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# Sea-level changes and ammonite faunal turnover during the Lias/Dogger transition in the western Tethys

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*Key words.* – Lias/Dogger transition, Ammonites, Faunal turnover, Eustatic changes, Mediterranean province, Submediterranean province.

*Abstract.* – The aim of this paper was to investigate the possible connections between ammonite faunal turnover and the eustatic events recorded in Tethyan sequences during the middle Toarcian/early Bajocian time interval. For this we have analysed the biostratigraphic ranges, at the subzone level, of approximately 600 ammonite species belonging to 160 genera from several selected sections of the western Tethys (Mediterranean and Submediterranean provinces). The analysis of taxon ranges enabled us to plot curves for ammonite faunal turnovers, inter-subzonal distance, and diversity. Comparing the mentioned curves with Tethyan sequences [Hardenbol *et al.*, 1998], we find that sea-level changes correlate well with origination and extinction events and faunal diversity. Most of the faunal turnovers correlate with stratigraphic events. Extinction events with their corresponding decrease in diversity correlate with regressive intervals and with major or minor sequence boundaries. Origination events and their corresponding increase in diversity were clearly connected with transgressions in Tethyan sequences. In several cases, the major sequence boundary and the subsequent transgressive phase correlate with major ammonite faunal turnover, whereas minor or medium sequence boundaries generally gave rise to minor or medium turnovers.

## Variations eustatiques et renouvellement des ammonites au passage Lias/Dogger dans la Tethys occidentale

*Mots clés.* – Passage Lias/Dogger, Variations eustatiques, Renouvellement faunique, Province Méditerranéenne, Province Subméditerranéenne.

*Résumé.* – Ce travail analyse les connections possibles entre la faune d'ammonites et les événements eustatiques enregistrés dans le domaine de la Tethys pendant le Toarcien moyen et le Bajocien inférieur. Pour cette étude nous avons révisé les répartitions stratigraphiques de 600 espèces et 160 genres d'ammonites par sous-zone sur des coupes stratigraphiques selectionées dans les provinces méditerranéenne et subméditerranéenne. Cette analyse nous a permis d'obtenir une courbe de renouvellement faunique, une courbe des distances inter-sous-zones et la variation de la diversité. Une comparaison entre ces courbes et les séquences stratigraphiques de la Téthys proposées par Hardenbol *et al.* [1998] a mis en évidence une magnifique corrélation entre les événements de renouvellement dans la faune des ammonites et les variations eustatiques enregistrées dans la Téthys. La plupart des renouvellements sont corrélés avec des événements stratigraphiques. Les extinctions correspondent ainsi avec les intervalles régressifs et avec les limites majeures ou mineures des séquences stratigraphiques. Les événements d'apparition, qui s'accompagnent des augmentations de la diversité, coïncident avec les phases transgressives. La majorité des cas analysés montrent que les limites principales des séquences se corrèlent avec les rénovations fauniques majeures, tandis que les limites mineures et intermédiaires des séquences coïncident avec des renouvellements fauniques peu importants.

## INTRODUCTION

Possible connections between sea-level changes and origination and extinction processes have long occupied researchers. After the publication of the Exxon curve [Haq *et al.*, 1987, 1988], papers have proliferated concerning the connection between sea-level fluctuations (eustatic changes) and faunal turnover (originations-extinctions) in Mesozoic ammonites. Concretely, Mouterde *et al.* [1989, 1990], analysed the possible relationships of evolution and ammonite turnover with sea-level changes in the Bajocian of the Vocontian trough, and showed the strong connection between the eustatic changes and ammonite faunal turnovers. Recently, O'Dogherty *et al.* [2000] and Sandoval *et al.* [2001] have reported a strong relationship between ammonite faunal turnover in the Betic Cordillera and the eustatic changes for the entire Jurassic.

The aim of the present study was to plot a curve showing ammonite faunal turnover, at the subzonal level, in the western Tethys during the middle Toarcian-early Bajocian time interval, and to examine its possible connections with sea-level changes. For this, we have analysed in detail the

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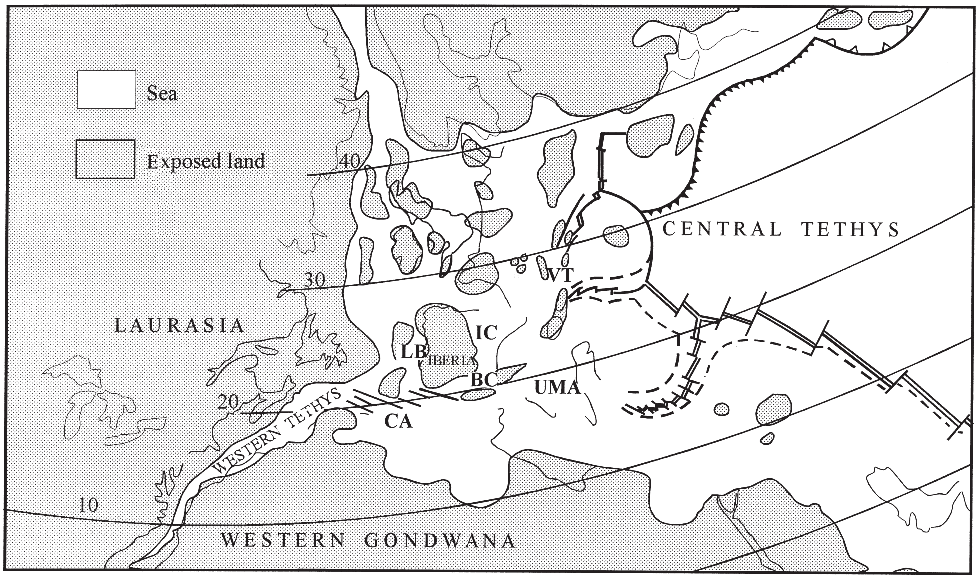


FIG. 1. – Paleogeographic reconstructions of the western Tethys (Toarcian) with the palaeogeographic location of the six basins analysed. BC : Betic Cordillera, CA : Central Atlas, IC : Iberian Cordillera, LB : Lusitanian basin, UMA : Umbria/Marche Apennines, VT : Vocontian trough [Modified from De Wever *et al.*, 1994].
FIG. 1. – *Reconstruction paléogéographique de la Téthys occidentale (Sinémurien-Aalénien) avec l'emplacement paléogéographique des six bassins analysés.* BC : *Cordillère bétique,* CA : *Atlas Central,* IC : *Cordillère ibérique,* LB : *Bassin lusitanien,* UMA : *Apennins d'Ombrie-Marches,* VT, *Bassin Vocontien [Simplifié d'après de De Wever* et al., *1994].*

stratigraphical range of approximately 600 ammonite species belonging to 160 ammonite genera (fig. 1) from several selected sections of the western Tethys, Mediterranean and Submediterranean provinces (fig. 2). The Mediterranean data come from Betic Cordillera [Linares and Sandoval, 1986, 1990, 1993, 1996; Linares *et al.*, 1988; Jiménez, 1986 ; Jiménez and Rivas, 1991, 1992; Sandoval, 1983, 1985, 1986; 1990; Goy *et al.*, 1988; García-Gómez *et al.*,

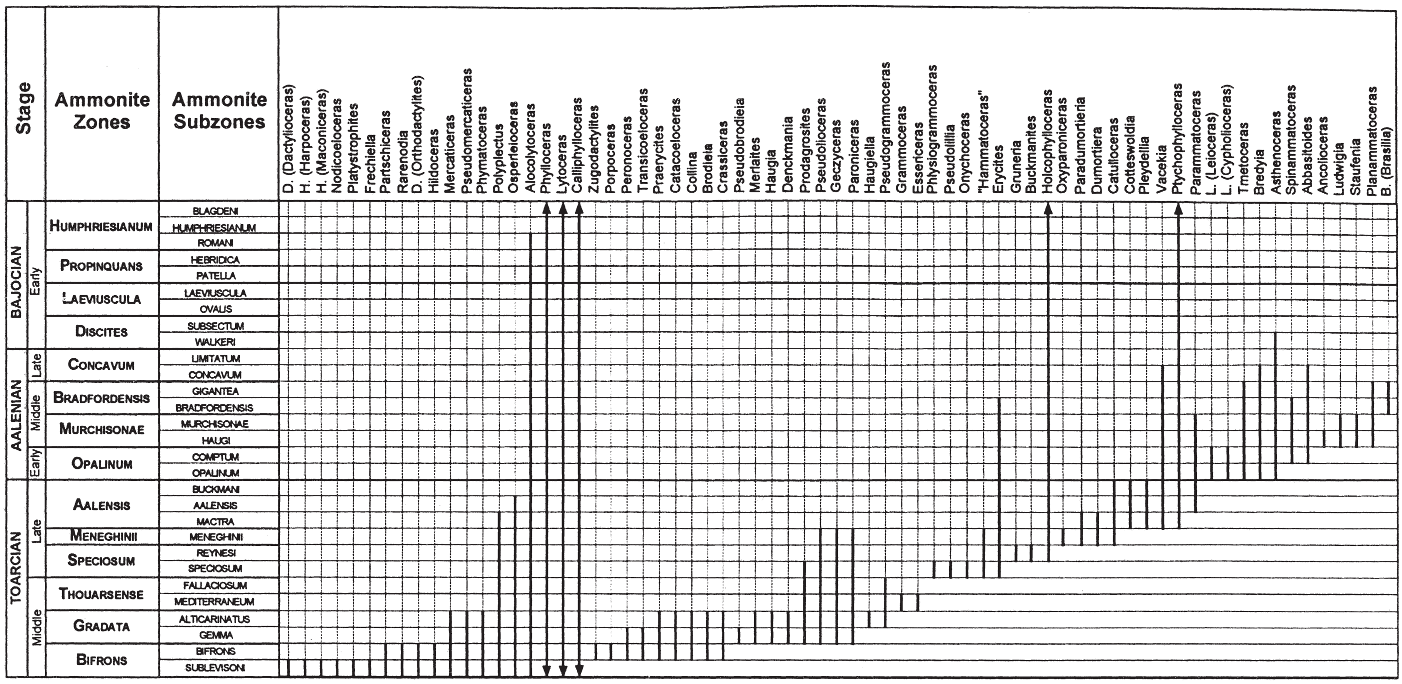


FIG. 2. – Biostratigraphic distribution of ammonite genera in the Submediterranean province. Zones and subzones (with minor modifications in the Aalensis and Laeviuscula Zones) proposed for the Submediterranean province [Contini *et al.*, 1997; Elmi *et al.*, 1997; Rioult *et al.*, 1997] in Groupe Français d'Étude du Jurassique [1997].
FIG. 2. – *Répartition stratigraphique des genres d'ammonites dans la province subméditerranéenne. L schéma zonal et subzonal est celui proposé par le Groupe Français d'Étude du Jurassique [Contini et al.,* 1997; Elmi *et al.,* 1997; Rioult *et al.,* 1997] avec de légères modifications pour les zones à Aalensis et Laeviuscula.

1994 ; Henriques *et al.*, 1996; Fernández-López *et al.*, 1999], Vocontian trough [Pavia, 1983], Umbro/Marchinian Apennines [Cresta, 1988, 1994; Cresta *et al.*, 1989, 1993; Nimi *et al.*, 1997; Parisi *et al.*, 1998; Macchioni and Venturi, 2000], Atlas [Benshili, 1989; Sadki, 1994, 1996]. The data on ammonite ranges analysed in the Submediterranean province are from Iberian Cordillera [Fernández-López, 1985; Fernández-López *et al.*, 1999; Goy and Martínez, 1990; Goy and Ureta, 1990, 1991; Goy *et al.,* 1988, 1994, 1996a,b; Ureta, 1985; Martínez, 1992, 1996; Henriques *et al.*, 1996; Comas-Rengifo *et al.,* 1996] and Lusitanian Basin [Fernández-López *et al.*, 1988a, b, 1999; Rocha *et al.*, 1990; Henriques, 1992, 1995, 2000; Henriques *et al.*, 1988, 1994, 1996]. In the Betic Cordillera, Iberian Cordillera and Umbro/Marchinian Apennines we analyse the complete time interval, in the Lusitanian Basin and in the Central Atlas we study the uppermost Toarcian (Aalensis Zone)-Lower Bajocian (Propinquans Zone) interval, and in the Vocontian trough we analyse the interval extending from the Concavum to Humphriesianum Zones (fig. 3). We selected these areas because they have been studied in detail; most of the stratigraphic sections were sampled bed by bed and the vertical range of the taxa are drawn. The sections are located in basins in which Upper Toarcian and/or Aalenian/Lower Bajocian sediments are well developed and provide a good stratigraphic and taxonomic record of the ammonite fauna.

In this study, we assume a potential bias generated by the taxonomic splitting, since the ammonite assemblages from each area were studied by different authors and we accept, at the species level, their taxonomic splitting and the chronostratigraphic range of the taxa they drawn. We have studied previously the Lias/Dogger ammonite faunas and, in revising the faunal assemblages, we have unified the generic taxonomy. Consequently, we believe that this potential bias is minimal, with little affect on the turnover and diversity curves.

## METHODOLOGY

For the time interval studied, we used, with minor modifications in the Aalensis and Laeviuscula Zones (figs. 2, 3, 4), the Mediterranean standard ammonite subzones [Contini *et al.*, 1997; Elmi *et al.*, 1997; Rioult *et al.*, 1997] in the "Groupe Français d'Étude du Jurassique". The successive biochronological units (subzones) of the time interval analysed have been numbered (from 1 for the Sublevisoni Subzone to 30 for the Banksi Subzone). Also we analysed the biochronological range of the ammonites from the data gathered in the selected sections. Figure 2 shows that the range of each taxon covers the entire subzone, although this may not necessarily be the case, since taxa with a FAD (first appearance datum) or LAD (last appearance datum) within a subzone are considered to have a time range that spans the entire interval.

The origination and extinction events identified in the studied interval were analysed in detail, starting from the data we have plotted, thereby rendering (a) curves of ammonite faunal turnover (b) inter-subzonal distances and (c) taxa diversity. These curves were later correlated with the Exxon curve, and more specifically with the Tethyan sequences [de Graciansky *et al.*, 1998; Hardenbol *et al.*, 1998].

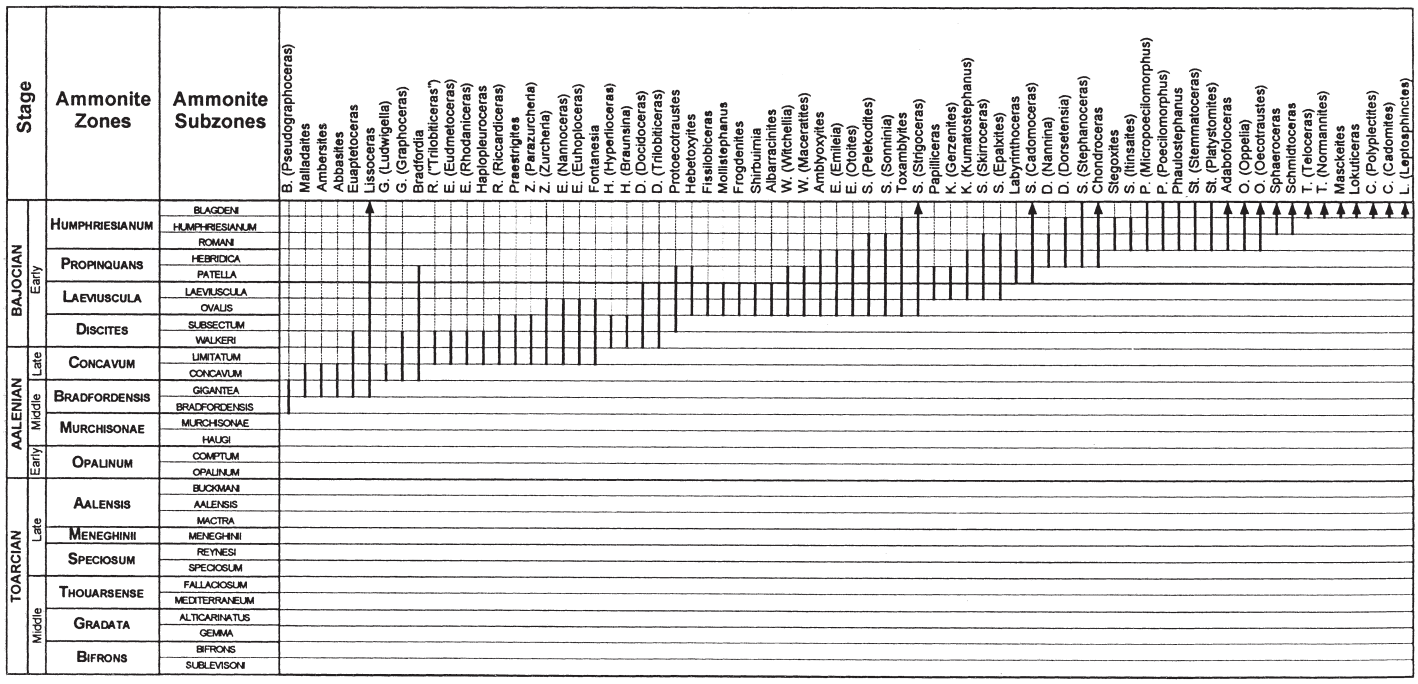
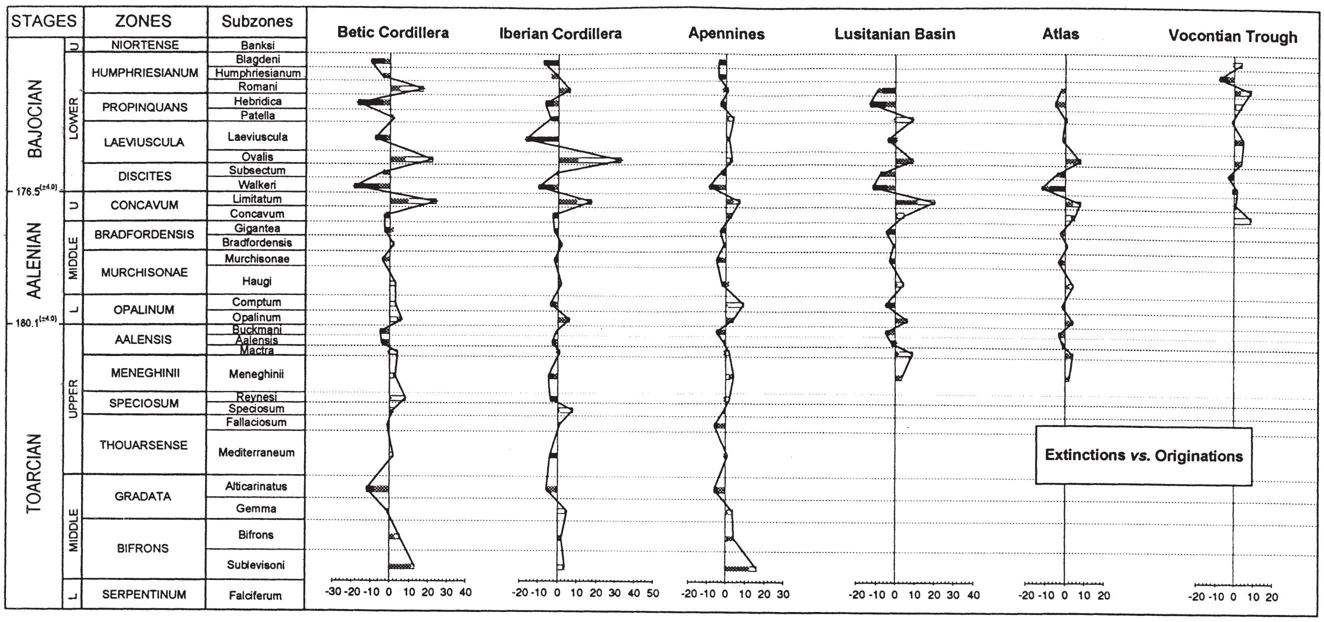


FIG. 2. (Continued)
FIG. 2. (suite)


STAGES
ZONES
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Atlas
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BRADFORDENSIS
MURCHISONAE
OPALINUM
AALENSIS
MENEGHINII
SPECIOSUM
THOUARSENSE
GRADATA
BIFRONS
SERPENTINUM
Banksi
Blagdeni
Humphriesianum
Romani
Hebridica
Patella
Laeviuscula
Ovalis
Subsectum
Walkeri
Limitatum
Concavum
Gigantea
Bradfordensis
Murchisonae
Haugi
Comptum
Opalinum
Buckmani
Aalensis
Mactra
Meneghinii
Reynesi
Speciosum
Fallaciosum
Mediterraneum
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Gemma
Bifrons
Sublevisoni
Falciferum
-30 -20 -10 0 10 20 30 40
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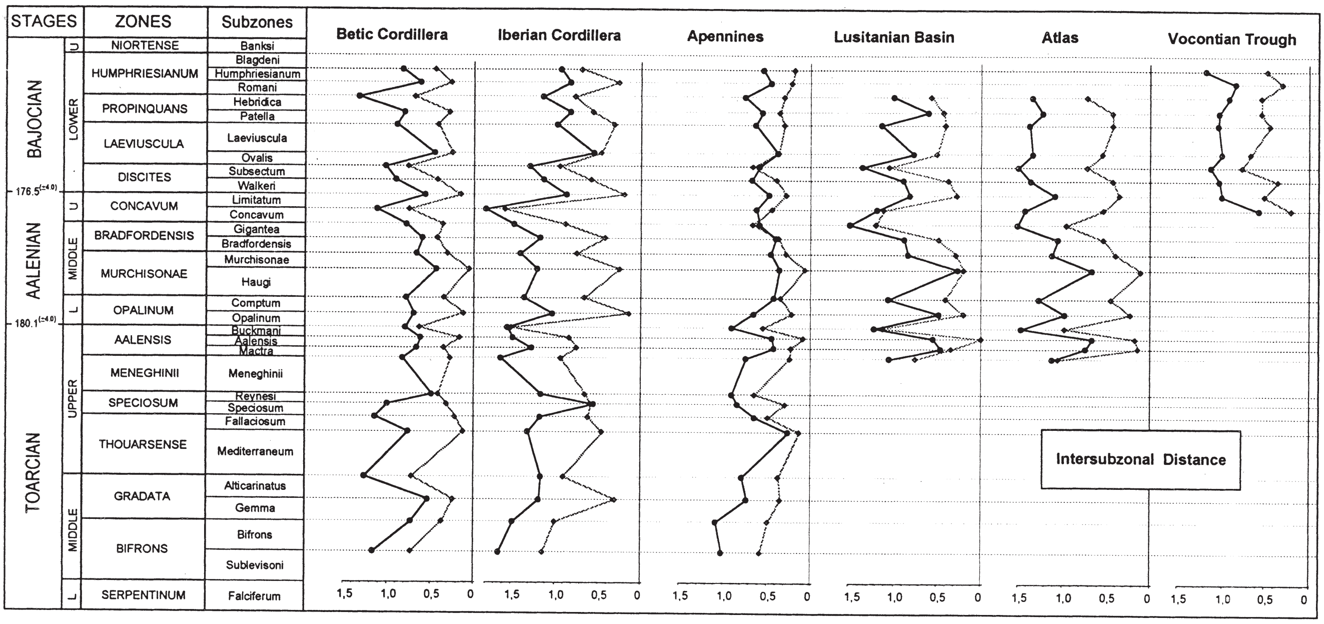
Extinctions *vs.* Originations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Walkeri
Limitatum
Concavum
Gigantea
Bradfordensis
Murchisonae
Haugi
Comptum
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Buckmani
Aalensis
Mactra
Meneghinii
Reynesi
Speciosum
Fallaciosum
Mediterraneum
Alticarinatus
Gemma
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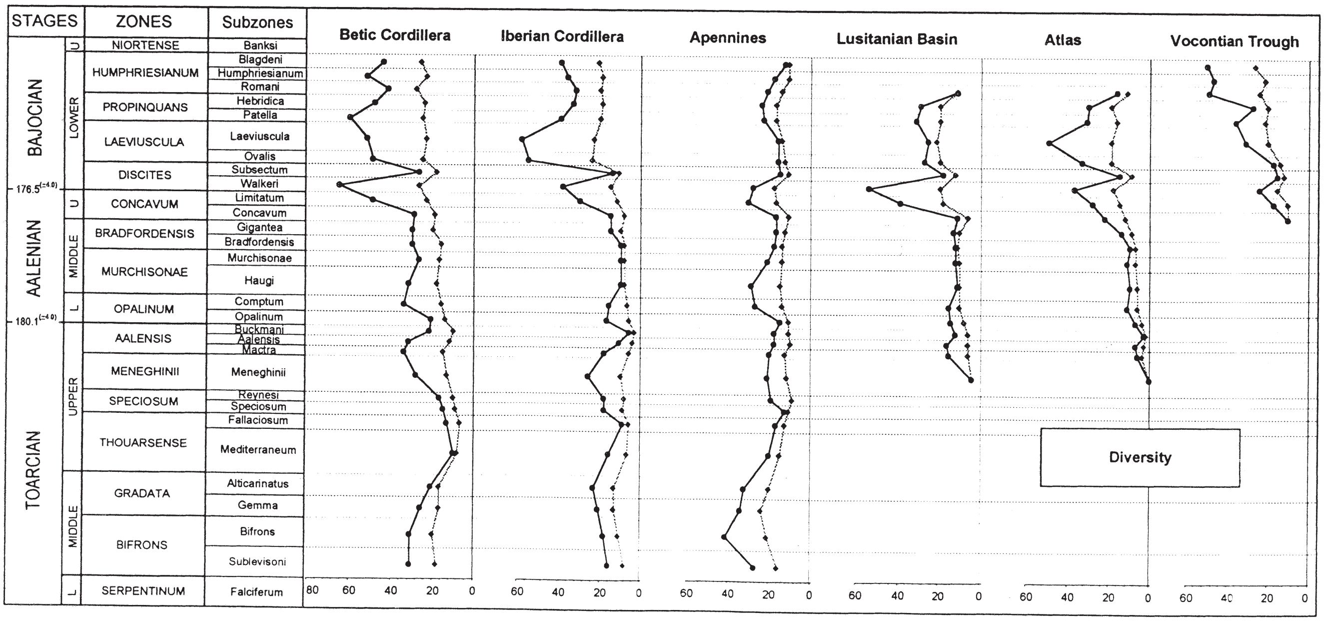
Intersubzonal Distance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Diversity

The **ammonite faunal turnover** (figs. 3, 4, curve A) was determined by comparing the origination and the extinction number of taxa in each subzone. For this, we calculated the differences between the numbers of first appearance datum's (FAD's) and last appearance datum's (LAD's). In this figure the black bars indicate that species originations exceeded species extinctions (positive values with FAD > LAD); white bars indicate species extinctions exceeded species appearances (negative values; LAD > FAD). Genus turnover analyses are also plotted in this bar diagram using the same axis, but now genera originations and extinctions are represented only by dotted bars (note that either species or genus bars show the same turnover trend but the latter consistently displays lower values). In our diagram the turnover curve (black line) results from maximum values (species-turnover rates). We found a good correlation between times of high origination values and maximum flooding surface in the Tethyan sequence analysis.

The ammonite faunal turnover was analysed also by studying faunal-assemblage similarities between two successive subzones (figs. 3, 4, curve B), which we called the **inter-subzonal distance**, [see Guex, 1991 for details]. This coefficient indicates the significance of faunal turnover rates by studying the dissimilarities between two adjacent biochronological units. This coefficient is determined by applying Guex's [1991] formula. Let i and j be two discrete biochronological units (in our case subzones). For each pair of adjacent units i and j, we can calculate a distance Dij defined as follows : Dij = Li/Ti +Fj/Tj, where Li = the number of LAD's in unit i, Ti = the total number of taxa in unit i, Fj = the number of FAD's in unit j and Tj = the total number of taxa in unit j. This coefficient varies between 0 and 2. Its lowest theoretical value 0 means that units i and j are identical (this is never the case because they must be distinct) and indicate a gradual faunal change and/or a good fossil record. Very high values (close to 2) signify that the two adjacent subzones are completely different and, having no common elements, express high faunal turnover rates and/or a poor vertical record and/or gaps in the stratigraphic record. The results need to be interpreted together with the regional stratigraphic data in order to differentiate peaks due to rapid faunal-turnover rates from that artefact resulting from the incompleteness of the stratigraphic record. The resulting curve (figs 3, 4, curve B) noticeably shows a direct correlation with the Tethyan sequences. In this curve, the intersubzonal distance curve could be comparable to curve A, but a basic difference is that in the construction of the former the diversity is also considered, giving a precise picture of the faunal turnover. The black lines indicate the species intersubzonal distance and the grey lines show the genera intersubzonal distance. Note the quasi-parallelism between the two curves, which results from the good taxonomic criteria followed. High values in the inter-subzonal distance index correlate with the transgressive interval and occur stratigraphically after a subzone characterized by high extinction rate and before a subzone with high origination rate. This is a common mechanism because there will be no common elements between both subzones (most of new species occur in the upper subzone). This coefficient has a low value during the regressive interval and is located after a subzone with a high origination rate and it precedes a subzone with a high extinction rate. This is the reason why we found many common elements (taxa) between the two subzones, in fact a part of the originated taxa still exist in the upper biozone.

To analyse **diversity,** we calculated the total number of taxa (genera and species) regardless of their population size while assuming that each taxon covers the entire biochronologic unit. The resulting curves (figs. 3, 4, curve C) show : (1) a marked parallel between genus and species diversity, and (2) a good correlation between the diversity and the Tethyan sequences of de Graciansky *et al.* [1998].

## AMMONITE TURNOVER AND EUSTATIC CYCLES : ANALYSIS

The first major faunal turnover analysed took place in the Middle Toarcian (Bifrons Zone, Sublevisoni Subzone) as revealed by the appearance of some genera and several species in the family Dactylioceratidae and the subfamilies Hildoceratinae, Bouleiceratinae and Phymatoceratinae (fig. 2). This peak in the appearance of ammonite genera and species coincides with a transgressive maximum in the curve of Haq *et al.* [1988], which can be correlated with a relative sea-level rise. In the Tethyan realm, the transgressive peak of the cycle Toa3 occurred during the upper part of the Sublevisoni Subzone [de Graciansky *et al.*, 1998; Hardenbol *et al.*, 1998]. This transgressive peak is detected in many areas of the Betic Cordillera, Apennines, Iberian Cordillera and Lusitanian Basin. In the Subbetic, the Bifrons Zone clearly corresponds to a transgressive maximum since, in several areas, Bifrons sediments are overlain (sometimes also underlain) by stratigraphic discontinuities.

Between the Bifrons Subzone and the lower part of Gradata Zone a faunal turnover took place; most Dactylioceratidae and of the Hildoceratinae (including the genus *Hildoceras*) became extinct and some new genera (*Pseudomercaticeras*, *Haugia, Haugiella, Denckmannia, Brodiea*) and some Grammoceratinae originated. The extinctions may be connected with a period of relatively low sea-level

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FIG. 3. – Ammonite faunal turnover in each of the analysed areas. The analysis of taxa origination-extinction (upper part) is indicated by the turnover curves which are made from the differences between the numbers of first appearance datum's (FAD's) and last appearance datum's (LAD's) (see text). Intersubzonal distance coefficient (middle part) ranges between 0-2. This coefficient tests the significance of faunal-turnover rates by studying the distance, or dissimilarity, between each adjacent discrete subzone (see text). The analysis of diversity (lower part) is based on the absolute number of taxa (genera or species) occurring in each ammonite subzone. The black graphs (left side) represent the species diversity and grey graphs (right side) represent the genus diversity (zones and subzones as in figure 2). Note the good correlation of all of the curves for the six areas analysed.

FIG. 3. – *Renouvellements fauniques des ammonites dans chacune des régions étudiées. L'analyse des spéciations/extinctions (partie supérieure) est donnée par la courbe des taux de renouvellement basée sur le nombre des apparitions (FAD's) et des disparitions (LAD's) (voir texte). Le coefficient de distance intersubzonale (milieu) oscille entre 0 et 2. Ce coefficient teste la signification des taux de changements fauniques en exprimant la distance (ou la dissimilarité) entre deux sous-zones discrètes adjacentes (voir texte). L'analyse de la diversité (partie inférieure) est basée sur le nombre absolu de taxa (genres et espèces) qui se trouvent dans chaque sous-zone. Les graphes noirs (partie gauche) représentent la diversité spécifique et les graphes gris (partie droite) représentent la diversité générique (les zones et sous-zones sont les mêmes que dans la figure 2). Noter la bonne corrélation entre toutes les courbes pour les six régions prises en considération.*

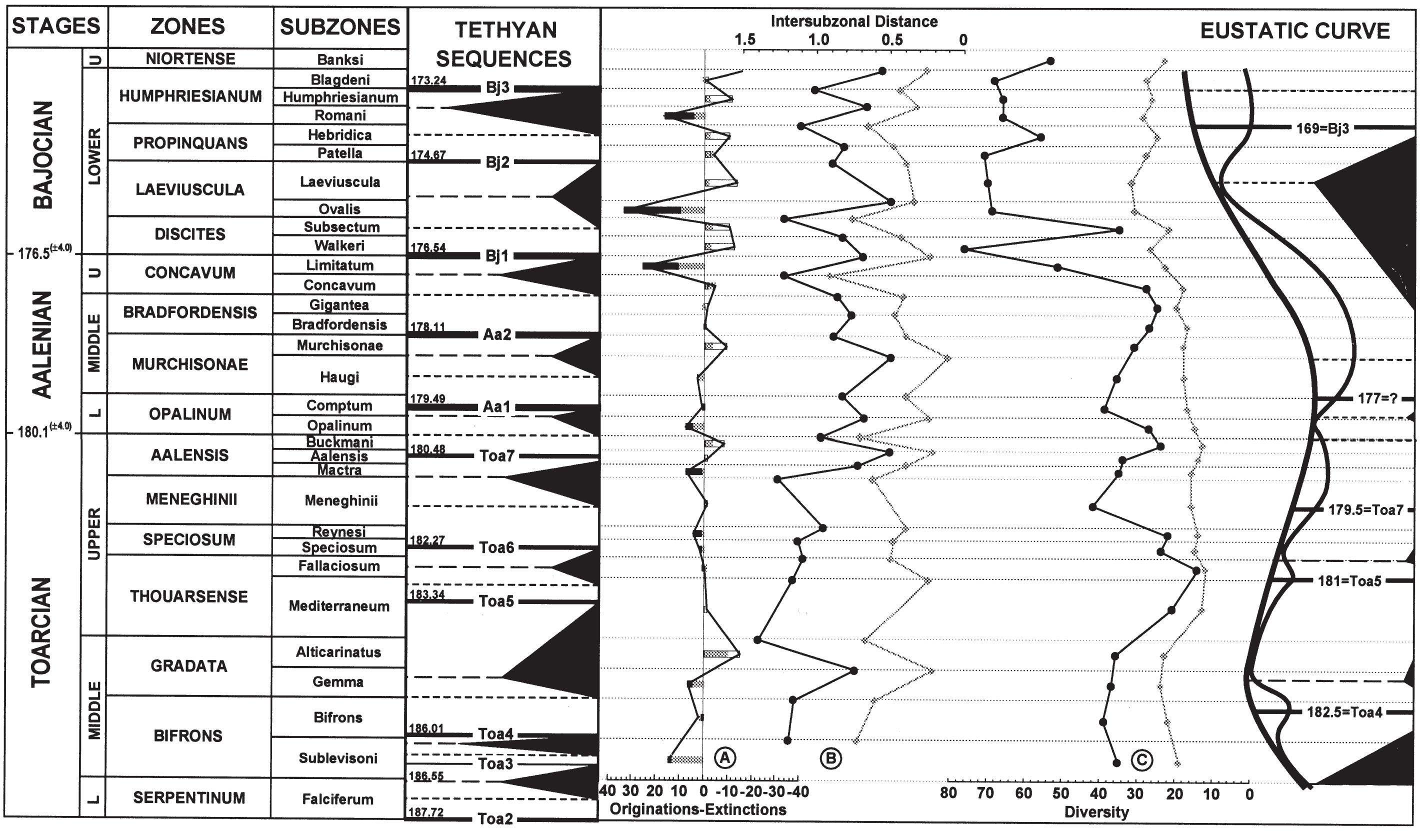

FIG. 4. – Ammonite faunal turnover compared with sea-level-change analysis. Zones and subzones as in figure 2. Sequence boundaries of Tethyan sequence according to Hardenbol *et al.* [1998]. Eustatic curve on the right side is that of Haq *et al.* [1988] [*in* Hardenbol *et al.*, 1998]. The analysis of taxa origination-extinction (curve A) is indicated by the turnover curve (black line), which is made from the differences between the numbers of first appearance datum's (FAD's) and last appearance datum's (LAD's) (see text). Curve B is expressed by means of the intersubzonal distance coefficient ranging between 0-2. This coefficient tests the significance of faunal-turnover rates by studying the distance, or dissimilarity, between each adjacent discrete zone (see text). The analysis of diversity (Curve C) is based on the absolute number of taxa (genera or species) occurring in each ammonite subzone. The black graph represents the species diversity and grey graph represents the genus diversity.

FIG. 4. – *Renouvellement de la faune d'ammonite comparé avec la courbe de variations eustatiques. La zonation employée est la même que celle de la figure 1. Les limites des séquences stratigraphiques sont celles établies par Hardenbol* et al. *[1998]. La courbe eustatique de la partie droite de la figure est celle de Haq* et al. *[1988] (in Hardenbol* et al. *[1998]. L'analyse des apparitions vs. extinctions dans la faune d'ammonites (courbe A) est représentée par la courbe de renouvellement (ligne noire), qui exprime la différence entre le nombre des premières apparitions (FAD's) et des dernières apparitions (LAD's). Les rectangles noirs indiquent que le nombre d'apparitions dépasse le nombre d'extinction (valeurs positives, FAD>LAD); les rectangles blancs montrent l'inverse : le nombre d'extinctions est plus élévé que celui des apparitions (LAD>FAD). L'analyse des renouvellements des genres a été aussi dessinée sur le diagramme précédent en employant le même axe de représentation, mais les valeurs sont indiquées par des rectangles gris. On peut observer comment la tendance entre genres et espèces est semblable, mis à part le fait que les données pour les espèces montrent toujours des valeurs plus élevées. La courbe noire est obtenue à partir des valeurs maximales des taux de renouvellements des espèces. La* courbe B *montre la distance intersubzonale, qui est un coefficient variant entre 0 et 2. Ce coefficient montre le renouvellement faunique en analysant la distance inter-zone, ou la non similitude entre deux sous-zones adjacentes. La courbe obtenue est comparable à la courbe A, mais pour la construction de la courbe de distance intersubzonale la diversité est un paramètre pris en considération et de cette façon la courbe montre une image précise du renouvellement. La ligne noire montre la distance intersubzonale pour les espèces et la ligne grise montre celle des genres. On notera le parallelisme entre les deux courbes qui est le résultat d'une excellente taxonomie. L'analyse de la diversité* (Courbe C) *est etablie à partir du nombre absolu des taxa (au niveau du genre ou de l'espèce) qui ont été enregistrés par sous-zone. La courbe noire montre la diversité pour les espèces et la courbe grise montre la diversité générique.*

[Hallam, 1990], which is slightly later than the Toa3/Toa4 sequence boundary and coincides with the lowstand deposits in Tethyan sequences located between the Bifrons and Gemma subzones [de Graciansky *et al.*, 1998; Hardenbol *et al.,* 1998]. The originations correlate well with the end of the transgressive phase of the Toa5 of Tethyan sequences. This transgressive phase was not significant, since in many areas of the Betic Cordillera (swells and locally, also in trough facies) and other Tethyan areas the discontinuity covers the complete Gradata and Thouarsense Zones.

In the upper part of the Gradata Zone (Alticarinatus Subzone) and the lower part of the Thouarsense Zone (Mediterraneum Subzone) a minor ammonite faunal turnover occurred, in which extinctions clearly surpassed originations (figs. 2, 3). The last Hildoceratinae, Dactylioceratidae and the Phymatoceratinae became extinct and several Grammoceratinae and Hammatoceratinae diversified and later radiated. Extinctions may have been connected to the Toa4/Toa5 sequence boundary and the diversification may have been related Hallam's [1988] transgressive phase (T7), which in turn is more or less equivalent to the transgressive phase of the UAB-4.4 cycle in the Exxon curve and with the transgressive phase of the Toa5 Tethyan sequence [de Graciansky *et al.*, 1998; Hardenbol *et al.*, 1998].

Between the upper part of the Thouarsense Zone (Fallaciosum Subzone) and the Meneghinii Zone a minor ammonite turnover occurred place. Some genera (*Pseudogrammoceras, Grammoceras, Hammatoceras, Gruneria, Pseu-*

*dolillia,* etc.) disappeared and new taxa (the family Erycitidae, new Hammatoceratidae and the first Graphoceratidae such as *Dumortieria* and *Catulloceras*) appeared and radiated within this time interval, and occupied the various palaeogeographical regions. This faunal turnover (figs. 2, 3 curve A) coincided with the Toa5/Toa6 sequence boundary and with the transgressive phase of the Toa6 of Tethyan sequences [de Graciansky *et al.,* 1998; Hardenbol *et al.*, 1998]. This transgressive phase re-established communication between the Boreal, the Submediterranean and the Mediterranean basins, and the faunal assemblages are therefore similar in different palaeogeographic domains.

At the transition between the Meneghinii and Aalensis Zones, another faunal turnover occurred. Some genera (*Polyplectus*, *Geczyceras*) disappeared and were replaced by new Graphoceratinae such as *Pleydellia* and *Cotteswoldia* (which predominated in the latest Toarcian) and new Hammatoceratinae. These minor biological events coincided with the end of a transgressive phase in the Exxon curve [Haq *et al*., 1988], and also coincide with a regressive interval in Hallam's [1988, 1990] curves, as well as with the end of the transgressive phase of the Tethyan sequence Toa6 [de Graciansky *et al.,* 1998; Hardenbol *et al.,* 1998]. Originations clearly surpassed extinctions in the Mactra Subzone, indicating a slightly transgressive character. However, Upper Toarcian sediments are generally well represented only in the Betic troughs, but on the swells a stratigraphic discontinuity appears, also covering the Lower and Middle Aalenian. This clearly shows the generally regressive character of this wide time interval, although Aalensis Zone sediments are generally better developed than are underlying or overlying ones.

In the Toarcian-Aalenian transition the *Pleydellia, Cotteswoldia and Catulloceras* genera, which were the dominant ammonite-fauna during the latest Toarcian, became extinct and Tmetoceratinae, Leioceratinae and several new Hammatoceratidae and Erycitidae appeared and radiated. These biological events, coinciding with a regression in Hallam's curve [1988], are represented in the western Tethys by a very poor record of the Buckmani and Opalinum Subzones, even in the typical trough facies. This ammonite turnover may correlate in turn with the Toa6/Toa7 boundary of the Tethyan sequence and with the transgressive interval of this latter sequence. The number of extinctions surpasses originations in the Buckmani Subzone (figs. 2, 3, 4, curve A) indicating a strong regressive character of this subzone. The lower part of the Comptum Subzone, which is well represented almost all over the world, corresponds to the end of a small transgressive interval (the end of the transgressive phase of the UAB-4.6 in the Exxon curve) and the end of the transgressive phase of Toa7 of the Tethyan sequence [de Graciansky *et al.*, 1998; Hardenbol *et al.*, 1998]. During the transgressive phase, originations clearly surpass extinctions (figs. 3, 4, Curve A) and this coincides with most widespread diversification of Leioceratinae, Tmetoceratinae, Erycitidae and Hammatoceratidae, which gave rise to a relative maximum in diversity (figs. 3, 4, curve C).

A medium turnover took place in the early/middle Aalenian transition, in which the more significant ammonite events were the isolation of ammonite faunas that may have caused the Leioceratinae to give way to Graphoceratinae, simultaneously with the appearance and radiation of some characteristically Mediterranean Erycitidae (*Spinammatoceras, Malladaites and Ambersites*, Sandoval *et al*. [2001]. This turnover, which correlates well with the boundary between the UAB and LZA super-sequences in the Exxon curve [Haq *et al*., 1988], coincides with a major sequence boundary (Toa7/Aa1) and with the transgressive phase of Aa1 of Tethyan sequences.

Between the upper part of the Middle Aalenian and the Aalenian/Bajocian transition a major ammonite-faunal turnover is recognizable. Some typical middle Aalenian ammonites (*Erycites, Spinammatoceras, Brasilia, Tmetoceras,* etc) went extinct and new groups such as the Haploceratidae, Strigoceratidae, Sonniniidae, Otoitidae and Stephanoceratidae as well as new Graphoceratidae and the last Erycitidae (*Haplopleuroceras*) and Hammatoceratidae originated and spread (fig. 2). Originations proliferated in the Limitatum Subzone so that originations clearly surpassed extinctions during this time interval, giving rise to a maximum in diversity at both the genus and especially the species level (figs. 2, 3, 4, curves A and C). The turnover coincides with a transgressive phase in the Exxon curve [Haq *et al*., 1988] and correlates well with the Aa1/Aa2 major sequence boundary and with the transgressive phase of this latter sequence in the Tethyan sequences [de Graciansky *et al*., 1998; Hardenbol *et al*., 1998].

From the Aalenian/Bajocian transition to Laeviuscula Zones a new major ammonite faunal turnover is discernible (figs 2 and 3, 4, curve A). Most of the ammonites (Graphoceratidae, Grammoceratinae, Hammatoceratidae and Erycitidae) that predominated in the late Aalenian disappeared in the Discites Zone (Walkeri Subzone), and a great diversification of the Haploceratidae, Strigoceratidae, Sonniniidae, Otoitidae, Stephanoceratidae together with the origination of the Sphaeroceratidae took place, especially in the Laeviuscula Zone (Ovalis Subzone). In comparing these faunal turnovers with the eustatic events, we find that the curves of Hallam [1988, 1990] [see O'Dogherty *et al.,* 2000] show a regressive interval which would be situated very close to the Aalenian/Bajocian boundary, followed by a transgression [$T_8$ in Hallam, 1988] in early Bajocian. The Exxon curve [Haq *et al*., 1988] shows a broad transgressive episode from the Murchisonae Zone to the Laeviuscula Zone. Tethyan sequences [de Graciansky *et al*., 1998; Hardenbol *et al*., 1998] show a major sequence boundary (Aa2/Bj1) near the Aalenian/Bajocian boundary, lowstand deposits in the upper part of the Discites Zone and a transgressive phase in the Laeviuscula Zone (fig. 4). Comparing Tethyan sequences with the diversity curve, we find that the maximum specific diversity coincides with a major sequence boundary (Aa2/Bj1) (figs. 3, 4, curve C). We believe that the major sequence boundary may be located within the Discites Zone rather than in the Aalenian/Bajocian boundary, since the major extinction events took place at the end of the Walkeri Subzone. The regressive interval, which is related to this sequence boundary, caused more extinctions than originations in the Discites Zone (figs. 3, 4, curve A) whereas in the transgressive phase of the Tethyan sequence Bj1 (Ovalis Subzone), originations clearly surpassed extinctions, giving rise to great diversity in the Laeviuscula Zone (figs. 2, 3, 4 curves A, C). These events (regression and later transgression) satisfactorily explain the faunal turnovers described above. In the Betic and other Mediterranean areas, the transgressive interval in the early Bajocian is easily recognised because in many areas (e.g. Betic swells), the Lower Bajocian materials lie directly on top of Lower Aalenian sediments or even older ones.

Near the boundary between the Propinquans and Humphriesianum Zones (Hebridica and Romani Subzones), another major faunal turnover marks the disappearance of the Otoitidae, Bradfordiinae, Sonniniidae –except for *Dorsetensia*– and some Stephanoceratidae such as *Kumatostephanus*, and the genus *Labyrinthoceras*. This extinction occurred slightly before the appearance of other taxa (e.g. Oppeliidae and some Sphaeroceratidae such as *Sphaeroceras* and *Chondroceras*) and also before the maximum diversification and abundance of the Stephanoceratidae. In the Exxon curve, high-stand deposits end at the boundary between Propinquans and Humphriesianum zones, where a medium sequence boundary is located (figs 3, 4). This event is concomitant with the end of $T_8$ and with the $R_6$ of the Hallam's curve [see O'Dogherty *et al.*, 2000]. The Tethyan sequences [de Graciansky *et al.,* 1998; Hardenbol *et al.,* 1998] show a regressive interval in the Propinquans Zone related with the lower boundary of Bj1 of the Tethyan sequences, followed by a major transgression in the Humphriesianum Zone (Romani and Humphriesianum Subzones). Clearly, this turnover is correlated with a drop in sea-level, followed by a rapid rise, as is shown by the Exxon and Hallam's [1988] curves and the Tethyan sequences [de Graciansky *et al.,* 1998].

Lastly, a new major faunal turnover took place at the early/late Bajocian transition, which can be accurately related to the lower boundary of the Tethyan sequence Bj3 (figs. 3, 4) and with the transgressive phase of this cycle.

## CONCLUSIONS

The faunal assemblages analysed in the Mediterranean and Submediterranean provinces (Betic Cordillera, Umbria-Marche Apennines, Vocontian Trough, Atlas, Iberian Cordillera, Lusitanian Basin) show that, during the middle Toarcian/early Bajocian times, ammonite faunal turnovers are well correlated with stratigraphic and eustatic events. Origination events with their corresponding increase of generic and specific diversity clearly correlate with transgressive intervals in Tethyan sequences. Extinction events with corresponding decrease of diversity correlate with regressive intervals and with sequence boundaries. The major faunal turnover took place in the Middle Toarcian (Bifrons Zone), latest Middle Toarcian-Late Toarcian (Bifrons-Gradata Zones), Toarcian-Aalenian boundary (Aalensis-Opalinum Zones), latest Middle Aalenian-earliest Bajocian (Bradfordensis-Walkeri Subzones), earliest early Bajocian (Discites-Laeviuscula Zones), early Bajocian (Propinquans-Humphriesianum Zones) and in the early/Late Bajocian Transition (Humphriesianum-Niortense Zones). In several cases (sequence boundaries Aa2, Bj3; see fig. 2, curve A), major sequence boundaries and subsequent transgressive phases correlate with major ammonite faunal turnover events, whereas medium or minor sequence boundaries generally correlate with minor, at times scarcely detectable, faunal turnover. Factors affecting the ammonite faunal turnover could be both biotic and abiotic, and, as Hallam and Wignall [1997] have shown, small marine environmental perturbations can strongly affect shallow organisms (most ammonites with the exception of Lytoceratina and Phylloceratina, which, in the analysed areas, are only abundant in typically Mediterranean areas such as the Subbetic and Apennines). A significant environmental event affecting the ammonite faunal turnover could be the climatic changes, since, as it is well known, eustatic changes are strongly affected by severe temperature changes and tectonic activity. If we assume, as the diversity and turnover curves show (fig. 4), that sea-level changes are the main cause affecting ammonite faunal turnover, we can easily deduce that climatic changes affected these turnovers both directly and, even more so, indirectly. In conclusion, our study shows the strong influence that the environment (in this case sea-level changes) exerted on faunal assemblages and general renovation biota, even for pelagic organisms such as the ammonites.

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## References

BENSHILI K. (1989). – Lias-Dogger du Moyen-Atlas plissée (Maroc). Sédimentologie, biostratigraphie et évolution paléogéographique. – *Doc. Lab. géol. Fac. Sci. Lyon,* **106,** 1-96.

COMAS-RENGIFO M.J., GÓMEZ J.J., GOY A., ARIAS C., BERNALD J., GARCÍA-JORAL F., HERRERO C., MARTÍNEZ G. & PERILLI N. (1996). – The Toarcian in the Rambla del Salto (Sierra Palomera) section. *In* : *1st Toarcian and 4th Aalenian Working Groups Meeting*. – Field-trip Iberian Range Guide-Book, 27-48. – Univ. Complutense, Madrid, 77 p.

CONTINI D., ELMI S., MOUTERDE R. & RIOULT M. (1997). – *In* : E. CARIOU & P. HANTZPERGUE (coords.), Biostratigraphie du Jurassique ouest-européen et méditerranéen : zonations parallèles et distribution des invertevrés et microfóssiles. *In* : Groupe Français d'étude du Jurassique : Aalénien, 25-36. – *Bull. Centre Rech. Explor. Prod. Elf Aquitaine*, *Mém*. **17**, 440 pp.

CRESTA S. (1988). – Associations d'ammonites et biostratigraphie de l'Aalénien et du Bajocien inférieur des Appenins d'Ombrie-Marches (Italie Centrale). *In* : R.B. ROCHA & A.F. SOARES Eds., *2nd International Symposium on Jurassic Stratigraphy*. – INIC, Lisboa, 209-224.

CRESTA S. (1994). – Distributions stratigraphiques des Hammatoceratidae au Toarcien et Aalénien des Apennins d'Ombrie Marches (Italie). – *Misc. Serv. Geol. Naz. Ital.,* **5,** 113-115.

CRESTA S., BASILICI G., BUSSOLETTI A., COMAS M.J., ELMI S., FERNÁNDEZ-LÓPEZ S., FERRETTI A., GOY A., HENRIQUES M.H., KALIN O., JIMÉNEZ A.P., MARTÍNEZ G., SANDOVAL J., URETA M.S. & VENTURI F. (1993). – Relazione sul Workshop "Paleontologia e Biostratigrafia dei sedimenti Toarciano-Bajociani in successioni di alto morfostructturale dell'Appennino Umbro-Marchigiano : l'area di Monte Nerone. Correlazioni con altre regioni della Tetide Occidentale (Piobbico, 2-14 agosto 1993). – *Bol. Serv. Geol. It.*, **112**, 129-139.

Cresta S., Pallini G. & Venturi F. (1989). – Associazioni ad ammoniti della sezione Giurassica di Valdobia. *In* : S. Cresta, S. Monechi & G. Parisi Eds., Mesozoic-Cenozoic stratigraphy in the Umbria-Marche area. – *Mem. Descr. Carta geol. Il.*, **39,** 89-94.

De Wever P., Azéma J. & Fourcade E. (1994). – Radiolaires et Radiolarites : Production primaire, diagenèse et paléogéographie. – *Bull. Centres Rech. Prod.-Explor Elf Aquitaine*, **18**, 315-379.

Elmi S., Rulleau L., Gabilly J. & Mouterde R. (1997). – *In* : E. Cariou & P. Hantzpergue, (coords.), Biostratigraphie du Jurassique ouest-européen et méditerranéen : zonations parallèles et distribution des invertevrés et microfósiles. *In* : Groupe Français d'étude du Jurassique, Toarcien, 37-40. – *Bull. Centre Rech. Explor. Prod. Elf Aquitaine,* **Mém. 17**, 440 p.

Fernández-López S. (1985). – El Bajociense en la Cordillera Ibérica. – PhD Thesis. Fac. Ciencias Geológicas univ. Madrid, 1-850.

Fernández-López S, Henriques M.H,. Linares A., Sandoval J. & Ureta M.S. (1999). – The genus *Tmetoceras* (Ammonoidea) from Iberia : taxonomy, habitats, and evolution. *In* : F. Olóriz & F.J. Rodríguez-Tovar Eds., Advancing research on living and fossil cephalopods, 91-108. – Kluwer Academic/Plenum Publishers, New York, 550 p.

Fernández-López S., Henriques M.H., Mouterde R., Rocha R.B. & Sadki D. (1988a). – Le Bajocien inférieur du Cap Mondego (Portugal), essai de biozonation. *In :* R.B. Rocha & A.F. Soares Eds., *2nd International symposium on Jurassic stratigraphy.* – INIC*,* Lisboa, 303-313.

Fernández-López S., Mouterde R. & Rocha R.B. (1988a) – Les *Zurcheria s.l.* (Ammonitina, Erycitidae) du Bajocien inférieur du Cap Mondego (Portugal). *In* : R.B. Rocha & A.F. Soares Eds., *2nd International symposium on Jurassic stratigraphy.*– INIC*,* Lisboa, 283-300.

García-Gómez R., Jiménez A.P., Linares A., Rivas P. & Sandoval J. (1994). – The Toarcian Aalenian boundary in the Betic Cordillera (southern Spain). – *Geobios*, Mém. sp. **17**, 211-222.

Goy A., Jiménez A.P., Martínez G. & Rivas P. (1988).– Difficulties in Correlating the Ammonite successions of the Iberian and Betic Cordilleras. *In :* R.B. Rocha & A.F. Soares Eds., *2nd International Symposium on Jurassic Stratigraphy.* – INIC*,* Lisboa, 155-178.

Goy A. & Martínez G. (1990). – Biozonación del Toarciense en el área de La Almunia de Doña Godina-Ricla (Sector Central de la Cordillera Ibérica). – *Cuad. Geol. Ibérica*, **14**, 9-44

Goy A., Martínez G., Arias C., Bernad J., , García-Joral F., Gómez J.J., Herrero C., Perilli N. & Ureta M.S. (1996a). – The Toarcian in the sector located between La Almunia de Doña Godina y Ricla. *In* : *1st Toarcian and 4th Aalenian Working Groups Meeting*, Fieldtrip Iberian Range Guide-Book, 1-24. – Univ. Complutense, Madrid, 77 p.

Goy A. & Ureta M.S. (1990). – El Aaleniense en la Cordillera Ibérica. – *Cahiers Univ. Catho. Lyon, sér. Sci*., **4**, 73-87.

Goy A. & Ureta M.S. (1991). – The lower boundary of the Aalenian in the Fuentelsaz section (Iberian range, Spain). *In* : N. Morton Ed., *Conference on Aalenian and Bajocian Stratigraphy.* – Birkbeck College, Univ. London, 81-95.

Goy A., Ureta S., Arias C., Bernad J., Barrón M.L., Canales M.L., García-joral F., Herrero C., Gialanella P.L., Gómez J.J., Martínez G., Perilli N. & Villalain J.J. (1996b). – The Toarcian/Aalenian transition in the Fuentelsaz section. *In* : *1st Toarcian and 4th Aalenian Working Groups Meeting*, Fieldtrip Iberian Range Guide-Book, 51-77. – Univ. Complutense, Madrid, 77 p.

Goy A., Ureta M.S., Arias C., Canales M.L., García-Joral F., Herrero C., Martínez G. & Perilli N. (1994). – The Toarcian Aalenian transition in the Fuentelsaz section (Iberian Range, Spain) : a possible stratotype for the base of the Aalenian Stage. – *Misc. Serv. Geol. Naz. Ita*., **5**, 1-31.

Graciansky P.C. de, Dardeau G., Dommerges J.L., Durlet C., Marchand D., Dumont, T., Hesselbo S.P., Jacquin J., Goggin V., Meister C., Mouterde R., Rey J. & Vail P.R. (1998). – Ammonite biostratigraphic correlation and Early Jurassic sequence stratigraphy in France : comparisons with some U.K. sections. *In* : P.C. de Graciansky, J. Hardenbol, J. Jacquin & P. R. Vail Eds, Mesozoic and Cenozoic sequence stratigraphy of European Basins. – *SEPM, Spec. Pub.*, **60,** 467-479.

Groupe Français D'Étude Du Jurassique (1997). – Biostratigraphie du Jurassique Ouest Européen et Méditerranéen. Zonations parallèles et distribution des invertébrés et microfossiles. *In* : E. Cariou, & P. Hantpergue (Coords.) – *Bull. Centre Rech. Explor. Prod Elf Aquitaine,* Mém **17**, 1-400.

Guex J. (1991) – Biochronological correlations. – Springer Verlag, Berlin, 250 p.

Hallam A. (1988). – A re-evaluation of Jurassic eustasy in the light of new data and the revised Exxon curve. *In* : C.K. Wilgus *et al.* Eds., Sea-level changes : an integrated approach*.* – *SEPM, Spec. Publ.*, **42,** 261-273.

Hallam A. (1990). – Biotic and abiotic factors in the evolution of early Mesozoic marine molluscs. *In* : R.M. Ross & W.D. Allmon Eds, Cause of evolution. A paleontological perspective. – Univ. Chicago Press, Chicago, 249-260.

Hallam A. & Wignal P.B. (1997). – Mass extinctions and their aftermath. – Oxford University Press, Oxford, 320 p.

Haq B.U., Hardenbol J. & Vail P.R. (1987). – Chronology of fluctuating sea levels since the Triassic. – *Science*, **235**, 1156-1167.

Haq B.U., Hardenbol J. & Vail P.R. (1988) – Mesozoic and Cenozoic chronostratigraphy and cycles of sea-level change. *In* : C.K. Wilgus *et al*. Eds., Sea-level changes : an integrated approach. – *SEPM, Spec. Pub.* **42,** 71-108.

Hardenbol J., Thierry J., Farley M.B., Jacquin T., de Graciansky P.-C. & Vail P.R. (1998). – Mesozoic and Cenozoic sequence chronostratigraphic framework of European basins. Jurassic sequence chronostratigraphy. *In* : P.C. de Graciansky, J. Hardenbol, T. Jacquin & P.R. Vail Eds., Mesozoic and Cenozoic sequence stratigraphy of European Basins. – *SEPM, Spec. Pub.*, **60,** chart 6.

Henriques M.H. (1992). – Biostratigrafía e Paleontología (Ammonoidea) do Aaleniano en Portugal (Sector Setemtrional da Bacia Lusitania). – PhD Thesis, Univ. Coimbra, 301 p.

Henriques M.H. (1995). – Les faunes d'ammonites d'Alénien portugais : composition et implications paléobiogéographiques. – *Geobios, Mém. Sp.* **18,** 229-235.

Henriques M.H. (2000). – Biostratigraphie (Ammonoidea) du passage Lias-Dogger dans la Bassin lusitanien : la coupe de S. Gião. – *Strata*, **10**, 31-35.

Henriques M.H., Gardin S., Soares A.F., Gomes C.R., Marques F.J., Lapa M.R. & Montenegro J.D. (1994). – The Aalenian-Bajocian boundary at Cabo Mondego (Portugal). – *Misc. Ser. Geol. Naz., Ital*, Roma, **5,** 63-78

Henriques M.H., Linares A., Sandoval J. & Ureta M.S. (1996). – The Aalenian in the Iberia (Betic, Lusitanian and Iberian Basins). *In* : A.C. Riccardi Ed., Advances in Jurassic research. – *GeoResearch Forum*, Transtec Publ., Zurich, **1-2**, 130-150**.**

Henriques M.H., Sadki D. & Mouterde R. (1988) – Graphoceratidés (Ammonitina) de la base du Bajocien portugueis. *In* : R.B. Rocha & A.F. Soares Eds., *2nd International Symposium on Jurassic stratigraphy.* – INIC*,* Lisboa, 243-254.

Jiménez A.P. (1986). – Estudio paleontológico de los Ammonites del Toarciense inferior y medio de las Cordilleras Béticas (Dactylioceratidae e Hildoceratidae). – Unpublished PhD Thesis, University of Granada, 252 p.

Jiménez A.P. & Rivas P. (1991). – Los Dactyliocerátidos del Toarciense inferior y medio de las Cordilleras Béticas, España. – *Bol. Real Soc. Esp. Hist. Nat.* (Sec. Geol.), **86**, 53-64.

Jiménez A.P. & Rivas P. (1992). – Hildoceratidae (Ammonitina) del Toarciense inferior y medio de las Cordilleras Béticas (España). – *Bol. Real Soc. Esp. Hist. Nat*. (Sec. Geol.), **87**, 37-113.

Linares A. & Sandoval J. (1986). – *Malladaites* nov. gen. et *Spinammatoceras* (Hammatoceratidae, Ammonitina) de l'Aalénien de la Zone Subbétique, sud de l'Espagne. – *Geobios*, **19**, 207-224.

Linares A. & Sandoval J. (1990). – The lower boundary of the Bajocian in the "Barranco de Agua Larga" section, (Subbetic Domain, southern Spain). – *Mem. Descr. Carta Geol. Ital.,* **40**, 13-22.

Linares A. & Sandoval J. (1993). – El Aaleniense de la Cordillera Bética (Sur de España) : Análisis bioestratigráfico y caracterización paleobiogeográfica. – *Rev. Soc. Geol. Esp.*, **6,** 177-206.

Linares A. & Sandoval J. (1996). – The genus *Haplopleuroceras* (Erycitidae, Ammonitina) in the Betic Cordillera, southern Spain. – *Geobios*, **29,** 287-305.

Linares A., Ureta M.S. & Sandoval J. (1988). – Comparison between the Aalenian ammonite associations from the Betic and Iberian Cordilleras : elements of correlation. *In :* R.B. Rocha & A.F. Soares Eds., *2nd International symposium on Jurassic stratigraphy.* – INIC, Lisboa, 193-208.

Macchioni F. & Venturi F. (2000). – Leukadiellinae, n. subfam. of the Lower and Middle Toarcian. Origin and evolution of the genera *Renziceras* Arkell (1957) and *Leukadiella* Renz (1913). – *Bol. Soc. Paleont. Ital.*, **39,** 319-339.

Martínez G. (1992). – Hammatoceratinae (Ammonitina) del Toarciense superior y Aaleniense en la Cordillera Ibérica. – PhD Thesis, Univ. Complutense Madrid. 331 p.

Martínez G. (1996). – Los Hammatoceratinae (Ammonitina) del Toarciense y Aaleniense en la Cordillera Ibérica y Cantábrica oriental. Implicaciones paleobiogeográficas. – *Rev. Españ. Paleont.*, Nº Extraordinario, 114-121

Mouterde R., Chevallier T, Corna M. & Sadki D. (1990). – Variations eustatiques et évolution des ammonites au Lias et au Bajocien.– *Bull. Soc. géol. Fr.* (8) **VI**, 985-988.

Mouterde R., Sadki D., Chevallier T. & Ferry S. (1989). – Sea level changes and ammonites turnovers in the Bajocian of the Vocontian trough (S-E France). *In* : Mesozoic eustacy record on western Tethyan margins. – *2º Cong. Franç. Sédiment.*, 48-50.

Nimi C., Nocchi M. & Venturi F. (1997). – Toarcian marly-calcareous succession in the M. Martani (northern Apennines) : lithostratigraphy, biostratigraphy, paleoecology and effects of Tethysian events on the depositional environments. – *Bol. Soc. Paleont. Ital.*, **35,** 281-319.

O'Dogherty L., Sandoval J. & Vera J.A. (2000). – Ammonite faunal turnover tracing sea level changes during the Jurassic (Betic Cordillera, southern Spain). – *J. Geol. Soc. London*, **157**, 723-736.

Parisi F., Baldanza A., Benedetti L., Mattioli E., Venturi F. & Cresta S. (1998). – Toarcian stratigraphy of the Colle d'Orlando section (Umbria, Central Italy, northern Apennine). – *Bol. Soc. Paleont. Ital.*, **37,** 3-39.

Pavia G. (1983). – Ammoniti e biostratigrafia del Baiociano superiore di Digne (France SE). – *Mus. Reg. Sci. Nat.*, **2**, 1-254.

Rioult M., Contini D., Elmi E. & Gabilly G. (1997). – *In* : E. Cariou & P. Hantzpergue (coords.), Biostratigraphie du Jurassique ouest-européen et méditerranéen : zonations parallèles et distribution des invertebrés et microfossiles. – Groupe Français d'étude du Jurassique, Bajocien, 41-53. – *Bull. Centre Rech. Explor. Prod. Elf Aquitaine*, Mém. **17**, 440 p.

Rocha R.B., Henriques M.H., Soares A.F., Mouterde R., Caloo B., Ruget C. & Fernández-López S. (1990). – The Cabo Mondego section as a possible Bajocian boundary stratotype. – *Mem. Descr. Carta Geol. Ital.* **40,** 49-60.

Sadki D. (1994). – L'Aalénien supérieur et le Bajocien inférieur du Haut Atlas marocain : Révision biostratigraphique et corrélations. – *Misc. Serv. Geol. Naz.* Roma, **5,** 161-176.

Sadki D. (1996). – Le Haut-Atlas central (Maroc). Stratigraphie et paléontologie du Lias supérieur et du Dogger inférieur. Dynamique du bassin et des peuplements. – *Doc. Lab. géol. Fac. Sci. Lyon,* **142,** 1-245.

Sandoval J. (1983). – Bioestratigrafía y paleontología (Stephanocerataceae y Perisphinctaceae) del Bajocense y Bathonense de las Cordilleras Béticas. – PhD Thesis, Servicio de Publicaciones, Univ. Granada, 613 p.

Sandoval J. (1985). – Los Strigoceratidae (Ammonitina) del Bajocense de la Zona Subbética (Sur de España). – *Mediterránea,* **4**, 85-112.

Sandoval J. (1986). – Middle Jurassic Haploceratidae (Ammonitina) from the Subbetic Zone (South Spain). – *Geobios,* **19**, 435-463.

Sandoval J. (1990). – A revision of the Bajocian divisions in the Subbetic Domain (southern Spain). – *Mem. Descr. Carta Geol. Ital.* **40,** 141-162.

Sandoval J., O'Dogherty L. & Guex J. (2001). – Evolutionary rates of Jurassic ammonites in relation to sea-level fluctuations. – *Palaios,* **16,** 330-363.

Ureta M.S. (1985). – Bioestratigrafía y paleontología (Ammonitina) del Aaleniense en el Sector Noroccidental de la Cordillera Ibérica. – PhD Thesis, Universidad Complutense, Madrid. 452 p.