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# Bioerosion in shell beds from the Pliocene Roussillon Basin, France: Implications for the (macro)bioerosion ichnofacies model

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The marine Pliocene at the locality of Nefiach (Roussillon Basin, SE France) includes several shell beds constituted by oysters and scallops that bear a diverse and abundant bioerosion trace fossil assemblage. The most abundant trace fossils are *Gnathichnus pentax* and *Radulichnus inopinatus*, produced by the grazing activity of echinoids and polyplacophorans upon algae and other microorganisms coating shell surfaces. Other bioerosion traces include polychaete dwellings (*Caulostrepsis taeniola* and *Maeandropolydora sulcans*), sponge boring systems (*Entobia* isp.), and rare bryozoan borings (*Pinaceocladichnus* isp.), predation structures (*Oichnus simplex* and repaired durophagous scars), and foraminiferal fixation pits (*Centrichnus* cf. *eccentricus*). The trace fossil assemblage records short-term bioerosion in shellgrounds in a moderate energy setting as evinced by the dominance of epigenic or shallow endogenic structures produced in most cases by “instantaneous” behaviors. The assemblage can be assigned to the *Gnathichnus* ichnofacies, and it contrasts with that found in Pliocene rocky shores in the same geographic area, which are examples of the *Entobia* ichnofacies. The *Gnathichnus* ichnofacies is validated as an archetypal one and its recurrence demonstrated since the Jurassic. *Entobia* and *Gnathichnus* ichnofacies have to be used in the Mesozoic and Cenozoic as substitutes of the previously existing *Trypanites* ichnofacies, which is still valid in the Palaeozoic.

**Key words:** Shell beds, ichnology, bioerosion, ichnofacies, *Gnathichnus*, *Radulichnus*, Pliocene, France.

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## Introduction

Biological erosion is an important process in both Modern and Ancient marine environments. The study of bioerosion trace fossils has brought up interesting insights on the ecological interactions between species (e.g., Hoffman and Martinell 1984; Kelley and Hansen 2006; Wisshak and Neumann 2006), palaeoenvironmental interpretation and basin analysis (e.g., Bromley and Asgaard 1993a; Vögel et al. 1995; Domènech et al. 2001), or the evolution of hard-substrate communities (e.g., Taylor and Wilson 2003; Benner et al. 2004). Nevertheless, the existence of bioerosion assemblages recurrent in time and space (Seilacherian or archetypal ichnofacies) is a problem poorly understood compared to the soft substrate (bioturbation) realm. Frey and Seilacher (1981) erected the *Trypanites* ichnofacies to include all trace fossil assemblages constituted by bioerosion structures upon hard substrates. This archetypal ichnofacies did not contain any ecological or environmental information beyond the nature of the substrate. Still, bioerosion is produced upon a variety of substrates (rockgrounds, synsedimentary hardgrounds, skeletal substrates, wood, etc.) and in a variety of depositional settings. Bromley et al. (1984) erected the

*Teredolites* ichnofacies for boring assemblages in woodgrounds, but further exploration in mineral (lithic or skeletal) substrates had to wait until Bromley and Asgaard (1993a). These authors defined two bioerosion ichnofacies with environmental significance in the Upper Pliocene of Rhodes. The *Entobia* ichnofacies, dominated by deep-tier dwelling borings, was found in lengthily exposed substrates (littoral rocky shore settings), while the *Gnathichnus* ichnofacies, constituted mainly by epigenic and shallow-tier structures, characterized briefly exposed substrates such as shells and lithoclasts in deeper water. Bromley and Asgaard (1993a) suggested that these two ichnofacies could come to substitute the *Trypanites* ichnofacies or rather become subdivisions of it. However, they did not demonstrate the recurrence of the assemblages, an essential requisite for the formal definition of a valid archetypal ichnofacies (e.g., Seilacher 1964; Bromley 1996; Pemberton et al. 2001). Later, Gibert et al. (1998) described several examples of the *Entobia* ichnofacies from the Lower Pliocene of the north-western Mediterranean and validated it by demonstrating its presence in rocky shores since the Jurassic to the Holocene. On the other hand, the *Gnathichnus* ichnofacies has been little used, since first defined (Mayoral and Muñiz 1996; Radley 2006).

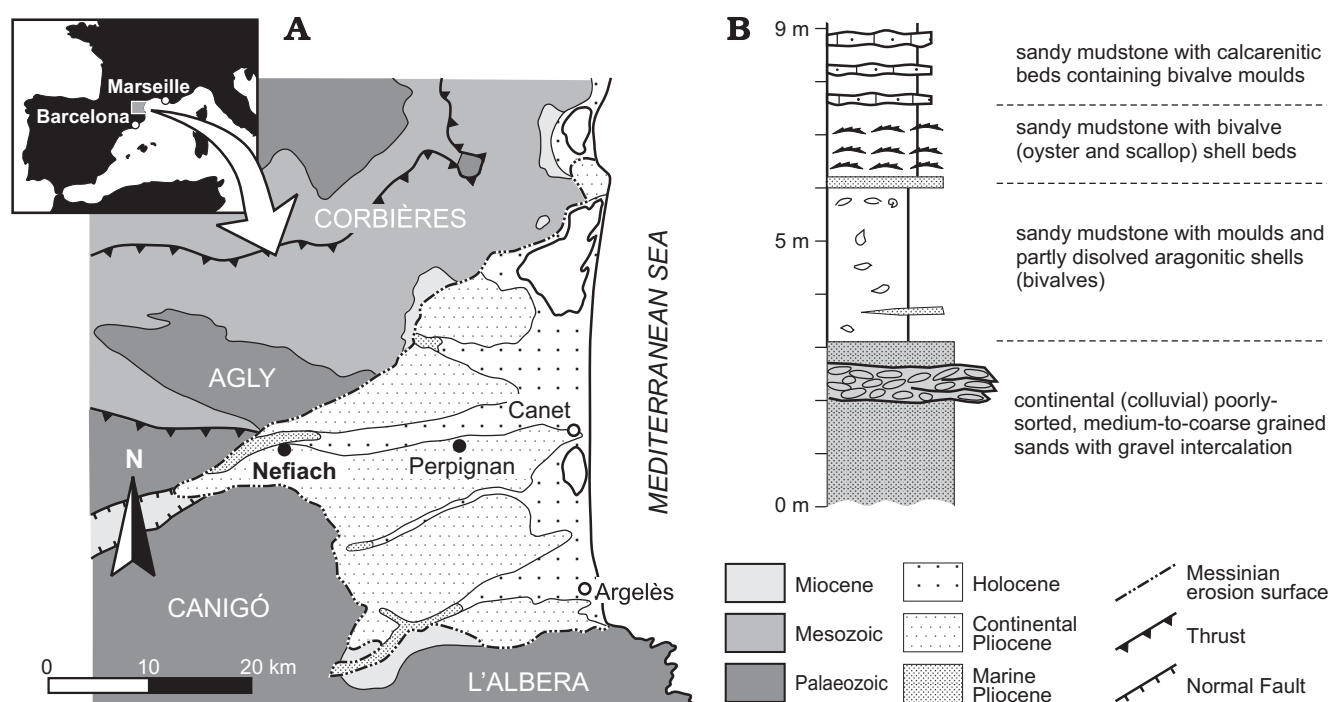


Fig. 1. **A.** Geological map of the Roussillon Basin, modified from Clauzon et al. (1987). **B.** Stratigraphic section of the Pliocene at Nefiach.

The objectives of the present paper are: (1) to describe an excellent example of the *Gnathichnus* ichnofacies in shell beds in the Pliocene Roussillon Basin (south-eastern France); (2) to interpret the genetic history of those shell beds; and (3) to analyze the validity of the ichnofacies as an archetypal one.

*Institutional abbreviation.*—JMC-UB, Jordi Martinell Neogene invertebrate collection, University of Barcelona, Spain.

## Geological setting

The Roussillon Basin is located in the southeast of France. Today, it corresponds to a plain, with the city of Perpignan in the centre, that coincides with the lower courses of the Tech and Têt rivers. The area is bounded to the northwest by the Corbières and to the south by the Pyrenean reliefs of Canigó and L'Albera (Fig. 1A). The Roussillon is a Neogene extensional basin active during the Miocene and located in the axial part of the Pyrenees. A very important event for the evolution of the basin was the so-called "Messinian Salinity Crisis" (Hsü et al. 1973; Ryan 1976; Clauzon 1982) that affected the whole Mediterranean area. In the latest Miocene a dramatic sea-level fall, due to the combination of a global eustatic lowering and a tectonic uplift in the Gibraltar region, resulted in the incision of deep canyons in the continental shelf that reached what today are onshore areas. Thus, the posterior transgression in the Early Zanclean (Early Pliocene) resulted in the flooding of important areas and the formation of several marginal basins in the Mediterranean area (Clauzon et al. 1990; Gibert and Martinell 1998a), the Roussillon being among them.

The Pliocene materials in the Roussillon basin overlie the Messinian erosional surface (Clauzon et al. 1987; Clauzon 1990). The Pliocene sequence begins with marine sandy mudstones, the thickness of which never reaches more than 20 m in the outcrops at the inner part of the basin but extends beyond 600 m at the Canet drill hole near the present shoreline (Duvail et al. 2005). This unit has yielded an abundant and diverse fossil macrofauna, mainly constituted by molluscs (Martinell and Domènech, 1984, 1987–88, 1990). Microfaunal analysis allowed to date these sediments as Lower Zanclean (Cravatte et al. 1984). Overlying the fully marine deposits, coarser-grained (sandy and gravelly) units exhibit a significant depositional dip (201–251) and have been interpreted as the foresets of a Gilbert delta (Clauzon 1990). The Pliocene infill is completed by topset units constituted by alluvial fan and alluvial plain deposits. They have also been assigned to the Lower Pliocene on the basis of rodent microfauna (Clauzon et al. 1989).

The locality that is the object of the present paper is located in the valley of the Têt, about 1 km north of the village of Nefiach (Fig. 1A). This locality was first described by Martinell and Domènech (1990) as Chemin de Saint Martin. The Pliocene section here (Fig. 1B) begins with about 3 m of continental (colluvial) sands and gravels that are abruptly overlain by marine sandy mudstones (3 m) with a variety of molluscs, preserved as moulds or partly dissolved shells. Bivalves are most abundant and include species of the genera *Acanthocardia*, *Corbula*, *Dosinia*, *Laevicardium*, *Solen*, and *Tellina*, while gastropods are scarcer and only *Architectonica* has been identified. The upper third of the exposed section contains beds (between a few and 10 cm thick) composed of calcitic bi-



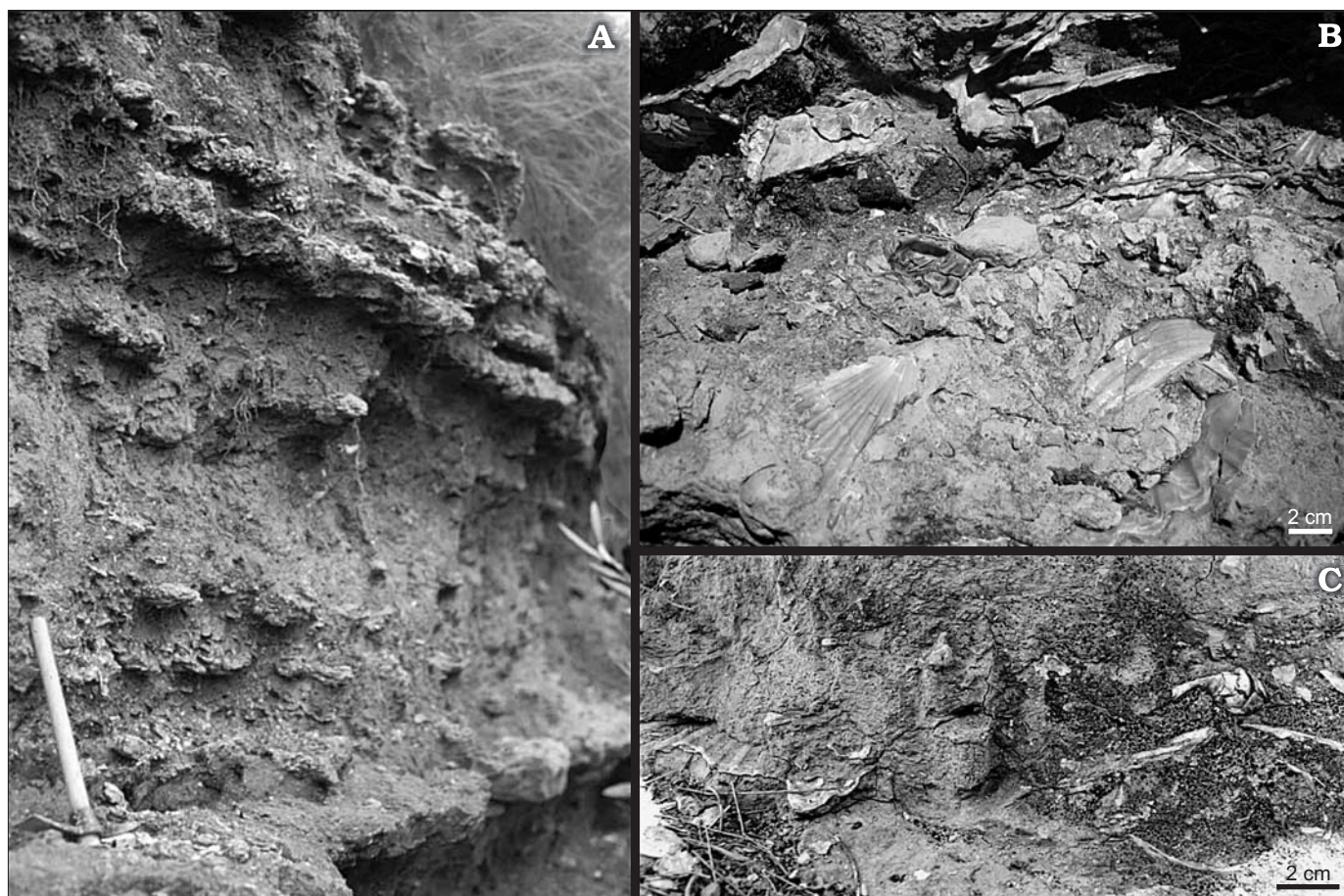


Fig. 2. Field appearance of the shell beds at Nefiach. **A**. View of the interval that includes several shell beds. **B**, **C**. Details of the shell beds showing the concordant attitude of the shells.

valve shells, including oysters and scallops (Fig. 2). These shells bear an abundant and diverse assemblage of macrobioerosion structures that are the object of this contribution.

## The shell beds at Nefiach

The shell beds that are object of this study are mainly constituted by a concentration of valves of three species of bivalves (Figs. 2 and 3). The oyster *Saccostrea cucullata* (Fig. 3C, E) and the scallop *Pecten benedictus* (Fig. 3A) are the most abundant, while another scallop, *Aequipecten scabrellus* (Fig. 3B, J), is also common. They form beds of a few centimetres where valves are organized parallel to bedding (concordant in the sense of Kidwell et al. 1986; Fig. 2C). The stacking of the shells supports the sediment fabric, while the matrix, composed of sandy mudstone, fills completely the spaces left between the skeletal remains. Shell preservation varies. Both fragments and complete, or nearly complete, shells are found. Valves are commonly separated but some articulated specimens also occur. There is no obvious size sorting but some valve selection has been recognized. Upper valves of *P. benedictus* and *S. cucullata* (left and right valves, respectively), and right valves of *A. scabrellus* are much better represented, con-

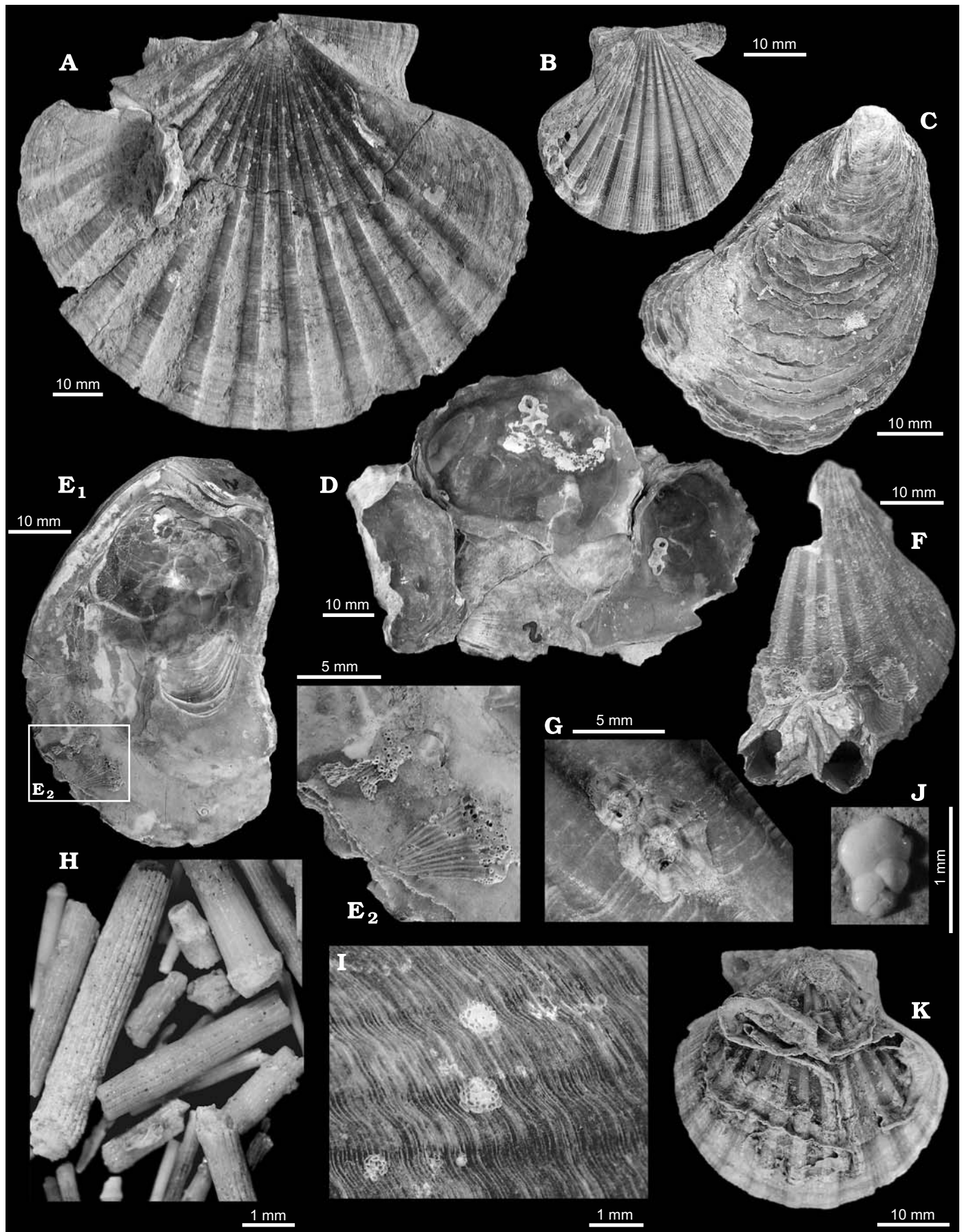
stituting approximately 75% of the total number of valves, and the same percentage is found for each species. Bioerosion is intense on *S. cucullata* and *P. benedictus*, but *A. scabrellus* valves usually occur pristine. In contrast, encrusters affect the three species. Mechanical abrasion is absent or very low.

Other molluscs include some anomiid bivalve shells (*Anomia ephippium* and *Monia patelliformis*) and moulds of small indetermined originally aragonite-shelled gastropods and bivalves.

Body fossils of encrusting organisms include some of the specimens of *S. cucullata* and Anomiidae, but also bryozoans, cirripedians, foraminiferans, and annelids. It has been possible to recognize two species of cheilostomate bryozoans, *Cellaria nebianii* and cf. *Conopeum reticulatum*, and several cyclostomates, *Diplosolen obellium* (Fig. 3E), *Exidmonea* cf. *disticha*, *Crisia* sp., and some other undetermined Tubuliporina. Barnacles are represented by at least two balanid species, *Balanus crenatus* and *B. concavus* (Fig. 3F, G), while encrusting foraminifera include *Dyocibicides biserialis* (Fig. 3J), *Cibicides lobatulus* and another species probably belonging to the genus *Planorbulina* (Fig. 3I). The serpulid polychaete, *Potamoceros triqueter*, is also a common encruster (Fig. 3K).

Finally, common regular echinoid spines are found in the sediment (Fig. 3H).





## Bioerosion trace fossils

Bioerosion trace fossils from the shell beds at Nefiach include a variety of ichnotaxa belonging to different ethological classes (see Gibert et al. 2004, for a review of the ethological classification of bioerosion structures). Pascichnia (grazing structures) are the most abundant, including two ichnospecies, *Gnathichnus pentax* and *Radulichnus inopinatus*. Dwelling borings (domichnia) of polychaetes are common and are represented by *Caulostrepsis taeniola* and *Maeandropolydora sulcans*. Other traces are less frequent. They include domichnia of endoskeletozoans (*Entobia* isp. and *Pinaceocladichnus* isp.), praedichnia (predation structures; *Oichnus simplex* and durophagous scars), and fixichnia (attachment structures; *Centrichnus* cf. *eccentricus*). Only bioerosion traces produced by macroorganisms are here considered. Microborings produced by microorganisms (fungi, algae, etc.) are also present but their study is beyond the scope of the present paper as techniques involved are very different than those needed to study macrobioerosion (Golubic et al. 1975; Beuck et al. 2007).

### Echinoid grazing traces: *Gnathichnus pentax*

The most common bioerosion structure consists of groups of pentaradiate grooves that may cover completely or extensively the surfaces of the shells (Fig. 4). The trace in its simplest form (the modular unit; e.g., Bromley 1975) is composed of five grooves arranged in a star-shaped pattern (Fig. 4A<sub>1</sub>). Angle between radial scratches is consistently of 72° and they do not meet in the centre. Each groove is rectilinear with a length between 0.8 and 1.5 mm and a width varying little around 150 µm, their distal end being acuminate. The diameter of the modular units varies between 1 and 5 mm. They rarely occur isolated, but most commonly overlap to cover the whole or most of the surface of the shell. In some cases, where bioerosion was not so intense, trails of overlapping stars can be recognized indicating directed movement of the tracemaker.

These features allow to identify these traces as *Gnathichnus pentax*, an ichnospecies erected and described by Bromley (1975) to name trace fossils produced by the grazing activity of regular echinoids. They feed upon epilithic and endolithic algae and other organisms by using their Aristotle lantern to gnaw them out of the substrate. Observation of modern echinoids demonstrates that this activity results in pentaradiate traces such as *Gnathichnus pentax* (Bromley 1975; Martinell 1981; Försterra et al. 2005; Wisshak et al. 2005). The finding of abundant regular echinoid spines in the

shell beds from the Roussillon provides additional evidence of the presence of such organisms.

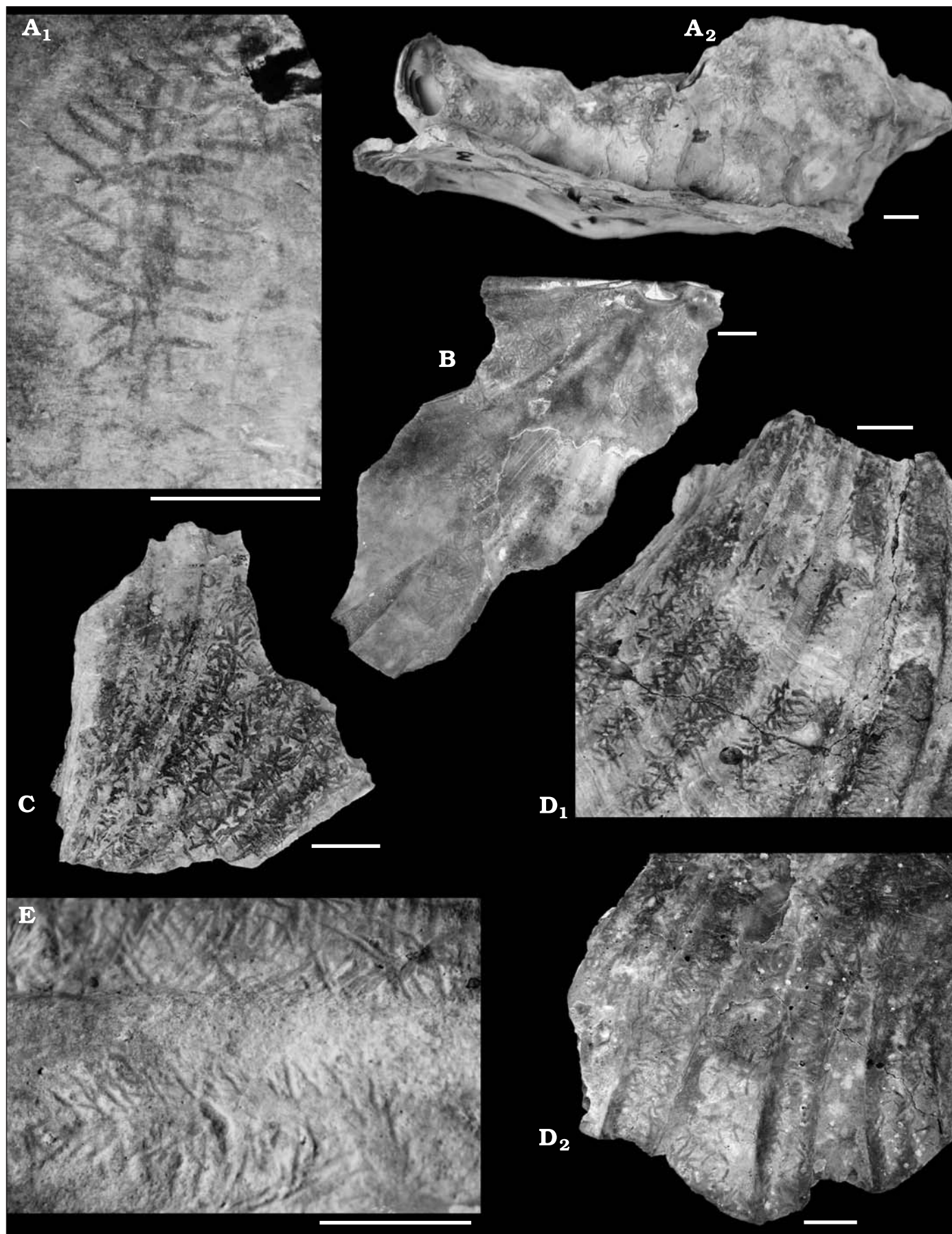
Approximately half of the shells with *Gnathichnus* at Nefiach bear the trace in both sides of the valves. Among the rest, the echinoid sculpture is mostly found only in the external side for oyster valves and left valves of *A. benedictus*, or in the internal side for right valves of *A. benedictus*. There seems to be a correlation between shell ornamentation and *Gnathichnus* preservation. Gnawing traces are deeper in external (stronger ornamented) sides of valves, something already pointed out by Martinell (1981) in his study of modern echinoid bioerosion. Additionally, the distribution of *Gnathichnus* in individual pectinid valves is also controlled by their ornamentation. It is present both in ribs and intercostal areas in the areas near the ventral margin of the shell, while it is restricted to the ribs in more central parts where intercostal areas are narrower, probably because of the impossibility to reach them. Finally, in the umbonal region where ribs are less marked and very close to each other, there is no difference between higher and deeper areas as their width is smaller than the diameter of the modular unit. In many cases, it can be observed that encrusters post-date echinoid bioerosion as their skeletons encrust *Gnathichnus* sculptures.

Michalík (1977) described Upper Triassic *Gnathichnus* from Slovakia as a new ichnogenus and ichnospecies, *Redersignus quinquerradialis*, but the same author (Michalík 1980) later put this name in synonymy with *G. pentax*. Breton et al. (1992) erected a new ichnospecies, *G. stellarum*, from material found in the Upper Cretaceous of France. As the authors stated, *G. stellarum* is morphologically identical to *G. pentax* and thus, it has to be considered a junior synonym. They upheld the erection of the new species based on the fact that their material was upon asteroid ossicles and then, they considered that the tracemaker was feeding upon the organic material contained in the stereome of the asteroid and not upon encrusting or boring organisms in a non-living substrate. Nevertheless, ichnotaxonomy should better be based on morphological rather than genetic (interpretative and thus, less stable) considerations.

The oldest known occurrence of *Gnathichnus* was recorded by Fürsich and Wendt (1977) from the Middle–Upper Triassic of the Alps. Other fossil occurrences of the ichnotaxon are known from the Upper Triassic (Michalík 1977, 1980) Jurassic (Nicosia 1986; Machalski 1998; Radwańska 1999; Radley 2006), Cretaceous (Breton et al. 1992; Wilson 2003), Palaeogene (Carrasco 2003), Neogene (Martinell 1982; Barrier and D'Alessandro 1985; Martinell and Domènech 1986; Bromley and Asgaard 1993a, b; Mayoral and Muñiz 1996, 2002), and Quaternary (Martinell and Domènech 1981). Most of these occurrences correspond to bioerosion

← Fig. 3. Body fossils from Nefiach, Pliocene. **A.** Left valve of *Pecten benedictus*, JMC-UB/I-0088. **B.** Right valve of *Aequipecten scabrellus*, JMC-UB/I-0089. **C.** Right valve of *Saccostrea cucullata*, JMC-UB/I-0090. **D.** *Pecten benedictus* encrusted by three *Saccostrea cucullata*, JMC-UB/I-0091. **E.** Internal side of a right valve of *Saccostrea cucullata* (E<sub>1</sub>) with an encrusted cyclostomate bryozoan *Diplosolen obellium* (E<sub>2</sub>), JMC-UB/I-0092. **F.** Balanid cirripedians, *Balanus crenatus*, on a pectinid shell, JMC-UB/I-0093. **G.** Two specimens of *Balanus concavus*, displaying traces of the original colour ornamentation, JMC-UB/I-0094. **H.** Spines of regular echinoids, JMC-UB/I-0095. **I.** Foraminifera, cf. *Planorbulina*, on pectinid shell, JMC-UB/I-0096. **J.** *Dyocibicides biserialis*, an encrusting foraminifera, JMC-UB/I-0103. **K.** The serpulid worm *Potamoceros triqueter* encrusted on *A. scabrellus*, JMC-UB/I-0097.





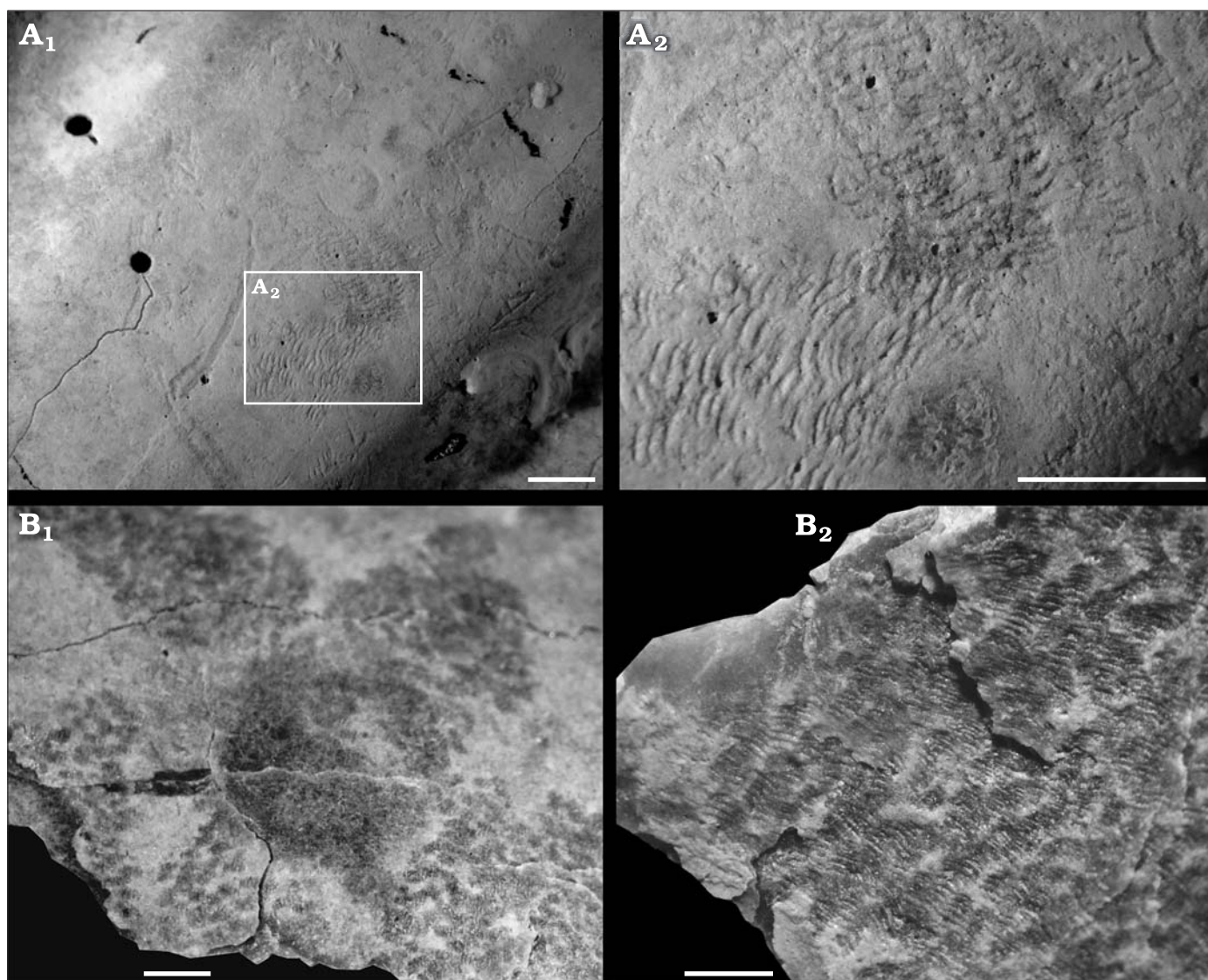


Fig. 5. Mollusc grazing traces *Radulichnus inopinatus* from Nefiach, Pliocene. **A.** Inner surface of a pectinid valve with areas covered by *Radulichnus* (A<sub>1</sub>) and detail of the specimen (A<sub>2</sub>), displaying the arrangement of scratches in groups, JMC-UB/I-0103. **B.** Oyster shell with dense patches of *Radulichnus* (B<sub>1</sub>) and sculpture resulting from pervasive, deep *Radulichnus* bioerosion (B<sub>2</sub>), JMC-UB/I-0098. Scale bars 1 mm.

sculptures upon shells and only more rarely upon lithic clasts. The stratigraphic range of *Gnathichnus* supports the fact that mobile lanterns with strong teeth able to scratch hard substrates evolved early in the Mesozoic, while Palaeozoic echinoids fed on surface detritus or used their teeth for scooping or biting rather than scraping (Smith 1984).

### Mollusc grazing traces: *Radulichnus inopinatus*

Less frequently than *Gnathichnus*, a different scratched sculpture is commonly found upon inner surfaces of oyster, and

more rarely *A. benedictus*, valves (Fig. 5). This may cover almost completely the surface of the shell or be restricted to clustered areas. Detailed examination of the surfaces led to the recognition of a modular unit (similarly to the stellate unit of *Gnathichnus*) that consistently repeats along the sculptured surface (Fig. 5A). This modular unit consists of a group of 4–6 individual scratches 100–200 µm long. They are rectilinear or slightly curved. They form groupings of subparallel traces with a length (perpendicular to the axis of the scratches) of 200–500 µm. In some cases, the scratches are sharply incised in the undisturbed surface of the shell but often they occur

← Fig. 4. Echinoid grazing traces *Gnathichnus pentax* from Nefiach, Pliocene. **A.** Detail showing the pentaradiate morphology of *Gnathichnus* in the inner side of an *Ostrea* valve (A<sub>1</sub>); outer side of the same valve with abundant *Gnathichnus* (A<sub>2</sub>), JMC-UB/I-0098. **B.** Traces in the inner side of the left valve of a pectinid, JMC-UB/I-0099. **C.** *Gnathichnus* sculpture in strongly ribbed (outer side) of a pectinid valve, JMC-UB/I-0100. **D.** Outer side of the umbonal area (D<sub>1</sub>) and inner side (D<sub>2</sub>) of a pectinid valve with pervasive *Gnathichnus* sculpture, JMC-UB/I-0101. **E.** Detail on the outer side of a pectinid valve, JMC-UB/I-0103. Scale bars 5 mm.



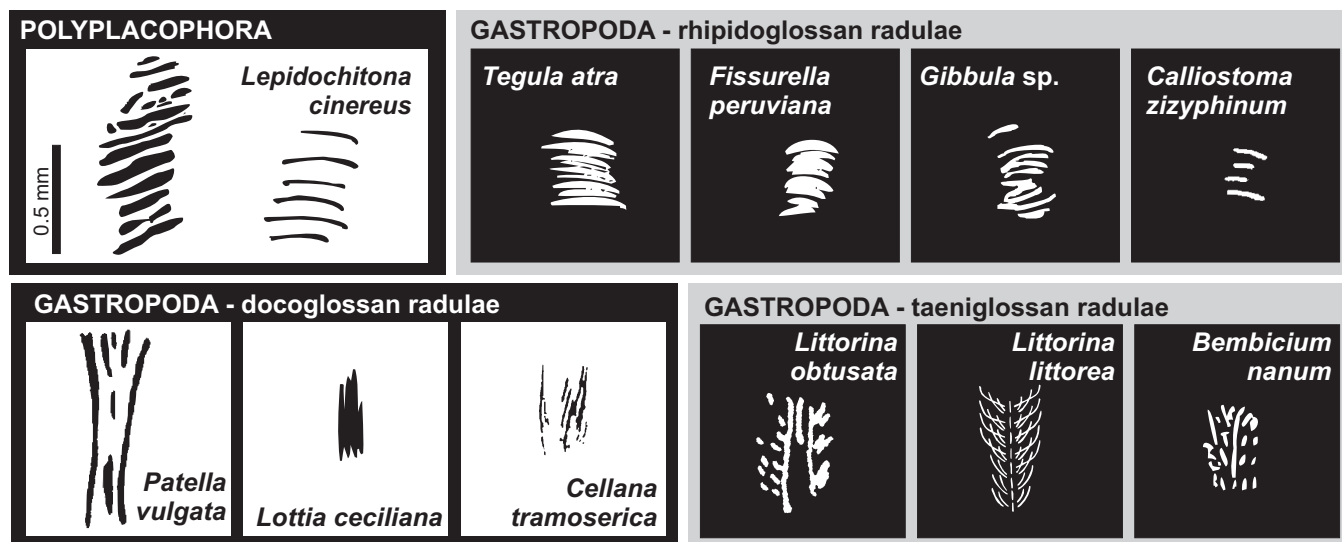


Fig. 6. Different morphologies of the modular unit of grazing traces produced by a species of polyplacophoran and several species of gastropods. Only those produced by polyplacophorans and patellogastropods (white boxes) are likely to be preserved as fossils, because other groups bear unmineralized radulae. Figures redrawn from Jüch and Boekschoten (1980; *L. cinereus* and *L. littorea*), Thompson et al. (1997; *P. vulgata*, *C. zizyphinum*, *Gibbula* sp., and *L. obtusata*), Forrest et al. (2001; *C. tramoserica* and *B. nanum*), and Reyes et al. (2001; *T. atra*, *F. peruviana*, and *L. cecilians*). In all cases, the direction of movement of the tracemaker would be towards the top of the page.

within ovate depressions (Fig. 5B). Both scratches and groupings exhibit a consistent orientation throughout the sculptured surface.

This trace fossil can be assigned to the ichnogenus *Radulichnus*, erected by Voigt (1977) and interpreted as produced by the radular grazing activity of herbivorous gastropods or polyplacophorans. Each one of the modular units records a single “bite” of the tracemaker when scraping the surface with its radula to feed upon epilithic or shallow endolithic algae or other microorganisms, while individual scratches correspond to the action of radular denticles. Ovate depressions represent deeper gnawing than more sharply incised scratches. The grazing activity of herbivorous molluscs and its ichnological product are well known since the pioneering papers by Voigt (1977) and Jüch and Boekschoten (1980). Several authors carried out observations and experiments with modern polyplacophoran and gastropod grazers (Thompson et al. 1997; Forrest et al. 2001; Reyes et al. 2001) that significantly improved our understanding of them. Different patterns in the modular unit of their traces can be correlated with different types of radula and to different groups of organisms (Fig. 6). Thus, gastropods with docoglossate radulae (order Patellogastropoda) leave very distinctive traces in which scratches are parallel to the longer axis of the modular unit. In contrast, species of the family Littorinidae (order Littorinimorpha), that bear taeniglossate radulae, leave traces with a rather complex bilaterally symmetrical set of scratches, some parallel to the axis of the grouping and other shorter and oblique. Radular marks left by gastropods with rhipidoglossate radulae, such as some belonging to the families Trochidae, Fissurellidae, and Calliostomidae (order Vetigastropoda), or Neritidae (order Cycloneritimorpha), are very different and the slightly arcuate denticular scratches are perpendicular to the longer axis of the grouping.

These latter are morphologically similar to those left by chitons (class Polyplacophora). Nevertheless, not all these different patterns are likely to be preserved in the fossil record as only some groups bear a mineralized, hardened radula. Iron and silica minerals are present in the tips of the radular denticles of polyplacophorans and patellogastropods (Guralnick and Smith 1999; Bromley 2004; Hua and Li 2007) and thus, they are the only living taxa able to leave their traces upon hard substrates such as calcareous shells. Considering all this, we can conclude that *Radulichnus* from the Roussillon were the result of the work of polyplacophorans. Polyplacophoran skeletal plates, belonging to the genus *Lepidopleurus*, have been found in other contemporaneous localities of the same basin where aragonite shells are preserved.

Voigt (1977) recognized two different morphologies in the fossil material he studied, and he correctly identified them as produced by polyplacophorans and patellogastropods. Nevertheless, he erected one single ichnospecies, *inopinatus*, for the whole material although leaving the door open to further ichnospecies as further material was studied in detail. The diagnosis of *Radulichnus inopinatus* includes then a variety of patterns of the modular unit, although the holotype clearly corresponds to the docoglossan pattern. Pending revision of type material, the present specimens from the Roussillon are assigned to the only available ichnospecies, *R. inopinatus*. Further research including examination of *Radulichnus* from different localities and ages will probably lead to the revision of the monospecific status of the ichnogenus.

True *Radulichnus* are known since the Jurassic (Voigt 1977; Radley 2006). They have been recorded in the Cretaceous (Voigt 1977; Akpan et al. 1982; Jagt 2003), Neogene (Voigt 1977; Mayoral 1987; Bromley and Asgaard 1993 a, b; Parras and Casadío 2006), and Quaternary (Martinell and

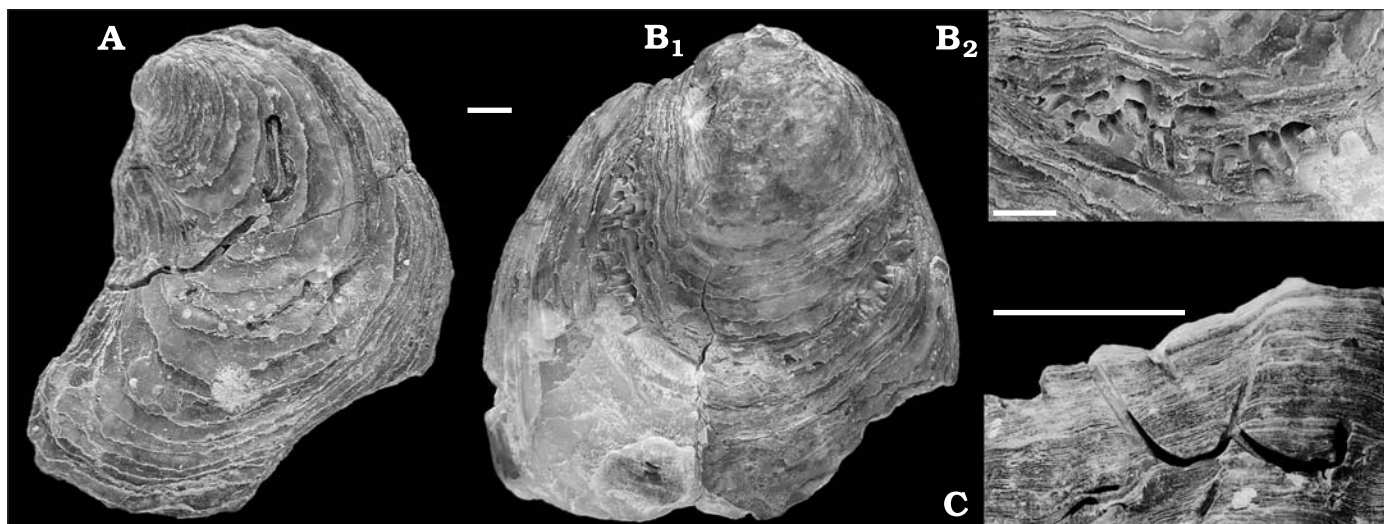


Fig. 7. Polychaete borings from Nefiach, Pliocene. **A.** Single specimen of *Caulostrepsis taeniola* on an oyster valve, JMC-UB/I-0104. **B.** Oyster valve with numerous *Caulostrepsis taeniola* borings arranged following growth lines (**B<sub>1</sub>**) and detail of the borings (**B<sub>2</sub>**), JMC-UB/I-0105. **C.** *Maeandropolydora sulcans* in a pectinid shell, JMC-UB/I-0096. Scale bars 10 mm.

Domènech 1981). They are most commonly found upon invertebrate (mostly molluscan) shells, but Jagt (2003) reported occurrences on vertebrate bones and teeth. Special mention has to be given to *Radulichnus*-like structures occurring in the Vendian and Cambrian (e.g., Seilacher 1997; Dornbos et al. 2004). They have been interpreted as produced by primitive molluscs grazing on microbial mats binding sedimentary substrates. They are much larger than Mesozoic and Cenozoic *Radulichnus* but morphologically comparable. Nevertheless, they are not bioerosion structures and thus their assignment to the same ichnogenus is, at least, arguable.

### Polychaete borings: *Caulostrepsis taeniola* and *Maeandropolydora sulcans*

Other than the grazing sculptures described above, the only bioerosion trace fossils that are common in the shell beds from Nefiach are polychaete dwelling borings (Fig. 7), in particular *Caulostrepsis taeniola*, although a few specimens of *Maeandropolydora sulcans* are also found.

*Caulostrepsis* is a pouch-shaped boring consisting of a U-bend gallery. Bromley and D'Alessandro (1983) revised the systematics of this ichnotaxon and recognized several ichnospecies. The material from Nefiach displays consistently a dumbbell-shaped transversal section all along its length. This allows assignment to the ichnospecies *C. taeniola*. The diameter of the limb is about 2 mm, while the aperture is near 4.5 mm-wide. Maximum observed length reaches 36 mm. All specimens are found in oyster shells except for one occurring in a valve of *A. benedictus*. Borings in oysters are mostly found in right (upper) valves, which are more abundant, and their position is near parallel to shell surface. Only the apertures are visible except when the shell is broken or eroded. In most cases, only one or two borings occur in each shell but in a few cases single valves may bear more than ten *Caulostrepsis*,

and even in one case more than thirty! When this abundance of *Caulostrepsis* is observed, it is interesting to see that the boring apertures tend to occur following the same growth line (Fig. 7B). This might indicate that traces were produced when the oyster was still alive and infested by boring polychaete worms with the apertures near the ventral margin.

*Maeandropolydora* is less common but also found in oyster shells. It consists of a single sinuous gallery lacking pouched-shaped components, which allows the material to be assigned to *M. sulcans* (Bromley and D'Alessandro 1983).

Both ichnogenera are assigned to polychaetes and living equivalents are well known, particularly among the Family Spionidae. *Caulostrepsis* is known from the Devonian, while the oldest *Maeandropolydora* is known from the Jurassic (Taylor and Wilson 2003; Bromley 2004).

### Other bioerosion trace fossils

Other bioerosion trace fossils are less common and found only in a few shells. Sponge borings, belonging to the ichnogenus *Entobia* (see Bromley and D'Alessandro 1984), occur in oyster shells. In most cases, the surface of the shells has not been weathered out or abraded and only the external apertures of the boring systems are seen (Fig. 8A, C). X-radiographies allow to examine in more detailed their tridimensional configuration (Fig. 8B), which is dominated by chambers rather than channels. Nevertheless, their stenomorphic character makes identification to ichnospecies level uncertain. Other domichnia are represented by bryozoan borings similar to those produced by the ctenostomate bryozoan *Terebripora* that have been assigned to the ichnogenus *Pinaeocladichnus* by Mayoral (1988; Fig. 9C).

The activity of predatory animals is recorded by *Oichnus simplex* in oyster shells and repaired durophagous scars in pectinid valves. *Oichnus simplex* are small cylindrical drill



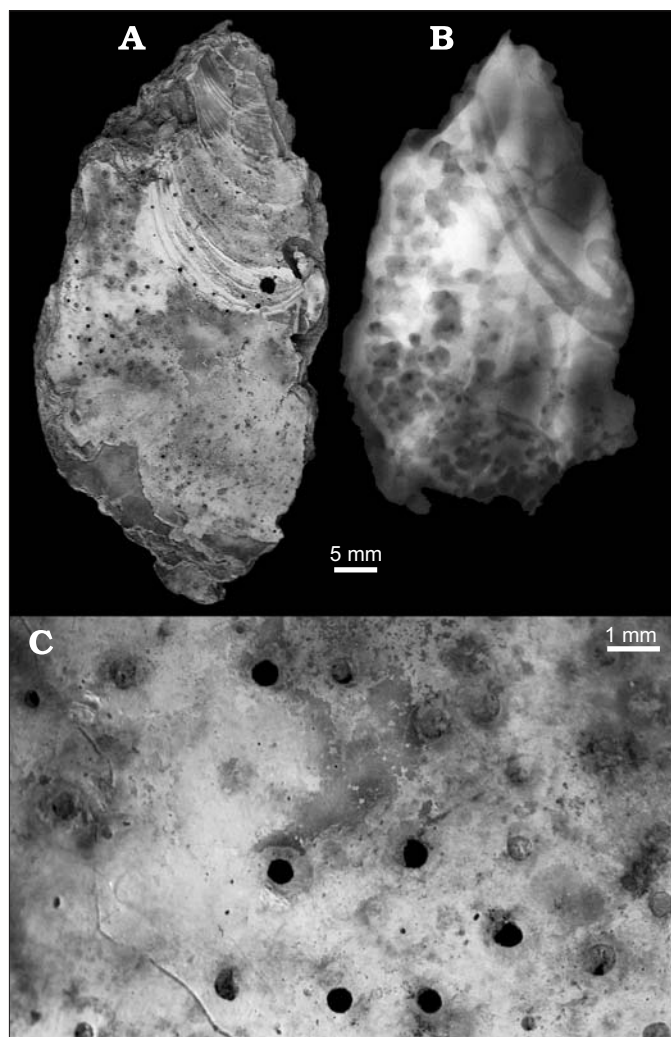


Fig. 8. Sponge borings from Nefiach, Pliocene. **A.** Oyster shell with *Entobia*, JMC-UB/I-0106. **B.** X-radiography of the same specimen displaying the structure of the sponge boring and revealing the presence of a *Caulostrepsis taeniola*. **C.** Detail of *Entobia* apertures in the same specimen.

holes (Fig. 9D) produced by carnivorous gastropods (Bromley 1981). The ichnospecies can be reasonably assigned to the activity of muricaceans (Bromley 2004). The durophagous scars are recognized as irregular fractures that interrupt the normal growing of the attacked bivalve (Fig. 9E). Probable attackers might have been fish or decapod crustaceans (Martinell et al. 1982).

Finally, despite the abundance of encrusting sclerozoans, attachment bioerosion structures (fixichnia *sensu* Gibert et al. 2004) are restricted to minute depressions left by cibicidid foraminifera (Fig. 9A, B). They are formed by a series of increasingly wider, arched furrows arranged perpendicularly to the axis of the trace. This configuration results in a water-drop-like morphology. Length of the etching varies between 1 and 1.5 mm, while maximum width may reach 0.5 to 1 mm. Narrowing of the trace is in the direction of the concavity of the furrows. Beside these structures, it is sometimes possible to recognize the test of the encrusting foraminifera still *in situ*. They have the same morphology and size that the

pit, which allows for a straightforward assignment of a trace maker for the traces. These foraminifera have been determined as *Dyocibicides biserialis*. Morphology of the attachment scars is very different from that of some ichnogenera described for foraminiferal fixichnia (Santos and Mayoral 2006). On the contrary, it is very similar to the ichnospecies *Centrichnus eccentricus*, erected by Bromley and Martinell (1991) to designate fossil bioerosion structures left by the anchoring of the calcified byssus of anomiid bivalves. The most obvious difference is size, as bivalve traces are one order of magnitude larger, with lengths that may reach 10 mm, but a more detailed examination reveals some other dissimilarities, such as the relative proportions of groove and inter-groove areas (grooves are much wider than the distance between them in foraminiferal pits, while the opposite happens in *C. eccentricus*), or a more rapid increase in width of the foraminiferal traces. Although these features could be reason enough to support the erection of a new ichnospecies, we prefer not to do it because of the scarcity of material what does not allow to recognize its variability. Thus, this traces are here referred to as *Centrichnus cf. eccentricus*.

## Discussion

### Genetic history of the shell beds at Nefiach

The taphonomic (biostratinomic) attributes that characterize the shell beds from Nefiach clearly indicate that they have to be considered as sedimentological concentrations (*sensu* Kidwell et al. 1986). Shell attitude, stacking, fragmentation and, particularly, sorting of valves indicate that this is not an autochthonous assemblage but rather an accumulation resulting from hydraulic factors, as was already stated by Martinell and Domènech (1990) in a previous study. Nevertheless, shells are well preserved (common complete valves, signs of mechanical abrasion rare or absent), size sorting is poor, and there is no preferential orientation, nor imbrication of shells, to indicate the presence of directional currents. Thus, the deposit is not the result of accumulation in a persistently energetic setting, but rather the product of a single hydraulic event, most likely a storm.

*Saccostrea cucullata* is an oyster that mostly lives today attached to rockgrounds or mangrooves in intertidal areas, although bioherms constructed by this species are known from the Pliocene (Aguirre 1998). In contrast, the two pectinid species must have lived bisally attached in loose sedimentary substrates, probably along a wider range of bathymetry. Hence, we can assume that the storm transported oysters to the shallow subtidal area from an adjacent rocky shore. Upper (free) valves would have been preferentially transported as lower valves would have remained attached to the substrate. No *in situ* palaeontological evidences have been found of the rockground community but geological mapping demonstrates that the Nefiach locality was located in the innermost part of the Roussillon basin very near to a shore constituted by the Palaeozoic rocks of the Agly (Fig. 1; Clauzon et

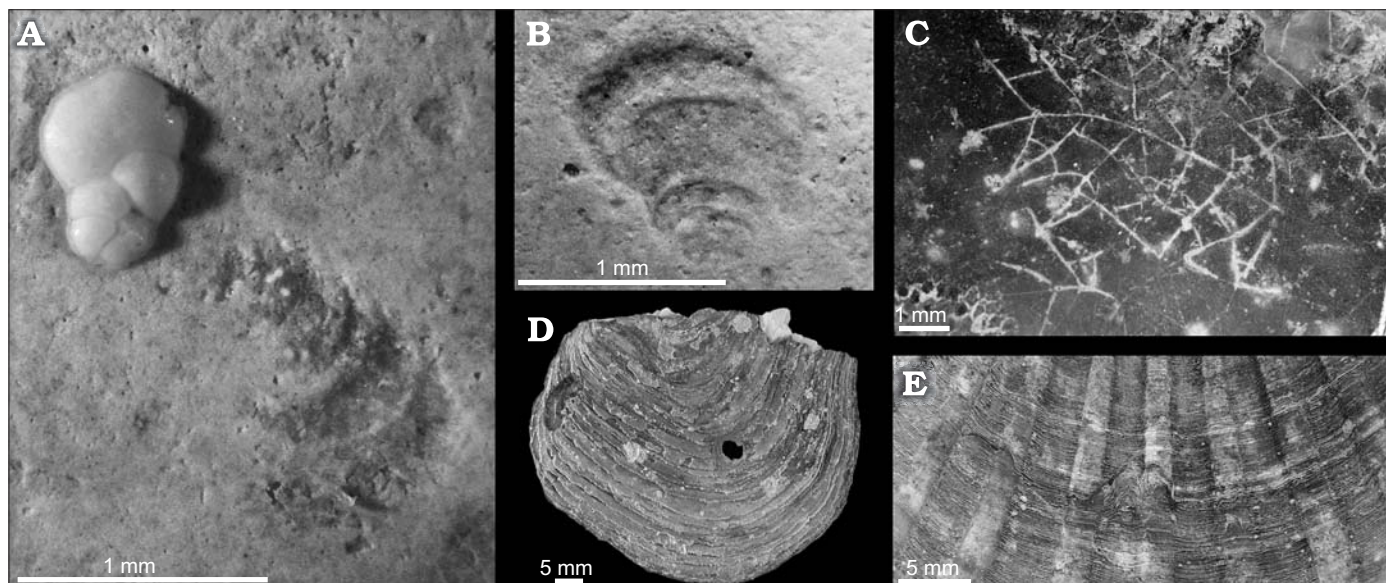


Fig. 9. Other trace fossils from Nefiach, Pliocene. **A.** *Centrichnus* cf. *eccentricus* beside an specimen of the foraminiferan tracemaker, *Dyocibicides biserialis*, still attached, JMC-UB/I-0103. **B.** Another specimen of *C.* cf. *eccentricus*, JMC-UB/I-0103. **C.** *Pinaceocladichnus*, a bryozoan boring, in a pectinid valve, JMC-UB/I-0107. **D.** *Oichnus simplex* on an oyster shell, JMC-UB/I-0108. **E.** Repaired scars produced by durophagous attacks in a pectinid valve, JMC-UB/I-0102.

al. 1987). In contrast, the source for pectinid valves had to be different, maybe more local. In this case, valve selection is not so easily explained, but it may have been a consequence of their different hydraulic behaviour.

Thus, the shell beds from Nefiach can be classified as event concentrations (*sensu* Kidwell 1991) and they are interpreted as the product of storms depositing clearly allochthonous (oyster) and parautochthonous/allochthonous shells (pectinidae) in a shallow subtidal setting. These depositional episodes would have led to the formation of a shellground on the sea floor, offering an opportunity for skeletozoans (encrusters and borers) to colonize it. The fact that most borings and encrusting shells are found in both sides of valves clearly indicates that they were produced after the death of the animals. The only clear exception to this are predation structures, particularly the repaired durophagous scars, and some *Caulostrepsis* borings. On the other hand, sponge and polychaete borings, which are found only in oyster shells, were probably produced before final deposition, presumably in the original rocky shore where the hosts had lived. Nevertheless, dominant traces (*Gnathichnus* and *Radulichnus*) record the activity of vagile grazers (echinoids and chitons, respectively) and their presence points to a relatively short colonization window (*sensu* Pollard et al. 1993). These conditions, together with the discrete character of the hard substrates (shells) and their mobility, prevented colonization by longer-term borers. The mobility of the substrates is demonstrated by the fact that they are encrusted and bored in both sides. Overturning might have been result of hydraulic reworking of the shells or, more likely, of the burrowing activity of macrofauna. Regular echinoids, for example, are known to manipulate and relocate all sort of clasts in modern settings (Martinell 1981), but also crustacean or fish might have been responsible.

Nevertheless, it cannot be ruled out that grazing and encrustation occurred before the final storm event. But even in this case, the previous episode would have had to be similar to the one described above. It is unlikely that the same type of skeletozoans colonized the shells of oysters and scallops in their respective original living habitats before their mixing by a storm. Thus, the most simple interpretation is that grazers and encrusters colonized the substrate during a relatively short colonization window after the formation of the shellground and its burial by finer-grained sediment.

### The *Gnathichnus* ichnofacies

The main features characterizing the Nefiach assemblage are: (1) dominance of epigenic traces (*Gnathichnus*, *Radulichnus*) recording the grazing activity of vagile herbivores/omnivores (pascichnia); (2) presence of several other ethological classes (domichnia, fixichnia, praedichnia) including only epigenic and shallow-tier structures; and (3) most traces are produced by “instantaneous” behaviours despite the presence of some more permanent structures. These features respond to the particular characteristics of the substrate already mentioned above: (1) short colonization window, (2) spatially restricted substrates, and (3) instability (mobility) of the substrates. Thus, the *Gnathichnus*-dominated assemblage described in Nefiach is very different from most bioerosion assemblages previously described in the Pliocene of the northwestern Mediterranean area (Fig. 10). Among them, those recording colonization of littoral rocky shores typically consist exclusively of deeper-tier domichnia, mainly *Gastrochaenolites* and *Entobia* (Gibert et al. 1998), which is consistent with long-term exposure of a stable substrate in a high-energy setting. Epigenic and shallow-tier structures, even if



| locality, basin           | substrate   | <div> <div>bivalves</div> <div>sponges</div> <div>worms s.l.</div> <div>echinoids</div> <div>bryozoans</div> <div>brachiopods</div> <div>bryozoans</div> <div>foraminiferans</div> <div>molluscs</div> <div>echinoids</div> <div>gastropods</div> <div>crustac. / fish</div> </div> |    |            |    |        |           |    |    |            |    |             |    |  |
|---------------------------|-------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|------------|----|--------|-----------|----|----|------------|----|-------------|----|--|
| Sant Onofre, BE           | rockground  |                                                                                                                                                                                                                                                                                     |    |            |    |        |           |    |    |            |    |             |    |  |
| Viladamat, AE             | rockground  |                                                                                                                                                                                                                                                                                     |    |            |    |        |           |    |    |            |    |             |    |  |
| St. Miquel / St. Mori, AE | rockground  |                                                                                                                                                                                                                                                                                     |    |            |    |        |           |    |    |            |    |             |    |  |
| St. Genís de Comolas, RH  | rockground  |                                                                                                                                                                                                                                                                                     |    |            |    |        |           |    |    |            |    |             |    |  |
| Vence, VA                 | rockground  |                                                                                                                                                                                                                                                                                     |    |            |    |        |           |    |    |            |    |             |    |  |
| Sant Onofre, BE           | gravel      |                                                                                                                                                                                                                                                                                     |    |            |    |        |           |    |    |            |    |             |    |  |
| Els Olivets, AE           | hardground  |                                                                                                                                                                                                                                                                                     |    |            |    |        |           |    |    |            |    |             |    |  |
| Vilacolum, AE             | shellground |                                                                                                                                                                                                                                                                                     |    |            |    |        |           |    |    |            |    |             |    |  |
| Nefiach, RO               | shellground |                                                                                                                                                                                                                                                                                     |    |            |    |        |           |    |    |            |    |             |    |  |
| ichnotaxa ▶               |             | Ga                                                                                                                                                                                                                                                                                  | En | Ca, Ma, Tr | Ci | Pi, Ir | Po        | Le | Ce | Ra         | Gn | Oi          | Ds |  |
| ethological class ▶       |             | DOMICHNIA                                                                                                                                                                                                                                                                           |    |            |    |        | FIXICHNIA |    |    | PASCICHNIA |    | PRAEDICHNIA |    |  |

Fig. 10. Bioerosion ichnoassemblages from the Pliocene basins of the northwestern Mediterranean: Baix Ebre (BE), and Alt Empordà (AE) in Spain, and Roussillon (RO), Rhône (RH), and Var (VA) in France. Black indicates dominant ichnotaxa, while gray corresponds to other present traces. Ichnotaxa abbreviations: Ca, *Caulostrepsis*; Ce, *Centrichnus*; Ci, *Circolites*; Ds, durophagous scars; En, *Entobia*; Ga, *Gastrochaenolites*; Gn, *Gnathichnus*; Ir, *Iranema*; Le, *Leptichnus*; Ma, *Maeandropolydora*; Oi, *Oichnus*; Pi, *Pinaceocladichnus*; Po, *Podichnus*; Ra, *Radulichnus*; Tr, *Trypanites*. Data from Martinell and Domènech (1986) and Gibert et al. (1998).

produced, would have had a very low preservation potential in such a setting due to overprinting and mechanical abrasion. The same *Gastrochaenolites*–*Entobia* assemblage is also found in deposits interpreted as gravel beaches, where, despite the discrete and unstable characteristics of the hard substrates, their long time of residence allowed for colonization by deeper-tier borers. Only one locality, Vilacolum in the Alt Empordà basin (NE Spain), displays an assemblage closer to that described from Nefiach. It records a variety of ethological classes, with dominance of epigenic and shallow-tier structures and with important presence of grazing structures (*Gnathichnus*). Interestingly, bioerosion at Vilacolum took place on a shellground as in Nefiach. Hence, two different ichnoassemblages are recognized in the northwestern Mediterranean Pliocene that can be correlated with the stability of the substrate, the level of hydrodynamic energy, and the duration of the colonization window.

Two bioerosion assemblages very comparable with those mentioned above, were described by Bromley and Asgaard (1993a, b) in the Upper Pliocene of Rhodes. On the basis of their detailed study, these authors described an *Entobia* ichnofacies, representing the work of a rocky shore community, and a *Gnathichnus* ichnofacies, recording the activity of organisms in less permanent substrates such as shells and pebbles. They proposed those ichnofacies to be subdivisions or maybe even substitutes of the existing *Trypanites* ichnofacies, described as an archetypal ichnofacies by Frey and Seilacher (1981) to encompass all bioerosion assemblages in hard substrates. The proposal of Bromley and Asgaard (1993a) contributed in providing a palaeoenvironmental significance to bioerosion ichnofacies that was lacking in the *Trypanites* ichnofacies. Gibert et al. (1998) demonstrated the recurrency of the *Entobia* ichnofacies since the Jurassic and its correlation with long-exposed

substrates, particularly in rocky shore settings. On the contrary, the validity of the *Gnathichnus* ichnofacies as an archetypal or Seilacherian ichnofacies still has to be tested.

Since it was introduced by Seilacher (1964), the ichnofacies concept has become a central paradigm for ichnologists. Over the years the model has evolved and numerous researchers have reviewed it, offering their own perspective (e.g., Frey and Pemberton 1985; Bromley and Asgaard 1991; Gibert and Martinell 1998b; Pemberton et al. 2001; MacEachern et al. 2007). There are some conditions that have to be met for the validation of an archetypal ichnofacies. These are discussed in the following paragraphs in relation to the *Gnathichnus* ichnofacies:

**An ichnofacies is subject to Walther's Law.**—Actual ichnofacies have to be comparable to sedimentary facies in having lateral continuity and displaying vertical succession (Bromley and Asgaard 1991; Pemberton et al. 2001). Based on this, MacEachern et al. (2007) considered invalid the *Gnathichnus* ichnofacies as it encompasses ichnocenoses on isolated clasts or skeletons, which are “structures that do not form continuous mappable surfaces and do not correspond to the classical meaning of the word facies”. We agree that a trace fossil assemblage on a single isolated substrate cannot be considered an ichnofacies, but field examples of the *Gnathichnus* ichnofacies (see below, section b) occur in shell beds (and a few in hardgrounds), deposits that do concur with that traditional view of the facies concept. Despite the discrete nature of the components, a shellground constitutes a continuous substrate available for skeletobiont colonization.

**An archetypal ichnofacies has to be recurrent in time and space.**—An archetypal ichnofacies can be considered as an epitome for a suite of local (existing) ichnofacies. Thus,

| authors                     | age         | <div> bivalves<br/>sponges<br/>worms s.l.<br/>cirripedians<br/>bryozoans<br/>brachiopods<br/>bryozoans<br/>cirripedians<br/>molluscs<br/>foraminiferans<br/>molluscs<br/>echinoids<br/>gastropods<br/>crustac. / fish </div> |    |            |    |            |           |    |    |        |    |            |    |             |    |             |    |
|-----------------------------|-------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|------------|----|------------|-----------|----|----|--------|----|------------|----|-------------|----|-------------|----|
|                             |             |                                                                                                                                                                                                                              |    |            |    |            |           |    |    |        |    |            |    |             |    |             |    |
| Martinell and Domènech 1981 | Pleistocene |                                                                                                                                                                                                                              |    |            |    |            |           |    |    |        |    |            |    |             |    |             | sg |
| Martinell and Domènech 1986 | Pliocene    |                                                                                                                                                                                                                              |    |            |    |            |           |    |    |        |    |            |    |             |    |             | sg |
| This paper                  | Pliocene    |                                                                                                                                                                                                                              |    |            |    |            |           |    |    |        |    |            |    |             |    |             | sg |
| Bromley and Asgaard 1993a   | Pliocene    |                                                                                                                                                                                                                              |    |            |    |            |           |    |    |        |    |            |    |             |    |             | sg |
| Mayoral and Muñiz 1996      | Miocene     |                                                                                                                                                                                                                              |    |            |    |            |           |    |    |        |    |            |    |             |    |             | hg |
| Wilson 2003                 | Cretaceous  |                                                                                                                                                                                                                              |    |            |    |            |           |    |    |        |    |            |    |             |    |             | sg |
| Jarvis et al. 1982          | Cretaceous  |                                                                                                                                                                                                                              |    |            |    |            |           |    |    |        |    |            |    |             |    |             | hg |
| Radley 2006                 | Jurassic    |                                                                                                                                                                                                                              |    |            |    |            |           |    |    |        |    |            |    |             |    |             | sg |
| ichnotaxa ▶                 |             | Ga                                                                                                                                                                                                                           | En | Ca, Ma, Tr | Ro | Fe, Ir, Pi | Po        | Le | Ce | Ce, Re | Ce | Ra         | Gn | Oi          | Ds | ▲ substrate |    |
| ethological class ▶         |             | DOMICHNIA                                                                                                                                                                                                                    |    |            |    |            | FIXICHNIA |    |    |        |    | PASCICHNIA |    | PRAEDICHNIA |    |             |    |

Fig. 11. Bioerosion ichnoassemblages from several localities and ages that can be assigned to the *Gnathichnus* ichnofacies. Grey boxes indicate presence. Ichnotaxa abbreviations: Ca, *Caulostrepsis*; Ce, *Centrichnus*; Ci, *Circolites*; Ds, durophagous scars; En, *Entobia*; Fe, *Feldmannia*; Ga, *Gastrochaenolites*; Gn, *Gnathichnus*; Ir, *Iranema*; Le, *Leptichnus*; Ma, *Maeandropolydora*; Oi, *Oichnus*; Pi, *Pinaceocladichnus*; Po, *Podichnus*; Ra, *Radulichnus*; Re, *Renichnus*; Ro, *Rogerella*; Tr, *Trypanites*. Substrate abbreviations: sg., shellground; hg., hardground.

demonstration of recurrence is essential to erect or validate an archetypal ichnofacies. Bromley and Asgaard (1993a) mentioned only one other example of *Gnathichnus* ichnofacies from an Upper Cretaceous hardground in France (Jarvis et al. 1982). To the knowledge of the authors, only two other studies have described bioerosion assemblages as examples of the *Gnathichnus* ichnofacies: Mayoral and Muñiz (1996), in an Upper Miocene hardground in southern Spain, and Radley (2006), in Lower and Middle Jurassic shellgrounds from England. Revision of literature allowed us to identify some other examples from the Cretaceous of Israel (Wilson 2003), the Pliocene of northeastern Spain (Martinell and Domènech 1986), and the Pleistocene of northeastern Spain (Martinell and Domènech 1981), all of them in shellgrounds. Thus, we have been able to recognize eight occurrences between the Jurassic and the Recent (Fig. 11). This demonstrates that the ichnofacies has some recurrence and probably more examples will be recorded when revisiting shell beds under an ichnological perspective.

**An archetypal ichnofacies must have palaeoenvironmental implications.**—The *Gnathichnus* ichnofacies occurs most frequently in shell beds, but also in hardgrounds, in shallow sublittoral settings. Most importantly, it records short periods of exposure of hard substrates before their burial. Thus, this setting is in contrast with that recorded by the *Entobia* ichnofacies that corresponds to long colonization windows in stable substrates with low sedimentation rate, particularly in rocky shore settings. Interestingly, not all shell concentrations are characterized by the *Gnathichnus* ichnofacies, and some authors have described boring assemblages in shell beds that can be assigned to the *Entobia* ichnofacies (Farinati and Zavala 2002; Parras and Casadío 2006). Thus, the presence of one ichnofacies or the other might be indicative of depositional

conditions and can be used to refine interpretations on shell concentrations.

A possible difficulty for the acceptance of the *Gnathichnus* recurrent assemblage as an archetypal ichnofacies is that local (actual) examples of the ichnofacies do not necessarily correspond to a single ichnocenosis. In the case described herein, some of the trace fossils are likely produced, at least part of them, in a different location before the formation of the shellground (*Caulostrepsis*, *Maeandropolydora*, *Entobia*). Frey and Pemberton (1985) stated that an ichnofacies was the preserved record of an ichnocenosis, but at least one of the traditional Seilacherian ichnofacies does not concur with this requirement. The *Nereites* ichnofacies typifies palimpsest assemblages consisting of a pre-depositional and a post-depositional suites. Bromley and Asgaard (1991) pointed out this “anomaly” and indicated the dual character of ichnofacies as biofacies and taphofacies. In any case, the diagnostic elements of the *Gnathichnus* ichnofacies (the grazing structures) were produced in an already deposited shellground, and are also present (although more rarely) in hardgrounds where the allochthonous or mixed nature of the substrate is out of the question.

## Towards a (macro)bioerosion ichnofacies model—conclusions

The trace fossil assemblage described herein from the Pliocene of the Roussillon constitutes an exceptional example of the *Gnathichnus* ichnofacies erected by Bromley and Asgaard (1993a) and offers an excellent opportunity to revisit archetypal ichnofacies in hard substrates.

The study of the ichnology of the shell beds at Nefiach



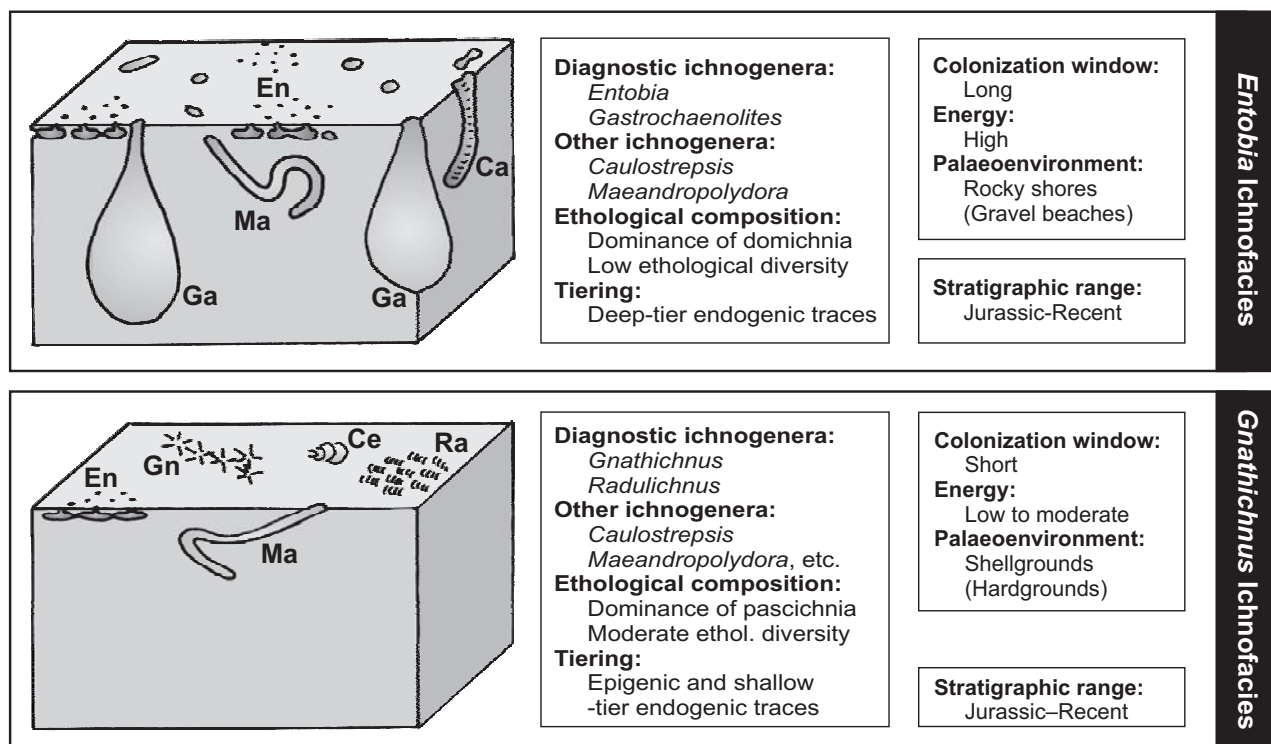


Fig. 12. Summary of attributes and significance of the *Entobia* and *Gnathichnus* ichnofacies. Abbreviations: Ca, *Caulostrepsis*; Ce, *Centrichnus*; En, *Entobia*; Ga, *Gastrochaenolites*; Gn, *Gnathichnus*; Ma, *Maeandropolydora*; Ra, *Radulichnus*.

complements previous works addressing bioerosion ichnology in the Pliocene of the northwestern Mediterranean area (Martinell and Domènech 1986; Gibert et al. 1998). The resulting picture allows the distinction of two recurrent assemblages: one dominated by domichnia recording long-term bioerosion in stable substrates (mostly rocky shores), and a second one characterized by the presence of pascichnia as a result of short-term bioerosion in shellgrounds. These assemblages coincide with those described by Bromley and Asgaard (1993a) as *Entobia* and *Gnathichnus* ichnofacies, respectively, in the Pliocene of Rhodes. The validity of the first was already demonstrated in a previous paper (Gibert et al. 1998), while the *Gnathichnus* ichnofacies is here shown to fulfill the requirements of an archetypal ichnofacies. The *Gnathichnus* ichnofacies is distinctive in taxonomic and ethologic composition, recurrent in time and space and has a palaeoenvironmental significance (Fig. 12). It is characterized by the dominant presence of grazing structures (Pascichnia) and the absence (or scarcity) of deep-tier borings. It typically occurs under conditions of short-term submarine exposure of shellgrounds (and, more rarely, hardgrounds) in moderate energy settings. These features contrast with those of the *Entobia* ichnofacies (Fig. 12), which is dominated by dwelling borings (Domichnia) commonly reaching deeper within the substrate, and characterizes long-term bioerosion in high energy settings. This duet of ichnofacies constitutes a powerful instrument for a better understanding of the palaeoecology of hard bottom communities and their palaeoenvironmental significance. Previously to the definition of these two ichnofacies,

the only one available for hard (mineral) substrates was *Trypanites*, which, in consequence, contained non palaeoenvironmental information other than the nature of the substrate.

Interestingly, oldest occurrences of both ichnofacies are known from the Jurassic. Other authors have previously pointed out that bioerosion assemblages in the Jurassic take on a “modern” aspect and are, thus, very different from Palaeozoic counterparts (e.g., Taylor and Wilson 2003). Palaeozoic bioerosion assemblages are usually poorly diverse and they are typified by the *Trypanites* ichnofacies. MacEachern et al. (2007) suggested an identity between the *Entobia* and the *Trypanites* ichnofacies because they both typified long-term bioerosion assemblages. Nevertheless, ignoring the obvious differences between both recurrent assemblages because of that reason, would result in an impoverishment of the (macro)bioerosion ichnofacies model. Both recurrent assemblages are different from a palaeoecological and evolutionary point of view. The time (evolutionary) component of the ichnofacies model is usually disregarded by ichnologists but it has to be an integral part of it if our goal is to construct a useful paradigm to understand time and space distribution of benthic communities.

Thus, in our present state of knowledge, the (macro)bioerosion ichnofacies model is composed of four archetypal ichnofacies. One (*Teredolites*) typifies woodgrounds, and three occur in mineral (lithic and skeletal) hardgrounds: *Trypanites*, which is valid for relatively low diverse Palaeozoic bioerosion assemblages, and *Entobia* and *Gnathichnus*, that extend from the Jurassic to the Recent.

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