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Echinoid grazing traces on ostreid shell-ground from the Pliocene Ficulle quarry (central Italy)

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ABSTRACT - Echinoid grazing traces present on ostreid valves constituting a shell-ground were studied. The shell-ground is preserved in sandy levels in the Pliocene clayey deposit cropping out near the Ficulle Village (central Italy). A dense frame made almost exclusively by rasping traces of regular echinoids referable to the ichnospecies *Gnathichnus pentax* Bromley was recognized. Ostreid shells dispersed in the surrounding clayey sediment show deep-tier endogenic traces, as *Entobia*, *Gastrochaenolites*, *Caulostrepsis* and *Meandropolydora*. Only on rare specimens rasping traces coexist with the latter ones. The different bioerosion trace-assemblages can be assigned to the two *Gnathichnus* and *Entobia* bioerosion ichnofacies as defined by Bromley and Asgaard (1993).

Key words: Bioerosion, ichnofacies, *Gnathichnus*, Pliocene, central Italy

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INTRODUCTION

Grazing or scraping is the usual food-gathering technique for regular echinoids, whose diet is omnivorous, consisting of attached and boring algae and plants, encrusting and boring small animals and organic detritus. Traces carved on the substrate by the grazing activity of the five teeth of the "Aristotle's lantern" are well recognizable by their pentastellate morphology and are grouped by Bromley (1975) in the ichnotaxon *Gnathichnus pentax*. The Bromley's ichnospecies contains all the pentastellate traces until now known, being the ichnospecies *G. quinqueradialis*, erected by Michalík (1977), and *G. stellarum,* erected by Breton et al. (1992), considered junior synonyms (Michalík, 1980; Gibert et al., 2007). Nevertheless, Wisshak et al. (2011) report different *Gnathichnus* traces on modern hard substrates, 60 m depth, from Azores. Echinoid grazing traces are known on marine shallow water hard substrates of Triassic-Recent ages (Gibert et al., 2007); sometimes preserved grazing traces are very frequent (Radley, 2006) and extensively cover hard substrates at the end of the Mesozoic times, supporting the idea that the grazing pressure has been a contributor in the decline of articulate Brachiopods (Radley, 2010). Today, the limiting role on coral reef growth by grazing pressure is well known (Mokady et al., 1996; Ruengsawang and Yeemin, 2000). *Gnathichnus* has been recognized on Eocene mollusk shells from Aragona (Carrasco, 2004); in Northwestern Mediterranean Plio-Pleistocene coastal deposits grazing traces are widespread (Martinell, 1982; Martinell and Domènech, 1986; Gibert and Martinell, 1998; Gibert et al., 2007). In Italy, *G. pentax* has been recognized on Pleistocene mollusk shells (Barrier and D'Alessandro, 1985) and on Jurassic ammonite shells (Nicosia, 1986).

Bromley and Asgaard (1993) introduced the *Gnathichnus* bioerosion ichnofacies, that, according to Gibert et al. (2007), is characterized by "the dominance of grazing structures (Pashichnia) and the absence (or scarcity) of deep-tier borings". The *Gnathichnus* bioerosion ichnofacies develops on exposures of shell-grounds and hard-grounds in shallow marine, low energy, water environments, through a short-term skeletobiont colonization window. According to Gibert et al. (2007), the *Gnathichnus* ichnofacies has been recognized in various outcrops, from Jurassic to Recent.

The aim of this paper is to describe the well preserved Echinoid grazing traces on ostreid shells of the Pliocene marine shallow water sediments cropping out in a clay quarry near the Ficulle village (Orvieto, central Italy; Fig. 1) and to analyze their depositional facies in the frame of the *Gnathichnus* ichnofacies concept.

GEOLOGICAL AND PALEOENVIRONMENTAL SETTING

The siliciclastic succession cropping out in the study area consists of marine, transitional and continental deposits filling the Plio-Pleistocene post-orogenic extensional Paglia-Tevere graben formed in the Lower Pliocene (Ambrosetti et al., 1987; Cavinato and De Celles, 1999). The clays cropping out in the Ficulle

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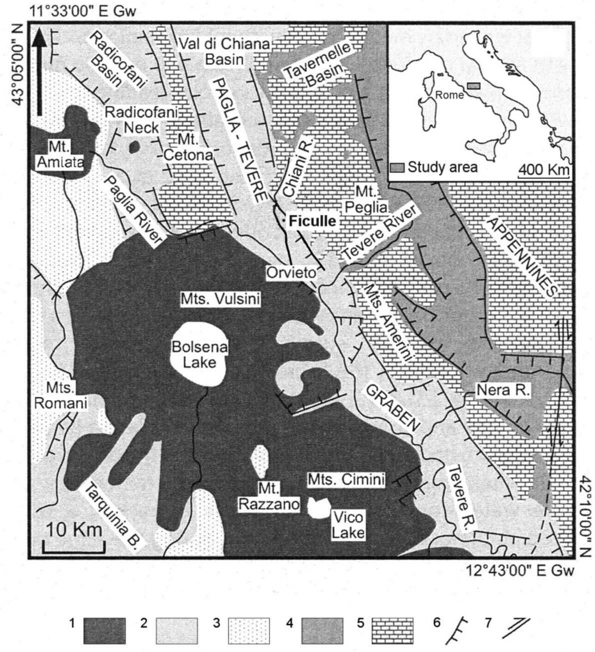

Fig. 1 - Geological sketch of central Italy: 1) Quaternary silica undersatured to intermediate volcanic rocks; 2) "Neoautochthonous" sedimentary successions, of the marine, transitional and non-marine environments (Early Pliocene-Quaternary); 3) Siliciclastic and carbonate successions of the Tuscan and Ligurid domains (Trias-Miocene); 4) Sedimentary successions of the intermontane basins (Middle Pliocene-Quaternary); 5) Carbonate and siliciclastic successions of the Umbro-Marchean domain (Trias-Miocene); 6) Normal fault; 7) Transcurrent fault (modified after Mancini et al., 2004 and Galiano and Ciccacci, 2011).

quarry belong to Pliocene sedimentary succession recognized in the Tyrrhenian margin of central Apennines and called "Tenaglie-Fosso San Martino Unit" by Mancini et al., (2003-2004). Two sedimentary cycles are recognized.

The first cycle, ranging from Early Pliocene to Early Pleistocene (Gelasian), overlies fluvio-deltaic conglomerates ("Basal conglomerates", late Messinian-Early Pliocene in age) and is made up of three units: "Argille di Fabro", "Sabbie a *Flabellipecten*" and "Conglomerato di Città della Pieve" (Ambrosetti et al., 1977; Carboni et al., 1992; Ambrosetti et al., 1987). The first unit, constituted of bioclastic clays, contains a diversified neritic molluscan assemblage (350 taxa, in Malatesta, 1974) and a microfaunistic content characterized by the presence of *Globorotalia puncticulata* and *G. aemiliana* (Ambrosetti et al., 1987). The second unit, whose siliciclastic content gradually increases, is characterized by horizons rich in pectinids and ostreids (mainly towards the top). The sedimentological and paleontological data suggest a shallow water environment. The third unit is made up of a coastal marine conglomerate, whose large-sized carbonate pebbles show polychaete dwellings, clionid borings, ostreid and balanid encrustations.

The second sedimentary cycle consists of marine deposits evolving in continental facies and it depletes in Early Pleistocene (Santernian). The two cycles are separated by the Acquatraversa erosional phase which spans 0.2-0.3 Ma (Bossio et al., 1998; Girotti and Mancini, 2003).

In the Ficulle quarry, the regional Plio/Pleistocene regressive sequence is represented by proximal deposits, more or less influenced by fluvial input. These sediments can be referred to a highstand progradational phase (early Gelasian?) characterizing the Apennine coastal area during the early Gelasian) (Mancini et al., 2003-2004). From the bottom to the top of the quarry wall, about 50-60 m thick (Fig. 2), a gradual transition develops from the basal sandy clays rich in mollusks, mostly in ostreids, to sands with ostreids and pectinids through a level of sandy clays rich in cerithids, which lies on a thin level with phanerogam remains; the top of the sands contains conglomeratic lenses with strongly bored pebbles. The foraminiferal assemblage becomes poor and scarcely diversified towards the top of the succession; only *Ammonia beccarii*, that is the dominant species, rare specimens of *Elphidium* spp. and *Nonion fabum* are found. Laterally, the basal sandy clays show a rapid transition to clayey sands and sands, which contain ostreids and scattered bored carbonate pebbles. The basal level of the cerithid interval is characterized by the richness of regular echinoid spines within the phanerogam remains; the proximal corresponding sandy level, characterized by thalassinoidal traces, contains a rich ostreid assemblage, with shells densely covered by echinoid bites.

The Pliocene deposits cropping out in the quarry constitute a progradational deltaic succession deposited in shallow water environment. According to Mancini et al. (2003-2004), all marine deposits of the Tenaglie-Fosso San Martino Unit are characterized by foraminiferal assemblages dominated by infralittoral species. The sands with ostreids show a foraminiferal assemblage poorly diversified and mainly composed by epifaunal sandy bottom dwellers (Murray, 1991; Bergamin et al., 2009) like *Ammonia inflata, A. beccarii*, *Lobatula lobatula*, *Asterigerinata planorbis, Rosalina globularis* and *Elphidium* spp. (Carboni et al., 1992).

The level with preserved roots of phanerogams, that is about 50 cm thick, probably represents a vegetated meadow developed at the passage from marine shallow water to brackish lagoonal environment. The sands with ostreids (*Ostrea lamellosa*, in Malatesta, 1974) and pebbles can be related to the proximal side of the *Posidonia*-like phanerogam meadow area. These deposits are rich in disarticulated valves and fragments. Locally, ostreid valves are arranged one near to the other, forming spatially limited horizons parallel to the substrate. The ostreids are accompanied only by scarce fragments of other mollusks; the prevalence of disarticulated valves, that lie parallel to the bedding planes, indicates transport and redeposition. These ostreid patches have to be interpreted as temporary shell-grounds. Articulated ostreid shells are common in the open marine clayey

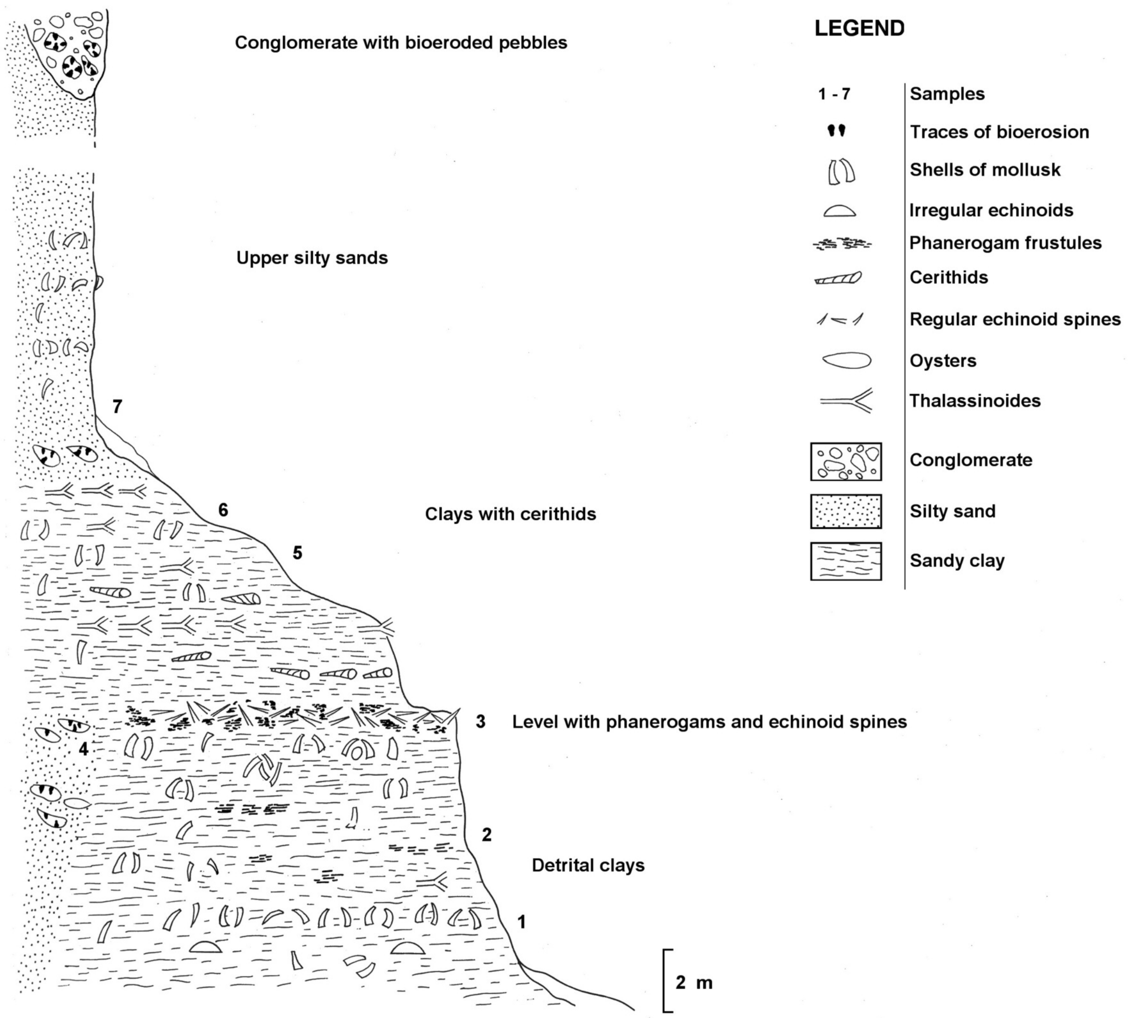

Fig. 2 - Schematic section of the outcrop at the quarry of Ficulle (modified after Carboni et al., 1992).

deposits underlying the phanerogam meadow horizon, and they are present less frequently in the overlying lagoon clayey sands. In these shells, entobian borings and encrustations are frequent, whereas grazing traces are rare. Mollusks are abundant and diversified (Malatesta, 1974); foraminiferal assemblage consists of infralittoral, mainly epiphytic, species (Fig. 3) as *Elphidium crispum, Ammonia beccarii*, *Nonion fabum* and miliolids (*Quinqueloculina* spp. and *Massilina* sp.).

MATERIAL AND METHODS

About twenty ostreid valves were sampled both from the sands with grazed shells and from the sandy clays with bored shells. For each specimen, qualitative and comparative analysis of the traces were performed on both sides of each single valve.

GRAZING TRACES

Grazing traces on the Ficulle ostreid shells perfectly correspond to those described by Bromley (1975) for the ichnotaxon *Gnathichnus simplex*, referred to the feeding action of regular echinoids. The pentaradiate organization of the bites is highly distinctive and it constitutes the basal feature of the taxon. As indicated by Bromley (1975), the grazing traces show various non pentaradiate arrangements, mainly in relation to the substrate characteristics, as flat or irregular surfaces and sharply curved rims.

In the examined material, (about twenty ostreid valves) pentaradiate traces (the "modular units", sensu Heinberg, 1973), with 72 degrees between rays (the so called stars), are numerous, often overlapping one to another; also the better distinguishable modules exhibit sometimes overlapping stars (Figs. 6a and 7d, e). The modular unit exhibits a maximum diameter of 0.8-1.0 mm, with single bites length of 2-4 mm; single bites can reach 6-8 mm in length. Successive stars along the supposed tracemaker trail (Fig. 4b) are easily recognizable while adjacent traces show often incomplete stars with few rays; incomplete stars, mainly with four or two rays (Fig. 5a, b) are very frequent, probably because of the irregularity of the morphology of oyster shell surfaces, mainly the external one; they display a constant alignment (Figs. 5a, b and 6b), as

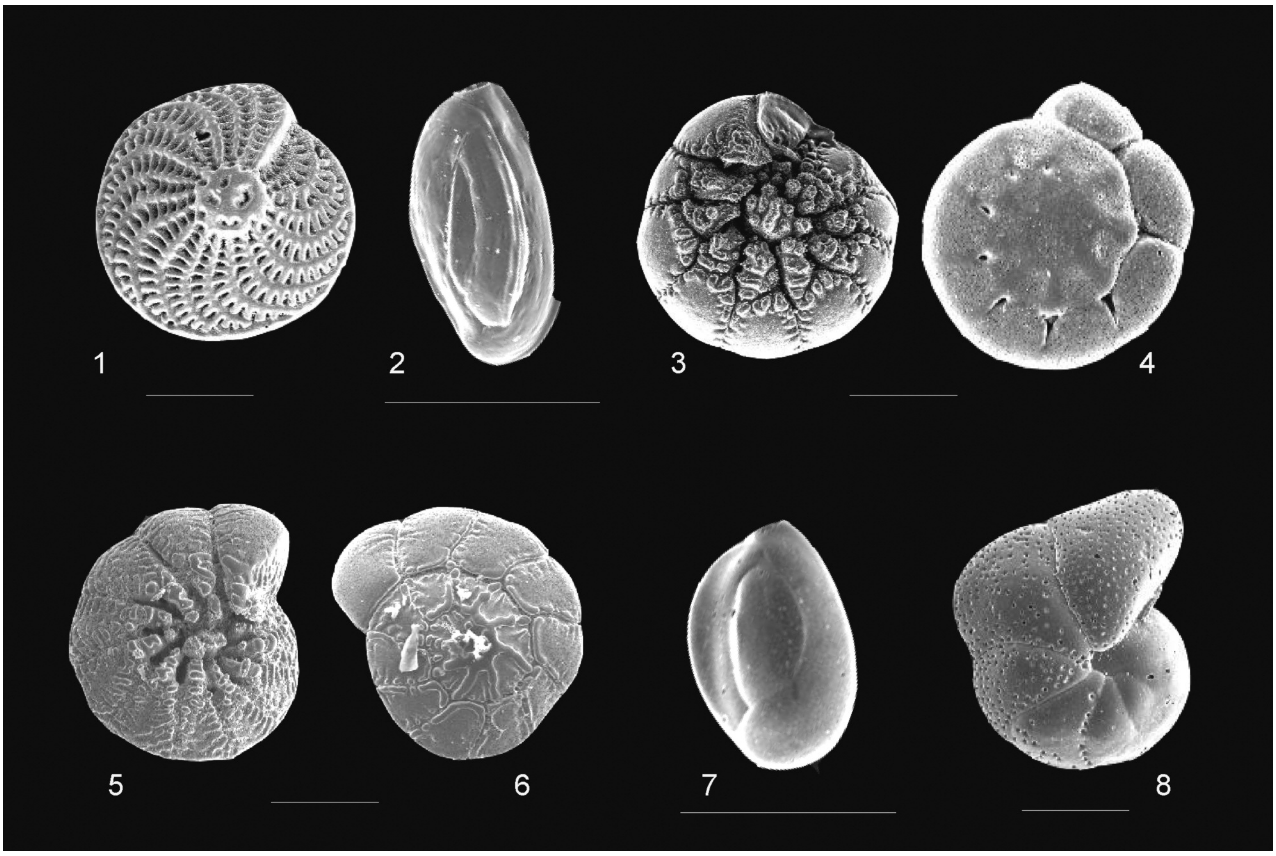

Fig. 3 - 1) *Elphidium crispum* (Linnè): lateral view, sands with ostreids; 2) *Quinqueloculina stelligera* (Schlumberger): lateral view, sandy clays; 3) *Ammonia inflata* (Seguenza): ventral view, sandy clays; 4) *Ammonia inflata* (Seguenza): spiral view, sandy clays; 5) *Ammonia beccarii* (Linnè): ventral view, sands with ostreids; 6) *Ammonia beccarii* (Linnè): spiral view, sands with ostreids; 7) *Quinqueloculina seminulum* (Linnè): lateral view, sandy clays; 8) *Lobatula lobatula* (Walker and Jacob): ventral view, sands with ostreids. Bar scale equals 250 μm.

observed by Krumbein and Van der Pers (1974) for living echinoids. The grazed shell margins show perpendicular bites (Figs. 4b and 6a), often densely aligned, as observed by Bromley (1975). In many specimens, the grazing traces cover almost entirely the external oyster surfaces (Figs. 4a and 7a). Bites around the *Caulostrepsis* borings of figure 7b, whose roof has been broken away, indicate a bioerosive attack in order to eat the boring worms. Density of superimposed scratches is very high, sometimes producing a dense, irregularly crossing, grooved surface (Figs. 4b, 6a and 7c). On scarcely grazed flat surfaces on which the single bites are well distinguishable, can be observed trails characterized by a series of one or two bites, roughly transverse to the trail but inclined as in the pentaradiate pattern (Fig. 5a, b). The use of two or one tooth does not change the inclination of their rasping movement in respect to that of the other four teeth of the "Aristotle's lantern". However, in some cases, single bites change more or less abruptly direction; there are also series of three or four single bites with the same changes in direction (Fig. 5b and 7f). Bite direction changes could be the response to the environmental stress due either to the shell-ground instability or to water energy rapid changes. Moreover incomplete bites on flat surfaces of the inner side of some ostreid valves can be interpreted as the result of a hasty exploration of the substrate along the trail, using "voluntarily" only one or two of the five available teeth. Thus the morphology of the traces depends not only on the substrate irregularities, but also on the adaptive behavior of the tracemaker.

On more grazed surfaces, bites of variable length, width and depth, overlapped one another , can be easily distinguished (Fig. 7a-f). Also the flatness and the depth of the single bites is very variable (Fig. 7d). Surely these morphologies can be ascribed to the environmental conditions during the single grazing movement and to the individual characteristics (age, force, hunger). According to Klinger and Lawrence (1985) the hardness of the teeth does not change significantly among different species, but can differ among the specimens of the same species; also the size of the teeth of the grazing species vary significantly (Mokady et al., 1996). So these features, together with the morphology of the teeth of the echinoid grazing groups and their evolution (Smith, 1984), can influence the morphology of grazing traces.

THE GNATHICHNUS AND ENTOBIA ICHNOFACIES

The *Gnathichnus* ichnofacies as defined by Bromley

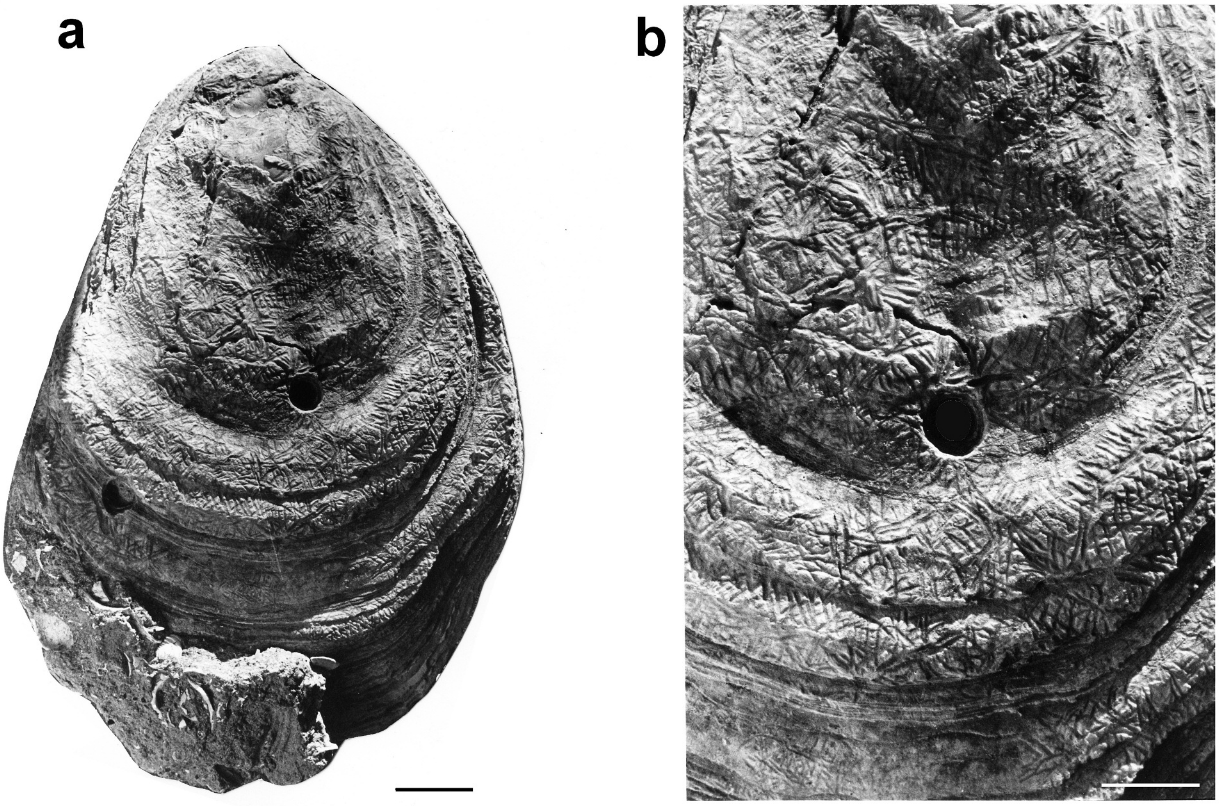

Fig. 4 - a) outer side of an *Ostrea* valve with pervasive *Gnathichnus* bioerosive traces and a predatory boring (*Oichnus*); b) detail showing some pentastellate traces (on the left side, under and above the *Oichnus* boring at the centre of the picture), but also, aligned bites (on the right side) and "rhomboidal" features of the dense rasped area above the *Oichnus* boring. Bar scale equals 1cm.

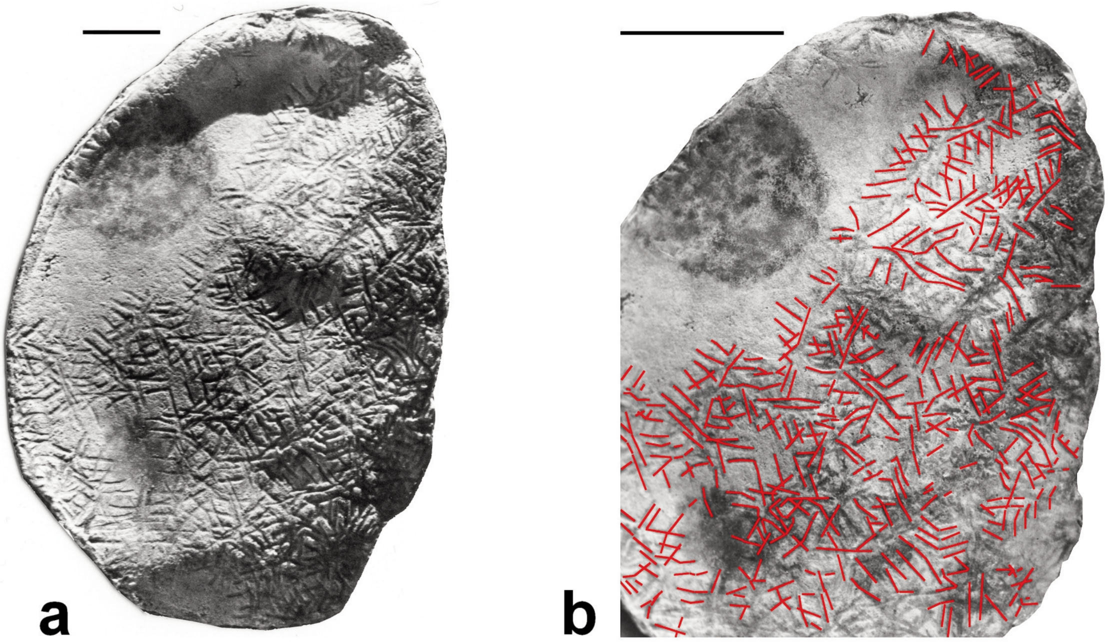

Fig. 5 - a) inner side of an *Ostrea* valve showing its almost complete sculptured surface; b) detail, showing various types of bites (red marks), from single curved ones to four, two and one rays rasping trails. Bar scale equals 1 cm.

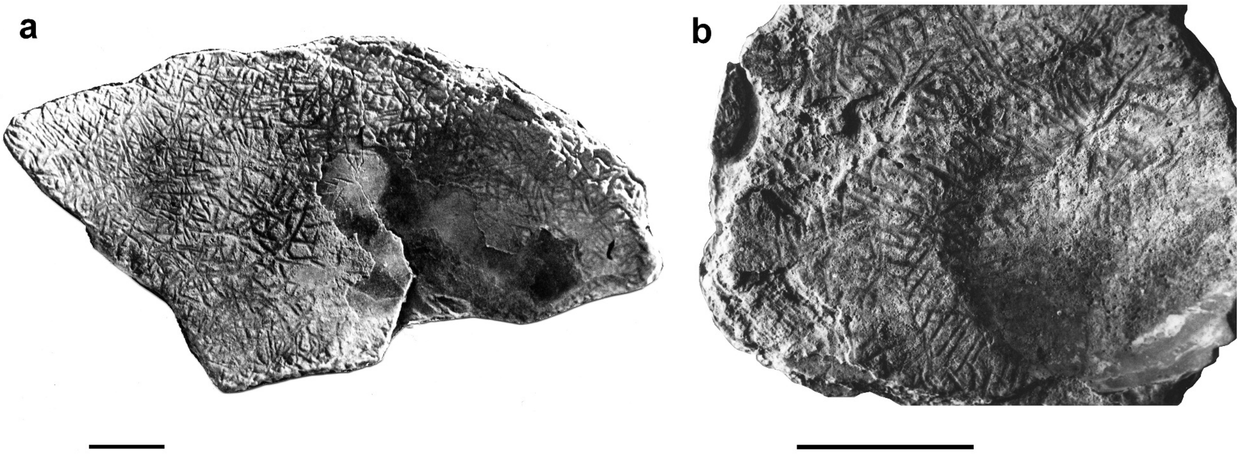

Fig. 6 - a) inner side of a pervasively bioeroded fragment of an *Ostrea* valve; note the superimposed pentastellate traces and the perpendicular bites along the edges; b) outer side of a fragment of a *Hyotissa* valve, exhibiting a "suite" of single or double bites along a concentric growth rim. Bar scale equals 1 cm.

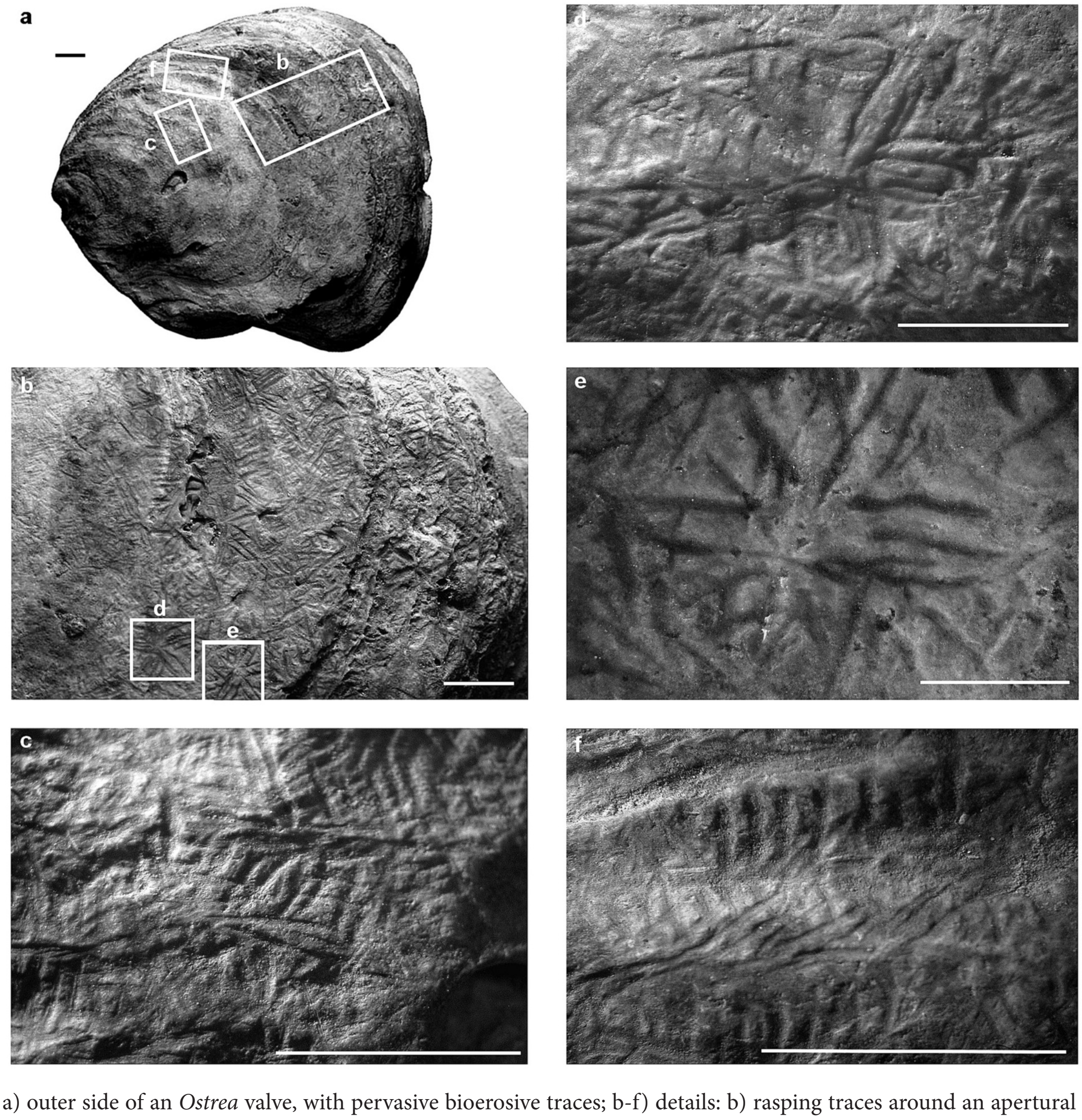

Fig. 7 - a) outer side of an *Ostrea* valve, with pervasive bioerosive traces; b-f) details: b) rasping traces around an apertural series of *Caulostrepsis* borings along one *Ostrea* growth rim; pentastellate traces are visible (bottom side of the picture); c) densely rasped area, with superimposed bites; note the long single bites running parallely; d, e) detail of pentastellate traces, due to multiple rasping acts; f) bites between two growing rims of the *Ostrea* shell; note the curved series of single bites, sculpted on the inclined surface between the two growing rims. Bar scale equals 1 cm.

and Asgaard (1991) is characterized by the dominance of the grazing traces produced by the activity of echinoids (*Gnathichnus*) and of mollusks (*Radulichnus*), whereas it shows rare boring traces (*Entobia*, *Caulostrepsis*). The latter together with *Gastrochaenolites* characterize the *Entobia* ichnofacies, mainly developed in rocky shores and gravel beaches.

In the Ficulle shell-grounds both the ichnofacies are represented. In the ostreid shell-ground of the sandy proximal level the echinoid grazing traces represent almost the only traces found; in fact only rare predatory (*Oichnus*), meandropolydorid, entobian traces and very rare *Gastrochaenolites* were found. However, gastropod and polyplacophoran grazing traces (*Radulichnus*) that, even if subordinately, usually characterize the ichnofacies (Gibert et al., 2007), here completely lack. We believe that the complete absence of *Radulichnus* can be due both to the relatively high energy conditions of the sandy deposit, and to the density of the *Gnathichnus* traces, which could have obscured the more delicate *Radulichnus* ones, superimposing on them. According to Ridley (2010), in the Jurassic *Gryphaea* shell beds, densely grazed by echinoids, only on one *Gryphaea* shell, *Radulichnus* traces are preserved. On the other hand, in the Nigerian brackish modern mangrove swamps, ostreid shell bioerosion is made up mainly by cyanobacteria and herbivorous gastropods, whereas regular echinoids and chitons are totally lacking (Apkan, 1990). Also in the Dutch Sea, *Littorina* and *Lepidochitona* traces dominate (Jüch and Boekschoten, 1980).

The deep-tier borings of the *Entobia* ichnofacies are numerous mainly in the *Ostrea* shells (Fig. 7a, b), but also in the very large *Glycymeris* (G. *bimaculata* according to Malatesta, 1974) valves that are abundantly present in the clayey sediments underlying and overlying the *Posidonia* horizon; entobian borings prevail, but other boring traces are frequent and moderately diversified. They are principally made by polichaetes (*Caulostrepsis, Meandropolydora)* and more rarely by bivalves *(Gastrochaenolites*). Polichaete borings are very frequent: *Caulostrepsis* mainly develops its pouch-shaped boring roughly parallel to the outer margin of the ostreid shells, often with apertures arranged along the ostreid growth lines, supporting the interpretation suggested by Gibert et al. (2007) of their infestation on alive specimens. Shells are variously infested: some exhibit only linear file of the small oscular apertures of initial entobian borings (Fig. 8), other are reduced to small fragments densely bored. Some specimens are also more or less encrusted by balanids, bryozoans, foraminiferids, serpulids as well as by *Cladocora caespitosa* small colonies. *Gnathichnus* traces are usually lacking, but rare bites can be recognized in some preserved ostreid shell surfaces; in these cases, borings superimpose on the *Gnathichnus* traces.

Also in the Ficulle outcrop, the two ichnofacies of Bromley and Asgard (1991) are well distinguished. The *Gnathichnus* ichnofacies developed in a probably

Fig. 8 - Outer and inner sides of the same *Ostrea* valve showing entobian and other (*Meandropolydora* and ?*Gastrochaenolites*) traces respectively signed by the 1, 2, 3 arrows. Bar scale equals 1 cm.

spatially restricted short term shell-ground; the *Entobia* ichnofacies developed in a more washed substrate as a beach shell-grounds and on shells acting as isolated firm grounds scattered in the soft sediment. The ostreid and *Glycymeris* shells found in the clayey sediments were almost all more or less strongly bored. Only rare bored specimens or fragments exhibit remnants of the *Gnathichnus* bites. The limited number of specimens with both domichnian and paschichnian traces and the superimposition of the former on the latter suggest that they are specimens reworked from the *Gnathichnus* in the *Entobia* domain, rather than representatives of an intermediate area between the two domains.

CONCLUSIVE REMARKS

The recognition and the definition of ichnofacies are useful tools for the restoration of the rocky and shelly grounds and of their environmental significance. *Gnathichnus* and *Entobia* facies are well distinguished and easily recognizable. Coexistence of the traces typical of the two facies can give information on their areal distribution and changes in time. *Gnathichnus* traces analysis (density, distribution, morphology and changes along the trails) can be useful in providing behavioral and microenvironmental information. In the analyzed outcrop the two ichnofacies are well represented: the *Gnathichnus* one is only preserved on a single horizon spatially restricted; the *Entobia* ichnofacies is developed on almost all the ostreid and *Glycymeris* shells dispersed in the lateral clayey deposit. Rare *Gnathichnus* traces are recognizable on the outer surfaces of ostreid shells of the *Entobia* ichnofacies; they could indicate shells displaced from the temporary *Gnathichnus* ichnofacies shell-ground towards more washed substrates.

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REFERENCES

Akpan E.B. 1990. Bioerosion of oyster shells in brackish modern mangrove swamps, Nigeria. Ichnos: 1, 125-132.

Ambrosetti P., Carboni M.G., Conti M.A., Esu D., Girotti O., La Monica G.B., Landini B., Parisi G. 1987. Il Pliocene e il Pleistocene inferiore del Bacino del fiume Tevere nell'Umbria meridionale. Geografia Fisica e Dinamica Quaternaria: 10, 10-33.

Ambrosetti P., Conti M.A., Parisi G., Kotsakis T., Nicosia U. 1977. Neotettonica e cicli sedimentari plio-pleistocenici nei dintorni di Città della Pieve (Umbria). Bollettino della Società Geologica Italiana: 96, 605-635.

Barrier P., D'Alessandro A. 1985. Structures biogèniques et physiques dans les Sables de Pavigliana, Reggio Calabria (Italie). Rivista Italiana di Paleontologia e Stratigrafia: 91, 379-408.

Bergamin L., Romano E., Finoia M.G., Venti F., Bianchi J., Colasant A., Ausili A. 2009. Benthic foraminifera from the coastal zone of Baia (Naples, Italy): Assemblage distribution and modification as tools for environmental characterization. Marine Pollution Bulletin: 59, 234-244.

Bossio A., Costantini A., Foresi L.M., Lazzarotto A., Mazzanti R., Mazzei R., Pascucci V., Salvatorini G., Sandrelli F., Terzuoli A. 1998. Neogene-Quaternary sedimentary evolution in the western side of the northern Apennines (Italy). Memorie della Società Geologica Italiana: 52, 513-525.

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 Palébiologie: 11, 219-229.

Bromley R.G. 1975. Comparative analysis of fossil and recent echinoid bioerosion. Palaeontology: 18, 725-739.

Bromley R.G., Asgaard U. 1991. Ichnofacies: a mixture of taphofacies and biofacies. Lethaia: 24, 153-163.

Bromley R.G., Asgaard U. 1993. Endolithic community replacement on a Pliocene rocky coast. Ichnos: 2, 93-116.

Bromley R.G., D'Alessandro T. 1983. Bioerosion in the Pleistocene of southern Italy: ichnogenera *Caulostrepsis* and *Meandropolydora*. Rivista Italiana di Paleontologia e Stratigrafia: 89, 283-309.

Carboni M.G., Di Bella L., Matteucci R., Palagi I. 1992. Ficulle. In Matteucci R. (Ed.), Fifth Symposium on ecology and paleoecology of benthic communities, Field guide book, Rome 28-30 September 1982, 14-18.

Carrasco J.F. 2003. Presencia dela icnoespecie *Gnathichnus pentax* sobre *Dimya richei* (Bivalvia) en el Eoceno inferior de la Puebla de Roda (Huesca). Batalleria: 11, 37-40.

Cavinato G.P., De Celles P.G. 1999. Extensional basins in the tectonically bimodal central Apennines fold-thrust belt, Italy: Response to corner flow above subducting slab in retrograde motion. Geology: 27, 955-958.

Galiano M., Ciccacci S. 2011. Recent morphoevolution of the Fabro calanchi badlands (Umbria, Italy). Journal of Mediterranean Earth Sciences: 3, 1-13.

Gibert J.M. de, Martinell J. 1998. Ichnofabrics of the Pliocene marginal marine basins of the northwestern Mediterranean. Revista de la Sociedad Geológica de España: 11, 43-56.

Gibert J.M., de, Martinell J., Domènech R. 1998. *Entobia* Ichnofacies in Fossil Rocky Shores, Lower Pliocene, Northwestern Mediterranean. Palaios: 13, 476-487.

Gibert L.M., de, Domènech R., Martinell J. 2004. An ethological framework for animal bioerosion trace fossils upon mineral substrata with proposal of a new class, Fixichnia. Lethaia: 37, 429-437.

Gibert J.M. de, Domènech R., Martinell J. 2007. Bioerosion in shell bed from the Pliocene Roussillon Basin, France: Implications for the (macro) bioerosion ichnofacies model. Acta Palaeontologica Polonica: 54, 783-798.

Girotti O., Mancini M. 2003. Plio-Pleistocene stratigraphy and relations between marine and non-marine successions in the middle valley of the Tiber river (Latium, Umbria). Il Quaternario, Italian Journal of Quaternary Sciences: 16, 89-106.

Heinberg C. 1973: The internal structure of the trace fossils *Gyrochorte* and *Curvolithus*. Lethaia: 6, 227-238.

Klinger T.S., Lawrence J.M. 1985. The hardness of the teeth of five species of echinoids (Echinodermata). Journal of Natural History: 19, 917-920.

Jüch J.W.M., Boekschoten G.J. 1980. Trace fossils and grazing traces produced by *Littorina* and *Lepidochitona*, Dutch

Wadden Sea. Geologie en Mijnbouw: 59, 33-42.

Malatesta A. 1974. Malacofauna pliocenica umbra. Memorie per Servire alla Descrizione della Carta Geologica d'Italia: 13, p. 464.

Mancini M., Girotti O., Cavinato G.P. 2003-2004. Il Pliocene e il Quaternario della Media Valle del Tevere. Geologica Romana: 37, 175-236.

Martinell J. 1982. Echinoid bioerosion from the Pliocene of NE Spain. Geobios: 15, 249-253.

Martinell J., Domènech R. 1986. Actividad bioerosiva en el Plioceno marino del Empordà (Catalunya). Paleontologia i Evolució: 20, 247-251.

Mayoral E., Muñiz F. 1996. Ichnofacies de Gnathichnus en el sector Suroccidental de la Cuenca del Guadalquivir. Coloqios de Paleontologia: COL PA, 48, 87-102.

Michalík J. 1977. Systematics and ecology of *Zeilleria* BAYLE and other brachiopods in the Uppermost Triassic of the West Carpathian. Geologica Carpathica: 28, 323-346.

Michalík J. 1980. A palaeoenvironmental and palaeoecological analysis of the West Carpathian part of the northern Tethyan nearshore region in the latest Triassic times. Rivista Italiana di Paleontologia e Stratigrafia: 85, 1047-1064.

Mokady, O., Lazar, B., Loya, Y. 1996. Echinoid Bioerosion as a Major Structuring Force of Red Sea Coral Reefs. Biological Bulletin: 190, 367-372.

Murray J.W. 1991. Ecology and Paleoecology of Benthic Foraminifera. Longman Scientific and Technical, London, p. 397.

Nicosia U. 1986. Ammonite/epizoans relationships in the Kimmeridgian of the Central Apennines. Geologica Romana: 25, 155-164.

Radley J.D. 2006. Grazing bioerosion on oyster concentrations (Lower and Middle Jurassic, England). Ichnos: 13, 47-50.

Radley J.D. 2010. Grazing bioerosion in Jurassic seas: a neglected factor in the Mesozoic marine revolution? Historical Biology: 22, 387-393.

Ruengsawang N., Yeemin T. 2000. Bioerosion caused by grazing activities on coral communities in the Gulf of Thailand. Proceedings of the 9th International Coral Reef Symposium, Bali, Indonesia 23-27 October 2000.

Smith A. 1984. *Echinoid Palaeobiology*. George Allen & Unwin, London, p. 190.

Wisshak M., Gektidis M., Freiwald A., Lundälv T. 2005. Bioerosion along a bathimetric gradient in a cold-temperate setting (Kosterfjord, SW Sweden): an experimental study. Facies: 51, 93-117.

Wisshak M., Tribollet A., Golubic S., Jakobsen J., Freiwald A. 2011: Temperate bioerosion: ichnodiversity and biodiversity from intertidal to bathyal depths (Azores). Geobiology: 9, 492-520.