

Grazing activity as taphonomic record of necrobiotic interaction: A case study of a sea turtle carapace from the Upper Jurassic of the Prebetic (south Spain)

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ABSTRACT

Bioerosion trace fossils can shed light on the ecological interactions between species. Here we describe an unusual case of bioerosion on a turtle carapace of *Hispaniachelys prebetica* from the Oxfordian (around 155 Ma, Upper Jurassic) of the Prebetic (Betic Cordillera, South Spain). The specimen was found in a limestone bed of a marl-limestone rhythmite. Morphological analysis of the bioerosive structures reveals the dominance of epigenic traces produced by the grazing activity of regular sea urchins (ichnospecies *Gnathichnus pentax*). No other bioerosion structures are present. From an ethologic point of view only epigenic traces (pascichnia) are present. *Gnathichnus pentax* records short-term bioerosion produced exclusively on the carapace before its burial. The ichnological assemblage recorded herein typifies the *Gnathichnus* Ichnofacies. The carapace was the most favourable hard substrate for grazers in comparison to the surrounding muddy soft bottom. The carapace was oriented convex-down when found in the rock. Therefore, pascichnial activity probably occurred early after the death and accumulation on the sea floor of the turtle remains, but before the carapace was overturned by large scavengers. The low degree of fragmentation and the low dispersion of skeletal components indicate a low-energy environment and early burial in the sea bottom.

Key words: Turtle carapace; bioerosion; *Gnathichnus*; gnawing organisms; regular echinoids; Upper Jurassic.

RESUMEN

Las pistas fósiles de bioerosión son una herramienta útil para interpretar las relaciones ecológicas entre especies. En este trabajo se describe un caso poco habitual de bioerosiones en un caparazón de tortuga (*Hispaniachelys prebetica*) del Oxfordiense (Jurásico superior, hace aproximadamente 155 Ma) del Prebético (Cordillera Bética, S España). El espécimen fue hallado en un banco calizo en una ritmita margoso-calcárea. El análisis morfológico de las estructuras bioerosivas revela la presencia de numerosas pistas epigénicas producidas por organismos raspadores, concretamente erizos regulares (ichnospecie *Gnathichnus pentax*). *Gnathichnus pentax* registra periodos cortos de

bioerosión producidos exclusivamente sobre el caparazón previamente a su enterramiento. La asociación registrada tipifica la icnofacies de *Gnathichnus*. El caparazón fue el sustrato duro más favorable para los erizos irregulares raspadores en comparación con el fondo blando circundante. El caparazón se encontró en el afloramiento en posición invertida dentro de la capa caliza. Así, la colonización del mismo probablemente ocurrió en una fase temprana, tras la muerte del organismo y su acumulación en el fondo, pero antes de que el caparazón fuera girado a una posición invertida, probablemente por la acción de grandes carroñeros. El bajo grado de fragmentación y la escasa dispersión de los elementos del esqueleto apuntan a una baja energía en el medio así como un enterramiento relativamente rápido.

Palabras clave: Caparazón de tortuga; bioerosión; *Gnathichnus*; organismos raspadores; equinoideos irregulares; Jurásico Superior.

INTRODUCTION

The breakdown of hard substrates by boring and gnawing organisms, known as bioerosion (Neumann, 1966), is important in understanding the biology of ancient ecosystems (Taylor and Wilson, 2003). Regular echinoids are among the most important of the epilithic grazers in both temperate and tropical marine ecosystems, where they cause considerable rock destruction in their quest for food. The work of these organisms is commonly preserved in the fossil record (e.g. Bromley and Asgaard, 1993a; Gilbert *et al.* 2007; Santos *et al.* 2008, 2011; Johnson *et al.* 2011; Gudveig Baarli *et al.* 2013) with two ichnotaxa named *Circolites* Mikuláš, 1992 and *Gnathichnus* Bromley, 1975. The latter, which is a characteristic star-shaped scratch resulting from grazing activity, is the one that concerns us here.

Known from the Middle-Late Triassic (Fürsich and Wendt, 1977) to the present, this bioerosive structure occurs mainly on skeleton of organisms (e.g., Bromley, 1975; Fürsich and Wendt, 1977; Radwański, 1977; Voigt, 1977, 1979; Martinell, 1981, 1982; Nicosia, 1986; Wilson, 2003; Radley, 2006; Gibert *et al.*, 2007; Lach *et al.*, 2014) and more rarely upon rock clasts (e.g., Bromley and Asgaard, 1993a, b; Mayoral and Muñiz, 1996; Steinthorsdottir *et al.*, 2006). Twitchett (1994) and Danise *et al.* (2014) identified and figured star-shaped gnawing traces

of regular echinoids on an ichthyosaur rib bone from the Upper Jurassic of England. A recent study by Cione *et al.* (2010) thoroughly describes our knowledge of *Gnathichnus* in vertebrate skeletal substrates. These authors reported evidence of etching on penguin bones from the Miocene of Argentina providing new information on taphonomic issues. Meyer (2011) reported the occurrence of the ichnotaxon *Gnathichnus pentax* on two specimens of Kimmeridgian marine turtles from Solothurn (Switzerland) and suggested the extinct echinoid *Hemicidaris mitra* (Agassiz) as the producer of these stellate grooves.

Here, we focus on a detailed description and interpretation of echinoid grazing traces on a fossil sea turtle carapace (*Hispaniachelys prebetica*) aged more than 155 Ma (Upper Jurassic) from the Prebetic (Betic Cordillera, South Spain). In this case, the trace fossils provide valuable data for the study of certain palaeoecological and taphonomic aspects in marine hard substrate communities. In this context, we characterize the ichnoassemblage recognized on the carapace and relate it with the taphonomic history of the sea turtle.

GEOLOGICAL SETTING

The turtle specimen was found in the upper Oxfordian (Upper Jurassic), at the Riogazas-Chorro section (RGCH) of the External Prebetic, the northernmost part of the Betic Cordillera in southeast Spain (Figure 1). The sequence is a well-stratified marl-limestone rhythmite measuring 22 m thick (Olóriz *et al.*, 2002, 2003), with a sponge-microbialite buildup at the base. The turtle was found in limestone bed 62, which according to the ammonite biostratigraphy of this section (Olóriz *et al.*, 1999) corresponds to the *Bimammatum* ammonite Biozone (upper Oxfordian). The rocks are sediments deposited in a mid-shelf environment on a carbonate epicontinental shelf system (Reolid *et al.*, 2008). According to taphonomic and palaeoecological analysis of the macroinvertebrate assemblages, the sedimentary setting has been interpreted as a softground with a depth of ~60–80m (Reolid, 2003; Olóriz *et al.*, 2006).

The microfacies is a fine-grained wackestone with peloids, and there are no sedimentary structures indicating turbulence. The marl-

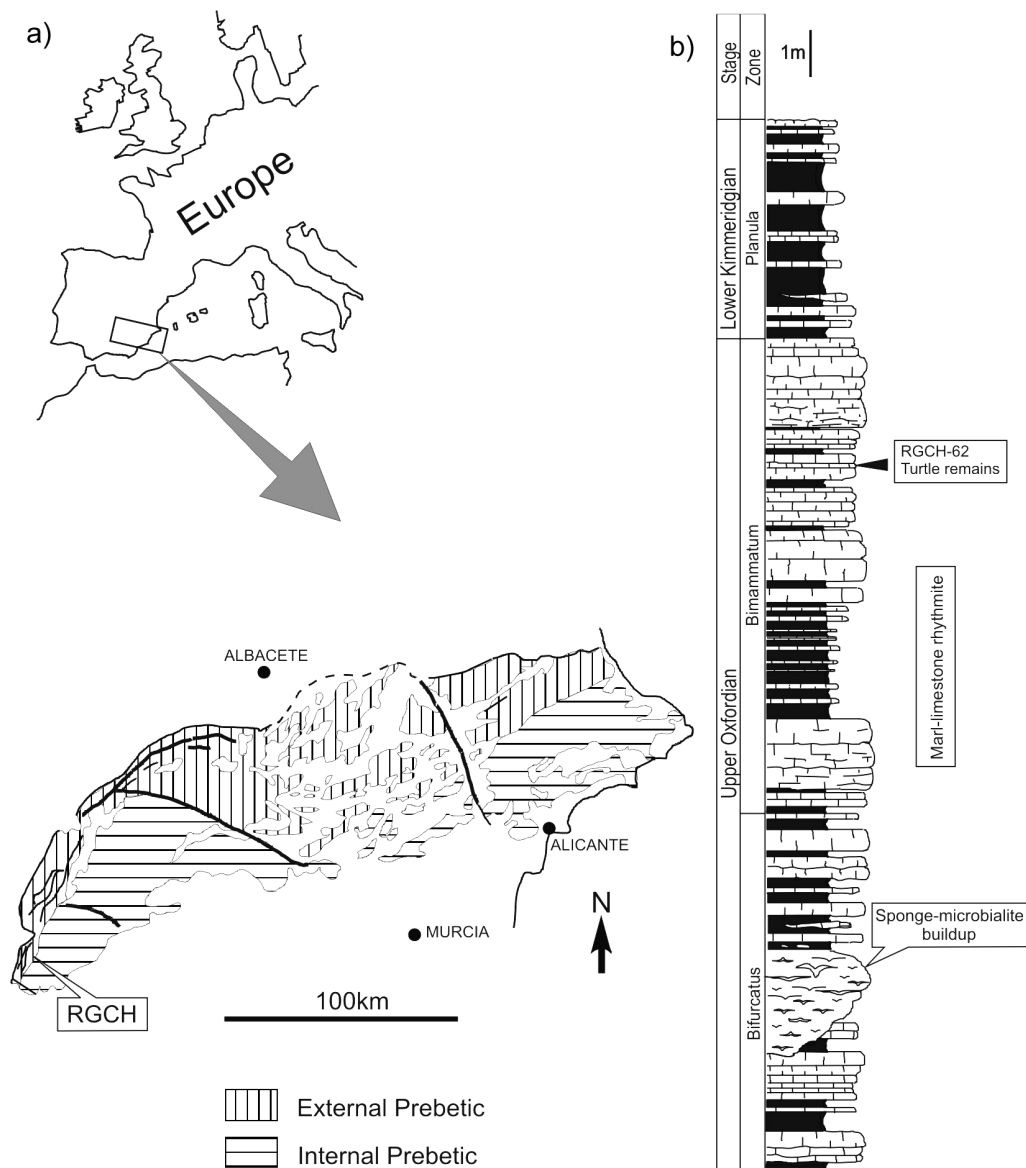


Figure 1. a) Geological setting of the Riogazas-Chorro section (RGCH) in the External Prebetic. b) Stratigraphic section with location of the level with fossil turtle remains.

limestone rhythmites represent fluctuations in carbonate productivity and delivery of siliciclastic material derived from the proximal Iberian palaeomargin, which is defined by the extent of the Triassic sediments composing the Tabular Cover immediately to the north (Olóriz *et al.*, 2003, 2006; Reolid *et al.*, 2008).

The rich fossil invertebrate fauna of the RGCH section has been extensively studied (Olóriz *et al.*, 2002, 2003, 2006; Reolid, 2003; Reolid *et al.*, 2008). *Hispaniachelys prebetica* is the only known tetrapod from the Jurassic of the Betic Cordillera and is the oldest turtle from southern Europe (Slater *et al.*, 2011).

The macroinvertebrate fossil assemblage in the RGCH section is clearly dominated by ammonoids (84%), followed by belemnites (13%). Benthic macroinvertebrates are in a minority (3%) being only abundant in the sponge-microbialite buildups (Reolid, 2011). *Chondrites* and *Planolites* ichnogenus are presented, whereas *Thalassinoides* is very rare. The proportions of macroinvertebrates (51 specimens) in the bed in which the turtle remains were recorded (RGCH-62) are also dominated by cephalopods (ammonites 78%, belemnites 10%) over benthics (12%). The ammonoids are mainly *Sowerbyceras* (45%), Haploceratacea (27%) and perisphinctoids (17%). Among the benthic forms, bivalves (50%) and irregular echinoids (17%) are most common; brachiopods and regular echinoids are rare.

ANALYSED MATERIAL

The material studied and illustrated here is the holotype of *Hispaniachelys prebetica* and is housed in the Museo de Paleontología of the Universidad de Granada (Spain) under the reference number RGCH-62-52. The specimen is a moderately large turtle including the majority of the carapace and plastron (Figure 2). The carapace is thick and fully ossified, measuring 43 cm long and

34 cm wide. In addition, some disarticulated cervical and thoracic vertebrae, some of the post cranial bones of the skeleton (such as the dorsal vertebrae, and the scapula) were recorded. A detailed description of the preserved elements of the skeleton is given by Slater *et al.* (2011).

The carapace does not show signs of flattening or disarticulation. The plastron collapsed into the carapace, as the specimen was preserved in a carapace-down orientation, and consequently the plastron is broken up but still relatively well preserved. A number of isolated fragments of the carapace are also present. The remains are preserved as phosphate (francolite). The degree of fragmentation is low and appears largely to affect the distal parts of bones, which are fractured and not rounded.

On the external surface of the carapace there are groups of pentaradiate grooves which cover it extensively, and which frequently overlap each other, covering areas of about 7–8 cm² (Figure 3a). Visual examination indicates that these bioerosive structures are epigenic traces produced by the grazing activity of regular echinoids (vagile herbivores/omnivores). No other bioerosion structures were identified on the surface of the carapace, although incorrectly Slater *et al.* (2011) identified the ichnofossil *Entobia*. The plastron and other bones do not have trace marks on their surfaces. Also, the surface of the carapace does not carry an episkeletozoan fauna.

ICHOLOGICAL STUDY ON THE TURTLE CARAPACE

Ichtnogenus Gnathichnus Bromley, 1975

Type. Ichnospecies *Gnathichnus pentax* Bromley, 1975

Diagnosis. Biogenic sculpture consisting of grooves, pits, and scratches on hard substrates (from Bromley, 1975).



Figure 2. General view of the Upper Jurassic turtle *Hispaniachelys prebetica*, RGCH-62-52 (Riogazas-Chorro section, Betic Cordillera, southeast Spain).

***Gnathichnus pentax* Bromley, 1975**

Figures 3b, 3c, 3d, 3e, 3f, 3g

Description. The most common trace is composed of five grooves arranged in a star-shaped pattern. Each groove is rectilinear, with a length between 3 mm and 10 mm and a width between 0.6 and 1.1 mm (Figure 3b). The repetition of overlapping stars can produce a compound stellate bioerosion sculpture, highly complex, and making it impossible to discern the individual stars (Figures 3c–3d). In these cases, all surfaces are completely covered by grooves of similar depth and length. Overlapping these complex stellate patterns some sinuous grooves are also commonly observed (Figures 3e–3f). These are relatively long, from 12.5 to 30 mm, but normally 20 mm on average. The angle between radial scratches has a median value of 72°. The diameter of modular units varies between 6.5 and 10 mm.

Remarks. Bromley (1975) mentioned that the stellate pattern has a diameter that rarely exceeds 5 mm and in most cases is less than 2 mm. Mayoral (1986) described diameters up to 1.4 mm with maximum length of the radius of 0.7 mm. Both authors comment that if the surfaces are sharply curved or irregular, the stellate pattern is commonly reduced to a smaller radius, maintaining a constant angle of 72° between the rays. In these cases, the lengths of the radius are longer and the grooves become densely packed and more or less parallel. In the studied material, this pattern is observed only in some points where the curvature is slightly greater or in the vicinity of suture lines (Figure 3g). In areas where the surface is more or less flat, the configuration of the structures is represented by the typical star-shaped pattern with regular morphologies.

DISCUSSION**The trace maker**

The close similarity of recent gnawing traces produced by regular echinoids allows us to interpret the trace fossils on the turtle carapace as the work of gnawing echinoids with a fair degree of confidence. The close morphological similarity of these superficial grazing traces with recent gnawing traces and, considering the extensive fossil record of such grazing traces back to the Triassic, it is reasonable to attribute our Jurassic traces to the work of these active grazers. Star-shaped grooves are typically produced today by sea urchins (Bromley, 1975), which employ mechanical techniques. According to Bromley (1975), the mode of employment of the echinoid tooth involves a powerful scraping action with characteristic and uniform width and depth. The simultaneous action of all five teeth produces a stellate pattern of grooves identical in form to the trace fossil. The sinuous grooves, which sometimes overlap the star-shape patterns, could be traces left by the sharp spines that are arranged around the mouth of the sea urchins.

According to Kier and Grant (1965), some fishes or grapsid crabs can produce groups of subparallel scratches. Yet, the result of such foraging is generally a series of highly irregular scratches, pits, and broken protuberances on the substrates that do not resemble the uniform, pentaradiate traces discussed here. Gastropods and polyplacophores are other groups of organisms that graze on hard substrates and could have produced sets of scratches on the turtle carapace, but their rasping traces produced by radular erosion do not produce a pentaradiate pattern.

In the studied outcrop, grazers are frequent only in relation to microbial-sponge buildups of the *Bifurcatus* Zone, but they are progressively scarcer in the *Bimammatum* and *Planula* zones, as is true of other epifaunal forms in general in softgrounds (Reolid, 2003; Olóriz et

al., 2006). The echinoids recorded are *Plegiocidaris* sp. and *Diplopodia* sp., which are most likely the producers of the gnaw traces according to size and shape of their lantern. Nevertheless, some feeding differences arise between these two species. *Plegiocidaris* sp. is a grazer and omnivore, while *Diplopodia* sp. is a grazer and deposit-feeder, which suggests that the first may be the species responsible for the production of these star-shaped grooves. In neighbouring sections, less common *Heterosalenia* sp. and *Acrocidaris* sp. have been recorded. Meyer (2011) interpreted *Hemicidaris mitra* as the producer of *Gnathichnus pentax* traces on Kimmeridgian carapaces from the Solothurn Turtle Limestone in Switzerland.

The producers of these bioerosions likely exploited all trophic resource on the surface of the turtle carapace. The outermost layer of the carapace mainly consists of the fibrous protein β -keratin (glycine-proline-tyrosine rich proteins) (Alexander, 1970; Espinoza et al., 2007; Dalla Valle et al., 2009) probably a source of protein for scavengers. Moreover, carapace epibionts colonizing this horny material composing the turtle scutes were probably present at the time of death. Studies of Recent turtles show that green and red algae grow epizoically on aquatic turtles (Neil and Allen, 1954; Caine, 1986; Frick et al., 1998; Pfaller et al., 2008; among others). This algal growth always supports a crustacean microcommunity, including cladocerans, copepods, ostracods and amphipods (Neil and Allen, 1954). Encrusting epizoo-bionts have been described on carapaces of Recent sea turtles such as *Caretta caretta* and *Dermochelys coriacea* (Frazier et al., 1985, 1992; Caine, 1986; Gramentz, 1988; Frick et al., 1998, 2000, 2004; Pfaller et al., 2008) including bivalves (e.g. *Ostrea* and *Crassostrea*), annelids (e.g. *Filograna*, *Sabellaria* and *Serpula*), cirripedes (e.g. *Balanus*) and bryozoa. Algal growths, microcrustacean and others epizoo-bionts were potential trophic resources for grazers and scavengers. However, they were fixed on the protein composing the turtle scutes and they are not recorded on the fossil material.

Moreover, the sea urchins *Arbacia punctulata* and *Lytechinus variegatus* have been reported as epizoo-bionts on specimens of *Caretta caretta* hosting the green algae *Acetabularia crenulata* and *Chaetomorpha linum* (Pfaller et al., 2008). These sea urchins were likely grazing algae from the carapace. However, in fossil specimens such as *Hispaniachelys prebetica* it is not possible to recognise this type of relationship.

Taphonomic interpretation

The low degree of fragmentation and the low dispersion of skeletal components of the turtle are consistent with a low-energy environment and rapid burial. This is congruent with the absence of any sedimentary structures indicating turbulence and is also supported by the micro-facies comprising a fine-grained wackestone with peloids. Previous taphonomic studies on macroinvertebrate assemblages (primarily ammonoids) have indicated a low energy and low degree of fragmentation within a softground in a mid-shelf environment (Reolid, 2003; Olóriz et al., 2006). A convex-down position of a turtle carapace prevents or slows down disarticulation, as shown in burial experiments using hawksbill turtles (Meyer, 1991).

The burial orientation of the *H. prebetica* may have arisen from post-mortem activity of large scavengers (Slater et al., 2011). The action of scavengers is cited as a further possible reason for carapace-down burial of terrestrial turtles in both modern and fossil death assemblages from fluvial deposits, in studies of turtle taphonomy by Corsini et al. (2006) and Corsini and Chamberlain (2009). However, Brand et al. (2000) observed high variability of orientations of turtle carapace in lacustrine deposits (Middle Eocene, Wyoming), with common upside down orientations. The fragmentation of some bones of *Hispaniachelys prebetica* could also be related to scavenging activity by larger organ-

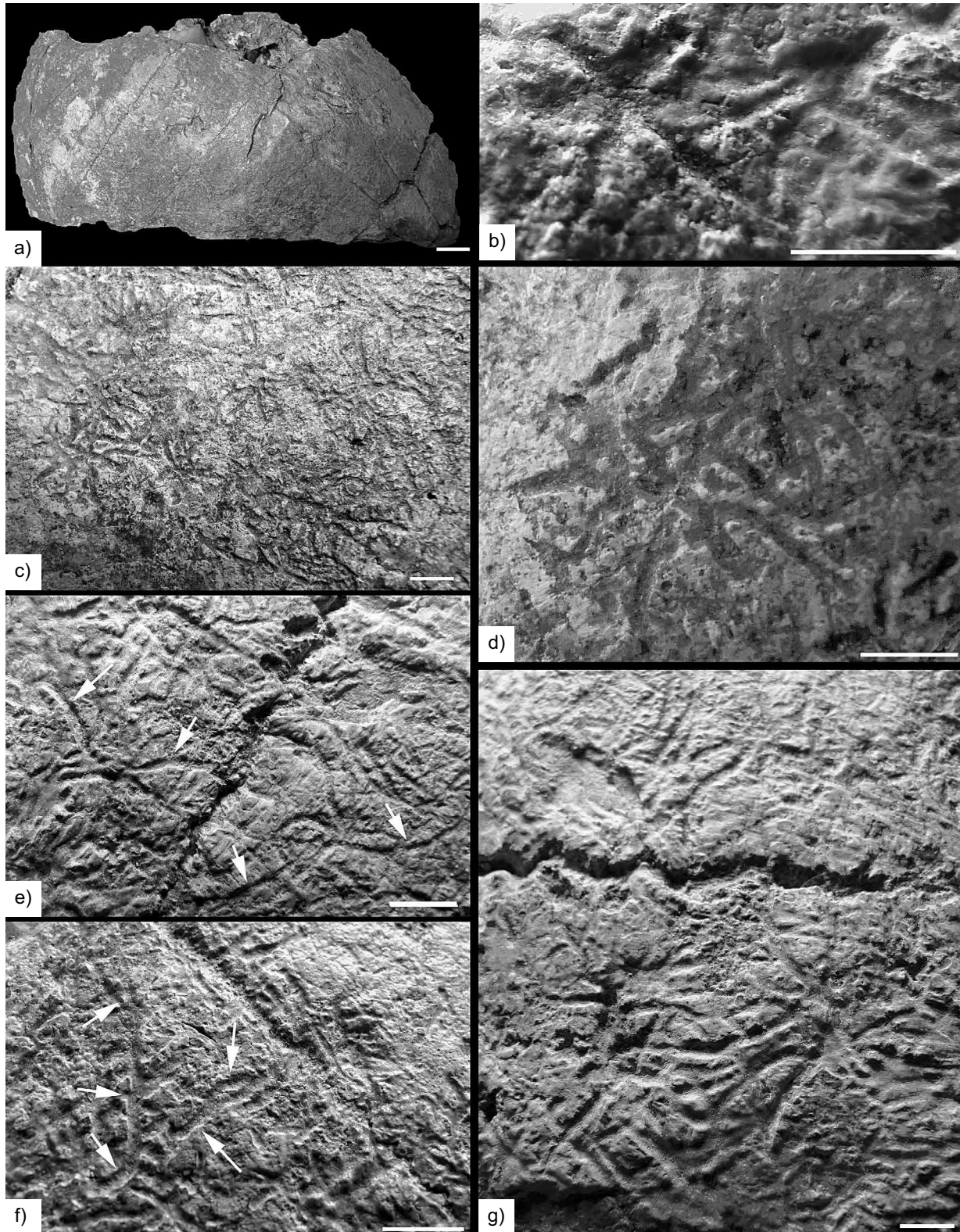


Figure 3. Echinoid grazing traces, *Gnathichnus pentax*, on the *Hispaniachelys prebetica* turtle carapace from the Prebetic (Betic Cordillera, South Spain). a) External surface of *Hispaniachelys prebetica* carapace entirely sculptured with traces produced by the grazing activity of regular echinoids (*Gnathichnus pentax*). Scale bar 20 mm. b) Detail of *Gnathichnus pentax* showing the characteristic pentaradiate morphology. Scale bar 5 mm. c) Compound star-shaped morphology produced by the repetition of overlapping pattern. Scale bar 5 mm. d) Detail of *Gnathichnus pentax* compound morphology. Scale bar 5 mm. e) Sinuous grooves overlapping star-shaped patterns of *Gnathichnus pentax*. f) Further detail of the sinuous grooves overlapping star-shaped patterns of *Gnathichnus pentax*. Scale bar 5 mm. g) Vicinity of a suture line on *Hispaniachelys prebetica* where the lengths of the radius are longer and the grooves became densely packed and more or less parallel. Scale bar 5 mm.

isms, since the water energy was likely too low to cause the breakage of bones (supported by the very low fragmentation present in ammonoids of the bed RGCH-62). The plastron presumably collapsed under sedimentary loading.

The distribution of bioerosion indicates preferential exploitation of the carapace. The external surface of the carapace was oriented downwards in the bed, and so pascichnial activity probably occurred prior to overturning of the carapace. According to the studies of Meyer (1991) in intertidal sandy environments, a carapace buried convex-up was completely disarticulated within ten days, whereas a carapace buried convex-down was still almost intact after fifteen days, although it has to be used with caution as an argument to understand the pre-burial taphonomic processes in this case study. However, Brand *et al.* (2003) conducted an experimental study of decay and disarticulation of freshwater turtles (*Trachemys scripta*) and the carapace was disarticulated in more than 15 weeks. The disarticulation times of Brand *et al.* (2003) have to be taken with care due the experiment eliminated scavenging and distort the taphonomic process, and the experiment was conducted in aquaria with a filter system to reduce the buildup of bacteria in the water. Therefore, following the disarticulation times proposed by Meyer (1991), the exploitation of the study carapace by regular echinoids likely occurred early after the accumulation of the turtle remains on the sea floor but before the overturning of the carapace by large scavengers. This presumably explains the absence of bioerosion on the plastron, which would have been buried and so sheltered from borers and grazers. The collapse of the plastron is congruent with the early burial beneath loose sediment, causing it to cave in to the internal cavities.

The grazer's action presumably occurred when the turtle carapace was already covered by algae during its stay on the sea floor. In an environment like this, where soft bottoms were widespread, the skeletal fragments were the only hard substrates, which were available for colonization by algae and then the exploitation by their grazers. However, the presence of thin algal mats on the turtle carapace (exposed to light) and their absence on the plastron (shadow surface) during life cannot be rejected, as shown in Recent aquatic turtles (Frick *et al.*, 1998; Pfaller *et al.*, 2008), also explaining the location of *Gnathichnus* on the carapace. Meyer (1991) noted that the costal plates of the carapace of modern hawksbill turtle skeletons are often covered in grazing traces formed by sea urchins as they remove algae and other organic material encrusting the carapacial bone. No epibionts were found encrusting the specimen, even though barnacles and algae are common encrusters in recent living turtles (Pfaller *et al.*, 2008; among others). Many barnacle species are found exclusively attached to turtle shells today, although these would be removed when the turtle died and the dermal scutes to which they were attached rotted away (Pfaller *et al.*, 2006, 2008).

According to Slater *et al.* (2011), the thick, heavily ossified carapace of *Hispanichelys prebetica* would have been a useful adaptation in a coastal marine habitat where manoeuvrability and protection are more important than weight reduction and energy conservation. Ocean wandering turtles today reduce drag by having a shallow streamlined shell. Probably the fossil turtle lived in shallow coastal environments within the shallow euphotic zone confirming the possibility of algal encrustation during life, which were exploited as a trophic resource by sea urchins after the death of the turtle.

Therefore, the bony plates of the carapace, the protein-rich scutes and algal encrustations could have been the trophic resource grazed by the sea urchins producing the *Gnathichnus pentax* trace fossil. However, bioerosion of the bone result an extra work if they were simply grazing on algae, and the grazing on the bone for obtaining phosphate is an additional possibility.

Palaeoenvironmental interpretation

Hard substrate ichnofacies characterized by epigenic and superficial grazing traces such as those recorded herein typify Bromley and Asgaard's (1993a) *Gnathichnus* Ichnofacies. According to Bromley (1975) the ichnogenus *Gnathichnus* is known to characterize shallow water substrates. Their producers, regular echinoids, are particularly common on hard substrates within the euphotic zone today, where they graze on algae (Smith, 1984). With increasing depth and reducing light penetration, the stands of algae disappear and algal grazers are confined to areas where there is a supply of drift algae supply (Smith *et al.*, 2006).

Previous studies of Oxfordian macroinvertebrate assemblages (Reolid, 2003; Oloriz *et al.*, 2006) as well as sponge-microbialite build-ups (Oloriz *et al.*, 2003; Reolid, 2011) in the Prebetic suggested a sea depth of 60 m in this area, *i.e.*, a mid-outer neritic biota. Nevertheless, the presence of both regular echinoids and grazing traces produced by them on the turtle carapace suggests that the deposit lay seaward of the proximal shallow euphotic zone (inner shelf), which is compatible with the relative transparency envisaged for the water column. Also, the presence of *Chondrites* and *Planolites*, and exceptionally *Thalassinoides* trace fossils, can be included in the *Cruziana* Ichnofacies, whose conditions typically range from moderate energy levels lying below fair weather wave base but above storm wave base, to lower energy levels in deeper, quieter waters (MacEachern *et al.*, 2007). The most common settings correspond to the offshore, extending to the very distal fringes of the lower shoreface (MacEachern *et al.*, 2007).

From an ethological point of view, only epigenic and shallow-tier structures (pascichnia) are present on the turtle carapace. This ichnoassemblage can be correlated with the stability of the substrate, the level of hydrodynamic energy as well as the time interval of the colonization window. The high density of *Gnathichnus* records a period of non-deposition of sediment and exposure of the turtle carapace before its burial, but is more controlled by the type of substrate. The physical properties of the carapace substrate as well as the surrounding softground controlled this ichnofacies, which is known to depend upon hard, exposed substrates. This is in agreement with Gibert *et al.* (2007), who suggested that the *Gnathichnus* producers responded to short periods of exposure of hard substrates, spatially restricted substrates, and instability of the substrate.

CONCLUSIONS

The present study of grazing structures on a sea turtle carapace from the Upper Jurassic of the south of Spain provides new insights into their taphonomic interpretation, by paying special attention to the palaeoecology of trace fossils. The carapace constituted an important substrate, especially after death, supporting several encrusting, boring or more frequently grazing organisms. In this work

Gnathichnus pentax is described for the first time upon an Oxfordian sea turtle carapace.

The *Gnathichnus* Ichnofacies records a short period of exposure of the turtle carapace before its burial. The high concentration of *Gnathichnus* on the external surface of the carapace resulted shows it was a favourable hard substrate in comparison to the surrounding soft bottom. Sea urchins grazed the carapace to obtain food from the bony material of the plates, the protein of scutes, or algal encrustations. The external surface of the carapace, where the bioerosion is located, was oriented downwards in the bed, and so pascichnial activity probably occurred early after the turtle remains accumulated on the sea floor and before the carapace was overturned. After the death of the turtle, early overturning of the carapace to the convex-down position avoided disarticulation and explains the subsequent collapse of the plastron.

The low degree of fragmentation, the absence of encrusters and the low dispersion of skeletal components are consistent with a low-energy environment and early burial after the accumulation of the remains on the sea floor.

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