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Borings are not boring: Examples of macrobioerosion in marine palaeo-ecosystems

Las perforaciones no aburren: Ejemplos de macrobioerosión en paleoecosistemas marinos

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Abstract: Bioerosion is an ecological process identifiable in the fossil record by means of traces left on hard substrates by producers, since Late Proterozoic times. It implies both the destruction and construction of information, and its analysis is a valuable tool to better understand the biodiversity and the (palaeo)ecological complexity of a given area at any moment of the Earth's history, as bioeroding organisms often lack a fossilisable hard skeleton. Moreover, bioerosion traces inform on two (reaction and coaction) of the three relationships established between organisms and their environment within the ecosystem. But bioerosion is also a first order taphonomic agent. Bioerosion and taphonomy follow one another as (palaeo)ecological and fossilisation processes, but at the same time they overlap and condition each other. This review aims to be a state-of-the-art treatise on bioerosion as both an ecological process and a taphonomic agent. The review mainly focuses on the fields of palaeomalacology, understanding molluscs both as producers and victims, or substrates of bioerosion, and of the rocky-shore environments, both centred in the Neogene period. Bioerosive studies of a palaeoecological and palaeoenvironmental nature are numerous and continue to increase. Research on bioerosion-taphonomy interaction still has a long way to go. As such, this contribution will demonstrate its value for both palaeoenvironmental interpretation and for understanding the sometimes-complex processes of fossilisation

Resumen: La bioerosión es un proceso ecológico identificable en el registro fósil mediante las trazas dejadas en sustratos duros por los productores, desde finales del Proterozoico. Implica tanto la destrucción como la construcción de información, y su análisis es una herramienta valiosa para entender mejor la biodiversidad y la complejidad (paleo) ecológica de una zona dada en cualquier momento de la historia de la Tierra, ya que los organismos bioerosivos a menudo carecen de un esqueleto duro fosilizable. Además, las trazas de bioerosión informan sobre dos de las tres posibles relaciones establecidas entre organismos y su entorno dentro del ecosistema. Pero la bioerosión también es un agente tafonómico de primer orden. La bioeroesión y la tafonomía se suceden como procesos (paleo)ecológicos y de fosilización, pero al mismo tiempo se superponen y condicionan mutuamente. Esta revisión tiene como objetivo ser un tratado sobre la bioerosión como proceso ecológico y agente tafonómico. La revisión se centra básicamente en los campos de la paleomalacología, comprendiendo a los moluscos tanto como productores como víctimas o sustratos de bioerosión, y de los medios de costa rocosa, ambos centrados en el periodo Neógeno. Los estudios bioerosivos de naturaleza paleoecológica y paleoambiental son numerosos y continúan aumentando. La investigación sobre la interacción bioerosión-tafonomía todavía tiene un largo camino por recorrer. Esta contribución demostrará su valor tanto para la interpretación paleoambiental como para comprender los a veces complejos procesos de fosilización.

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INTRODUCTION

About fifty years ago I published my first scientific paper (Martinell, 1973), basically dedicated to the taphonomy and palaeoecology of a marine Pliocene outcrop in the northeast of the Iberian Peninsula. I included a chapter on the bioerosive activity of naticid gastropods. At that time, the bibliographic information on bioerosion was very scarce (Boekschoten, 1967). Currently, the situation has changed radically and bioerosion is the subject of thematic congresses, books, and articles published in major scientific journals. In any case, there is still a strong bias in general palaeontology books, in which bioerosion is treated in a limited way at most, while bioturbation — the most traditional area of ichnology— receives all the attention. In the present

review I propose a brief tour of macrobioerosion, both from the palaeoecological and taphonomic fields, where it plays a leading role. For reasons related to my scientific background, I have limited this journey to the Cenozoic and mainly (although not exclusively) in relation to the position of molluscs as bioeroders or bioeroded agents.

The study of bioerosion is a valuable tool to understand the biodiversity and the ecological or palaeoecological complexity of a given area at any moment of the Earth's history. As bioeroding organisms often lack a fossilisable hard skeleton, it is the trace they leave on the substrate that enables determination of their existence in the past, and furthermore, to interpret the biotic interactions established with the substrate.

Bioerosion is a widespread ecological process that has transformed and modified habitats in all biomes of the Earth from the Late Proterozoic to Recent, by means of physical and/or chemical mechanisms. Much bioerosion takes place through the process of boring (also referred to as drilling) by organisms. Carbonates are the most common substrate into which they bore. Nevertheless, some examples are known from other lithologies (Masuda, 1968; Martinell, 1981; Ledesma-Vázquez & Johnson, 1994; Johnson *et al.*, 2010; Mayoral *et al.*, 2020). Wood is considered a special type of hard substrate (Noda & Lee, 1989; Evans, 1999; Taylor & Wilson, 2003). Bioeroders belong to numerous taxa including microbes (bacteria, algae, fungi, protists), lichens, vascular plants, invertebrates and vertebrates (Warme, 1975; Bromley, 1978; Ekdale *et al.*, 1984; Mayoral, 1988a,1998b; Bromley, 2004; Glaub *et al.*, 2007; Cockell & Herrera, 2008). The structures produced by epiliths (organisms adapted to life upon a hard substrate) are primarily raspings, scrapings, superficial etching scars, and breakages; borings and bioclaustrations are mainly due to endoliths (organisms that dwell *within* a hard substrate, which can be inorganic or organic in origin) (Neumann, 1966; Ekdale *et al.*, 1984; Martinell, 1989; Bromley, 1996; Gibert *et al.*, 2004; Wilson, 2007; Bertling *et al.*, 2007; Santos *et al.*, 2012a; Baarli *et al.*, 2017; Wisshak *et al.*, 2019).

Organisms and their environment form a reciprocating system, the ecosystem. Within it, three and only three types of interactions are possible: (1) living organisms that affect other living organisms (coaction), (2) living organisms that affect the abiotic environment (reaction), and (3) the inorganic environment that affects living organisms (action) (Lawrence, 1971; De Renzi, 1978). Ecology and palaeoecology must be logically defined as the study of these three interacting pairs, and bioerosion particularly is framed within the analysis of both coaction and reaction. Bioerosion is also a first order taphonomic agent that is feasible in all main phases of the process (Fig.1).

Researchers use numerous non-exclusive terms to describe the many processes by which organisms alter, break down, and erode hard substrates. These

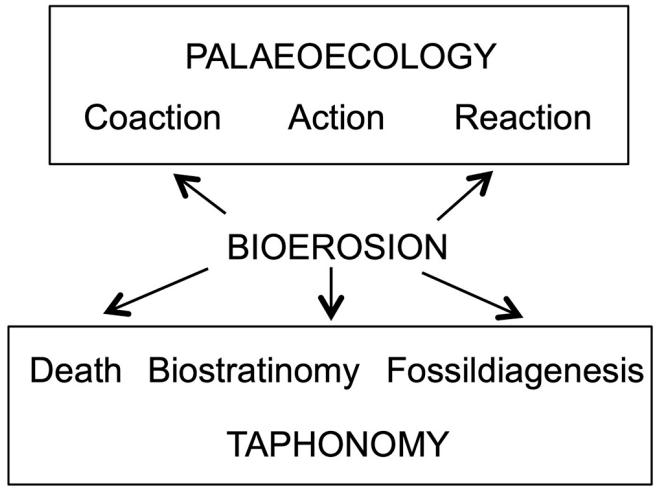

Figure 1. Graphical representation of formal relationships between bioerosion, taphonomy, and palaeoecology.

terms vary in function of the scope, scale, substrate type, and the discipline of study. For example, the erosive activities of fungi, lichens, and microbes on mineral substrates is called "biotic weathering" (Viles, 1995); the erosive effects of organisms on human-made substrates is termed "biodeterioration" (Allsop *et al.*, 2004); the destruction or damage of a material due to a chemical reaction in front of an invasive organism is called "biocorrosion" (Beech & Gaylarde, 1999); "biogeomorphology" refers to the interactions and feedbacks between the landscape's living and non-living components (Coombes, 2016); and the resulting cavity provoked by the growth-interfering behaviour of a symbiont that lives in the growing skeleton of the host is called "bioclaustration" (Tapanila, 2004; Tapanila & Ekdale, 2007). The destruction and removal of consolidated mineral or lithic substrate by the direct action of organisms is referred to as "bioerosion" (Neumann, 1966). Indeed, the term itself has been reinterpreted, expanded, and/or redefined by multiple authors over the last half century (Ekdale *et al.*, 1984; Tapanila, 2008; Schönberg *et al.*, 2017). Nowadays, the term bioerosion is used by several authors to denote the breakdown of any hard substrate by biological activities, whether by microorganisms, invertebrates, vertebrates, or plants in marine, fresh water, or continental environments from the Late Proterozoic to Recent (Brasier *et al.*, 1994; Montalvo, 2002; Farlow & Holtz, 2002; Bromley, 2004; Hasiotis *et al.*, 2007; Mangano *et al.*, 2012; Davidson *et al.*, 2018; Wisshak *et al.*, 2019). More specifically, traces that are less than 1 mm produced by euendolithic microorganisms are referred as "microbioerosion" (Ekdale *et al.*, 1984; Glaub *et al.*, 2007; Wisshak, 2012) whereas "macrobioerosion" relates primarily to marine invertebrate bioeroders (McHuron, 1976; Ekdale *et al.*, 1984; Wilson, 2007; Wisshak *et al.*, 2019).

BIOEROSION *VERSUS* PALAEOECOLOGY

Reaction

Bioerosion in inorganic hard substrates. Bioeroders alter landscape features as a direct consequence of their activities and indirectly by accelerating erosional processes, causing substantial alterations to the morphology of landforms and habitats (Naylor *et al.*, 2012; Coombes, 2016; Domènech & Martinell, 2019). This activity is especially evident on the current and fossil carbonate rocky shores and on organic calcareous structures such as dead corals and shells. Macrobioerosion trace fossils are important indicators of intertidal and shallow subtidal marine palaeo-environments (Wilson & Palmer, 1990; Taylor & Wilson, 2003; Bromley, 2004; Santos *et al.*, 2011a; Schönberg & Wisshak, 2014). Rocks containing macroborings are not exclusive indicators of marine palaeo-ecosystems, but may also reflect freshwater habitats (Bolotov *et al.*, 2018, 2021).

The drilling activity of lithophagous bivalves in ancient cliffs had already been noted by Renaissance malacologists. According to Brocchi (1814), the Tertiary European pholadids had been cited by classical authors such as Aldrovandi, Targioni, Allioni, and Baldasieri, with studies based on the descriptive aspects of bivalves, but without delving into their boring activity.

The geological importance of the bioerosive activity of lithophagous molluscs was demonstrated as early as in Charles Lyell's *Principles of Geology* (Lyell, 1830), who started his seminal masterpiece with a reproduction of the abundant "*Lithodomi*" borings found in the columns of the Temple of Seraspis in Italy (currently known as Macellum of Pouzuoli), using them as a proof of relative sea level changes. Afterwards, Johnston (1850) classified the species responsible for those specific perforations as *Lithophaga lithophaga*.

Since the end of the 20th Century, bioerosive activity has been mainly used to characterize unconformable surfaces in the Palaeozoic (Pojeta & Palmer, 1976; James *et al.*, 1977; Kobluk *et al.*, 1977; Narbonne, 1984; Pemberton *et al.*, 1980; Johnson *et al.*, 1988; Desrochers & James, 1988; Webb, 1994; Rong & Johnson, 1996; Johnson *et al.*, 2010); the Mesozoic (De La Beche, 1846; Kahrs, 1927; Hecker, 1965; Palmer & Fürsich, 1974; Bromley, 1975; Chudzikiewicz & Wieczorek, 1985; Ager, 1986; Gruszczynski, 1986; Breton *et al.*, 1992; Mikuláš, 1992; Wilson & Palmer, 1994; Cole & Palmer 1999; Farris *et al.*, 1999; Wilson *et al.*, 2005; Zatoń *et al.*, 2011; Krajewski *et al.*, 2017) and the Cenozoic (Lutzeier, 1922; Kiderlen, 1931; Lessertisseur, 1955; Aubert, 1972; Libbey & Johnson, 1997). It is clear nowadays that rocky-shore surfaces and their associated deposits are present throughout the entire geological register, commonly related to transgressive episodes (Johnson, 1988, 1992, 2006; Johnson & Baarli, 1999; Pemberton *et al.*, 2004; Santos *et al.*, 2008a; Santos & Mayoral, 2009). The ichnotaxonomic composition of rocky-shore assemblages changed throughout the Phanerozoic, although some taxa (*Trypanites*, *Gastrochaenolites*) are recurrent in the record. Figure 2 illustrates this evolution with three archetypical assemblages based on bibliographic data (see details in Gibert *et al.*, 2012).

Neogene and Quaternary examples on fossil rocky-shore deposits are by far the most abundant and best documented ones (Pierçon, 1932; Denizot, 1952; Radwanski, 1970; Ballesio, 1972; Gutowski & Machalski, 1984; Rangheard, *et al.*, 1985; Watkins, 1990; Bromley & Asgaard, 1993a, 1993b; Uchman *et al.*, 2002; Titschack *et al.*, 2005; Charollais *et al.*, 2006; Johnson *et al.*, 2011; Demircan, 2012; Santos *et al.*, 2012b; Pineda-Salgado *et al.*, 2015; Brlek *et al.*, 2016; Abbel-Fattah & Assal, 2016; Santos & Mayoral, 2016; Steinthorsdottir & Håkansson, 2017; Hoffmann & Friedrich, 2017; El-Hedeny & El-Sabbagh, 2018; Martinell *et al.*, 2021b). In particular, there is a wealth of studies dealing with boring ichnoassemblages in Neogene rocky shores of the Iberian Peninsula (Martinell & Domènech, 1986, 1995; Silva *et al.*, 1995; Mayoral & Muñiz, 1996; Perry, 1996; Aguirre & Jiménez, 1997; Gibert *et al.*, 1998; Domènech *et al.*, 1999; Silva *et al.*, 1999; Domènech *et al.*, 2001; Cachão *et al.*, 2009; Santos *et al.*, 2008b, 2010, 2011b; Gibert *et al.*, 2012; Aguirre *et al.*, 2014; Rodríguez-Tovar *et al.*, 2015; Aguirre *et al.*, 2017; Giannetti, *et al.*, 2020).

The complex structures excavated by bioeroders can provide habitat for diverse and abundant

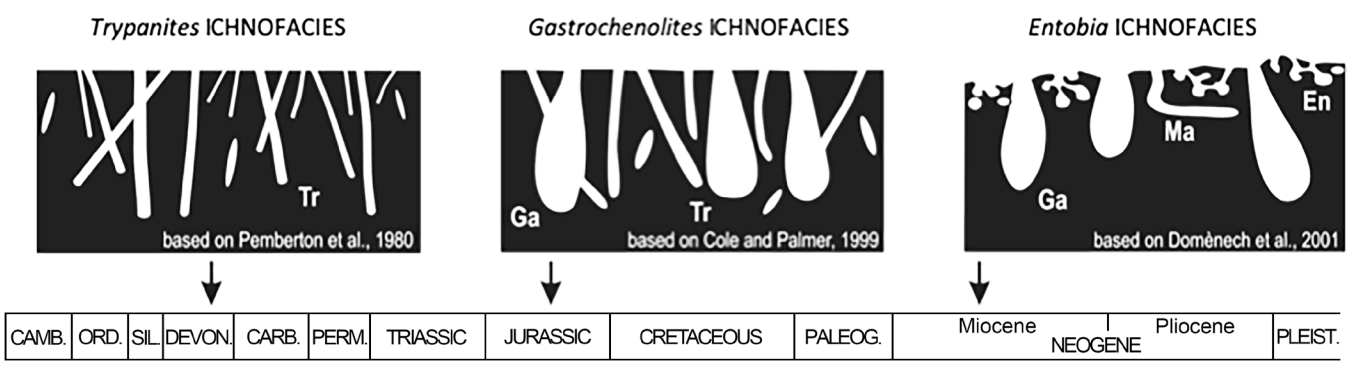

Figure 2. Evolution of the composition of rocky-shores trace fossil assemblages through the Phanerozoic, represented by three successive archetypical assemblages (see details in Gibert *et al.*, 2012).

species assemblages: recent communities inhabiting boreholes grated by bivalves in the rocky intertidal (mostly assigned to the ichnogenus *Gastrochaenolites* in the fossil record) contain 2.7 times more species than assemblages on bare rocks (Pinn *et al.*, 2008). However, intensive bioerosion can also impoverish biodiversity when such activity diminishes structural complexity or eliminates a habitat entirely.

Bioerosion of lithic substrates dominated by *Gastrochaenolites* indicates shallow marine environments. While lithophagous clams may also bore in deeper waters, a heavy infestation in a lithic substrate is largely a shallow water phenomenon (Kleemann, 1973).

As mentioned above, rocky shores in the fossil record appear associated with regional unconformities. The best palaeoenvironmental scenario for their formation and preservation occurs during major transgressive events capable of flooding rocky palaeoreliefs that are devoid of sedimentary cover. Marine evidence of submersion (bioerosion, body fossils, tidal or wave erosion) commonly overprints other features formed during the period of subaerial exposure (*e.g.*, karstification in carbonate rocks) preceding the transgression (Bromley & Asgaard, 1993a,1993b; Domènech *et al.*, 2001). Although it is possible to identify sedimentary deposits linked to rocky shores, these environments are essentially erosional, and bioerosion is often the best aid for their identification in the geological record. Bioeroded rocky-shore surfaces can be extensive and, given adequate outcrop conditions, can be recognized and correlated across different localities in a basin, thus contributing to its palaeogeographic reconstruction (Martinell *et al.*, 2021b). Such large surfaces are often time-averaged due to the overprinting of successive communities as the transgression proceeded. Bioerosion is also a very precise indicator of maximum sea level in those areas, since borings are observed to disappear above a certain altitude, a feature that can be related with other morphological characteristics that are indicative of sea-level limit, such as erosional notches. Identifying these palaeo sea-level positions may also be important to interpret eustatic changes, or relative changes due to tectonic activity (Gibert *et al.*, 1998, 2012; Domènech *et al.*, 2001; Cachão *et al.*, 2009; Giannetti *et al.*, 2020). Moreover, the density of coeval bioerosion combined with the estimation of the percentage of affected area allows one to precisely characterise the biological activity and to better calibrate palaeoenvironmental conditions (Domènech *et al.*, 2001; Martinell *et al.*, 2021b).

Regarding palaeoecological studies, rocky-shore assemblages offer the important advantage that organisms cementing to and boring into hard substrates generally retain their original positions on it during fossilisation, as represented by body fossils or by the traces themselves. In a transgressive situation, surfaces are exposed to deeper waters and new traces overprint former ones. Later structures may cut across and destroy earlier ones, and endoliths can penetrate and modify previous structures (Bromley & Asgaard, 1993a; Domènech *et al.*, 2001; Gibert *et al.*, 2012; Silva *et al.*, 2019; Giannetti *et al.*, 2020). Thus, bioerosion itself leads to a masking or an elimination that does not always reflect the sequence of events (Bromley & Asgaard, 1993b; Domènech *et al.*, 2001). However, the morphologies of the borings that remain partial—those of the intact ones and those of the overlapped ones—have in some cases allowed estimation of the overall erosion on a linear scale. Thus, Domènech *et al.* (2001) proposed a denudation of several cm in the mid-marine Miocene wave-cutting platforms of Tarragona (Spain), based on the numerous and truncated *Gastrochaenolites* and *Phryxichnus* (both attributed to the action of lithophagous bivalves) present in them. The resulting surface exhibits *Entobia* (produced by endolithic but surficial boring sponges) and *Maeandropolydora* (due to the action of epilithic worms), which reveal a final stage of bioerosion (Fig. 3).

A transgressive situation often prevents identifying the ecological relationships that were established in the geological past for a given area. In the case of cliffs, erosion removes the skeletons of encrusters as well as many traces, so that only the most recent and/or deeper perforations can be observed. However, some examples exist where these relationships have been preserved. Thus, in the Jura marine Miocene, the ichnological record on Cretaceous limestone cliffs within the transgressive sequence has been studied. There are frequent dwelling buckets (*Circolites kotoucensis* Mikuláš) of regular echinids, which contain numerous specimens of *Calulostrepsis* drilling that were produced by polychaetes (Bromley & D'Alessandro, 1983; Domènech *et al.*, 2008). Johnson *et al.* (2011) mentioned for the first time the presence of the ichnogenus *Caulostrepsis* in the concave surfaces of *Circolites* in the fossil record. These authors found rare specimens inside *C. kotoucensis* in the Upper Miocene rocky shores on the north coast of Menorca (Balearic Islands). On the contrary, this association is well developed at the Les Bez outcrop. U-shaped annelid galleries are distributed in different patterns inside echinoid bowls, in some cases covering the entire surface, and in others being limited to their external rim. Fifty-five percent of the *C. kotoucensis* at the site host *Caulostrepsis*, although the distribution in not regular, increasing towards the upper part of the cliff. This situation suggests an ecological relationship between the involved organisms—a relationship that has been preserved despite the erosional environment (Martinell *et al.*, 2021b). In the fossil record, *Caulostrepsis* has often been attributed to the spionid *Polydora* or the cirratulid *Dodecaceria*. At present, there is no documented relationship between *Polydora* and echinoid cavities, while different authors have highlighted this association with *Dodecaceria*

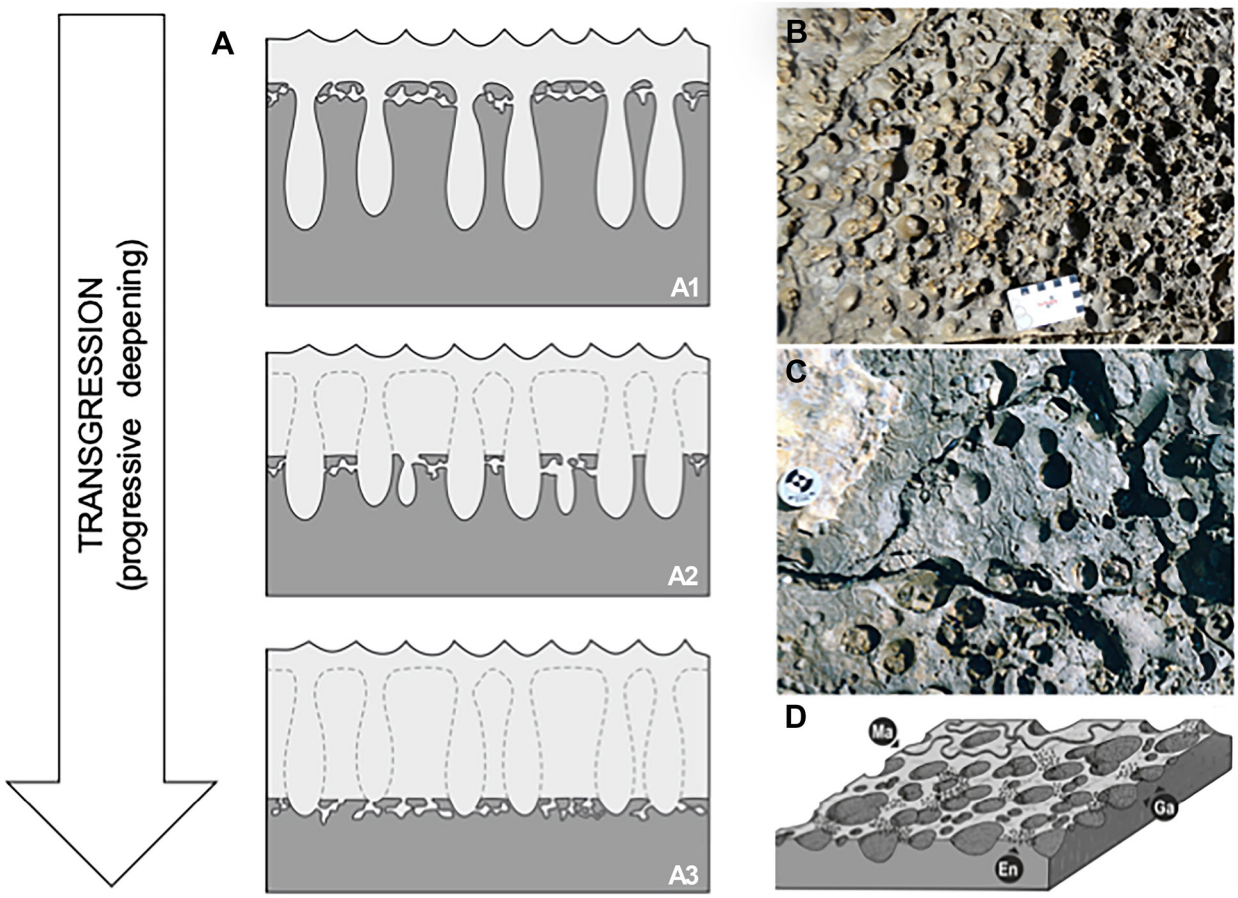

Figure 3. Bioerosive succession within the *Gastrochaenolites* Ichnocoenosis during a trangressive episode on a marine rocky-shore, Middle Miocene, Tarragona. **A,** From 1 to 3, evolution from the bivalve-dominated community (represented by *Gastrochaenolites*) to a sponge-dominated community (represented by *Entobia*); **B**–**C,** general overviews of the bored and abraded platform; **D,** Diagram of the final abrasion platform. **Ma,** *Maeandropolydora*; **Ga,** *Gastrochaenolites*; **En,** *Entobia*.

(Kempf, 1962; Voigt, 1970, 1971; Gibson, 2017; Gravina *et al.*, 2019). *Dodecaceria* infests encrusting calcareous algae, whereas regular echinoids feed on them. Therefore, in this case the association polychaete/echinoid could be explained by their mutual relationship to such algae. In several cases at Les Bez outcrop, the position of *Caulostrepsis* is limited to the distal zone of *Circolites*. That can be interpreted to be a result of the cohabitation between the producers, the echinoid offering passive protection to the worm against predators and/or the high energy environment (Davidson & Grupe, 2014).

Bioerosion in biological entities (organic remains). Skeletal remains (shells, bones, wood) deposited on the seabed act as islands for organisms that need a hard substrate to live. Although bioeroders may partially or totally destroy these remains, through their traces they also provide valuable information needed to reconstruct the biodiversity in ancient ecosystems. Known from the Late Proterozoic, species belonging to many groups of marine invertebrates and vertebrates have adopted a living habitat of boring, with up to 65 catalogued ichnogenera (Bromley, 2004; Wilson, 2013).

Sessile epilithic organisms attach themselves to the substrate in many ways. Permanently cementing species may secrete a carbonate skeleton in intimate contact with the substrate. When the organism requires a permanent location, an organic contact anchoring shallow superficial structures into a carbonate substrate provides the most durable bond. Such groups include verrucid barnacles (Darwin, 1854; Radwanski, 1977; Bromley & Martinell, 1991; Martinell & Domènech, 2022), eunicid polychaetes (Zibrowius, 1987; Martin & Britayev, 1998; Martinell & Domènech, 2009; Naimi *et al.*, 2021a), annelids (Santos *et al.*, 2003a), brachiopods (Bromley & Surlyk, 1973; Martinell, 1982a; Taddei Ruggiero & Annunziata, 2002; Jagt *et al.*, 2007; Bromley, 2008; Mergl, 2021), bryozoans (Mayoral, 1987a, 1988b; Mayoral & Reguant, 1995; Taylor *et al.*, 1999; Bromley & Heinberg, 2006), anomid bivalves (Bromley & Martinell, 1991; Taddei Ruggiero & Annunziata, 2002; Blissett & Pickeril, 2007; Neumann *et al.*, 2015) and vermetids (Mayoral, 1987b; Uchman *et al.*, 2017, 2018; Verde *et al.*, 2022).

Some groups of epilithic and endolithic organisms identifiable through their perforations have restricted environmental tolerances in terms of the bathymetric and sedimentary conditions. Invertebrate herbivores

that depend on epilithic and endolithic algae leave characteristic traces in the biological entities that indicate the photic zone. Therefore, the abundant presence of *Gnatichnus* (browsing and foraging traces attributed to dental erosion by regular echinoids) and/or *Radulichnus* (shallow fossil traces that have been attributed to the grazing activity of the radula of mollusks: chitons and gastropods) on hard surfaces such as the remains of shells or rocks indicate the epipelagic zone (Bromley, 1975; Voigt, 1977; Martinell & Domènech, 1981; Martinell, 1982b; Forrest *et al.*, 2001; Jagt, 2003; Gibert *et al.*, 2007; Cione *et al.*, 2010; Breton *et al.*, 2017; Lopes & Pereira, 2019).

Entobia (boring sponges), the most important ichnotaxon in advanced taphonomic stages of shell degradation, is abundant in both shallow and deep-water settings, as it seems to be particularly dependent on a sustained lack of sedimentation (De Groot, 1977; Wisshak, 2008; Garilli *et al.*, 2022). *Entobia* can involve the entire shell, resulting in stenomorphic borings (*sensu* Bromley & D'Alessandro, 1984, 1989). In this case, the destruction of the shell can be total (Belaústegui *et al.*, 2018). On certain surfaces, sponge borings are conspicuously absent, and worm borings (*Caulostrepsis, Trypanites*, etc.) predominate (Domènech *et al.*, 2008). These cases would represent situations in which sedimentation is problematic for some animals, being enough to prevent the colonization by sponges, but insufficient to prevent the proliferation of certain types of worms (Evans, 1969; Ekdale *et al.*, 1984; Hutchings, 2008).

Coaction

Traces of bioerosion present on skeletal remains could have been carried out during the life of the organism, indicating the cause of its death, or been produced *post-mortem*. The former ones correspond to predation or parasitism and commensalism (symbiosis), the latter are related to the activities of epizoans (endo- and epibionts) that use skeletal remains (shells, bones, wood) as a substrate. In this case, it is worth referring to it as taphonomic feedback (Kidwell & Jablonski, 1983). Proper recognition of shell damage is seminal since direct observations of predation are infeasible, but preserved shells with injuries are common in the fossil record.

Predation. The palaeontological marine record contains numerous examples of interspecific relationships (*e.g.*, Tevesz & McCall, 1983; Boucot, 1990; Briggs & Crowther, 1990, 2003; Boucot & Poinar, 2010). Many of them correspond to exploitation pairs (predation and parasitism) among invertebrates, in which one member benefits at the expense of the other. The importance of predation as a selective influence on the evolution, diversification, mineral biomineralization and ecology of metazoans has been the focus of intensive research. Vermeij (1987), Kowalewski *et al.* (1998), Conway-Morris and Bengston (1994), Kowaleski and Kelly (2002), Leighton (2001, 2011), Kelley *et al.* (2003), Zuschin *et al.* (2003), and Martinell *et al.* (2010, 2012) are some examples of different approaches to the study of marine invertebrate predation in the fossil record.

The earliest evidence of predation in the fossil record comes from drill holes in *Cloudina* specimens from Ediacara strata of China (Bengtson & Zhao, 1992; Hua *et al.*, 2003), the oldest known skeletal fossil. Boring predators became geographically widespread during the Cambrian, having already attacked a variety of organisms (Kobluk *et al.*, 1978; Conway-Morris & Bengston, 1994; Skovsted et al, 2007). During the Late Cretaceous and Early Cenozoic, specialized marine durophagous taxa increased in diversity within the marine benthic ecosystems (Vermeij 1977; Bambach, 2002; Walker & Brett, 2002; Oji *et al.*, 2003; Harper, 2006; Zatoń & Salamon, 2008).

The Phanerozoic record of marine predation consists of both direct and indirect evidence. Indirect evidence is mostly based on predatory borings, shell repairs, skeletal regenerations, coprolites, and fossilized regurgitates (Conway Morris & Robinson, 1988; Baumiller & Gahn, 2004; Huntley & Kowalewski, 2007; Vallon, 2012; Zatoń & Rakocinski, 2014). Direct evidence in vertebrates corresponds to gut contents (Prikryl & Novosad, 2009; Zatoń *et al.*, 2017; Smit *et al.*, 2018; Vinn, 2018; Carnevale *et al.*, 2019; Hoffmann & Stevens, 2020).

In recent years, the concerted efforts of palaeontologists and ecologists have considerably advanced our knowledge of drilling predation and have demonstrated that drilling is a feeding mechanism employed by many groups of predators and that many shell-bearing groups of prey/host are drilled (Kabat, 1990; Kowalewski, 2002). In particular, the groups that have been most extensively studied as predators or hosts include molluscs (Vermeij, 1987; Dietl & Alexander, 2000; Kelley & Hansen, 2007; Martinell *et al.*, 2010; Naimi *et al.*, 2021b), brachiopods (Baumiller *et al.*, 1999; Taddei Ruggiero, 1999; Leighton, 2001; Harper, 2005; Kowalewski, 2002), and echinoderms (McClintock & Marion, 1993; Baumiller, 1996; Nebelsick & Kowalewski, 1999; Złotnik & Ceranka, 2005; Belaústegui *et al.*, 2017a).

Predators that drill holes in shells of marine invertebrates can provide quantitative data on various aspects of the predator-prey interactions, having produced one of the longest and richest fossil records in this scope (Palmer, 1982; Kitchell, 1986; Kelley & Hansen, 1993; Kowalewski *et al.*, 1998; Ceranka & Złotnik, 2003; Chattopadhyay & Baumiller, 2010).

Round drill-holes in shells made by predatory gastropods (dominantly, naticids and muricids) are among the few cases of direct evidence for behavioural interspecific interactions found in the fossil record. Such borings first appear in the Mesozoic and are very common in the Cenozoic fossil marine assemblages.

Morphologically, they can be classified into cylindrical (*Oichnus simplex* Bromley) and paraboloid borings (*Oichnus paraboloides* Bromley). The morphological consistency of fossil borings with those produced by Recent gastropods permits their approximate assignment to specific groups of predatory drilling gastropods (*O. simplex* to the muricids, *O. paraboloides* to the naticids) (Bromley, 1981; Hoffman & Martinell, 1984; Bromley, 2004). Although many other invertebrate groups produce similar borings, the reliability of the assignment can be further increased by the existence of associated body fossils of the suspected predators to the preys. However, it is prudent to consider other well-known producers and traces: Octopopid cephalopods that generate *O. ovalis* Bromley; eulimid gastropods that parasitise echinoderms and their traces, *O. halo* Nemann & Wisshak; or *Oichnus*-like holes of cassid gastropods in echinoids (Bromley, 1981; Neumann & Wisshak, 2009; Petsios *et al.*, 2021).

Traces of gastropod predation have been studied extensively at both Mesozoic and Cenozoic sites and for a variety of marine invertebrate preys, including annelids (Villegas-Martín *et al.*, 2016), ostracods (Reyment *et al.*, 1987; Reyment & Elewa, 2003; Baldanza *et al.*, 2020), barnacles (Gordillo, 2013; Klompmaker, *et al.*, 2015), decapod crustaceans (Pasini & Garassino, 2012; Klompmaker, *et al.*, 2013), brachiopods (Leighton, 2003; Harper, 2005; Baumiller *et al.*, 2006), bivalves and gastropods (Vermeij, 1982, 1994; Kabat, 1990; Dietl & Alexander, 2000; Kingsley-Smith *et al.*, 2003; Martinell *et al.*, 2010; Klompmaker, *et al.*, 2016), scaphopods (Yochelson *et al.*, 1983; Klompmaker, 2011), chitons (Rojas *et al.*, 2014), and echinoids (Neumann & Wisshak, 2009; Petsios *et al.*, 2021).

Naticids are the best studied group of molluscs regarding their predatory activity. Individually, they especially attack infaunal bivalves, but also other epifaunal molluscs—mainly gastropods—by means of drilling into their shells. The result is an O-shaped bore named *Oichnus paraboloides* (Bromley, 1981). The ability of naticids to move on or within the substrate allows them to easily locate their prey. Studies in aquariums allowed us to observe how they wrap the prey inside the foot in a mucus coat and then bury, drill and consume it completely in the sediment (unpublished personal observations). The naticids boring rate depends especially on the thickness and the ornamentation of the prey's shell (Reyment, 1967; Ansell, 1983; Kabat, 1990; Kabat, & Kohn, 1986; Kingsley-Smith *et al.*, 2003). Ziegelmeier (1954) and Kitchell *et al.* (1981) obtained similar drilling rates (0.6 mm/day) in Recent specimens of *Euspira nitida* Donovan and *Neverita duplicata* Say with an almost constant value regardless of prey species, predator size, or elapsed time.

Naticid gastropods are capable of an efficient selection of their prey. They preferably attack some of the potential prey species, select the size range of a particular prey depending on their own size, and selectively drill at suitable areas of the prey shell. They are also expected to exclusively attack live individuals, the frequency of failed attacks (based on incomplete boreholes) being very low (Martinell, 1973; Martinell & Marquina, 1978; Kitchell *et al.*, 1981; Hoffman & Martinell, 1984; Kitchell *et al.*, 1986; Batllori & Martinell, 1992; Kingsley-Smith *et al.*, 2003; Kelley & Hansen, 2006). Prey can also detect the presence of naticids and try to escape predation. Observations on the behaviour of the bivalve *Callista chione* Linnaeus in terms of specimens of *Naticarius hebraeus* Martyn that were carried out in aquariums, showed that *C. chione* dug out and, with the help of its foot, moved around the aquarium when the naticids were introduced. Finally, being in a closed space, predators captured and subsequently consumed them (unpublished personal observations) (Fig. 4A–4C).

Naticids also feed on other naticids, but drillholes made by different species are almost identical. That makes it difficult to distinguish between confamilial, congeneric, or conspecific naticid predation based on the holes, and it is then better to consider it as confamilial predation rather than cannibalism among naticids (Fig. 4D). The confamilial predation among naticids has received notable attention from palaeoecologists and evolutionary palaeobiologists (*e.g.*, Kelley, 1991; Dietl & Alexander, 2000; Kelley & Hansen, 2007; Fortunato, 2007; Martinell *et al.*, 2010; Mondal *et al.*, 2017). This is because confamilial predation among drilling gastropods provides quantitative and qualitative data in the context of important evolutionary and ecological concepts, including optimal foraging, escalation, size refuge, coevolution of dangerous prey, and behavioural ecology. The naticids' drilling patterns in confamilial depredation are similar to those observed in other prey. Although common, confamilial naticid predation intensity is not very prominent in the geological record (Kitchell *et al.*, 1981; Vermeij, 1982, 1994; Hoffman & Martinell, 1984; Kabat, 1990; Kelley, 1991; Kowalewski, 1993; Dietl & Alexander, 2000; Das *et al.*, 2014; Brezina *et al.*, 2016).

The Cretaceous radiation of naticids is part of the Mesozoic marine revolution, involving the increase in diversity of many modern marine predators due to the increase in shelled food supply (Palmer, 1982; Vermeij, 1977, 1982, 1987, 1994; Kabat, 1990; Kelley & Hansen, 1993; Walker & Brett, 2002; Bambach, 2002; Kase & Ishikawa, 2003).

The predatory activity of muricids is well known both in the Recent and in the fossil record. They attack epifaunal species of other gastropods, bivalves (especially ostreids and mytilids) and crustaceans (barnacles). Its predatory behaviour clearly differs from that of naticids. Their perforations are cylindrical and perpendicular to the shell thickness and the result is a conical-shaped borehole named *Oichnus simplex* (Bromley, 1981). Muricids can attack individually or in groups (causing several holes in the prey's shell), they neither select the location of the drilling that much, nor do they select the size of the prey, and they are rarely selective of

the prey itself (Bromley, 1981; Palmer, 1982; Dunkin & Hughes, 1984; Guerrero Alba & Reyment, 1988; Kowalewski, 2004; Yanes & Tyler, 2009; Martinelli *et al.*, 2013; Gordillo, 2013; Klompmaker *et al.*, 2015; Xu *et al.*, 2017).

The Muricidae evolutionary radiation preceded that of the balanomorphs during the Cretaceous. The evolutionary tendency of barnacles to reduce the number of their exoskeletal plates (from 8 to 4–6) since their appearance in the fossil record is probably a response to the predatory pressure of muricids that drilled into the imbrication zone of the plates (Palmer, 1982; Gale & Sørensen, 2015; Klompmaker *et al.*, 2015).

Echinoids are important prey for several vertebrate and invertebrate predatory groups in modern marine ecosystems. Carnivorous cassid gastropods are known to produce drill holes (*Oichnus*-like) in the process of preying upon echinoids, although other invertebrate groups have also been proposed as originators (Nebelsick & Kowalewski, 1999; Kowalewski & Nebelsick, 2003; Donovan & Pickerill, 2004; Złotnik & Ceranka, 2005; Meadows *et al.*, 2015). On the other hand, the parasitism of eulimid gastropods also produces drill holes, although significantly smaller, named *Oichnus halo* (Neumann & Wisshak, 2009).

The study of the distribution of the holes made by large and small *Cassis* (Gastropoda, Cassidae) on fossil echinoids from the Jurassic to the Recent verifies that, as in the case of naticids, the drilling activity was and is selective both for the size and place. Large cassids bore into and consume their prey almost always individually, whereas small cassids sometimes prey in groups upon urchins. Large cassids also display a higher site-selectivity. They more frequently bore into the petals and the apical disc. Larger cassids prey more habitually on larger echinoids (Farrar *et al.*, 2020). However, many trace morphologies observed on fossil echinoids cannot been associated with a possible predator. A better understanding of the morphology and distribution of these traces will allow us to carry out evaluations of the ecological and evolutionary importance of biotic interactions in benthic marine ecosystems (Złotnik & Ceranka, 2005; Tyler *et al.*, 2018; Farrar *et al.*, 2020; Petsios *et al.*, 2021).

Several modern octopod species belonging to the widespread genera *Octopus* and *Eledone* are known to drill into at least some of their shelled molluscan and crustacean prey. Drill holes made by octopods vary considerably in morphology, in part related to the microstructure and mineralogy of the affected shell (Wodinsky, 1973; Boyle & Knobock, 1981; Nixon & Maconnchie, 1988; McQuaid, 1994; Smith, 2003; López-Uriarte *et al.*, 2008; Fee *et al.*, 2023). All the first authors describe *Octopus* borings as oval. Wodinsky (1969), however, mentions that borings can vary from oval, circular, cross-shaped, and multi-sided polygons to extremely irregular ones. However, octopods are the only known predators to bore a distinctive ovoid and bevelled hole (*Oichnus ovalis*). *Octopus* activity has been thoroughly neglected by palaeontologists because, having no skeleton, they are virtually unrepresented by body fossils. Thus, *O. ovalis* may be used to gain some insight into ancient octopod-feeding behaviour (Bromley, 1993; Harper, 2005; Pasini & Garassino, 2012; Klompmaker *et al.*, 2013, 2014; Klompmaker & Landman, 2021).

Crustaceans (stomatopods and decapods) are active predators of molluscs. The common injuries they cause to shells are chipping and peeling (*Caedichnus*) (Frey, 1987; Stafford *et al.*, 2015). Crustaceans produce still other injuries to shells, such as the holes (*Belichnus*) originating in gastropods and bivalves from blows produced by the chelipods of stomatopods (Geary *et al.*, 1991; Baluk & Radwanski, 1996). Successful chipping or peeling attacks can leave distinctive damage on the shells, whereas unsuccessful attacks are often repaired, leaving characteristic repair scars on the shell (Fig. 4E–4J) (Vermeij *et al.*, 1980, 1982; Vermeij, 1982; Allmon *et al.*, 1990; Turra *et al.*, 2005; Cintra-Buenrostro, 2007). As predation represents a major cause of death within marine ecosystems, shell-crushing predation by decapods has been shown to be an important process in the evolution of shells and crab claw designs (Vermeij, 1977; Vermeij *et al.*, 1981; Bertness & Cunningham, 1981; LaBarbera & Merz, 1992; Molinaro *et al.*, 2014). However, in cases other than predatory boreholes, it is often difficult to differentiate between *ante-* and *post-mortem* mechanical damage and *ante-mortem* predatory damage. Thus, it has proven difficult to attribute marginal shell damage in bivalves to predation by crustacean decapods, particularly crabs (Alexander & Dietl, 2003). However, a high incidence of death by breakage does not necessarily mean that breakage is evolutionarily significant. For example, if all attempts by predators to break shells resulted in the prey's death, the shell would be useless as a protection structure. The persistence of the prey populations facing such predation would occur not by virtue of the protective role of the shell, but in spite of it. The only way in which traits conferring resistance to cracking could spread through a population is by the survival and subsequent reproduction of individuals that have withstood onslaughts by shell-breakers. In other words, the evolution of anti-predatory protection is contingent upon predator failure (Vermeij, 1994). Repair scars also occur after non-lethal shell damage due to causes other than predation, *e.g.*, impact by stones, or self-inflicted damage during predation and burrowing.

Durophagous shell breakage is abundant in the Neogene record (Martinell, 1989; Geary *et al.*, 1991; Baluk & Radwanski, 1996). Papp *et al.* (1947) described and illustrated numerous examples of predation by the peeling activities of decapods mainly related to Tortonian gastropod prey, highlighting that certain naticid gastropod species are more prone to shell repair than others. Martinell *et al.* (1982) reached similar conclusions for the marine Pliocene of Catalonia—the

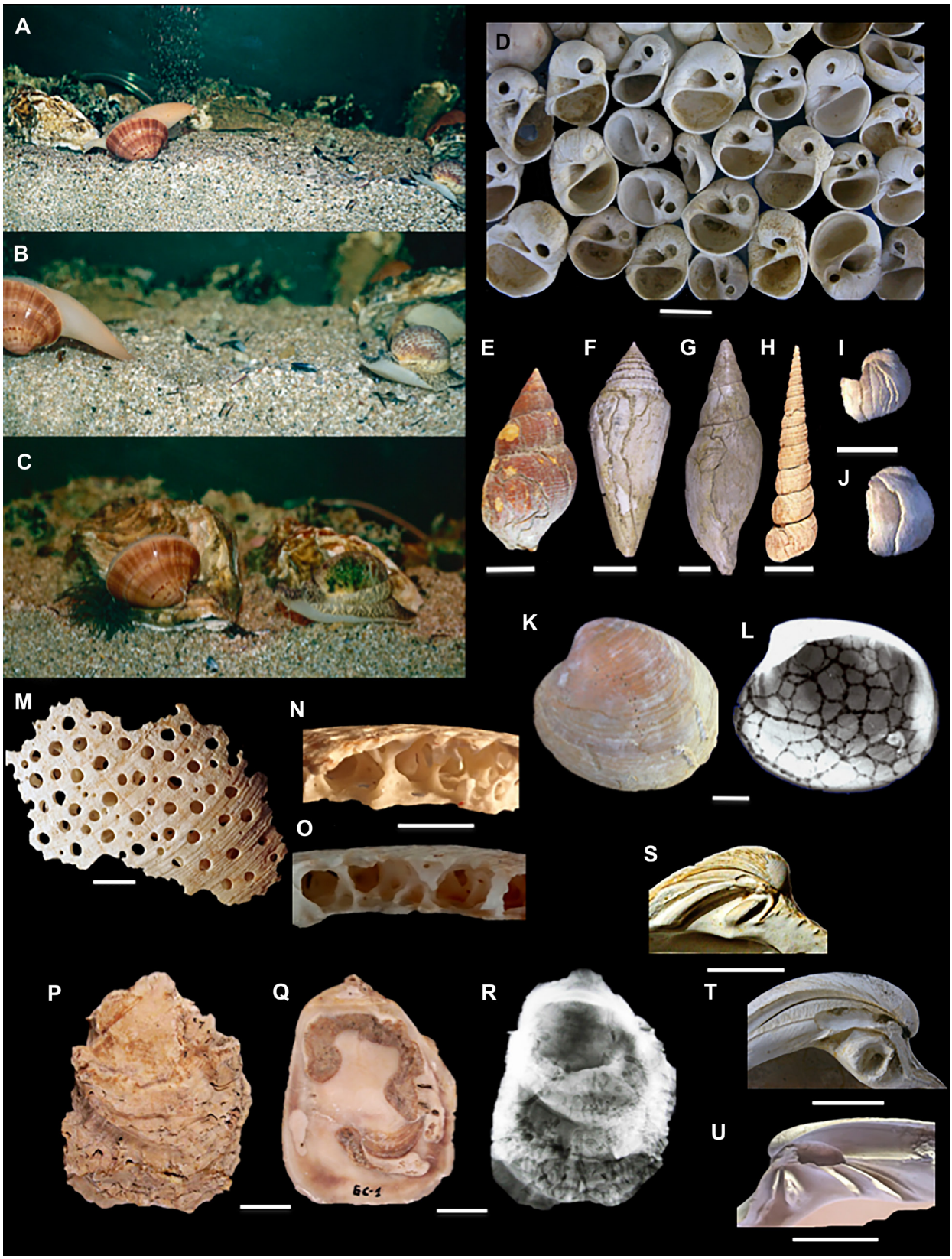

Figure 4. A–C, Attack sequence of the gastropod *Naticarius hebraeus* on the bivalve *Callista chione* in aquarium*;* **D,** *Cochlis pseudoepiglotina* shells showing naticid borings (*Oichnus paraboloides*), Pliocene, Roussillon, France; **E–J,** some predation scars made by crabs on Pliocene gastropods, and repaired; **E,** *Buccinum*; **F,** *Conus*; **G,** *Scaphella*; **H,** *Turritella*; **I–J,** *Cochlis*; **K–L,** *Arctica islandica* with *Entobia*; **K,** outer view of the shell; **L,** x-ray image to show the boring network in the shell; Pleistocene, Girona coast; **M–O,** *Entobia* boreholes in a shell fragment of a Recent *Glycymeris*, El Perelló, Tarragona; **P–R,** *Crassostrea rhizophorae* with *Maeandropolydora*; **Q,** clear mud blister; **R,** x-ray image to show the weakened interior of the shell; Pleistocene, Colombia; **S–U,** *Umbichnus* in bivalve shells; **S,** *Venericardia planicosta*, Eocene, Île-de-France, France; **T,** *Pelecyora gigas*, Pliocene, Huelva, Andalucía; **U,** *Dosinia concentrica,* Pleistocene, Sarasota, Florida; scale bars = 1 cm.

gastropod species with the most shell repairs being those belonging to turritellids, naticids, and nassarids, while also highlighting that between 45% and 99% of the injured specimens exhibit more than one repaired scar.

Using the Plio-Pleistocene fossil record of crab predation on morphologically similar pairs of right-coiled and left-coiled gastropod species, it has been noted that the rare sinistral coiling snail promotes survival from attacks by right-handed crabs. Dextral busyconid and conid species typically have higher shell repair frequencies than sinistral ones (Dietl & Hendricks, 2006).

Parasitism. Bivalves and gastropods are known to be hosts for various parasites that live in their mantles or within their shells (Blake & Evans, 1973; Carroll & Finelli, 2015; Diez *et al.*, 2011; Sato-Okoshi *et al.*, 2012). Parasites, by definition, are harmful to their host to a certain degree. Negative effects can vary from minor metabolic changes to more important soft tissue damage and reduced shell strength. Parasites recognizable in the fossil record are those that leave traces of their activity on/in the shell of their hosts. Among them, the best known are sponges, polychaetes and bivalves (Cremonte, 2011).

Boring sponges belong to the Clionaidae family and nowadays are the dominant endolithic sponges. *Cliona* is the Recent genus with the largest number of species, and specimens are capable of boring into a variety of substrates, including live and dead shells. They mainly parasitise epifaunal molluscan species (ostreids, pectinids, and mytilids) (Evans, 1969; Rützler & Rieger, 1973; Rützler, 2002; Rohde, 2005), and brachiopods (Bromley *et al.*, 2008). Sponges penetrate the periostracum forming 0.5–4 mm diameter circular holes on the surface and excavating a network of interconnected chambers or galleries with a series of globular chambers connected by canals and with external apertures, which appear as pores in shell surfaces (Fig. 4K–4O). In the fossil record they are registered under the ichnogenus name *Entobia* and its numerous ichnospecies. Apertures are invariably multiple, either linear or pepper pot-like in their distribution. The trace commonly appears parallel to the structure of the shells (De Groot, 1977; Bromley, 1970; Bromley & D'Alessandro, 1984, 1989; Garilli *et al.*, 2022).

Polychaete worms are active and widespread bioeroders, especially members of the family Spionidae. *Polydora websteri* Hartman is capable of boring into a variety of substrates, including coral, limestone, and live and dead shells (both bivalves and gastropods) (Voigt, 1975; Blake, 1971; Wargo & Ford, 1993). Its borehole is U-shaped, elongate and straight or sinuous, with the two parallel tubes separated by a central raised vane. The bore aperture has an eight-shaped outline. They commonly appear parallel to the layered structure of the shells. When the tubes reach the inner part of the valve, the infested mollusc reacts by secreting conchiolin layers in their attempt to isolate the polychaete, which may contain mud and debris from polychaetes (mud blisters) (Fig. 4P–4R). The presence of mud blisters in fossil ostreid valves would be indicative that the drilling activity was carried out while the bivalve was alive, allowing identification of a parasitism relationship (Domènech *et al.*, 2008).

Various ichnotaxa have been described related to bioerosion caused by worms in general, *Maeandropolydora* and *Caulostrepsi*s ichnogenera being associated with spionid polychaetes. They basically differ by the proximity (*Caulostrepsis*) or separation (*Maeandropolydora*) between the entrance and exit orifices and by the existence or not of a central raised vane along the route of the tunnels (Bromley & D'Alessandro, 1983). When infestation has occurred in a living shell, it is interpreted as parasitism and the producers are described as endoskeletozoans (Taylor & Wilson, 2002). As a reaction to the boring activity of the spionids, a thickening of the infected shell occurs. In the case of scallops, this thickening reduces their ability to swim, making them more accessible to predators (Mori *et al.*, 1985). Ishikawa and Kase (2007) proposed *Polydorichnus* as a new ichnogenus for spionid boreholes in gastropod shells. *Umbichnus inopinatus* Martinell *et al.* is another common ichnospecies located in an unusual but consistent position in the bivalve shells. The borehole is sack-shaped and is emplaced in and between the opposed hinge plates of the two shell valves, just beneath the umbo and dorsal to the hinge teeth. The size of the boring varies considerably, both within the same species of host, and according to the size of the host species. In large hosts, such as *Pelecyora islandicoides* Lamarck the borehole may reach a length of almost 2 cm (Martinell *et al.*, 1999) (Fig. 4S–4U). While the producer is still unknown, it has been attributed to some group of commensal polychaetes, probably spionids (Martinell *et al.*, 1999). The host bivalve is invariably a heterodont, 85 of the host species have been identified, distributed among the carditids, arcticids and venerids, from the Paleocene to the Recent (Martinell & Domènech, 2023). This borehole today appears to have a world-wide distribution, whereas in the geological record it has only been reported from the Mediterranean and northern Atlantic areas (Pereira *et al.*, 2009; Richiano *et al.*, 2012; Wisshak *et al.*, 2019; Martinell & Domènech, 2023).

Some solitary caryophylliid and flabellid scleractinian corals from the Pliocene of the Western Mediterranean exhibit epigenic groove-shaped bioerosional structures running along the surface of the thecae. Martinell and Domènech (2009) named them *Sulcichnus* and attributed them to the activity of polychaetes. Currently, similar structures are produced by the eunicid *Helmutneris flabellicola* Fage which maintains a commensalistic relationship with solitary corals. In the fossil record, *Sulcichnus* occurs associated to

shallow marine environments whereas their Recent counterparts are described for deep-marine corals. Martinell and Domènech (2009) interpreted this as a change in the environmental requirements of the coral/worm pair. *Sulcichnus* has been also found on Messinian rhodolith beds of the Western Mediterranean (Naimi *et al.*, 2021a, 2021b), though in this case the producer's commensalism habit must be discarded.

Lithophagous bivalves can drill into the upper valve of large ostreids, mainly occupying the umbonal area. These borings (*Gastrochaenolites*) can become numerous, weakening the shell structure (Lauckner, 1983). Kleemann (2009) described *Gastrochaenolites* in corals as *Favia* from the Lower Eocene of Wascheberg (Austria) and *Montastrea* from the Miocene of Seggauberg (Austria), which have presented a slight S-like bending in the basal (old part) of the boring, indicating an adaptation of the boring axis to the change in direction of the host coral growth. It also could be evidence of parasitism of the lithophagous bivalve in the coral.

BIOEROSION *VERSUS* TAPHONOMY

Death

Death is the initial stage from which the processes of taphonomy begin. In other words, it is the initiation of the transition of an organic entity towards the fossil register (Emig, 2002).

As seen in the Predation section, some traces of bioerosion, *e.g.*, complete drill holes produced by carnivorous gastropods, are obvious signs of the prey's death. Others, such as the traces of parasitism produced by spionid polychaetes (*Polydora*), can cause the death of the host even when the infestation only markedly weakens its shell. However, this fact is more complicated to verify since the activity of the spionids can continue to affect the host's shell after death. In addition, spionid polychaetes also pierce the shells of already dead molluscs, which would at this point simply be acting as a substrate.

The taphonomic processes on terrestrial vertebrate remains have received substantial attention both in the field and the laboratory (Weigelt, 1928, 1989; Behrensmeyer & Hill, 1980; Brain, 1981; Shipman, 1981; Andrews, 1990; Allison & Briggs, 1991; Lyman, 1994; Martin, 1999; De Renzi *et al.*, 2002; Fernández-Jalvo & Andrews, 2016). Mikuláš *et al.* (2006) erected three new ichnotaxa for bite and gnaw marks recognized in animal fossil hard tissues: *Machichnus* (shallow serial or subparallel grooves, interpreted as gnaw marks), *Nihilichnus* (circular or oval attack marks in compact bone), and *Brutalichnus* (strong impact marks, characterized by breaking the cortical bone towards its inner part). Jacobsen and Bromley (2009) proposed a new ichnogenus for tooth impressions, *Linichnus* (unique elongated toothed groove on bone surface). Taphonomic processes in marine aquatic environments differ markedly from those in terrestrial environments. Due to the complexity of developing underwater observations, studies on the alteration of the skeletal remains of current marine vertebrates are very scarce and are basically concentrated on the study of the pre-burial stages of cetacean carcasses (Allison *et al.*, 1991; Smith & Baco, 2003; Rouse *et al.*, 2004; Haag, 2005; Dahlgren *et al.*, 2006; Amon *et al.*, 2013; Muñiz *et al.*, 2020). Unfortunately, fossil cetaceans with a significant part of the skeleton preserved are relatively rare and consequently the few documented cases of possible shark bite marks (*Nihilichnus*, *Linichnus* and/or *Brutalichnus*) prevalently correspond to fragmentary remains (Lambert & Gigase, 2007; Noriega *et al.*, 2007; Ehret *et al.*, 2009; Esperante *et al.*, 2009; Godfrey & Lowry, 2021), being challenging to differentiate whether they respond to predation or scavenging. Shark teeth are sometimes found associated along with cetacean remains. This could be direct evidence of shark attacks (Ehret *et al.*, 2009; Muñiz *et al.*, 2009). Bianucci *et al.* (2001) describe a specimen of *Astadelphis* (Cetacea, Delphinidae) from the Italian Pliocene with well-defined predation bite marks produced by a shark, including striae (*Linichnus*), sulci (*Nihilichnus*) and abrasions (*Brutalichnus*)—visible on the right dentary, on several ribs and on vertebrae—having lethal consequences.

Biostratinomy

Around 40 animal species can coexist within the carcasses of today's whales, including different types of fish (sharks, hagfish, etc.) and invertebrates (crabs, ophiuroids, molluscs, polychaetes, etc.), which feed on their remains (Dahlgren *et al.*, 2006). In the fossil record, traces of bone eater *Osedax* (Siboglinidae, Polychaeta) activity are found in whales, fish, and bird bones (Kiel *et al.* 2010, 2013; Higgs *et al.*, 2011). They have been described as *Clavichus ionassi* (Muñiz *et al.*, 2010, 2017; Höpner & Bertling, 2017). The presence of the scavenger cassid gastropod *Liracassis*, found in close association with Oligocene mysticete whale skeletons, indicate a novel trophic relationship (Nesbitt, 2005). Possible traces of osteophagous activity of potential decapod crustaceans have been reported in the scapula of a mysticete whale from the lower Pliocene of Southern Spain (Esperante *et al.*, 2009; Belaústegui *et al.*, 2017b). Clavate borings (*Gastrochaenolites* isp.) found in a cetacean skull from the Miocene of Tarragona provide the first evidence of bioerosion by pholadid bivalves on an autochthonous marine mammal skeleton (Belaústegui *et al.*, 2011, 2012a). Cione *et al.* (2010) reported *Gnatichnus and Radulichnus* grazing traces on penguin bones from the Argentinian Miocene. The echinoids and molluscs responsible for these two ichnogenera grazed on the substrate to feed upon exo- and endoskeletal algae and other microorganisms.

The remains of different organisms are transported in many ways. At the same time, similar organic

remains are transported in different ways in different environments. Most *post-mortem* transport of bottom-dwelling marine organisms depends on currents. In relatively shallow waters where currents are strong, a skeleton may be carried a considerable distance to its final burial site. Sorting or selection during the *post-mortem* transport is important because it influences the composition of the final fossil assemblage.

The left-right valve sorting by currents in bivalves varies depending on the size, the symmetry, and the perimeter of the shells (Martin-Kaye, 1951; Brenchley & Newall, 1970; Shimoyama & Fujisaka, 1993; Chattopadhyay *et al.*, 2013; Angseesing, 2020). Lever (1958) and Lever and Thijssen (1968) carried out extensive research on the transport behaviour of pierced valves (with *Oichnus*), concluding that there is a drill hole effect. The unpierced valves had a different behaviour compared to the bored ones, with differences depending on the number, location and diameter of the hole(s). The proportion of drilled/non-drilled valves, rather than strictly being an ecological factor, may have a taphonomic bias.

Although bioerosion is recognized to cause significant destruction of hard substrates, as of yet, few studies have assessed the loss of biological entities due to a taphonomic bias in relation to shells with predatory perforations (*Oichnus*). Some studies have assumed that drilled and non-drilled bivalve shells do not have the same preservation potential, indicating that valves with *Oichnus* are significantly weaker than those without them, considering factors such as transport, compaction, etc. (Roy *et al.*, 1994). On the contrary, Kowalewski and Hoffmeister (2004) tested whether drilling frequencies were independent of the taphonomic condition with shells from the Holocene beach ridges of Baja California and from mollusc assemblages of the European Miocene. These authors concluded that drilling did not affect the pre-burial survival of shells. The results from Kelley (2008) were similar, finding that the bias unfavourable to the specimens containing *Oichnus* was not significant in fossil shell beds examined—neither from the Miocene of Maryland nor the Plio-Pleistocene of Florida.

The transport of more delicate skeletons (*e.g.*, scaphopods, polychaete tubs), which were also attacked by boring predators, can easily provoke their breakage across the borehole. In a quantitative analysis of predation in the serpulid polychaete *Ditrupa arietina* Müller from the Pliocene of Southeastern Spain, Martinell *et al.* (2012) observed that between 29% and 38% of drilled tubes had broken across the boring. These figures reveal, on the one hand, that information on the intensity of predation can be lost due to breakage while, on the other hand, that the skeletons could be more broken than would correspond to the same environmental conditions but without being affected by bioerosion.

On present-day beaches it has been observed that shells of certain species of bivalves appear with the umbo worn away, giving an *Oichnus*-like structure. These are shells with prominent umbos (*Acanthocardia*, *Glycymeris*, etc.) that, once the animal is dead and the skeleton is subjected to sea currents, are eroded by friction at the umbonal end (Fig. 5A–5D). This breakage can be confused morphologically with naticid borings. However, its position at the umbonal end, and often its size, indicate with greater certainty that the hole is of mechanical origin (Martinell *et al.*, 2021a).

The transport of biological entities can also be carried out by living organisms. In marine ecosystems, hermit crabs play a major role in this process. Throughout the “life” of a gastropod shell, numerous hermit crabs may inhabit it, subjecting it to different ecological and environmental conditions than those of the gastropod’s own habitat. This process effectively extends the “shelf life” of the shell far beyond that of the initial gastropod (Walker, 1989). Shells inhabited by hermit crabs are susceptible to damage from predators that attack both gastropods and hermit crabs. These shells can also be affected by environmental agents, such as wave action and potential colonisation by boring organisms like sponges and spionid worms. Unlike living gastropods, hermit crabs cannot defend themselves against them (Bertness, 1982; Walker, 1989, 1992). Certain boring organisms—including foraminifera, sponges, polychaetes, barnacles or bryozoans—can penetrate shells of both living gastropods and those inhabited by hermit crabs, potentially producing visible holes and weakening the shell’s structure, and thus increasing its vulnerability to environmental damage. While skeletal dissolution and boring represent types of non-predatory damage, which is distinct from predatory damage, they can still weaken the shell’s integrity, making it more susceptible to environmental damage (Smyth, 1990). Effective shell availability to hermit crabs depends on the causes of gastropod death. The hermit crab population may utilize almost all shells, even those drilled and otherwise damaged, so that all habitable shells are exposed to the same types of taphonomic damage (Zuschin *et al.*, 2003; Ishikawa *et al.*, 2004; Stafford & Lighton, 2011). Hermit crabs can select which species’ empty shells they use. In the rocky supralittoral zone of the coast of Cabo Huertas (Alicante), practically out of the water, we observed monospecific groups of hundreds (almost 400) of *Cerithium lividulum* Risso shells occupied by the hermit crab *Clibanarius erythropus* Lastreille (Fig. 5E). Obviously, this habitat does not correspond to that of the living *C. lividulum*, a species who inhabits shallow but water-covered rocky bottoms. The result is the alteration of the molluscan taphocenosis and, thus, the loss or masking of palaeoecological and palaeoenvironmental information.

A variety of marine bivalves (clavagellids, mytilids, tridacnids, pholadids, myids, petricolids, arcids, and gastrochaenids) actively bore into invertebrate skeletal remains, using chemical and/or mechanical techniques, while producing club-shaped dwellings

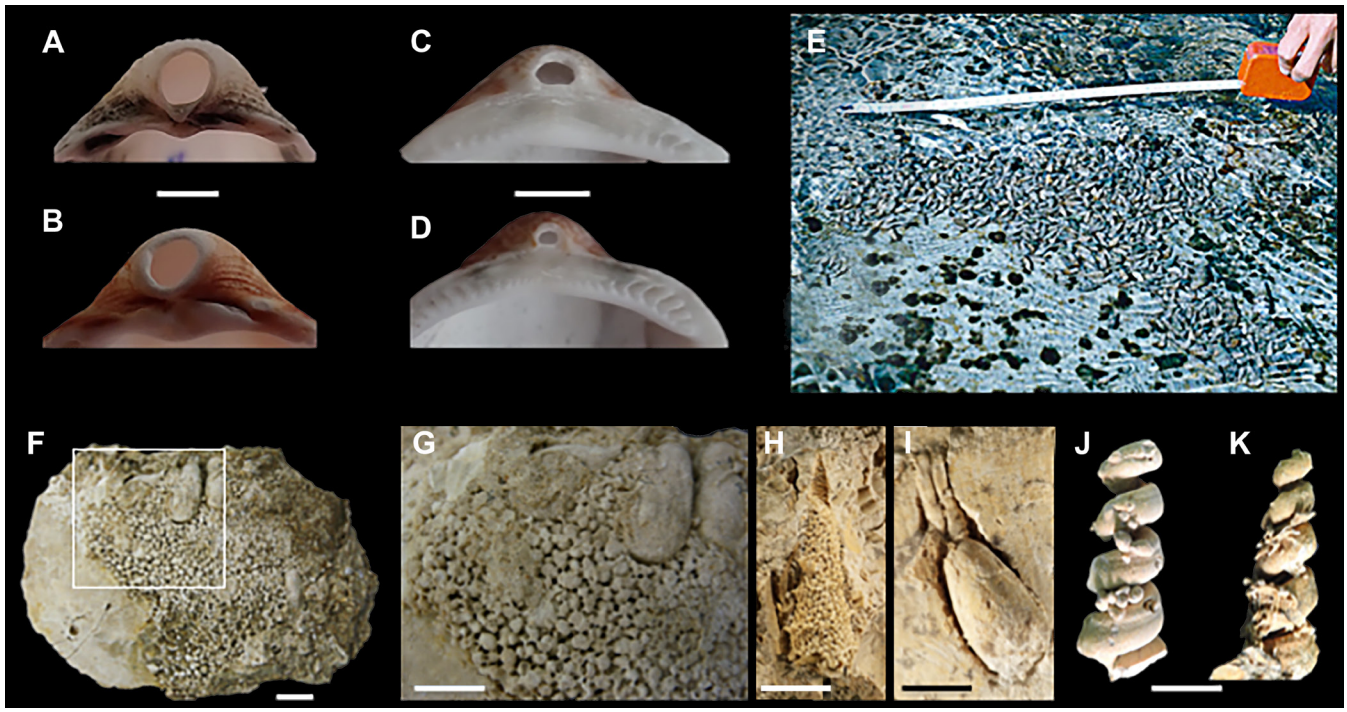

Figure 5. A–D, Bivalve shells with umbones "bored" by inorganic marine abrassion; **A–B,** *Acanthocardia*; **C–D,** *Glycymeris*; El Remolar beach, Baix Llobregat; **E,** *Cerithium lividulum* shells concentration by the hermit crab *Clibanarius erythropus*, Cabo de las Huertas, Alacant; **F–G,** inner mould of *Entobia* (detail in G) and some small moulds of *Gastrochaenolites* in a bivalve mould; **H,** *Entobia* mould completely covering a turritellid gastropod inner mould; **I,** mould of *Gastrochaenolites* including the siphons conducts; **J,** turritellid inner mould with small *Gastrochaenolites* moulds; **K,** turritelid inner mould with *Caulostrepsis* moulds. Specimens in F to K from Middle Miocene, Garraf, Barcelona; scale bars = 1 cm.

(*Gastrochaenolites*). Large and thick epifaunal bivalve shells (rudists, clams, oysters) have been described from the Mesozoic to the Recent, showing weakened shells due to perforations by lithophagous bivalves (Kleemann, 1994; Bromley, 2004; Villegas-Martín *et al.*, 2022). Several Miocene species of *Ostrea* from Patagonia (Argentina) have been reported with abundant *Gastrochaenolites*, usually in the upper valve (Farinati & Zavala, 2002; Mauna *et al.*, 2005; Domènech *et al.*, 2014; Romero *et al.*, 2017). Mauna *et al.* (2005) suggested that the absence of *Gastrochenolites* in the inner side of the valves would indicate that the drilling activity of lithophages occurred while the oysters were still alive and, at the same time, that the oyster shells were quickly buried after death. Lopes (2011) reached similar conclusions through studying the bioerosive activity in *Ostrea puelchana* D'Orbigny and *Crassostrea virginica* Gmelin from the Pleistocene-Holocene of Rio Grande do Sul (Brazil).

The abundance of clypeasteroids in the fossil record is attributed to a variety of distinctive characteristics that enhance their preservation, in addition to the formation of mass aggregations. These characteristics include: (1) their tendency to gather in groups; (2) the strength of their skeletal structure; (3) their high mobility; and (4) their preference for inhabiting shoreface environments, which favour its redistribution and accumulation (Belaústegui *et al.*, 2012b). The dome-shaped tests of *Clypeaste*r thus represented the commonest, largest, and most stable hard substrates on an otherwise soft, shifting, sandy sea bottom, and have therefore been considered as benthic islands or preferential spots for settlement and growth of boring skeletozoans in the Neogene. *Gastrochaenolithes* is one of the commonest bores in clypeasteroids fossil tests (Santos *et al.*, 2003b; Belaústegui *et al.*, 2013; Rahman *et al.*, 2015). The distribution of modern wood-boring bivalves is mainly controlled by salinity, temperature, and availability of wood (Lavigne, 1999). Teredinids thrive in exclusively marine conditions but can survive in brackish waters with salinities over 10 ppt and grow at higher rates in warmer water conditions.

Wood-boring teredinid and pholadid bivalves produce clavate or club-shaped borings, which are collectively assigned to the ichnogenera *Teredolites* (Kelly & Bromley, 1984) and *Apectoichnus* (Donovan, 2018), being present in the stratigraphic record since the Jurassic. *Teredolites* is taphonomically informative because it provides evidence for the timing and position of wood prior to burial. Heise *et al.* (2011) observed that (on average and after two years on the sea bottom) the 74% loss of original volume in modern wood samples was due to teredinid colonization. *Teredolites* have been found both in *in situ* composite wood substrates (Bromley *et al.*, 1984; Savrda *et al.*, 1993), in individual allochthonous fossil log-grounds, and as ghost log-grounds (*Teredolites* liberated from their original wood-substrates) (Pickerill *et al.*, 2003;

Kříž & Mikuláš, 2006). Because of the relative ease with which logs are transported in aquatic systems, *Teredolites* found in allochthonous trunks is by far the most common situation (Radwanski, 2009; Donovan *et al.*, 2009; Monaco *et al.*, 2011; Villegas-Martín & Rojas-Consuegra, 2011; Kumar *et al.*, 2011; Villegas-Martín *et al.*, 2012; Leszczynski, 2018; Serrano-Brañas *et al.*, 2019; Belaústegui *et al.*, 2020a).

Fossildiagenesis

Resedimentation of preserved elements is a biostratinomic process, whereas the reelaboration of those elements (named reworking in many papers) is a fossildiagenetic process (Fernández López, 1984a, 1984b)

The reelaboration of fossils is commonly associated with "poor" preservation, as processes such as breakage, abrasion, corrosion, encrustation and boring could affect them after exhumation and transport. Reelaborated fossils commonly correspond to robust skeletal remains (shells, bones, wood) or to fossil moulds that were eroded out from a sedimentary rock. Reelaborated fossils may remain buried in either younger or older strata, depending on their taphonomic journey. The character of reworked fossils is easily deduced through their bioerosive structures when these affect skeletal moulds (Akpan *et al.*, 1982; Fernández López, 1984b). The analysis must be more precise when the perforations directly affect the shell, as for example in the case of corals, oysters, rudists or clypeastoroids, where it must be discerned whether the traces are contemporary with the skeletal remains or were produced during the reworking process (Donovan *et al.*, 2010; Villegas-Martín *et al.*, 2022). On modern beaches, limited by sedimentary sequences, it is not unusual to find a mixture of present-day fauna and recently drilled fossils (Donovan, 2012; Donovan *et al.*, 2014; Lopes, 2024).

A paradigmatic case would be that of underwater deposits with perforated mollusc shells from the marine Pleistocene of the NE of the Iberian Peninsula (Domènech & Martinell, 1982; Martinell & Domènech, 1981, 2023; Molinu, 2015; Belaústegui *et al.*, 2020b). The typical fauna of cold waters appears exposed in the canyons of the marine platform, where they could have been used as a substrate by today's macro- and micro-borers. Distinguishing between the activity that took place in the vital or biostratinomic phases from that which would have occurred in the last stages of the fossildiagenetic phase is relevant for the interpretation of the taphonomic assemblage, given the different environmental conditions that would correspond to different drillers/encrusters. It is therefore hard to deduce the drilling sequence and, consequently, to know the actuation order for each producer.

Ekdale *et al.* (1984) defined lithoturbation as a process of successive episodes of bioerosion-sedimentation-cementation-bioerosion. As such, lithoturbation is a perfect example of the relationships among biological, biostratinomic and diagenetic processes. The deciphering of the successive events permits the interpretation of a depositional environment as well as the reconstruction of the fossilisation path. Belaústegui *et al.* (2018) describe and interpret a multi-episodic marine shell accumulation in the Pi Gros Miocene outcrop (Garraf, NE Iberian Peninsula) where both bioerosional, biostratinomic and diagenetic processes act successively and repeatedly on skeletons, moulds and substrate (Fig. 5F–5K). Most notably, bioerosion traces due to different endoskeletozoans gave clues regarding the sequence. Boreholes produced in shells by sponges, polychaetes and bivalves were simultaneous, but the presence of semi-endoskeletal dwellings and isolated casts implies episodes with higher sedimentation rates. Furthermore, clusters of intersecting clavate-boring *G. dijugus* proved the occurrence of different bioerosive episodes. Due to diagenesis, fossil molluscs were preserved as internal and external moulds, while traces were preserved as positive casts. This site provided an excellent example of how both destructive (dissolution) and constructive (cementation of boring casts) diagenetic processes may result in the exceptional preservation of bioerosion trace fossils, which at the same time explains a complete multi-episodic sequence. Taxonomic, ichnologic and taphonomic approaches have allowed the interpretation of the depositional environment and the fossilisation succession.

Romero Baena *et al.* (2022) also present an extraordinary case of *Gastrochaenolites* preservation in opaline silica. The borings were produced by pholadid bivalves in volcanic tuff pebbles deposited in a marine subtidal environment after a tsunami event (Oligocene, Ica, Peru). The mineralization affected both the pholadid shells and the borings and allows for the precise interpretation of the diagenetic environment.

SOME REFLECTIONS, BY WAY OF CONCLUSIONS

Bioerosion studies are in good health. A handful of researchers from all over the world have been specializing in this field and both basic ichnotaxonomic results and those applied to palaeontology and geology have been increasing in recent years. This means that the future of this field can be faced with optimism.

Bioerosion is a destructive-constructive process of palaeobiological information present in all the Phanerozoic marine ecosystems. Bioeroders modify substrates (rocky, skeletal, or wood) through destruction, but at the same time build new (palaeo) biological information that needs to be interpreted carefully.

Macroperforations may not be as spectacular as other groups of ichnofossils (*e.g.*, dinosaur footprints) or most body fossils, but their study provides valuable information about the biodiversity and ecology of

past marine ecosystems, and moreover about the taphonomic processes which affected the organic remains.

The ichnotaxonomic composition of rocky-shore assemblages changed through the Phanerozoic (*Typanites-Gastrochaenolites-Entobia*). Macrobioerosion in rocky shores is mainly used to characterize unconformity surfaces, which is of great interest from a geological point of view. Nevertheless, I believe that more detailed studies on the possible relationships among the rock borers themselves are needed as they could contribute new information on ancient rocky ecosystems. A few articles have been published in this sense and there is still much terrain to explore.

The study of depredation through the investigation of bioerosion traces in skeletal remains is seminal in order to see tendencies, coevolution, etc. in the geological past, but it is also important to take into account the fact that we are dealing with organisms that do not always follow the same behaviour. For example, when we are registering naticid traces on the shell of their victims, it is worth considering that they do not always need to bore to obtain food. In this case, predation activity is not reflected in the palaeontological record, although it had existed.

The drill hole effect regarding the transport of the bivalves by marine currents is a taphonomic bias that must be taken into account in palaeoecological studies, whether they are approached from a global or analytical alternative.

From the taphonomical point of view, is relevant to assess the response of bioeroded skeletal remains—especially those affected by endolithic drillers—being weakened shells, which are more fragile when transported by sea currents and which, consequently, can fragment more easily even with weak currents.

The study of bioerosional processes in present-day coastal environments and beaches is very useful for interpreting biostratinomic processes (transport, fragmentation, etc.) in ancient, shallow environments. Beaches are authentic changing laboratories of taphonomic processes that marine dynamics modify depending on the characteristics of the currents, their intensity and direction, and which in turn modify the components of biological entities. We can see the results in the thanatocoenoses accumulated on today's beaches (from the shoreface to the backshore), usually riches in mollusc remains. They are particularly evident after storms or episodes of rough seas, but they also occur under calmer conditions.

Donovan *et al.* (2010) have reported that "Reworked macrofossils are rare and fascinating components of the record that can preserve evidence of unique *postmortem* histories." I agree with the concept of fascinating, but I do not think that reworked (*sensu* reelaborated) macrofossils are rare but, rather, that they have not yet received enough attention. Until this point, we have only taken into account all the present-day planetary rocky shores built by sedimentary rocks that are potentially rich in fossils. Marine erosion is occurring to a greater or lesser extent, and it produces reelaboration of fossils that fall into the present sea and can be used as settlement sites for many organisms, encrusters, and bioeroders; we find them in the present-day beaches. Over more than 600 Ma of regular erosion in rocky shores, the production of reelaborated entities must have been really important. I think this is a fascinating field in which the study of bioerosion can make a significant contribution to our knowledge of the past and present.

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REFERENCES

Abbel-Fattah, Z. A., & Assal, E. M. (2016). Bioerosion in the Miocene Reefs of the northwest Red Sea, Egypt. *Lethaia, 49*, 398–412. doi: 10.1111/let.12157

Ager, D. (1986). A reinterpretation of the basal "Littoral Lias" of the Vale of Glamorgan. *Proceedings of the Geologists Association*, *97*, 29–35. doi: 10.1016/S0016-7878(86)80003-7

Aguirre, J., & Jiménez, A. P. (1997). Census assemblages in hard-bottom coastal communities: a case study from the Plio-Pleistocene Mediterranean. *Palaios, 12*, 598–608. doi: 10.2307/3515415.

Aguirre, J., Belaústegui, Z., Domènech, R., Gibert, J. M. de, & Martinell, J. (2014). Snapshot of a lower Pliocene *Dendropoma* reef from Sant Onofre (Baix Ebre Basin, Tarragona, NE Spain). *Palaoegeography, Palaeoclimatology, Palaeoecology*, *395*, 9–20. doi: 10.1016/j.palaeo.2013.12.011.

Aguirre, J., Domènech, R., Martinell, J., Mayoral, E., Santos, A., & Pérez-Asensio, J. N. (2017). Witnesses of Early Pliocene Sea-level Rise in the Manilva Basin (Málaga, S Spain). *Spanish Journal of Palaeontology, 32*, 35–52. doi: 10.7203/sjp.32.1.17029

Akpan, E. B., Farrow, G. E., & Morris, N. (1982). Limpet grazing on Cretaceous algal-bored ammonites. *Palaeontology*, *25*, 361–367.

Alexander, R. R., & Dietl, G. P. (2003). The fossil record of shell-breaking predation on marine bivalves and gastropods. In P. H. Kelley, M. Kowalewski, & T. A. Hansen (Eds.), *Predator-prey Interactions in the Fossil Record* (pp. 141–176). Kluwer Academic/Plenum Publishers. doi: 10.1007/978-1-4615-0161-9_7

Allison, P. A., & Briggs, D. E. G. (Eds.) (1991). *Taphonomy. Releasing the Data Locked in the Fossil record*. Topics in Geobiology, 9, Plenum Press.

Allison P. A., Smith C. R., Kukert H., Deming J. W., & Bennett B. A. (1991). Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina Basin. *Paleobiology, 17*, 78–89. doi: 10.1017/S0094837300010368

Allmon, W. D., Nieh, J. C., & Norris, R. D. (1990). Drilling and peeling of turrritelline gastropods since the Late Cretaceous. *Palaeontology*, *33*, 595–611.

Allsop, D., Seal, K. J., & Gaylarde, C. C. (2004). *Introduction to Biodeterioration*. Cambrige University Press. doi: 10.1017/CBO9780511617065

Amon, D. J., Glover, A. G., Wiklund, H., Marsh, L., Linse, K., Rogers, A. D., & Copley, J. T. (2013). The discovery of a natural whale fall in the Antarctic deep sea. *Deep Sea Research Part II: Topical Studies in Oceanography, 92*, 87–96. doi: 10.1016/j.dsr2.2013.01.028

Andrews P. (1990). *Owls, Caves and Fossils: Predation, preservation and accumulation of small mammal bones in caves, with an analysis of the Pleistocene cave faunas from Westbury-Sub-Mendip, Somerset, UK*. University of Chicago Press.

Ansell, A. D. (1983). Prey selection by the naticid gastropod, *Polinices catena. Journal of Molluscan Studies*, *49*, Issue supp12A, 1. doi: 10.1093/oxfordjournals.mollus.a065725

Angseesing, J. (2020). Left-right sorting in bivalves–a comparison of elongate versus non-elongate shells. *Proceedings of the Cotteswold Naturalists Field Club, XLVIII*, 233–242.

Aubert, D. (1972). Le lapié fossile des Verrières (Doubs). *Annales Scientifiques de l'Université de Besançon*, *3 G*éologie, *17*, 85–88.

Baarli, G., Malay, M. C., Santos, A., Johnson, M., da Silva, C. M., Meco, J., Cachão, M., & Mayoral, E. (2017). Miocene to Pleistocene transatlantic dispersal of *Ceratoconcha* coral-dwelling barnacles and North Atlantic island biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *468*, 520–528. doi: 10.1016/j.palaeo.2016.12.046

Baldanza, A., Bizzarri, R., Posati, F., & Ravoni, M. (2020). Evidence of Predation on Early Pleistocene Freshwater Ostracods (Umbria, Central Italy). *Geosciences, 10*, Article 416. doi: 10.3390/geosciences10100416

Ballesio, R. (1972). Étude stratigraphique du Pliocène rhodanien. *Documents des Laboratoires de Geólogie de la Faculté des Sciences de Lyon, 53*, 1–333.

Baluk, W., & Radwanski, A. (1996). Stomatopod predation upon gastropods from the Korytnica Basin, and from other classical Miocene localities in Europe. *Acta Geologica Polonica*, *46*, 279–304.

Bambach, R. K. (2002). Supporting predators: changes in the global ecosystem inferred from changes in predator diversity. In M. Kowalewski, & P. H. Kelley, (Eds.), The fossil record of predation. *The Paleontological Society Papers*, *8*, 319–352. doi: 10.1017/S1089332600001145

Batllori, J., & Martinell, J. (1992). Actividad predadora en moluscos del Mioceno del Penedès (Catalunya). *Revista Española de Paleontología*, *7*, 24–30. doi: 10.7203/sjp.24775

Baumiller, T. K. (1996). Boreholes in the Middle Devonian blastoid *Heteroschisma* and their implications for gastropod drilling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *123*, 343–351. doi: 10.1016/0031-0182(95)00124-7

Baumiller, T. K, & Gahn, F. J. (2004). Testing predation-driven evolution using mid-paleozoic crinoid arm regeneration. *Science, 305*, 1453–1455. doi: 10.1126/science.1101009

Baumiller, T. K., Bitner, M. A., & Emig, C. C. (2006). High frequency of drill holes in brachiopods from the Pliocene of Algeria and its ecological implications. *Lethaia*, *39*, 313–320. doi: 10.1080/00241160600847546

Baumiller, T. K. Leighton, L. R, & Thompson, D. (1999). Boreholes in brachiopods of the Fort Payne Formation (Lower Mississippian, central USA). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *147*, 283–289. doi: 10.1016/S0031-0182(98)00165-5

Beech, I. B., & Gaylarde, C. C. (1999). Recent in advances in the study of biocorrosion: an overview. *Revista de Microbiología, 30*, 177–190. doi: 10.1590/S0001-37141999000300001

Behrensmeyer, A. K., & Hill, A. P. (Eds.) (1980). *Fossils in the Making. Vertebrate Taphonomy and Paleoecology*. The University of Chicago Press.

Belaústegui Z., Doménech R., & Martinell J. (2018). An ichnofossil-lagerstätte from the Miocene Vilanova basin (NE Spain): taphonomic and paleoecologic insights related to bioerosion structures. *Palaios*, *33,* 16–28. doi: 10.2110/palo.2017.082

Belaústegui, Z., Gibert, de J. M., Domènech, R., Muñiz, F., & Martinell, J. (2011). Tafonomía y contexto paleoambiental de los restos de un cetáceo del Mioceno medio de Tarragona (NE España). *Geobios*, *44*, 19–31. doi: 10.1016/j.geobios.2010.07.002

Belaústegui, Z., Gibert, de J. M., Domènech, R., Muñiz, F., & Martinell, J. (2012a). Clavate borings in a Miocene cetacean skeleton from Tarragona (NE Spain) and the fossil record of marine bone bioerosion. *Palaeogeography, Palaeoclimatology, Palaeoecology, 323–325*, 68–74. doi: 10.1016/j.palaeo.2012.01.031

Belaústegui, Z., Gibert, J. M. de, Nebelsick, J. H., Domènech, R., & Martinell, J. (2013). Clypeasteroid tests as benthic islands for gastrochaenid bivalve colonization: Evidences from the Middle Miocene of Tarragona (NE Spain). *Palaeontology*, *56*, 783–796. doi: 10.1111/pala.12015

Belaústegui, Z., Muñiz, F., Nebelsick, J. H., Domènech, R., & Martinell, J. (2017a). Echinoderm ichnology: bioturbation, bioerosion and other related processes. *Journal of Palaeontology*, *9*, 643–661. doi: 10.1017/jpa.2016.146

Belaústegui, Z., Muñiz, F., Domènech, R., & Martinell, J. (2017b). Icnogenia, nuevos ejemplos a partir de estructuras de bioerosión. In L. O'Dogherty (Coord.), *XXXIII Jornadas de Paleontología* (pp. 28–31). Cádiz.

Belaústegui, Z., Muñiz, F., Domènech, R., & Martinell, J. (2020a). Ichnogeny and bivalve bioerosion: examples from shell and wood substrates. *Ichnos*, *27*, 277–283. doi: 10.1080/10420940.2020.1744584

Belaústegui, Z., Muñiz, F., Domènech, R., & Martinell, J. (2020b). Tafonomia de Icnofósseis. In D. Sedorko, & H. Francischini (Eds.), *Icnologia: Interaçöes entre organismos e substrates* (pp. 49–74). Editora CRV Ltd.

Belaústegui, Z., Nebelsick, J. H., Gibert, J. M. de, Domènech, R., & Martinell, J. (2012b). A taphonomic approach to the genetic interpretation of clypeasteroid accumulations from Tarragona (Miocene, NE Spain). *Lethaia*, *45*, 548–565. doi: 10.1111/j.1502-3931.2012.00314.x

Bengtson, S., & Zhao, Y. (1992). Predatorial borings in Late Precambrian mineralized exoskeletons. *Science*, *257*, 367–369. doi: 10.1126/science.257.5068.367

Bertling, M., Brady, S. J., Bromley, R. G., Demathieu, G. R., Genise, J., Mikuláš, R. Nielsen, J. K., Nielsen, S. S., Rinsberg, A. K., Schlirf, M., & Uchman, A. (2007). Names for trace fossils: a uniform approach. *Lethaia*, *39*, 265–286. doi: 10.1080/00241160600787890

Bertness, M. D. (1982). Shell utilization, predation pressure, and thermal stress in panamanian hermit crabs: An interoceanic comparison. *Journal of Experimental Marine Biology and Ecology, 64*, 159–187. doi: 10.1016/0022-0981(82)90151-4

Bertness, M. D., & Cunningham, C. (1981). Crab shell-crushing predation and gastropod architectural defense. *Journal of experimental marine Biology and Ecology*, *50*, 213–230. doi: 10.1016/0022-0981(81)90051-4

Bianucci, G., Sorce, B., Storai, T., & Landini, W. (2010). Killing in the Pliocene: shark attack on a dolphin from Italy. *Palaeontology*, *53*, 457–470. doi: 10.1111/j.1475-4983.2010.00945.x

Blake, J. A. (1971). Revision of the genus *Polydora* from the East coast of North America. *Smithsonian Contributions to Zoology*, *75*, 1–32. doi: 10.5479/si.00810282.75

Blake, J. A., & Evans, J. W. (1973). *Polydora* and related genera as borers in molluscan dshells and other calcareous substrates. *The Veliger*, *15*, 235–249.

Blissett, D. J., & Pickeril, R. K. (2007). Systematic ichnology of microborings from the Cenozoic White Limestone Group, Jamaica, West Indies. *Scripta Geologica*, *134*, 77–108.

Boekschoten, G. J. (1967). Paleoecology of some Mollusca from the Tielrode Sand (Pliocene, Belgium). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *3*, 311–362. doi: 10.1016/0031-0182(67)90024-7

Bolotov, I. N., Aksenova, O. V., Bakken, T., Glasby, C. J., Gofarov, M. Y., Kondakov, A. V., Konopleva, E. S., Lopes-Lima, M., Lyubas, A. A., Wang, Y., Bychkov, A. Y., Sokolova, A. M., Tanmuangpak, K., Tumpeesuwan, S., Vikhrev, I. V., Shyu, J. B. H., Win, T., & Pokrovky, O. S. (2018). Discovery of a silicate rock-boring organism and macrobioerosion in fresh water. *Nature Communication, 9*, Article 2882. doi: 10.1038/s41467-018-05133-4

Bolotov, I. N., Kondakov, A. V., Konopleva, E. S., & Vikhrev, I. V. (2021). A new genus of ultra-elongate freshwater mussels from Vietnam and eastern China (Bivalvia: Unionidae). *Ecologica Montenegrina, 39*, 1–6. doi: 10.37828/em.2021.39.1

Boucot, A. J. (1990). *Evolutionary Paleobiology of Behavior and Coevolution*. Elsevier.

Boucot, A. J., & Poinar, G. O. (2010). *Fossil Behavior Compendium*. CRC Press. doi: 10.1201/9781439810590

Boyle, P. R., & Knobock, D. (1981). Hole boring of crustacean prey by the octopus *Eledone cirrhosa* (Mollusca, Cephalopoda). *Journal of Zoology*, *193*, 1–10. doi: 10.1111/j.1469-7998.1981.tb01486.x

Brain, C. K. (1981). *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. The University of Chicago Press.

Brasier, M. D., Cowie, J. W., & Taylor, M. E. (1994). Decision on the Precambrian-Cambrian boundary. *Episodes*, *17*, 3–8. doi: 10.18814/epiiugs/1994/v17i1.2/002

Brenchley, P. J., & Newall, G. (1970). Flume experiments on the orientation and transport of models and shell valves. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 7,185–220. doi: 10.1016/0031-0182(70)90093-3

Breton, G., Neraudeau, D., & Cuenca-Boulat, C. (1992). *Gnathichnus stellarum* ichnosp. nov., trace de broutage d'un echinide du Campanien des Charentes (France). *Revue de Paleobiologie*, *11*, 219–229.

Breton, G., Wisshak, M., Néraudeau, D., & Morel, N. (2017). Parasitic gastropod bioerosion trace fossil on Cenomanian oysters from Le Mans, France and its ichnologic and taphonomic context. *Acta Palaeontologica Polonica*, *62*, 45–57. doi: 10.4202/app.00304.2016

Brezina, S. S., Cech, N., Martín Serralta, D., & Casadío, S. (2016). Cannibalism in Naticidae from the La Meseta Formation (Eocene, Antarctica). *Antarctic Science*, *28*, 1–11. doi: 10.1017/S0954102015000656

Briggs, D. E. G., & Crowther, P. R. (Eds.) (1990). *Palaeobiology. A synthesis*. Blackwell Scientific Publications.

Briggs, D. E. G., & Crowther, P. R. (Eds.) (2003). *Palaeobiology II*. Blackwell Scientific Publications.

Brlek, M., Špišić, M., Brčić, V., Mišur, I., Kurečić, T., Miknić, M., Avanić, R., Vrsaljko, D., & Slovenec, D. (2016). Mid-Miocene (Badenian) transgression on Mesozoic basement rocks in the Mt. Medvednica area of northern Croatia. *Facies*, *62*, Article 18. doi: 10.1007/s10347-016-0470-z

Brocchi, G. B. (1814). *Conchiologia fossile subapenninacon observaqzione geologichi sugli Appennini e sul suclo adiacente.* Stamperia Reale. doi 10.5962/bhl.title.11569

Bromley R. G. (1970). Borings as trace fossils and Entobia cretacea Portlock, as an example. In T. P. Crimes, & J. C. Harper (Eds.), Trace Fossils. *Geological Journal*, *Special Issue*, *3*: 49–90.

Bromley, R. G. (1975). Comparative analysis of fossil and rent echinoid bioerosion. *Palaeontology*, *18*, 725–739.

Bromley, R. G. (1978). Bioerosion in Bermuda reefs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *23*, 169–197. doi: 10.1016/0031-0182(78)90093-7

Bromley, R. G. (1981). Concepts in ichnotaxonomy illustrated by small round holes in shells: *Acta Geologica Hispanica*, *16*, 55–64.

Bromley, R. G. (1993). Predation habits of *Octopus* past and present and a new ichnospecies, *Oichnus ovalis*. *Bulletin of the Geological Society of Denmark, 40,* 167–173. doi: 10.37570/bgsd-1993-40-07

Bromley, R. G. (1996). *Trace Fossils: Biology, Taphonomy and Applications*. Chapman & Hall. doi: 10.1007/978-1-4899-2875-7

Bromley, R. G. (2004). A stratigraphy of marine bioerosion. In D. McIlroy (Ed.), The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis,

Geological Society of London Special Publications, *228*, 455–481. doi: 10.1144/GSL.SP.2004.228.01.20

Bromley, R. G. (2008). The trace fossil *Podichnus obliquus*, attachment scar of the brachiopod *Terebratulina retusaa*: Pleistocene, Rhodes, Greece. *Fossil and Strata, 54*, 227–230. doi: 10.18261/9781405186643-2008-24

Bromley, R. G., & Asgaard, U. (1993a). Endolithic community replacement on a Pliocene rocky coast. *Ichnos, 2*, 93–116. doi: 10.1080/10420949309380081

Bromley, R. G., & Asgaard, U. (1993b). Two bioerosion ichnofacies produced by early and late burial associated with sea-level change. *Geologische Rundschau*, *82*, 276–280. doi: 10.1007/BF00191833

Bromley, R. G., & D'Alessandro, A. (1983). Bioerosion in the Pleistocene of Southern Italy: Ichnogenera *Caulostrepsis* and *Maeandropolydora*. *Rivista Italiana di Paleontologia e Stratigrafia*, *89*, 283–309.

Bromley, R. G., & D'Alessandro, A. (1984). The ichnogenus *Entobia* from the Miocene, Pliocene and Pleistocene of southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, *90*, 227–296.

Bromley, R. G., & D'Alessandro, A. (1989). Ichnological study of shallow marine endolithic sponges from the Italian coast. *Rivista Italiana di Paleontologia e Stratigrafia*, *95*, 279–340.

Bromley, R. G., & Heinberg, C. (2006). Attachment strategies of organisms on hard substrates: A palaeontological view. *Palaeogeography, Palaeoclimatology, Palaeoecology, 232*, 429–453. doi: 10.1016/j.palaeo.2005.07.007

Bromley, R. G., & Martinell, J. (1991). *Centrichnus*, new ichnogenus for centrically patterned attachment scars on skeletal substrates. *Bulletin of the geological Society of Denmark*, *38*, 243–252. doi: 10.37570/bgsd-1990-38-21

Bromley, R. G., & Surlyk, F. (1973). Borings produced by brachiopod pedicles, fossil and Recent. *Lethaia, 6*, 349–365. doi: 10.1111/j.1502-3931.1973.tb01203.x

Bromley, R. G., Beuck, L., & Taddei Ruggiero, E. (2008). Endolithic sponge versus terebratulid brachiopod, Pleistocene, Italy: accidental symbiosis, bioclaustration, deformity and death. In M. Wisshak, & L. Tapanila (Eds.), *Current Developments in Bioerosion* (pp. 361–368), Springer Verlag. doi: 10.1007/978-3-540-77598-0_18

Bromley, R. G., Pemberton, G., & Rahmani, R. A. (1984). A Cretaceous woodground: The Teredolites ichnofacies. *Journal of Paleontology*, *58*, 488–498.

Cachão, M., Silva, C. M. da, Santos, A., Domènech, R., Martinell, J., & Mayoral, E. (2009). The bioeroded megasurface of Oura (Algarve, south Portugal): Implications for the Neogene stratigraphy and tectonic evolution of southwest Iberia. *Facies*, *55*, 213–225. doi: 10.1007/s10347-008-0172-2

Carnevale, G., Farrés, F., Belaústegui, Z., Cabello, P., Colombo, F., Vidal, A., & Martinell, J. (2019). Fish-bearing deposits from the Upper Eocene Terminal Complex of the Plana de Vic (Catalonia, NE Spain): Sedimentary context and taphonomy. *Geological Journal*, *54*, 1638–1652. doi: 10.1002/gj.3257

Carroll, J. M., & Finelli, C. M. (2015). Impacts of ectoparasitic snail *Boonea impressa* on growth of potsset juvenile oysters. *Journal of Molluscan Studies, 81*, 161–163. doi: 10.1093/mollus/eyu070

Ceranka, T., & Złotnik, M. (2003). Traces of cassid snails predation upon the echinoids from the Middle Miocene of Poland. *Acta Palaeontologica Polonica*, *48*, 91–496.

Charollais, J., Wernli, R., Chene. R. J. D., Von Salis, K., & Steiner, F. (2006). La molasse marine supérieure de la Combe d'Evuaz et de la Pesse (Jura méridional, France). *Archives des Sciences, 59*, 21–46.

Chattopadhyay, D., & Baumiller, T. (2010). Effect of durophagy on drilling predation: a case study of Cenozoic molluscs from North America. *Historical Biology*, *22*(4), 367–379. doi: 10.1080/08912961003600445

Chattopadhyay, D., Rathie, A., & Das, A. (2013). The effect of morphology on postmortem transportation of bivalves and its taphonomic implications. *Palaios*, *28*, 203–209. doi: 10.2110/palo.2012.p12-103r

Chudzikiewicz, L., & Wieczorek, J. (1985). Bored and encrusted clasts in the Lower Kimmeridgian carbonates at Sobków (SW margin of the Holy Cross Mts., Poland). *Annales Societatis Geologorum Poloniae*, *55*, 295–306.

Cintra-Buenrostro, C. E. (2007). Trampling, peeling and nibbling mussels: An experimental assessment of mechanical and predatory damage to shells of *Mytilus trossulus* (Mollusca: Mytilidae). *Journal of Shellfish Research, 26*, 221–231. doi: 10.2983/0730-8000(2007)26[221:TPANMA]2.0.CO;2

Cione, A. L., Hospitaleche, C. A., Pérez, L. M., Laza, J. H., & César, I. (2010). Trace fossils on penguin bones from the Miocene of Chubut, southern Argentina. *Alcheringa*, *34*, 433–454. doi: 10.1080/03115511003793470

Cockell, C. S., & Herrera, A. (2008). Why are some microorganisms boring? *Trends in Microbiology*, *16*, 101–106. doi: 10.1016/j.tim.2007.12.007

Cole, A. R., & Palmer, T. J. (1999). Middle Jurassic worm borings, and a new giant ichnospecies of *Trypanites* from the Bajocian/Dinantian unconformity, southern England. *Proceedings of the Geologists' Association, 110*, 203–209. doi: 10.1016/S0016-7878(99)80070-4

Conway-Morris, S., & Bengston, S. (1994). Cambrian predators: possible evidence from boreholes. *Journal of Paleontology*, *68*, 1–23. doi: 10.1017/S0022336000025567

Conway-Morris, S., & Robinson, R. A. (1988). More soft-bodied animals from the Middle Cambrian of Utah and British Columbia. *The University of Kansas Palaeontological Contributions*, *122*, 1–48.

Coombes, M. (2016). Biogeomorphology: diverse, integrative and useful. *Earth Surface Processes and Landforms, 41*, 2296–2300. doi: 10.1002/esp.4055

Cremonte, F. (2011). Enfermedades de Moluscos Bivalvos de interés comercial causadas por Metazoos. In A. Figueras, & B. Novoa (Eds.), *Enfermedades de moluscos bivalvos de interés en Acuicultura* (pp. 331–396), Publicaciones Científicas y Tecnológicas de la Fundación Observatorio Español de Acuicultura.

Dahlgren, T. G., Wiklund, H., Kallstrm, B., Lundälv, T., Smith, C. R., & Glover, A. G. (2006). A shallow-water whale-fall experiment. *Cahiers de Biologie Marine*, *47*, 385–389.

Darwin, C. (1854). *A monograph on the subclass Cirripedia, with figures of all the species. The Balanidae, the Verrucidae, etc*. The Ray Society.

Das, A., Mondal, S., & Bardhan, S. (2014). A note on exceptionally high confamilial naticid drilling frequency on *Natica gualteriana* from the Indian subcontinent. *Historical Biology*, *26*, 758–764. doi: 10.1080/08912963.2013.841684

Davidson, T. M., & Grupe, B. M. (2014). Habitat modification in tidepools by bioeroding sea urchins and implications

for fine-scale community structure. *Marine Ecology*, *36*, 185–194. doi: 10.1111/maec.12134

Davidson, T. M., Altieri, A. H., Ruiz, G. M., & Torchin, M. E. (2018). Bioerosion in a changing world: a conceptual framework. *Ecology Letters*, *21*, 422–438. doi: 10.1111/ele.12899

De Groot, R. A. (1977). Boring sponges (Clionidae) and their trace fossils from the coast near Rovinj (Yugoslavia). *Geologie en Mijnbouw*, *56*, 168–180.

De La Beche, H. T. (1846). On the formation of the rocks of south Wales and south western England. *Memoirs of the Geological Survey of Great Britain*, *1*, 1–296.

De Renzi, M. (1978). La problemática de la fundamentación de la Paleoecología. *Estudios Geológicos*, *34*, 559–570.

De Renzi, M., Pardo, M. V., Belinchón, M., Peñalver, E., Montoya, P., & Márquez Aliaga, A. (Eds.) (2002). *Current topics on Taphonomy and fossilization*. *Col·lecció Encontres, 5*. Oficina de Publicaciones, Ayuntamiento de Valencia.

Demircan, H. (2012). Determination of a Late Miocene rocky palaeoshore by bioerosion trace fossils from the Bozcaada Island, Çanakkale, Turkey. *Comptes Rendus-Palevol*, *11*, 331–344. doi: 10.1016/j.crpv.2011.11.002

Denizot, G. (1952). Le Pliocène dans la vallée du Rhône. *Revue de géographie de Lyon*, *27*, 327–357. doi: 10.3406/geoca.1952.1144

Desrochers, A., & James, N. P. (1988). Early Paleozoic surface and subsurface paleokarst: Middle Ordovician carbonates, Mingan Islands, Quebec. In N. P. James, & P. W. Choquette (Eds.), *Paleokarst* (pp. 183–210), Springer. doi: 10.1007/978-1-4612-3748-8_10

Dietl, G. P., & Alexander, R. R. (2000). Post-Miocene shift in stereotypic naticid predation on confamilial prey from the mid-Atlantic shelf: Coevolution with dangerous prey. *Palaios*, *15*, 414–429. doi: 10.1669/0883-1351(2000)015<0414:PMSISN>2.0.CO;2

Dietl, G. P., & Hendricks, J. R. (2006). Crab scars reveal survival advantage of left-handed snails. *Biology Letters*, *2*, 439–442. doi: 10.1098/rsbl.2006.04

Diez, M. E., Radashevsky, V. I., Orensanz, J. M., & Cremonte, F. (2011). Spionid polychaetes (Annelida:Spionidae) boring into shells of molluscs of commercial interest in northern Patagonia, Argentina. *Italian Journal of Zoology, 78*, 497–504. doi: 10.1080/11250003.2011.572565

Domènech, R., & Martinell, J. (1982). Fauna malacològica submergida del Würm del litoral gironí. Descriptiva i sistemàtica. *Butlletí de la Institució Catalana d'Història Natural*, *48*(*Secció Geologia, 3*), 31–60.

Domènech, R., & Martinell, J. (2019). La bioerosión, clave en el reconocimiento de las paleocostas rocosas. In R. Durán, J. Guillén, & G. Simarro (Eds.), X *Jornadas de Geomorfología Litoral, libro de ponencias* (pp. 233–236). Castelldefels.

Domènech, R., Farinati. E., & Martinell, J. (2014). *Crassostrea patagonica* (d'Orbigny, 1842) shell concentrations from late Miocene of Rio Negro province, NE Patagonia, Argentina. *Spanish Journal of Palaeontology*, *29*, 165–182. doi: 10.7203/sjp.29.2.17799

Domènech, R., Gibert, J. M. de, & Martinell, J. (2001). Ichnological features of a marine transgression: Middle Miocene rocky-shores of Tarragona, Spain. *Geobios*, *34*, 99–107. doi: 10.1016/S0016-6995(01)80051-6

Domènech, R., Martinell, J., & Porta de, J. (2008). Bioerosión por Poliquetos Espiónidos (Polychaeta, Spionidae) en moluscos del Cuaternario caribeño de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*,*124*, 411–419.

Domènech, R., da Silva, C. M., Cachão, M., & Martinell, J. (1999). Una megasuperficie bioerosionada en Oura (Albufeira): Implicaciones para la evolución sedimentaria del Mioceno de Algarve (S de Portugal). *Temas Geológico-Mineros ITGE*, *26*, 226–230.

Donovan, S. K. (2012). Taphonomy and significance of rare Chalk (Upper Cretaceous) echinoderms preserved as beach erratics, north Norfolk, UK. *Proceedings of the Yorkshire Geological Society*, *59*, 109–113. doi: 10.1144/pygs2012-313

Donovan, S. K. (2018). A new ichnogenus for *Teredolites longissimus* Kelly and Bromley. *Swiss Journal of Palaeontology*, *137*, 95–98.

Donovan, S. K., & Pickerill, R. K. (2004). Traces of cassid snails predation upon the echinoids from the Middle Miocene of Poland: Comments on Ceranka and Złotnik (2003). *Acta Palaeontologica Polonica*, *49*, 483–484.

Donovan, S. K., Blissett, D. J., & Jackson, T. A. (2010). Reworked fossils, ichnology and palaeoecology: an example from the Neogene of Jamaica. *Lethaia*, *43*, 441–444. doi: 10.1111/j.1502-3931.2010.00215.x

Donovan, S. K., Harper, D. T. H., & Rasmussen, J. A. (2009). Taphonomy of Logs Bored with *Teredolites longissimus* Kelly and Bromley in the Danian (Lower Paleocene) of West Greenland. *Ichnos*, *16*, 186–192. doi: 10.1080/10420940802686020

Donovan, S. K., Harper D. T., Portell, R. W., & Renema, W. (2014). Neoichnology and implications for stratigraphy of reworked Upper Oligocene oysters, Antigua, West Indies. *Proceedings of the Geologists' Association*, *125*, 99–106. doi: 10.1016/j.pgeola.2013.10.002

Dunkin, S. De B., & Hughes, N. R. (1984). Behavioural components of prey-selection by dogwhelks, *Nucella lapillus* (L.), feeding on barnacles, *Semibalanus balanoides* (L.), in the laboratory. *Journal of Experimental Marine Biology and Ecology*, *79*, 91–103. doi: 10.1016/0022-0981(84)90032-7

Ehret, D. J., Macfadden, B. J., & Salas-Gismondi, R. (2009). Caught in the act: trophic interactions between a 4-million-year-old white shark (*Carcharodon*) and mysticete whale from Perú. *Palaios*, *24*, 329–333. doi: 10.2110/palo.2008.p08-077r

Ekdale, A. A., Bromley, R. G., & Pemberton, S. G. (1984). Bioerosion. In A. A. Ekdale, R. G. Bromley, & S. G. Pemberton (Eds.), *Ichnology: The Use of Trace Fossil in Sedimentology and Stratigraphy* (pp. 108–128). Society of Economic Paleontologists and Mineralogists. doi: 10.2110/scn.84.15.0108

El-Hedeny, M., & El-Sabbagh, A. (2018). *Entobia* ichnofacies from the Middle Miocene carbonate succession of the Northern Western desert of Egypt. *Annales Societatis Geologorum Poloniae*, *88*, 1–19. doi: 10.14241/asgp.2018.002

Emig, C. C. (2002). Death: A key information in marine palaeoecology. In M. De Renzi, M. V. Pardo Alonso, M. Belinchón, E. Peñalver, P. Montoya, & A. Márquez-Aliaga (Eds.), *Current Topics on Taphonomy and Fossilazation*. *Col·lecció Encontres*, *5*, 21–26.

Esperante, R., Muñiz Guinea, F., & Nick, K. E. (2009). Taphonomy of a Mysticeti whale in the Lower Pliocene

Huelva Sands Formation (Southern Spain) *Geologica Acta*, *7,* 489–504.

Evans, J. W. (1969). Borers in the shell of the sea scallop, *Placopecten magellanicus*. *American Zoologist, 9*, 775–782. doi: 10.1093/icb/9.3.775

Evans, S. (1999). Wood-boring bivalves and boring linings. *Bulletin of the Geological Society of Denmark, 45*, 130–134. doi: 10.37570/bgsd-1998-45-14

Farinati, E., & Zavala, C. (2002). Trace fossils in shelly substrate. An example from the Miocene of Patagonia, Argentina. *Acta Geolológica Hispánica, 37*, 29–36.

Farrar, L., Graves, E., Petsios, E., Portell, R. W., Grun, T. B., Kowalewski, M., & Tyler C. L. (2020). Characterization of traces of predation and parasitism on fossil echinoids. *Palaios*, *35*, 215–227. doi: 10.2110/palo.2019.088

Farris, M. A., Oates, M. J., & Torrens, H. S. (1999). New evidence on the origin and Jurassic age of palaeokarst and limestone breccias, Loch Slapin, Isle of Skye. *Scottish Journal of Geology*, *35*, 25–29. doi: 10.1144/sjg35010025

Farlow, J. O., & Holtz, T. R. (2002). The Fossil Record of Predation in Dinosaurs. *The Paleontological Society Papers*, *8*, 251–266. doi: 10.1017/S108933260000111X

Fee, G. N., Mather, J., Landschoff, J., & Griffiths, C. (2023). Finding the sweet spot: drilling precision on shelled molluscs by *Octopus vulgaris* type III in False Bay, South Africa. *Marine Biology*, *170*, 22. doi: 10.1007/s00227-022-04152-6

Fernández-Jalvo, Y., & Andrews, P. (2016). *Atlas of Taphonomic Identifications. 1001+ Images of fossil and Recent Mammal Bone Modification. Vertebrate Paleobiology and Paleoanthropology Series.* Springer Nature. doi: 10.1007/978-94-017-74-32-1

Fernández López, S. (1984a). Nuevas perspectivas de la Tafonomia Evolutiva: Tafosistemas y asociaciones conservadas. *Estudios Gelógicos, 40*, 215–224.

Fernández López, S. (1984b). Criterios elementales de reelaboración tafonómica en ammonites de la Cordillera Ibérica. *Acta Geológica Hispánica*, *19*, 105–116.

Forrest, R. E., Chapman, M. G., & Underwood, A. J. (2001). Quantification of radular marks as a method for estimating grazing of intertidal gastropods on rocky shores. *Journal of Experimental Marine Biology and Ecology*, *258*, 155–171. doi: 10.1016/S0022-0981(01)00212-X

Fortunato, H. (2007). Naticid gastropod predation in the Gatun Formation (late middle Miocene), Panama: Preliminary assessment. *Palaeontologische Zeitschrift*, *81*, 356–364. doi: 10.1007/BF02990184

Frey, R. W. (1987). Hermit Crabs: Neglected Factors in Taphonomy and Paleoecology. *Palaios*, *2*, 313–322. doi: 10.2307/3514756

Gale, A. S., & Sørensen, A. M. (2015). Taxonomy and palaeoecology of thoracican cirripedes (Crustacea) from a Campanian rocky shoreline at Ivö Klack, southern Sweden. *Cretaceous Research, 54*, 212–242. doi: 10.1016/j.cretres.2014.09.004

Garilli V., Dávid Á., & Dominici S. (2022). Natural casts of *Entobia* from the late Caenozoic of Sicily. *Rivista Italiana di Paleontologia e Stratigrafia*,*128*, 211–228. doi: 10.54103/2039-4942/15175

Geary, D., Allmon, W. D., & Reaka-Kudla, M. L. (1991). Stomatopod predation on fossil gastropods from the Plio-Pleistocene of Florida. *Journal of Paleontology*, *65*, 355–360. doi: 10.1017/s0022336000030341

Giannetti, A., Falces-Delgado, S., & Baeza-Carratalá J. F. (2020). Bioerosion pattern in a nearshore setting as a tool to disentangle multiphase transgressive episodes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *554*, Article 109820. doi: 10.1016/j.palaeo.2020.109820

Gibert, J. M. de, Domènech, R., & Martinell, J. (2004). An ethological framework for animal bioerosion trace fossils upon mineral substrates with proposal of a new class of Fixinichia. *Lethaia*, *37*, 429–438. doi: 10.1080/00241160410002144

Gibert, J. M. de, Domènech, R., & Martinell, J. (2007). Bioerosion in shell beds from the Pliocene Roussillon Basin, France: implications for the (macro)bioerosion Ichnofacies model. *Acta Paleontologica Polonica*, *52*, 783–798.

Gibert, J. M. de, Domènech, R., & Martinell, J. (2012). Rocky shorelines. In D. Knaust, & R. G. Bromley (Eds.), Trace Fossils as Indicators of Sedimentary Environments, *Developments in Sedimentology*, *64*, 441–462. doi: 10.1016/B978-0-444-53813-0.00015-0

Gibert, J. M. de, Martinell, J., & Domènech, R. (1998). *Entobia* ichnofacies in fossil rocky shores, Lower Pliocene, northwestern Mediterranean. *Palaios*, *13*, 476–487. doi: 10.2307/3515475

Gibson, P. H. (2017). A search for trace fossils of the burrowing cirratulid polychaetes *Dodecaceria fimbriata* and *D. concharum*. *Ichnos*, *24*, 83–90. doi: 10.1080/10420940.2015.1137215

Glaub, I., Golubic, S., Gektidis, M., Radtke, G., & Vogel, K. (2007). Microboring and microbial endoliths: Geological implications. In W. Miller III (Ed.), *Trace Fossils: Concepts, Problems, Prospects* (pp. 368–381). Elsevier. doi: 10.1016/B978-044452949-7/50147-9

Godfrey S. J., & Lowry A. J. (2021). The ichnospecies *Linichnus bromleyi* on a Miocene baleen whale radius preserving multiple shark bite-shake traces suggests scavenging. *Carnets de Geologie*, *21*, 391–398. doi: 10.2110/carnets.2021.2117

Gordillo, S. (2013). Muricid boreholes in Pleistocene acorn barnacles from the Beagle Channel: trophic interactions during the Last Interglacial in southern South America. *Journal of Palaeontology*, *37*, 479–486. doi: 10.1080/03115518.2013.792458

Gravina, M. F., Antonelli, F., Sacco Perasso, C., Cesaretti, A., & Casoli, E. (2019). The role of polychaetes in bioerosion of submerged mosaic floors in the Underwater Archaeological Park of Baiae (Naples, Italy). *Facies*, *65*, 19. doi: 10.1007/s1034 7-019-0563-6

Gruszczynski, M. (1986). Hardgrounds and ecological succession in the light of early diagenesis (Jurassic, Holy Cross Mts., Poland). *Acta Palaeontologica Polonica*, *31*, 163–212.

Guerrero Alba, S., & Reyment, R. A. (1988). Differentiation between the traces of predation of muricids and naticids in Spanish Pliocene *Chlamys*. *Estudios Geológicos*, *44*, 317–328. doi: 10.3989/egeol.88443-4549

Gutowski, J., & Machalski, M. (1984). A new littoral locality within the Middle Miocene (Badenian) Korytnica Basin (Holy Cross Mountains, Central Poland). *Acta Geologica Polonica*, *34*, 195–203.

Haag, A. (2005). Marine biology: Whale fall. *Nature*, *433*, 566–567. doi: 10.1038/433566a

Harper, E. M. (2005). Evidence of predation damage in Pliocene *Apletosia maxima* (Brachiopoda). *Palaeontolgy*, *48*, 197–208. doi: 10.1111/j.1475-4983.2004.00433.x

Harper, E. M. (2006). Dissecting Post-Paleozoic arms races. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *232*, 322–343. doi: 10.1016/j.palaeo.2005.05.017

Hasiotis, S. T., Platt, B. F., Hembre, D. I., & Everhart, M. J. (2007). The Trace-Fossil Record of Vertebrates. In W. III Miller, (Ed.), *Trace Fossils: Concepts, Problems, Prospects* (pp. 196–218). Elsevier. doi: 10.1016/B978-044452949-7/50138-8

Hecker, R. F. (1965). *Introduction to Paleoecology*. Elsevier.

Heise, E. A., Raymond, R., Parsons-Hubbard, K., Walker, S. E., Staff, G., Powell, E. A., Brett, C., & Ashton-Alcox, K. A. (2011). Wood taphonomy in a tropical marine carbonate environment: Experimental results from Lee Stocking Island, Bahamas *Palaeogeography, Palaeoclimatology, Palaeoecology*, *312*, 363–379. doi: 10.1016/j.palaeo.2011.04.031

Higgs, N. D., Little, C. T. S., Glover, A. G., Dahlgren, T. G., Smith, C. R., & Dominici, S. (2011). Evidence of *Osedax* worm borings in Pliocene (~3 Ma) whale bone from the Mediterranean. *Historical Biology*, *24*, 269–277. doi: 10.1080/08912963.2011.621167

Hoffman, A., & Martinell, J., (1984). Prey selection by naticid gastropods in the Pliocene of Empordà (Northeast Spain). *Neues Jahrbuch für Geologie und Paläontologie*, *7*, 393–399. doi: 10.1127/njgpm/1984/1984/393

Hoffmann, M., & Friedrich A. M. (2017). Erosional and tectonic overprint of the mid-Miocene marine cliff line and its applicability as a paleo-geodetic marker of regional-scale tilting, Swabian Alb, southwestern Germany. In M. Hoffmann (Ed.), *Young tectonic evolution of the Northern Alpine Foreland Basin, southern Germany, based on linking geomorphology and structural geology* (pp. 67–116). (PhD Thesis, Universität München). Available at https://edoc.ub.uni-muenchen.de/21123/1/Hoffmann_Markus.pdf

Hoffmann, R., & Stevens, K. (2020). The palaeobiology of belemnites – foundation for the interpretation of rostrum geochemistry. *Biological reviews of the Cambridge Philosophical Society*, *95*, 94–123. doi: 10.1111/brv.12557

Höpner, S., & Bertling, M. (2017). Holes in Bones: Ichnotaxonomy of Bone Borings. *Ichnos*, *24*, 1–24. doi: 10.1080/10420940.2017.1289937

Hua, H., Pratt, B. R., & Zhang, L. Y. (2003). Borings in *Cloudina* Shells: Complex Predator-Prey Dynamics in the Terminal Neoproterozoic. *Palaios*, *18*, 454–459. doi: 10.1669/0883-1351(2003)018<0454:BICSCP>2.0.CO;2

Huntley, J. W., & Kowalewski, M. (2007). Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proceedings of the National Academy of Sciences*, *104*, 15006–15010. doi: 10.1073/pnas.0704960104

Hutchings, P., (2008). Role of polychaetes in bioerosion of coral substrates. In M. Wisshak, & L. Tapanila (Eds.), *Current Developments in Bioerosion* (pp. 249–264). Springer-Verlag. doi: 10.1007/978-3-540-77598-0_13

Ishikawa, M., & Kase, T. (2007). Spionid bore hole *Polydorichnus subapicalis* new ichnogenus and ichnospecies: a new behavioral trace in gastropod shells. *Journal of Paleontology*, *81*, 1466–1475. doi: 10.1666/05-137.1

Ishikawa, M., Kase, T., Tsutsui, H., & Tojo, B. (2004). Snails versus hermit crabs: a new interpretation on shell-peeling predation in fossil gastropod assemblages. *Paleontological Research, 8*, 99–108. doi: 10.2517/prpsj.8.99

Jacobsen, A. R., & Bromley, R. G. (2009). New ichnotaxa based on tooth impressions on dinosaur and whale bones. *Geological Quarterly*, *53*, 373–382.

James, N. P., Kobluk, D. R., & Pemberton, S. G. (1977). The oldest macroborers: Lower Cambrian of Labrador. *Science*, *197*(4307), 980–983. doi: 10.1126/science.197.4307.980

Jagt, J. W. M. (2003). The ichnofossil genera *Radulichnus* and *Renichnus* in the Maastrichtian of The Netherlands and Belgium. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, *73*, 175–184.

Jagt, J. W. M., Dortangs, R., Simon, E., & Knippenberg, P. V. (2007). First record of the ichnofossil *Podichnus centrifugalis* from the Maastrichtian of northeast Belgium. *Bulletin de l'Institut Royal des Sciences Naturelles de Belqique, Sciences de la Terre*, *77*, 95–105.

Johnson, M. E. (1988). Why are ancient rocky shores so uncommon? *The Journal of Geology*, *96*, 469–480. doi: 10.1086/629241

Johnson, M. E. (1992). Studies of ancient rocky shores: a brief history and annotated bibliography. *Journal of Coastal Research*, *8*, 797–812.

Johnson, M. E. (2006). Uniformitarianism as a guide to tocky-shore ecosystems in the geological record. *Canadian Journal of Earth Sciences*, *43*, 1119–1177. doi: 10.1139/e06-045

Johnson, M. E., & Baarli, B. G. (1999). Diversificationof rocky-shore biotas through geologic time. *Geobios*, *32*, 257–273. doi: 10.1016/S0016-6995(99)80040-0

Johnson, M. E., Baarli, B. G., Santos, A., & Mayoral, E. (2011). Ichnofacies and microbial build-ups on Late Miocene rocky shores from Menorca (Balearic Islands), Spain. *Facies*, *57*, 255–265. doi: 10.1007/s10347-010-0240-2

Johnson, M. E., Skinner, D. F., & Macleod, K. G. (1988). Ecological zonation during the carbonate transgression of a Late Ordovician rocky shore (Northeastern Manitoba, HudsonBay, Canada). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *65*, 93–114. doi: 10.1016/0031-0182(88)90115-0

Johnson, M. E., Wilson, M. A., & Redden, J. A. (2010). Borings in quartzite surf boulders from the Upper Cambrian basal Deadwood Formation, Black Hills of South Dakota. *Ichnos*, *17*, 48–55. doi: 10.1080/10420941003659618

Johnston, G. (1850). *An introduction to conchology*. John Van Voorst.

Kabat, A. R. (1990). Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia*, *32*, 155–193.

Kabat, A. R., & Kohn, A. J. (1986). Predation on Early Pleistocene naticid gastropods in Fiji. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *53*, 255–269. doi: 10.1016/0031-0182(86)90062-3

Kahrs, E. (1927). Zur Paläogeographie der Oberkreidein Rheinland-Westfalen. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, *58B*, 627–687.

Kase, T., & Ishikawa, M. (2003). Mystery of naticid predation history solved: Evidence from a "living

fossil" species. *Geology*, *31*, 403–406. doi: 10.1130/0091-7613(2003)031<0403:MONPHS>2.0.CO;2

Kelley, P. H. (1991). Apparent cannibalism by Chesapeake Group naticid gastropods: Predictable result of selective predation. *Journal of Paleontology*, *65*, 75–79. doi: 10.1017/S0022336000020229

Kelley, P. H. (2008). Role of bioerosion in Taphonomy: effect of predatory drillholes on preservation of molluscan shells. In M. Wisshak, & L. Tapanilla (Eds.), *Current Developments in Bioerosion* (pp. 451–470). Springer-Verlag. doi: 10.1007/978-3-540-77598-0_23

Kelley, P. H., & Hansen, T. A. (1993). Evolution of the naticid gastropod predator-prey system: An evaluation of the hypothesis of escalation. *Palaios*, *8*, 358–375. doi: 10.2307/3515266

Kelley, P. H., & Hansen, T. A. (2006). Comparisons of class- and lower taxon-level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the US Coastal Plain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *236*, 302–320. doi: 10.1016/j.palaeo.2005.11.012

Kelley, P. H., & Hansen, T. A. (2007). A case for cannibalism: Confamilial and specific predation by naticid gastropods, Cretaceous through Pleistocene of the United States Coastal Plain. In A. M. T. Elewa (Ed.), *Predation in Organisms: A Distinct Phenomenon* (pp. 151–170). Springer. doi: 10.1007/978-3-540-46046-6_8

Kelley, P. H., Kowalewski, M., & Hansen, T. A. (Eds.) (2003). *Predator–Prey Interactions in the Fossil Record. Topics in Geobiology*, 20. Springer. doi: 10.1007/978-1-4615-0161-9

Kelly, S. R. A., & Bromley, R. G. (1984). Ichnological nomenclature of clavate borings. *Palaeontology*, *27*, 793–807.

Kempf, M. (1962). Recherches d'écologie comparée sur *Paracentrotus lividus* (Lmk) et *Arbacia lixula* (L.) (I). *Recueil des Traveaux de la Station Marine d'Endoume, 25*, 47–116.

Kiderlen, H. (1931). Beitrage zur Stratigraphie und Paläogeographie des süddeutschen Tertiärs. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, *66*, 215–384.

Kidwell, S. M., & Jablonski, D. (1983). Taphonomic Feedback Ecological Consequences of Shell Accumulation. In M. J. S. Tevesz, & P. L. McCall (Eds.), Biotic Interactions in Recent and Fossil Benthic Communities. *Topics in Geobiology*, *3*, 195–248. Springer. doi: 10.1007/978-1-4757-0740-3_5

Kiel, S., Goedert, J. L., Kahl, W-A., & Rouse, G. W. (2010). Fossil traces of the bone-eating worm *Osedax* in early Oligocene whale bones, *PNAS*, *107*, 8656–8659. doi: 10.1073/pnas.1002014107

Kiel, S., Kahl, W-A., & Goedert, J. l. (2013). Traces of bone-eating annelid *Osedax* whale teeth and fish bones. *Paläontologische Zeitschrift*, *87*, 161–167. doi: 10.1007/s12542-012-0158-9

Kingsley-Smith, P. R., Richardson, C. A., & Seed, R. (2003). Stereotypic and size selective predation in *Polinices pulchellus* (Gastropoda: Naticidae) Risso 1826. *Journal of Experimental Marine Biology and Ecology*, *295*, 173–190. doi: 10.1016/S0022-0981(03)00294-6

Kitchell, J. A. (1986). The evolution of predator-prey behavior: Naticid gastropods and their molluscan preys. In M. H. Nitecki, & J. A. Kitchell (Eds.), *Evolution of animal behavior: Paleontological and field approaches* (pp. 88–110). Oxford Press.

Kitchell, J. A., Boggs, C. H., Kitchell, J. F., & Rice, J. A. (1981). Prey selection by naticid gastropods: experimental tests and application to the fossil record. *Paleobiology*, *7*, 533–552. doi: 10.1017/S0094837300025574

Kitchell, J. A., Boggs, C. H., Rice, J. A., Kitchell, J. F., Hoffman, A., & Martinell, J. (1986). Anomalies in naticid predatory behavior: a critique and experimental observations. *Malacologia*, *27*, 291–298.

Kleemann, K. H. (1973). Der Gesteinsabbau durch Ätzmuscheln an Kalkküsten. *Oecologia*, *3*, 377–395. doi: 10.1007/BF01825527

Kleemann, K. H. (1994). Associations of corals and boring bivalves since the Late Cretaceous. *Facies*, *31*, 131–140. doi: 10.1007/BF02536937

Kleemann, K. H. (2009). *Gastrochaenolites hospitium* isp. nov., trace fossil by a coral-associated boring bivalve from the Eocene and Miocene of Austria. *Geologica Carpathica*, *60*, 339–342. doi: 10.2478/v10096-009-0025-0

Klompmaker, A. A. (2011). Drilling and crushing predation on scaphopods from the Miocene of the Netherlands. *Lethaia*, *44*, 429–439. doi: 10.1111/j.1502-3931.2010.00254.x

Klompmaker, A. A., & Landman, N. (2021). Octopodoidea asa predators near the end of Mesozoic Marine Revolution. *Biological Journal of the Linnean Society*, *132*, 894–899. doi: 10.1093/biolinnean/blab001

Klompmaker, A. A., Karasawa, H., Portell, R. W., Fraaije, R. H. B., & Ando, Y. (2013). An overview of predation evidence found on fossil decapod crustaceans with new examples of drill holes attributed to gastropods and octopods. *Palaios*, *28*, 599–613. doi: 10.2110/palo.2013.p13-026r

Klompmaker, A. A., Portell, R. W., & Hiroaki, K. (2014). First fossil evidence of a drill hole attributed to an octopod in a barnacle. *Lethaia*, *47*, 309–312. doi: 10.1111/let.12072

Klompmaker, A. A., Portell, R. W., Lad, S. E., & Kowalewski, M. (2015). The fossil record of drilling predation on barnacles. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *426*, 95–111. doi: 10.1016/j.palaeo.2015.02.035

Klompmaker, A. A.; Portell, R. W., & van der Meij, S. E. T. (2016). Trace fossil evidence of coral-inhabiting crabs (Cryptochiridae) and its implications for growth and paleobiogeography. *Scientific Reports*, *6*, Article 23443. doi: 10.1038/srep23443

Kobluk, D. R., James N., & Pemberton G. S. (1978). Initial Diversification of Macroboring Ichnofossils and Exploitation of the Macroboring Niche in the Lower Paleozoic. *Paleobiology*, *4*, 163–170. doi: 10.1017/S0094837300005832

Kobluk, D. R., Pemberton, S. G., Karolyi, M., & Risk, M. J. (1977). The Silurian–Devonian disconformity in southern Ontario. *Bulletin Canadian Petroleum Geology*, *25*, 1157–1186.

Kowalewski, M. (1993). Morphometric analysis of predatory drillholes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *102*, 69–88. doi: 10.1016/0031-0182(93)90006-5

Kowalewski, M. (2002). The fossil record of predation: An overview of analytical methods, In M. Kowalewski, & P. H. Kelley (Eds.), The Fossil Record of Predation. The Paleontological Society. *Special Papers*, *8*, 3–42. doi: 10.1017/S1089332600001030

Kowalewski, M. (2004). Drill holes produced by the predatory gastropod *Nucella lamellosa* (Muricidae): Paleobiological and ecological implications. *Journal of Molluscan Studies*, *70*, 359–370. doi: 10.1093/mollus/70.4.359

Kowalewski, M., & Hoffmeister, A. (2004). Taphonomy and time-averaging of drill holes: assessing the quality of the fossil record left by hunting gastropods. *Geological Society of America Abstracts with Programs*, *36*, 478.

Kowaleski, M., & Kelly, P. H. (Eds.) (2002). *The Fossil Record of Predation.* The Paleontological Society Papers, *8*. doi: 10.1017/S1089332600001030

Kowalewski, M., & Nebelsick, J. H. (2003). Predation on Recent and Fossil Echinoids. In P. H. Kelley, M. Kowalewski, & T. A. Hansen (Eds.), Predator-Prey Interactions in the Fossil Record. *Topics in Geobiology*, *20*, 279-302. Springer. doi: 10.1007/978-1-4615-0161-9_12

Kowalewski, M., Dulai, A., & Fürsich, F. (1998). A fossil record full of holes: Phanerozoic history of drilling predation. *Geology*, *26*, 1091–1094. doi: 10.1130/0091-7613(1998)026<1091:AFRFOH>2.3.CO;2

Krajewski, M., Olchowy, P., Zatoń, M., & Bajda, T. (2017). Kimmeridgian ha rdground-sequence boundary from the Mesozoic margin of the Holy Cross Mountains (central Poland): implications for the evolution of the northern Tethyan carbonate shelf. *Facies*, *63*, Article 15. doi: 10.1007/s10347-017-0496-x

Kříž, J., & Mikuláš, R. (2006). Bivalve Wood Borings of the Ichnogenus *Teredolites* Leymerie from the Bohemian Cretaceous Basin (Upper Cretaceous, Czech Republic). *Ichnos*, *13*(3), 159–174. doi: 10.1080/10420940600851594

Kumar, K., Singh, H., & Rana, R. S. (2011). Ichnospecies *Teredolites longissimus* and Teredinid Body Fossils from the Early Eocene of India—Taphonomic and Palaeoenvironmental Implications. *Ichnos*, *18*, 57–71. doi: 10.1080/10420940.2011.573601

LaBarbera, M., & Merz, R. A. (1992). Postmortem changes in strength of gastropod shells: evolutionary implications for hermit crabs, snails, and their mutual predators. *Paleobiology*, *18*, 367–377. doi: 10.1017/S0094837300010940

Lambert, O., & Gigase, P. (2007). A monodontid cetacean from the Early Pliocene of the North Sea. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, *77*, 197–210.

Lauckner, G. (1983). *Diseases of Mollusca: Bivalvia Diseases of Marine Animals*. Biologische Anstalt Helgoland.

Lavigne, J. M. (1999). *Aspects of marginal marine sedimentology, stratigraphy and ichnology of the Upper Cretaceous Horseshoe Canyon Formation, Drumheller, Alberta*. (MS Thesis, University of Alberta). doi: 10.7939/R32N4ZN6J

Lawrence, D. R. (1971). The nature and structure of Paleoecology. *Journal of Paleontology*, *45*, 593–607.

Ledesma-Vázquez, J., & Johnson, M. E. (1994). Late Pliocene abrasion platform from the Cantil Costero Formation of Baja California. *Ciencias Marinas*, *20*, 139–157. doi: 10.7773/cm.v20i2.964

Leighton, L. R. (2001). New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *165*, 53–69. doi: 10.1016/S0031-0182(00)00153-X

Leighton, L. R. (2003). Predation on brachiopods. In P. H. Kelley, M. Kowalewski, & T. A. Hansen (Eds.), *Predator-Prey Interactions in the Fossil Record* (pp. 215–237). Topics in Geobiology, *20*. Kluwer Academic/Plenum Publishers. doi: 10.1007/978-1-4615-0161-9_9

Leighton, L. R. (2011). Analyzing Predation from the Dawn of the Phanerozoic. In M. Laflamme, J. Schiffbauer, & S. Dornbos (Eds.), *Quantifying the Evolution of Early Life* (pp. 73-109). Topics in Geobiology, *36*. doi: 10.1007/978-94-007-0680-4_4

Leszczynski, S. (2018). Integrated sedimentological and ichnological study of the Coniacian sedimentation in North Sudetic Basin, SW Poland. *Geological Quaterly*, *62*, 767–816. doi: 10.7306/gq.1440

Lessertisseur, J. (1955). Traces fossiles d'activité animale et leur signification paléobiologique. *Société Géologique de France. Nouvelle Edition. XXXIV*(74), 1–150.

Lever, J. (1958). Quantitative beach research I. The "left-right phenomenon": sorting of Lamellibranch valves on sandy beaches. *Bastria*, *22*, 21–68.

Lever, T., & Thijssen, R. (1968). Sorting phenomena during the transport of shell bivalves on sandy beaches studied with the use of artificial valves: *Symposia of the Zoological Society of London*, *22*, 259–271.

Libbey, L. K., & Johnson, M. E. (1997). Upper Pleistocene rocky shores and intertidal biotas at Playa La Palmita (Baja California Sur, Mexico). *Journal of Coastal Research*, *13*, 216–225.

Lopes, P. R. (2011). Ichnology of fossil oysters (Bivalvia, Ostreidae) from the southern Brazilian coast. *Gaea-Journal of Geoscience*, *7*, 94–108. doi: 10.4013/gaea.2011.72.02

Lopes, R. P. (2024). Bioerosion and Bioincrustation in body fossils from the coastal plain of Rio Grande do Sul State, Southern Brazil. *Sociedade Brasileira de Paleontología, Monografias*, *2*, 179–194.

Lopes, R. P., & Pereira, J. C. (2019). Molluskan Grazing Traces (Ichnogenus *Radulichn*us Voigt, 1977) on a Pleistocene Bivalve from Southern Brazil, With the Proposal of a New Ichnospecies. *Ichnos*, *26*, 1–17. doi: 10.1080/10420940.2018.1532898

López-Uriarte, E., Ríos-Jara, E., & González-Rodríguez, M. E. (2008). Diet and feeding habits of *Octopus hubbsorum* Berry, 1953, in the Central Mexican Pacific. *The Veliger*, *51*, 26–42.

Lutzeier, H. (1922). Beiträge zur Kenntnis der Meeresmolasse in der Ulmer Gegend. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage Band*, Abt. B, *46*, 117–180.

Lyell, C. (1830). *Principles of Geology, Being an Attempt to Explain the Former Changes of the Earth's Surface, by References to Causes Now in Operation*, *1*. John Murray. doi: 10.5962/bhl.title.50860

Lyman, R. (1994). *Vertebrate Taphonomy*. Cambridge University Press. doi: 10.1017/CBO9781139878302

Mangano, M. G., Buatois, L. A., & MacNaughton, R. B. (2012). Ichnostratigraphy. In D. Knaust, & R. G. Bromley (Eds.), *Trace Fossils as Indicators of Sedimentary Environments* (pp. 195–212). Developments in Sedimentology, *64*. Elsevier. doi: 10.1016/B978-0-444-53813-0.00007-1

Martin, R. E. (1999). *Taphonomy. A Process Approach*. Cambridge Paleobiology Series, 4. Cambrige University Press. doi: 10.1017/CBO9780511612381.011

Martin, D., & Britayev, T. A. (1998). Symbiotic polychaetes: Review of known species. *Oceanography and Marine Biology: An Annual* Review, *36*, 217–340.

Martin-Kaye, P. (1951). Sorting of lamellibranch valves on beaches in Trinidad, B.W.I. *Geological Magazine London*, *886*, 432–434. doi: 10.1017/s0016756800069995

Martinell, J. (1973). Algunos datos paleoecológicos y tafonómicos de un yacimiento pliocénico del Ampurdán. *Acta Geológica Hispánica*, *VIII*, 16–20.

Martinell, J. (1981). Actividad erosiva de *Paracentrotus lividus* (Lmk.) (Echinodermata, Echinoidea) en el litoral gerundense. *Oecologia Aquatica*, *5*, 219–225.

Martinell, J. (1982a). Borings produced by presumed brachiopods from l´Empordà. (Catalunya). *Butlletí de la Institució Catalana* d´Història Natural, *46*, 91–97.

Martinell, J. (1982b). Echinoid bioerosion on the Pliocene materials from N.E. Spain. *Geobios*, *15*, 249–253. doi: 10.1016/S0016-6995(82)80026-0

Martinell, J. (1989). Interacción organismos/sustrato duro: La Bioerosión y sus aplicaciones. In E. Aguirre (Ed.), *Paleontología. Nuevas Tendencias*, *10*, 205–222.

Martinell, J., & Domènech, R. (1981). Boring activity of epibionts in an early Holocene molluscan fauna of Spanish Catalunya. *Acta Geológica Hispánica*, *XVI*, 145–149.

Martinell, J., & Domènech, R. (1986). Actividad bioerosiva en el Plioceno del Empordà (Catalunya). *Paleontologia i Evolució*, *20*, 247–251.

Martinell, J., & Domènech, R. (1995). Bioerosive structures on the Pliocene rocky shores of Catalonia (Spain). *Revista Española de Paleontología*, *10*, 37–44. doi: 10.7203/sjp.24096

Martinell, J., & Domènech, R. (2009). Commensalism in the fossil record: Eunicid polychaete bioerosion on Pliocene solitary corals of the Westen Mediterranean. *Acta Paleontologica Polonica*, *54*, 143–154. doi: 10.4202/app.2009.0115

Martinell, J., & Domènech, R. (2022). Bioerosió en mol·luscs pleistocens de la plataforma marina catalana. *Nemus, 12*, 237–261.

Martinell, J., & Domènech, R. (2023). Revisitant *Umbichnus inopinatus*, una perforació enigmàtica a la xarnera de bivalves heteroconquis. *Nemus*, *13*, 81–95.

Martinell, J., & Marquina, M. J. (1978). Señales de depredación en los Gastropoda procedentes de un yacimiento pliocénico de Molins de Rei (Barcelona). Implicaciones paleoecológicas. *Acta Geológica Hispánica, XIII*, 125–128.

Martinell, J., Domènech, R., & Bromley, R. G. (1999). Mysterious boring hidden within the hinge plates of Heterodont Bivalves. *Bulletin of the Geological Society of Denmarck*, *45*, 161–163. doi: 10.37570/bgsd-1998-45-21

Martinell, J., Domènech, R., Aymar, J., & Kowalewski, M. (2010). Cannibalistic drilling in Pliocene naticid gastropods from Southern France: Utility of preexisting collections in quantitative paleoecology. *Palaios*, *25*, 221–228. doi: 10.2110/palo.2009.p09-124r

Martinell, J., Gili, C., & Domènech, R. (2021a). Arqueomalacología: reflexiones desde la paleomalacología. *Monografies de la Societat d'Història Natural de les Balears*, *32*, 31–65.

Martinell, J., Juilleret, J., & Domènech, R. (2021b). The Early Miocene (Burdigalian) Marine Rocky-shores at the French Jura Massif: a palaeoecological and paleoenvironmental contribution. *Facies*, *67*, 1–15. doi: 10.1007/s10347-020-00610-z

Martinell, J., Kowalewski, M., & Domènech, R. (2012). Drilling predation on serpulid polychaetes (*Ditrupa arietina*) from the Pliocene of the Cope Basin, Murcia Region, southeastern Spain. *PLoSONE*, *7*, Article e34576. doi: 10.1371/journal.pone.0034576

Martinell, J., Marquina, M. J., & Domènech, R. (1982). Moluscos y crustáceos: una relación traumática. Evidencias en el Plioceno catalán. *Acta Geològica Hispànica*, *XVII*, 11–19.

Martinelli, J. C., Gordillo, S., & Archuby, F. (2013). Muricid drilling predation at high latitudes: insights from the Southernmost Atlantic. *Palaios*, *28*, 33–41. doi: 10.2110/palo.2012.p12-087r

Masuda, K. (1968). Sandpipes penetrating igneous rocks in the environs of Sendai, Japan. *Transactions and Proceedings of the Paleontological Society*, *72*, 351–361.

Mauna, C., Casadío, S., Parras, A., & Pascual, M. (2005). Abundance and distribution of *Lithophaga* (Mytilidae) in extant and fossil oysters: taphonomic and paleobiological implications. *Ameghiniana, 42*, 395–405.

Mayoral, E. (1987a). *Stellichnus* nov. icnogen., huellas de incrustación atribuidas a *Paravinella* nov. gen. (Bryozoa, Ctenostomata) de la Formación *Arenas de Huelva* (Plioceno Inferior) en la cuenca del Bajo Guadalquivir (España). *Revista Española de Paleontología*, *2*, 33–40. doi: 10.7203/sjp.25213

Mayoral, E. (1987b). Acción bioerosiva de Mollusca (Gastropoda, Bivalvia) en el Plioceno inferior de la Cuenca del Bajo Guadalquivir. *Revista Española de* Paleontología, *2*, 49–58. doi: 10.7203/sjp.25215

Mayoral, E. (1988a). Microperforaciones (Tallophyta) sobre Bivalvia del Plioceno del Bajo Guadalquivir. Importancia paleoecológica. *Estudios Geologicos, 44*, 301–316. doi: 10.3989/egeol.88443-4548

Mayoral, E. (1988b). *Pennatichnus* nov. icnogen.; *Pinaceocladichnus* nov. icnogen. e *Iramena.* Huellas de bioerosión debidas a Bryozoa perforantes (Ctenostomata, Plioceno Inferior) en la Cuenca del Bajo Guadalquivir. *Revista Española de Paleontología*, *3*, 13–22. doi: 10.7203/sjp.25139

Mayoral, E., & Muñiz, F. (1996). La icnofacies de *Gnatichnus* en el sector suroccidental de la Cuenca del Gualquivir (Lepe, Huelva, España). *Coloquios de Paleontología*, *48*, 87–102.

Mayoral, E., & Reguant, S. (1995). Palaeoecology and taphonomy of bivalves, mainly *Glycymeris insubrica* (Brocchi), and bryozoans from Huelva sands Fm (Lower Pliocene, SW Spain). *Revista Española de Paleontología, Nº Homenaje al Dr. Guillermo Colom*, 31–47.

Mayoral, E., Santos, A., Gámez Vintaned, J. A., Wisshak, M., Neumann, Ch., Uchman, A., & Nel, A. (2020). Bivalve bioerosion in Cretaceous-Neogene amber around the globe, with implications for the ichnogenera *Teredolites* and *Apectoichnus*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *538*, 109410. doi: 10.1016/j.palaeo.2019.109410

McClintock, J. B., & Marion, K. R. (1993). Predation by the King Helmet (*Cassis tuberosa*) on Six-Holed Sand Dollars (*Leodia sexiesperforata*) at San Salvador, Bahamas. *Bulletin of Marine Science*, *52*, 1013–1017.

McHuron, E. J. (1976). *Biology and paleobiology of modern invertebrate borers*. (Unpublished PhD Thesis, Rice University, Houston).

McQuaid, C. D. (1994). Feeding behavior and selection of bivalve prey by *Octopus vulgaris* Cuvier. *Journal* of *Experimental Marine Biology and Ecology*, *77*, 187–220. doi: 10.1016/0022-0981(94)90236-4

Meadows, C. A., Fordyce, R. E., & Baumiller, T. K. (2015). Drill holes in the irregular echinoid, *Fibularia,* from the Oligocene of New Zealand. *Palaios*, *30*, 810–817. doi: 10.2110/palo.2015.043

Mergl, M. (2021). Dead or alive? Brachiopods and other shells as substrates for endo- and sclerobiont activity in the early Devonian (Lochkovian) of the Barrandian (Czechia). *Bulletin of Geosciences*, *96*, 401–429.

Mikuláš, R. (1992). Early Cretaceous borings from Stramberk (Czechoclovakia). *Casopis pro mineralogii a geologii*, *37*, 297–323.

Mikuláš, R., Kadlecová, E., Fejfar, O., & Dvorák, Z. (2006). Three new ichnogenera of biting and gnawing traces on Reptilian and Mammalian bones: A case study from the Miocene of the Czech Republic. *Ichnos,* 13, 113–127. doi: 101080/1040940600850729

Molinaro, D. J., Stafford, E. S., Collins, B. M. J., Barclay, K. M., Tyler, C. L., & Leighton, L. R. (2014). Peeling out predation intensity in the fossil record: A test of repair scar frequency as a suitable proxy for predation pressure along a modern predation gradient. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *412*, 141–147. doi: 10.1016/j.palaeo.2014.07.033

Molinu, A.R. (2015). Microbioerosión en substratos esquelèticos del Neógeno y Cuaternario marinos del Mediterráneo *Occidental*. (PhD Thesis, Universitat de Barcelona, Barcelona). Available at https://www.tdx.cat/handle/10803/396601

Monaco, P., FaMiani, F., Bizzarri, R., & Baldanza, A. (2011). First documentation of wood borings (*Teredolites* and insect larvae) in Early Pleistocene lower shoreface storm deposits (Orvieto area, central Italy). *Bollettino della Società Paleontologica Italiana*, *50*, 55–63.

Mondal, S., Goswami, P., & Barham, S. (2017). Naticid confamilial drilling predation trough time. *Palaios*, *32*, 278–287. doi: 10.2110/palo.2016.050

Montalvo, C. I. (2002). Root traces in fossil bones from the Huayquerian (Late Miocene) faunal assemblage of Telén, La Pampa, Argentina. *Acta Geologica Hispanica*, 37, 37–42.

Mori, K., Sato, W., Nomuray, T., & Imajima, M. (1985). Infestation of the Japanese scallop *Patinopecten yessoensis* by the boring polychaetes, *Polydora*, on the Okhotsk Sea coast of Hokkaido, especially in Abashiri waters. *Bulletin of the Japanese Society of Scientific Fisheries*, *51***,** 371–380. doi: 10.2331/suisan.51.371

Muñiz, F., Belaústegui, Z., Toscano, A., Ramirez-Cruzado, S., & Gámez Vintaned, J. A. (2020). New ichnospecies of *Linichnus* Jacobsen & Bromley, 2009. *Ichnos*, *27*, 344–351. doi: 10.1080/10420940.2020.1744585

Muñiz, F., Gibert, J. M. de, & Esperante, R. (2010). First trace-fossil evidence of bone-eating worms in whale carcasses. *Palaios*, *25*, 269–273. doi: 10.2110/palo.2009.p09-112r

Muñiz, F., Toscano, A., Bromley, R. G., & Esperante, R. (2009). Excepcional caso de interacción trófica entre tiburones hexanchiformes y una ballena Balaenoptera en el Plioceno Inferior de Huelva (SO de España). In P. Palmqvist, & J. A. Pérez-Claros (Eds.), *Comunicaciones de las XXV Jornadas de la Sociedad Española de Paleontología* (pp. 242– 244). Málaga.

Naimi, M. N., Cherif, A., Vinn, O., & Bendaho, D. E. (2021a). Polychaete macrobioerosion in the Messinian (Late Miocene) rhodolith beds of the western Mediterranean. *Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen*, *301*, 307–315. doi: 10.1127/njgpa/2021/1013

Naimi, M. N., Vinn, O., & Cherif, A. (2021b). Bioerosion in *Ostrea lamellosa* shells from the Messinian of the Tafna basin (NW Algeria). *Carnets Géologie*, *21*, 127–135. doi: 10.2110/carnets.2021.2105

Narbonne, G. M. (1984). Trace fossils in Upper Silurian tidal flat to basin slope carbonates of Arctic Canada. *Journal of Paleontology*, *58*, 398–415.

Naylor, L. A., Coombes, M. A., & Viles, H. A. (2012). Reconceptualising the role of organisms in the erosion of rock coasts: a new model. *Geomorphology*, *157–158*, 17–30. doi: 10.1016/j.geomorph.2011.07.015

Nebelsick, J. H., & Kowalewski, M. (1999). Drilling predation on Recent clypasteroid echinoids from the Red Sea. *Palaios*, *14*, 127–144. doi: 10.2307/3515369

Nesbitt, E. A. (2005). A novel trophic relationship between cassid gastropods and mysticete whale carcasses. *Lethaia*, *38*, 17–25. doi: 10.1080/00241160510013132

Neumann, A. (1966). Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge *Cliona lampas. Limnology and Oceanography, 11*, 92–108. doi: 10.4319/lo.1966.11.1.0092

Neumann, C., & Wisshak, M. (2009). Gastropod parasitism on Late Cretaceous to Early Paleocene holasteroid echinoids. Evidence from *Oichnus halo* isp.n. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *284*, 115–119. doi: 10.1016/j.palaeo.2009.09.010

Neumann, B., Wisshak, M., Aberhan, M., Girod, P., Rösner, T., & Bromley, R.G. (2015). *Centrichnus eccentricus* revisited: A new view on anomiid bivalve bioerosion. *Acta Palaeontologica Polonica*, *60*, 539–549. doi: http://dx.doi.org/10.4202/app.00079.2014

Nixon, M., & Maconnchie, E. (1988). Drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Mediterranean. *Journal of Zoology*, *216*, 687–716. doi: 10.1111/j.1469-7998.1988.tb02466.x

Noda, H., & Lee, Y. G. (1989). Wood-boring bivalve Martesia striata from the Middle Miocene Sinhyeon Formation in the Ulsan Basin, Korea. *Institute of Geosciences, University of Tsukuba*, *Annual Report*, *15*, 61–67.

Noriega, J. I., Cione, A. L., & Aceñolaza, F. G. (2007). Shark tooth marks on Miocene balaenopterid cetacean bones from Argentina. *Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen*, *245*, 185–192. doi: 10.1127/0077-7749/2007/0245-0185

Oji, T., Ogasya, C., & Sato, T. (2003). Increase of shell-crushing predation recorded in fossil shell fragmentation. *Paleobiology*, *29*, 520–552. doi: 10.1666/0094-8373(2003)029<0520:IOSPRI>2.0.CO;2

Palmer, A. R. (1982). Predation and parallel evolution: recurrent parietal plat reduction on balanomorph barnacles. *Paleobiology*, *8*, 31–44. doi: 10.1017/S0094837300004334

Palmer, T. J., & Fürsich, F. T. (1974). The Ecology of a Middle Jurassic hardground and crevice fauna. *Palaeontology*, *17*, 507–524.

Papp, A., Zapfe, H., Bachmasyer, F., & Tauber, A. F. (1947). Lebenspuren mariner Krebse. *Sitzungsberichte, Akademie der Wissenschaften in Wien*, *155*, 281–317.

Pasini, G., & Garassino, A. (2012). Naticid gastropod and octopodid cephalopod predatory traces: evidence of drill holes on the leucosid crab *Ristoria pliocaenica* (Ristori, 1891), from the Pliocene of the "La Serra" quarry (Tuscany, Italy). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*. *153*, 257–266. doi: 10.4081/19

Pemberton, S. G., Kobluk, D. R., Yeo, R. K., & RIisk, M. J. (1980). The boring *Trypanites* at the Silurian-Devonian disconformity in southern Ontario. *Journal of Paleontology*, *54*, 1258–1266.

Pemberton, G. S., MacEachern, J. A., & Saunders, T. (2004). Stratigraphic applications of substrate-specific ichnofacies: delineating discontinuities un the rock record. In D. McIlroy (Ed.), The application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. *Geological Society Special Publication*, *228*, 29–62. doi: 10.1144/GSL.SP.2004.228.01.03

Pereira, S., Mocho, P., & Lourenço, J. (2009**).** Bioerosão sobre *Megacardita jouanetti* (Bivalvia) do Miocénico da Foz do Rego (Costa de Caparica, Portugal). *Paleolusitana*, *1*, 327–338.

Perry, C. T. (1996). Distribution and Abundance of Macroborers in an Upper Miocene Reef System, Mallorca, Spain: Implications for Reef Development and Framework Destruction. *Palaios*, *11*, 40–56. doi: 10.2307/3515115

Petsios, E., Portell, R. W., Farrar, L., Tennakoon, S., Grun, T. B., Kowalewski, M., & Tyler, C. L. (2021). An asynchronous Mesozoic marine revolution: the Cenozoic intensification of predation on echinoids. *Proceedings of the Royal Society*, *B 288*, Article 20210400. doi: 10.1098/rspb.2021.0400

Pickerill, R. K., Donovan, S. K., & Portell, R. W. (2003). *Teredolites longissimus* Kelly & Bromley from the Miocene Grand Bay Formation of Carriacou, the Grenadines, Lesser Antilles. *Scripta Geologica*, *125*, 1–9.

Pierçon, M. (1932). Le Miocène marin de la Haute-Chaîne du Jura. *Bulletin de la Société* d›Histoire Naturelle du Doubs, *41*, 54–85.

Pineda-Salgado, G., Quiroz-Barroso, S. A., & Sour-Tovar, F. (2015). Analysis of bioerosion in clasts from a Miocene rocky-shore, Concepción Formation, Veracruz, México. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *439*, 50–62. doi: 10.1016/j.palaeo.2015.06.010

Pojeta J. R., & Palmer, T. J. (1976). The origin of the rock boring in mytilacean pelecypods. *Alcheringa*, *1*, 167–179.

Prikryl, T., & Novosad, B. (2009). Direct evidence of cannibalism in the Oligocene cutlassfish *Anenchelum glarisianum* Blainville, 1818 (Perciformes: Trichuridae). *Bulletin of Geosciences*, *84*, 569–572. doi: 10.3140/bull.geosci.1114

Radwanski, A. (1970). Dependence of rock-borers and burrows on the environmental conditions within the Tortonian littoral zone of Southern Poland. In T. P. Crimes, & J. C. Harper (Eds.), Trace Fossils. *Geological Journal Special Issues*, *3*, 371–390.

Radwanski, A. (1977). Present-day types af trace in the Neogene sequence; their problems of nomenclature and preservation. In T. P. Crimes, & J. C. Harper (Eds.), Trace fossils 2. *Geological Journal Special Issues*, *9*, 226–264.

Radwanski, A. (2009). *Phoenix szaferi* (palm fruitbodies) reinterpreted as traces of wood-boring teredinid bivalves from the Lower Oligocene (Rupelian) of the Tatra Mountains, Poland. *Acta Paleobotanica*, *49*, 279–286.

Rahman, A. R., Belaústegui, Z., Zamora, S., Nebelsick, H. J., Domènech, R., & Martinell, J. (2015). Miocene *Clypeaster* from Valencia (E Spain): Insights into the taphonomy and ichnology of bioeroded echinoids using X-ray micro-tomography. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *438*, 168–179. doi: 10.1016/j.palaeo.2015.07.021

Rangheard, Y., Demarcq, G., Mongereau, N., Pharisat, A., Pouyet, S., & Truc, G. (1985). Le Miocène du Val des Verrières et du Bief des Lavaux (Jura central, Haute-Chaîne): événements paléobiogéographiques et géo-dynamiques. *Geobios*, *18*, 769–785. doi: 10.1016/S0016-6995(85)80034-6

Reyment, R. A. (1967). Paleoethology and Fossil Drilling Gastropods. *Transactions of the Kansas Academy of Science*, *70*, 33–50. doi: 10.2307/3627612

Reyment, R. A., & Elewa, A. M. T. (2003). Predation by drills on Ostracoda. In P. H. Kelley, M. Kowalewski, & T. A. Hansen (Eds.), Predator-Prey Interactions in the Fossil Record. *Topics in Geobiology Series*, *20*, 93–112. Kluwer Academic/Plenum Publishers. doi: 10.1007/978-1-4615-0161-9_5

Reyment, R. A., Reyment, E. R., & Honigstein, A. (1987). Predation by boring gastropods on Late Cretaceous and Early Palaeocene ostracods. *Cretaceous Research*, *8*, 189–209. doi: 10.1016/0195-6671(87)90021-8

Richiano, S., Aguirre, M., & Farinati, E. (2012). Bioerosion structures in Quaternary marine mollusks from Argentina. In R. G., Netto, N. B., Carmona, & F. M. Tognoli (Eds.), Ichnology of Latin America Selected Papers. *Monografias da Sociedade Brasileira de Paleontologia, 2*, 159–177.

Rodríguez-Tovar, F., Uchman, A., & Puga-Bernabéu, A. (2015). Borings in gneiss boulders in the Miocene (Upper Tortonian) of the Sorbas Basin, SE Spain. *Geological Magazine*, *152*, 287–297. doi: 10.1017/S0016756814000302

Rohde, K. (ed.) (2005). *Marine Parasitology*. Cabi Publishing. doi: 10.1079/9780643090255.0000

Rojas, A., Verde, M., Urteaga, D., Scarabino, F., & Martínez, S. (2014). The first predatory drillhole on a fossil chiton plate: an occasional prey item or an erroneous attack? *Palaios*, *29*, 414–419. doi: 10.2110/palo.2014.030

Romero, M. V., Brezina, S. S., Bremec, C., & Casadío, S. (2017). Sclerobionts on Patagonian Oysters from the Puerto Madryn Formation (Early-Late Miocene, Argentina). *Ameghiniana*, *55*, 179–196. doi: 10.5710/AMGH.29.08.2017.3081

Romero Baena, A., Muñiz Guinea, F., Ayala Arias, A. J., Ramírez-Cruzado, S., Esperante Caamaño, R., & Figueroa Martínez, F. (2022). Composición y microestructura de la sílice opalina en icnofósiles del Oligoceno de Ica (Perú). *Macla: revista de la Sociedad Española de Mineralogía*, *26*, 168–169.

Rong, J., & Johnson, M. E. (1996). A stepped karst unconformity as an Early Silurian rocky shoreline in Guizhou Province (South China). *Palaoegeography, Palaeoclimatology, Palaeoecology*, *121*, 115–129. doi: 10.1016/0031-0182(95)00082-8

Rouse G., Goffredi S. K., & Vrijenhoek R. C. (2004). *Osedax*: bone-eating marine worms with dwarf males. *Science*, *305*, 668–671. doi: 10.1126/science.1098650

Roy, K., Miller, D. J., & LaBarbera, M. (1994). Taphonomic Bias in Analyses of Drilling Predation: Effects of Gastropod drill Holes on Bivalve Shell Strength. *Palaios*, *9*, 413–421. doi: 10.2307/3515059

Rützler, K. (2002). Family Clionaidae D'Orbigny, 1851. In J. N. Hooper, & R. M. van Soest (Eds.), *Systema Porifera: A Guide to the Classification of Sponges* (pp. 173–185). Kluwer Academic/Plenum Publishers. doi: 10.1007/978-1-4615-0747-5_19

Rützler, K., & Rieger, G. (1973). Sponge burrowing: Fine structure of *Clione lampa* penetrating calcareous substrata. *Marine Biology*, *21*, 144–162. doi: 10.1007/BF00354611

Santos, A., & Mayoral, E. (2009). Paleoacantilados y Bioerosión: Dos ejemplos en el Neógeno Superior de la Cordillera Ibérica. *Revista de la Sociedad Geológica de España*, *22*, 13–22.

Santos, A., & Mayoral, E. (2016). Two remarkable examples of Portuguese Neogene bioeroded rocky shores: new data and synthesis. *Comunicações Geológicas*, *103*, 121–130.

Santos, A., Mayoral, E., Muñiz, F., Vera-Peláez, J. L., & Lozano-Francisco, M. C. (2003a). Estructuras bioerosivas de anélidos poliquetos (Serpulidae) en el Neogéno superior del Sur de la Península Ibérica. *Geogaceta*, *33*, 27–30.

Santos, A., Mayoral, E., Muñiz, F., Bajo, I., & Adriaensens, O. (2003b). Bioerosión en erizos irregulares (Clypeasteroidea) del Mioceno Superior en el sector suroccidental de la cuenca del Guadalquivir (Provincia de Sevilla). *Revista Española de Paleontología*, *18*, 131–141. doi: 10.7203/sjp.18.2.21639

Santos, A., Mayoral, E., Domènech, R., Martinell, J., & Aguirre, J. (2008a). Bioerosional evidence of a marine transgression (Early Pliocene, South Spain). *Second International Congress on Ichnology*, *Abstracts Book* (p. 112). Cracow.

Santos, A. Mayoral, E., Marques da Silva, C., Cachão, M., Domènech, R., & Martinell, J. (2008b). Trace fossil assemblages on Miocene rocky shores of southern Iberia. In M. Wisshak, & L. Tapanila (Eds.), *Current Developments in Bioerosion* (pp. 431–450). Springer Verlag. doi: 10.1007/978-3-540-77598-0_22

Santos, A., Mayoral, E., Silva, C.M. da, Cachão, M., & Kullberg, J. C. (2010). *Trypanites* ichnofacies: Palaeoenvironmental and tectonic implications. A case study from the Miocene disconformity at Foz da Fonte (Lower Tagus Basin, Portugal). *Palaoegeography, Palaeoclimatology, Palaeoecology*, *292*, 35–43. doi: 10.1016/j.palaeo.2010.03.023

Santos, A., Mayoral, E. J., da Silva, C. M., Cachão, M., Johnson, M. E., & Baarli, B. G. (2011a). Miocene intertidal zonation on a volcanically active shoreline: Porto Santo in the Madeira Archipelago, Portugal. *Lethaia*, *44*, 26–42. doi: 10.1111/j.1502-3931.2010.00222.x

Santos, A., Mayoral, E., & Bromley, R. G. (2011b). Bioerosive structures from Miocene marine mobile-substrate communities in Southern Spain, and description of a new sponge boring. *Palaeontology*, *54*, 535–545. doi: 10.1111/j.1475-4983.2011.01040.x

Santos, A., Mayoral, E., Baarli, G., da Silva, C. M., Cachão, M., & Johnson, M. E. (2012a). Symbiotic association of a pyrgomatid barnacle with a coral from a volcanic Middle Miocene shoreline (Porto Santo, Madeira Archipelago, Portugal). *Palaeontology*, *55*, 173–182. doi: 10.1111/j.1475-4983.2011.01105.x

Santos, A., Mayoral, E., Johnson, M., Baarli, B. G., Cachão, M., Da Silva, C. M., & Ledesma-Vázquez, J. (2012b). Extreme habitat adaptation by boring bivalves on volcanically active paleoshores from North Atlantic Macaronesia. *Facies*, *58*, 325–338. doi: 10.1007/s10347-011-0283-z

Sato-Okoshi, W., Okoshi, K., Koh, B.-S., Kim, Y.-H., & Hong, J.-S. (2012). Polydorid species (Polychaeta: Spionidae) associated with commercially important mollusk shells in Korean waters. *Aquaculture*, *350–353*, 82–909. doi: 10.1016/j.aquaculture.2012.04.013

Savrda, E. C., Ozalas, K., Demko, T. H., Huchison, R. A., & Scheiwe, T. D. (1993). Log-Grounds and the Ichnofossil *Teredolites* in Transgressive Deposits of the Clayton Formation (Lower Paleocene), Western Alabama. *Palaios*, *8*, 311–324. doi: 10.2307/3515263

Schönberg, C. H. L., Fang, J. K. H., Carreiro-Silva, M., Tribollet, A., & Wisshak, M. (2017). Bioerosion: the other ocean acidification problem. *ICES Journal of Marine Science*, *74*, 895–925. doi: 10.1093/icesjms/fsw254

Schönberg, C. H. L., & Wisshak, M. (2014). Marine bioerosion. In S. Goffredo, & Z. Dubinsky (Eds.), *The Mediterranean Sea. Its History and Present Challenges* (pp. 449–461). Springer Verlag. doi: 10.1007/978-94-007-6704-1_26

Shipman, P. (1981). *Life History of a Fossil: An Introduction to Taphonomy and Paleoecology*. Harvard University Press.

Pinn, E., Thompson, R., & Hawkins, S. (2008). Piddocks (Mollusca: Bivalvia: Pholalidae) increase topographical complexity and species diversity in the intertidal. *Marine Ecology Progress Series, 355*, 173–182. doi: 10.3354/meps07248

Serrano-Brañas, C. I., Espinosa-Chávez, B., & Maccracken, S. A. (2019). *Teredolites* trace fossils in log-grounds from the Cerro del Pueblo Formation (Upper Cretaceous) of the state of Coahuila, Mexico. *Journal of South American Earth Sciences*, *95*, Article 102316. doi: 10.1016/j.jsames.2019.102316

Shimoyama, S., & Fujisaka, H. (1993). A New Interpretation of the Left-Right Phenomenon during Spatial Diffusion and Transport of Bivalve Shells. *The Journal of Geology*, *100*, 291–304. doi: 10.2307/30078381

Silva, C. M. da, Cachão, M., Martinell, J., & Domènech, R. (1995). Estruturas Bioerosivas como indicadores de Paleolitorais rochosos. O exemplo do Miocenico da Foz da Fonte (Sesimbra, Portugal). Dados preliminares. *Memórias do Museu e Laboratório Mineralógico e Geoloógico da FCUP*, *4*, 133–137.

Silva, C. M. da, Cachão, M., Martinell, J., & Domènech, R. (1999). Bioerosional evidence of rocky palaeoshores in the Neogene of Portugal. *Bulletin of the Geological Society of Denmark*, *45*, 175–179. doi: 10.37570/bgsd-1998-45-19

Silva, C. M. da, Cachão, M., Rebelo, C., Johnson, M., Baarli, G., Santos, A., & Mayoral, E. (2019). Paleoenvironment and taphonomy of Lower Miocene bivalve and macroid assemblages: The Lagos Biocalcarenite (Lagos-

Portimão Formation, Southern Portugal). *Facies*, *65*, 6–15. doi: 10.1007/s10347-018-0550-3

Skovsted, C. B., Brock, G. A., Lindström, A., Peel, J. S., Paterson, J. R., & Fuller, M. K. (2007). Early Cambrian record of failed durophagy and shell repair in an epibenthic mollusc. *Biology Letters*, *3*, 314–317. doi: 10.1098/rsbl.2007.0006

Smit, K. T., Schaal, S. F. K., & Habersetzer, J. (2018). *Messel. An Ancient Greenhouse Ecosystem.* Senckerber Gasellsschaft für Naturforschung.

Smyth, M. J. (1990). Incidence of boring organisms in gastropod shells on reef around Guan. *Bulletin of Marine Science*, *46*, 432–449.

Smith, C. D. (2003). Diet of *Octopus vulgaris* in Fale Bay, South Africa. *Marine Biology*, *143*, 1127–1133. doi: 10.1007/s00227-003-1144-2

Smith, C. R., & Baco, A. R. (2003). Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology: An Annual Review*, *41*, 311–354. doi: 10.1201/9780203180594.ch6

Stafford, E. S., & Lighton, L. R. (2011). Vermeij Crushing Analysis: A new old technique for estimating drushing in gastropod assemblages. *Palaoegeography, Palaeoclimatology, Palaeoecology*, *305*, 123–137. doi: 10.1016/j.palaeo.2011.02.026

Stafford, E. S., Dietl, G. P., Gingras, M. P., & Leighton, L. R. (2015). *Caedichnus,* a New Ichnogenus Representing Predatory Attack on the Shell Aperture. *Ichnos*, *22*, 87–102. doi: 10.1080/10420940.2015.1031899

Steinthorsdottir, M., & Håkansson, E. (2017). Endo- and epilithic faunal succession in a Pliocene–Pleistocene cave on Rhodes, Greece: record of a transgression. *Palaeontology*, *60*, 1–19. doi: 10.1111/pala.12312

Taddei Ruggiero, E. (1999). Bioerosive processes affecting a population of brachiopods (Upper Pliocene, Apulia). *Bulletin of the Geological Society of Denmark*, *45*, 169–172. doi: 10.37570/bgsd-1998-45-23

Taddei Ruggiero, E., & Annunziata, G. (2002). Bioerosion on a *Terebratula scillae* population from the Lower Pleistocene of Lecce (Southern Italy). *Acta Geologica Hispanica*, *37*, 43–51.

Tapanila, L. (2004). The earliest *Helicosalpinx* from Canada and the global expansion of commensalism in Late Ordovician sarcinulid corals (Tabulata). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *215*, 99–110. doi: 10.1016/S0031-0182(04)00454-7

Tapanila, L. (2008). The endolithic guild: an ecological framework forresidual cavities in hard substrates. In M. Wisshak, & L. Tapanila (Eds.), *Current Developments in Bioerosion* (pp. 3–20). Springer. doi: 10.1007/978-3-540-77598-0_1

Tapanila, L., & Ekdale A. (2007). Early History of Symbiosis in Living Substrates: Trace-Fossil Evidence from the Marine Record. In W. Miller (Ed.), *Trace Fossils: concepts, Problems, Prospects* (pp. 345–355). Elsevier. doi: 10.1016/B978-044452949-7/50145-5

Taylor, P. D., & Wilson, M. A. (2002). A new terminology for marine organisms inhabiting hard substrates. *Palaios*, *17*, 522–525. doi: 10.1669/0883-1351(2002)017<0522:ANTFMO>2.0.CO;2

Taylor, P. D., & Wilson, M. A. (2003). Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews*, *62*, 1–103. doi: 10.1016/S0012-8252(02)00131-9

Taylor, P. D., Wilson, M. A., & Bromley, R. G. (1999). A new ichnogenus for etchings made by cheilostome bryozoans into calcareous substrates. *Palaeontology*, *42*, 595–604. doi: 10.1111/1475-4983.00087

Tevesz, M. J. S., & McCall, P. L. (Eds.) (1983). *Biotic Interactions in Recent and Fossil Bentic Communities*. *Topics in Geobiology*, 3. Plenum Press. doi: 10.1007/978-1-4757-0740-3

Titschack, J., Bromley, R. G., & Freiwald, A. (2005). Plio-Pleistocene cliffbound, wedge-shaped, warm-temperate carbonate deposits from Rhodes (Greece): sedimentology and facies. *Sedimentary Geology*, *180*, 29–56. doi: 10.1016/j.sedgeo.2005.06.009

Turra, A., Denadai, M. R., & Leite, F. P. P. (2005). Predation on gastropods by shell-breaking crabs: effects on shell availability to hermit crabs. *Marine Ecology Progress Series*, *286*, 279–291. doi: 10.3354/meps286279

Tyler, C. l., Dexter, T. A., Portell, R. W., & Kowalewski, M. (2018). Predation-facilitated preservation of echinoids in a tropical marine environment. *Palaios*, *33*, 478–486. doi: 10.2110/palo.2018.046

Uchman, A., Demircan, H., Toker, V., Derman, A. S., Sevim, S., & Szulc, J. (2002). Relative sea level changes recorded in borings from a Miocene rocky shore of the Mut Basin, southern Turkey. *Annales Societatis Geologorum Poloniae*, *72*, 263–270.

Uchman, A., Kleemann, K., & Rattazzi, B. (2017). Macroborings, their tracemakers and nestlers in clasts of a fan delta: The Savignone Conglomerate (lower Oligocene), Northern Apennines, Italy. *Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen*, *283*, 35–51. doi: 10.1127/njgpa/2017/0625

Uchman, A., Stachacz, M., & Salamon, K. (2018). *Spirolites radwanskii* n. igen., n. isp.: Vermetid gastropod attachment etching trace from the middle Miocene rocky coast of the Paratethys, Poland. *Journal of Paleontology*, *92*, 883–895. doi: 10.1017/jpa.2017.95

Vallon, L. H. (2012). Digestichnia (Vialov, 1972): an almost forgotten ethological class for trace fossils. In A. P. Hunt, J. Milan, S. G. Lucas, & J. A. Spielmann (Eds.), *Vertebrate coprolites*. *New Mexico Museum of Natural History and Science Bulletin*, *57*, 131–135.

Verde, M., Castillo, C., Martín-González, E., Cruzado-Caballero, P., Mayoral, E., & Santos, A. (2022). A new miocene–pliocene ichnotaxon for vermetid anchoring bioerosion structures. *Frontiers in Earth Science*, *10*, Article 906493. doi: 10.3389/feart.2022.906493

Vermeij, G. J. (1977). The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology, 3*, 245–258. doi: 10.1017/S0094837300005352

Vermeij, G. J. (1982). Unsuccessful predation and evolution. *The American Naturalist, 120*, 701–720. doi: 10.1086/284025

Vermeij, G. J. (1987). *Evolution and escalation. An ecological history of life.* Princenton University Press. doi: 10.1515/9780691224244

Vermeij, G. J. (1994). The evolutionary interaction among species: Selection, escalation, and coevolution. *Annual Review of Ecology and Systematics, 25*, 219–236. doi: 10.1146/annurev.es.25.110194.001251

Vermeij, G. J., Schindel, D. E., & Zipser, E. (1981). Predation Through Geological Time: Evidence from Gastropod Shell Repair. *Science*, *214*, 1024–1026. doi: 10.1126/science.214.4524.1024

Vermeij, G. J., Zipser, E., & Dudley, E. C. (1980). Predation in time and space: peeling and drilling in terebrid gastropods. *Paleobiology*, *6*, 352–364. doi: 10.1017/S0094837300006850

Vermeij, G. J., Zipser, E. & Zardini, R. (1982). Breakage-Induced shell repair in some gastropods from the Upper Triassic of Italy. *Journal of Paleontology*, *56*, 233–235.

Viles, H. A. (1995). Ecological perspectives on rock surface weathering towards a conceptual method. *Geomorphology*, *13*, 21–35. doi: 10.1016/0169-555X(95)00024-Y

Villegas-Martín, J., & Rojas-Consuegra, R. (2011). Presencia del icnogénero *Teredolites* en un megabloque de la Formación Peñalver, límite Cretácico–Paleógeno (K/Pg), Cuba occidental. *Revista Española de Paleontología*, *26*, 45–52. doi: 10.7203/sjp.26.1.18468

Villegas-Martín J., Gibert, J. M. de, Rojas-Consuegra, R., & Belaústegui, Z. (2012). Jurassic *Teredolites* from Cuba: New trace fossil evidence of early Wood-boring behavior in bivalves. *Journal of South American Earth Sciences*, *38*, 123–128. doi: 10.1016/j.jsames.2012.06.009

Villegas-Martín, J., Rojas-Consuegra, R., & Klompmaker, A. A. (2016). Drill hole predation on tubes of serpulid polychaetes from the Upper Cretaceous of Cuba. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *455*, 44–52. doi: 10.1016/j.palaeo.2016.05.009

Villegas-Martín J., Rojas-Consuegra, R., Verde, M., Belaústegui, Z., Ritter, M., & Scalise Horodyski, R. (2022). Bioerosion on rudist shells from the Upper Cretaceous of Cuba: Paleobiological, paleoecological andtaphonomic implications. *Journal of South American Earth Sciences*, *113*, Article 103665. doi: 10.1016/j.jsames.2021.103665

Vinn, O. (2018). Traces of predation in the Cambrian. *Historical Biology*, *30*, 1043–1049. doi: 10.1080/08912963.2017.1329305

Voigt, E. (1970). Endolithische Wurm-Tunnelbauten (*Lapispecus cuniculus* n.g. n.sp. und *Dodecaceria* [?] sp.) in Brandungsgeröllen der oberen Kreide im nördlichen Harzvorland. *Geologische Rundschau*, *60*, 355–380. doi: 10.1007/BF01820950

Voigt, E. (1971). Fremdskulpturen an Steinkernen von Polychaeten-Bohrgängen aus der Maastrichter Tuffkreide. *Paläontologische Zeitschrift*, *45*, 144–153. doi: 10.1007/BF02989572

Voigt, E**.** (1975). Tunnelbaue rezenter und fossiler Phoronidea. *Paläontologische Zeitschrift*, *49*, 135–167. doi: 10.1007/BF02988072

Voigt, E. (1977). On grazing traces produced by the radula of fossil and Recent gastropods and chitons. In T. P. Crimes, & J. C. Harper (Eds.), Trace Fossils 2. *Geological Journal Special Issues*, *9*, 335–346.

Walker, S. E. (1989). Hermit Crabs as Taphonomic Agents. *Palaios*, *4*, 439–452. doi: 10.2307/3514588

Walker, S. E. (1992). Criteria for recognizing marine hermit crabs in the fossil record using gastropod shells. *Journal of Paleontology*, *66*, 535–558. doi: 10.1017/S0022336000024410

Walker, S. E., & Brett, C. E. (2002). Post-Paleozoic patterns in marine predations was there a Mesozoic and Cenozoic marine predatory revolution? In M. Kowalewski, & P. H. Kelley (Eds.), The fossil record of predation. *The Paleontological Society Papers*, *8*, 119–193. doi: 10.1017/S108933260000108X

Wargo, R. N., & Ford, S. E. (1993). The Effect of Shell Infestation by *Polydora* sp. and Infection by *Haplosporidium nelsoni* (MSX) on the Tissue Condition of Oysters, *Crassostrea virginica*. *Estuaries*, *16*, 229–234. doi: 10.2307/1352494

Warme, J. E. (1975). Borings as trace fossils, and the processes of marine bioerosion. In R. W. Frey (Ed.), *The Study of Trace Fossils* (pp. 181–227). Springer-Verlag. doi: 10.1007/978-3-642-65923-2_11

Watkins, S. R. (1990). Paleoecology of a Pliocene rocky shore-line, Salton Trough Region, California. *Palaios*, *5*, 167–175. doi: 10.2307/3514813

Webb, G. E. (1994). Paleokarst, paleosol, and rocky shore deposits at the Mississippian-Pennsylvanian unconformity, northwestern Arkansas. *Geological Society of America Bulletin*,*106*, 634–648. doi: 10.1130/0016-7606(1994)106<0634:PPARSD>2.3.CO;2

Weigelt, J. (1928). Die Pflanzenreste des mitteldeutshen Kupferschiefers und *ihre* Einschaltung ins Sediment. *Forstschritte der Geologie und Palaontologi*, *6*, 95–592.

Weigelt, J. (1989). *Recent Vertebrate Carcasses and Their Paleobological Implications*. University of Chicago Press. doi: 10.7208/chicago/9780226881683.001.0001

Wilson, M. A. (2007). Macroborings and the evolution of bioerosion. In W. Miller III (Ed.), *Trace Fossils: Concepts, Problems, Prospects* (pp. 356–367). Elsevier. doi: 10.1016/B978-044452949-7/50146-7

Wilson, M. (2013). Bioerosion Bibliography. Marine Bioerosion Bibliography (updated February 27, 2013). The College of Wooster, Ohio. Available at https://markwilson.voices.wooster.edu/bioerosion-bibliography-5/

Wilson, M. A., & Palmer, T. J. (1990). A Review of Evolutionary Trends in Carbonate Hardground Communities. *The Paleontological Society Special Publications*, *5*, 137–152. doi: 10.1017/S2475262200005475

Wilson, M. A., & Palmer, T. J. (1994). A carbonate hardground in the Carmel Formation (Middle Jurassic, SW Utah, USA) and its associated encrusters, borers and nestlers. *Ichnos*, *3*, 79–87. doi: 10.1080/10420949409386375

Wilson, M. A., Wolfe, K. R., & Avni, Y. (2005). Development of a Jurassic rocky shore complex (Zohar Formation, Makhtesh Qatan, southern Israel). *Israel Journal of Earth Sciences*, *54*, 171–178. doi: 10.1560/71EQ-CNDF-K3MQ-XYTA

Wisshak, M. (2008). The new dwarf *Entobia* ichnospecies in a diverse aphotic ichnocoenosis (Pleistocene/ Rhodes, Greece). In M. Wisshak, & L. Tapanila (Eds.), *Current developments in bioerosion* (pp. 213–233). Springer Verlag. doi: 10.1007/978-3-540-77598-0_11

Wisshak, M. (2012). Microbioerosion. In D. Knaust, & R. Bromley (Eds.), Trace Fossils as Indicators of Sedimentary Environments. *Developments in Sedimentology*, *64*, 213–243, Elsevier. doi: 10.1016/B978-0-444-53813-0.00008-3

Wisshak, M., Knaust, D., & Bertling, M. (2019). Bioerosion ichnotaxa: review and annotated list. *Facies*, *65*, 24. doi: 10.1007/s10347-019-0561-8

Wodinsky, J. (1969). Penetration of the shell and feeding on gastropods by *Octopus*. *American Zoologist*, *9*, 997–1010. doi: 10.1093/icb/9.3.997

Wodinsky, J. (1973). Mechanism of hole Boring in *Octopus vulgaris*. *The Journal of General Psychology*, *88*, 179–183. doi: 10.1080/00221309.1973.9920727

Xu, X-Y., Yip, K. R., Shin, P. K. S., & Cheung, S. G. (2017). Predator–prey interaction between muricid gastropods and mussels under ocean acidification.

Marine Pollution Bulletin, *124,* 911–916. doi: 10.1016/j.marpolbul.2017.01.003

Yanes, Y., & Tyler, C. L. (2009). Drilling predation intensity and feeding preferences by *Nucella* (Muricidae) on limpets inferred from dead-shell assemblage. *Palaios*, *24*, 280–289. doi: 10.2110/palo.2008.p08-074r

Yochelson, E. L., Dockery, D., & Wolf, H. (1983). Predation on sub-Holocene scaphopod mollusks from southern Louisiana. *Geological Survey Professional Paper*, *1282*, 1–13.

Zatoń, M., & Salamon, M. A. (2008). Durophagous predation on Middle Jurassic molluscs, as evidenced from shell fragmentation. *Palaeontology*, *521*, 63–70.

Zatoń, M., & Rakocinski, M. (2014). Coprolite evidence for carnivorous predation in a Late Devonian pelagic environment of southern Laurasia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *394*, 1–11. doi: 10.1016/j.palaeo.2013.11.019

Zatoń, M., Wilson, M. A., & Zavar, E. (2011). Diverse sclerozoan assemblages encrusting large bivalve shells from the Callovian (Middle Jurassic) of southern Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *307*, 232–244. doi: 10.1016/j.palaeo.2011.05.022

Zatoń, M., Broda, K., Niedźwiedzk, G., Qvarnstr, M. M., & Ahlberg, P. E. (2017). The first direct evidence of a Late Devonian coelacanth fish feeding on conodont animals. *Science of Nature*, *104*, 1–5. doi: 10.1007/s00114-017-1455-7

Zibrowius, H. (1987). Scléractiniares et polychètes serpulidae des faunes bathyales actuelles et plio−pleistocènes de Meditérrannée. *Documents et Travaux de l'Institut Géologique Albert de Lapparent*, *11*, 255–257.

Ziegelmeier, E. (1954). Beobachtungen über den Nahrungserwerb bei der Naticide *Lunatia nitida* Donovan (Gastropoda, Prosobranchia). *Helgoländer Wissenschaftliche Meeresuntersuchungen*, *5*, 1–33. doi: 10.1007/BF01609105

Złotnik, M., & Ceranka, T. (2005). Patterns of drilling predation of cassid gastropods preying on echinoids from the middle Miocene of Poland. *Acta Palaeontologica Polonica*, *50*, 409–428.

Zuschin, M., Stachowitsch, M., & Stanton, J. (2003). Patterns and processes on shell fragmentation in modern and ancient environments. *Earth-Science Reviews*, *63*, 33–82. doi: 10.1016/S0012-8252(03)00014-X