and even there have been cases where some individuals have lost an entire leg (Hay, 1904; McArthur, 2004; Rothschild et al., 2013). There are many records of extant turtles that live long and productive lives with injuries in their shells, or even with one of their limbs amputated (Balazs, 1980). It is not possible to confirm whether *Rionegrochelys caldieroi* would have hibernated or not, but at least it can be assumed that it would not have done it in the terrestrial environment, given the co-existence of theropods and

crocodiles, both large predators. Given that *Rionegrochelys caldieroi* had semi-aquatic habits, if it had hibernated, it probably would have done so underwater. Among extant chelids, *Hydromedusa tectifera* possesses high plasticity to adapt to extreme condition (de la Fuente, 1999). Some specimens of this species can hibernate under the water in the southern range of its distribution (such as around tributaries streams in the Samborombón Bay, in Buenos Aires province, Argentina) in small creeks because it support more decelerated metabolism.

In general, turtles are primary or secondary consumers in trophic networks, and, both in marine and terrestrial communities, constitute a component of the diet for several predators (Bondavalli and Ulanowicz, 1999; Heithaus et al., 2002; Milàn et al., 2010, 2011; Cruz-Escalona et al., 2013; Botfalvai et al., 2014). It would be expected that the same ecological situation happened in the paleo-communities, being part of several trophic chains of a large trophic network.

Taking into account both the morphology of the trace fossil in the ridge (MPCA-AT 700-2) and the paleofauna of the upper Coniacian−lower Santonian Plottier Formation from the El Anfiteatro area (see Section 2.2), the identity of the predator of *Rionegrochelys caldieroi* can be discussed. For instance, other remains related to the chelids of the group *Hydromedusa-Chelodina-Yaminuechelys* have been recovered from the locality (de la Fuente et al., 2017). Current chelids are usually omnivores, and even can attack other turtles (Buhlmann, 1995), but the members of the group lack teeth so it is not possible that they were the predator. Titanosaurian sauropod and ornithopod dinosaurs are also discarded as possible predators, as they were herbivorous components of the paleofauna.

Two taxonomic groups with carnivorous and predatory habits were recorded in the locality and nearby from the Plottier Formation, namely, the crocodyliforms and diverse theropods. There are abundant data about extant crocodiles preying on chelonians (e.g. Cott, 1961; Neill, 1971; Erickson, 1982, 1984; Bondavalli and Ulanowicz, 1999; Rothschild et al., 2013); the same happens with corvids, raptors and shorebirds (e.g. Harding and Bloomer, 1979; Clark, 1982), which are descendants of some theropods, although

Fig. 6. Speculative in vivo reconstruction of the predation attempt on *Rionegrochelys caldieroi*. A crocodylomorph is trying to prey on an individual of *Rionegrochelys caldieroi*, flexing its limbs to get as close as possible to the prey. However, the turtle reacts, protects its neck and head, and manages to escape from the predation attempt. Artwork by Elia Smaniotto.
Speculative in vivo reconstruction of the predation attempt on Rione-grochelys caldieroi por < span xmlns:cc = "http://creativecommons.org/ns#" property = "cc:attributionName">Elia Smaniotto se distribuye bajo una Licencia Creative Commons Atribución-CompartirIgual 4.0 Internacional.

clear evidence relating theropods and turtles in a trophic structure with confidence is lacking.

Taking into consideration the circular outline of the teeth traces, crocodyliforms might be the best candidate as potential tracemaker (Fig. 6). The record of crocodyliforms from the Plottier Formation comprises Crocodyliformes, including indeterminate specimens (Salgado et al., 2009) and Peirosauridae indet. (Filippi et al., 2013a), and Mesoeucrocodylia indet. (Arcucci et al., 2011). Among the record from the unit, peirosaurids display a premaxillar alveolar distance (i.e. diastema) that could fit in the scar representing the distance between teeth observed in the ridge in the wounded area (see Barrios et al., 2016). Alveolar distance was already suggested as putative proxy for associate crocodyliform tracemakers and bite traces in previous papers (Erickson, 1984; Noto et al., 2012).

The evidence relating crocodyliforms and turtles as predator-prey in a trophic structure was previously reported both in modern settings (e.g. Balazs, 1980; Ortiz et al., 1997; Heithaus et al., 2008) and in the fossil record (e.g. Fuentes, 2003; Mead et al., 2006; Hastings et al., 2015). Regarding the latter, fossil records of cured, healed wounds (non-lethal interactions for the prey) or injuries made with the individual still alive are relatively scarce (Neumann, 1966; Erickson, 1982, 1984; Buffetaut, 1983; Alonso et al., 2006; Schwimmer, 2010; McCoy et al., 2012; Rothschild and Depalma, 2013). They are unequivocal evidence of predation (Kowalewski, 2002), and not of scavenging. Some of the most relevant examples of crocodyliforms-turtle interaction as predator-prey are mentioned herein. Several puncture wounds with thickened bone on posterior and posterodorsal shell of *Protochelydra Erickson, 1973* suggest predation interactions between this turtle and *Leidyosuchus formidabilis Erickson, 1976* as possible predator, recorded from the late Paleocene Bullion Creek Formation, in the Wannagan Creek Quarry, North Dakota, USA (Erickson, 1982, 1984; Rothschild et al., 2013). At least two sets of parallel grooves preserved in a symphysis of a crocodilian jaw, from the Eocene of Mali, West Africa, has been interpreted as possible intraspecific fighting (Buffetaut, 1983). Trace fossils and evidence of tissue regeneration in abundant bones and shell plates from the middle Eocene Corrales del Vino, Zamora, Spain, have been cited by Alonso et al. (2006). A fragmentary plastron belonging to *Chedighaii barberi* (Schmidt, 1940), from the Campanian Blufftown Formation, from Georgia, USA, has a healed semi-circular trace fossil, assigned to a crocodilian predatory action (Schwimmer, 2010). A wound healed on a fragment of skin, found in association with a hadrosaur skull, from the upper Maastrichtian Hell Creek Formation, has been described as evidence of probable failed predation (Rothschild and Depalma, 2013). A complete specimen of *Eurysternum wagleri Meyer, 1839*, from the Upper Jurassic Mörnsheim Formation, from Germany, displays a series of pits that would fit with a crocodile bite (Neumann, 1966).

Based on the fossil record, it supports a recurrent trophic interaction between crocodyliforms and testudines, at least since the Late Jurassic to date. It would not be surprising that this ecological relationship has existed even before that period, closer to the origin of both groups.

5.2. Ichnological significance

Neumann (1966) has defined bioerosion as every form of biologic penetration into hard substrates. These substrates can be biogenic, such as shells, wood, teeth and bones, or non-biogenic, as cemented sediments, rocks and clasts (Taylor and Wilson, 2003; de Gibert et al., 2004). Within biogenic substrates, bones are characterized by a quite large variability of structure, mineralogy, nutritional value, and hardness (Taylor and Wilson, 2003; Hopner and Bertling, 2017). Specifically, the bioerosion trace fossils in bones

are biogenic structures that cut or destroy hard osseous tissue structures as the result of mechanical and/or chemical processes (Pirrone et al., 2014).

If a bone tissue is injured and then this bone has the chance to heal, it may generate a scar or callus, as in the ridge preserving MPCA-AT 700-2. Another option is not to form a scar but to produce cortical or compact tissue, like in the edge of MPCA-AT 700-1. Biting and gnawing punctures and scratches caused by predation are considered trace fossils, while pathological structures and results of diseases visible in skeletal parts are not (Bertling et al., 2006). In the holotype of *Rionegrochelys caldieroi*, the absence of part of the plastron with a semicircular cut line is the evidence of bioerosion associated with an attempt of predation. However, the bone cell regeneration itself, which produces both the healed scar in the visceral surface of the plastron and the cortical tissue in the edge of the wound, is not a trace fossil. In any case, the scar forming the ridge is reflecting at least partially the shape and number of the teeth that would have caused the wound, namely, an undulating or sinuous line of healing. This sinuosity showing the teeth of the predator and its attempt of predation are considered as trace fossils.

6. Conclusions

The shape and arrangement of two distinct but synchronously produced trace fossils in the anterior right portion of the plastron of the semi-aquatic pleurodire turtle *Rionegrochelys caldieroi*, allow to discuss an attempt of predation. These trace fossils are the product of the bite action: one is semicircular and indicates where the bone has been broken, while the other presents a zigzagging line that reflects the predator teeth morphology.

Moreover, the CT analysis has shown the presence of regenerated tissue related to the trace fossils, suggesting that the wound healed and, therefore, the turtle survived the attack.

Taking into account both the vertebrate diversity of the Plottier Formation and the characteristics of the wounded area, a member of Crocodyliformes, probably a peirosaurid, is proposed as a putative predator. Nowadays, the unambiguous predator-prey relationship between crocodyliforms and turtles is common. On the other hand, the fossil record shows this relationship at least since the Late Jurassic, so it would be expected this ecological predator-prey relationship goes back even closer to the origin of both groups.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2019.104290.