Pseudoborings in Ammonite Molds: The Combined Result of Predation and Taphonomic-reworking (Bajocian, Normandy, N. France)

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Unusual structures, observed on taphonomically-reworked ammonite molds collected in the Oolithe Ferrugineuse de Bayeux Formation (Bajocian, Normandy), are described. They appear as depressions in the mold, located below "holes" in the shell, and they are filled with a sediment plug texturally different from the mold. These structures are called "pseudoborings" because of their similarity in both external shape and size (from 2 mm to over 10 mm in diameter) to bivalve borings. Detailed analyses of polished surfaces and thin sections cut through the mold show that the depth of penetration of pseudoborings and the irregularity of the plug-mold boundary exclude a bioerosional origin. The origin of pseudoborings is hypothesized to be due to erosion of unlithified sediments and exhumation of sediment-filled ammonite shells, previously damaged by attacks by cephalopod predators, resulting in a partial emptying of the conch.

INTRODUCTION

The Bajocian strata of the region around Bayeux, N France (Fig. 1), have been studied for more than 150 years (d'Orbigny, 1842–51) because of their very rich fossil content. In addition, this area has been proposed as the Bajocian stratotype (e.g. Rioult, 1964; 1980). More recently, however, it has been shown that the Bajocian of Normandy does not fulfill the requirements of a Global Boundary Stratotype Section (Pavia, 1994) because the strata are mostly highly condensed calcareous sediments rich in ferruginous ooids ("Oolithe Ferrugineuse de Bayeux"). Moreover, sedimentologic analyses by Fürsich (1971) and recent detailed taphonomic studies by Pavia (1994) and Martire and Pavia (1996), in the classical localities of Sully and Port-en-Bessin (Fig. 1), have shown that most of the ammonite molds on which biostratigraphic scales are based are taphonomically-reworked and mixed, hence, no simple stratigraphic division can be made.

In the course of new studies, that include consideration of new stratigraphic exposures (Revellino, 1995; Quaglia, 1997; Boscolo, 1998; Torta, 1999), enigmatic structures have been observed on some ammonite internal molds. Some of these structures were described by Pavia (1994) who interpreted them as bivalve borings. More detailed analyses directed at verification of the origin of these structures revealed that they show complex features probably due to the combined action of predation and reworking. The object of this paper is the description and intepretation of these structures that also could be present in other marine condensed sequences.

THE "OOLITHE FERRUGINEUSE DE BAYEUX"

The Bajocian of Normandy comprises two formations (Fig. 2): the Maliére and the Oolithe Ferrugineuse de Bayeux, from oldest to youngest, respectively. The Maliére Formation (MF) is represented by grey cherty limestones. Glauconite-rich sediments, known as "Couche Verte," fill depressions less than 15 cm deep and firm-ground burrows in the top of the MF at the unconformable boundary between MF and the overlying Oolithe Ferrugineuse de Bayeux (OFB). The OFB consists of grey to yellow limestones rich in ferruginous or phyllitic ooids. Ooids range in size from 0.3 to 2 mm and may be variably abundant in different beds, but they are never in sufficient abundance that would result in a supporting framework. The intergranular matrix is represented by wackestones to packstones containing thin-shelled bivalves, echinoderm fragments, benthic foraminifera, peloids, and a scarce to absent detrital quartz fraction. The ammonite molds described here were collected from the OFB. The OFB may be subdivided in two parts, with the boundary marked by a burrowed omission surface. The lower part only contains ferruginous ooids, whereas the upper part is characterized by white phyllitic ooids and a higher mud fraction in the matrix (Rioult et al., 1991).

The facies of the OFB is monotonous and the only lateral changes concern total thickness and number of beds. In the classical localities close to the English Channel coast (Sully, Port-en-Bessin; Fig. 1) the OFB does not exceed 40 cm organized in not more than 4 beds, whereas the thickness reaches 170 cm with up to 13 beds in the newly studied section of Bretteville (Fig. 1). The boundary of the OFB with the overlying formation ("Calcaires à Spongiaires") may be transitional similar to that seen at Sully, or sharp where it corresponds to another omission surface as at Bretteville (Fig. 2).

The great majority of the ammonites collected in the OFB are taphonomically reworked (= reelaborated *sensu* Fernàndez-Lòpez, 1984; see also Gòmez and Fernàndez-Lòpez, 1994, and Fernàndez-Lòpez and Melendez, 1994). They have been exhumed after initial burial, in response to an erosional event, and buried again in younger sediments. The main diagnostic features for taphonomically-reworked ammonites in the OFB, according to Pavia (1994) and Martire and Pavia (1996), are: fractures, borings, and abrasion traces on internal molds; textural difference between mold and matrix; iron oxide coatings; and contrasting geopetal fills in different chambers.

Taphonomic reworking has important implications on the bio-chronostratigraphy of the OFB. Taphonomically reworked fossils are, by definition, always older than the surrounding sediments and, therefore, must be used with caution (Fernàndez-Lòpez, 1991; Salvador, 1994). On the basis of an analysis of the ammonite association, Pavia (1994) was able to distinguish taphonomically reworked and non-reworked fossils, and concluded that the OFB at Sully belongs to the Upper Bajocian, *Parkinsonia parkinsoni* Zone. This is in contrast with previous authors (Rioult

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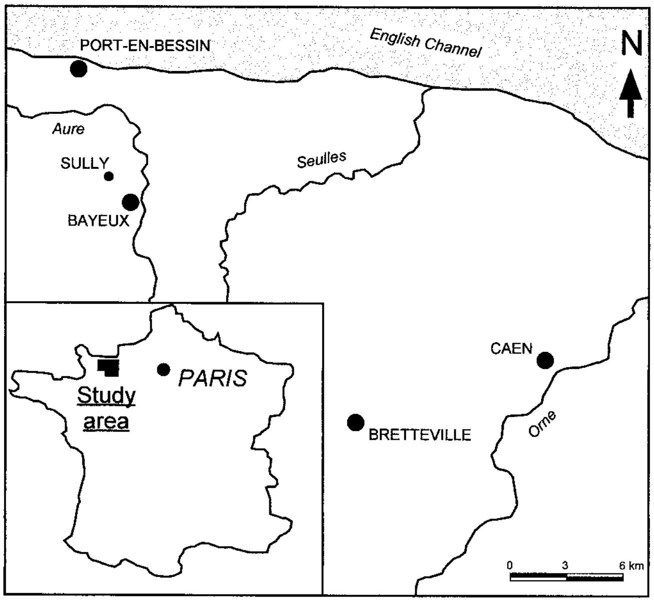

FIGURE 1—Schematic map of the study area.

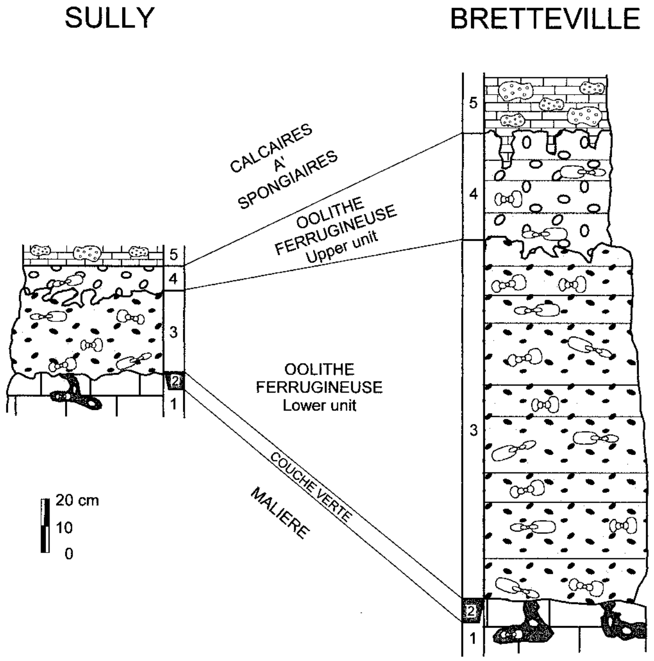

FIGURE 2—Stratigraphic logs of the studied sections.

et al., 1991) who considered that three biozones (*Strenoceras niortense, Garantiana garantiana,* and *Parkinsonia parkinsoni* Zones) are represented as a condensed thin succession at Sully. A different situation is present in the Bretteville section that is less condensed. However, a detailed description of this section and of the ammonite assemblages it contains is beyond the scope of this report and will be the object of future research.

PSEUDOBORINGS: DESCRIPTION, DEFINITION, AND INTERPRETATION

The great majority of the ammonites of the OFB consists of internal molds with calcitized shells. The aragonite-to-calcite transformation may have proceeded through inversion or dissolution and precipitation of limpid spar depending on individual specimens (Martire and Pavia, 1996). In all the sections studied, 12 specimens (approximately 2 % of the collected ammonites) show unusual structures, that appear as sharply edged "holes" in the shell (Fig. 3) or, if the shell has been lost during sampling, as subcircular portions or "plugs" in the mold in which the sediment is lithologically distinct from the mold itself (Fig. 4). The "plug" of these holes, in fact, is filled with the same Fe-oolitic sediment as the enclosing bed. The shape of these structures is mainly circular to elliptical, but more irregular margins (e.g., arched shapes) also occur (Fig. 5). These holes have a long axis that ranges from 2 mm to more than 10 mm. Pavia (1994) observed these features in a few ammonoid specimens from the Sully section, and because of the size and the rounded shape of the holes, and the textural difference between the fine grained mold and the Fe-oolite-bearing fill of the hole, concluded that their origin was by bivalve borings on taphonomically reworked fossils. Recently, additional sampling in the same sections and at Bretteville has provided new examples of such ammonoids exhibiting a greater morphological variety of these structures.

Analysis of these holes and "plugs" included preparation of several thin sections and of polished surfaces cut through the molds perpendicular to the plane of symmetry, highlighting the discontinuities that exist between "plugs" and molds. Such discontinuities often are accentuated by a yellow brown band that is due to impregnation of the mold by Fe-oxides/hydroxides. The band decreases in pronouncement away from the plug- mold boundary (Fig. 6). There are four features of this discontinuity, however, that contrast with the boring hypothesis proposed by Pavia (1994). These four features are: (1) The depth of the plug is usually less than what is normally shown by the flask-shaped bivalve borings which have a vertical penetration greater than the apertural diameter; (2) the irregularity of the plug-mold boundary markedly differs from the typically clear-cut, smooth profile of *Gastrochaenolites;*

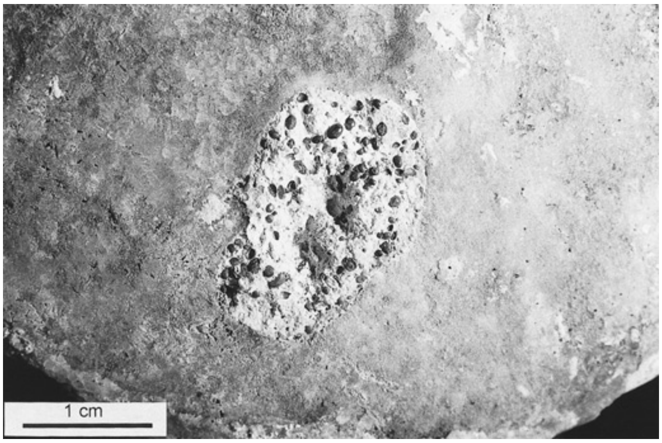

FIGURE 3—Detail of a "hole" in the calcitized shell of a *Oppelia bajociensis* FAVRE (Fig. 5 b). Note the sharp and rounded edges of the "hole" and the infill by a non-mineralized Fe oolitic limestone.

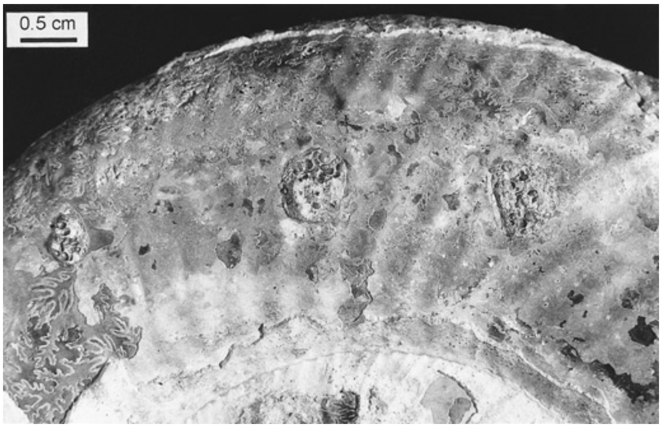

FIGURE 4—Detail of three aligned "holes" on the mold a *Prorsisphinctes reparator* (BUCKMAN)(ex *Leptosphinctes leptus* non BUCKMAN in Pavia, 1994, Pl. 1, fig. 1; Fig. 5 a). Note the textural difference between the fine-grained mold and the Fe-oolitic infill of the "hole".

(3) the small-scale features of the plug-mold boundary show that the grains are not truncated across the boundary (Fig. 6) as a result of bivalve boring activity ; and (4) there is no difference in the cathodoluminescence observed across the boundary. This indicates that differential cementation did not take place, and that the plug and the mold were co-cemented during diagenesis.

The term pseudoboring is herein proposed to indicate structures, subcircular to more irregular in shape and filled with a sediment different from the mold, that are not due to bioerosion, but may be mistaken for borings when examined in hand specimen.

The interpretation of pseudoborings in the Bajocian ammonites of the OFB requires that two aspects be analysed separately. These are: (1) the origin of the hole in the shell; and (2) the origin of the microdiscontinuity between the plug and the mold.

Origin of the Hole in the Shell

Some ammonites in the OFB exhibit only one pseudoboring whereas others have up to eight. When multiple pseudoborings are present, they occur on both sides of the ammonite and often correspond to each other, as the camera lucida line drawings clearly demonstrate (Fig. 5). Moreover, pseudoborings may be aligned resulting in rows of two or three holes coincident on opposite sides of the shell (Fig. 4). Three mechanisms may be responsible for producing such damage in ammonoid shells. These include: (1) Impact of the shell against hard objects; (2) Drilling by carnivorous gastropods; and (3) Predation by the teeth of durophagous predators.

Impact During Transport

Platform environments, such as those where the OFB deposition took place (e.g. Chan, 1992; Burkhalter, 1995), commonly are characterized by episodic high energy events such as storms that, in the biostratinomical phase, could have caused ammonoid shells to have impacted against other transported objects or hard substrates. The resulting damage to the shell, however, should show irregular and angular shapes that are localized randomly on the most fragile parts of the conch, such as the body chamber or the venter. The rounded, often neatly elliptical, nature of the holes, their alignment and position on the flanks of the shell, mainly corresponding with the phragmocone where the septal walls reinforce the conch, indicate that this mechanism does not apply to the studied examples (Figs. 3, 4, 5).

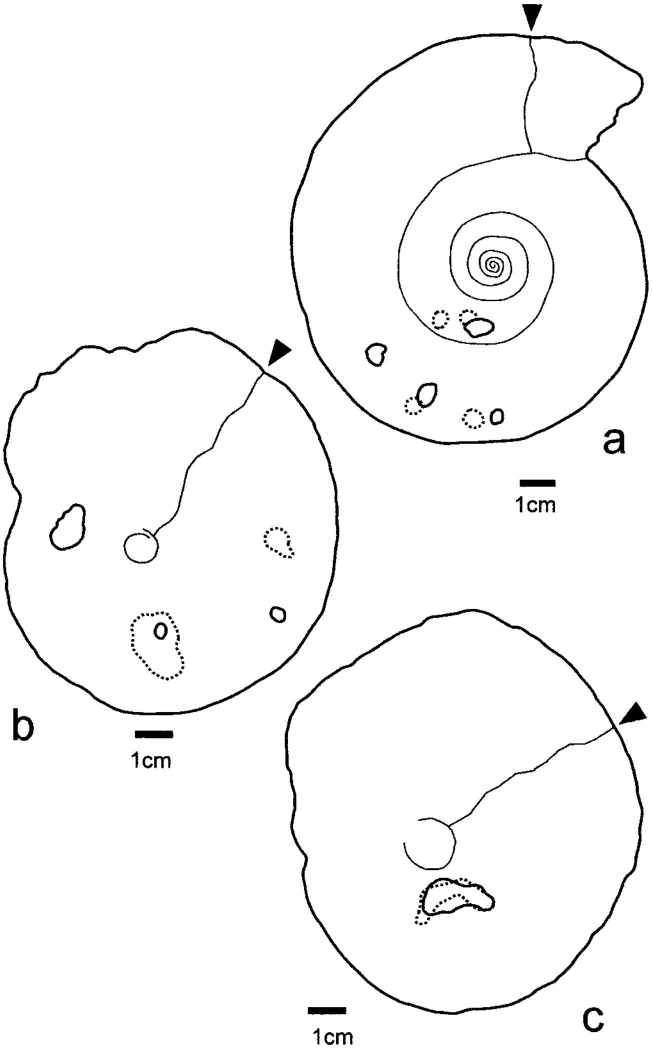

FIGURE 5—Camera lucida line drawings of three ammonites showing the location of several pseudoborings. Solid and stippled lines refer to pseudoborings observed on opposite flanks. Note that pseudoborings often correspond to each other on the opposite sides of the mold. Although the circular or oval shape is the commonest, some pseudoborings show an arcuate shape (c) possibly due to biting of arch-shaped jaws. The arrows point to the phragmocone-body chamber boundary. (a) *Prorsisphinctes reparator* (BUCKMAN); (b) *Oppelia bajociensis* FAVRE; (c) *Oppelia subcostata* BUCKMAN.

Carnivorous Predation

Predatory boring activities by gastropods have been considered as an explanation for holes in cephalopod shells (Mapes and Hansen, 1984). Boreholes by drilling gastropods, however, are usually only a few millimeters in

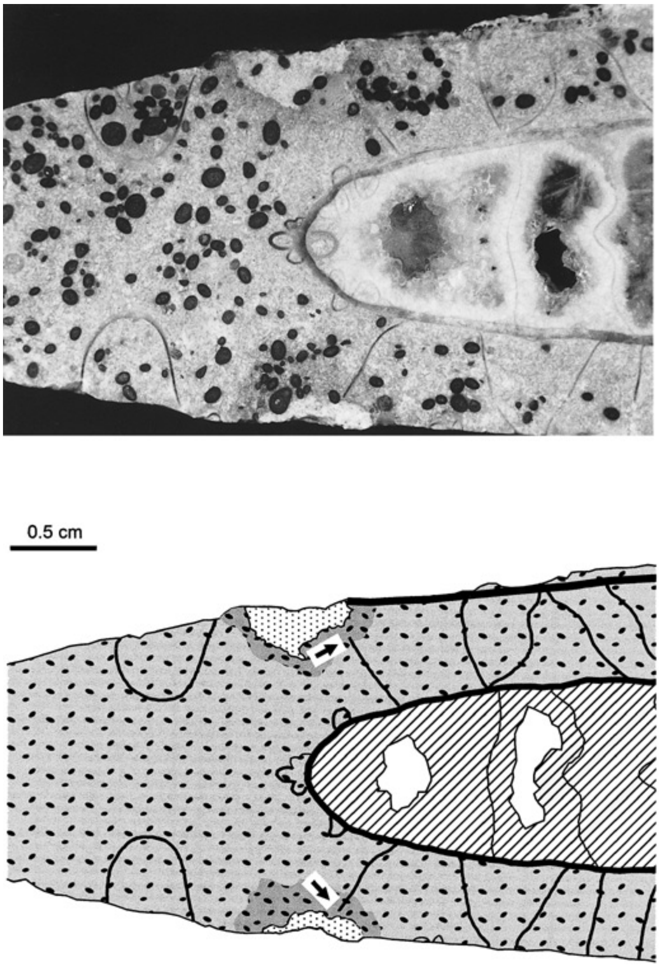

FIGURE 6—Photograph and line drawing of an axial section of a mold of *Oppelia subcostata* BUCKMAN (Fig. 5c) passing through two pseudoborings located on opposite flanks of the ammonite. Note: the different texture and colour of the mold and of the pseudoboring infill; the dark halo of the pseudoboring due to Fe oxide impregnation of the mold; the irregularity of the pseudoboring-mold boundary, with Fe-oolites crossing it; and the breakage of septa (arrows) below pseudoborings.

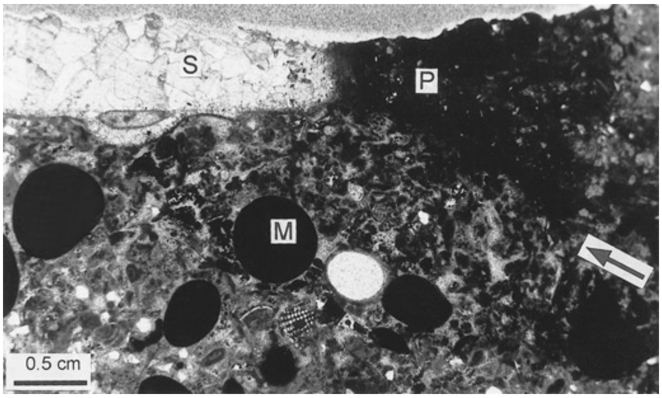

FIGURE 7—Axial section through a pseudoboring in *Oppelia bajociensis* FAVRE (Fig. 5b). Note the textural contrast between the mold (M) and the pseudoboring infill (P), and the sharp contact between the broken shell, now calcitized (S), and the "plug" of the pseudoboring (P). The arrow indicates the boundary. (Thin section, positive print).

diameter, only one per shell, and are very smooth and perfectly circular (e.g. Bishop, 1975). These features are not found on any OFB ammonites and this mechanism must be dismissed.

Durophagous Predators

The features of the holes (size range, subcircular shape, alignment, and correspondence on opposite flanks) found as pseudoborings observed in the OFB ammonoids allows comparison with circular-to-oval holes interpreted as bite marks that were produced by predatory vertebrates preying upon cephalopods (Kauffman and Kesling, 1960; Mapes and Hansen, 1984; Hewitt and Westermann, 1990; Martill, 1990; Mapes et al., 1995). The same holds true with the results of "biting" experiments conducted on *Nautilus* shells using a mosasaur robot (Kase et al., 1998). The breakage of septa in the phragmocone below pseudoborings (Fig. 6) seems to further support the vertebrate predation hypothesis. Doubt over the intepretation of bite marks on Cretaceous ammonites have been raised (Kase et al., 1998), but the recent finding of cephalopod jaws together with gastroliths in the stomach region of a plesiosaur provides further evidence to the hypothesis of reptile predation activity on cephalopods (Sato and Tanabe, 1998).

It is not possible to interpret the pseudoborings of the OFB ammonites as home depressions of patellogastropods subsequently crushed by compaction during burial, as suggested by Kase et al. (1994; 1998). There are several reasons to support this conclusion. The first concerns the absence of limpets in the OFB. Evidence for these organisms has not been observed on the ammonites, although epibionts, such as serpulids, bryozoa, and oysters, are common. The second reason is that the pseudoborings are sharply defined holes through the shell (Fig. 7) and, except for rare cases that are discussed below, no trace of fragmented ammonoid shell are present within the perforation. A third reason is that neither concentric fractures are present around the hole nor is there a mesh-like cracking pattern on the shell, reflecting diagenetic flattening of the OFB ammonite shells. A final reason to reject the patellogastropod organism concerns the morphology of the shell. The cross section of the shell shows a stepped, funnel-shaped profile that enlarges towards the mold (Fig. 8). This shape is in agreement with a puncturing of a multilayered, nacreous shell, as shown by the experiments of Kase et al. (1998).

Even though the exact identity of the predator is impossible to determine, it is herein concluded that the origin of the holes in the shells of the OFB ammonites is related to attacks by cephalopod predators with sharp, pointed teeth. Such predators include fishes, sharks, marine reptiles (such as plesiosaurs, ichthyosaurs), or those with untoothed, arch-shaped beaks, in the case of the pseudoborings illustrated in Fig. 5C (Lehmann, 1981).

Origin of the Microdiscontinuity Between the Plug and the Mold

The sediment textures of both ammonite molds and lithologies vary from wackestone to packstone-grainstone

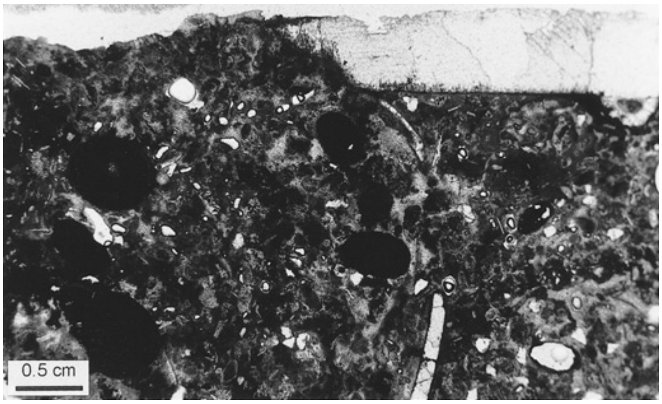

FIGURE 8—Axial section through a pseudoboring in *Oppelia bajociensis* FAVRE (Fig. 5b). Note the stepped, funnel-shaped morphology of the broken edge of the shell due to the external punching of a multilayer structure such as the ammonite shell. (Thin section, positive print).

that contain a mixture of different grains, mainly represented by thin-shelled bivalves, echinoderm fragments, benthic foraminifera, peloids, and a minor detrital quartz fraction. Therefore, the lithology is relatively uniform. Nevertheless, a clear textural and/or compositional difference between the mold and the plug is always recognizable. The plug is either more or less rich in micrite than the mold, depending on particular specimens (Fig. 7). In addition to this, the mold immediately below the boundary with the plug always shows a dark halo due to the impregnation of yellowish brown iron oxides (Fig. 6) and /or phosphates. The textural contrast and the mineralization document a discontinuity between the plug and the mold.

To explain such discontinuities and the irregular geometries of pseudoborings, the following hypothesis is proposed (Fig. 9). The punctured, but still entire, shell of a predated ammonoid was buried and partially or totally filled with sediment. After a variably long period, during which no appreciable cementation of the sediment occurred, an erosional event removed a certain volume of sediment and exhumed the subfossil/fossil. This probably occurred when the mold was stiff, but not lithified. In all the points where the shell did not exert a sheltering action, the unlithified sediment in the ammonoid was partially removed. This removal was particularly effective in the body chamber aperture region and at punctures in the conch. Sediment removal in the body chamber is supported by the presence of a discontinuity with the same characteristics of the mold "plug" described in the punctured areas of the conch (Fig. 10). A partial emptying of the body chamber, therefore, must have taken place while a depression was formed in the unlithified sediment below the punctures. This depression was variably deep and regular, depending on the hydrodynamic energy and the size of the hole. It is worth noting that pseudoborings occurring on both sides of the ammonite mold imply that the current responsible for the exhumation had to be strong enough not only to expose the upper part of the fossil but to overturn it. Subsequently, prolonged exposure on the oxygenated sea floor produced the staining at the microdiscontinuity, within the body chamber and at the pseudoboring boundary. At the time of the discontinuity staining, the entire

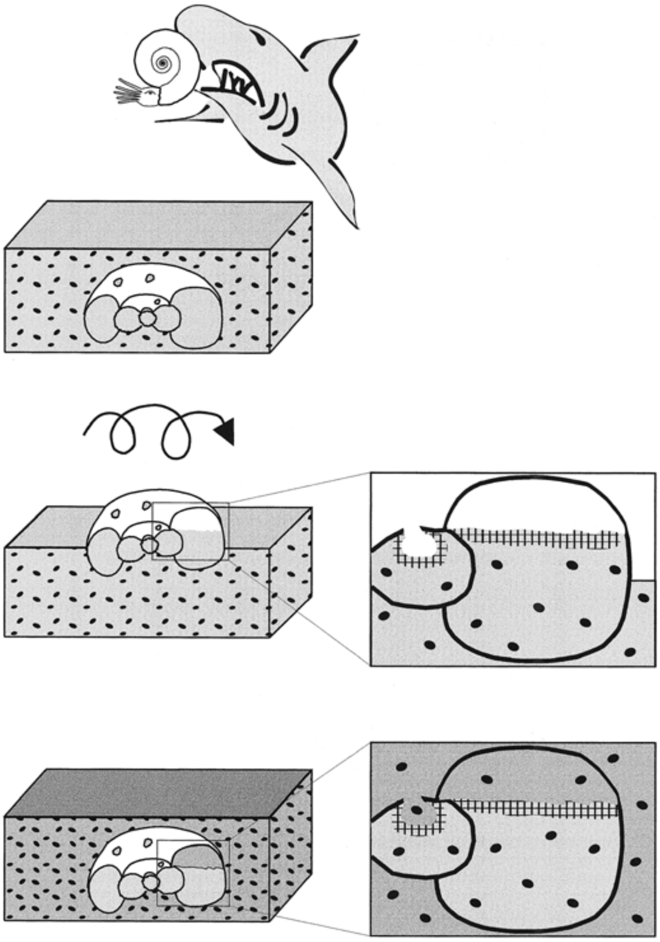

FIGURE 9—Schematic representation of the formation of pseudoborings. The grid overprint in the enlargements on the right indicates Fe-oxide staining of the mold. For details see text.

FIGURE 10—Axial section of the mold of a *Oppelia subcostata* BUCKMAN (Fig. 5c). Note that the internal discontinuity in the body chamber (small arrow) shows the same Fe-staining as the pseudoboring halo (large arrow).

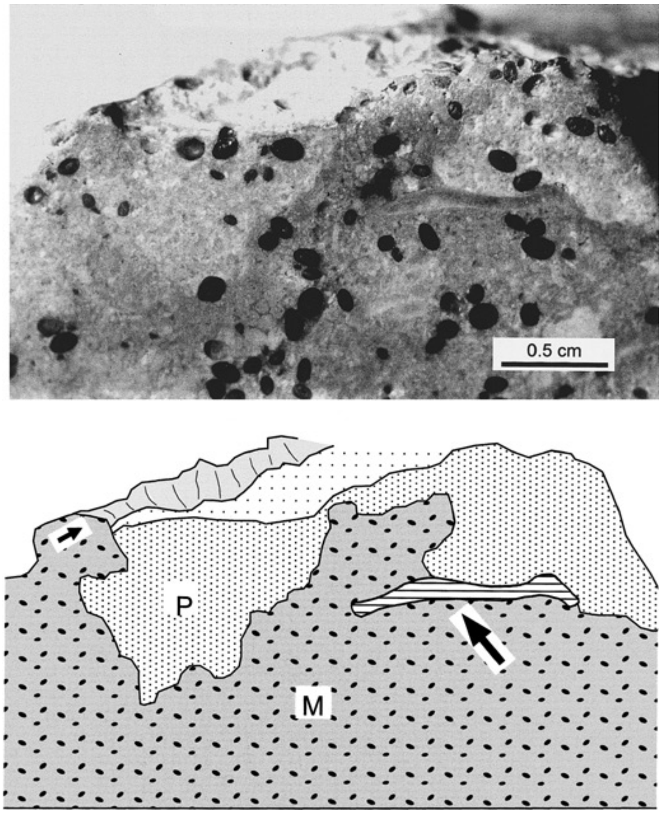

FIGURE 11—Photograph and line drawing of an axial section of a mold of *Prorsisphinctes* aff. *martiusi* (d'ORBIGNY; Fig. 5c) passing through a pseudoboring. In the background (upper part of the photo), slightly out of focus, the external part of the mold of the last whorl can be seen. Note: the different texture and colour of the mold and of the pseudoboring infill; the ''microslope'' of the pseudoboring depression (small arrow) where the sediment of mold ''crops out''; and the fragment of shell (large arrow) at the pseudoboring-mold boundary.

external of the shell was coated with iron oxide. The formation of the "plug," then, took place with the renewal of sedimentation and the reburial of the shell.

In one case, a shell fragment has been found below a pseudoboring at the boundary between the mold and plug (Fig. 11). The ornamentation, thickness of the shell, and spacing of ribs displayed by the fragment perfectly corresponds with the part of conch where the pseudoboring occurs. This shows that the shell was broken after initial burial, specifically when the phragmocone already was filled with sediment. Moreover, this is additional proof that the sediment fill was not lighified before reworking. Thus, the fragment of shell must have collapsed into the chamber and partially sank into the stiff, unlithified sediment in the chamber without leaving any void (Fig. 12). Such breakage of the shell also could be explained as a result of predatory attack on a reworked ammonite. This hypothesis seems unrealistic for biological reasons, but should not be ruled out. Durophagous predators are known to have fed on benthic, shelled, organisms such as *Inoceramus* (Kauffmann, 1972) or brachiopods (Alexander, 1981). It is also possible that taphonomically reworked ammonites likely had a "fresh" appearance, due to the effective winnowing of the uncemented sediment, and were attacked during active movement by bottom currents.

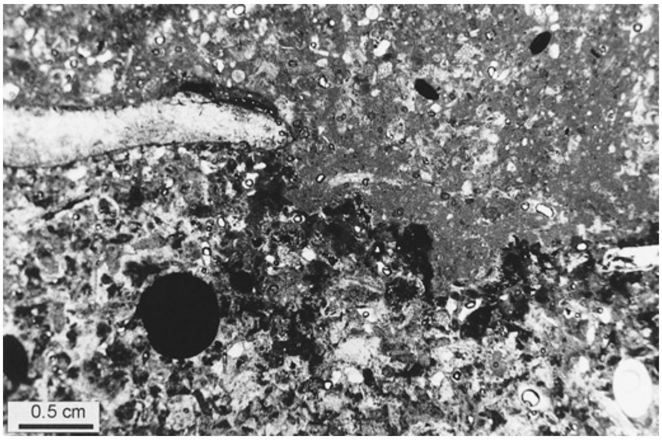

FIGURE 12—Close up of Figure 11 showing the fragment of shell at the pseudoboring-mold boundary. Note that both the latter and the external part of the shell are coated by black Fe oxides.

CONCLUSIONS

Unusual structures, herein named pseudoborings, have been described on ammonite molds. Their genesis is complex and involve several phases and probably due to the combination of biological and mechanical (taphonomic reworking) factors. This report is just one example of how paleontologists, stratigraphers, and sedimentologists can benefit from the taphonomical study of fossils (cf. Fernàndez-Lòpez and Melendez, 1994; Gòmez and Fernàndez-Lòpez, 1994; Fernàndez-Lòpez, 1997).

The recognition of pseudoborings goes beyond the pure paleontological curiosity. These structures, in fact, bear implications for several fields of study including paleobiology, taphonomy, and sedimentology.

(1) Paleobiology—pseudoborings provide additional evidence to the hypothesis that ammonites were preyed upon by durophagous organisms, a hypothesis that has recently been questioned (Kase et al., 1998);

(2) Taphonomy—pseudoborings are *per se* a proof of taphonomic reworking. This may be of great importance in ammonite assemblages, especially when many of the clues for recognition of taphonomically reworked fossils are absent (Fernàndez-Lòpez, 1984). This may be due to the absence of early lithification of the molds before exhumation, and/or to a lithological similarity of molds and matrix. Moreover, taphonomically-reworked fossils are, by definition, older than the encasing sediment. Accordingly, they must not be used to draw biostratigraphic or chronostratigraphic conclusions. Distinguishing taphonomically reworked fossils is of paramount importance in stratigraphy (e.g., Fernàndez-Lòpez, 1991; Pavia and Martire, 1997);

(3) Sedimentology—the formation of a pseudoboring implies the following scenario: burial of a predated ammonite shell; retardation of early lithification during the early burial phase; erosional events causing fossil exhumation by currents strong enough to overturn shells at least partially filled with sediment and up to 15 cm in diameter; a prolonged period of non-deposition allowing for the precipitation of authigenic Fe oxides-hydroxides; and final buri-

al. Most of this complex depositional-erosional-non-depositional history has scarce, if any, evidence in the lithostratigraphical record.

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