The importance of taphonomic studies on biochronology: examples from the European Middle Jurassic

La importancia de los estudios tafonómicos en biocronología: ejemplos del Jurásico Medio europeo

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ABSTRACT

Biochronology deals with the organisms of the past and is used to subdivide geological time on the basis of biological evolution that is a continuous and irreversible process. Given the importance of biochronological scales, one cannot just assume the contemporaneity of fossils and enclosing sediments: the stratigraphic record and the paleontological one do not necessarily coincide and must be considered separately. In the same way, also the chronological relationships among fossils cannot be simply derived from their relative stratigraphical position: the first occurrence of two taxa in a bed, for example, may not correspond to a real contemporaneous appearance. The possibility exists, in fact, of reorganization i.e. of exhumation after a first phase of burial. Reorganized fossils are, by definition, non contemporaneous with the host sediment and the other fossils not affected by reorganization present in the same bed. Therefore taphonomic analysis is an absolute prerequisite to biochronological reconstructions.

Two examples of ammonite-bearing calcareous successions from the Middle Jurassic of Northern Europe (Poitou, France and Dorset, England) are discussed. In the first case an increase of information results from taphonomic studies: a correct chronostratigraphy may be reconstructed, the
biochronological meaning of taxa reconstructed, the presence of discontinuities recognized, and the causes of taphonomic condensation understood. In the second example, it transpires that a detailed taphonomic analysis is needed before taking a succession as a reference for identifying boundaries and durations of biochronologic intervals.

**Key words:** Taphonomy, biochronology, reelaboration, condensation, ammonites, Middle Jurassic, north-western Europe.

**RESUMEN**

La Biocronología se ocupa de los organismos del pasado y se utiliza normalmente para subdividir el tiempo geológico sobre la base de la evolución biológica, que es un proceso continuo e irreversible. La enorme importancia de las escalas biocronológicas establecidas hace que no sea posible asumir directamente la contemporaneidad de los fósiles y las rocas sedimentarias que los contienen. El registro fósil y el registro estratigráfico constituyen dos entidades distintas y disociables, que deben ser analizadas y consideradas independientemente. De un modo semejante, las relaciones cronológicas entre los fósiles no pueden reducirse simplemente a las derivadas de su posición estratigráfica relativa. Por ejemplo, el primer registro de dos taxones en una capa puede no corresponderse en la realidad con una verdadera aparición contemporánea de los mismos: Es preciso tener en cuenta la posibilidad real de reelaboración, es decir: exhumación con posterioridad a una primera fase de enterramiento. Los fósiles reelaborados, por definición, no son contemporaneos con la roca sedimentaria que los engloba ni con los fósiles no-reelaborados (*i.e.* acumulados y/o resedimentados) que se encuentran con ellos en su misma asociación y en su misma capa. De tal manera, el análisis tafonómico constituye un prerequisito absolutamente fundamental en cualquier reconstrucción biocronológica.

En este trabajo se describen dos ejemplos de sucesiones carbonatadas con ammonites del Jurásico Medio de Europa septentrional (Poitou en Francia, y Dorset, en Inglaterra). En el primero de los casos el análisis tafonómico da lugar a un incremento sustancial de información: la reconstrucción de una cronostratigrafía más correcta que permite una mejor comprensión del significado biocronológico de los taxones, así como reconocer la presencia de discontinuidades y comprender las causas de la condensación tafonómica. El segundo ejemplo evidencia la necesidad de realizar un análisis tafonómico detallado antes de proponer una sucesión
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INTRODUCTION

Taphonomy and biochronology are two important branches of the palaeontological sciences. Taphonomy deals with the processes that transform the remains, or traces, of organisms of the past into fossils embedded in sedimentary rocks (from biosphere to lithosphere: Efremov, 1940) and is classically subdivided after Lawrence (1968) in biostratinomy and fossil-diagenesis (e.g. Muller, 1979). Biostratinomy has been largely employed essentially as a fundamental premise to paleoecological analyses, in order to ascertain to which extent oxicocenoses reflect past living communities (e.g. Martinelli et al., 1980). On the other hand, fossil diagenetic studies have been much rarer and seem to have been considered little more than a curiosity about how a fossil acquires its final aspect with scarce, if any, relevance to other important branches of sedimentary geology such as biostratigraphy and paleoenvironmental reconstructions. In the last decade Fernández López (1984a, 1989, 1991) has shown that a more dynamic and evolutionary approach to taphonomy is not only possible but strictly necessary: fossils must be investigated in order to reconstruct all the states, and the responsible mechanisms, through which they have passed while changing from skeletal remains (or traces) of an organism to a recorded entity (fossil). Moreover, temporal relationships among fossils and organisms of the past may only be stated on the basis of their taphonomic properties.

Biochronologic studies deal with the reconstruction of life times of organisms and, as a goal, with the recognition of bioevents defined by evolutionary changes and time-correlations. They can be reliably done only after the chronological relationships between the production of the fossil remains and their record in a stratigraphic succession are unravelled.

The aim of this paper is to show how taphonomic analyses are fundamental in the study of sedimentary successions since they provide the sole means to understand the way of formation of the embedded fossil assemblages, on which any biostratigraphic and possibly chronostratigraphic definition is based. In this analysis we will refer to some particular cases

Palabras clave: Tafonomía, biocronología, reelaboración, condensación, ammonites, Jurásico Medio, noroeste de Europa
studied in the Middle Jurassic of western France (Pavia 1994; Martire & Pavia, 1996a). Both cases are very favourable for this purpose, because the analysis concerns fossil associations mainly consisting of chambered shells (ammonites) which, on the one hand, evolved very rapidly making possible a detailed subdivision of geologic time in biochronological units and, on the other hand, acted as sedimentary traps witnessing the successive taphonomic modifications and processes.

SOME CONCEPTS, DEFINITIONS AND PROBLEMS

Biochronology deals with a matter of prime importance and great complexity: the measurement of geological time. It hence deserves a detailed treating of concepts, definitions and problems. The purpose of geochronology is to build and continuously refine a conceptual time scale which enables us to frame, in a time sequence, events of various nature that happened during earth history. Stratigraphers deal essentially with rocks successions which are per se a discontinuous record of geological time, even in the most complete stratigraphic column: stratigraphic successions. Consequently, a geochronological scale is inherently incomplete because it is composed of time intervals corresponding to the formation of given chronostratigraphical units (Hedberg, 1976; North American Commission on Stratigraphic Nomenclature, 1983). A different task is the quantitative measurement of geologic time (geochronometry): any geological event of the past can be, as a result, characterized by a numerical value representing how many years before present it happened. At the present state of knowledge, only two phenomena are characterized by continuity and irreversibility, i.e. the two properties on which the geologic clock must be based, at least theoretically: the decay of radiogenic isotopes and the evolution of living organisms. The former provides the basis for geochronometry, the latter does the same for biochronology. In fact, time-correlation of Phanerozoic sedimentary bodies, which are only occasionally datable chronometrically, is mainly made on the basis of their fossil content. Of course, this type of dating is not easy and straightforward to achieve because of the many factors controlling the fossil record, the main ones being ecological, biogeographical and preservational factors.

Now, fossils are contained within rock bodies and hence, it could be argued, the fossil record is at least as discontinuous as the lithostratigraphic record. This statement is implicitly founded on the assumption of contemporaneity of fossils and enclosing sediments which is differently expressed
in the principle of positional relationships stating that «the only proof that one fossil is younger than another lies in the relative position of the two in a sequence of rocks» (McLaren, 1977 in Schoch, 1989). It is always remarked that fossils may be «out of context in stratigraphic sections» (Schoch, 1989) because of reworking (older fossils within younger rocks) or of bioturbation (younger fossils within older sediments). At the same time, however, it is stressed that the fear of deleterious effects of biochronologically «displaced» fossils is quite unfounded: fossils, in fact, are recognized as «displaced» if the degree of temporal (stratigraphic) displacement is detectable biochronologically; otherwise, it means that the displacement is very slight and falls within the noise level of resolution. In both cases it is supposed not to matter any relevant deviation from the biochronological position of the fossil (Shaw, 1963 in Haq & Worsley, 1982). This approach, however, is methodologically incorrect since reworking, intended as exhumation after burial and better called reelaboration as will be discussed in detail later, must be verified by taphonomical analysis and not by a priori, biochronological criteria (Fernández López, 1984a). Actually such an approach may not result in significant mistakes when working with assemblages of microfossils (e.g. planktic foraminifera) embedded in thick successions of fine-grained hemipelagic sediments. The opposite is true when thin, stratigraphically condensed, mainly calcareous units are studied in such richly fossiliferous sections that they may be, and indeed have historically been, proposed as reference sections for bio—and chronostratigraphical—units (e.g. Pavia, 1994). In such cases, if reelaborated (taphonomically reworked) fossils are not recognized and orictocenoses are interpreted as composed by the remains of contemporaneous organisms, mistaken conclusions of paramount importance are made which may result in huge problems of bio—and chronostratigraphic—correlation. As it has been deeply investigated and clearly stated by Fernández López (1991), if the possibility of reelaboration is assumed, one is forced to conclude that the stratigraphical record (rock bodies) and the fossil record have to be considered separately. They are independent records of the passing of geological time and they are both discontinuous, but the discontinuities need not correspond to each other.

It appears thus unacceptable for biochronology to be simply derived from biostratigraphic successions. Biochronology aims to reconstruct the succession of living organisms of the past whereas biostratigraphy deals with rock bodies and tries to characterize them on the basis of their paleontological content. Biostratigraphy, therefore, should not take into consideration (should not be based on) reelaborated fossils, which are always
non contemporaneous, to varying degrees, with enclosing rock, while defining or correlating biozones of whatever nature (North American Commission on Stratigraphic Nomenclature, 1983). In the last edition of the In-

Fig. 1.—Graphic representation of fossilisation processes. The main phases through which the remain generated by an organism (paleobiological entity) is transformed into a fossil (recorded entity) which can be found by a palaeontologist (obtained entity) are indicated, (modified after Fernández López, 1991).

Fig. 1.—Representación gráfica de los procesos de fosilización. En el gráfico se muestran las principales fases por las cuales el resto generado por un organismo (entidad paleobiológica) se transforma en un fósil (entidad registrada) que llega a ser conocida por el paleontólogo (entidad obtenida). Modificado, según Fernández-López, 1991.
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International Stratigraphic Guide (Salvador, 1994), however, it has been remarked that re-ellaborated fossils must not be ignored. No indication about how to use them, however, is explicitly given. Reelaborated fossils may in fact be the only witness of an interval of geological time whose corresponding sediments have been completely eroded or swept away, leaving just a residue of exhumed fossils which add a tessera to, and contribute to refine, the mosaic of the geochronological scale (Fernández López, 1991).

Time relationships between paleontological entities and the host beds must be specified on the basis of the relationships between the times of production and fossilization (or record) of the taphonomic entities preserved in the stratigraphic succession (Fig. 1). In fact, a basic premise strongly underlined by Fernández López (1989, 1991) is the sharp distinction to be made between the organism of the past i.e. the producer of the remains and/or traces, and the recorded entity (fossil) that is found in a stratigraphic succession. On the basis of what has been discussed so far, it is obvious that the chronological relationships of selected taxa are not derived from the stratigraphical relationships between fossil-bearing beds but from the topological relations (anterior to; posterior to) verifiable between the successive different recorded entities by determining their successive time of production (Fernández López, 1991). In other words, any biochronological scale can be constructed, improved or refined only after sorting out, by means of an accurate taphonomic analysis, the succession of paleobiological, taphonomical and depositional events.

The distribution of the fossil content in a given stratigraphic succession is commonly defined by the data of First Appearance (FAD) and Last Appearance (LAD) of more or less selected taxa. By definition, FADs and LADs are controlled by organic evolution and hence, conceptually, treated as if they were globally synchronous; the corresponding biohorizons might be considered as time lines useful for biochronological correlations (Salvador, 1994). It is commonly acknowledged that FADs and LADs can be diachronous because of factors intrinsically linked to the biology of the organisms of the past, such as rates of biogeographic spreading and ecologic limitations. In fact, what is found in a succession are actually First and Last Occurrences (FO and LO): they refer to a stratigraphic section that is subject to local discontinuities in both the rock and the fossil record. Discontinuities in the fossil record may be due to two groups of factors, besides sampling deficiencies: one controls the presence of the living organisms in the paleoenvironment (biogeographic and ecologic biases), the second affects the preservation of organic remains, before and after burial in sediments (biostratinomic and fossil-diagenetic biases). For these reasons biochrono-
logical scales and correlations must take advantage of the integration of different methods (geochronometric dating of volcanoclastic beds, magnetostratigraphy, etc.: Berggren & Van Couvering, 1978) in addition to paleontology (e.g. Tauxe et al., 1983). However, before taking such important step as connecting FOs and LOs to FADs and LADs, a preliminary study is needed. This deals with the testing of the contemporaneity of sediments and fossils through taphonomic analysis and, more particularly, through the identification of reealaborated fossils. The FO of the latter in a stratigraphic succession is in fact apparent because it is related to a bed which is always younger than the actual time of production of the organic remains. Once the FO of a taxon is correctly positioned in a chronological succession, one can try to correlate it with FOs in other sections and infer the real FAD.

Stratigraphic successions in fact could contain mixed assemblages with groups of fossils derived from different phases of taphonomic production and record: (A) a first stock of fossils which is contemporary to the enclosing sedimentary rock; (B) a second group of fossils due to exhumation and displacement of preserved entities from a layer previously deposited (reelaborated fossils). The latter have experienced at least two chronologically successive events of burial.

Of course mixed fossil-assemblages are well known and documented in the literature. It is interesting to review how approaches may be diverse, depending on different disciplinary traditions, overall geological setting and objects of research. Some examples can be cited:

1) The association of e.g. Late Cretaceous to Early Oligocene planktic foraminifers with Late Oligocene ones (Premoli Silva & Violanti, 1981) is referred as due to «reworking» and the age of the enclosing sediment is attributed according to the range of the younger fossils.

2) The co-occurrence of the Toarcian ammonites Hildoceras gr. lusitanicum and Hildaites undicosta has been regarded by Della Bruna & Martire (1985) as a case of condensed layer, where the H. serpentinus and H. bifrons Zones are condensed.

3) The presence of the early Bajocian ammonite Stephanoceras umbilicum is by itself enough to assign the enclosing bed to the S. humphriesianum Zone (Gauthier et al., 1995).

All these approaches are methodologically wrong. In fact: (1) the younger foraminifers may be reelaborated too; (2) it is necessary to precise what kind of condensation we are dealing with, as three different meanings for condensation phenomena have recently been demonstrated (Gómez &
Fernández López, 1994); (3) there are no guarantees for the taphogenic production of a fossil to be contemporaneous with the deposition of the sediment. In other words, before reaching any conclusion which could be important for a genetic interpretation of the fossil assemblage, it is necessary to carry on a detailed taphonomic analysis of the material.

TAPHONOMIC ANALYSIS

In our purpose, taphonomic study can be simply addressed to verify the homogeneity of the preserved elements which compose the fossil assemblage and, in particular, to distinguish between fossils contemporaneous with the enclosing matrix and fossils which, after previous burial and diagenesis, were exhumed and buried again together with younger preserved elements. Fernández López (1984a, 1991) proposed a simple scheme to classify fossils according to their state of preservation. Three main categories are established:

— Accumulated fossils: elements lying in or on the bottom sediments after a phase of biogenic production.
— Resedimented fossils: previously accumulated elements displaced on the sedimentary bottom, prior to their burial. Demic and ademic, autochtonous and allochtonous, accumulated and resedimented are adjectives which are referred to different stages of the taphonomic process and thus to different entities, i.e. paleobiological, preserved and recorded ones respectively (Fig.1). Therefore they are neither synonymous nor partly overlapping and must not be mistaken. A detailed discussion of this subject is out of the scope of this paper. The interested reader is addressed to Fernández López (1990, 1991).
— Reelaborated fossils: elements exhumed and displaced after burial as a consequence of denudation of a certain volume of previously deposited sediments.

As far as the third category is concerned, there are many terms used for naming the phenomenon of fossil exhumation. The most common one is the English reworking, but its employment in the stratigraphical literature seems too large for being adopted in taphonomic analysis. In fact, the definition of the term «reworking» applies to both sedimentary and biogenic particles and does not indicate precisely whether displacement took place in a pre or postburial phase (Bates & Jackson, 1987). For this reason,
waiting for an eventual (if necessary) proposal by anglosaxon authors to replace this neologism with a corresponding word, we support Fernández López's nomenclature (reelaboration = taphonomic reworking) which refers just to recorded elements exhumed after a previous phase of burial, without any reference to sedimentologic processes.

There are many criteria for recognizing reelaborated fossils and an exhaustive list has been reported by Fernández López (1984b). Chambered shells of ammonites, protozoans, etc. (Martire & Pavia, 1996b) are actually very favourable to recognize reelaboration processes. Their internal moulds may be lithological different, i.e. showing a lithological, textural and/or structural discontinuity, from the matrix as they record previous phases of sediment filling and diagenesis. Cathodoluminescence analyses (Martire & Pavia, 1996a) increase the possibility of recognizing reelaboration, when skeletal remains show modification in the mineral structure due to different diagenetic histories.

What kind of information can we obtain from the taphonomic analysis of a mixed fossil-assemblage? In such assemblage the mixing of biogenically produced entities in successive time intervals (taphonomic condensation: Gómez & Fernández López, 1994) may be due, for example, to colonization of a previously deposited fossiliferous bed by endobenthic organisms: This will result in a consequent juxtaposition of non-reelaborated fossil remains referable to different times of production (time averaging, e.g. Fürsich & Aberhan, 1990). However, when dealing with remains of nekto-planktic organisms such as many ammonites, a taphonomically condensed assemblage most likely corresponds to a mixing of accumulated and/or resedimented plus reelaborated fossils. The assemblage can be subdivided into different taphonomic groups (taphorecords) composed of fossils showing homogeneity in their preservational features. Each taphorecord has diagnostic characters which can be related to a well-defined set of biostratinomic and/or fossil-diagenetic processes.

From a mixed fossil assemblage it is possible to reconstruct the chronologic order of the separate taphonomic events, from the biogenic or taphogenic production to the final record in the sedimentary rock: Fig. 1. This succession is recognizable from the taphonomic features shown by the recorded elements in the studied association. This ordering will produce the so-called registratic succession (Fernández López, 1986). The registratic succession is integrated by the topologically and chronologically successive recorded entities mixed in a single layer, each one of them referring to a rock-body which may be the same as, or different (and older) from the rock-body where the elements are found (Fig. 2). In particular, internal
moulds of accumulated and/or resedimented fossils, showing no differences and/or textural discontinuities with the enclosing matrix, are to be regarded as coeval with the enclosing rock-body and then will take the hig-

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Fig. 2.—The mixed fossil assemblage of bed B2 can be split into five taphorecords (TR1-TR5) each one showing different preservational states or referable to the same phase of burial. The chronologic relationships of these taphorecords allow to recognize the registratic succession in the right column where four assemblages (A1-AIV), corresponding to as many time intervals (T1-TIV), are distinguished. The assemblage A11 gathers two taphorecords (TR3 and TR4) produced contemporaneously. (modified after Gómez & Fernández López, 1990). TR1: reeaborated fossils possibly related to erosion of the topmost bed B1. TR2: reeaborated fossils referable to a bed younger than B1 but older than B2, not any more represented in the stratigraphic succession. TR3: accumulated fossils. TR4: resedimented fossils. TR5: accumulated fossils stratigraphically referred to bed B2, but topologically successive because pertaining to an organism which excavated a burrow after sedimentation of the bed B2.
hast position in the registratic succession. On the contrary, the sedimentary events corresponding to the reelaborated fossils bearing evidence of one or more previous phases of sedimentation / diagenesis, are no longer recorded in the stratigraphic succession by a discrete lithological layer but just by the matrix trapped in their internal moulds.

Let us come back to the problem of FOs and FADs, discussed in the preceding chapter, and to the importance of a taphonomic study for biochronological statements. In Fig. 2 the paleontological sampling of a hypothetical stratigraphic succession shows the presence of the single fossiliferous bed B2 with selected taxa. Taphonomic study of the assemblage B2 indicates the mixing of accumulated (AC), resedimented (RS) and reelaborated (RL) fossils, and the registratic succession displays the relative chronologic position of each taphorecord. From this study it follows that we cannot consider each fossil found as the FO of the related taxon. Such an inference is justified only for TRs 3 and 4, i.e. the non-reelaborated fossils. The real FO of TR1 and 2, in fact, pre-date the FOs of TR3 and 4 as can clearly be seen on the registratic succession. Even younger is TR5, although it is accumulated, because it is clearly referable to a subsequent colonization phase. Otherwise, if the FOs of all the taxa were regarded as being essentially contemporaneous, the assemblage of bed B2 would represent a faunal horizon i.e. «a fairly homogeneous horizon representing the fauna that lived during a relatively short time» (Callomon & Cope, 1995: 61). In our opinion, «relatively short» is an expression not to be used because it is impossible to define precisely. A fossil assemblage, in fact, may be interpreted as a faunal horizon only when it can be demonstrated to be composed of fossils produced by contemporaneous paleobiological entities. The sole powerful tool able to verify, by independent criteria, the chronological order among fossils is taphonomic analysis. If we just assume that a fossil assemblage is homogeneous, giving it a precise biochronological meaning, and taking it as a reference for biochronological scales we fall into circular reasoning with serious consequences.

The practical consequences of such a conclusion, for both biostratigraphy and biochronology, will be shown in the following examples referring to ammonite assemblages of the Middle Jurassic of north-western Europe.

SELECTED EXAMPLES

Two similar situations will be discussed in order to demonstrate the consequences of detailed taphonomic analysis for interpretation of the
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evolution of a stratigraphic succession (A: Aalenian-Bajocian of Poitou) and how essential it is before describing a particular fossiliferous sequence as a standard reference for biochronology (B: Upper Bajocian of Dorset).

A) Saint Maixent, Poitou (western France)

Generality

La-Grande-Palisse quarry near Saint-Maixent-l’Ecole, some 30 km WSW of Poitiers, has been described by Branger (1989; see also Martire & Pavia, 1996a). The Aalenian and Bajocian stages are represented by a carbonate succession nearly 15 m-thick. The section basically consists of bioclastic limestones, slightly glauconitic in the lower part, with significant fossil species referable to the latest Aalenian and to different Bajocian biochrons. The ground level of the quarry corresponds to the top of a thick calcareous bed of middle Aalenian age or, locally, to the overlying thin Fe-oolithic bed referred to the Aalenian-Bajocian transition.

No detailed taphonomic analyses have so far been published on the Saint-Maixent succession, except for the preliminary results summarized by Martire & Pavia (1996a). Our attention has been focused on the Fe-oolithic beds 2-4 which contain very rich fossil assemblages, mainly represented by ammonites. From bottom to top (Fig. 3a):

1) Compact bioclastic wackestone. Middle Aalenian in age according to Cariou et al. (1991).
2) Fe-oolithic-bioclastic packstone to wackestone (8-13 cm) draping the irregular and bored discontinuity surface at the top of bed 1. Taking into account the fossil content, sampled in different points of the quarry, two subunits have to be supposed which must be separated by a minor discontinuity surface hardly identifiable in the field. The fossil assemblages 2A and 2B indicate respectively latest Aalenian and earliest Bajocian age.
3) Reddish marls with reworked Fe-oolithic pebbles (1-2 cm). No fossils, undeterminable age.
4) Bioclastic wackestone with sparse and small Fe-ooids which are mainly concentrated at the base of the bed to form a characteristic reddish layer. The paleontological content is indicative of the Early Bajocian, late Laeviuscula Chron.
### Stratigraphic Succession

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### Biochronology

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<td>A 2A (TR 2/1)</td>
<td>late Concavum Ch.</td>
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<td>A 2' (TR 2/2)</td>
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### Chronostratigraphy

- BED 4: uppermost W. laeviuscula Zone
- BED 3: ??
- BED 2B: lowermost H. discites Zone
- BED 2A: uppermost G. concavum Zone
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TAPHONOMIC ANALYSIS OF BEDS 2 AND 4

The state of preservation of ammonites has been studied in beds 2 and 4. Several taphorecords with distinct biochronological meanings (Fig. 3b,c) can be distinguished, the recognition of which is in some cases possible directly in the outcrop, whereas in others it needs detailed observations carried out in the laboratory. Only macroscopic analyses for taphonomic purposes are reported here; microscopic and further lithologic observations are omitted (see Martire & Pavia, 1996a for details on taphorecords of bed 4). In the following description RS and RL refer respectively to resedimented and reelaborated fossils. Taxonomic study of the ammonites is in progress.

— Taphorecord 2/3 (RL)—Moulds are fragmented, abraded, bioencrusted, bored, coated by a thin Fe-crust and filled with the bioclastic wackestone typical of bed 1 (Pl. 1, figs. 1, 2). These occur both in layers 2A and 2B. Taxonomy: Brasilia similis, B. gr. gigantea. Biochronology: Bradfordensis Chron.

— Taphorecord 2/2 (RL)—The mould matrix is similar to the Fe-ooidal lithofacies of bed 2; moulds are fragmented by disarticulation (Pl. 1, fig. 3) and show abrasion facets and traces of encrusting organisms. It is present only in layer 2A. Taxonomy: Euapetoceras euapetum, Graphoceras concavum. Biochronology: early Concavum Chron.

— Taphorecord 2/1 (RS)—Neomorphic shells are always present. Neither abrasion, disarticulation or bioencrustation of moulds nor differences between filling and surrounding sediment are recognizable. The taxonomic content of bed 2 can be subdivided into two groups, respectively referred to

Fig. 3.—Summary of stratigraphic results from taphonomical analysis of the Upper Aalenian to Lower Bajocian succession exposed in La Grande Palissee quarry, Saint-Maixent, Poitou. a: The stratigraphic succession. b: The registratic succession lists the different fossil assemblages recognized in beds 2 and 4 and the corresponding taphorecords. c: Biochronological meaning of each topologically successive fossil assemblage. d: Beds and fossil assemblages are interpreted in terms of biostratigraphic units. The position of bed 3 is undefined. Ruled intervals represent hiatuses. A: fossil assemblage. Ch: biochrons. TR: taphorecord.

Fig. 3.—Resumen de los datos estratigráficos resultantes del análisis faconómico de la sucesión del Aaleniano Superior: Bajociano Inferior de la cantera de la Grande Palissee (Saint Maixent, Poitou). a: Sucesión estratigráfica. b: Sucesión registrática. Esta sucesión comprende la sucesión de asociaciones registradas topológicamente sucesivas reconocidas en las capas 2 y 4, y los correspondientes taforregistros. c: Significado biocronológico de cada una de las asociaciones registradas topológicamente sucesivas. d: Interpretación bioestratigráfica de los niveles estudiados y de las correspondientes asociaciones registradas. La posición bioestratigráfica de la capa 3 es indeterminada. El rayado vertical representa la extensión de las lagunas estratigráficas. A: asociación registrada. Ch: biocronos. TR: Taforregistro.

— Taphorecord 4/3 (RL)-Moulds are disarticulated, abraded, biocrusted and filled with multiple generations of texturally different sediment; they also show darker color than the enclosing matrix and thin glauconitic/ferruginous coating (Pl. 1, figs. 4, 6). Taxonomy: Euhoploceras crassicostratum, E. tridactylum, Fissilobiceras fissilobatum, F. ovalis, F. undiferum. Biochronology: early Laeviuscula Chron.


— Taphorecord 4/1 (RS)-Neomorphic shells are always present. No physical discontinuity is present between internal moulds and the surrounding matrix which are petrographically identical. Shells are either complete, with the peristome, or broken along an irregular fracture never corresponding to a septum. Frequently, the phragmocone is occupied by coarse calcite spar and only the body chamber is filled with sediment (Pl. 1, fig. 5). Taxonomy: Papilliceras cf. arenatum, P. mesacanthum, Somninia sp., Witchellia cf. laeviuscula, W. patefactor, W. rubra, W. sayni, Maceratites costulatosus, M. macer, M. moysisy, M. spatians, Lissiceras semicosulatum, Otoites sp. Biochronology: late Laeviuscula Chron.

**DISCUSSION**

The taphonomic analysis of a tract of the Aalenian-Bajocian at Saint Maixent has allowed for recognition of three taphorecords in both beds 2 and 4: in each of them, two reelaborated taphorecords and one resedimented taphorecord occur (Fig. 3b). The two reelaborated taphorecords show clearly different features mainly due to less marked evidence of exposure at the sediment-water interface (borings, authigenic mineral coatings, etc.); taphorecords 2/3 and 4/3 bear more evident proof of reelabo-
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tation than 2/2 and 4/2. On the basis of these taphonomic features, a chronological order of the fossils in each mixed assemblage may be recognized which reflects order in their taphogenic production, e.g. 4/3, 4/2 and 4/1, from the oldest to the youngest to be produced. An interesting relationship exists between taphorecords and biochronological units: each taphorecord (TR), in fact, consists of a taphonomically homogeneous fossil assemblage that corresponds to, and is exclusive of, a single geochronologic unit (a subchron), even though reelaborated fossils may be found in different layers (e.g. TR2/3 occurs in both bed 2A and 2B Fig. 3b, c). Moreover in a single taphorecord (TR2/1) taphonomically identical resedimented fossils are grouped which are partly referable to the Concavum Chron and partly to the Discites Chron. This enables distinction of two different subbeds, 2A and 2B, mostly unconspicuous in the field.

On the basis of these analytical data, the following conclusions may be drawn. Firstly, a correct biostratigraphy may be reconstructed on the basis only of resedimented fossils (Fig. 3d). This leads us to recognize several surfaces of discontinuity in the beds and to constrain more closely the age of bed 3, which is barren of fossils. In spite of these gaps, reelaborated fossils constitute records of stratigraphic intervals not represented by sediment except for the ammonite infillings. The chronoregistratic succession, i.e. the succession of the topologically successive fossil units, is a more complete record of geological time than the stratigraphic succession. This may greatly help in increasing our degree of knowledge about both sedimentary and biological evolution of the basin studied. Finally beds 2 and 4 are good examples of taphonomic condensation (Gómez & Fernández López, 1994) due to reelaboration and not to other, theoretically plausible, mechanisms such as extremely low sedimentation rates leading to accumulation on the sea floor, side by side, of remains of organisms which lived in different times. In addition to this, a stratigraphic condensation of the Saint Maixent section compared to many other coeval sections in Europe, is also demonstrably due in part to the presence of prolonged sedimentary hiatuses (Fig. 3d).

B) Dorset (southern England)

GENERALITY

The county of Dorset, along and just inland of the English Channel coast, is a classical area for the Jurassic geology of Europe (Arkell, 1933; Callomon & Cope, 1995). Rocks spanning almost the whole Jurassic system
are displayed in cliff exposures; their successions are important for many geological purposes, mainly due to their rich paleontological content and for being considered as the reference sections for establishing standard biochronological scales based on ammonite assemblages. This is particularly true for the middle Jurassic and, especially, for the Aalenian and Bajocian ammonite successions which have been the subject of detailed studies carried out by Callomon & Chandler (1990).
The Aalenian and Bajocian stages are represented by the well-known formation the Inferior Oolite, which consists of a relatively thin limestone succession between the Toarcian Bridport Sands and the thick Bathonian Fuller’s Earth formations. The Inferior Oolite succession has been summarized by Callomon & Cope (1995: 61). It consists of a series of relatively thin beds of varying calcareous lithologies, sharply delimited by partings or erosion-planes... each bed typically has its own ammonite assemblage, and in most cases such assemblage gives the impression... of being fairly homogenous, i.e. representing the fauna that lived during a relatively short time... The succession is therefore «highly condensed», but in a very particular way. It has the appearance of the record of but brief instants of time in a long history. Different localities record different instants, and hence... a tolerably complete history can be reconstructed». The conclusion of Callomon & Chandler (1990; up-to-date version reported by Callomon & Cope, 1995, fig. 7) was a table of faunal horizons; it lists the ammonite horizons that have been distinguished so far for the British Aalenian and Bajocian. This biohorizon table is becoming more and more basic for any biochronological, and then chronostratigraphical interpretation of the European Middle Jurassic (Pavia & Enay, in press). Its importance is also enhanced by the fact that the paleobiological content of Dorset successions is intermediate between the Boreal and Tethyan realms and could make correlations easier.

Nevertheless, we have seen that the possibility of taphonomic mixing (condensation) in Fe-oolithic rocks, mainly due to reelaboration, is very high (Martire & Pavia, 1996a). This is particularly true when we consider that the Dorset succession belongs to the so-called Anglo-Parisian basin like that of Bayeux (Rioult et al., 1991; Pavia, 1994), the evolution of which had been possibly controlled by the same tectonic influences (e.g. the Armorican uplift: Callomon & Cope, 1995). To be confident of using the English ammonite succession as the standard biochronological reference, we thus need to know whether those faunal ammonite horizons actually consist of homogenous assemblages, in terms of taphonomic production time, or if they constitute mixed fossil assemblages. In other words, whether a detailed taphonomic analysis is missing and needed.

Many fossiliferous beds of the Dorset Inferior Oolite are suspected to contain mixed fossil assemblages. Among them, we draw our attention to the so-called «Astarte Bed», well represented in the Burton Bradstock section (Fig. 5) and precisely described by Callomon & Cope (1995: 64). This layer, Late Bajocian in age, is widely represented in southern England (Cope et al., 1980); it is the key, for English authors (Torrens, 1969), to as-
sign the *P. acris* Subzone to the *G. garantiana* Zone instead of to the succeeding *P. parkinsoni* Zone, as variously reported by continental authors. In fact, the ammonite content of this bed shows the co-occurrence of such taxa (among others, *Parkinsonia acris* and *Garantiana garantiana*) which
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are usually referred elsewhere (Spain, France) as representatives of the two subsequent biozones.

**THE ASTARTE BED IN DORSET**

First described by Hudleston (1887 in 1887-96: 37) at Vinney Cross near Bridport, the biostratigraphic meaning of this layer had been described by Buckman (1910: 67) as «dated exactly as Garantiana Beds». This lithostratigraphic acronym was not in current use for many decades (Donovan & Hemingway, 1963: 29) and it was not cited by Arkell (1956) either. Nevertheless, some notes published in the seventies (Senior et al., 1970; Parsons, 1975a) gave a detailed account of the paleontological content of the layer. The acronym *Astarte Bed* was then inserted in the Geological Society's Correlation charts (Cope et al., 1980: fig. 3a) as one of the most widely distributed horizons in southern England (Dorset and Somerset). On the basis of its rich ammonite assemblages, it has been biocorrelated with, and thus considered time-equivalent to, other lithological units such as the «Upper Trigonia Grit» in the Cotswolds (Parsons, 1976) or the «Maes Knoll Conglomerate» of Dundry, Avon (Parsons, 1979).

The ammonite content of the *Astarte* Bed can be deduced from different works of Buckman (1891, 1893, 1909-30). Recent contributions record: *Strigoceras compressum*, *S. septicaratum*, *Oppelia aff. pleurifer*, *Oecotraustes umbilicatus*, *Sphaeroceras brongniarti*, *S. tutthum*, *Garantiana garantiana*, *G. longidens*, *G. tetragona*, *Pseudogarantiana minima*, *Parkinsonia acris*, *P. rarecostata*, *Spiroceras waltoni*, *Prorisorphinctes glyphus*, *P. meseres*, *P. cf. pseudomartinsi*, *P. subdivisus*, *P. stomphus*.

According to the classical acceptance of the European continental Late Bajocian (e.g. Pavia, 1973; Galacz, 1980; Sandoval, 1983; Fernández López, 1985), these species should be separated into different biochronological groups. In particular: (1) *G. garantiana* is usually referred to the middle part of the *G. garantiana* Zone; (2) *G. longidens*, *G. tetragona*, *P. minima*, *P. meseres*, *P. stomphus* are indicative of the upper part of the same zone (*G. tetragona* Subzone), or even of the passage to the overlying *P. parkinsoni* Zone (Gabilly et al., 1971); (3) *P. acris* and *P. rarecostata*, including also the last representatives of the genus *Garantiana* characterise the base of the *P. parkinsoni* Zone (*P. acris* Subzone). Such biostratigraphic subdivision is confirmed by Gauthier et al. (in press) in the unusually expanded section of Feuguerolles (Normandy) of the same Anglo-Parisian basin as the Dorset sector.
DISCUSSION

The historical importance of the Astarte Bed has been recently highlighted by Callomon (1990, pers. comm. as errata corrigi of notes in Callomon & Chandler, 1990), who reminded that it had been «the basis for the first definition of the Garantiana Zone, in Britain» introduced by Buckman (1893: 483-484). This sentence summarizes what was already discussed in the paper of Parsons (1976: 48) in which the P. acris Subzone had been justified as necessarily placed at the top of the G. garantiana Zone instead of at the base of the P. parkinsoni Zone as advocated at that time by Sturani (1971) and Pavia (1973). Parsons (op. cit.) in fact specified that «... The faunas recorded from this horizon... [P. acris Subzone]... show that it is correlated with the Astarte Bed of south Dorset and the Marl Bed and part of the Sherborne Building-Stone of north Dorset. Since these latter horizons were the very basis for the foundation of the G. garantiana Zone, the P. acris Subzone must be considered, by original definition, as an integral part of the G. garantiana Zone».

Parson's interpretation could be taken into consideration if taphonomic studies prove that the fossil assemblage is homogenous, according to the production time of its ammonite elements. Some arguments, however, raise doubts about this hypothesis. Firstly the presence in the Astarte Bed of taxa biochronologically distributed in two different zones (G. garantiana and P. parkinsoni Zones) in many other European sections as discussed before. Secondly, the results of a detailed taphonomic analysis of coeval ammonites in the sections of Normandy which consist of very similar lithostratigraphic successions (Pavia, 1994; Martire & Pavia, 1996a): many reelaborated taphorecords have been identified often corresponding to wonderfully preserved ammonites. Two alternatives are theoretically possible. One would explain the fossil mixing (taphonomic condensation) as a result of sedimentary condensation, i.e. of an extremely reduced accumulation of sediment; this however contrasts with the classical interpretation of episodic deposition (Callomon & Cope, 1995). The other alternative would instead call upon reelaboration and mixing.

In conclusion, detailed taphonomic studies are urgently needed on the Inferior Oolite successions of southern England and, more particularly, on the Astarte Bed, to verify if it contains a mixing of reelaborated ammonites typical of the G. garantiana Chron with younger ammonites of the P. acris Subchron. Should this hypothesis be confirmed, the result would be that the sedimentation of the Astarte Bed is more recent than the time of production of the G. garantiana remains and it would be necessary to
abandon the definition of the Astarte Bed as the type-horizon of the G. ga-
rantiana Zone. As a consequence, the P. acris Subzone would refer to a
biostratigraphical unit well separated from the latter by the onset of the ge-
nus Parkinsonia; it could thus be placed at the base of the P. parkinsoni
Zone as it has been usually done in the European late Bajocian. A final
comment is necessary: the Astarte Bed is the type-horizon of many am-
onites described by Buckman (1909-30), e.g. P. glyphus (Parsons, 1975b:
203); the determination of the taphonomic state (i.e. the mechanical state of
preservation) of these type-specimens is therefore needed, particularly for
all the taxonomic, evolutionary and biochronological implications.

CONCLUDING REMARKS

The exposed data have shown how important taphonomic studies are in
stratigraphy and, in particular, in such a delicate subject as biochrono-
logy. At Saint Maixent (Poitou), the taphonomic analysis of the recorded
associations of ammonites, with special reference to the taphonomic fea-
tures shown by the internal moulds, have provided a more coherent and cor-
correct chronostratigraphical frame, allowing the recognition of several so far
undescribed stratigraphic discontinuities, and an understanding of the cau-
ses of taphonomic condensation. This analysis results in a noteworthy in-
crease of information, which is specially useful for both stratigraphic cor-
relation, and in the reconstruction of the sedimentary evolution of the
basin. Conclusions of more general interest result from a reexamination, in
the light of the established principles and methodologies of evolutionary
taphonomy (Fernández López, 1991), of the well-known Jurassic succes-
sions of Southern England. Comparisons with the preservational states of
coeval ammonites from comparable sections (Normandy), and discrepan-
cies with biostratigraphic and biochronological successions from many
other European sections evidence the need of a detailed taphonomic analy-
sis of the important Jurassic succession in Dorset, in order to ascertain what
kind of fossil assemblages are being studied, and to precise the state of pre-
servation of the studied fossils before taking them as a reference for stan-
dard biochronologic scales.

To sum up, it can be stated that taphonomic analysis may greatly help
to clarify the relationships between biochronology and biostratigraphy. It
allows distinction between fossils which are contemporaneous with the en-
closing sedimentary rock (accumulated and resedimented fossils) and fos-
sils which were produced at a previous time and exhumed, and are thus ol-
der than the actual host bed (reelaborated fossils). Biostratigraphy must be founded only on accumulated and/or resedimented fossils.

Because many beds are barren of fossils, the chronostratigraphic succession is supposed to be more complete than the biostratigraphic one. Furthermore, sedimentary successions are affected by unconformities which make both records discontinuous. Some pieces of the «lost history», however, are preserved as reelaborated fossils. Most important, the latter are remains of organisms of the past which are often taxonomically significant. This means that not only are reelaborated fossils the unique record of time slices otherwise unpreserved in the stratigraphic record, but they may be put into ordinal sequence providing a precious supplementary information to the knowledge of evolution of life and passage of time on Earth. Careful taphonomic analyses are needed, especially in those fossiliferous successions to be chosen as reference sections (e.g. boundary stra-

Plate 1.—Ammonites from the Aalenian-Bajocian of Saint Maixent, Poitou. Fig. 1.—Brasilia similis (Buckman). Reelaborated specimen: note the encrusting bivalves on the mould (arrows). Assemblage A 2'. Taphorecord 2/3. Bradfordensis Chron. (0.55x). Fig. 2.—Brasilia gr. gigantea (Buckman). Reelaborated specimen: note the boring on the mould (arrows). Assemblage A 2'. Taphorecord 2/3. Bradfordensis Chron. (0.47x). Fig. 3.—Euapotoceras euquetum Buckman. Reelaborated specimen: note that the mould is disarticulated along a septum (arrows). Assemblage A 2'. Taphorecord 2/2. Early Concavum Chron. (0.47x). Fig. 4.—Fissilobiceras fissilobatum (Waagen). Reelaborated specimen: note the dark colour of the filling of internal chambers due to glauconitization. Assemblage A 4'. Taphorecord 4/3. Early Laeviuscula Chron. (0.47x). Fig. 5.—Volutellina sp. Resedimented specimen: note that the body chamber is filled with the same sediment as the enclosing matrix and that the phragmocone is plugged with coarse calcite spar. Assemblage A 4'. Taphorecord 4/3. Early Laeviuscula Chron. (0.95x). Fig. 6.—Fissilobiceras sp. Reelaborated specimen: note different colours and textures in the mould. Assemblage A 4'. Taphorecord 4/3. Early Laeviuscula Chron. (0.95x). Fig. 7.—Eohoploceras aff. modestum (Buckman). Resedimented specimen. Assemblage A 2B. Taphorecord 2/1. Early Discites Chron. (0.95x).

Lámina 1.—Ammonites del Aalenien-Bajociense de Saint Maixent, en Poitou. Fig. 1.—Brasilia similis (Buckman). Ejemplar reelaborado. Nótese los bivalvos encostrando el molde interno (flechas). Asociación registrada A 2'. Taforregistro 2/3. Cron Bradfordensis. (x 0.55). Fig. 2.—Brasilia gr. gigantea (Buckman) Ejemplar reelaborado. Nótese las perforaciones sobre el molde interno (flechas). Asociación registrada A 2'. Taforregistro 2/3. Cron Bradfordensis. (x 0.47). Fig. 3.—Euapotoceras euquetum (Buckman) Ejemplar reelaborado. Nótese que el molde interno muestra una faceta de desarticulación a favor de un septo (flechas). Asociación registrada A 2'. Taforregistro 2/2. Cron Concavum. (x 0.47). Fig. 4.—Fissilobiceras fissilobatum (Waagen) (Buckman) Ejemplar reelaborado. Obsérvese el color oscuro del reflejo de las cámaras internas del fragmocono, debido a la glauconización. Asociación registrada A 4'. Taforregistro 2/3. Cron Laeviuscula inferior. (x 1.17). Fig. 5.—Volutellina sp. Ejemplar resedimentado. Obsérvese que la cámara de habitación se encuentra rellenada con el mismo material que la matriz, o roca sedimentaria, que lo rodea y que el fragmocono muestra un revestimiento interno de gruesos cristales de calcita. Asociación registrada A 4'. Taforregistro 4/1. Cron Laeviuscula superior. (x 0.78). Fig. 6.—Fissilobiceras sp. Ejemplar reelaborado. Obsérvese los diferentes colores y texturas en el material que forma el molde interno. Asociación registrada A 4'. Taforregistro 4/3. Cron Laeviuscula inferior. (x 0.95). Fig. 7.—Eohoploceras aff. modestum (Buckman). Ejemplar resedimentado. Asociación registrada A 2B. Taforregistro 2/1. Cron Discites inferior. (x 0.95).
totypes) in order to reconstruct a correct biostratigraphy and to refine biochronological scales.

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