

Evidence of predation in Early Cretaceous unionoid bivalves from freshwater sediments in the Cameros Basin, Spain

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Here, we present evidence of possible vertebrate predation on freshwater bivalves from the Lower Cretaceous strata of the Cameros Basin (Spain). The described collection contains the largest number of vertebrate-inflicted shell injuries in freshwater bivalve shells yet reported in the Mesozoic continental record. Several types of shell damage on fossil shells of *Protopleurobema numantina* (Bivalvia: Unionoida) are described and their respective modes of formation interpreted in the context of morphological attributes of the shell injuries and the inferred tooth morphology of predators that could have inflicted such injuries. Detailed study of these bite marks shows similarities with the well-documented injuries in the shells of marine molluscs, namely ammonoids, that have likewise been attributed to reptilian predators. The most parsimonious interpretation suggests crocodiles as the vertebrates interacting with the bivalves in the Cameros Basin. \Box Barremian–Aptian; bite marks; freshwater bivalves; predation; reptile; Unionoida.

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During the development of taxonomic studies on the molluscs of the Early Cretaceous Valdeperillo site (Cameros Basin), carried out by Delvene & Araujo (2009), some peculiar marks were detected in part of the material collected. Consistent characteristics of these marks pointed to some kind of biogenic interference with the bivalve shells. Given the rarity of this kind of mark in the Early Cretaceous freshwater record, this article describes them and identifies a potential producing agent.

The sedimentary succession of the Cameros Basin (Northwest of the Iberian Range, Spain) (Fig. 1A) consisting mainly of continental sediments is divided into eight depositional sequences, DS1–DS8 in ascending order (Mas *et al.* 1993, 2002, 2011). The studied bivalve remains come from the Valdeperillo site, close to the town with the same name in the La Rioja province. Lithostratigraphically, the interval from which our bivalves were collected corresponds to Unit D of the Urbión Group, the uppermost of four units (A–D in ascending order) in the scheme of Barrenechea (1993). Among depositional sequences, our section (Fig. 1B) is included in the DS7 depositional sequence, whose age is approximately latest Barremian–Early Aptian (Mas *et al.* 2002, 2011).

The freshwater bivalves are assigned to the genus *Protopleurobema* (Superfamily Unionoidea), of which all known specimens were collected exclusively from Unit D of the Urbión Group in the Cameros Basin (Delvene & Araujo 2009, and this study). Meticulous examination of the available material has revealed injuries on 34 of the specimens.

Taphonomic context

The shells of *Protopleurobema numantina* (Palacios & Sánchez 1885) are trigonal in shape, with a posterior slight wing and a robust hinge with massive pseudo-cardinal teeth and grooves on the teeth and sockets. The largest specimens attain a maximum shell length of up to 120 mm and a maximum umbonal thickness of 12.6 mm.

As for most known unionoids, *P. numantina* has been interpreted as a shallow infaunal suspension feeder (Delvene & Araujo 2009). This species is abundant in strata exposed at the Valdeperillo site with both juvenile and adult growth stages represented. Articulated specimens in 'butterfly' position are common and the proportion of right and left valves is approximately equal for disarticulated specimens. These taphonomic observations suggest a low degree of post-mortem physical transport disturbance, and thus an assemblage of parautochtonous character. As such, it is reasonable to assume that the faunal composition of the assemblages closely approximates that of the original living community from which the shells were derived.

At Valdeperillo, *P. numantina* has been recorded at two different stratigraphic levels (Fig. 1B) that together constitute the greater part of the fossil record of this species. In both cases, the fossil assemblages represented are dominated by *P. numantina* to the extent of near monospecificity, with large but poorly preserved specimens of *Viviparus* being the only other macrofaunal elements associated with these bivalves (Delvene & Araujo 2009).

The umbonal-anterior part of *P. numantina* constitutes the maximum thickness of the shell, coinciding with the area of the underlying visceral mass in which soft parts would have been most concentrated in the living organism. The convexity of the shell is pronounced in the shoulder of the shell and the injuries are frequent on this area. The posterior region of the shell is usually broken and/or missing, but such damage is likely more a function of sedimentological/taphonomic factors (i.e. reflecting the greater fragility of this relatively thin part of the shell) than biogenic agents such as predation.

Material and methods

The studied collection consists of 805 bivalve specimens (Delvene & Araujo 2009), 34 of which bear evidence of injuries (Table 1). According to the rules of the La Rioja Government, the specimens include the prefix VDPR (an abbreviation for the Valdeperillo site), followed by a capital letter indicating the stratigraphic level of collection (e.g. 'A' for level A) and a unique distinguishing number. All specimens have been loaned to the Instituto Geológico y Minero de España and will ultimately be deposited at the 'Centro Paleontológico de Enciso' (Enciso locality, La Rioja province) when the study is finished and the results published.

The specimens of injured bivalves described herein were collected from two different stratigraphical levels: nine from level A (VDPR-A) and 25 from level C (VDPR-C). Levels A and C correspond to fine-grained sandstones and marls respectively (Fig. 1B). The proportion of injured valves to the total number of specimens collected from each level (125 in A and 680 in C), was calculated to be 7.2 and 3.68% for levels A and C respectively.



Fig. 1. Geographical and geological setting. A, Geographical location of the Cameros Basin and Valdeperillo site. B, Studied log at Valdeperillo site (Urbión Group, Cameros Basin).

Table 1. List of injured specimens indicating the fossil type (LV = left valve; RV = right valve; A = articulated specimen; Juv = juvenile) and kind of the identified marks: Den. = dents; (dd) = double dent; (m) = mark located on the internal mould; Perf. = perforations; Tri. pr. = triangular projection; L. dep. = linear depressions; L. gash. = linear gashes; R. frac. = radial fractures; Notc. = notched edges; Spal. = spall marks; Pres. = pressure deformation; X= presence; -= absence; VDPR-A = Valdeperillo level A; VDPR-C = Valdeperillo level C.

Specimen	Fossil type	Den.	Perf.	Tri. pr.	L.dep.	L.gash.	R.frac.	Notc.	Spal.	Pres.
VDPR-A-2	A (RV)	1(m)	_	_	_	_	_	_	_	_
VDPR-A-9	LV	_	1	-	-	_	_	х	_	_
VDPR-A-10	RV	1	_	-	-	_	_	_	_	_
VDPR-A-11	RV	_	1	_	_	_	_	х	х	-
VDPR-A-12	А	1	_	_	_	_	_	_	_	-
VDPR-A-13	А	1	_	_	_	_	_	_	_	-
VDPR-A-16	LV	_	_	_	_	_	_	_	_	х
VDPR-A-17	RV	_	1	_	_	_	_	_	_	-
VDPR-A-19	RV	2(m)	_	_	_	_	_	_	_	-
VDPR-C-7	RV	_	_	_	1	_	_	_	_	-
VDPR-C-11	RV	_	_	_	_	1	_	_	_	-
VDPR-C-14	RV	1	_	_	_	_	_	_	_	-
VDPR-C-22	A (Juv)	1	_	_	_	_	_	_	_	х
VDPR-C-27	A (Juv)	1(dd)	_	_	_	_	_	_	_	-
VDPR-C-33	RV (Juv)	1	1	_	_	_	_	_	_	-
VDPR-C-36	LV	1	_	_	_	_	_	_	_	х
VDPR-C-61	RV	-	1	х	_	-	X	-	х	-
VDPR-C-62	LV	2	_	_	_	_	_	х	х	-
VDPR-C-63	RV (Juv)	1	1	х	_	-	X	X	х	-
VDPR-C-64	LV	1	1	х	_	-	-	X	-	-
VDPR-C-66	RV	1	-	_	_	1	-	-	-	-
VDPR-C-67	LV	1	-	_	_	-	-	-	-	-
VDPR-C-68	LV	-	-	_	1	-	-	-	-	-
VDPR-C-69	LV	1	-	_	_	-	-	-	-	-
VDPR-C-70	LV	2	1	_	_	-	X	X	-	-
VDPR-C-72	RV	1	-	_	_	-	-	-	-	-
VDPR-C-79	LV	2	-	_	_	-	-	-	-	-
VDPR-C-88	LV	1	-	_	1	-	-	-	-	-
VDPR-C-89	LV	1	-	_	-	-	-	-	-	-
VDPR-C-91	RV	-	-	-	1	-	-	-	-	-
VDPR-C-93	RV	-	1	-	_	-	х	X	-	х
VDPR-C-94	LV	-	1	-	_	-	_	-	-	-
VDPR-C-98	RV (Juv)	1	-	-	_	-	_	-	-	-
VDPR-C-110	RV	-	-	-	-	2	-	-	-	-

Of the total 34 injured bivalve specimens, five are articulated ones. Of the remaining 29 (disarticulated) specimens, 16 are right valves and 13 are left valves (Table 1).

Although effects of re-crystallization and dissolution are both obvious and extensive in all injured bivalve specimens examined for this study, the shell injuries themselves are quite well preserved. Even so, there are examples where the injury marks appear to have been partially obscured by the effects of dissolution and we recognize that it may be difficult to discriminate these features from others solely caused by dissolution. To reduce the risk of such misidentification, several specimens bearing dubious evidence of true injury were excluded from this study. As such, it should be noted that in addition to the specimens included in Table 1, there are probably many specimens in our collection that preserve true injuries, but for which evidence of this has been blurred by the effects of dissolution.

As discussed below, although predation or scavenging appears to be the most obvious possible cause of patterns of shell damage in our bivalve specimens, we also recognize that physical deformation could potentially modify shell features in ways that mimic predation-related shell damage. We use the term pressure deformation to anomalies in shell shape that do not appear to have been produced by one or more isolated elements (e.g. individual teeth) and thus are unlikely to have a biogenic origin. Four of these specimens show injuries in addition to the pressure deformation (Table 1). The effects of the pressure deformation are more evident just behind the shoulder of the shell, where its thickness decreases, as it can be observed in specimen VDPR-C-65 (Fig. 2A, B).

Shell injury terminology and description

Significant research has been conducted on the characteristics of bite marks inflicted in skeletal tissues of mammals by mammalian carnivores (e.g. Bindford 1981; Lyman 1994) and recent studies have attempted to characterize patterns of bone damage in bite marks produced by reptiles on mammals (e.g. Njau & Blumenschine 2006). In comparison, however, studies of bite marks produced by vertebrate predators on invertebrate prey (notably, molluscs), remain relatively slim. Most such studies have dealt exclusively with marine faunas and, of these, many have focussed primarily on mosasaur bite marks on ammonoids (e.g. Kauffman & Kesling 1960; Hewitt & Westermann 1990; Kauffman 2004). As pointed by Gorzelak *et al.* (2010), data of predation on non-marine fossil molluscs are almost completely lacking, with significant studies limited to those of Kear & Godthelp (2008), Bermúdez-Rochas *et al.* (2009) and Gorzelak *et al.* (2010) (see below).

For the purpose of comparing types of predation-related shell injuries in molluscs of different taxonomic groups, age and geographical occurrence, a common terminology is necessary. To that end, we have adopted Tsujita & Westermann's (2001) terminology that, although originally used in the context of bite mark features in ammonoid shells, is applicable to analogous features observed in the bivalve shells described herein. With an aim of unifying the existing terminology on bite marks and associated features, we also consider a number of terms employed by other authors (especially those used in disciplines of study other than our own) that may be regarded as synonyms. Individual types of shell injuries recognized by us are defined, and described in detail below.

Dents

Dents represent circular or oval depressions on the shell surface that are not perforated (Fig. 3A, B). A mark of this type manifests the damage inflicted by point loading on a shell in cases where the shell resisted puncture, but was rendered permanently indented due to partial failure of the shell structure. As such, a dent can retain its original thickness in the affected location of the shell, as opposed to showing an obvious thinning of the shell that would otherwise indicate a diagenetic origin in some cases (e.g. by dissolution). The term 'dent' was used by Kauffman & Kesling (1960), Ward & Hollingworth (1990) and Tsujita & Westermann (2001), and is likewise favoured by us. Terms used by other authors that may be considered synonyms to 'dent' include 'indentation' (as used by Kauffman 1972; Ward & Hollingworth 1990; and Kear & Godthelp 2008) and 'indentation without puncture' (Kase et al. 1998). 'Dent' could also be considered equivalent to the terms 'pit' and 'pitting' (Bindford 1981; Njau & Blumenschine 2006), or 'shallow pitting' (Maguire et al. 1980), as used specifically in studies on nonperforated bite marks in mammalian remains.

We have identified 22 specimens with dents (Figs 4A–D, 5A–C). In ideal cases where both axes of the dent are preserved, the measurement recorded is the length of the minor axis (see Discussion). The best-preserved dents vary in diameter from 2.8 mm (VDPR-C-62 and VDPR-C-63) to 4.5 mm (VDPR-C-64) (Figs 4A–C, 5A–C).

Seventeen specimens bear a single dent and five of them bear two dents in the same specimen (VDPR-A-19, VDPR-C-62 [Fig. 4A–C], VDPR-C-70, VDPR-C-79, VDPR-C-27). VDPR-C-27, an articulated specimen also preserves two dents (Fig. 4D), but it is unique in that the individual dents not only occur on separate valves but are sufficiently close to one another to be regarded together as a double dent. Here, the term 'double dent' is akin to the 'double perforation', of Tsujita & Westermann (2001), but it is distinguished by not exhibiting evidence of full penetration of a shell by the dent-producing object. The resulting morphology in so proximal marks could completely obliterate the two individual dents.



Fig. 2. Pressure deformation on VDPR-C-65 (left valve), in internal (A) and external (B) views.



Fig. 3. Schematic diagram showing the formation of dents and perforations in bivalve shells affected by perpendicular point loading by a tooth. A1–A2, formation of a dent, without the development of adjacent fractures. B1–B2, development of a dent with inward fractures and partial displacement of the shell. C1–C2, formation of a perforation with complete detachment of the shell affected by point loading, with formation of inward-diverging fractures in the perforation's perimeter. D1–D2, development of a perforation with adjacent spall marks.



Fig. 4. Specimens showing dents, notched edge, and double dent. A–C: VDPR-C-62 (left valve) showing dents (d) and notched edge, in external (A), posterior (B) and internal (C) views. D: VDPR-C-27 (articulated specimen) in anterior view, showing a double dent.

Taken collectively, the dents preserved in our specimens show no evidence of preferential siting on particular areas of the shell, but do tend to be more deeply impressed in the posterior and shoulder areas of the shell than elsewhere. This may simply reflect the tendency of this thinner walled part of the shell to succumb to the bending stresses generated during tooth impact; thicker areas of the shell would presumably have been more resistant to failure by point loading. Consistent with this interpretation, some of these posteriorly sited dents show some gradation to true perforations (see below).

Although dents are most conspicuous on the shell surface, two bivalve specimens (VDPR-A-2 and VDPR-A-19) preserve impressions of these features in their internal moulds (Table 1). This suggests that the dents were made in the shell before soft sediments penetrated and filled the cavity between the articulated shell, and thus also prior to the onset of significant diagenetic processes such as sediment induration. As such, we think it more likely that the observed dents were produced on the shell as a consequence of shell impact by predator teeth than by post-burial phenomena associated with diagenesis.

Specimens VDPR-C-62 and VDPR-C-63 (Figs 4A– C, 5A–B) preserve deep dents on the external surface of the shell, which have penetrated towards the shell interior. The result is a local spalling of the inner shell layer on the internal side of the valve. This is probably due to the dissolution or detachment of the fractured inner layer after the projection of the dent from the exterior. Both specimens, VDPR-C-62 and VDPR-C-63, show preferential dissolution in the thinnest areas of the shell. The result is a dent on the external and internal sides of the shell, deeper in the external part of the specimen, allowing us to determine the direction of the injury from the outside to the inside of the bivalve.

Perforations

We use the term 'perforation' to describe discrete punctures of the shell with well-defined margins that

typically range in shape from approximately circular to oval in outline (Fig. 3C-D). Such features record the brittle failure and subsequent penetration of the shell by an impacting object in cases where the point load pressure exerted by that object greatly exceeded the resistance of the shell material against local bending stresses. 'Perforation', our preferred term for these features, has been used to describe analogous features in ammonoid shells by Kauffman & Kesling (1960) and by subsequent authors such as Tsujita & Westermann (2001). The term 'puncture' as used by Ward & Hollingworth (1990), Kase et al. (1998), and in mammalian bite mark studies (e.g. Bindford 1981; or Njau & Blumenschine 2006) can be regarded as synonymous. Likewise, equivalent are the 'punctuate depressions' of Maguire et al. (1980), and the 'round holes' described by Saul (1979).

Ten specimens in our collection clearly preserve perforations (Figs 5A-C, 6A-E); of these, three specimens also preserve a single dent (VDPR-C-63, VDPR-C-64, VDPR-C-33), and one preserves two dents (VDPR-C-70). The remaining six specimens bear partial outlines of perforations preserved as arc-shaped crenulations along a broken edge in the thin-walled, posterior part of the shell (e.g. Fig. 5A-C; see below). The diameter of the perforations ranges from 3.3 mm (in specimen VDPR-C-93) to 4.0 mm (in specimen VDPR-C-63). Specimen VDPR-C-94 features a 4.2mm diameter perforation on the anterior commissural edge of the shell (Fig. 6C). In only one of our specimens (VDPR-C-61) is the entire outline of the perforation preserved; located approximately in the central area of the shell, this perforation has a minor axis of 3.9 mm (Fig. 6A, B, D, E).

Dents or perforations with triangular projections. – This term is applied to a dent or perforation that



Fig. 5. Specimens showing dents (d) with triangular projections, perforations (p), notched edges and spall marks. A, B, VDPR-C-63 (right valve) in external (A) and internal (B) views. C, VDPR-C-64 (left valve) in external view.



Fig. 6. Specimens showing perforations. A, B, D, E, VDPR-C-61 (right valve) showing perforation, spall marks and radial fractures, in external (A–B), and internal views (D–E), and details of radial fractures (B) and spall marks (D). C, VDPR-C-94 (left valve), specimen showing a perforation in the commissure, in anterior view.

exhibits some degree of angularity in the shape of its outline. We here modify the Njau & Blumenschine's (2006) term 'perforation with triangular projection', to include not only perforations, but also their nonperforated counterparts (i.e. dents).

Individual dents present in specimens VDPR-C-63 (Fig. 5A–B), VDPR-C-64 (Fig. 5C) and VDPR-C-67 each feature a unique triangular projection. However, the perforation in specimen VDPR-C-61 (Fig. 6A–B, D–E) shows two visible triangular projections. We regard the latter example as analogous to the 'angular or triangular holes' and the 'eye-shaped perforations' noted previously in ammonoid shells by Saul (1979), and Tsujita & Westermann (2001) respectively. We speculate that the triangular projections associated with the dents and perforations reflect a bicarinate tooth morphology in the vertebrate predator that produced these injuries (see Njau & Blumenschine 2006).

Linear depressions

Associated with dents and perforations in some bivalve shells of our collection are shallow elongated depressions. Four specimens show linear depressions (Table 1) that range in length from 7.4 mm in VDPR-C-88 to at least 10.3 mm in VDPR-C-7 (Fig. 7A, B), with the latter incomplete specimen representing only part of a longer depression that must have existed on the original shell. The depths of linear depression range from a minimum of 1 mm in VDPR-C-7 to a maximum of 2 mm in VDPR-C-88, and vary in cross-sectional profile from U-shaped (VDPR-C-68, VDPR-C-7, VDPR-C-91) to almost V-shaped (VDPR-C-88). We interpret these linear depressions as having been produced by the dragging of a predator's tooth (or teeth) against the shell (Tsujita & Westermann 2001). The term 'shell scarring', as used by



Fig. 7. Specimens showing linear marks. A, B, VDPR-C-7 (right valve) showing a linear depression, in external (A) and postero-ventral (B) views. C, VDPR-C-66 (right valve) in anterior view, showing a linear gash.

Gorzelak *et al.* (2010) may be regarded equivalent to the 'linear depressions' we describe above.

Linear gashes

These features, although similar to the shallow linear depressions described above, are distinguished by their direct association with tear features in the shell.

Three specimens show linear gashes of markedly different dimensions and overall shape. In the specimen VDPR-C-110, it measures 9 mm; 26.3 mm in specimen VDPR-C-11; and it reaches 27 mm in length in VDPR-C-66 (Fig. 7C). All three are curved and with a U-shaped cross section. The width ranges from 3 mm (VDPR-C-110) to 3.8 mm (VDPR-C-11); and the maximum depth is 1 mm in specimen VDPR-C-66. This kind of mark is similar to deep 'linear depressions', but part of the shell has been torn out along the mark (see Tsujita & Westermann 2001; Fig 5). Other terms used to describe different elongated depressions, frequently used in mammal bibliography are: 'scoring' or 'score' (e.g. Bindford 1981; Njau & Blumenschine 2006); 'striations' or 'gouge marks' (Maguire et al. 1980); and 'tooth scratches' (Shipman 1981; see Lyman 1994). These terms should be avoided in the description of mollusc marks.

Additional features associated with main bite marks

Associated with the main injuries observed in the studied bivalve shells are a variety of structural

features to which a predator-related origin can also be ascertained. These are as described below.

Radial fractures. – These fractures, normally grouped in sets of two or more fractures, are seen clearly emanating in radial pattern from dents and perforations, and are synonymous to the 'radial cracks' of Kear & Godthelp (2008). Four specimens in our collection show radial fractures (Table 1) on the external surface of the shell. Of these, specimen VDPR-C-61 (Fig. 6A– B) is particularly notable in preserving six prominent radial fractures.

Notched edges. – This term is applied to the irregular, broken edge of a shell (of which the complementary portion of the damaged shell is missing), that preserve the borders of one or more dents and/or perforations.

Seven specimens in our collection preserve notched edges (Table 1). All except for the VDPR-C-62 (Fig. 4A–C), whose notched edge is associated to a dent, are related to perforations (Fig. 5A–C). These irregular fractures may well have developed in response to the same point loading event that produced their associated perforation/dent. However, we cannot completely discount the possibility that dents or perforations created local structural weaknesses within the shell and, in turn, simply enhanced the tendency for fractures to be generated during sediment compaction. 'Notched edge' could be considered synonymous to the term 'crenulated edge', the latter term commonly used in mammal taphonomic literature (e.g. Bindford 1981). *Spall marks.* – Some specimens show evidence of localized delamination and/or detachment of the inner layer in direct association with perforations and/or dents. These marks, preserved on the interior surface of shells as pits with polygonal edges are interpreted by us as features of localized areas of shell failure that were generated ahead of point loads as they penetrated through the shell. In the case of a perforation, a spall mark could be considered to approximate the exit point of the perforating object.

Four specimens show spall marks on the internal part of the shell (Table 1), one associated to a dent and three associated to perforations. The former (VDPR-C-62; Fig. 4C) measures 0.9 mm (measured radially from the external limit of the dent/perforation). Spall marks in the latter specimens vary from 1.3 mm in VDPR-C-63 (Fig. 5B) to 5.4 mm in VDPR-A-11. Arguably, the best example of a spall mark in our collection, measuring approximately up to 5.1 mm in extension around the perforation and having a roughly pentagonal outline, is featured in specimen VDPR-C-61 (Fig. 6D, E).

Discussion

Origin of the injuries

We acknowledge that without the direct association of vertebrate remains with Valdeperillo bivalve specimens, it is not possible to identify the producer of the marks described here with absolute certainty. However, it is possible to identify some potential candidates and to deduce which of these would have been the more likely predator.

The attributes of shell injuries noted among unionoid bivalve shells from Valdeperillo do not seem consistent with those that could be realistically expected from any known invertebrate. And, as unionoids are clearly freshwater organisms, we can immediately exclude any known marine predator.

The morphological attributes of the bite marks described herein differ markedly from boring gastropod's marks. The drilling activities of carnivorous gastropods on the shell of other molluscs are well known (Bromley 1981). According to this author, among the major groups of gastropods in which boring habits are known, Naticidae, Muricoidea, Tonnoidea, Capulidae and nudibranchs, are exclusively marine. All marine mentioned groups and, according to Carriker & Yochelson (1968), some Pulmonata (freshwater) are indeed capable of boring into the bivalves' shells to acquire food (from bivalve soft tissues) and minerals (specifically calcium carbonate from the bivalve shell). However, at odds with the injuries described herein, the physical and mechanical processes involved in such activity result in well-rounded holes with no associated fractures, and sometimes with micro-rasping marks associated (Schiffbauer *et al.* 2008). No *Radilichnus*-like micro-rasping marks were observed in our studied bite marks. Furthermore, no carnivorous pulmonate gastropod has been recorded at the same stratigraphic horizons as *P. numantina*. As noted above, *Viviparus*, a known filter-feeder (Dillon 2000), is the only gastropod that has been found in direct association with this bivalve.

Two other major groups of freshwater taxa known to produce holes in shells are turbelarians and nematodes (Bromley 1981), although neither of them are likely to have made the holes observed in the Valdeperillo bivalves. Turbelarian borings are too dissimilar in cross-sectional shape (and more comparable to naticid gastropods borings; Bromley 1981) and nematode borings are simply too minute in size to be realistically confused with the holes described here. Thus, we rule out these organisms as producers of the observed injuries as well.

Patelliform gastropods are known from various non-marine aquatic habitats, and although these are unrelated to true patellogastropods, one might speculate that they could produce home scar structures comparable to those alleged to occur on ammonoid shells. A few authors (e.g. Kase et al. 1998; Seilacher 1998; Machalski 1999; Tsujita & Westermann 2001; Wahl 2008) have commented on the idea that such home scars could be modified during sediment compaction to give the illusion that they were punctured by teeth of large predators. However, other authors have regarded this mode of hole formation secondary to tooth impact as the most common perforating agent (at least among ammonoids). We agree with Tsujita & Westermann (2001) in their assertion that the mosasaur predation hypothesis of Kauffman & Kesling (1960) provides the parsimonious explanation for the occurrence and morphological characteristics of the perforations observed in ammonite shells. This hypothesis does not exclude the possibility of some marks that were produced by the collapse of home scars of patellogastropods, as seen in Kase et al. (1994, 1998). But, this seems unlikely in the context of our material as it fails to account for several associated characters, such as radial fractures, spall marks and linear depressions and gashes. In addition, we have not found any evidence to suggest the former presence of patelliform gastropods or their expected radular grazing marks in the bivalve-bearing unit.

Semionotiform fishes (ganoid scales) have been recovered in a lower level of the stratal unit exposed at the Valdeperillo site (Bermúdez-Rochas *et al.* 2006). However, the large number of specimens bearing

single, isolated marks seems to exclude actinopterygian fishes (like semionotiforms or pycnodontiforms) and durophagous sharks as the potential predators of the unionids. The fact that the teeth of such fishes are so closely spaced indicates that the production of a single, isolated mark caused by the insertion of a single tooth is unlikely. Non-durophagous sharks have been inferred as predators of ammonoids and nautiloids in the Pennsylvanian (Mapes & Hansen 1984; Mapes et al. 1995) and in the Late Jurassic (Vullo 2011), but the thickness of Protopleurobema shells renders this possibility unlikely as well. Gorzelak et al. (2010) state that Late Triassic freshwater bivalves may have been preved upon by ceratodont lungfishes, and add that ceratodont tooth plates would be expected to produce 'radiate tooth marks' in bivalves (Gorzelak et al. 2010). There is no presence of ceratodont lungfishes in the Urbión Group; and in any case, the tooth plates of lungfishes could not have been the producers of individual circular to oval dents or perforations, as the ones found in Valdeperillo.

In summary, individual injury marks observed on the Valdeperillo bivalve shells appear to have been produced by the pressure of isolated elements (e.g. teeth) with a more or less conical morphology. Variations in the orientation and/or loading pressure of these elements against a shell could account for the different marks observed: (1) if the pressure was applied perpendicular to the shell surface, a dent (reflecting low pressure of loading and/or high resistance of the shell) or a perforation (reflecting high pressure and/or low resistance of the shell) would have been produced; and, (2) if the pressure was applied at an oblique angle to the shell surface, the result would have varied in form from a linear depression (reflecting low pressure of loading and/or high resistance of the shell) to a linear gash (reflecting high pressure and/or low resistance of the shell).

Marks preserved in specimens VDPR-C-62 and VDPR-C-63 (Figs 4A-C, 5A-B) might, at first glance, appear to conflict with this interpretation. Both specimens feature a single dent with an inward sloping margin and concentric fractures on the shell interior (Fig. 4C). These injuries could be interpreted as the outer border of the home scars of patellogastropods; or as the 'large crater-like structures, with an inwardsloping margin bounded by concentric fractures' reported by Hewitt & Westermann (1990), and previously mentioned by Kauffman & Kesling (1960) in shells of the ammonoid Placenticeras. Tsujita & Westermann (2001) agree with Kauffman & Kesling (1960) in interpreting such features as the result of the impact of the 'flared base of a mosasaur's tooth'. Significantly, this mark in Figure 4C is matched on the internal part of the shell by a dent that can clearly be observed on the opposite part (external) of the shell. Detailed examination of this feature indicates that the 'circular' outer border simply reflects the smoothing effect of dissolution on a spall mark.

Scavenging seems quite improbable (but not impossible) as an explanation to the studied marks. Bivalves open when they become dead, implying that if we would be dealing with scavenging activity, we should have encountered some indication of injuries going from the inside of the shell to the external part. In all the specimens, when the direction of the injury can be determined, we find just the contrary. So, it is more logical to think that the bivalves were closed (i.e. alive) at the moment when the activity of the vertebrates took place. In fact, some of them are still closed, as it is the case of specimen VDPR-C-27 (Fig. 4D). We consider these reasons enough to claim that predation seems a much more parsimonious explanation to the marks studied in Valdeperillo than scavenging, but accept that a mixture of both activities could have taken place.

As described above, the outlines of the dents and perforations range from circular to oval in shape. The difference in the shape of the injuries could manifest variations in the inclination of elements (the tooth) that penetrate the shell. As such, the minor axis of an oval-shaped mark would be expected to approximate the minimum diameter of the predator's tooth. It should be emphasized, however, that while this may be true in some cases, the dimensions of such marks may also vary according to the different pressures inflicted by the predator on the shell during the bite. This interpretation agrees with Tsujita & Westermann (2001; Fig. 14, p. 263).

One of the perforations (VDPR-C-61) (Fig. 6A, B, D, E) shows two triangular projections, so we can infer that the teeth of the predator were probably bicarinate. The only possible predator with a tooth shape consistent with this interpretation, and in the environmental setting represented in strata at our collection site, would have been a reptile.

Fossil record of bivalves preyed upon by reptiles

The literature on known bivalve-eating reptiles is rather scant and mainly deals with marine species. Carter (1968) regards placodonts and rhyncosaurs as bivalve predators, although this is largely based on their crushing teeth, and no direct evidence has yet been provided to confirm this claim. Likewise, McRoberts (2001) lists Triassic ichthyosaurs and placodont as potential bivalve predators, but the specific hardshelled items eaten by these vertebrates remains unclear (Motani 2005). Moreover, placodonts have been very recently reinterpreted as macroalgae feeders (Diedrich 2012; but see Salamon *et al.* 2012).

Reptile gut contents with bivalve remains have been brought to light recently. For example, McHenry *et al.* (2005) described pterioid bivalve remains (*Macoyella*) in the gut content and a bromalite of a Cretaceous elasmosaurid plesiosaur skeleton; and Kear (2006) documented inoceramid bivalve remains in the gut contents of a Cretaceous protostegid turtle (cf. *Notochelone*). Also, Martin & Fox (2007) reported bivalve shells (inoceramids, oysterlike fragments and the pterioid *Anomia*) in gut contents of the mosasaur *Globidens schurmanni*.

Reported specimens of fossil bivalves with bite marks have also been small in number, and those described have been primarily marine forms (e.g.: Speden 1971; Kauffman 1972). Predation studies on non-marine bivalves are limited even further, with only three major works having been published recently. Of these, Kear & Godthelp (2008) inferred feeding marks in Early Cretaceous unionoid bivalves; Bermúdez-Rochas *et al.* (2009) cited the existence of bite marks in the Cretaceous of Spain (with preliminary observations of the material described here) and Gorzelak *et al.* (2010) described similar marks in the Triassic of Poland.

Identifying the bite maker of Protopleurobema *shells*

The typical shape of the bite marks studied, relatively circular to oval in morphology, indicates that the predator had stout conical teeth. The triangular projections in some marks could be interpreted as reflecting the presence of carina in the tooth of the predator (see Njau & Blumenschine 2006; Fig. 1). The absence of these triangular projections in the majority of specimens in our collection could indicate that: (1) the teeth that produced the marks were rounded by wear, thus reducing the distinctness of the carinate elements (see Njau & Blumenschine 2006; Fig. 1); (2) there was some degree of heterodonty in the bite maker, such that it possessed both carinate and non-carinate teeth; or, (3) the teeth of predators tended to impact the external surface of the shell at an oblique angle (i.e. not orthogonal).

Several fossil terrestrial reptiles are known to have bicarinate teeth but only crocodyliforms possess stout conical ones. Theropod dinosaurs, even the semiaquatic fish-eating spinosaurids (Rayfield *et al.* 2007; Amiot *et al.* 2010), which are frequent in the Early Cretaceous of the Iberian Península (*Baryonyx*, and indeterminate spinosaurids, spinosaurines and baryonychines; e.g. Milner 2003; Buffetaut 2007; Sánchez-Hernández *et al.* 2007; Canudo *et al.* 2008), have labiolingually compressed crowns (Sander 1997). Besides being too small to produce the perforations in the shells of *P. numantina*, the teeth of Early Cretaceous toothed birds are not bicarinate (e.g. Chiappe & Witmer 2002).

Several genera of terrestrial crocodyliforms are known in the Early Cretaceous of the Iberian Peninsula, including *Goniopholis, Theriosuchus, Bernissartia, Lisboasarus, Montsecosuchus* and *Unasuchus* (Buscalioni & Sanz 1990; Brinkmann 1992; Buscalioni *et al.* 2008; Schwarz & Fechner 2008). Of these, *Bernissartia, Lisboasaurus, Unasuchus* and the atoposaurids *Theriosuchus* and *Montsecosuchus* are too small in size (from <0.4 m for *Lisboasaurus* up to no more than 1 m for *Bernissartia, Theriosuchus, Unasuchus*; Buscalioni & Sanz 1990; Schwarz & Fechner 2008) to account for the tooth dimensions implied from the bite-mark sizes measured by us.

Goniopholis, on the other hand, is larger (approximately 3-m snout-tail length; Andrade *et al.* 2011), and a mixture of juvenile and adult individuals could well have produced the range of bite marks described in Valdeperillo unionoids. *Goniopholis* is indeed the only crocodyliform that has been recorded, up to date, in the Urbión Group D unit (Moratalla *et al.* 1994; Ortega *et al.* 1996). *Goniopholis* teeth may reach more than 15 mm in mesiodistal width in the base of the crown in big specimens (see Andrade *et al.* 2011, and references therein), so the apexes of the crowns are able to produce the dents seen in the Valdeperillo shells (up to 4.5 mm).

Durophagy in fossil crocodiles

Several extinct crocodyliforms (among other reptiles of the 'crush' and 'crunch' guilds recognized by Massare 1987) have posteriorly positioned tribodont (Buffetaut & Ford 1979) or molariform (Buscalioni *et al.* 2008) teeth characterized by blunt and rounded morphology that point to a crushing function and thus an adaptation towards a durophagous mode of feeding (Motani 2009). Such teeth are also known from extant crocodiles as *Osteolaemus tetraspis* and *Caiman latirostris* (Osi & Weishampel 2009; p. 918) that exhibit life habits consistent with those inferred for their ancient blunt-toothed counterparts.

Although several of studies have alluded to hard food items in the diets of Mesozoic and Cenozoiccrocodyliform reptiles, most have specifically focused on turtles as hard-shelled prey candidates (e.g. Carpenter & Lindsey 1980; Meyer 1994; Joyce 2000; Karl & Tichy 2004).

Carpenter & Lindsey (1980; p. 1216), for example identified *Glyptops*, an aquatic turtle as a probable prey for the crocodile *Goniopholis*, an interpretation

based, in part by the co-ocurrence of their remains in the Upper Jurassic Morrison Formation (USA), although *Goniopholis* has not been taken into account in a recent revision of fossil chelonivorous crocodiles made by Karl & Tichy (2004).

Although a malacophagous diet has been suggested for several durophagous-teeth-bearing fossil crocodyliforms (e.g. *Bernissartia* in the Early Cretaceous, see Buffetaut & Ford 1979; or alligatorines in the Late Cretaceous and Palaeogene, see Brochu 2004, and references therein), there is no evidence, in the fossil record (neither gut contents nor predation marks), of crocodyliforms predation in molluscs prior to this article.

Dietary factors that might have influenced the predation of Protopleurobema

Several extant generalist crocodyliforms, including the Chinese alligator (*Alligator sinensis*, Groombridge & Wright 1982), the mugger crocodile (*Crocodylus palustris*, Whitaker & Whitaker 1989; table 2) and the gharial (*Gavialis gangeticus*, Shrestha 2001), are known to prey on freshwater bivalves. We suggest that the producer of the bite marks preserved in the Valdeperillo unionids was a crocodyliform reptile that was also a generalist predator.

Insights to why such a predator, even a generalist, would have bothered to pursue bivalves as a food source while larger and non-shelled prey would have presumably required less effort to acquire may be sought through observations made on such modern forms such as the mugger crocodile. This extant crocodile is a generalist predator whose typical diet consists of arthropods, snails, bivalves, fishes, frogs, snakes, turtles, birds and small and big mammals (Groombridge & Wright 1982; Whitaker & Whitaker 1989; Shrestha 2001). However, as noted by Shrestha (2001), the mugger will resort to eating harder shelled prey such as crabs, snails and bivalves when fish decline in abundance. It is not unreasonable to surmise that Goniopholis, a crocodyliform known from the same strata unit from which the described bivalves come (and indeed the only crocodyliform known from the Cameros Basin) faced similar circumstances and resorted to similar measures in its attempts to meet its nutritional demands.

Conclusions

The types of damage preserved in fossil shells of the unionoid bivalve *Protopleurobema numantina* from the Lower Cretaceous of Valdeperillo (Cameros Basin, Spain), are here attributed to the feeding activities of a vertebrate predator. The Valdeperillo specimens collectively represent the first evidence of a unionoid predation by megavertebrates in the Early Cretaceous record of Laurasia, and the largest assemblage of bite mark-bearing mollusc shells yet documented from the Mesozoic continental record.

Among the possible predators of this unionoid, we regard the crocodilian *Goniopholis* as the most logical candidate, based on the close match (in both the size and shape) between the teeth of this reptile genus and the injuries observed on the shells. Also, remains of this genus are known from the same stratigraphic unit (Urbión Group, D unit) as that from which the bivalve described here were derived, implying their coexistence in the same general environmental setting. Furthermore, in consideration of the currently accepted view, *Goniopholis* was a generalist in its feeding habits, it is conceivable that it fed on freshwater bivalves, especially at times when more substantial prey was in scarce supply, as do modern crocodiles.

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