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# BIOERODED AND/OR ENCRUSTED AMMONITE MOULDS AND THEIR TAPHONOMIC IMPLICATIONS

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*Key-words:* taphonomy, encrustation, bioerosion, composite moulds, reelaboration, Toarcian, Rosso Ammonitico.

*Riassunto*: In diversi campioni di ammoniti, provenienti da livelli del Toarciano inferiore-medio, della successione di Migiana di M. Malbe (Massicci Perugini; Umbria, Appennino Settentrionale), sono stati riscontrati fenomeni di incrostazione e/o bioerosione. La maggior parte di queste strutture è dovuta all'azione di vermi policheti; i casi di incrostazione s.s. infatti, sono imputabili all'azione di serpulidi mentre, i fenomeni di bioerosione s.s., sono simili a quelli prodotti da *Maeandropolydora decipiens* Voigt. Una terza categoria di policheti infine, ha prodotto strutture di bioerosione-incrostazione. L'osservazione del diverso grado di riproduzione dei dettagli ornamentali nei due lati di alcuni campioni, ha permesso di stabilire che i loro lati superiori sono replicati sotto forma di modelli compositi, ovvero modelli in cui elementi ornamentali esterni si sono sovrimpressi su quelli interni. I lati inferiori invece sono sempre conservati come normali modelli interni. Lo stile deformativo tramite il quale si realizza la formazione dei modelli compositi è di tipo plastico e verticale, con deformazione laterale impedita. Si ritiene pertanto che il processo avvenga in condizioni di compattazione diagenetica.

La presenza di boring e/o incrostazione nei lati inferiori di modelli interni è classicamente interpretata come evidenza di rielaborazione. Nel caso in questione, la duplice natura di alcuni dei modelli rinvenuti e alcune considerazioni puramente meccaniche, inducono a pensare che tali fenomeni siano avvenuti prima della dissoluzione del guscio e non implichino necessariamente rielaborazione. Tranne nei casi di bioerosione s.s., risulta impossibile stabilire se la conchiglia fosse più o meno riempita. Addirittura, non si può escludere che l'incrostazione da parte dei serpulidi sia avvenuta durante il post-mortem drifting o sul fondale prima del seppellimento nel sedimento. La similitudine tra i fenomeni di bioerosione s.s. riscontrati e quelli di altri ichnogeneri colonizzatori di substrati duri, suggerisce che, non è necessario invocare l'esumazione totale di un fossile per permettere l'azione di organismi perforanti.

*Abstract.* Encrustation and/or bioerosion have been observed on both sides of several ammonites sampled from Lower-Middle Toarcian Rosso Ammonitico of the Umbria-Marche Apennines (Central Italy). The majority of these features are due to the activity of polychaete worms: the encrusting s.s. is due to serpulids, whilst bioerosion s.s. is similar to *Maeandropolydora decipiens* Voigt, and a third category of polychaetes has produced bioerosion-encrustation structures. The ornamentation features of the samples studied allowed us to establish that the upper sides are preserved as composite moulds and the lower sides as internal moulds. The overprinting of the external shell structures on the internal infillings took place during burial diagenesis; the deformation style is plastic and only vertical, lateral deformation being impeded.

The presence of boring and/or encrustation on the lower side of internal moulds is classically interpreted as evidence of reelaboration. Regarding these Toarcian specimens, the nature of the composite moulds would seem to confirm that the phenomena of encrusting and/or boring by polychaete worms occurred before the dissolution of the shells. Except in the cases of pure bioerosion, it is impossible to ascertain whether the shell was already infilled or not. The encrustation by polychaete worms probably occurred during post-mortem drifting or when the shell was exposed on the sea floor.

The similarity between the observed bioerosion phenomena and other hard and/or firm material borers gives us reason to think that the complete re-exhumation of the shell is not necessary to permit the boring action; however, a partial re-exhumation might have helped the borer to detect the presence of a shell test.

## Introduction.

Taphonomy has always been a part of Palaeontology, the progress in the study of preservation features, on occasions exceptional, has furnished more and more information concerning both palaeobiological richness and paleoenvironmental (chemical-physical) features. Furthermore, fossils are clues to the reconstruction of depositional conditions and diagenetic evolution of sediments: for example, different types of infillings in the chambered shells of some cephalopods may reveal depositional-erosional events not recognisable utilising other fossil taxa.

The biostratigraphic implications of taphonomic investigations were "officially" accepted rather late in the context of progress in palaeontologic analyses. The acceptability of reworked (reelaborated, sensu Fernández López & Meléndez, 1994) fossils in biostratigraphic investigations was actually refuted by the N.A.C.S.N. (North American Commission on Stratigraphic Nomenclature) as recently as 1983 and in Salvador (1994), whilst erosion/reelaboration phenomena, for example, had already been documented by Bigot (1940) in Normandy.

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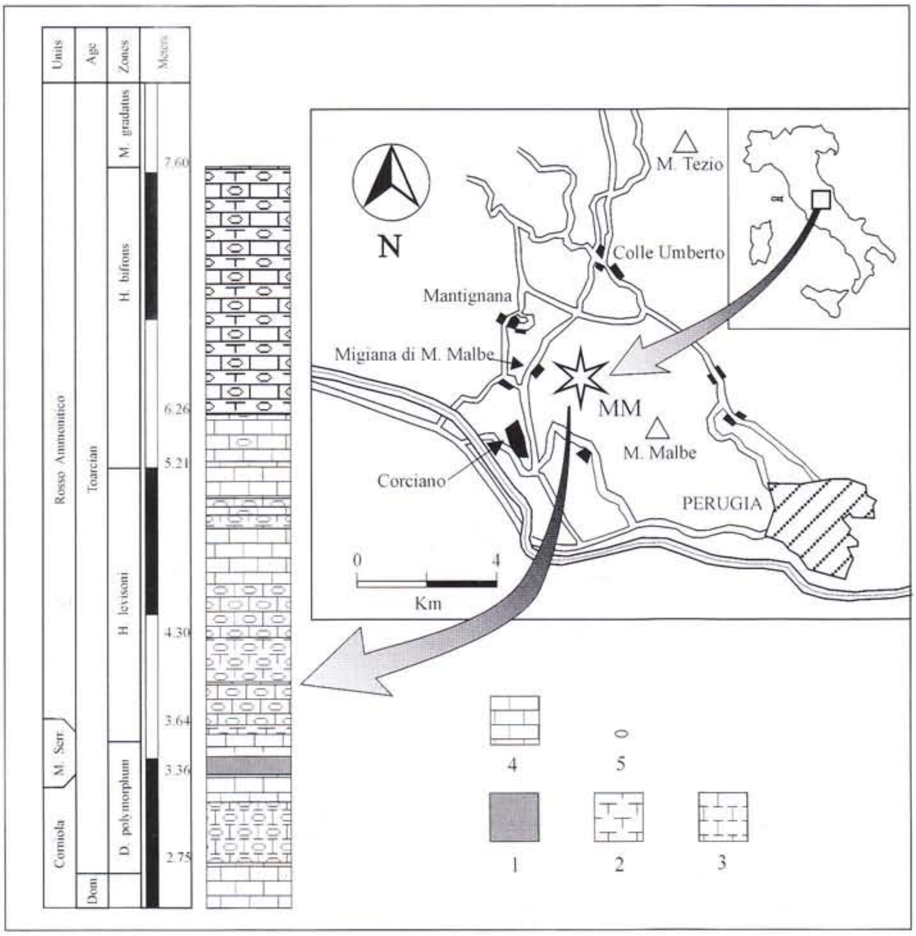

Fig. 1 - Location maps and the stratigraphic section of Migiana di M. Malbe (MM); 1 - poor oxygen clay; 2 - marl; 3 - calcareous marl; 4 - limestone; 5 - nodules. In the column of the stratigraphic units, M. Serr. stands for Marne di Monte Serrone.

A conceptual framework of field working and conceptual remobilization (resedimentation and reelaboration) criteria has been listed by Fernández López (1984; 1986; 1987a, b; 1997), Fernández López & Meléndez (1994) and Maeda & Seilacher (1996). Resedimentation pertains to the biostratinomic phase, whilst reelaboration occurs during the fossil diagenesis (Fernández López, 1984). Therefore, only reelaborated fossils have lower biostratigraphic significance.

This study was initiated during the execution of a biostratigraphic investigation, taking the above-cited criteria into account. During this phase samples displaying contrasting features have been found: evidence of reelaboration was found, together with other evidence indicating absence of remobilization after the first sedimental burial.

A careful study of ammonite preservation features, revealed the importance of taking the diagenetic effects into consideration when attempting to reconstruct the biostratinomic excursus of fossils.

## Geological setting.

The area studied (Fig. 1) is located in the Massicci Perugini (Perugia, Central Italy), which are the central portion of the internal successions of the Umbria-Marches domain (Lavecchia et al., 1989; Minelli & Menichetti, 1990). The latter is a Mesozoic-Cenozoic thrust and fold chain, prevalently oriented NW-SE and NNW-SSE, where carbonate and terrigenous sediments, Triassic-Neogenic in age, are prevalent.

The study examines ammonites collected from the "Migiana di M. Malbe" section, which can be considered to be midway between type 2 and 3 successions of Colacicchi et al. (1988). A detailed description of stratigraphical and palaeoecological aspects of Umbria-Marchean successions is provided in the latter work and in Cresta et al. (1988). The samples were extracted from the interval referable to the *D. polymorphum* Zone and *H. bifrons* Zones, with most of them coming from the lower part of *H. levisoni* Zone and the upper-middle portion of *H. bifrons* Zone.

This timespan includes the Corniola Unit, the Marne di Monte Serrone and the Rosso Ammonitico Umbro-Marchigiano (RAUM). As defined in Nini et al. (1997) the RAUM includes three members, respectively A, B and C. In the Migiana di M. Malbe section the A member is replaced by a calcareous stratified lithofacies, with variable nodularity.

## General preservation features.

Some taphonomic aspects of the ammonites collected from the section studied have already been discussed in Macchioni et al. (1996). On the basis of chemical-textural features, homogenous, partial and differentiated moulds were identified: the last two may generate infillings of geopetal meaning. Ammonite homogeneous infillings determine completely calcareous ammonite internal moulds, whilst in ammonite differentiated infillings the phragmocones are to some extent calcareous (in the lower side of some chambers) and partially marly. Ammonite partial infillings are composed of calcareous sediment and late sparite in the upper part of some phragmocone chambers.

Traditionally, ammonite samples collected from the RAUM were defined as internal moulds. Nevertheless, remains of neomorphic shell, were observed in some specimens collected from the upper part of *D. polymorphum* Zone and from the lower part of *H. levisoni* Zone. In this case, the transformed shell is sparitic, yellowish in colour. In specimens collected from other level of the succession thin crusts, brownish to yellowish in colour, are almost always visible in the specimens collected here. Normally, after the extraction of the specimens from the rock matrix, these crusts remain attached to the external mould and only few portions remain on the internal one (Pl. 1, Fig. 7). These crusts must be considered the consequence of diagenetic precipitation of carbonate deriving from the dissolution of the shell and other sedimental elements during the diagenetic compaction phase, either because, they do not follow exactly the surface of the moulds or, conversely, they also replicated bioerosion grooves. Furthermore, they are also thicker in the venter than in the rest of the mould surfaces (zones of lesser value of overburden), they are sometimes separated from the mould surface by clayey films and are identical to others contained in the surrounding matrix. The latter aspect confirms their common diagenetic evolution and that the crust found in a specimen cannot be considered the residue of recrystallisation of only the test of itself.

Indeed, many apparently internal moulds were also collected which showed delicate ornamental details (Pl. 1, fig. 1-3; Pl. 2, fig. 1-2, 4-5) only on the upper sides, even though they were free of erosion and corrosion effects on the lower side. Therefore the absence of these ornamental details on one of the two sides can not be attributed to one of the latter two phenomena. The comparison of the collected specimens with others which have been documented in literature reveal that these ornamental details are normally preserved only in external moulds or casts, and therefore these samples can not be considered to be simple internal moulds. In the majority of cases these structures are striae, and are superimposed on internal features such as suture lines and the internal replicas of ribs. Of these samples, some are partial and differentiated moulds (Macchioni et al., 1996), indicating a polarity consistent with the stratigraphic section.

## Outline of fossil replica processes and terminology.

The different types of replica of organism remains, and the occasional differences in their taxonomic importance, have led to the establishment in Palaeontology of a distinction between internal and external moulds.

A particular case of fossilisation was described for the first time by McAlester (1962) in some Palaeozoic pelecypods. The discovery in many moulds of rib impressions replicated from the external moulds on muscle impressions normally present only in internal moulds, prompted the author to coin the term 'composite mould'. In these, external structures previously separated by the test would come into contact with internal ones, one superimposing on the other on the same surface.

Other examples of composite mould formation were reported later by Pavia (1983), on Bajocian ammonites collected in the Calcaires à *Cancellophycos* fm. of Digne. Following the author, the major role in the formation of these composite mould is played by the nacreous layer which during the diagenetic compaction phase was rigid and left its impression in the infilled sediment that was still plastic.

One can expect that the periostracum of pelecypods of McAlester may have played the same role replicating the shell ornamentation. Nevertheless, it was impossible in the case of absence of cementation of the sediment matrix. Indeed, the bivalve periostracum is the external layer and the cavity resulting from dissolution of the aragonitic test, on which are impressed the muscle scars seems to have been closed up without leaving evidence of the original structure. We must therefore allow that the sediment was already partly cemented when the shell dissolution occurred. Remembering that 'plastic' does not mean 'soft', the bivalve periostracum and the ammonite nacreous layer are deformed plastically during burying conditions, when the aragonite dissolution occur they perfectly fit together with the sediment matrix below.

Due to the differing patterns of the three layers which make up ammonoid tests, definitions of the ornamental details on the two sides, internal and external, of the test may differ. For example, as described by Howarth (1973) and Birkelund (1981), in some genera of ammonites the external prismatic and the nacreous layers show identical patterns, while the internal layer is detached from the former where the various reliefs occur, creating an interspace (Fig. 2). As a result, the ribs reproduced in an internal mould are less in relief, and are more spaced out than is seen externally (Howarth, 1973; Gabilly, 1976); this translates into a loss of detail in reproducing of ornamental structures.

The existence of different modes of preservation on the two sides of individual samples, and the comparison of these with others documented in literature suggest that the structures of their tests are similar to that

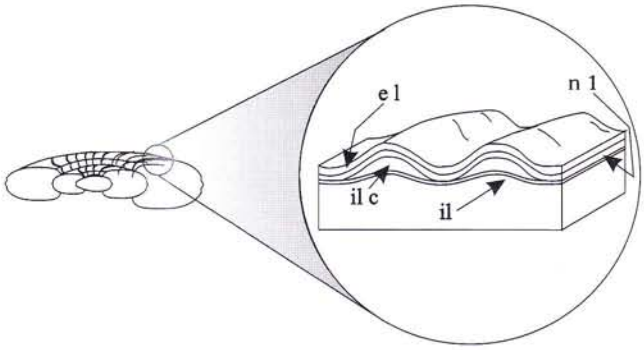

Fig. 2 - Details of the ammonite ornamentation structure: el: external (prismatic) layer; nl: nacreous layer; il: internal (prismatic) layer; il c: inter-layer cavity. After Howart (1973) and Birkelund (1981), modified.

of the forms described by Howarth (1973) and Birkelund (1981). Let us compare the specimens of *Hildaites wrighti* (Spath) here figured in Pl. 2, Fig. 1-2, with the holotype shown by Howarth (1992; pl. 30, fig. 7a-b), which has neomorphic test preserved. In the first one ribs are only replicated in the upper side. In the same manner, we can contrast the two sides of the example of *Alocolytoceras dorcadis* (Meneghini) in Pl. 1, Fig. 1-5, in which extremely delicate striae are preserved only on the right-hand side, and the internal moulds shown by Pinna (1968, pl. 1, fig. 15; 1969, pl. 6, fig. 5), which are absolutely lacking in any ornamental element.

Reassuming, the formation of a composite ammonite mould can come about:

1. due to the impression of the external mould on the internal (e.g. Mc Alester, 1962);
2. due to the impression of the lower side of the nacreous layer, that is to say the side facing the inter-layer cavity, on the internal mould (e.g. Pavia, 1983);
3. due to adherence between the infilling of the inter-layer cavity and the internal mould (e.g. Pl. 2, Fig. 1, 4, 5).

All three processes must occur due to load, when the moulds have undergone cementation and in a null lateral deformation condition ($\varepsilon x = \varepsilon y = 0$). These conditions occur with deep burial. This can be easily seen in specimen 257MM3.69, *Hildaites wrighti* (Spath), in which the original shell has been infilled only in the lower half, with the exception of the body chamber and the last two chambers of the phragmocone. Both ribs of the neomorphic test (Pl. 2, Fig. 4, right side of Fig. 5) and replicated in the chamber infilling (Pl. 2, left side of Fig. 5, Fig. 7) are deformed plastically and only vertically.

## Encrustation and Encrustation-Bioerosion.

Cases of encrustation in internal and external moulds are reported in many works, and encrustation of living ammonites was documented in very few cases by Seilacher (1960), Heptonstall (1970; see Donovan, 1989; for a critical comment of those encrustations) and Schindewolf (1934, in Arkell et al., 1957).

Encrustation occurring during the biostratinomic and fossildiagenetic phases were documented to have occurred both during post-mortem drifting and on the

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Fig. 1 - Specimen 1386MM6.86 *Alocolytoceras dorcadis* (Meneghini) x 1, lower side. On the basis of its infilling features, this specimen is a partial mould, as the upper parts of some phragmocone chambers are infilled by sparry cement. The example shows an ellipsoidal abrasion facet (located where the numbering is placed) which was consistent with its lying conditions.

Fig. 2 - Upper side of the same specimen as Fig. 1.

Fig. 3 - Detail of Fig. 2, a serpulid tube encrusted above the striae which are impressed on the infilling of shell, forming a composite mould.

Fig. 4 - Detail of Fig. 2, settling facets of a serpulid tube encrusted above the striae.

Fig. 5 - Detail of Fig. 1; two serpulid tubes are encrusted directly on the internal mould of the specimen.

Fig. 6 - Specimen 200MM3.76, *Hildaites murley* (Moxon), upper side x 1, the upper portion of the phragmocone chambers of first half of the last whorl are infilled by marl. Note the superimposition of ribs also in the later portion.

Fig. 7 - Lower side of the same specimen, x 1.

Fig. 8 - Detail of Fig. 5.

Fig. 9 - Detail of Fig. 6, body chamber. An intrathalamic settling of a polychaete tube is visible below (upper left corner of the photo) and above (centre of the photo) some calcitic crusts representing the remnants of the re-crystallised shell (see text for more detailed explanation).

Fig. 10 - Lower side of the specimen 1140MM7.10. Boring/encrusting polychaete tubes are settled on the surface of the mould, partly cutting into its surface in a manner analogous to that in Fig. 8. Just below the middle of the photo, on the left, a serpulid tube is also encrusted on the mould infilling.

Fig. 11 - Detail of Fig. 5, phragmocone. A boring/encrusting polychaete tube cuts into the rib reliefs. It is presumed that the settling of the tube occurred before sediment infilling; the thin void between the ammonite infilling and the polychaete tubes is thought to represent the void left by the dissolution of the latter's shell test.

Fig. 12 - Same specimen as in Fig. 11: both the settlements of a boring/encrusting polychaete are identical in the body chamber and in the phragmocone (Fig. 11).

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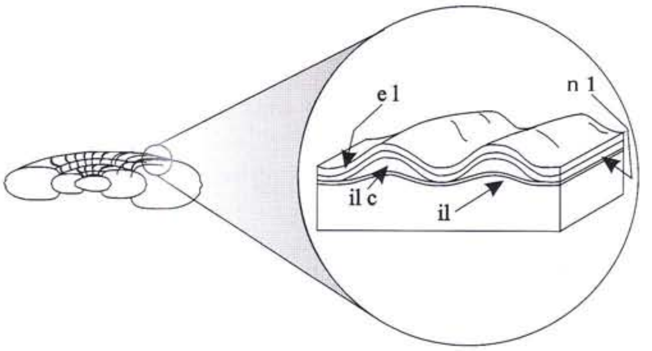

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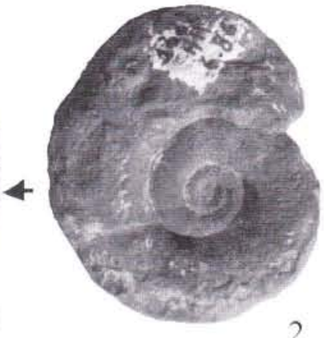

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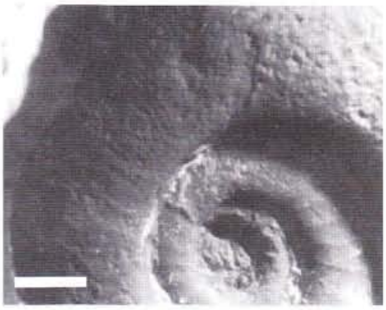

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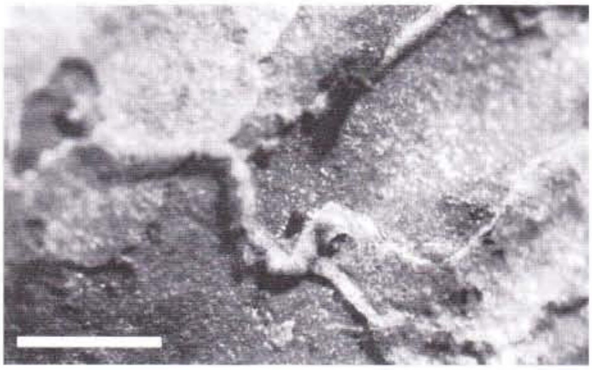

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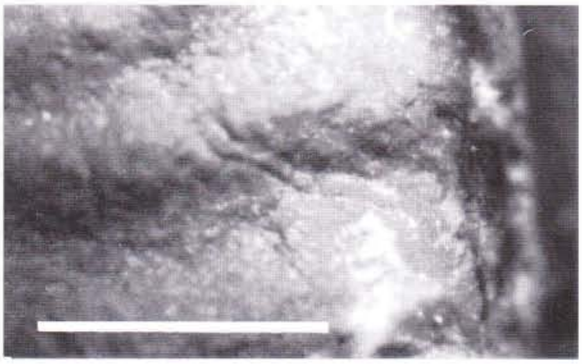

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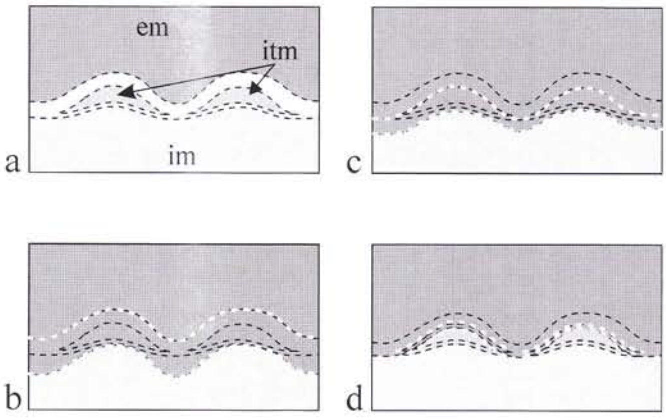

Fig. 3 - Formation of the three different types of composite moulds. a) The test of an ammonite is buried in the sediment. The three grey tones identify: the material which surrounds the test externally (external mould= em); that which penetrates internally (internal mould= im); and lastly, the sediment that has penetrated into the inter-layer cavity (inter-layer cavity mould= itm). During the diagenetic compaction phase, three types of mould can be created: b) by the impression of the external mould on the internal one; c) by impression of the lower side of the nacreous layer (i.e. the side facing the inter-layer cavity) on the internal mould; d) by adhesion between the infilling of the inter-layer cavity and the internal mould. There are only slight differences between the effects of the former two, which are seen in slight variations in the relief of the ornamentation. Note that with a decrease in the radius of curvature of the external ornamentation there is an increase in the radius of the internal: for this reason thin ribbing or striae may not be replicated in the internal mould.

sediment floor (Seilacher, 1971; Nicosia, 1986; Fernández López, 1987a; Manni et al., 1991). The presence of encrustations in some cases was utilised to establish the substrate conditions, and ammonites were identified as the unique lithified "isles" where encrustation was possible (Fernández López, 1987a). In other cases, tropic relationships have been delineated between encrusters and different kinds of substrate (Manni et al., 1991).

Examination of the samples studied revealed the presence of various types of encrustation by polychaetes and, more rarely, by crinoid implantations (Pl. 3, Fig. 7-8). Settling features allow us to distinguish serpulid tubes from those attributable to other polychaete worms (Fig. 4). The latter are more frequent than the former, and their tubes develop in a random and twisted (Pl. 1, Fig. 7-9; Pl. 2, Fig. 3, 5-7), without apparent changes in diameter. They are borers/encrusters at the same time because the tubes can partly cut through the moulds, either following or not following ornamentation reliefs independently of the side of settling (Pl. 1, Fig. 8; Pl. 2, Fig. 5-6, 8); as a result they are more or less deeply enclosed by the infilling sediment. Serpulid tubes, on the other hand, are relatively straight and grow radially in the ammonite coiling plane, without superimposition (Pl. 1, Fig. 4-5, 8, 10). In general, the polychaete tubes are preserved as internal moulds, but in some cases, on the lower sides of the ammonite specimens, there can also be present remnants of their tests (Pl. 1, Fig. 5, 8, 9, 13), or there may only be their settling facets (Pl. 2, Fig. 7). In the latter case, they are more probably the remains of completely internal (intrathalamic sensu Fernandez Lopez, 1987a) settling or simply non-infilled tubes.

## Bioerosion.

Bioerosion phenomena on ammonites collected from the section studied are very frequent, affecting approximately 80% of the total number collected. In general, the traces are almost exclusively settled in the life chamber infilling, sometimes affecting the last one or two phragmocone chambers of both composite and internal moulds (Pl. 3, Fig. 10). The majority of the traces is attributable to an unidentified ichnogenus, which the real nature of borer is clear in examining the Fig. 5. These appear to anastomose from a deeper and larger excavated section, normally developed along the umbilical border or located in the internal half of the sides of whorls in the body-chamber, from which mean-

PLATE 2

Fig. 1 - Specimen 257MM3.69, *Hildaites wrighti* (Spath), upper side: except for the last two chambers the phragmocone is infilled only for half or less of its height. Note the sparry calcite ribs directly superimposed on the infilling material without fragile deformation.

Fig. 2 - Lower side of the same specimen as Fig. 1: note the total absence of ornamentation reliefs in the last preserved whorl.

Fig. 3 - Effect of compaction on the upper side of an ammonite specimen, which forms a quasi-sutured contact between the surrounding matrix and the infilling rock. The section cuts through the boundary between the body chamber and the phragmocone. Smear slide.

Fig. 4 - Detail of the phragmocone of the specimen in Fig. 1. Boring/encrusting polychaete tubes are settled upon and below the ribs. Both ribs and tubes are filled by sparry cement.

Fig. 5 - Detail of the specimen in Fig. 1.

Fig. 6 - Probably intrathalamic settling facets of polychaete tube in the body chamber of specimen 1403MM7.39 *Hildoceras semipolitum* Buckman.

Fig. 7 - Same specimen as Fig. 1, last two phragmocone chambers: note ribs superimposed above the suture line, cut by the polychaete tubes. In this portion, both ribs and tubes are non-sparitic.

Scale bar 1mm, except in Fig. 3, where is 0,5 mm.


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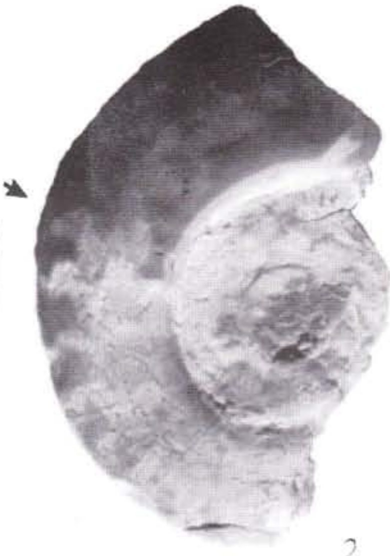
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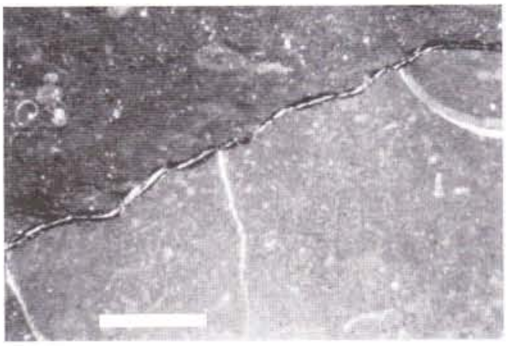
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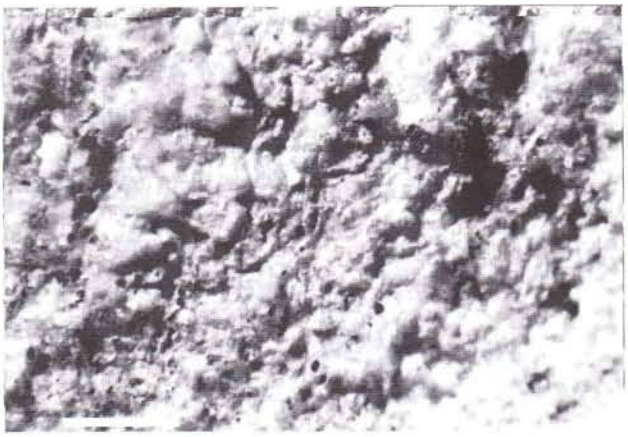
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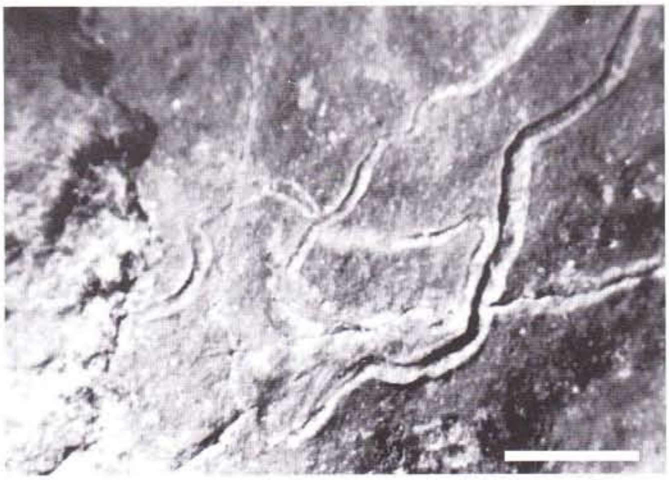
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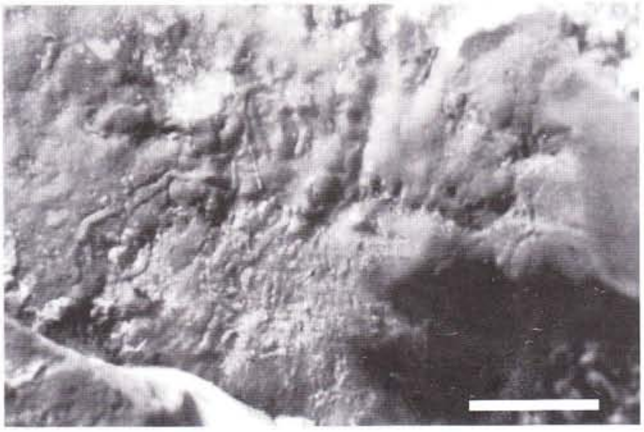
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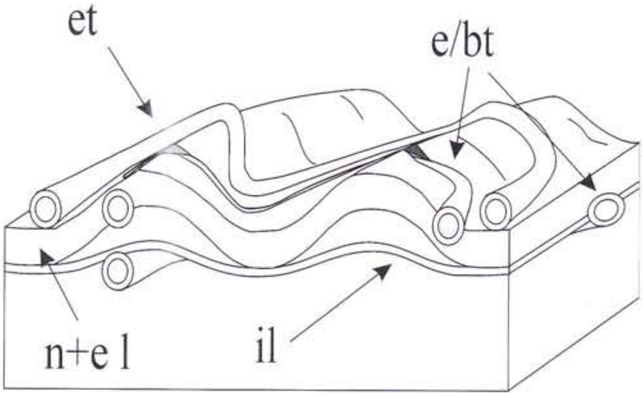

Fig. 4 - Different settling of polychaetes tubes on an ammonite shell: et: encrusted tube (serpulid); e/bt: an encruster/bioeroder tube; n+el: external (prismatic) and nacreous ammonite layers; il: internal (prismatic) layer.

dering minor branches lead. Some of them can pass beyond the sides of the whorls and extend into the neighbouring one (Pl. 3, Fig. 1-3, 7, 9, 10). Observation of fossils with different degrees of bioerosion gives us to understand that the boring action starts on either the lower or the upper side and may or may not extend to the other side. There are some similarities between these traces and *Maeandropolydora* Voigt, in the moulds the latter appear normally as grooves and, at less degree, as galleries. In both cases the organism predominantly acted in one area then expanding its action in others, but in *Maeandropolydora* the trend is bended, whilst in these specimens the development is more branched and less curved, but never meandering. Furthermore in the latter, the width of the sulci is approximately the double of those of *Maeandropolydora* (see Bromley & D'Alessandro (1983), pl. 24).

Other rare case of bioerosion detected (Pl. 3, Figs 3, 4-6) are attributable to clionid sponge (see Raffi & Serpagli, 1993; p. 46, fig. 2.17).

The meaning of the prime traces has already been discussed in Macchioni (1996) and Macchioni et al. (1996), who hypothesised that the bioerosion phase took place after an increase in environmental energy which exhumed the historic layer and the cemented moulds.

## Taphonomic implications.

The case-studied specimens are associated with others of the same species which are not encrusted and/or bored, and their stratigraphic succession is in congruent with other ammonite successions known in literature as biozonal reference base. With the exception of the fossils presenting truncational facets (e.g. Pl. 1, Fig. 2), none of the ammonites studied display any dis-

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PLATE 3

Fig. 1 - Specimen (x 1) 1057MM6.23 *Hildoceras lusitanicum* (Meister), lower side. As shown in Text-Fig. 3, the specimen was found inclined in the rock and had experienced deformation congruent with its condition of burial. The crushed part (upper part of the photo) probably protruded from the sediment surface. The discontinuity between the life-chamber and the sediment was effected artificially during preparation.

Fig. 2 - Specimen (x 1) 92MM3.00 *Protogrammoceras* aff. *meneghinii* (Bonarelli), lower side. The *Maeandropolydora*-like borings are more deeply incised in the vicinity of the umbilical border and some meandering branches extend toward the venter.

Fig. 3 - Upper side of the specimen in the last figure (x 1,1). Note the great degree of incision which results in the almost complete destruction of the preserved infilling of the body chamber. The completely absence of conservation of shell structure in the more external portion of the body chamber, is due to pressure dissolution phenomena. These can be or not to be related to bioerosion or bioturbation phenomena, otherwise it is also postulated that the presence of the bioerosion galleries on the other side may emphasise the effects of burial dissolution. It is possible that some minor branches extending outer of the more dare due to the action of clionid sponges like in Fig. 4-6.

Fig. 4 - Cast (x 1) of the upper side of the specimen 340MM3.86 *Polyplectus apenninicus* (Haas). Bioeroded branched galleries, here in positive relief have developed in the body chamber (see Fig. 6), probably attributable to a clionid sponge.

Fig. 5 - Detail of Fig. 6: the floor of the galleries is in relief with respect to the mould surface.

Fig. 6 - Upper side of the 340MM3.86 *Polyplectus apenninicus* (Haas). The ribs are not cut and continue through the galleries, this confirms that the boring occurred in the shell test. The galleries are here in negative relief.

Fig. 7 - Lower side of specimen 097MM3.13 *Petranoceras mariotti* Venturi, x 0,9. It was bioeroded by a *Maeandropolydora*-like borer and encrusted by a crinoid (centre of the lateral side of the whorl towards the bottom of the figure). The shell was broken during the biostratinomic phase, part of the sediment infilled is protruding out of the phragmocone.

Fig. 8 - Detail of the crinoid root, now settled directly on the mould surface of the specimen 097MM3.13.

Fig. 9 - Lower side (x 1,1) of the specimen 330MM4.14 *Harpoceras mediterraneum* (Pinna). A minor branch of bioerosion gallery protruding from the upper to the lower side.

Fig. 10 - A bioerosion groove without meandering branches or a trace of predation developed in the phragmocone of the upper side of the specimen 086MM 3.13 *Protogrammoceras bassanii* (Fucini). Some meandering branches are visible anyway in the lower side of the picture and in the other side of the specimen. The specimen is deformed in a manner consistent with its burying conditions. It must be observed that the contacts between the casts and the surrounding matrix are made of dissolution seams (Pl. 2, Fig. 3). In case of presence of original breakage of the shell, the seam can develop inside or outside the ideal extension of the test, leaving a cavity or a bulge (Fig. 7) indifferently.

Scale bar 1mm.

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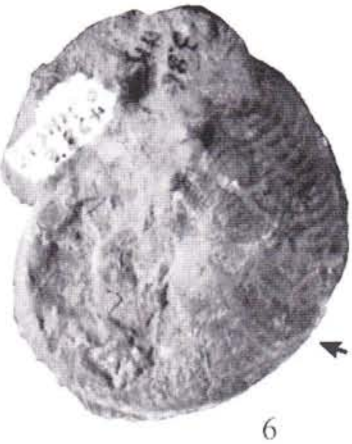

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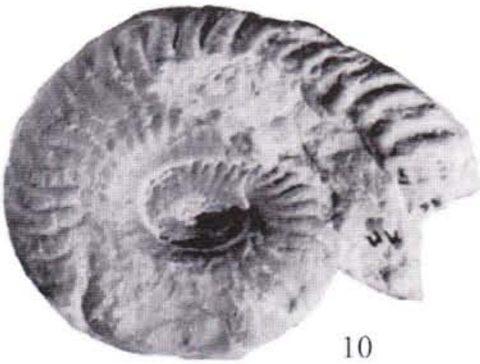

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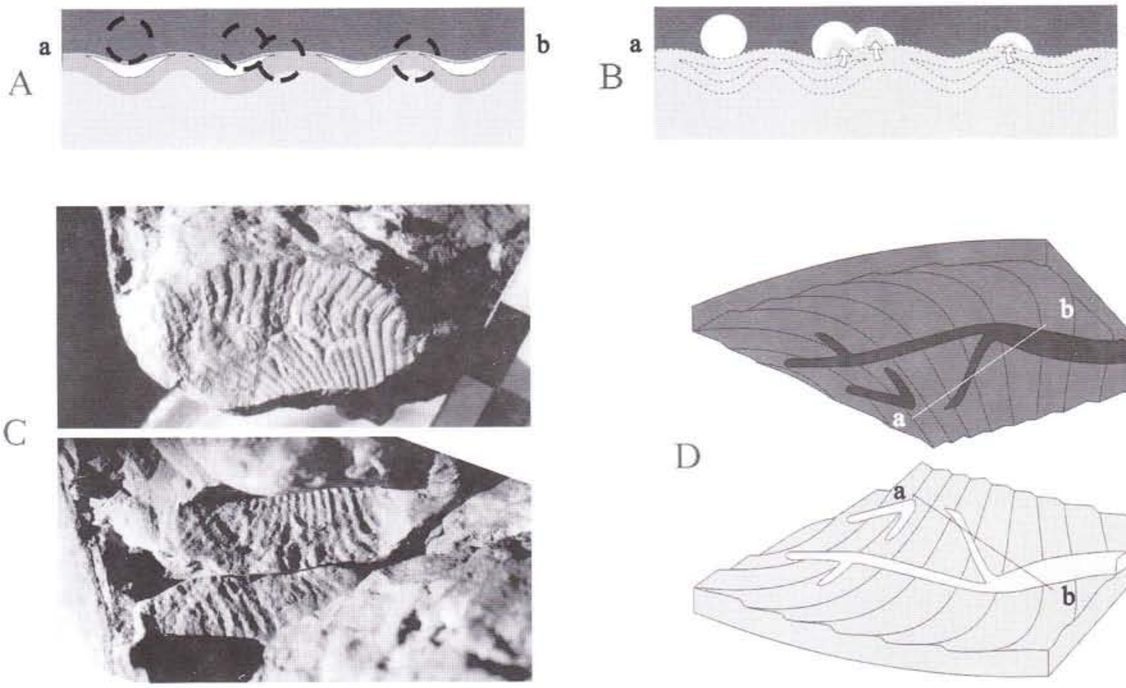

Fig. 5 - Evolution diagram of the formation of the replica of bioerosion grooves on an ammonite mould. The scheme is a based on what is visible in Fig. 5 C, where in the upper photograph is visible the mould made of limestone of shell fragment which lain in the rock convex downward. The matrix below (in the lower picture) is marly and replicates the shell ornamentation and partly the grooves. It is clear that the borer acted principally along the test and partly on the limestone cemented mud. The galleries drilled close to lower shell surface or directly in contact with lower marly matrix (Fig. 5 A, central and right side) were filled during the burying diagenesis when the aragonitic shell disappears (Fig. 5 B). Those bored more closely to the upper limestone mud were later infilled laterally and were not replicated in the marly mud (Fig. 5 A, left side). The quasi-complete replica of the boring galleries confirms that the boring was exerted on a test later disappeared.

continuity between the body chamber infilling and the surrounding rock, and some of them display a geopetal fabric consistent with the polarity of the stratigraphic succession. Following Fernández López (1986) and Fernández López & Meléndez (1994), the above cited aspects can be utilised to assess that these fossils were not reelaborated. Furthermore, it is here suggested that both encrustation and bioerosion took place when the shell was still present, not necessarily, in the first case, in the presence of sediment infilling. However, as encrustation and bioerosion of the lower side of internal moulds constitute reelaboration criteria of Fernández López (1986) and Fernández López & Meléndez (1994), it is of crucial importance to reconstruct the taphonomic excursus of the fossils collected.

### Encrustation.

The apparent contradiction is resolved by reconstructing the diagenetic evolution of the specimens which preserve external ornamentation details. Specimen 1328MM6.86 is encrusted on both sides (Pl. 1, Fig. 1-5): on the upper side serpulid tubes are directly settled on the striae which are the replica of external shell ornamentation, which is superimposed on the shell infilling sediment, while those present on the lower side of the specimen are settled on a replica (i.e. internal mould) of the internal structure (Fig. 2). As noted in paragraph 4, the presence of ornamental details superimposed on a replica of the internal structure means that the specimen is a composite rather than an internal mould. It must be pointed out that if the settling of the serpulid tubes on the lower side of the sample took place on what is now an internal mould, it must have occurred after the formation of the composite mould. As stated above, the latter process takes place during deep burying conditions, so it might have been assumed that this specimen would have been reelaborated from a different stratigraphic position.

### Bioerosion.

The same reasoning as above can be applied in these cases: specimen 1328MM6.86 also has grooves attributable to an ichnogenus similar to *Maeandropolydora* Voigt, which provides evidence that reelaboration is not necessary to explain or allow this phenomenon (Pl. 1, Fig. 1). This process can be better understood by the examination of its mechanical evolution, which can be achieved by analysis of the specimen 1057MM6.26, *H. lusitanicum* Meister (Fig. 3; Pl. 3, Fig. 1-2). The specimen is an internal mould and as suggested by Macchioni et al. (1996) was initially buried and then probably exhumed, which would allow the borer to detect the shell and perforate it in a downward direction (Fig. 7). The specimen is in this case complete, showing the peristome and a rostrum in the venter; at the same time it is deformed in a manner consistent with its burying conditions, and there was no discontinuities between the rock matrix and the shell infilling (Pl. 3, Fig. 1; see also Pl. 3, Fig. 10). The two latter aspects confirm the common diagenetic evolution of fossil and sediment, excluding reelaboration (Fernández López & Meléndez, 1994). The above is a very special case: ammonite specimens are normally inclined dipping toward the first quarter (from the aperture) of the last preserved whorl. In these cases, as shown in Pl. 3 (Fig. 2, 3, 7, 9, 10) the *Maeandropolydora-like* borers start their action from the ammonite shell aperture, which was closer to the sediment/water interface or protruded from it.

### Encrustation-Bioerosion.

Instead to be encrusted directly on the mould surface (internal and/or composite) some tubules are partly inserted inside the shell infilling. Those located in the body chamber are likely intrathalamic settling (Pl. 1 fig. 9, Pl. 2, Fig. 6), at the contrary those found in the phragmocone worms were shell encrusters and borers simultaneously. In fact, breakages of the shell which could have allowed the polychaete to go inside the chambers are absent. These apertures would be evidenced by the presence of fusion zones or discontinuities (Pl. 3, Fig 7, 10) between the shell infilled sediment and the surrounding matrix.

Their very nature bars us from establishing whether settling occurred before or after the infilling of the shell, or on/through the shell or on the internal mould itself. In the cases of samples 257MM3.69 e 200MM3.76, we can accept that settling occurred directly on the shell.

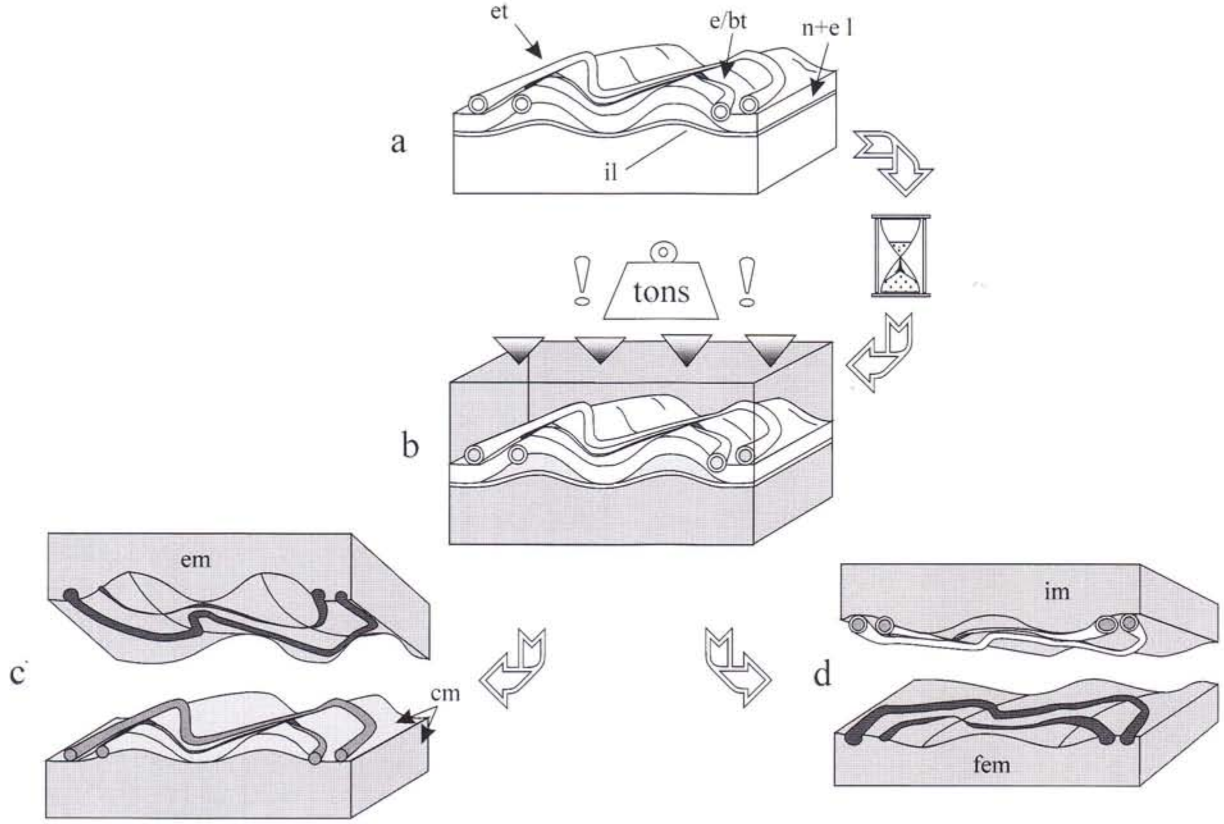

Fig. 6 - Evolution diagram of the formation of a mould with detail of a portion of a shell. For simplicity and for reasons of drafting, the polychaetes tubes are drawn smaller than the inflection of the ornamentation and the external and nacreous layers are not differentiated. a) A shell test is encrusted and encrusted/bioeroded, the firsts are settled upon the external (prismatic) layer, the seconds are settled upon it and/or throughout the test and/or below the internal (prismatic) layer. b) After the shell is filled the pressure from above causes the dissolution of the shell; c) On the upper side the external cast is superimposed on the internal mould and the polychaetes tube tests dissolve. In this case, the external mould is a quasi-exact replica of the external ammonite ornamentation. d) On the lower side the polychaete tubes can partly survive dissolution but the same process settles them directly on the internal mould surface. In the diagram none of the three criteria for formation of composite moulds has been adopted in particular. The infilling of the inter-layer cavity and the dark line that separates it from the internal mould s.s. have been drawn in order to make them stand out. It must be noted that in this case the external cast is not a true external mould because it is an exact replica of the inner ammonite structure. Terminology: et: encrusted tube (serpulid); e/b t: an encruster/bioeroder tube; e+n l: external (prismatic) and nacreous layers; il: internal (prismatic) layer; cm: composite mould; im: internal mould; fem: false external mould.

In the former, where a portion of the neomorphic shell is preserved (Pl. 2, Fig. 4-5), polychaete tubes (infilled with sparry calcite) are partly settled on the preserved shell test and partly disappear into it. On the other hand, where the shell test structures are only impressed, tubes are completely visible and appear to cut through the infilling sediment, and the suture line is completely visible (Pl. 2, Fig. 7). It must be noted that the phragmocone of this specimen was only infilled in its lower half, and the external structures are superimposed on it without fragile deformation like the neomorphic shell test. This confirms that the deformation and the superimposing take place during the deep burial compaction phase.

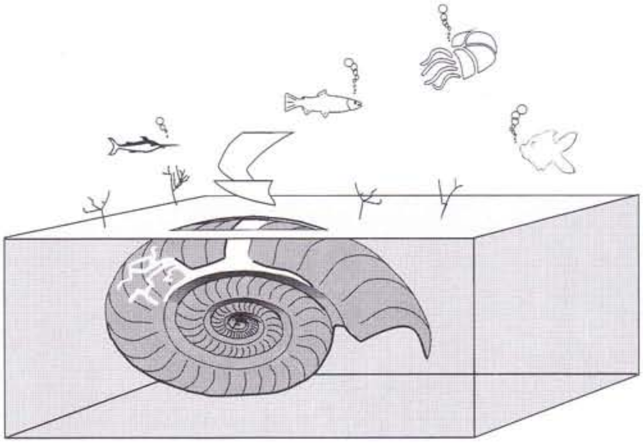

Fig. 7 - Reconstruction of a possible way of settling of the *Maeandropolydora* Voigt-like borer, based on the preservation features of specimen 1057MM6.23 shown in Pl. 3, Fig. 1-2. A small portion of the specimen probably protruded from the sediment surface allowing the borer (twisted arrow) to detect the shell test and to bore into its lower side as well. The ammonite is inclined toward the centre of the paper.

Specimen 200MM3.76 (Pl. 1, Fig. 6-7, 9, 11-12) is a pàrtial mould (sensu Macchioni et al., 1996) and preserves encrustation-boring tubes on both sides. In the last phragmocone chambers, first half of the external whorl, the sides of the upper half are filled by marl in which the rib traces are impressed. The marl is delicate to say the least, and it must be assumed that it would have been unable to stand up to a reelaboration phase as it can be removed easily during water washing.

## Conclusions.

The presence of boring and/or boring-encrustation in the lower side of internal moulds can be interpreted as evidence of reelaboration. Regarding the specimens in question, which have the double feature of composite and internal moulds, it can be said that, if the colonisation phase in their lower sides took place on the internal moulds, it must have occurred after the diagenetic compaction phase which is characteristic of deep burying. If this was the case, there should have been a significant anomaly in the stratigraphic position of the encrusted and bored moulds, or at least there would be other taphonomic evidence of reelaboration.

The presence of composite moulds on the upper sides of ammonite specimens provide evidence of the survival of a test until the compaction phase, so it is clear that the settlement of polychaetes (encrusting and boring-encrusting) occurs directly on the shells and not on their infillings.

With regard to the lower sides of these same specimens, now preserved as internal moulds, it must be concluded that the settling of serpulids on the internal ammonite shell replica is due to an adhesion of structures that were previously separated by the shell test. This was dissolved during compaction at the same time as the formation of composite moulds on the upper sides of the same fossils (Fig. 2). The same conclusion can be drawn for tubes of boring-encrusting polychaetes, which originally were partly settled inside the shell.

A simple process of adhesion of parts that were originally separated by the shell, occurring in the diagenetic compaction phase, may also be hypothesised in cases where we do not have the simultaneous formation of composite moulds on one of the two sides; in other words, it could be much more common than is thought. It can also be applied to the encrusted crinoid root specimens reported here (Pl. 3, Figs 6, 7). Indeed, the same process must be invoked if one accepts the hypothesis that Seilacher's specimen of *Buchiceras bilobatum* Hyatt was colonised on its shell test either during its life (Seilacher, 1960; Heptonstall, 1970) or during post-mortem-drifting (Donovan, 1989). As it is clear from the drawing by the authors mentioned, the Ostreidae which encrust this specimen are settled directly onto an internal mould.

Even if not attributable to any of the known species of *Maeandropolydora*, or perhaps not even to this ichnogenus itself, settling methods and developing structures of pure bioerosion structures share some similarities in their operation manner. Cases of bioerosion of *Maeandropolydora decipiens* Voigt have been observed by Bromley & D'Alessandro (1983, pl. 24, fig. 1, 3) on the attachment surfaces of certain encrusted bivalve shells and also as boring galleries developed along the separation surface between the aragonitic and calcitic layers in other bivalve shells. The preservation of only half of the boring galleries in the meandering branches present in the case-studied samples probably means that, also in these case, the separation surface between the infilling and the test was a sort of a guideline for the borers. Nevertheless, their action was not restricted to the test but was developed more or less deeply on the shell infilling. Even though the depth of incision of the galleries can be exaggerated by dissolution phenomena but above all the dissolution effects must not to be confused with borings (Pl. 3, Fig. 3). Their similarity to hard and/or firm material borers gives us reason to think that complete exhumation of the shell need not have taken place to permit the boring action; a small exhumation might however have helped the borer in detecting the presence of a shell test (Fig. 3).

In conclusion, encrusting and bioerosion of lower-side internal moulds cannot univocally be considered to be reelaboration criteria without taking into account other taphonomic evidence, for example incongruent truncation facets, geopetal infilling, or, as shown in a specimen documented by Fernández López (1984, fig. 8), xenomorphic growth of encrusters on ammonite suture lines. This is due to diagenetic processes, which can provoke superimposing of originally separated structures. Furthermore, in cases of pure bioerosion the mechanical impossibility of the borer reaching the lower sides of buried internal mould must always be demonstrated.

It can be seen that the validity of encrustation reelaboration criterion, set out by Fernández López (1984) and Fernández López & Meléndez (1994), is here reinforced: the lower sides of the samples studied (now internal moulds), which are now encrusted, were not originally the surfaces in contact with the substrate at the time of the last sedimental burial.

The reason for the formation of composite moulds on only the upper side of fossils only remains unclear. A different degree of diagenetic action, apparently conditioned by the polarity, was also discovered by Garrison & Kennedy (1977), who assessed also that the dissolution rate was higher on the upper sides of the nodules.

In the studied case, it is retained that the fossils deposition occur mainly during period of interruption or lower calcareous mud rate of sedimentation. This period were later emphasised by the formation of swarms of dissolution seams due to the different cementation degree of each layer, which create thin marly levels on which ammonites lie (for an extended tratement see Wanless, 1979; Clari et al., 1984; Bathurst, 1987, 1991; Martire, 1989; Ricken & Eader, 1991; Clari & Martire, 1996). During the diagenetic compaction phase the lower sides of fossils were subject to a major degree of dissolution which in some cases provoked the fusion of the sediment shell infilling and other elements which were earlier settled on the shell. On the upper sides of ammonites the major degree of cementation allowed the formation of composite moulds both by overprinting and adherence.

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