Evolutionary Rates of Jurassic Ammonites in Relation to Sea-level Fluctuations

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An analysis is presented of the diversity and faunal turnover of Jurassic ammonites related to transgressive/regressive events. The data set contained 400 genera and 1548 species belonging to 67 ammonite zones covering the entire Jurassic System. These data were used in the construction of faunal turnover curves and ammonite diversities, that correlate with sea-level fluctuation curves. Twenty-four events of ammonite faunal turnover are analyzed throughout the Jurassic. The most important took place at the Sinemurian-Carixian boundary, latest Carixian-Middle Domerian, Domerian-Toarcian boundary, latest Middle Toarcian-Late Toarcian, Toarcian-Aalenian boundary, latest Aalenian-earliest Bajocian, latest Early Bajocian-earliest Late Bajocian, Early Bathonian-Middle Bathonian boundary, latest Middle Bathonian-earliest Late Bathonian, latest Bathonian-Early Callovian, earliest Early Oxfordian-Middle Oxfordian, earliest Late Oxfordian-latest Oxfordian, latest Early Kimmeridgian, Late Kimmeridgian, middle Early Tithonian and Early Tithonian-Late Tithonian boundary. More than 75 percent of these turnovers correlate with regressive-transgressive cycles in the Exxon, and/or Hallam's sea-level curves. In most cases, the extinction events coincide with regressive intervals, whereas origination and radiation events are related to transgressive cycles. The turnovers frequently coincide with major or minor discontinuities in the Subbetic basin (Betic Cordillera).

INTRODUCTION

The possible connection between origination and extinction processes (turnovers) and changes in sea level have occupied researchers since the early years of the 20th century (Suess, 1906; Grabau, 1936). However, it was only after studies by Hallam (1961, 1963, 1988), Kennedy (1977), Guex (1981) and Haq et al. (1987, 1988) that a connection between fluctuations in sea level and faunal turnovers (evolution or extinction) in Mesozoic ammonites began to proliferate (Hallam, 1989, 1990, 1992, 1997; Hallam and Wignal, 1997; Mouterde et al., 1989, 1990; Collom, 1990; Reboulet et al., 1992; Rawson, 1993; Branger and Gonnin, 1994; Hoedemaeker, 1995; O'Dogherty et al., 2000).

Ammonites were more stenotypic than other groups of invertebrates and were affected by small environmental changes. This is the main reason why they show such high rates of renovation (extinction-speciation events) during their evolutionary history (Hallam, 1988, 1990). The well-studied extinctions appear to be clearly linked to stages of shallowing water and sea-level regressions, which reduced the habitats of those forms living on epicontinental platforms. Deepening processes due to a rise in sea level, on the contrary, produced new habitats, origination and radiation of new taxa, and/or immigration of taxa already existing in other regions (Hallam, 1981, 1990, 1992, 1996, 1997; Donovan, 1985; Bayer and McGhee, 1985; House, 1989, 1993; Ward, 1996; Wiedmann and Kullmann, 1996). Anoxic phenomena, possibly connected with the first stages of transgressive phases, may have had effects similar to those during regressive phases (Hallam, 1987, 1990; House, 1993; Ward, 1996; Wiedmann and Kullmann, 1996; Jiménez et al., 1996), in which some taxa disappeared.

The aim of the present study is to investigate the possible interconnections between the evolutionary history of Jurassic ammonites observed in the Betic Cordillera and global eustatic events. But, prior to presenting the analysis of ammonite faunal turnover, the possible potential biases generated by the taxonomic splitting and taphonomic process they undergone must be discussed. (1) It may be assumed that the ammonite groups analyzed are colored by the "monograph effect" generated by the amount of taxonomic splitting they have received. In the present case, most of the ammonites analyzed at the specific and generic level come from the same area (Betic Cordillera) and, moreover, all ammonite groups (Ammonitina, Lytoceratina and Phylloceratina) that occur in a wide stratigraphic interval were studied only by one author or team (e.g., Sandoval or Linares and Sandoval studied all Middle Jurassic ammonites). This implies that all ammonites from these stratigraphic intervals, especially at a specific level, were studied with the same taxonomic criteria and, therefore, are not colored by taxonomic splitting. Divisions at the genus or subgenus level can be partially colored, especially in those groups that present marked dimorphism. In this case, a single genus can be separated into two morphologic subgenera [e.g., *E.* (*Emileia*) and *E.* (*Otoites*)]. Ammonite dimorphism is very common throughout the

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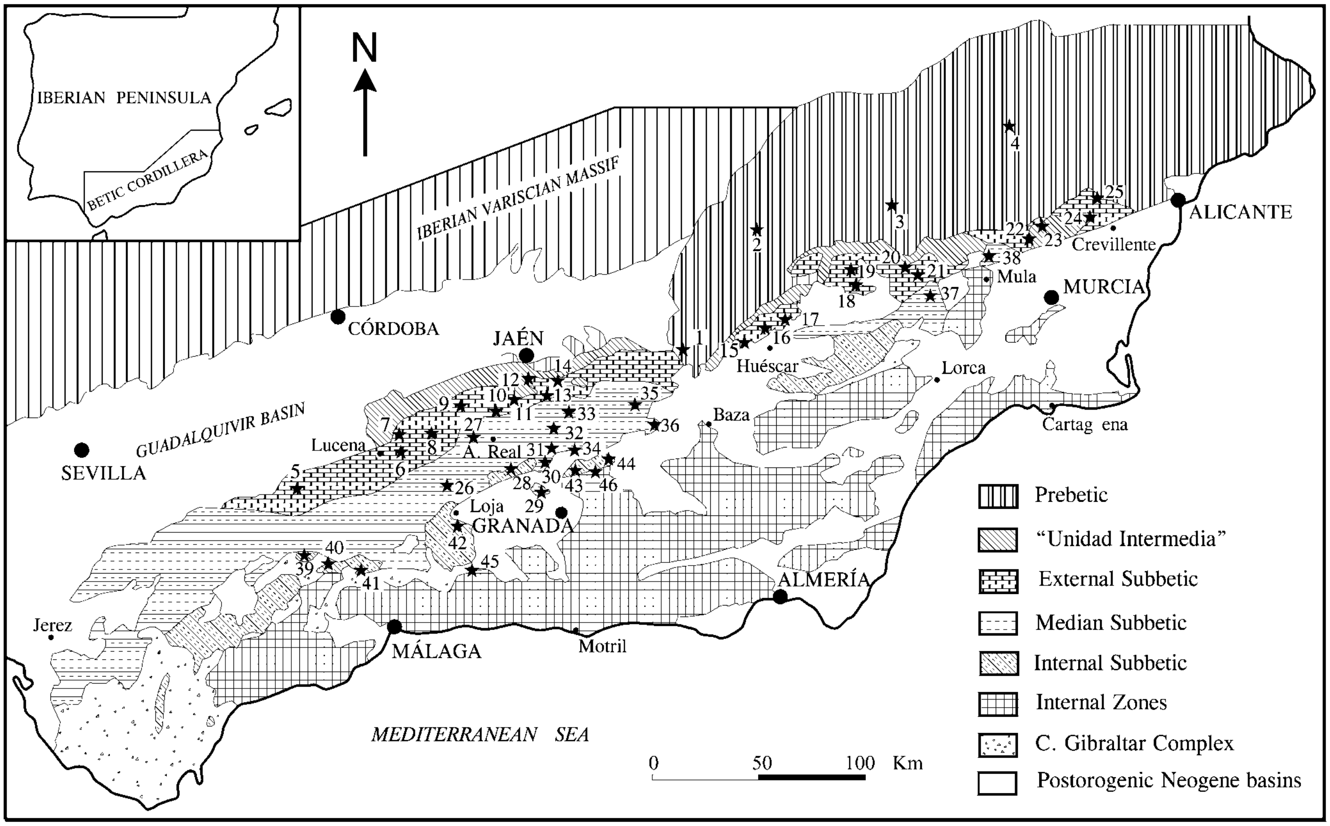

FIGURE 1—Sketch map of the Betic Cordillera (southern Spain) showing the different paleogeographic domains and the position (numbers on the map) of the areas in which the stratigraphic sections analyzed are located. See key localities in Table 1.

Jurassic (especially during the Middle Jurassic), a fact that may alter the total number of genera. However, the number of dimorphic pairs in each of the biochronologic unit analyzed is quite homogeneous. Therefore, the potential bias from taxonomic splitting is minimal and the data are scarcely affected. (2) Also, there could be a potential bias introduced by taphonomic processes. Most ammonites analyzed are from the Betic Cordillera, and specifically from the Subbetic basin. Hence, these all originate from the same paleogeographic domain (Fig. 1). For the complete Jurassic, Subbetic sediments are characterized by Tethyan pelagic facies. From the latest Early Jurassic to Late Jurassic, the Subbetic basin had well-defined pelagic troughs and swells. In these paleogeographic domains the possibility of fossils being affected by sea-level changes is lower than in shallow water platforms, in which during sea-level falls, fossils deposited shoreward during high sea-level intervals will be exposed to powerful taphonomic processes. Based upon these parameters, it is assumed that in such a paleogeographic domain, as analyzed here, taphonomic processes do not introduce a notable bias in to the analyses.

ANALYSIS OF FAUNAL TURNOVER: METHODOLOGY

Recently, O'Dogherty et al. (2000) plotted a curve based on the quantification of ammonite diversity and faunal turnover related to major discontinuities recorded in the Betic Cordillera. For this, it is hypothesized, as Hallam (1987, 1990, 1989, 1990) indicated, that ammonite faunal turnovers reflect global eustatic changes. This curve was used to trace changes in sea level during the Jurassic in the Betic Cordillera, and compared with the curves of Hallam (1988) and Haq et al. (1988). In the present study, the objective is a different one: here sea-level changes on a global scale were analyzed and the influence of these on ammonoids evolutionary processes (origination and extinction events) are demonstrated. In the present study, a synthesis of biochronological data from scientific papers and Ph.D. theses written since the early 70's, providing a data set of 400 genera and 1548 ammonite species coming from 67 ammonite zones covering the entire Jurassic, have been used. Figure 1 indicates the approximate geographic locations of the Betic areas in which Jurassic sections were sampled bed by bed; Table 1 (same numbers as in Figure 1) shows the stratigraphic interval represented in each area and the authors who studied (from a biostratigraphic standpoint) the localities listed.

Taking this database as a starting point, biochronological charts for genera (Fig. 2) have been constructed. Such data are used as points of reference in the analysis of faunal turnover (extinctions *vs.* originations, see below). A more detailed range chart for ammonite species is presented in Appendix 1, to provide a precise picture of ammonite distribution in the Betic Cordillera. It should be noted that the time-range chart of the ammonite genera that appear in Figure 2, and species (Appendix 1) refer only to taxa recovered from the Betic Cordillera and does

TABLE 1—Study areas, sampled intervals in each area, and authors who have studied each area. The column on the left side indicates the different Betic areas from which data about the distribution vertical range of the ammonites were obtained (same numbers as Figure 1). The central column shows the stratigraphic intervals studied in each locality. The column on the right side indicates the authors who made biostratigraphic studies of the localities.

Localities	Studied interval	Authors
1, 2, 3, 4.–Puerto Lorente, Segura de la Sierra, Elche de la Sierra, Fuente Álamo	Oxfordian-Kimmeridgian	Rodríguez-Tovar, 1993
5.–Sierra de Estepa	Upper Callovian-Oxfordian	Sequeiros, 1974; Sequeiros and Olóriz, 1979; Olóriz, 1978.
6.–Sierra de Gaena-Carcabuey	Domerian-Tithonian	Rivas, 1972; Sequeiros, 1974; Olóriz, 1978; Olóriz and Tavera, 1979; Mangold, 1979; Braga, 1983; Sandoval, 1983, 1986, 1990; Checa, 1985; Tavera, 1985; Jiménez, 1986; Caracuel, 1996.
7.–Sierra de Cabra	Callovian-Tithonian	Sequeiros, 1974, 1979, 1987; Sequeiros and Olóriz, 1979; Olóriz, 1978; Tavera, 1985.
8.–Sierra de los Judíos	Upper Bajocian-Tithonian	Sequeiros, 1974; Olóriz, 1978; Sandoval, 1983.
9.–Sierra del Ahillo	Toarcian-Tithonian	Sequeiros, 1974; Olóriz, 1978; Sandoval, 1983.
10, 11.–La Coronilla-Collado de Gracia, Cornicabra-Ventisquero	Upper Bajocian-Tithonian	Sequeiros, 1974; Olóriz, 1978; Sandoval, 1983, 1990; Tavera, 1985.
12.–Otiñar-Río Frío	Carixian-Tithonian	Rivas, 1972, 1979; Olóriz, 1978; Braga, 1983; Sandoval, 1983; Tavera, 1985; Jiménez, 1986; Linares and Sandoval, 1993.
13.–Carchel-Las Pilas-Puerto Rico	Carixian-Tithonian	Olóriz, 1978; García-Hernández et al., 1979; Braga, 1983; Sandoval, 1983; Tavera, 1985.
14.–La Cerradura	Domerian-Toarcian	Braga et al., 1982; Braga, 1983; Jiménez, 1986; Jiménez and Rivas, 1991, 1992.
15.–Puente Duda	Carixian-Toarcian	Braga, 1983; Jiménez, 1986; Jiménez and Rivas, 1991, 1992.
16.–Cortijo Mazagrán-Sierra de la Sagra	Domerian-Tithonian	Braga, 1983; Sandoval, 1983; Tavera, 1985; Jiménez, 1986.
17.–Sierra de Jorquera	Carixian-Toarcian	Braga, 1983; Jiménez, 1986; Jiménez and Rivas, 1991, 1992.
18, 19.–Sierra de Mojantes, Cortijo Majarazán	Carixian-Tithonian	Seyfried, 1978; Braga, 1983; Tavera, 1985; Jiménez, 1986; Jiménez and Rivas, 1991, 1992.
20, 21.–Cerro de May Valera, Sierra de Quípar	Domerian-Tithonian	Seyfried, 1978; Mangold, 1979; Sandoval, 1983; Tavera, 1985; Caracuel, 1996.
22, 23.–Sierra de Lugar, Sierra del Corque	Carixian-Tithonian	Seyfried, 1978; Braga, 1983; Mangold, 1979; Checa and Sequeiros, 1990; Sandoval, 1990; Caracuel, 1996; Caracuel et al., 2000.
24.–Sierra de Crevillente	Carixian-Tithonian	Seyfried, 1978; Mangold, 1979; Braga, 1983.
25.–Sierra del Reclot	Carixian-Tithonian	Seyfried, 1978; Sandoval, unpublished data.
26.–Sierra de Chanzas	Carixian-Aalenian	Rivas, 1972; Braga, 1983; Jiménez, 1986.
27.–Sierra de San Pedro	Aalenian-Lower Bajocian	Linares and Sandoval, 1986, 1990, 1993.
28.–Illora-Sierra Pelada	Carixian-Toarcian	Rivas, 1972; Braga, 1983; Jiménez, 1986
29.–Sierra Elvira	Carixian-Toarcian	Rivas, 1972; García-Hernández et al., 1979; Braga, 1983; Jiménez, 1986; Jiménez and Rivas, 1979.
30.–Colomera	Domerian-Toarcian	Rivas, 1972; García-Hernández et al., 1979; Jiménez and Rivas, 1979, 1991, 1992; Braga et al., 1982; Braga, 1983; Jiménez, 1986.
31.–Puerto del Zegrí, Sierra de las Cabras	Domerian-Aalenian.	Rivas, 1972; Braga, 1893; Jiménez, 1986; Jiménez and Rivas, 1979, 1991, 1992; Linares and Sandoval, 1993; García-Gómez et al., 1994.
32, 33.—Montillana, Sierra de Alta Coloma.	Domerian-Tithonian	Rivas, 1972; Sequeiros, 1974; Olóriz, 1978; Braga, 1983; Sandoval, 1983, 1986, 1990; Linares and Sandoval, 1990, 1993, 1996; Tavera, 1985; Jiménez, 1986.
34.–Iznalloz	Domerian-Toarcian	Rivas, 1972; Braga, 1983; Jiménez, 1986.
35.–Cerro Méndez	Toarcian-Lower Bajocian	García-Hernández et al., 1979; Jiménez, 1986; Jiménez and Rivas, 1979, 1992, 1993; Sandoval, 1983; Linares and Sandoval, 1993; García-Gómez et al., 1994.
36.–Río Fardes	Aalenian-Lower Bajocian	Hernández-Molina et al., 1991; Linares and Sandoval, 1993.
37.–Sierra de Ponce	Toarcian-Lower Bajocian	Seyfried, 1978.
38.–Sierra de Ricote	Toarcian-Tithonian	Olóriz, 1978; Seyfried, 1978; Sandoval, 1983, 1990; Linares and Sandoval, 1977, 1990, 1993; Braga et al., 1985; Tavera, 1985; Jiménez, 1986; Jiménez and Rivas, 1992, 1993; García-Gómez et al., 1994.
39, 40, 41.–Cañete-Teba, Sierra de Huma, Toscal	Oxfordian-Tithonian	Sequeiros, 1974; Sequeiros and Olóriz, 1979; Olóriz, 1978.
42.–Sierra Gorda	Upper Aalenian-Tithonian	Sequeiros, 1974, 1979; Olóriz, 1978; Sandoval, 1983, 1990; Checa, 1985; Tavera, 1985; Linares and Sandoval, 1993.
43, 44.–Sierra Harana (Internal Subbetic)	Bajocian-Tithonian	Sequeiros, 1974; Sequeiros and Olóriz, 1979; Olóriz, 1978; Sandoval, 1983, 1986, 1990; Checa, 1985; Tavera, 1985.
45.–Baños de Alhama	Hettangian-Sinemurian	Braga et al., 1984a, b, c.
46.–Sierra Harana (Penibetic)	Hettangian-Sinemurian	Braga et al., 1984a, b, c.

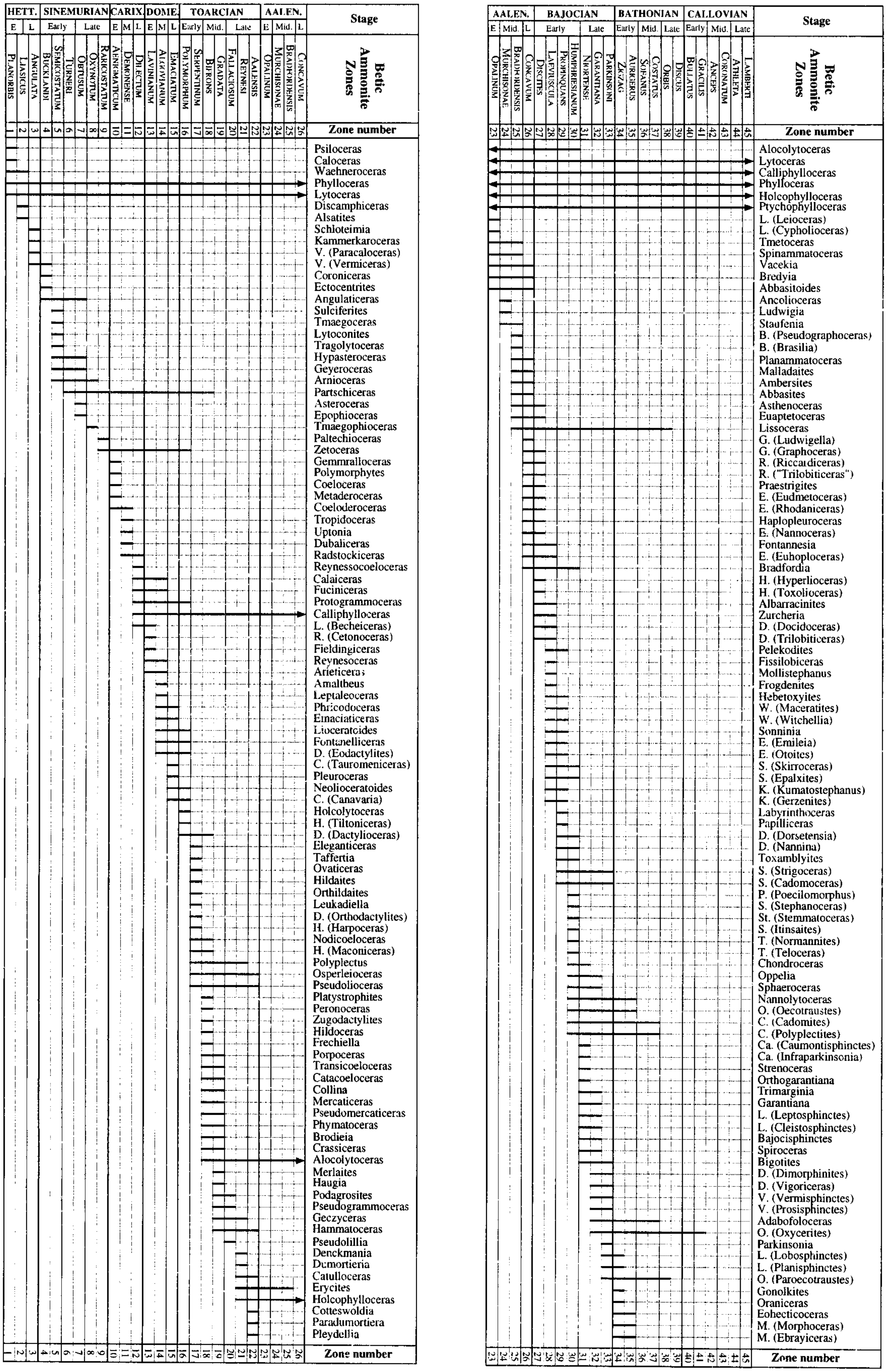

FIGURE 2—Temporal distribution of ammonite genera recorded in the Betic Cordillera sorted by first occurrence data.

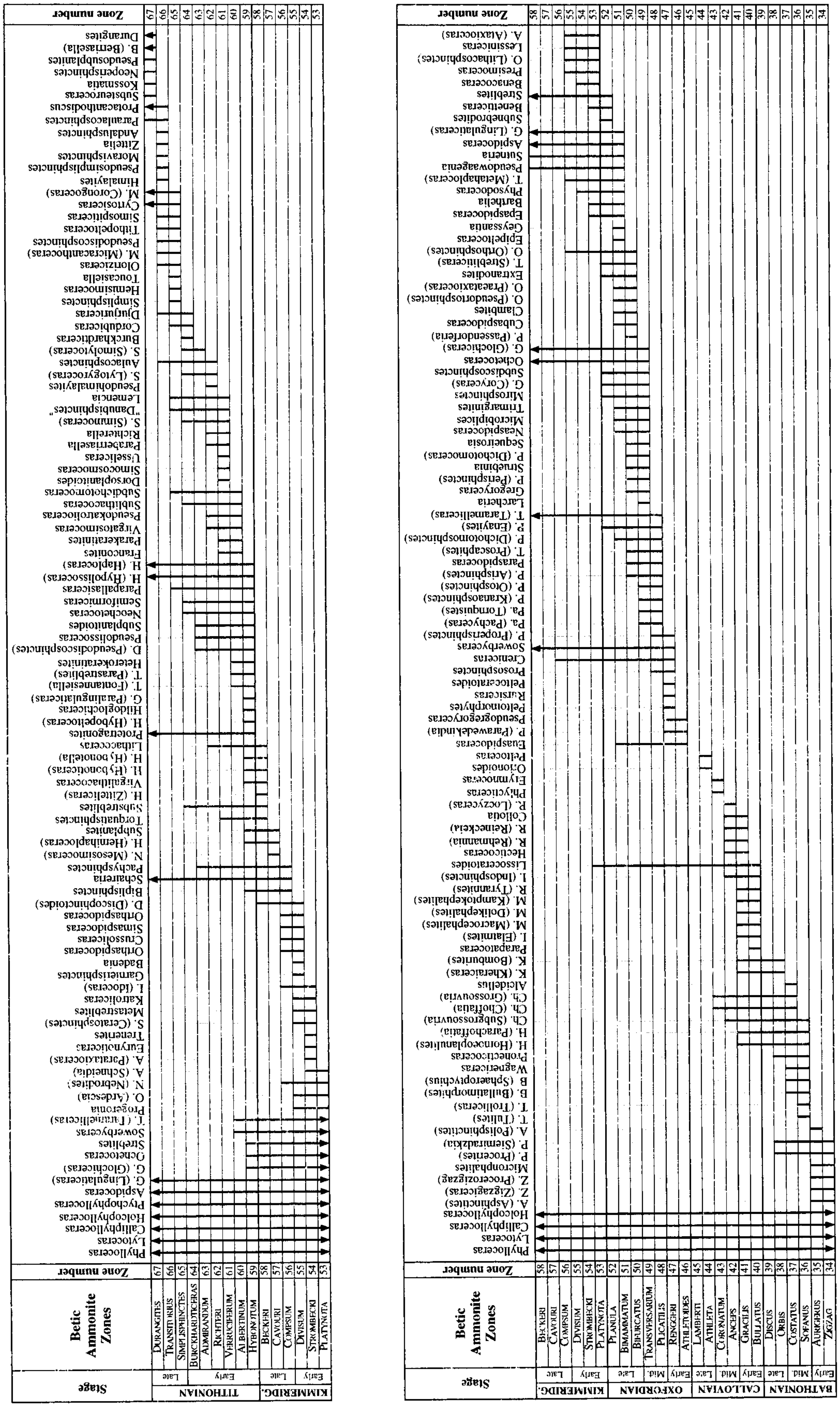

FIGURE 2—Continued.

not reflect taxon global ranges. Figure 2 shows that the taxon-distribution range covers the entire zone, although this necessarily may not be the case, because taxa with a FAD (first appearance datum) or LAD (last appearance datum) within a zone are considered to have a time range that covers the entire zone. Numbers 1 to 67 in successive figures indicate (with minor local modifications) the Mediterranean standard ammonite zones (Cariou and Hantzpergue, 1997), as listed in Figure 2.

Herein diversity is defined as the number of different species or genera present in each zone. These raw data are used in the elaboration of a synthetic diversity curve (Fig. 3B, re-drawn from O'Dogherty et al., 2000) on which the rate of turnover as the number of originations minus the number of extinctions during each ammonite zone is plotted.

This method has two minor drawbacks: (1) the subjectivity involved in tracing the curves; and (2) the fact that this empirical approach does not take into account the magnitude of the extinction or origination related to total diversity. The faunal turnover means could be biased if the extinction-origination curves were constructed when only FAD's were subtracted from LAD's, especially when a great number of extinctions and originations are involved. To test a previous interpretation (O'Dogherty et al., 2000), the present study introduces a new approach that analyzes the faunal-assemblage similarity between two successive zones.

Interzonal Distance Expressed by Means of a New Faunal-similarity Coefficient

Guex (1987) proposed a method for testing the significance of faunal turnover rates by studying the distance, or dissimilarity, between each adjacent discrete zone.

Let i and j be two discrete biochronological units (zones in this case). For each pair of adjacent units i and j, a distance measure can be calculated—D_{ij}—defined as follows:

$D_{ij} = L_i/T_i + F_j/T_j$

Where L_i = the number of LAD's in unit i

T_i = the total number of taxa in unit i

F_j = the number of FAD's in unit j and

T_j = 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 (however, this is never the case), and its maximum value 2 means that i and j have no common elements.

Low *D* values indicate a good fossil record and/or gradual faunal change; in other words, there is a high degree of similarity between two successive zones. Very high *D* values indicate that there are few common elements between two successive zones, and express either a poor vertical record, and/or high extinction and origination rates, and/or gaps in the stratigraphic record. Of course, the results obtained by this method need to be interpreted together with the stratigraphic data available in a region (analysis of major discontinuities, stratigraphic position within the sequence stratigraphic context, changes in sedimentation rate, stratigraphic gaps, hard-grounds, quality and quantity of the fossiliferous contents, etc.). This is required to differentiate D peaks due to rapid faunal-turnover rates from those that exist as an artifact of the stratigraphic record (Holland, 1995).

The D_{ij} coefficient has been applied to the data compiled in the present paper, in particular to originations and extinctions of species occurring in each ammonite zone (Table 2, Fig. 3A). The curve (D = interzonal distance, Fig. 3A) is used to distinguish the major extinction and radiation events, and it is compared with the curve of faunal turnover proposed by O'Dogherty et al. (2000; Fig. 3B). It is noted in curve 3A that the high values (close to 2) in the Lower Lias can be explained by the poor ammonoid records in this interval. In the Middle-Late Toarcian transition (Gradata Zone), a major faunal change as well as a minor lacuna in several areas of the Subbetic generate the high value of D. Other high values of D_{ij} (e.g., between Discites-Laeviuscula Zones or between Propinquans-Humphriesianum Zones) are related to major faunal turnover where a great number of extinctions and originations are involved and, consequently, the relative number of common elements (species or genera) between two successive units are extremely low.

Rate of Faunal Turnover: Tivariate FAD-LAD Diagrams

The method used in the present study differs from previous ones (Chaloner and Hallam, 1994; Larwood, 1988; Donovan, 1989; Kauffman and Walliser, 1990; Lawton and May, 1995) in that it allows a precise evaluation of the relationships between sub-contemporaneous extinctions and originations in the fossil record. Such an approach (see Guex, 1991) was designed for quantitative studies concerned with the relationship between extinction and origination events occurring within the same zone. Guex's (1991) method was designed to differentiate between extinction and minimal diversity. From the vertical taxa distribution given by the range chart in Figure 2 (also Appendix 1), bivariate cumulative graphs (Fig. 4) relating the number of genera (Fig. 4A) and species (Fig. 4B) originating and disappearing in each ammonite zone have been constructed. The extinction events are identified in these plots by the steepest parts of the curve (great accumulated number of disappearances versus low number of appearances), and the diversification episodes are characterized by the flattest parts of the curve (great accumulated number of appearances versus low number of disappearances). The number of disappearances divided by the number of originations in each zone gives the slope variations of the faunal turnover curve for each zone considered (see bottom curves of Fig. 4A, B). These variations at the bottom of the diagrams show some peaks, which serve to identify major ammonite-extinction events throughout the time interval analyzed. Several major ammonite-extinction events in the Betic Jurassic are indicated in Figure 4 by arrows and the corresponding ammonite zone number.

The graphs show relative consistency of the ammonite faunal-turnover rates throughout the Jurassic. Figure 4, diversification episodes are followed by extinction phases of equal duration and vice-versa. The general trend of the curve is approximately 45º in all the diagrams considered (genera or species). This observation reinforces the idea of equal zone duration, as first proposed by Westermann (1984).

Survivorship curve plots also have been constructed by using a sample of 400 ammonite genera and 1548 species recorded in the Betic Jurassic, and the survivorship dura-

TABLE 2—Table of Interzonal distance. In this table, n indicates the number assigned to each ammonite Zone; T, refers to total diversity by unity, the total number of genera or species recorded in each ammonite zone; L, last-appearance data, number of extinction in each zone; F, first-appearance data, number of first appearance by zone; Dij, is the interzonal distance, Dij = Li/Ti + Fj/Tj, (see text).

			Genera			Species			Interzonal distance (Dij)		
Substage	Zone	n	T	L	F	T	L	F	Interzone	Species	Genera
Early Berriasian	Jacobi	68	16	5	9	18	18	3			
	Durangites	67	20	4	6	41	24	21	$D_{67\,68}$	0,75	0.76
Late Tithonian	Transitorius	66	24	11	7	69	49	44	$D_{66\,67}$	1,22	0,76
	Simplisphinctes	65	36	8	9	65	40	44	$D_{65\,66}$	1,25	0,51
	Burckhardticeras	64	25	8	3	57	36	24	$D_{64\,65}$	1,31	0,57
	Admirandum	63	26	4	1	50	17	17	$D_{63\,64}$	0,76	0,27
Early Tithonian	Richteri	62	31	6	3	48	15	8	$D_{62\,63}$	0,65	0,23
	Verruciferum	61	34	6	8	75	35	42	$D_{61\,62}$	0,63	0,27
	Albertinum	60	32	6	7	61	28	32	$D_{60\,61}$	1,02	0,42
	Hybonotum	59	38	13	15	82	53	44	$D_{59\,60}$	1,17	0,56
	Beckeri	58	27	4	7	71	33	41	$D_{58\,59}$	1,00	0,54
Late Kimmeridgian	Cavouri	57	21	1	3	41	11	15	$D_{57\,58}$	0,85	0,31
	Compsum	56	25	7	3	47	21	9	$D_{56\,57}$	0,81	0,42
	Divisum	55	34	12	6	87	49	50	$D_{55\,56}$	0,75	0,47
Early Kimmeridgian	Strombecki	54	34	6	6	61	24	27	$D_{54\,55}$	0,97	0,35
	Platynota	53	31	4	10	63	28	33	$D_{53\,54}$	0,89	0,31
	Planula	52	29	7	4	61	32	22	$D_{52\,53}$	1,05	0,56
Late Oxfordian	Bimammatum	51	34	10	9	79	40	47	$D_{51\,52}$	0,87	0,43
	Bifurcatus	50	34	9	7	74	40	31	$D_{50\,51}$	1,14	0,53
Middle Oxfordian	Transversarium	49	31	4	14	69	28	45	$D_{49\,50}$	0,82	0,33
	Pilcatilis	48	20	2	9	35	11	26	$D_{48\,49}$	0,97	0,55
Early Oxfordian	Renggeri	47	17	6	7	23	14	15	$D_{47\,48}$	1,35	0,80
	Athletoides	46	11	0	4	11	3	5	$D_{46\,47}$	0,92	0,41
Late Callovian	Lamberti	45	7	0	1	8	2	2	$D_{45\,46}$	0,70	0,36
	Athleta	44	9	3	3	11	5	5	$D_{44\,45}$	0,70	0,48
Middle Callovian	Coronatum	43	10	4	2	12	6	4	$D_{43\,44}$	0,95	0,73
	Anceps	42	16	9	3	37	29	20	$D_{42\,43}$	1,12	0,76
Early Callovian	Gracilis	41	27	13	7	77	60	57	$D_{41\,42}$	1,32	0,67
	Bullatus	40	22	1	9	35	16	25	$D_{40\,41}$	1,20	0,30
Late Bathonian	Discus	39	13	0	1	14	1	1	$D_{39\,40}$	0,79	0,41
	Orbis	38	17	4	2	28	17	11	$D_{38\,39}$	0,68	0,31
Middle Bathonian	Costatus	37	23	8	3	62	45	42	$D_{37\,38}$	1,12	0,47
	Sofanus	36	22	2	9	34	14	22	$D_{36\,37}$	1,09	0,22
Early Bathonian	Aurigerus	35	23	10	1	49	37	18	$D_{35\,36}$	1,40	0,84
	Zigzag	34	26	4	11	54	23	32	$D_{34\,35}$	0,79	0,20
	Parkinsoni	33	21	8	4	41	19	22	$D_{33\,34}$	1,06	0,80
Late Bajocian	Garantiana	32	27	8	6	39	20	16	$D_{32\,33}$	1,05	0,49
	Niortense	31	26	5	11	68	45	56	$D_{31\,32}$	1,07	0,41
	Humphriesianum	30	30	15	15	56	44	48	$D_{30\,31}$	1,61	0,92
Early Bajocian	Propinquans	29	25	11	7	65	57	39	$D_{29\,30}$	1,73	0,94
	Laeviuscula	28	27	8	14	55	29	42	$D_{28\,29}$	1,13	0.58
	Discites	27	25	12	5	56	43	30	$D_{27\,28}$	1,53	1,00
Late Aalenian	Concavum	26	27	7	12	53	27	37	$D_{26\,27}$	1,05	0,46
Middle Aalenian	Bradfordensis	25	22	7	8	41	25	23	$D_{25\,26}$	1,31	0,76
	Murchisonae	24	17	3	4	31	13	12	$D_{24\,25}$	0,98	0,54
Early Aalenian	Opalinum	23	15	2	7	31	12	21	$D_{23\,24}$	0,77	0,37
	Aalensis	22	13	7	5	36	26	25	$D_{22\,23}$	1,40	1,01
Late Toarcian	Reynesi	21	14	4	5	25	14	17	$D_{21\,22}$	1,25	0,67
	Fallaciosum	20	12	3	1	21	13	14	$D_{20\,21}$	1,30	0,61
Middle Toarcian	Gradata	19	23	12	7	29	22	14	$D_{19\,20}$	1,43	0,61
	Bifrons	18	25	9	15	42	27	33	$D_{18\,19}$	1,13	0,66
Early Toarcian	Serpentinum	17	18	8	13	24	15	19	$D_{17\,18}$	1,41	1,04
	Polymorphum	16	14	9	3	22	17	8	$D_{16\,17}$	1,56	1,37
Late Domerian	Emaciatum	15	16	5	4	48	34	31	$D_{15\,16}$	1,07	0,53
Middle Domerian	Algovianum	14	18	6	8	49	32	38	$D_{14\,15}$	1,30	0,58
Early Domerian	Lavinianum	13	19	3	4	23	12	13	$D_{13\,14}$	1,30	0,60
Late Carixian	Dilectum	12	11	2	6	25	15	21	$D_{12\,13}$	1,17	0,39
Middle Carixian	Demonense	11	9	4	4	15	11	11	$D_{11\,12}$	1,57	0,99
Early Carixian	Aenigmaticum	10	9	4	5	13	9	12	$D_{10\,11}$	1,43	0,89
	Raricostatum	9	6	2	3	7	6	6	$D_{9\,10}$	1,78	0,89
Late Sinemurian	Oxynotum	8	5	2	1	6	2	1	$D_{8\,9}$	1,52	0,83
	Obtusum	7	10	6	3	10	8	8	$D_{7\,8}$	1,13	0,77
	Turneri	6	7	0	1	7	5	4	$D_{6\,7}$	1,51	0,30
Early Sinemurian	Semicostatum	5	10	4	7	13	10	11	$D_{5\,6}$	1,34	0,54
	Bucklandi	4	6	3	3	9	7	7	$D_{4\,5}$	1,62	1,20
Late Hettangian	Angulata	3	6	3	4	10	8	9	$D_{3\,4}$	1,58	1,00
	Liasicus	2	5	3	2	12	11	11	$D_{2\,3}$	1,82	1,27
Early Hettangian	Planorbis	1	5	2	5	5	4	5	$D_{1\,2}$	1,72	0,80

tion has been measured (Fig. 5). As absolute timescales present diverse problems, especially at zone or subzone levels, ammonite zones instead of absolute time have been used when plotting of these curves. Each zone has been considered to be of equal duration, although this is not necessary certain (McArthur et al., 2000; see also Fig. 7). Likewise, the taxon-distribution range is considered to have covered the entire ammonite zone, which is often not the case because many ammonites species cover less than a zone. The curves plot the number of genera or species surviving by zones throughout the Jurassic. The duration of a great number of genera (up to 150) is limited to one zone. The slope of the survivorship curves only corroborates a rapid evolutionary rate for the ammonites, which is typical of taxa that easily are affected by small environmental changes, such as is the case with several eustatic changes. Both species and generic curves present the same pattern: a rapid decrease in slope (approximately 80% of the species or genera survived less than 2 time zones), which is typical of a fast-evolving group.

SEA-LEVEL CHANGES AND EPISODES OF MAJOR FAUNAL TURNOVER: ANALYSIS

In this section, a detailed analysis of successive ammonite extinction, origination, and radiation processes in the Western Tethys is presented, based upon the chronological data of the taxa (Table 2, Fig. 2, Appendix 1) recorded in the Betic Cordillera and in nearby areas with similar paleogeographic characteristics. Faunal turnovers are compared with the sea-level changes that are documented in the Exxon curves (Haq et al., 1988) and those of Hallam (1988), and with the curves plotted in other regions (Hesselbo and Jenkyns, 1998; De Graciansky et al., 1998; Jacquin et al., 1998; Hardenbol et al., 1998), as well as with other stratigraphic events (discontinuity and condensation) registered in the Betic Cordillera.

In addition, with the data from a study on distribution ranking (Fig. 2; Appendix 1), a diversity curve both at the generic and at the species levels has been developed, showing the maximum ammonite diversity intervals during the entire Jurassic (Fig. 6). Moreover, Figure 7 shows the diversity and origination-extinction curves (from Fig. 3B) plotted against the global sea-level change curves proposed by Haq et al. (1988) and Hallam (1988).

At the end of the Triassic, the Ceratitida went extinct

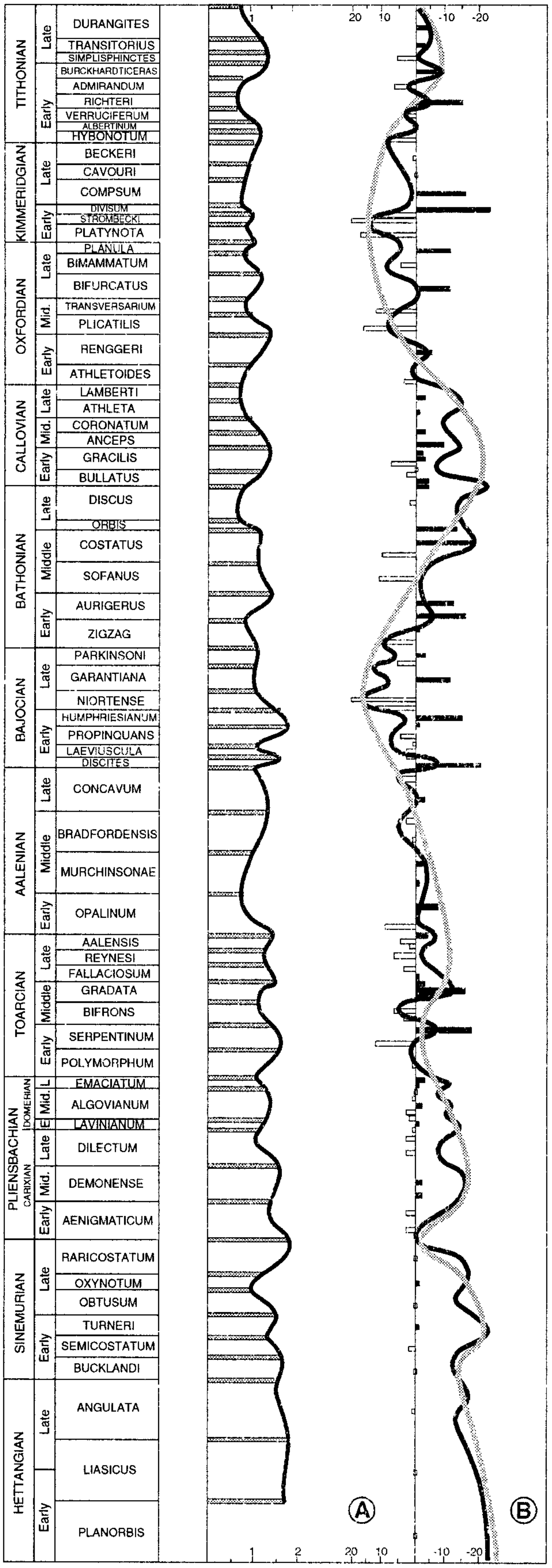

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FIGURE 3—Origination-extinction (species turnover) curves made by analytical (interzonal distance; A) and empirical (B) approaches (B from O'Dogherty et al., 2000). In curve (A), most of the very high values of interzonal distance (gray bars) indicate high extinction and origination rates (major species turnover) for two adjacent zones; low values indicate a high degree of similarity (minor species turnover) between two successive ammonite zones. The species turnover curve (B) indicates the differences between the numbers of FAD's (first appearance datum's) and LAD's (last appearance datum's) in each zone or subzone, with an indication of corresponding values (numbers) on both sides of the vertical axis (numbers at the left side and the right side of the vertical axis). The black bars indicate that extinctions exceeded new appearances (negative values with LAD> FAD) and decrease of diversity; white bars indicate appearances exceeded extinctions (positive values; FAD>LAD) and the consequent increase of diversity.

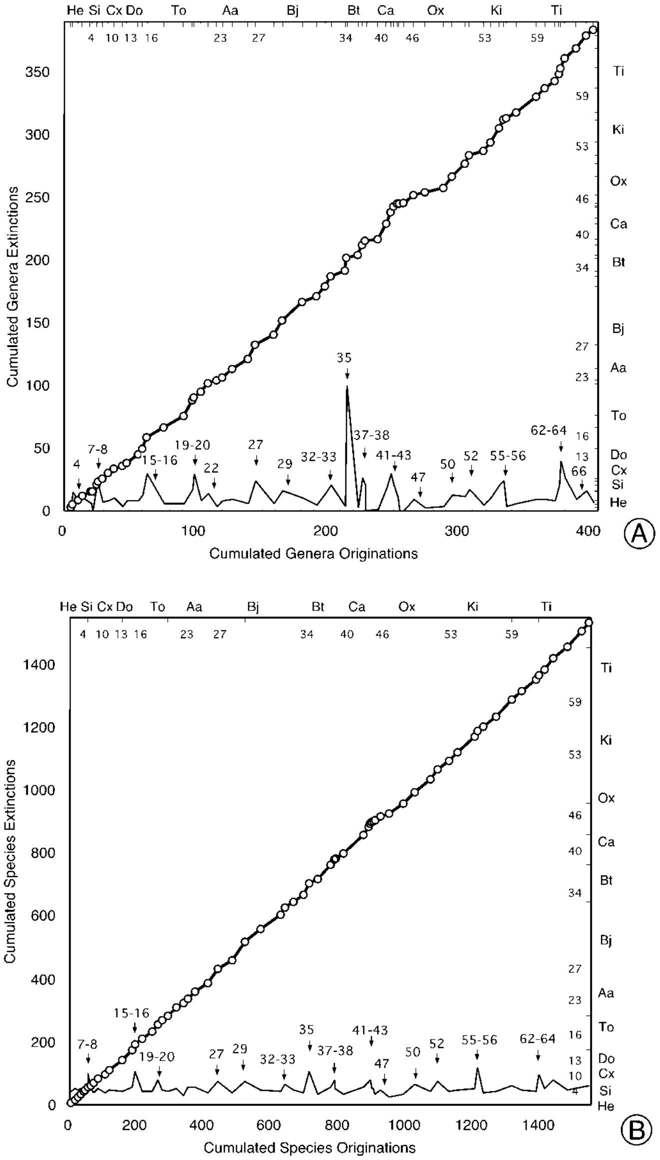


FIGURE 4—Bivariate cumulative extinctions vs. cumulative origination diagrams used in the analysis of the rate of faunal turnover. Based on data from range charts given in Figure 2 (genera) and Appendix 1 (species). (A) Faunal turnover of genera by zone. (B) Faunal turnover of species by zone. Dotted curve at the bottom of each diagram represents the slope of the curve at each ammonite zone, high values indicate major extinction events (enlarged x10). The observed major extinctions are as follows (numbers indicate the same ammonite zone than in Figure 2): Early Sinemurian, Bucklandi Zone (4); Late Sinemurian, Obtusum-Oxynotum Zones (7–8); Domerian-Toarcian boundary, Emaciatum-Polymorphum Zones (15–16); Middle Toarcian-Late Toarcian boundary, Gradata–Fallaciosum Zones (19–20); latest Toarcian, Aalensis Zone (22); earliest Bajocian, Discites Zone (27); Early Bajocian, Propinquans Zone (29); Late Bajocian, Garantiana-Parkinsoni Zones (32–33); latest Early Bathonian, Aurigerus Zone (35); Middle-Late Bathonian boundary, Costatus-Orbis Zones (37–38); Early-Middle Callovian, Gracilis-Coronatum Zones (41–43); latest Early Oxfordian, Renggeri Zone (47); earliest Late Oxfordian, Bifurcatus Zone (50); latest Oxfordian, Planula Zone, (52); Early-Late Kimmeridgian boundary, Divisum-Compsum Zones (55–56); latest Early Tithonian, Richteri-Burckhardticeras Zones (62–64); mid Late Tithonian, Transitorius Zone (66), only genera.

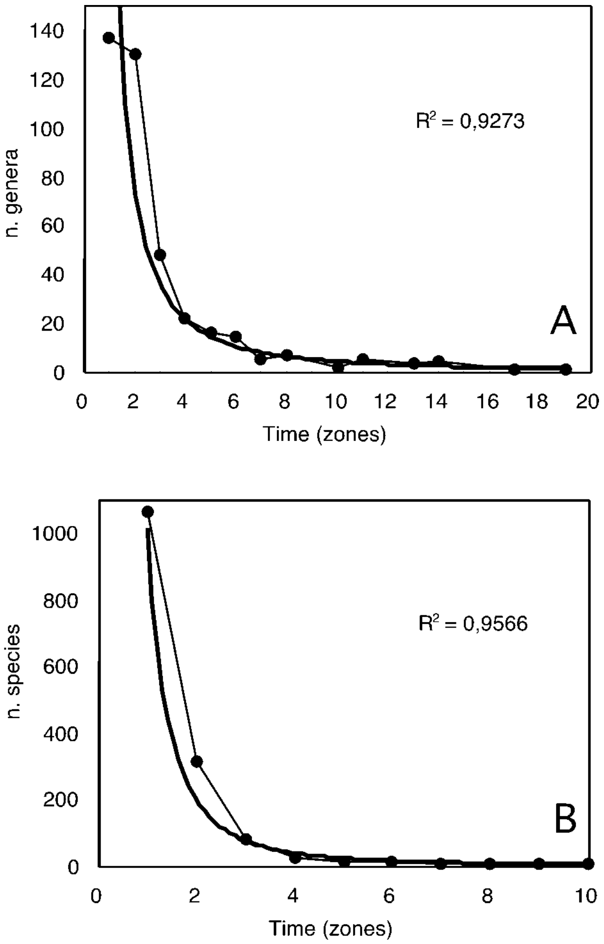


FIGURE 5—Ammonite survivor curves. (A) Survivor curve of genera by zones based on 400 ammonite genera recorded in the Betic Cordillera covering the entire Jurassic; (B) Survivor curve of species by zones. Data based on 1548 ammonite species recorded in the Betic Cordillera covering the entire Jurassic. Note that 35% of ammonite genera and almost 70% of species limit their stratigraphic range to a single biochronological unit.

and were replaced in the Early Lias by the first Ammonitida. This turnover took place during a strongly regressive phase followed by a long transgression (R_1 and T_1 in Hallam, 1989, 1990) and with the lower limit of the UAB-1 and UAB-2 mega-sequence boundary of the Exxon curve. Beginning in the Hettangian onwards, a series of evolutionary processes (extinctions, originations, and radiations) occurred, and it is these events and their possible connection with global sea-level changes that will be discussed. In the transgressive phase of the UAB-2.1 cycle, the diversification and expansion of the first Ammonitina (Psiloceratidae) took place. From this first Jurassic ammonite expansion, 24 major ammonite turnover events have been recorded in the entire Jurassic of the Betic Cordillera.

1. Early Sinemurian (Bucklandi-Semicostatum Zones)

The first important turnover of Jurassic ammonoids took place near the Hettangian/Sinemurian boundary (high D_{ij} values at generic and specific levels between the

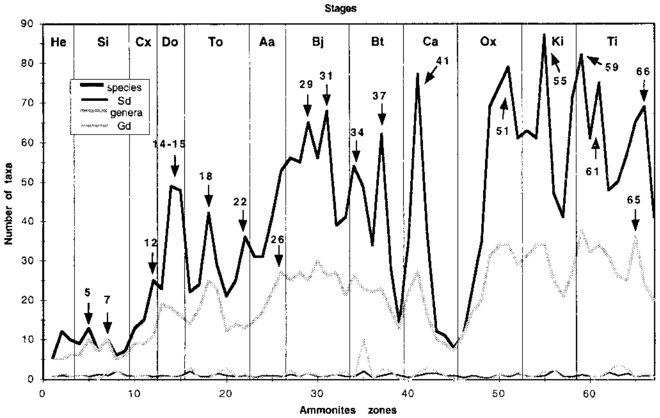


FIGURE 6—Generic and specific diversity with reference to major extinction events (as in Figure 4, numbers indicate the ammonite zone). The intervals of maximum relative diversity correspond to: Early Sinemurian, Semicostatum Zone (5); Late Sinemurian, Obtusum Zone (7); Late Carixian, Dilectum Zone (12); Middle-Late Domerian, Algovianum-Emaciatum Zones (14–15); Middle Toarcian, Bifrons Zone (18); latest Late Toarcian, Aalensis Zone (22); Late Aalenian, Concavum Zone (26), only generic level; Early Bajocian, Propinquans Zone (29); earliest Late Bajocian, Niortense Zone (31); Early Bathonian, Zigzag Zone (34); Middle Bathonian, Costatus Zone (37); Early Callovian, Gracilis Zone (41); earliest-mid Late Oxfordian, Bifurcatus-Bimammatum Zones (50–51); Early Kimmeridgian, Divisum Zone (55); Late Kimmeridgian-Early Tithonian, Beckeri-Hybonotum Zones (58–59); Early Tithonian, Verruciferum Zone (61); earliest Late Tithonian, Simplisphinctes Zone (65), only generic level; Late Tithonian, Transitorius Zone (66), only species level. Bottom curves as in Figure 5 (slope of the faunal turnover curve, where high values signify major extinction events). Sd = species level, Gd = generic level. A conspicuous correlation appears between extinction peaks (bottom curves) and drop in diversity.

Bucklandi-Semicostatum Zones; Table 2, Fig. 3A), when the forms belonging to the family Psiloceratidae and many Schlotheimiidae went extinct and were later replaced by Arietitidae. According to Hallam (1988, 1990), this turnover was connected with the latest Hettangian regression (Hallam's R_2, 1990) which caused the extinction, and with the Early Sinemurian transgressive phase (Hallam's T_2, 1988; Figs. 3, 7) which favored originations and radiation. This turnover also fits with the boundary between the UAB-2 and UAB-3 super-cycles, and with the transgressive phase of this latter cycle of the Exxon curve (see Mouterde et al., 1990; Hardenbol et al., 1998). Few ammonites have been recorded in the Betic Cordillera in the Lower Lias, and these have been found nearly always in overlapping areas between the internal and external zones of the Cordillera (Braga et al., 1984a, b, c). Nevertheless, these areas present the clearest examples of ammonite turnovers in this time interval.

2. Late Sinemurian (Obtusum-Oxynotum Zones)

The extinction of Arietitinae, Agassiceratinae, and Asteroceratinae and the radiation of the last Psilocerataceae (Echioceratidae and Oxynoticeratidae) and of the first Eoderocerataceae occurred in the Early-Late Sinemurian. This turnover is marked by high values of the D_{ij} coefficients between the Obtusum and Oxynotum Zones (Table 2, Fig. 3A). This turnover is related to the inter-Sinemurian discontinuity, which appears at some locations within of the Betic Cordillera (Rey, 1993; Nieto, 1997). Also, this turnover correlates with (1) Hallam's regressive phase R_2, which caused extinction, (2) with transgressive phase T_3 (Hallam, 1988), which, possibly, produced originations and radiations, and with (3) the boundary between the UAB-3.1 and UAB-3.2 cycles and with the transgressive phase of this cycle in the Exxon curve (Fig. 7). For the same period, significant changes also are detected in the curve of Hesselbo and Jenkyns (1998).

3. Sinemurian-Carixian Boundary (Raricostaum-Aenigmaticum Zones)

At the Sinemurian-Carixian boundary, the Echioceratidae and most of the Oxynoticeratidae became extinct, whereas Coeloceratinae, Polymorphitidae, Phricodoceratinae, and Liparoceratidae originated (Fig. 2; see also Mouterde et al., 1990). In the outer zones of the Betic Cordillera, this event occurs slightly before the demise of the carbonate platform, and there is an important stratigraphic discontinuity related to this event (Vera, 1988; Rey, 1993; Nieto, 1997). This faunal turnover, with high D_{ij} values, especially at the species level, between Raricostaum-Aenigmaticum Zones (Table 2, Fig. 3A), correlates very well with a regressive interval in the Late Sinemurian (Hallam's R_3, 1988) and with a third-order boundary (UAB-3.2/UAB3.3 in the Exxon curve). This is followed by a transgressive interval in the Early Pliensbachian (Hallam's T4, 1988; Fig. 7), which is also reflected in the Exxon curve. In addition, Hesselbo and Jenkyns (1998) located a maximum flooding surface near the Sinemurian/Carixian boundary, equivalent to the Si5/Pl1 sequence boundary and Pl1 transgressive phase of Tethyan sequences (Hardenbol et al., 1998).

4. Middle-Late Carixian (Demonense-Dilectum Zones)

In the Middle-Late Carixian transition, the extinction of the Acanthopleuroceratinae (*Tropidoceras, Metaderoceras, Duvaliceras*) and Polymorphitidae (*Uptonia,* etc.) took place, followed by the origination of the Hildoceratidae (the Harpoceratinae *Protogrammoceras* and *Fuciniceras*) and of the Dactylioceratidae (*Cetonoceras, Reynesocoeloceras*). In terms of sea-level fluctuations, this major turnover, with high interzonal distance (D_{ij} coefficient) between the Demonense and Dilectum Zones (Table 2, Fig. 3A) can be placed within Hallam's (1988) T_4 transgressive phase. It coincides with the boundary between the UAB-3.3 and UAB-3.4 cycles and with the transgressive phase of the UAB-3.4 cycle in the Exxon curve (Fig. 7). Similar events occurred in the Paris Basin (De Graciansky et al., 1998). Except for the faunal turnover, no significant stratigraphic event has been recorded in the Betic Cordillera during this time interval.

5. Latest Carixian-Middle Domerian (Dilectum to Algovianum Zones)

At the Early-Late Pliensbachian (Carixian-Domerian) boundary, the last Oxynoticeratidae and the Liparoceratidae disappeared in the Betic Cordillera (although Liparoceratidae range until Mid-Domerian in the Submediterranean). In the Betic Cordillera, this event coincides with the maximum abundance of Harpoceratinae (e.g., *Protogrammoceras, Fuciniceras, Lioceratoides*). The Arieticeratinae, which predominated in the Mediterranean domain (and in the Betic Cordillera), appeared later, as did the Amaltheidae, which predominated in the Sub-Boreal domain. The latter reached the Mediterranean basins only intermittently, and are preserved only within transgressive sequences. High values of D_{ij} coefficient, especially at the species level, appear between the Dilectum-Lavinianum and the Lavinianum-Algovianum Zones (Table 2, Fig. 3A), indicating a major turnover. In this turnover, originations surpass extinctions with a corresponding increase of diversity in the Algovianum and Emaciatum Zones (Fig. 6). The extinction processes may correspond to Hallam's (1988) R_4 regressive phase and to the boundary between the Exxon curve cycles UAB-3 and UAB-4 (Fig. 7). The radiations of the Amaltheidae and Arieticeratinae appear to correspond quite closely to Hallam's T_5 transgressive phase and to the transgressive phase in the UAB-4.2 third-order cycle in the Exxon curve.

In the Betic Cordillera, the regressive phase of the Carixian-Domerian boundary (Early-Middle Pliensbachian) is reflected by reduced facies and by stratigraphic discontinuities that are very well expressed in some areas of the Subbetic (Braga, 1983; Braga et al., 1982; O'Dogherty et al., 2000). The Middle-Late Domerian matches a transgressive phase that allowed the Arieticeratinae to migrate to the Sub-Boreal domain and the Amaltheidae to the Mediterranean domain (Braga, 1983; Braga et al., 1982).

6. Domerian-Toarcian Boundary—Middle Toarcian (Emaciatum-lower part of the Bifrons Zones)

A large number of the ammonoids from the Domerian disappeared at the Domerian-Toarcian boundary. Only a few genera (e.g., *Neolioceratoides, Fontanelliceras, Dactylioceras*) survived into the Polymorphum Zone, particularly in the Mediterranean (Jiménez, 1986; Jiménez and Rivas, 1992; Jiménez et al., 1996; Fig. 2). This extinction may be connected with a relative fall in sea level (Hallam's r_6, 1990) which may correspond to the limit of the UAB-4.2/UAB-4.3 cycles of the Exxon curve near the Pliensbachian-Toarcian boundary (Fig. 7). In fact, the extinction preceded the anoxia, which is concomitant with the subsequent transgressive phase.

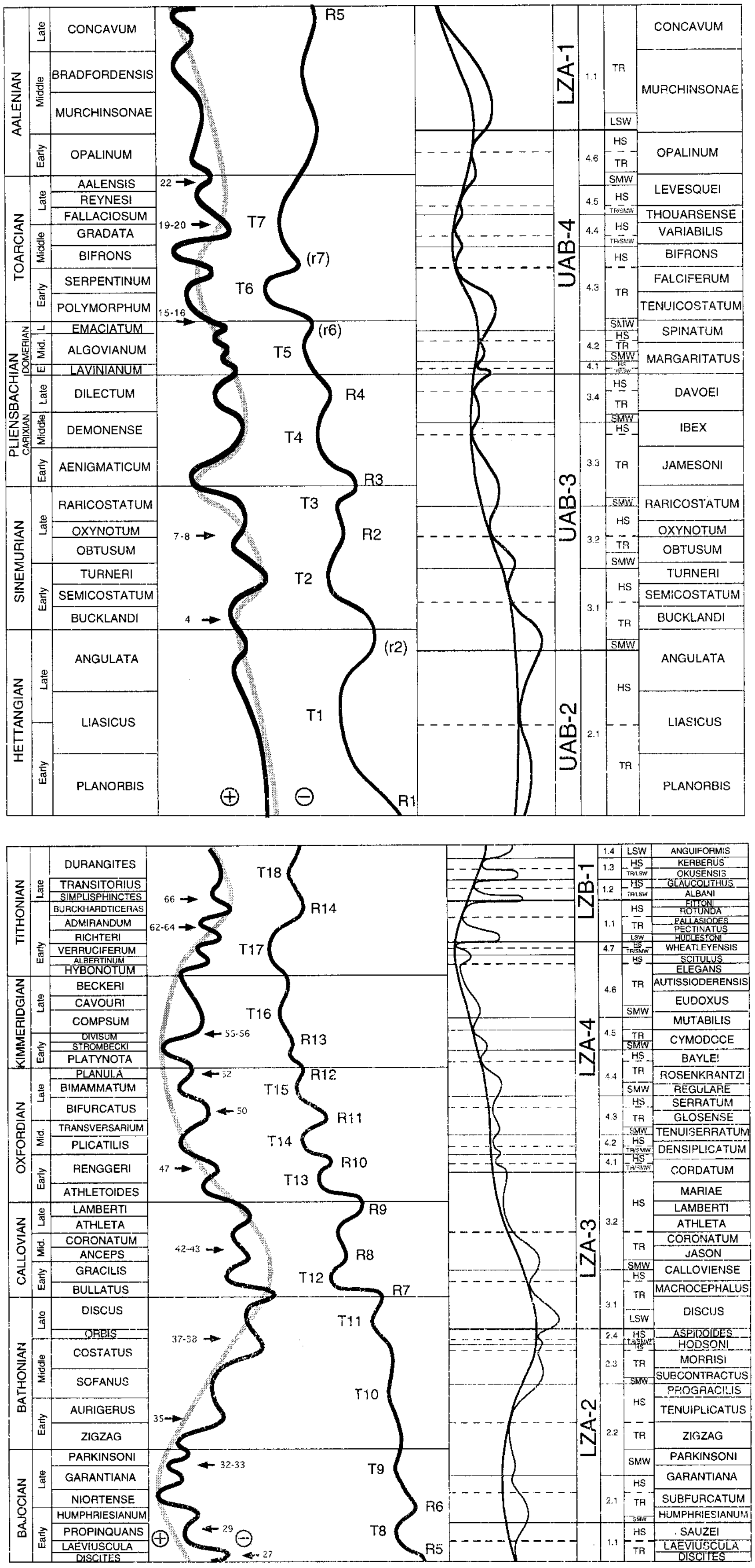
After this extinction, a new phase of ammonite diversification began in the Serpentinum Zone, both at generic (Fig. 2) and specific levels, giving very high values of D_{ij} between the Polymorphum and Serpentinum Zone (Table 2, Fig. 3A). This is true even though the fossils registered in the Betic Cordillera are both scarce and sporadic (Jiménez and Rivas, 1991, 1992). The appearance of new ammonites (various Dactylioceratidae, Harpoceratinae, and Hildoceratinae) may be connected with the fact that during the transgressive interval (UAB-4–3 of Haq et al.'s [1988] curve and T_6 [Hallam, 1988]) the marine habitats would have expanded, especially in marginal basins, where these taxa may have originated. The taxa that originated in the marginal basins would later have entered the Mediterranean basins (including the Betic). In fact, almost all the ammonites, especially platicones and serpenticones, appear to be diachronous in the Betic Cordillera with respect to marginal basins such as the Iberian Cordillera (Goy et al., 1988). Throughout this transgressive phase, a profound turnover in ammonite associations took place and the originations became even more important in the Bifrons Zone (a maximum relative in specific and generic diversity) than in the Serpentinum Zone (Figs. 2, 6, 7). This turnover affected mainly platicone and serpenticone forms (possibly linked to shallow environments; Westermann, 1990, 1996). Genera such as *Catacoeloceras, Zugodactylites, Peronoceras,* and *Collina* appeared among the Dactylioceratidae; *Hildoceras, Mercaticeras,* and *Pseudomercaticeras* among the Hildoceratinae; and the first Phymatoceratinae and Bouleiceratinae also originated (Fig. 2). The oxycone forms, mainly Harpoceratinae (*Polyplectus, Pseudolioceras*) which might have been adapted to deeper environments and, thus, less susceptible to fluctuations in sea level, underwent only minimal changes.

7. Latest Middle Toarcian-Late Toarcian (Bifrons to Aalensis Zones)

An important ammonite turnover took place between the Bifrons and Gradata Zones (with maximum extinction, almost coinciding with the upper limit of the Gemma Subzone). Extinctions clearly surpassed originations (Fig. 6) in this turnover (very high values of D_{ij} between the Bifrons-Gradata and Gradata-Fallaciosum Zones; Table 2, Figs. 2, 3A). The Dactylioceratidae and most of the Hildoceratinae (including *Hildoceras*) went extinct (Jiménez and Rivas, 1991) between the Bifrons-Gradata. During the Bifrons Zone, these taxa predominated in the Western Tethys (*Collina* also predominated in the base of the Gradata Zone). These extinctions may be connected with a period of relatively low sea-level (Hallam's r_7, 1990, Fig. 7) and with the regressive phase of the To4 cycle of Tethyan sequences (Jacquin et al., 1998; Hardenbol et al., 1998), which is recorded in the Betic Cordillera as a stratigraphic discontinuity. This event is consistently present in the Subbetic swells and may appear locally in basin facies (Median Subbetic), where it may cover the lower part of Gradata Zone and the Fallaciosum Zone.

In the lower part of the Fallaciosum Zone (in the Mediterranean), the Grammoceratinae and Hammatoceratinae became diversified and later radiated. This diversification may be related to Hallam's T_7 transgressive phase which, in turn, is connected with the transgressive phase of the UAB-4.4 cycle in the Exxon curve. However, this transgressive phase was apparently not major, and the communication pathways between the Mediterranean and the Central European basins continued to be restricted, given that there are hardly any common elements between the two basins.

The transgressive phase of the UAB-4.5 cycle, which was probably greater than reflected in the Exxon curve, and which would be included in Hallam's (1988) T_7 transgressive interval, reestablished communication between the Boreal, the Submediterranean, and the Mediterranean basins. New taxa (Erycitidae and Graphoceratidae, such as *Dumortieria* and *Catulloceras*) appeared and radiated within this interval, and occupied the various paleogeographic regions. Only forms associated with relatively deeper environments, such as the Phylloceratidae and fine-ribbed Lytoceratidae, are not yet found (or only


AALENIAN
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Middle
Early
CONCAVUM
BRADFORDENSIS
MURCHINSONAE
OPALINUM
TOARCIAN
AALENSIS
REYNESI
FALLACIOSUM
GRADATA
BIFRONS
SERPENTINUM
POLYMORPHUM
PLIENSBACHIAN
DOMERIAN
CARIXIAN
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ALGOVIANUM
LAVINIANUM
DILECTUM
DEMONENSE
AENIGMATICUM
SINEMURIAN
RARICOSTATUM
OXYNOTUM
OBTUSUM
TURNERI
SEMICOSTATUM
BUCKLANDI
HETTANGIAN
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THOUARSENSE
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BIFRONS
FALCIFERUM
TENUICOSTATUM
SPINATUM
MARGARITATUS
DAVOEI
IBEX
JAMESONI
RARICOSTATUM
OXYNOTUM
OBTUSUM
TURNERI
SEMICOSTATUM
BUCKLANDI
ANGULATA
LIASICUS
PLANORBIS
TITHONIAN
DURANGITES
TRANSITORIUS
SIMPLISPHINCTES
BURCKHARDTICERAS
ADMIRANDUM
RICHTERI
VERRUCIFERUM
ALBERTINUM
HYBONOTUM
KIMMERIDGIAN
BECKERI
CAVOURI
COMPSUM
DIVISUM
STROMBECKI
PLATYNOTA
OXFORDIAN
PLANULA
BIMAMMATUM
BIFURCATUS
TRANSVERSARIUM
PLICATILIS
RENGGERI
ATHLETOIDES
CALLOVIAN
LAMBERTI
ATHLETA
CORONATUM
ANCEPS
GRACILIS
BULLATUS
BATHONIAN
DISCUS
ORBIS
COSTATUS
SOFANUS
AURIGERUS
ZIGZAG
BAJOCIAN
PARKINSONI
GARANTIANA
NIORTENSE
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PECTINATUS
HUDLESTONI
WHEATLEYENSIS
SCITULUS
ELEGANS
AUTISSIODERENSIS
EUDOXUS
MUTABILIS
CYMODOCE
BAYLEI
ROSENKRANTZI
REGULARE
SERRATUM
GLOSENSE
TENUISERRATUM
DENSIPLICATUM
CORDATUM
MARIAE
LAMBERTI
ATHLETA
CORONATUM
JASON
CALLOVIENSE
MACROCEPHALUS
DISCUS
ASPIDOIDES
HODSONI
MORRISI
SUBCONTRACTUS
PROGRACILIS
TENUIPLICATUS
ZIGZAG
PARKINSONI
GARANTIANA
SUBFURCATUM
HUMPHRIESIANUM
SAUZEI
LAEVIUSCULA
DISCITES

very seldom present) in areas outside the Mediterranean region.

At the boundary between the Reynesi and Aalensis Zones, *Dumortieria* and *Polyplectus* disappeared and were replaced by new Grammoceratinae, such as *Pleydellia* and *Cotteswoldia,* which predominated in the latest Toarcian. These events occurred at almost the same time as the end of the UAB-4.5 transgressive phase in the Exxon curve, and coincide with a regressive interval in Hallam's curve (Fig. 7) and with transgressive phase of Toa6 in Hardenbol et al. (1998). In the Betic Cordillera, Upper Toarcian sediments generally are well represented in the Median Subbetic, but in swell areas this sub-stage usually accompanies a stratigraphic discontinuity that may cover up the Lower and Middle Aalenian, which clearly shows the generally regressive character of this interval.

8. Toarcian/Aalenian Boundary-Middle Aalenian (Aalensis to Bradfordensis Zones)

The genera *Pleydellia, Cotteswoldia,* and *Catulloceras* became extinct near the Toarcian-Aalenian boundary, and Tmetoceratinae and Leioceratinae appeared and radiated (Fig. 2). High D_{ij} values, at generic and specific levels, occur between the Aalensis and Opalinum Zones (Table 2, Fig. 3A). The Toarcian/Aalenian boundary coincides with a regressive period that can be seen in Hallam's (1988) curve and in the Betic Cordillera, where the Buckmani (latest Toarcian) and Opalinum Subzones (earliest Aalenian) are very poorly represented, even in a typical trough facies such as the Median Subbetic. In turn, these sea-level fluctuations may correlate with the UAB-4.5 and UAB-4.6 Exxon curve cycle boundaries (Fig. 7) and with the boundary of the sequences Toa6 and Toa7 (Hardenbol et al., 1998), and would appear to be responsible for faunal extinction.

The Comptum Subzone, which is well represented both in the Betic Cordillera and almost all over the world (Linares and Sandoval, 1993), corresponds to a small transgressive interval (the end of the transgressive phase of the UAB-4.6 Exxon curve cycle). This coincides with the most widespread diversification of Leioceratinae, Tmetoceratinae, and Erycitidae (*Spinammatoceras* appears for the first time). This transgressive interval is followed by a regression that reaches its peak near the lower part of the Murchisonae Zone (the boundary between the UAB and LZA super-cycles in the Exxon curve; Fig. 7). The events connected with this cycle boundary, together with the transgressive phase of the LZA-1.1 cycle (transgressive phase of Aa2 in Hardenbol et al., 1998), which developed during the Bradfordensis and Concavum Zones (Fig. 7), first brought about the isolation of, and later communication between, different basins. Change in basinal configuration may have caused a minor turnover event between the Murchisonae and Bradfordensis Zones (Table 2, Figs. 2, 3A) with the evolution of Leioceratinae to Graphoceratinae. Also possibly connected with this event is the appearance and radiation of some characteristically Mediterranean Erycitidae (*Abbasitoides, Malladaites* and *Haplopleuroceras*), of the last Grammoceratinae (*Vacekia, Asthenoceras* and *Fontannesia*), and others. At the same time as these forms characteristic of the Mediterranean ocean basins appear, other genera originated, such as *Staufenia,* that are found only in the epicontinental seas and must have arisen in small isolated marginal basins within these domains (Bayer and McGhee, 1985).

9. Latest Aalenian-earliest Bajocian (Concavum-Laeviuscula Zones)

Between the Concavum and Laeviuscula Zones, one of the most important faunal turnovers in the evolutionary history of Mesozoic ammonoids took place (Fig. 2A, Appendix 1) although their diversity barely changed (Figs. 6, 7). Very high D_{ij} values can be seen between the Concavum-Discites and, especially between the Discites-Laeviuscula Zones. Near the Aalenian Bajocian boundary, all the ammonite groups that predominated in the Aalenian (Graphoceratidae, Grammoceratinae, Tmetoceratinae, Hammatoceratidae and Erycitidae) disappeared. Subsequently, new groups originated and spread (among them the superfamilies Haplocerataceae and Stephanocerataceae) such as the Haploceratidae (Haploceratinae and Bradfordiinae), Strigoceratidae, Sonniniidae, Otoitidae, and Stephanoceratidae. A broad transgressive episode can be seen in the Exxon curve (Haq et al., 1988; LZA-1.1 cycle transgressive interval) which ranges from the Bradfordensis to the Laeviuscula Zone. However, the curves presented by Hallam show a regressive interval (Hallam's R_5, 1988, and r_8, 1990) which would be placed very near to this boundary, followed by a transgression (T_8 in Early Bajocian; Fig. 7). Also, in Tethyan sequences, Hardenbol et al. (1998) differentiate a sequence boundary in the Discites Zone. In the Betic Cordillera, the Aalenian is well represented only in the Median Subbetic; in the swells, the Internal Subbetic, and most of the External Subbetic, it coincides with a discontinuity (Linares and Sandoval, 1993). The transgressive interval in the Early Bajocian is easily recognizable so that in many areas of the Subbetic swells the Lower Bajocian lithologies lie directly on top of Lower Aalenian or even older strata (Sandoval, 1983; Linares and Sandoval, 1993; Rey, 1993; Nieto, 1997). These events (the regression and later transgression) offer a satisfactory explanation for the turnovers described above. Almost all the ammonoids first recorded in the latest Aalenian or at the beginning of the Bajocian could have originated in the ocean basin (Tethys), because they appear earlier in the Betic than in the Central European continental basins. During the transgressive phase (T_8, Hallam's, 1988), the migration of taxa from the Mediterranean to Central

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FIGURE 7—Curves for diversity (grey left) and for origination-extinction (black left) against global sea-level-change curves proposed by Haq et al. (1988; right) and Hallam (1988; middle, including the transgression and regression—T, R—and regression—r—in Hallam, 1990). (A) Hettangian to Aalenian times; (B) Bajocian to Tithonian times. Ammonite zonation on the left corresponds to the standard Mediterranean zones (Cariou and Hantzpergue, 1997) with local modifications. Ammonite zonation of the right is that used by Haq et al. (1988). Arrows and numbers indicate the ammonite zone.

Europe may have been facilitated (Sandoval and Chandler, 2000).

10. Early Bajocian (Propinquans-Humphriesianum Zones)

An important faunal turnover took place (Table 2, Figs. 2, 3A, 6,) near the boundary between the Propinquans and Humphriesianum Zones (Hebridica and Romani Subzones) which can be seen in the disappearance of the Otoitidae, Bradfordiinae, Sonniniidae (except for *Dorsetensia*), and *Labyrinthoceras*. This extinction occurred slightly before the appearance of other taxa (e.g., Oppeliidae and Sphaeroceratidae), and also before the maximum diversity and abundance of the Stephanoceratidae. In the Exxon curve, high-stand deposits end at the boundary between the Propinquans and Humphriesianum Zones where a sequence boundary (LZA-1.1/LZA-1.2) appears. This event, coinciding approximately with the end of Hallam's (1988) T_8 and R_6 (Fig. 7), do not explain satisfactorily this ammonite turnover. Mouterde et al. (1989), Gonnin et al. (1992, 1993) and Tethyan sequences (De Graciansky et al., 1998; Hardenbol et al., 1998) show a regressive interval in the Propinquans Zone, which is followed by a major transgression in the lower part of the Humphriesianum Zone (Hebridica Subzone). These events—a drop in sea level followed by a rise—explain this important turnover. In the Betic Cordillera, this event is detected as a discontinuity in some sectors of the Subbetic (O'Dogherty et al., 2000).

11. Latest Early Bajocian-earliest Late Bajocian (Humphriesianum-Niortense Zones)

At the Early-Late Bajocian boundary (the final stage of the Humphriesianum Zone-Niortense Zone), another important ammonite turnover took place (Fig. 2) although diversity scarcely varies (Fig. 6). High D_{ij} values, at both the generic and specific levels, appear between the Humphriesianum-Niortense Zones (Table 2, Fig. 3A). The most important events were the extinction of most Stephanoceratidae (except for the dimorph pair *Cadomites-Polyplectites*) and of the last Sonniniidae, on the one hand, and the origination and radiation of the Perisphinctidae (Leptosphinctinae), Parkinsoniidae, and Spiroceratidae on the other. The sphaerocones (Sphaeroceratidae) and oxycones (Oppeliidae, Haploceratidae and Strigoceratidae), which probably lived in deeper environments, survived almost unaffected (Sandoval, 1983, 1986). According to the Exxon curve (Haq et al., 1988), this turnover took place during the transgressive interval of the LZA.2.1 cycle, which extended from the Humphriesianum Zone to the middle part of the Garantiana Zone. In Hallam's (1988) curve, these events co-occur with R_9 (the inter-Humphriesianum regression) and T_8 (the Late Bajocian transgression; Fig. 7). Hardenbol et al. (1998) show a regressive interval, which includes the upper part of the Humphriesianum Zone and the lower part of the Niortense Zone, and a relative maximum transgressive in the middle part of Niortense Zone. A discontinuity appears in many areas of the Subbetic swells in the Betic Cordillera which, depending on paleogeography, ranges from the upper part of the Humphriesianum Zone to the lower part of the Niortense Zone, while the remainder of this zone and part of the Garantiana are transgressive. This last transgressive phase would explain the origination of the Perisphinctidae and Parkinsoniidae from Stephanoceratidae, which probably occurred in marginal basins of the Tethys (the Hispanic Corridor or Protoatlantic; Sandoval and Westermann, 1986). The transgressive phase would further explain the communication between the Central European basins and the Tethys and, indeed, that between the Tethys and the Eastern Pacific (via the Hispanic Corridor) with frequent migration among the different paleobiogeographic realms and provinces.

12. Latest Bajocian (Garantiana-Parkinsoni Zones)

Between the Garantiana and the base of the Parkinsoni Zone, the Garantianinae went extinct, the Sphaeroceratidae disappeared in the Western Tethys (they continued in the Eastern Pacific), the Leptosphinctinae were replaced by the Zigzagiceratinae, *Spiroceras* also went extinct, and the Morphoceratidae (*Dimorphinites-Vigoriceras*) originated and radiated in the Mediterranean (Fig. 2), although this turnover is minor at generic and specific levels (Table 2, Fig. 3A). In the curve proposed by Haq et al. (1988), and within a generally transgressive context, a sequence boundary appears between third-order cycles (LAZ-2.1/LAZ-2.2) in the upper part of the Garantiana Zone, while the whole of the Parkinsoni Zone coincides with a low-stand system tract (Fig. 7). In Hallam's (1988, 1990) curves, a small regressive interval can be distinguished within a major transgressive interval (T_9) near the Bajocian/Bathonian boundary, which also covers the Lower Bathonian (Fig. 7). In the Mediterranean province, the upper part of the Garantiana Zone coincides with a maximum regressive of the Bj4 sequence, and the transgressive phase occurs in the lower part of the Parkinsoni Zone (Hardenbol et al., 1998). In the Betic Cordillera, there is no major stratigraphic discontinuity in the Parkinsoni Zone, because uppermost Bajocian lithologies are found in many areas of the Subbetic swells. All these stratigraphic events, especially Tethyan sequences, satisfactorily explain the turnover.

13. Early Bathonian—Middle Bathonian Boundary (Aurigerus-Sofanus Zones)

Near the boundary between Early and Middle Bathonian another major turnover in the ammonite associations took place, with very high values of D_{ij} coefficients between the Aurigerus and Sofanus Zones (Table 2, Figs. 2, 3A). The most important events of this turnover were the extinction of the Parkinsoniidae (which were predominant in Central Europe throughout the Late Bajocian and Early Bathonian), the Morphoceratidae, *Nannolytoceras* (the predominant genus during the uppermost Bajocian and Lower Bathonian in the Betic Cordillera), and the extinction of several Tethyan Phylloceratina. These extinctions were followed by the first appearance of the Tulitidae (*Bullatimorphites, Tulites, Morrisiceras, Lycetticeras*), Hecticoceratinae (*Eohecticoceras* and *Prohecticoceras*) and several Perisphinctidae (*Wagnericeras, Choffatia, Homoeoplanulites*). A third-order boundary (LZA-2.2/LZA-2.4) between the Progracilis and Subcontractus Zones appears in the Exxon curve (Haq et al., 1988), while we find no major event on Hallam's (1988) curve, which shows a generally transgressive tendency (T_{10}) throughout the Early and Middle Bathonian (Fig. 7). However, in Tethyan sequences, Hardenbol et al. (1998) recognize a cycle boundary in the Aurigerus Zone, which co-occurs with extinction events. In the Betic Cordillera, this event coincides with a minor stratigraphic lacuna, that covers at least the earliest Middle Bathonian.

14. Latest Middle Bathonian—earliest Late Bathonian (Costatus-Orbis Zones)

Between the latest Middle Bathonian (Costatus Zone) and the earliest Late Bathonian, *Cadomites* went extinct in the Western Mediterranean, although it continued in Central Europe (Dietl and Herold, 1986). The genera *Wagnericeras, Procerites,* and *Bullatimorphites* also became extinct while *Epistrenoceras, Hemigarantia,* and various Andean forms (Eurycephalytinae and Neuqueniceratinae) appeared. This relatively major turnover (high values of D_{ij} coefficients between the Costatus and Orbis Zones; Table 2, Figs. 2, 3A) coincides with a third-order cycle boundary (LZA-2.3/LZA-2.4) which occurs in the upper part of the Hodsoni Zone (Costatus) in the Exxon curve (Haq et al., 1988), with the transgressive phase of the LZA-2.1 cycle, the Bat4 in the Tethyan sequences (Hardenbol et al., 1998), and also with a small regressive interval followed by another transgression (T_{11}) appearing in the last third of the Late Bathonian in the Hallam's (1988) curve (Fig. 7). A notable discontinuity appears in the Subbetic swells in the lower part of the Upper Bathonian and/or in the upper part of the Middle Bathonian. This discontinuity, in some areas, may cover the Late Bathonian to Middle Oxfordian interval while, in other places, part of the Upper Bathonian (Orbis Zone), the Callovian, and the Lower Oxfordian are present. This regression in the earliest Late Bathonian and the later transgression in the Orbis Zone would explain the minor turnovers that took place during this interval.

15. Latest Bathonian—Early Callovian (Discus to Gracilis Zones)

No deposits belonging to the Discus Zone (very poorly represented in the world) have been found in the Subbetic swells, which indicates the zone to be a broadly regressive interval. Even in those areas where this zone is present, low ammonite diversity is recorded (Mangold, 1970; Mangold and Rioult, 1997). The most notable faunal events in the Western Tethys during this interval include the extinction of *Epistrenoceras, Hemigarantia, Clydoniceras,* and several Perisphinctidae. According to the Exxon curve, the last important change in sea level recorded in the Bathonian was a conspicuous regression related to the boundary of the super-cycles LZA-2/LZA-3 in the Discus Zone, which is an equivalent boundary of the Tethyan sequence Bat5 of Hardenbol et al. (1998). However, Hallam's (1988) curve does not show any regressive interval (R_7) until the Bathonian/Callovian boundary (Fig. 7).

In Early Callovian (Bullatus and, especially, Gracilis Zones) in the Western Tethys, widespread diversification of the Perisphinctidae and the Tulitidae took place together with the first record of Macrocephalitidae and Reineckeiidae. These forms presumably migrated from the Western Pacific, because similar forms appeared in the Upper Bathonian in the Andean province and in Mexico (Cariou, 1984; Sandoval et al., 1990; Riccardi and Westermann, 1991), or in the Western Tethys (Westermann and Callomon, 1988). Several Boreal and Andean groups (Kosmoceratidae and Eurycephalytinae, respectively) diversified during the Early Callovian. High values of D_{ij} occur between the Bullatus and Gracilis and Anceps Zones (Table 2, Figs. 2, 3A). This faunal turnover occurred at the same time as Hallam's (1988) R_7 regressive and T_{12} phases, and the transgressive phase of the LZA-3.1 cycle in the Exxon curve (Haq et al., 1988; Fig. 7) equivalent to the transgressive cycle of Call1 of the Tethyan sequences (Hardenbol et al., 1998). In the Betic Cordillera, this turnover is connected with a major stratigraphic event that appears to mark the beginning of a transgressive phase after a long regressive interval. This is based upon materials from the Bullatus Zone that overlie the Middle Bathonian or even older strata in some areas of the Subbetic swells, while in other areas the oldest Callovian materials belong to the Gracilis Zone.

16. Middle-Late Callovian (Anceps to Lamberti Zones)

A major ammonite turnover occurred in Middle-Late Callovian (Fig. 2); the most significant events include the successive extinctions of the Macrocephalitidae, Tulitidae, Reineckeiidae, Strigoceratidae, Hecticoceratinae, and various groups of Perisphinctidae (Zigzagiceratinae and Grossouvriinae), all of which were the dominant ammonite groups during Early-Middle Callovian and earliest Late Callovian. These forms were replaced by Peltoceratinae, Euaspidoceratinae, Taramelliceratinae, and others. Throughout this turnover extinctions clearly surpass originations (Table 2, Fig. 3A) and, consequently, diversity decreases (Fig. 6). This may be linked to a regressive interval (R_8; Hallam, 1988) which covers the Middle and earliest Late Callovian and to a moderately transgressive interval (placed between R_8 and R_9) in Upper Callovian (Fig. 7). These intervals are more or less equivalent to the lowstand system tract of the third-order cycle LAZ.3.2 in the Exxon curve and the transgressive phase of this same cycle, likewise equivalent with the lower boundary of the sequence Call3 and with the transgressive cycle of the Tethyan sequences of Hardenbol et al. (1998). In the Betic Cordillera, there is a well-developed discontinuity in the Middle and Upper Callovian, such that the Upper Callovian materials rarely are found in the Subbetic swells. When such materials are found, they are limited to banks a few centimeters thick and are only in small areas of the Internal Subbetic (Sequeiros, 1974, 1987; Sequeiros and Olóriz, 1979) or the External Subbetic (Checa and Sequeiros, 1990).

17. Early Oxfordian-earliest Middle Oxfordian (Renggeri-Plicatilis Zones)

During the Early Oxfordian, ammonite associations were similar to those found in the latest Callovian when Peltoceratinae and Euaspidoceratinae (*Euaspidoceras*) predominated. In the central sector of the Betic Cordillera, the Lower Oxfordian (as in the Upper Callovian) coincides with a stratigraphic gap (Sequeiros, 1974, 1987; Sequeiros and Olóriz, 1979), while in the eastern sector it is present, but poorly represented (Checa and Sequeiros, 1990; Caracuel, 1996). The Late Callovian–Early Oxfordian discontinuity may correspond to the super-cycle LZA-3/LZA-4 boundary in the Exxon curve (Fig. 7) and with Ox1/Ox2 sequence boundary of Tethyan sequences.

In the earlier half of the Middle Oxfordian (Plicatilis Zone), a diversification of the Haploceratidae, Taramelliceratinae, Ochetoceratinae, Pachyceratidae, Euaspidoceratinae, and Perisphinctinae took place, together with the appearance of the first representatives of Passendorferiinae. Although the diversity is low (Fig. 6), the values of D_{ij} between the Renggeri and Plicatilis Zones are highs (Table 2, Fig. 3A). This diversification coincides with the T_{14} transgressive phase, which appears in the Middle Oxfordian in the Hallam's (1996) curve; this would correspond to the transgressive phase of the LZA-4.3 in the Exxon curve (Fig. 7).

18. Earliest Late Oxfordian-latest Oxfordian (Bifurcatus to Planula Zones)

In the early Late Oxfordian, a new ammonite turnover occurred that is characterized by the extinction of most of the Euaspidoceratinae, Peltoceratinae, Perisphinctinae, and several Taramelliceratinae, all of which predominated in the Middle Oxfordian. These were replaced by other forms such as the Ochetoceratinae, Epipeltoceratinae, Aspidoceratinae, Physodoceratinae, Idoceratinae, Ataxioceratinae, Aulacostephaninae, Streblitinae, and new Taramelliceratinae (*Metahaploceras*), which dominated in the Late Oxfordian, together with the Phylloceratina. Major turnovers took place between the Bifurcatus and Bimammatum Zones where originations overpass extinction (maximum in diversity, Fig. 6) and high values of D_{ij} are recorded (Table 2, Fig. 3). In studies carried out in the Subbetic basin, condensed sediments from the Transversarium and Bifurcatus Zones are found, but no major discontinuity in the deposits belonging to this time interval are noted (Sequeiros, 1974; Caracuel, 1996). This turnover may have been caused by a sea-level fall in the Late Oxfordian (Bimammatum and Planula Zones): R_{11} on Hallam's (1988) curve. At the same time, these events may be correlated with the boundary between the LZA-4.3 and LZA-4.4 sequences, the transgressive phase of this cycle in the Exxon curve (Fig. 7), with the Ox5/Ox6 boundary, and with the transgressive cycle of Ox6 of Tethyan sequences (Hardenbol et al., 1998).

19. Early Kimmeridgian (Platynota-Divisum Zones)

During the Kimmeridgian, the ammonoid associations underwent several turnovers at both the genus and the species levels. At the Oxfordian/Kimmeridgian boundary some taxa became extinct and others originated (Table 2, Fig. 2), a fact that may be related to the R_{12} regression and to a slight transgressive phase that appears in Hallam's curve (Fig. 7). The first major turnover occurred between the Platynota and Strombecki-Divisum Zones, in which some common Late Oxfordian and Early Kimmeridgian forms went extinct and there were a major diversifications within the Taramelliceratinae, Passendorferiinae (*Nebrodites, Mesosimoceras*) and Streblitinae (Olóriz, 1978, 1979; Rodríguez-Tovar, 1993; Caracuel, 1996), resulting in maximum diversity in the Divisum Zone (Table 2, Figs. 2, 3A, 6). This extinction and the subsequent diversification may be connected with the R_{13} regressive phase of the Early Kimmeridgian, and with the T_{16} transgressive phase of the Early-Late Kimmeridgian boundary on Hallam's (1988) curve. In turn, it may correspond to the third-order sequence boundary between the LZA-4.4 and LZA-4.5 cycles (Strombecki Zone) and the transgressive phase of this cycle on the curve (Haq et al., 1988), which covers the Divisum Zone and lower part of the Compsum (Fig. 7).

20. Late Kimmeridgian (Compsum-Beckeri Zones)

Another turnover, almost as important as that described above (Fig. 2), took place in the Late Kimmeridgian (Compsum and Beckeri Zones). The Aulacostephaninae, Idoceratinae, Passendorferiinae, and Ataxioceratinae, as well as several Ochetoceratinae and Taramelliceratinae, went extinct during the Compsum and Cavouri Zones. These were replaced by two new subfamilies of the Perisphinctidae (Lithacoceratinae and Torquatisphinctinae) and by the Hybonoticeratinae, all of which were to predominate during latest Kimmeridgian and most of the Early Tithonian (see Olóriz, 1978; Caracuel, 1996). This turnover was especially significant between the Cavouri and Beckeri Zones with high values of D_{ij} coefficients (Table 2, Fig. 3A). No notable discontinuity for this time interval has been recognized in the Betic Cordillera, but the Subbetic swells show all the cycles represented in the Exxon curve (Caracuel, 1996). This turnover can be correlated readily with the LZA-4.5/LZA-4.6 cycle boundary, equivalent to Kim3/Kim4 Tethyan sequence boundary (Compsum Zone), and with the transgressive phase of this cycle, which developed in Late Kimmeridgian (Cavouri and Beckeri Zones; Fig. 7). However, it does not coincide with any important event on Hallam's (1988) curve, where the entire interval is included in the T_{16} transgressive phase.

21. Earliest Early Tithonian (Hybonotum-Albertinum Zones)

No major stratigraphic gaps or discontinuities are recorded in the Tithonian sediments from the Subbetic swells, where all the Mediterranean standard ammonite zones have been recognized (Olóriz, 1978; Tavera, 1985; Caracuel, 1996, etc.). In that domain, Caracuel (1996) registered all the cycles that appear in the Exxon curve. In the Early Tithonian (in the upper part of the Hybonotum Zone and in the lower part of the Albertinum Zone), *Sowerbyceras,* which predominated throughout the Kimmeridgian, and the Hybonoticeratinae went extinct (Fig. 2). This extinction coincided with the origination of the Simoceratinae, but extinction events dominated over originations with a consequent decrease in diversity (Fig. 6). High D_{ij} values are recorded between the Hybonotum and Albertinum Zones (Table 2, Fig. 3A). On his curves, Hallam records no eustatic change that can be correlated with this turnover. The turnover may be connected with the boundary between the LZA-4.6 and LZA-4.7 cycles in the Exxon curve, with the transgressive phase of the LZA-4.7 cycle (Fig. 7), the boundary between sequences Kim5/Ti1, and the transgressive phase of Ti1 in the Tethyan sequences (Hardenbol et al., 1998).

22. Mid-Early Tithonian (Albertinum-Verruciferum Zones)

In the upper part of the Albertinum Zone and the lower part of the Verruciferum Zone, the Taramelliceratinae, Glochiceratidae, and most of the Aspidoceratinae and Physodoceratinae disappeared. The greatest diversification of the Simoceratinae and a major generic turnover within the Haploceratidae, Lithacoceratinae, and Torquatisphinctinae followed this extinction (Fig. 2). At the specific level, the D_{ij} value is high between the Albertinum-Verruciferum Zones (Table 2, Fig. 3A). Originations clearly surpassed extinctions, thereby increasing diversity (Fig. 6). In turn, this turnover coincides with the boundary between the second-order sequences LZA-4.7 and LZB-1.1 and with a small stratigraphic gap that has been detected in the Betic Cordillera (Rey, 1993; Nieto, 1997). The turnover does not fit in with any significant event in Hallam's (1988) curve (Fig. 7). The originations coincide with the transgressive phase of LZB-1.1.

23. Early Tithonian-Late Tithonian Boundary

At the boundary between Early and Late Tithonian (Burckhardticeras and Simplisphinctes Zones), the Ochetoceratinae, Streblitinae, Simoceratinae, and Torquatisphinctinae disappeared, whereas the Himalayitidae and Aulacostephaninae originated and became predominant during the Late Tithonian (Fig. 2). This turnover, notable at the species level (Table 2, Fig. 3A), may be connected with the R_{14}, the T_{18} intervals of Hallam's (1988) curve, and with the boundary between the LZB-1.1 and LZB-1.2 of the transgressive phase in the Exxon curve (Fig. 7). These are equivalents to the boundary between Ti3/Ti4 cycles and transgressive phase of Ti4 in Tethyan sequences (Hardenbol et al., 1998).

24. Late Tithonian (Transitorius-Durangites Zones)

A minor ammonite turnover occurred in the Late Tithonian with the extinction of the last representatives of the Perisphinctidae (Lithacoceratinae and later Paraulacosphinctinae) and the appearance of Berriasellidae and Spiticeratinae (Table 2, Figs. 2, 3A). This is the last Jurassic ammonite turnover recorded in the Western Tethys, a fact that may be correlated with the LZB-1.2 and LZB-1.3 sequence boundary and with the transgressive phase of the LZB-1.3 cycle in the Exxon curve (Ti4/Ti5 sequence boundary of Tethyan sequences in Hardenbol et al., 1998). These events are not shown in Hallam's curves (Fig. 7).

As indicated in Figure 6, with rare exceptions (e.g., Concavum, Simplisphinctes, and Transitorius Zones), the intervals of maximum generic and specific diversity coincide. Highest diversities occur especially in the Middle-Late Domerian, Middle Toarcian, Early Bajocian-earliest Late Bajocian, Early Bathonian, latest Middle Bathonian, Early Callovian, early Late Oxfordian, latest Early Kimmeridgian, latest Kimmeridgian-earliest Tithonian, mid-Early Tithonian and Late Tithonian. Minimal relative diversities occur in the Late Sinemurian, earliest Toarcian, Middle-Late Toarcian boundary, Early-Middle Aalenian boundary, latest Bathonian, Late Callovian-Early Oxfordian, latest Oxfordian, Late Kimmeridgian, and latest Early Tithonian. A comparison of the diversities with global sea-level-change curves (Fig. 7) shows that maximum relative diversities coincide mostly with transgressive peaks (e.g., Bifrons, Niortense, Gracilis, Divisum, Hybonotum, and Verruciferum Zones) in the Exxon, Hallam (1988) or Hardenbol et al. (1988) curves, whereas regressive peaks (e.g., Murchisonae, Discus, Lamberti-Atletoides Zones) correlate with minimal relative diversities.

The origination-extinction curve (Fig.7, black left curve) indicates that most extinction events are related to regressive intervals (cycle boundaries in the Exxon curve), and that origination and radiation events appear to be correlated well with transgressive intervals of Hallam's curve (1988) and with transgressive cycles in the Exxon curve (Haq et al., 1988). Comparison of the origination-extinction curve with Tethyan sequences (Hardenbol et al., 1998) results in a better correlation.

DISCUSSIONS

A study of ammonite associations recorded in the Jurassic lithologies of the Betic Cordillera reveals a series of faunal turnover events. The most common pattern consists of periods in which extinctions predominate followed by periods during which new taxa appeared and radiated. For many time intervals in the Betic Cordillera there is a direct relationship between stratigraphic gaps and faunal turnover. The causes for ammonite faunal turnover could be quite diverse. Decreases in diversity and extinction events can be strongly affected both by biotic and abiotic factors, although the latter play a more important role (i.e., competition with other taxa, environmental perturbations, such as thermal stress, tectonic events, alterations of the distribution areas, etc.). Likewise, biotic and abiotic events can be the factors generating the originations and radiation of new taxa. It should be noted that many of these factors are affected by others (e.g., climatic changes directly affect to biotic events but, at times, climatic changes can act on sea level which in turn may alter the distribution and area of continental and marine environments). Likewise, two or more factors can generate the same effect (e.g., sea-level fall and climatic cooling can accelerate extinction processes). As shown by Hallam and Wignall (1997), small environmental perturbations can strongly affect shallow-water organisms, a habitat in which many ammonites lived (Westermann, 1990, 1996). The comparative analysis of intervals in which ammonite turnovers took place, on the one hand, and global changes in sea level, on the other, demonstrates that most major faunal turnovers are correlated with eustatic cycles. Extinction almost always coincided with regressive phases, while the origination and radiation of new taxa (species, genera, etc.) were connected with transgressive episodes. Consequently, it is concluded that sea-level fall and the corresponding regression were the main causes of ammonite extinctions in the Subbetic basin. High sea-level with corresponding transgression, which resulted in the origination of new habitats, are the main factors influencing ammonite origination and radiation.

Exactly how these changes came about, however, is not yet clear. In many cases the regressive events (well documented in the Betic Cordillera by discontinuities) increased the isolation of the marine biota and, in turn, extinguished many taxa and decreased the diversity. Such extinctions are particularly important in taxa that lived in shallow environments (usually heavily ornamented serpenticone forms), precisely those that were more prone to undergo evolutionary changes. The observed data might suggest that the Phylloceratina, Lytoceratina, and many oxyconic Haplocerataceae (conservative and very abundant in Betic Cordillera, also in other typically basin areas) were unaffected by sea-level changes in terms of evolution and extinction. The adaptation of these groups to deep-water habitats may satisfactorily explain this fact.

On the other hand, the isolation of ammonite populations in marginal basins, either towards the end of regressive phases or, more probably, during the early stages of transgressive cycles, favors origination and the later appearance of new taxa, as was shown by Bayer and McGhee (1985).

These new taxa (isolated in marginal basins during periods of low sea level) would have taken advantage of the following transgressive cycles to radiate and occupy new areas. It may be during these latter intervals that taxa reached their widest geographical distribution and, in most cases, where they are first recorded.

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APPENDIX 1

Ranges of genera and species recorded in the Betic Jurassic. Numbers 1 to 69 indicate the Mediterranean standard ammonite zones.

Psiloceras	1	1
Psiloceras gr. naumanni	1	1
Caloceras	1	1
Caloceras sp.	1	1
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Parapallasiceras euscultum	60	60
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