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Eustatism and faunal associations. Examples from the South Iberian Margin during the Late Jurassic (Oxfordian-Kimmeridgian)

By FEDERICO OLÓRIZ¹⁾, BEATRIZ MARQUES²⁾ and FRANCISCO J. RODRÍGUEZ-TOVAR¹⁾

ABSTRACT

This paper analyses the relation between the eco-sedimentary dynamics, induced by relative sea level changes and the eco-evolutionary responses of the marine macro-invertebrate associations, especially ammonites. Analysis was made of cases recognized in materials from the Upper Jurassic (Oxfordian-Kimmeridgian) deposited on the South Iberian margin. Three orders of geo-biological interaction were recognized.

1) Major paleogeographical configurations to which the main physiographical features are related and which determine the large ecological differentiations.

2) In a determined ecological ambitus the influence of long term eustatic dynamics on the composition of the faunal associations is revealed; interaction between tectonics and eustatism is also considered, as is their ecological incidence over moderately long (10–12 m.y.) time intervals.

3) Geo-biological dynamics over intervals of 1–4 m.y., i.e. at the observational level of the third order depositional sequence. This permits consideration of the relations between eco-sedimentary evolution and the deviation of the associations in medium range ecostratigraphic intervals.

Eco-sedimentary control exists over the composition and variation of the macroinvertebrate associations. The critical volumes of the environment and the ecological parameters associated with them in each case seem to be determining factors. Thus relatively long period ecological effects are determined, giving rise to the complex relation between the eco-evolutionary dynamics of ammonites and the sedimentary breaks.

RÉSUMÉ

Dans ce travail, on analyse le rapport entre la dynamique éco-sédimentaire, induite par l'évolution du niveau relatif de la mer, et les réponses éco-évolutives des associations de macro-invertébrés marins, spécialement des ammonites. On a analysé des cas reconnus dans des matériaux du Jurassique supérieur (Oxfordien-Kimmeridgien) déposés dans la marge sudibérique. On a reconnu trois ordres d'interaction géo-biologique:

1) Configurations paléogéographiques les plus importantes auxquelles on relationne les caractéristiques physiographiques principales et on détermine les différenciations écologiques basiques persistantes.

2) Dans un «ecological ambitus» déterminé se révèle l'influence de la dynamique eustatique à long terme sur la composition des associations faunistiques; on considère également les interactions tectonique/eustatisme et leur incidence écologique dans des intervalles de période relativement longue (10–12 m.a.).

3) Dynamique géo-biologique au niveau de séquence de dépôt dans des intervalles de 1–4 m.a. Elle permet de considérer les rapports entre l'évolution éco-sédimentaire et la déviation des associations dans des intervalles éco-stratigraphiques de période moyenne.

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On conclue sur l'existence de contrôle éco-sédimentaire sur la composition et la déviation des associations de macro-invertébrés. On a trouvé également un rapport certain, mais pas simple, entre des ruptures sédimentaires (discontinuités) et la dynamique éco-évolutive des ammonites. Des facteurs déterminants semblent être les volumes critiques du milieu et les paramètres écologiques qui leur sont associés dans chaque cas. On détermine ainsi des effets écologiques de période relativement grande et de là le rapport complexe entre la dynamique éco-évolutive des ammonites et les discontinuités.

Introduction

Eustatism has taken on an increasing importance in the analysis of sedimentary successions, particularly because of the recognized influence it has on the sedimentary environment, inasmuch as we can deduce this environment at the present time (analysis of depositional conditions and associated processes). However, as VAIL and his collaborators have repeatedly pointed out, eustatism should be considered together with other geodynamic factors which affect the region under study for any fixed interval.

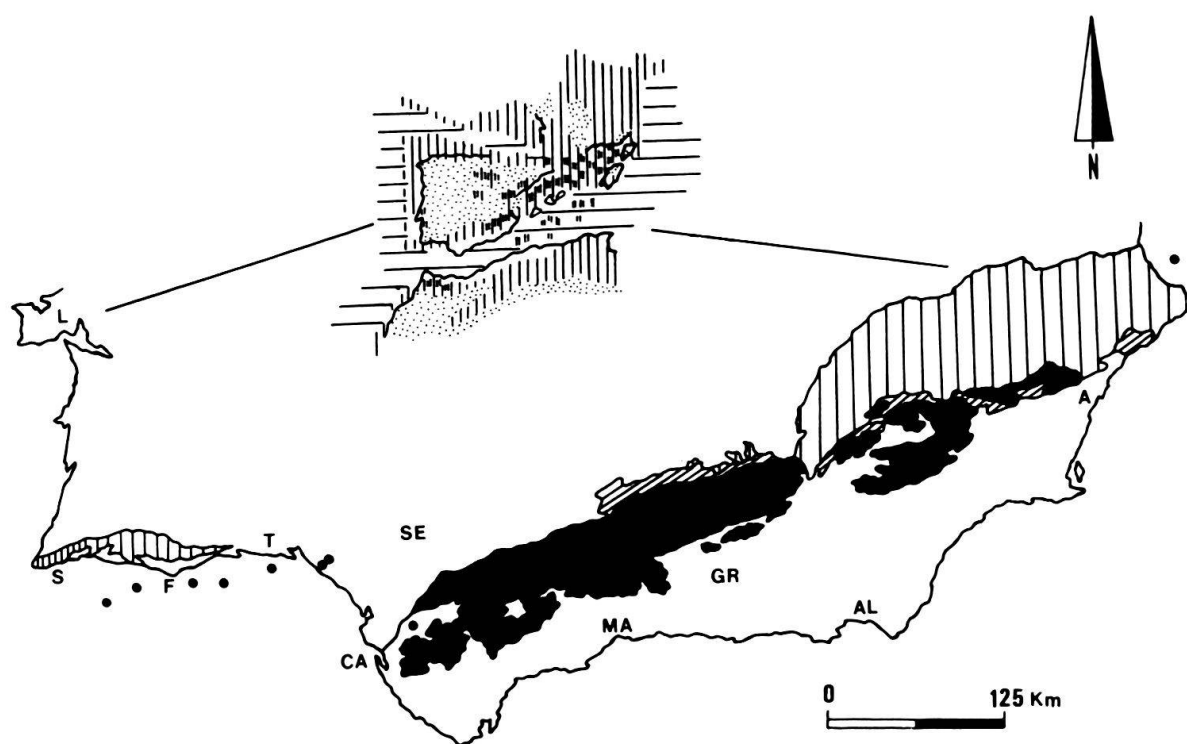
If we consider the climatic conditions during the Jurassic, it seems appropriate to relate eustatism with changes in the volume of the oceanic basins. MARQUES et al. (1989) have demonstrated the existence of different orders of interaction between tectonics and eustatism in the South Iberian margin during the Upper Jurassic (Fig. 1). In the 1970's, the relationship between global tectonics and eustatism had already been suggested in studies such as those by ROMA (1973), HAYS & PITMAN (1973), AGER (1973) and PITMAN (1978). It is significant that, in the publications of this time, reference was already being made to the impact which the interaction between tectonics and eustatism would foreseeably have on the biosphere and the atmosphere. Accordingly, it seems of interest to analyse the possible influence of the changes in relative sea-level, which are not exclusively eustatic, on marine macro-invertebrate associations. We have restricted ourselves to data obtained from the Upper Jurassic in the South Iberian margin for the purposes of this study.

In this paleomargin we found that the main difference between macroinvertebrate associations belonging to epicontinental areas and those from distal-pelagic swell areas was the scarce representation of benthic faunas in the latter (Fig. 2). Moreover, ammonite associations have been proved to fluctuate stratigraphically, whether or not benthic macroinvertebrates are present, and, on the whole, in inverse proportion to benthic faunas if these are present. Consequently we shall focus on the quantitative record of other macroinvertebrates against ammonoids, of which we only differentiate significant groups at different taxonomical level (Figs. 3, 4, 5, 6 and 8). We also pay special attention to ammonite faunas in order to provide biostratigraphy and correlations.

Eustatism and relative sea level. Ecological considerations

Two aspects related to eustatic dynamics and relative sea level, at each moment and in each area, are of particular interest in the analysis presented here: the sedimentary trends with their associated ecological variations, and the sedimentary discontinuities.

With no tectonic activity, the progradational sedimentary systems in the schemes of sequence stratigraphy (HAQ et al. 1987, 1988; VAIL et al. 1984, 1987 amongst others)



Above: epicontinental seas (shelf environments), very shallow and/or emerged areas, main land areas, oceanic environments.

Below: Eastern and Central Prebetic (right), Eastern and Western Algarve basins (left), Intermediate Units, Subbetic and lateral equivalents, • shelf environment sites (subsurface geology).

A= Alicante; AL= Almería; CA= Cádiz; F= Faro; GR= Granada; L= Lisboa;

MA= Málaga; S= Sagres; SE= Sevilla; T= Tavira.

Fig. 1. Present and paleogeographical distribution of upper Jurassic materials in the South Iberian margin.

should be related to regressive effects and, to a certain extent, to reductions in the area and the volume of the marine environment on shelves. In this scheme, the increase of ecological stress should affect the well adapted populations ("captured" cf. OLÓRIZ 1987) by means of the increase in the *Platform Effect* (OLÓRIZ 1985, 1987) which refers to deviations (variations) both in the phenotype variability and the composition of faunal spectra when the ecological environment fluctuates (for examples from the South Iberian margin see OLÓRIZ et al. 1988 and Fig. 3). Also, in the absence of tectonic activity, the aggradational systems in the schemes of sequence stratigraphy should be related to transgressions and, to a varying degree according to the association considered, with increases in the environmental volume. The relation of this process to the *Platform Effect* (OLÓRIZ 1985, 1987) may vary, and it is also possible that the ecological stress selectively increases for peripheral faunas in cases of biogeographical

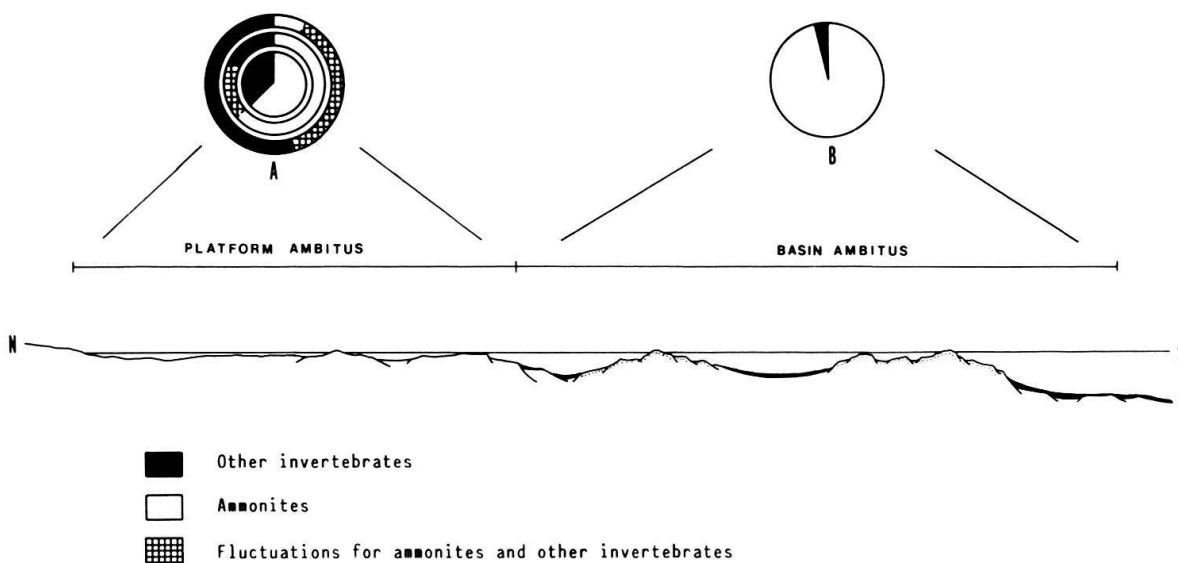


Fig. 2. Idealized physiographical section of the South Iberian margin during the upper Jurassic with differentiation of the two basic ecological environments.

A) Epicontinental areas with dominant marl-limestone rhythms, local buildups and shallow carbonate banks; episodically and areally restricted sandy and conglomerate levels. Westward a carbonate platform is well recognized in the Algarve (S. Portugal). Epicontinental areas belong ecologically to the *Platform Ambitus*.

B) Distal pelagic margin with comparatively shallow and locally emerged swells where ammonitico rosso and associated facies dominated; in low areas siliciclastics and/or turbidite sediments developed, with or without siliceous components ("radiolarites"), and conglomerates/breccias close to high areas. Distal-pelagic-swallow areas belong ecologically to the *Basin Ambitus*.

Diagrams represent faunal spectra for macroinvertebrates: The only diagram in B alludes to homogeneous composition of the faunal spectra during the Oxfordian and lower Kimmeridgian. In A the inner diagram represents the faunal spectrum for the upper Oxfordian (Bimammatum-Planula Zones); the intermediate diagram shows the standard composition for the lower Kimmeridgian (Platynota Zone), and the external diagram displays the same for the Hypselocyclum Zone (lower Kimmeridgian).

expansion and colonization of marginal areas. The latter reveals a relation which is not simple, but rather specific according to the faunal group under consideration, between the total area and volume of the platform environment at a given moment and the rate of the *Platform Effect* at that same moment.

If we consider the extra effect of tectonic disturbance, the scheme becomes more complex, but can practically be reduced to the simplification of two extreme cases:

- a) the tectonic distortion reinforces the eustatic trend, and
- b) the tectonic distortion reduces or counteracts the eustatic trend, and even goes so far as to invert the sedimentary trend.

In both cases secondary distortions or variations may appear linked, for example, to the new rate of siliciclastic inflows etc., which would mean a possible deviation of the *Platform Effect* in the epicontinental environments. In distal environments, the ecological fluctuations linked to these phenomena would be comparatively subtle and therefore there was environmental stability as far as vagile faunas are concerned, benthic faunas being directly affected only by major relative sea level falls or indirectly by related effects (Fig. 2).

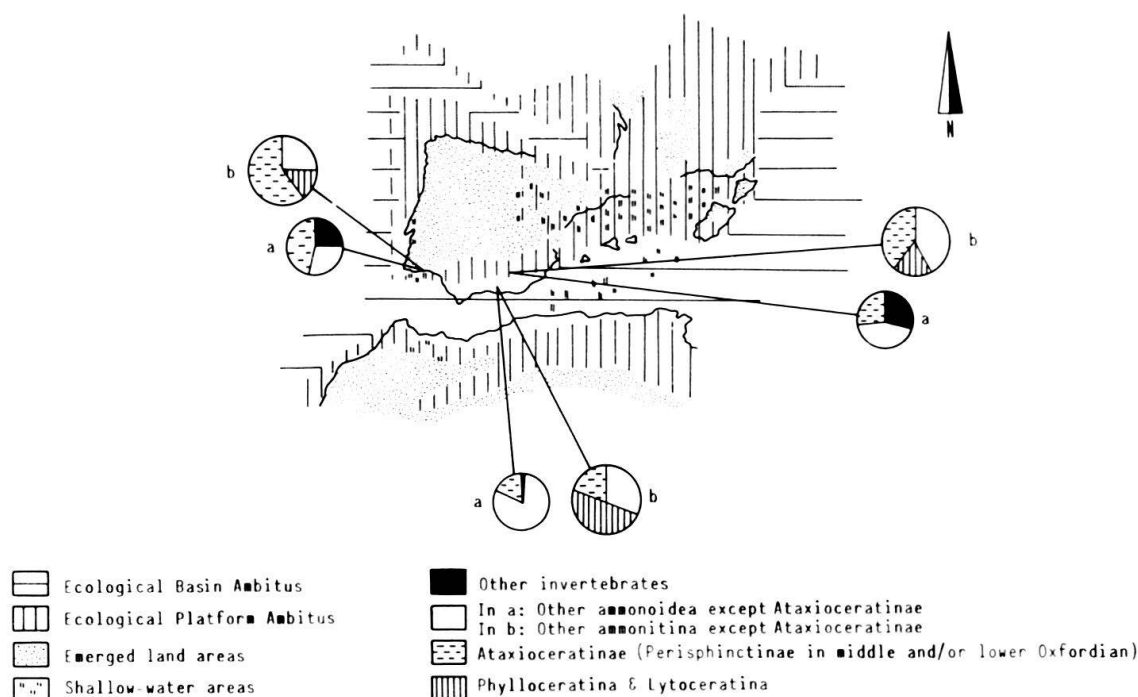


Fig. 3. Paleogeography, ecological configuration and faunal spectra in the South Iberian margin during the lowermost Kimmeridgian (Platynota Zone).

With regard to the unconformities/discontinuities, these being considered according to MARQUES et al. (1989), the interest lies in their relation to possible changes in the previously recorded sedimentary trend (i.e. inversions or changes of intensity in the aggradational/progradational trends) and/or in relation to the magnitude of the associated hiatuses. In comparatively distal sites, in which the unconformities *sensu lato* may be progressively reduced, the incidence of their causal factors may be evaluated by means of the ecological sensitivity of the associations subject to the new eco-sedimentary conditions.

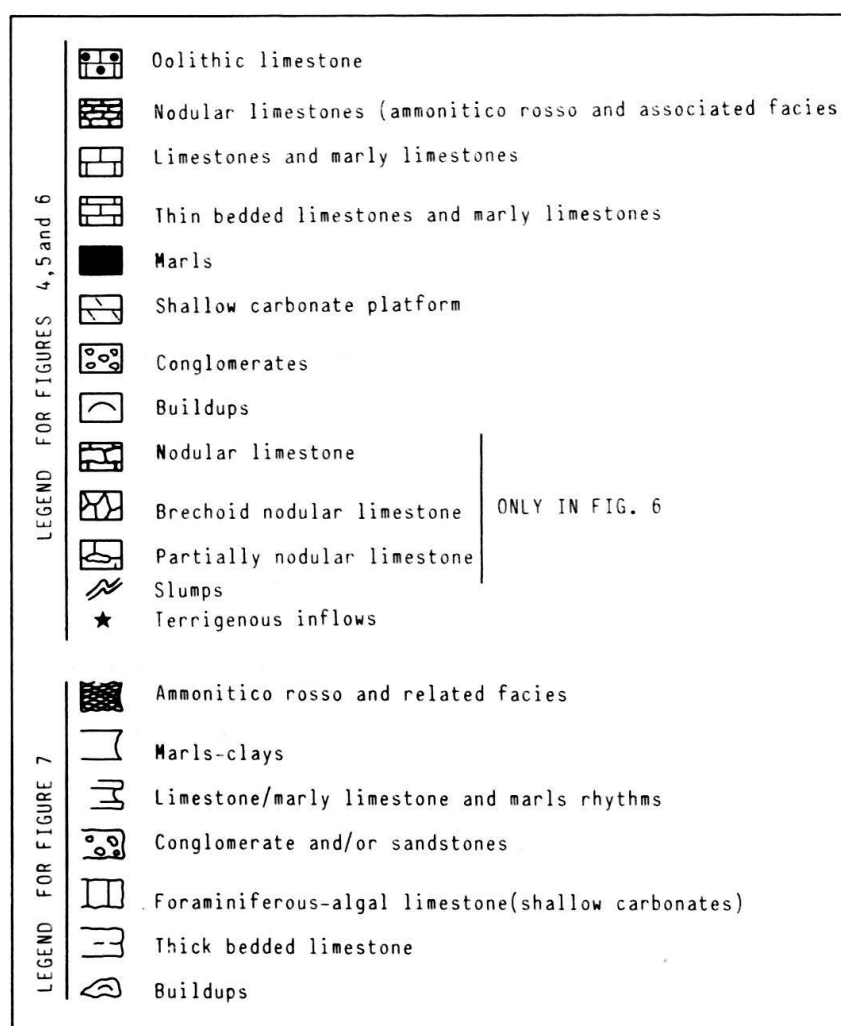
The eco-sedimentary context in the South Iberian Paleomargin

To deduce an eco-sedimentary context it is necessary to recognize the general paleogeography and stratigraphy of the area under study, as well as to have sedimentological, taphonomic and paleoecological data. With regard to the South-Iberian paleomargin, a recent and synthetic view was given by VERA (1988). The general stratigraphy and biostratigraphy of the Oxfordian and the Kimmeridgian (up to the Acanthicum or Compsum Zones) are known from the papers by BEHME (1970), AZEMA et al. (1971), LÓPEZ-GARRIDO (1971), JEREZ-MIR (1973), SEQUEIROS (1974), OLÓRIZ (1978), SEYFRIED (1978), GARCÍA-HERNÁNDEZ et al. (1979), SEQUEIROS & OLÓRIZ (1979), OLÓRIZ & TAVERA (1981) and MARQUES (1983, 1985). A synthetic view from standard profiles is given in Figs. 4, 5, 6 and 7. More recent biostratigraphical papers only provide minor adjustments to the biostratigraphy previously proposed by these authors (Tab. 1). Concerning the sedimentology of the Oxfordian and Kimmeridgian,

the papers by SEYFRIED (1978, 1979, 1980, 1981), COMAS et al. (1981), GARCÍA-HERNÁNDEZ et al. (1981), MARTÍN-ALGARRA (1987), MOLINA (1987) and GARCÍA-HERNÁNDEZ et al. (1988a) are relevant.

Given that there exists a general consensus on depositional conditions and the ecological environment to which the Tethyan ammonitico rosso and associated facies belonged (for recent comparative studies with other equivalent facies from the Paleozoic cf. WENDT et al. 1984), we shall concentrate on the taphonomy of the fossil associations collected from the epicontinental platforms, where the heterogeneity of the ecological and sedimentary environment was undoubtedly greater.

The levels on which the epicontinental ammonites were collected are rhythmic successions of mudstones with intercalations of marls and, occasionally, of wackstones. No gradations were observed, nor were structures due to currents nor coquina beds or preferential orientations of the bivalves. The average sedimentation rate fluctuated between 10 and 85 mm/10³ years in the Platynota Zone, in which the majority of the samples for taphonomical observations were obtained. As an usual practice, we con-



Legend to Figs. 4-7.

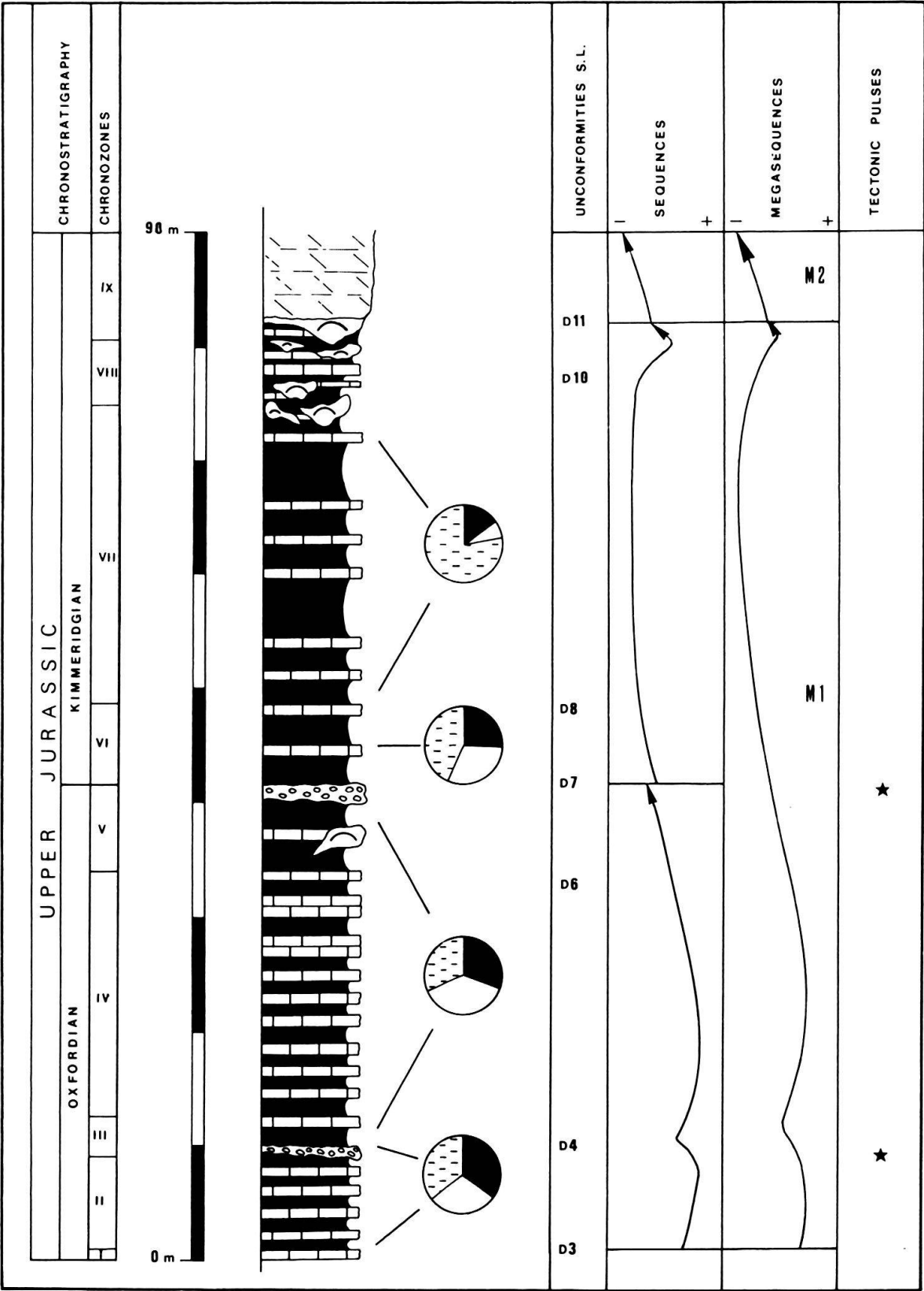


Fig. 4. Synthetic profile for middle Oxfordian to lower upper Kimmeridgian (Acanthicum Zone) in medial parts belonging to epicontinental shelves of the SW Iberian margin (East-central Algarve, Portugal).

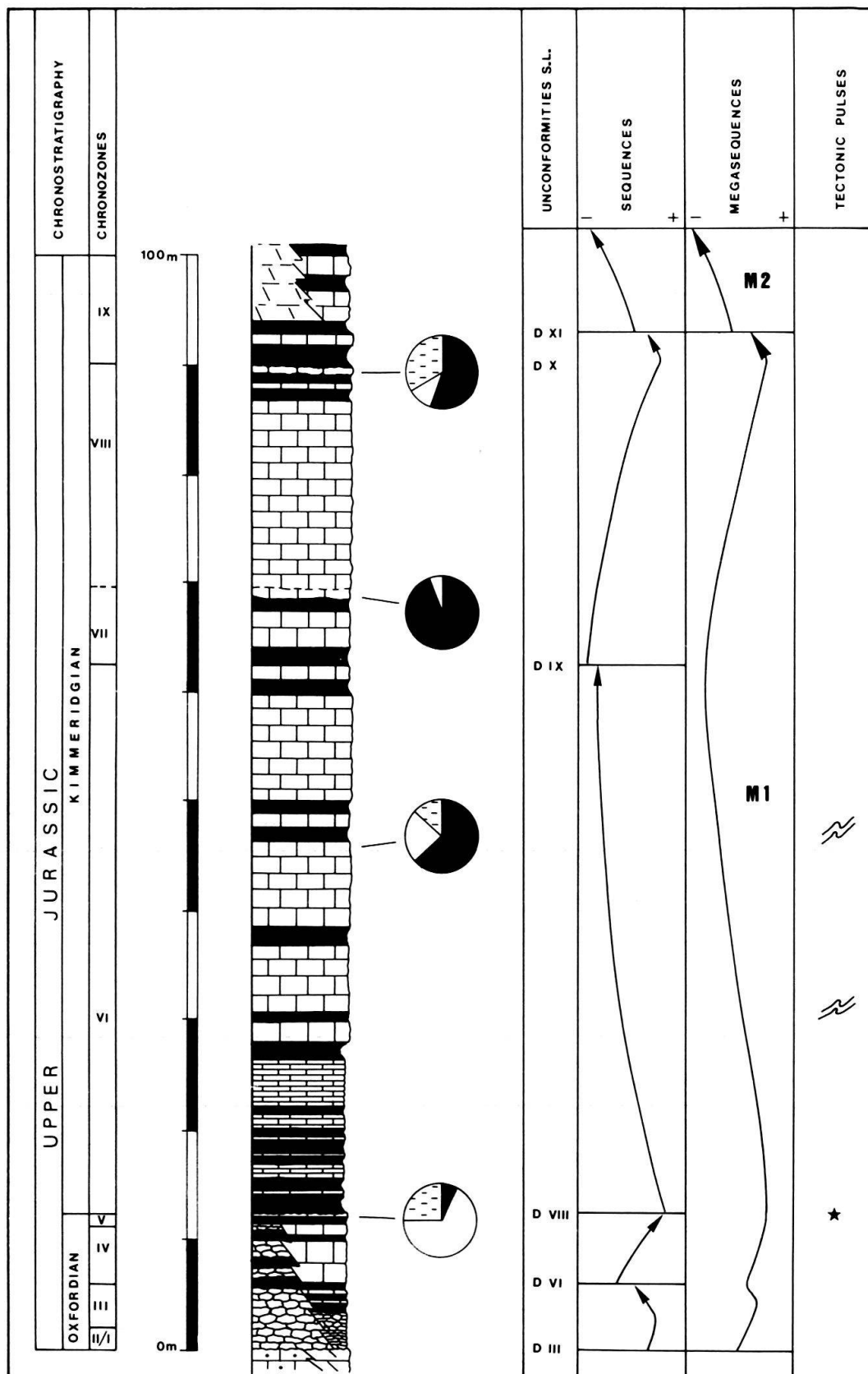


Fig. 5. Synthetic profile for middle Oxfordian to lower upper Kimmeridgian (Acanthicum Zone) in medial parts belonging to epicontinental shelves of the Central sector of the Prebetic Zone (S. Spain).

sider firstly the duration for all the Kimmeridgian (*sensu gallico* = 4×10^6 years), then we divided by the number of chronozones (6), and finally we obtained a duration of 700.000 years aprox. per chronozone. All of this can only be accepted by considering a constant time-duration for Kimmeridgian chronozones. The next step was to obtain the ratio thickness/700.000 years, again considering a “constant” sedimentation rate through the analysed chronozone.

The fossils (ammonites, bivalves, gasteropods and others in lesser proportion) are mainly preserved as internal casts. Fragmentation is infrequent, except in the ammonites, where it is selective, affecting more often larger size serpenticones and pla-

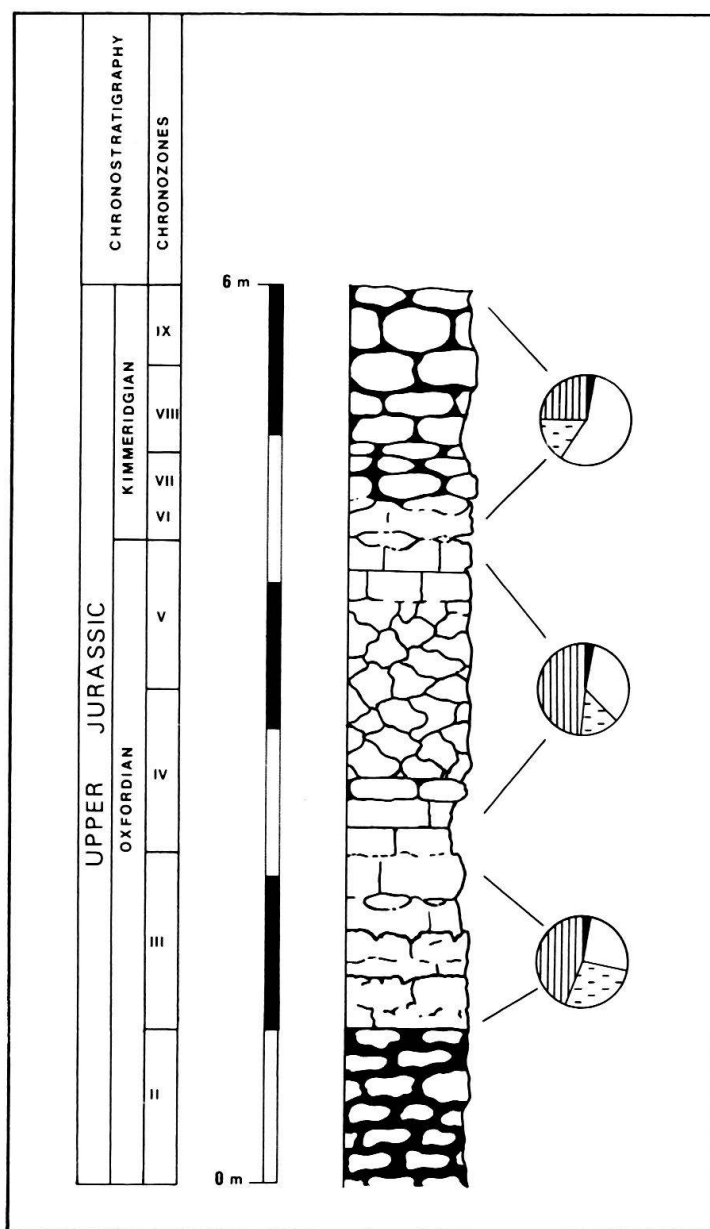


Fig. 6. Synthetic profile for middle Oxfordian to lower middle Kimmeridgian (Compsum Zone = lower upper Kimmeridgian, Acanthicum Zone, in shelves) in distal-pelagic-swell areas of the Subbetic Zone (S. Spain).

nulates (Ataxioceratinae, *Nebrodit*es and related forms), but forms with delicate and pedunculate peristome (*Sutneria*, *Glochiceras*) were usually preserved. The orientation of the fossil remains is parallel/subparallel to bedding in the larger size ammonites, but diverse orientations are frequent in smaller forms. Hyporeliefs of vermiform epizoa were sometimes observed, as too were serpulids and, occasionally, small ostreids adhering to the upper flank of the ammonite casts. Serpulids were only found once in the ventral region of a macroconch with a 50 mm thick whorl section. With regard to

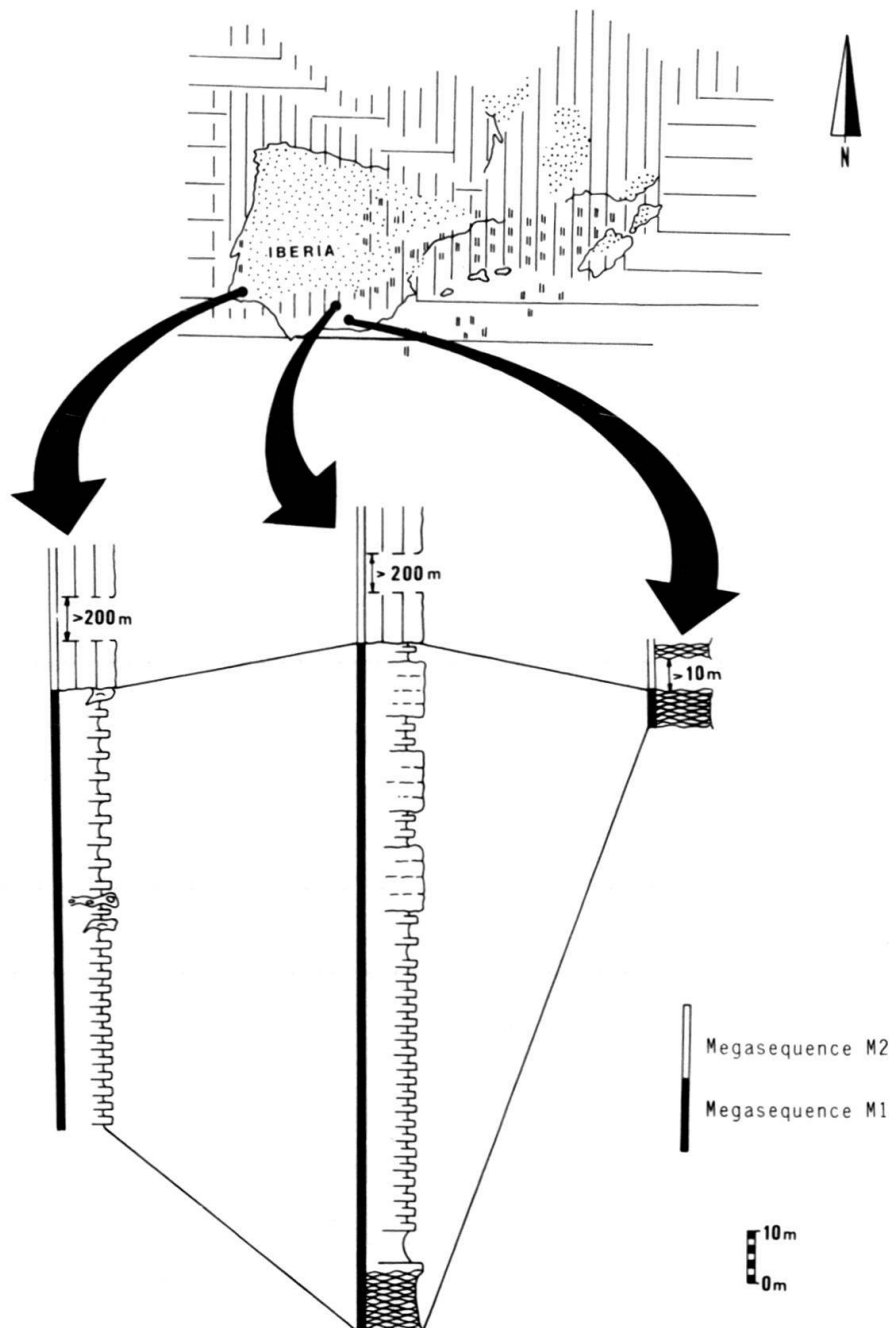


Fig. 7. Correlations of megasequences in synthetic profiles from the South Iberian margin.

Table 1: Significant ammonites, chronostratigraphy and correlations.

	CHRONOSTRATIGRAPHY			SIGNIFICANT AMMONITES. ONLY SOME SPECIES ARE MENTIONED. REFERENCES TO FAMILIES/SUBFAMILIES OR GENERA IN CASES OF ABUNDANT RECORD.
	EPICONTINENTAL AREAS	DISTAL-PELAGIC-SWELL AREAS		
KIMMERIDGIAN	ACANTHICUM	COMPNUM	IX	Aspidoceras acanthicum; Taramelliceras compsum; Orthaspidoceras; Nebrodites; Mesosimoceras; Aspidoceratidae; Physodoceratinae.
	UHLANDI	UHLANDI	VIII	Crussoliceras divisum; Garnierisphinctes; I. trachynotum; Orthaspidoceras uhlandi; Idoceras balderum; Ceratospinctes rachystrophus; Nebrodites; Mesosimoceras; Aspidoceratidae; Physodoceratinae.
	DIVISUM	DIVISUM		
	HYPSELOCYCLUM	STROMBECKI	VII	Ataxioceras Hypselocyclum; Metahaploceras strombecki; Parataxioceras gr. lothari; Lithacosphinctes Nebrodites; Mesosimoceras; Metastrebiles; Physodoceratinae; Aspidoceratinae.
	PLATYNOTA	PLATYNOTA	VI	Sutneria platynota; Orthosphinctes polygyratus; Ardesia; Schneidia; Physodoceras altenense; Parataxioceras; Lithacosphinctes; Nebrodites; Aspidoceras; Metahaploceras.
	PLANULA	PLANULA	V	Subnebrodites planula; S. minutum; Sutneria galar; Orthosphinctes; Lithacosphinctes; Taramelliceras; Metahaploceras gr. wenzeli; Metahaploceras; Geyssantia; Enayites.
OXFORDIAN	BIMAMMATUM	BIMAMMATUM	IV	Epilloceras bimammatum; Euaspidoceras hypselum; Praetaxioceras; Lithacosphinctes; Pseudorthosphinctes; Orthosphinctes; Enayites; Euaspidoceras; Ochetoceras marantianum; I. hauffianum; Metahaploceras; Aspidoceratinae; Physodoceratinae; Glochiceratidae.
	BIFURCATUS	BIFURCATUS	III	Dichotomoceras bifurcatus; Gregoriceras fouqueti; Passendorferia; Dichotomosphinctes; Subdiscosphinctes; Mirospinctes gr. bukowskii; Ochetoceras hispidiforme; Euaspidoceras.
	RIAZI/TRANSVERSARIUM	RIAZI	II	Gregoriceras riazii; G. transversarium; Arisphinctes; Dichotomosphinctes elisabethae; D. wartae; Subdiscosphinctes; Otophinctes birmensdorfensis; Perisphinctes (s.str.); Euaspidoceras.
	ANTECEDENS	ANTECEDENS	I	Dichotomosphinctes antecedens; Arisphinctes plicatilis; Kranaosphinctes; Iornquistes; D. wartae; Cardioceras; Oppeleidae.
<p>○ Only recorded from epicontinental areas.</p> <p>● Only recorded from distal-pelagic-swell areas.</p>				

the possible paleoecological interpretation of the faunal spectra obtained, the extremely scarce record of aptychi (0.4–0.6%) even in ammonite dominant associations is particularly interesting. Traces of stratigraphic contamination (mixing of faunas from different stratigraphic horizons) were not encountered in any instance, not even in ranges within the ammonite horizon (150.000 years approximately). No cases were found of internal casts whose facies was different to that of the rock containing them, nor of associations in which some type of component were selectively colonized by epizoa, or, on the other hand, exempt of them, or showed different phases of colonization, all of which could be interpreted as an indication of reworking and procedence different to that of the place in which the association was found.

In the condensed levels on the platforms (terminal Oxfordian and terminal lower Kimmeridgian) the only signs of reworking (internal casts of different composition to the rock which contains them) were detected at intra-zonal level in the terminal Oxfordian. This was not identified in the condensed levels of the lower Kimmeridgian. Specimens with peristome are preserved in these levels and the fragmentation of the fauna is associated with a prolonged exposure of the accumulation of shells due to the low rate of sedimentation; sedimentary load effects previous to lithification brought about the interpenetration of some ammonites.

In general, on the epicontinental platforms and in a sedimentary context of low energy near the sea-floor, taphonomic analysis allows the interpretation that the accumulation of fossil remains took place on soft bottoms without important resedimentation events. The shells were in some cases colonized before burial, for which we only have evidence of the occupation of the interior of the living chambers when their position was subhorizontal. With a maximum average sedimentation rate of 1 mm/year, common events of winnowing uncovered the casts occasionally allowing their colonization, mainly by serpulids.

In this context, the virtual absence of aptychi among the material collected is of special significance. We interpret this as a sign of limited transport of the ammonites before their fall to the sea-floor. Given that the bivalves are abundant and that there is no evidence of considerable transport, we interpret that the shells of the ammonites were deposited, in general, in an area more proximal than that in which they lived on the platform. Following a presumably short period of necroplanktonic drifting, the importance of this is consequently that, in the possible paleoecological interpretation of the faunal spectra obtained, the evaluation of the depth may reasonably become closer to the lesser values of the interval indicated in traditional models (e.g. ZIEGLER, 1967).

Studies dealing with Upper Jurassic paleoecology in the South Iberian paleomargin are rare, probably because of the scarcity of significant benthic faunas in the well-known ammonitico rosso facies so widely developed in the Subbetic Zone (Figs. 2, 3, 6 and 8). Moreover, paleoecological studies on epicontinental shelves of Southern Iberia are recent and only focus on more or less local buildups (ROSENDAHL 1985, 1988) and there is no accurate (systematic) information about the generally poorly preserved benthic faunas outside reefal sites.

In this context, and in an attempt to recognize ecostratigraphical models in the Upper Jurassic of the South Iberian margin, quantifications of more than 12.000 ammonoids with minor numbers of benthic faunas were reported by SEQUEIROS &

OLÓRIZ (1979) and OLÓRIZ & TAVERA (1981) from the Subbetic Zone. MARQUES & OLÓRIZ (1988a) characterized the Oxfordian and the Kimmeridgian, up to the Acanthicum Zone, in the Algarve with 1.500 ammonites and mainly bivalves among the other invertebrates, the ammonites being biostratigraphically controlled according to MARQUES (1983). A comparison of the epicontinental records from East Iberia and East-Central Algarve with those from the Subbetic which characterize the standard for the Platynota Zone was given by OLÓRIZ et al. (1988) on the basis of a sample of slightly more than 1.000 specimens (Fig. 3).

All the preceding information provides a reliable basis on which to consider eco-sedimentary frames which developed in the South Iberian paleomargin during the Oxfordian and the Kimmeridgian before the beginning of the shallow carbonate shelf phase which characterizes uppermost Jurassic sedimentation on epicontinental areas surrounding Iberia (for South Iberia see Fig. 7). Even at a more general level, the analysis of benthic invertebrates and those others which lived at differing heights in the water column requires the consideration of ecological and depositional factors. While the ecological factors will affect, by their very definition, the totality of the associations, the depositional conditions will necessarily have a greater impact on the benthic faunas and those others which, in one way or another, are most related with the sea bottom. Therefore, the more disconnected the way of life is from the sea bottom, the more secondary or indirect the influence of the depositional conditions on the fauna under consideration will be.

In studies such as this, it is standard practice to deduce the ecological configuration mainly from the composition of the faunal (and floral) associations, due to the difficulties entailed in the record of the purely physical ecological factors. On the other hand, the depositional conditions are better known and allow reconstructions of the sedimentary environments, which are comparatively more reliable since they include more general geological and paleontological data. We therefore control faunal spectra both stratigraphically and geographically as quoted below.

In order to obtain an integrated vision of environmental evolution in relation to the relative changes in sea level, MARQUES et al. (1989) have recently recognized the importance of ecological and sedimentary differentiation in the South Iberian margin during the Upper Jurassic. Basically, it is interesting to distinguish between *epicontinental platforms* and *distal pelagic swell areas* (Figs. 1 and 2), which coincide well with the two major ecological subdivisions of the Upper Jurassic marine environment, the *Platform Ambitus* and the *Basin Ambitus* respectively, the latter being distal areas subjected to comparatively oceanic ecological conditions (OLÓRIZ 1985, 1987). In both these regions of the margin the depositional and ecological conditions, the stability of the sea floor and, finally, the sedimentary environment, were significantly different. As a result, both the macro-invertebrate associations and the traces of the relative changes in sea level were also different.

In the *epicontinental platforms* (Algarve and the Prebetic Zone) the sedimentary environment was comparatively well supplied by siliciclastic inflows in proximal and medial areas (Figs. 4 and 5). In distal areas, the productivity of carbonates was frequently high. Topographical differentiations of the sea floors are easily recognizable and at times caused more or less persistent ecological differentiations (MARQUES & OLÓRIZ 1988a, MANUPELLA et al. 1988). The macro-invertebrate associations (particu-

larly ammonites) correspond to the submediterranean type (GARCÍA-HERNÁNDEZ et al. 1979, MARQUES 1983). The regions subjected to this ecological-depositional regime correspond to examples of the *Platform Ambitus sensu* OLÓRIZ (1985), whose dynamics have begun to be studied in detail (OLÓRIZ et al. 1988, MARQUES & OLÓRIZ 1988a and continuing research by the authors). In epicontinental areas of the South Iberian paleomargin we counted 3.000 specimens, biostratigraphically controlled at ammonite intra-biozone level in the central Prebetic, the sector in which a fine biostratigraphy was obtained. From the Algarve we quantified 1.500 specimens previously studied by OLÓRIZ et al. (1988) and MARQUES & OLÓRIZ (1988a) according to the biostratigraphy by MARQUES (1983) with only slight modifications. Therefore, a total sample of 4.500 specimens belonging to the *Platform Ambitus* has been studied.

In the *distal pelagic swell areas* (Subbetic Zone) the rate of sediment supply was very low, and the sedimentary successions are thin (Figs. 6 and 7), even though the productivity of carbonates was locally high in shallow enclaves. The topographical differentiation was a noteworthy and characteristic feature (SEYFRIED 1978, COMAS et al. 1981 and MARTÍN-ALGARRA 1987 amongst others). The ecological environment was comparatively stable and the macroinvertebrate associations, which are especially dominated by ammonites with poor representation of other groups (Figs. 2, 3, 6 and 8), corresponded to the Mediterranean type *sensu stricto*. The regions of the South Iberian margin subjected to this type of ecologic-depositional regime correspond to examples of the *Basin Ambitus* occupied by representatives of the *Distal Association* (OLÓRIZ 1985). A sample of slightly more than 7.000 specimens (SEQUEIROS & OLÓRIZ 1979, OLÓRIZ & TAVERA 1981) has been taken into account to characterize

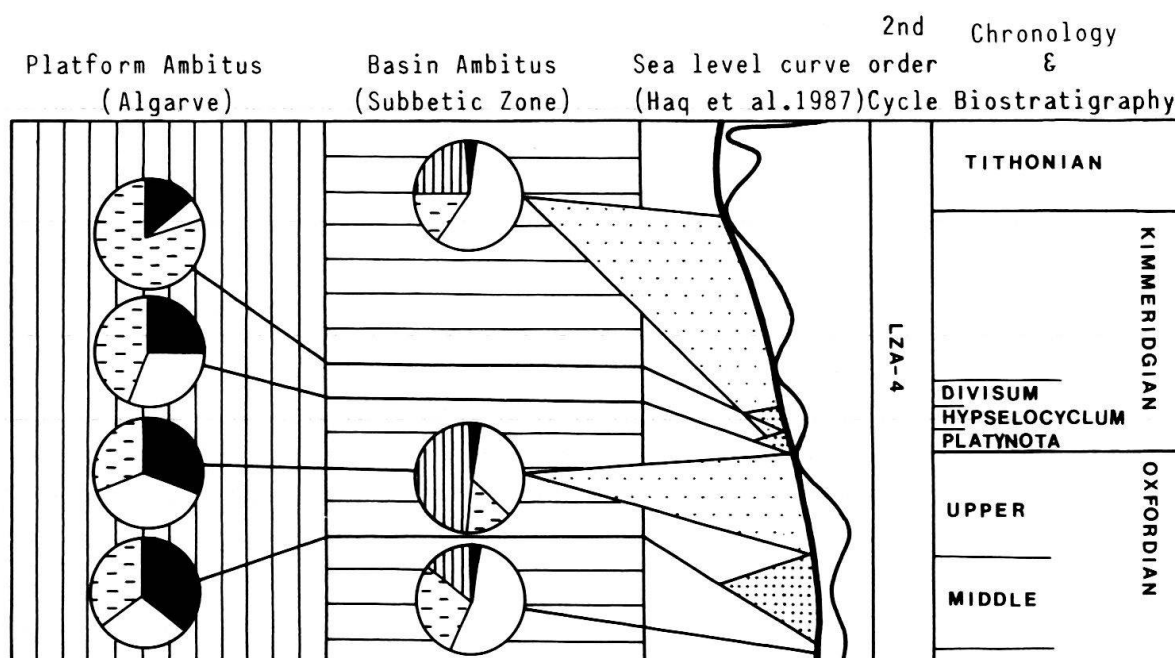


Fig. 8. Long Term eustatic curve for supercycle LZA-4 and average diagrams for faunal spectra. *Platform Ambitus* data from MARQUES & OLÓRIZ (1988a); faunal representation as type *a* diagram in Fig. 3. *Basin Ambitus* data from SEQUEIROS & OLÓRIZ (1979) and OLÓRIZ & TAVERA (1981); faunal representation as type *b* diagram in Fig. 3. Dotted for the referred time interval (dense for Algarve and sparse for Subbetic). LZA-4 (only mainly conserved part in the South Iberian margin is represented).

macroinvertebrate associations of the Oxfordian and the Kimmeridgian up to the Compsum Zone in this ecological environment.

As a whole, the eco-sedimentary context described above reveals, potentially at least, certain difficulties for the detailed correlation of both the traces of the relative changes in sea level and the evolution of the macro-invertebrate associations, the latter is particularly complicated by the differing rate and continuity of sedimentation.

Sequence stratigraphy and faunal associations in the South Iberian Margin during the Oxfordian and Kimmeridgian. Some remarks

Integrated stratigraphical studies on materials of the Upper Jurassic in the South Iberian margin have been undertaken in recent years (GARCÍA-HERNÁNDEZ & LÓPEZ-GARRIDO 1988, LÓPEZ-GARRIDO & GARCÍA-HERNÁNDEZ 1988, OLÓRIZ et al. 1988, MARQUES & OLÓRIZ 1988a, 1988b, MARQUES et al. 1989). Significant unconformities and third order depositional sequences have been characterized and the general features of the geo-biological evolution at different levels have been recognized by the authors (Figs. 4 and 5).

In this paleomargin, outcrops belonging to distal-pelagic-swell areas (first studied by BEHME 1970, SEQUEIROS 1974, OLÓRIZ 1978, SEYFRIED 1978, MARTÍN-ALGARRA 1987) in which ammonitico rosso facies are developed (Fig. 6), make it difficult to recognize the system tracts of the 3rd order depositional sequences. In the outcrops belonging to relatively medial epicontinental areas in the Algarve and the Prebetic Zone (Figs. 4 and 5), previously described by LÓPEZ-GARRIDO (1971), GARCÍA-HERNÁNDEZ et al. (1981), MARQUES (1983), MARQUES et al. (1989) and ACOSTA (1989), the sedimentary successions are composed of the *transgressive system tract* and a progradational complex made up of the *high stand system tract* and the *proximal part of the shelf margin wedge system tract* according to MARQUES et al. (1989). This also agrees with the frequently subtle record of discontinuities and unconformities. On the whole, the relatively reduced area for observations, in particular land-outcrops, also impedes immediate recognition of the geometrical downlap surfaces. In the light of the foregoing, it seems appropriate to proceed according to the "*procedure inverse*" of VAIL et al. (1987) when the sedimentary materials are rich in guide-fossils (e.g. ammonites). The recognition in detail, timing included, of minor surfaces (e.g. parasequence boundaries) is now beginning to be obtained. For the moment, in any case, we can only deal with general aspects of the mutual significance of sequence stratigraphy analyses and the preserved macro-invertebrate associations according to the recorded spectra. The context of studies belonging to this approach is that of geobiological evolution and, specifically, the eco-stratigraphical aspects. A hierarchization in three orders has been found to be significant.

First order: In the South Iberian margin, as in any other continental margin, the first order geo-biological frame of reference corresponds to the major paleogeographic configurations, that is to say, the major features of the physiography.

1) the *epicontinental platforms* (the Algarve and the Prebetic Zone) occupied relatively shallow regions in proximal position, with a complete eco-sedimentary gradation in an onshore-offshore direction, as proved by lithofacies and macroinvertebrate changes linked to relative sea level fluctuations (see Figs. 2, 4, 5, 8 and 9); deviations of

the general trend were induced by minor morphological features (cf. ALMERAS & ELMÍ 1981, for examples from the Lower and Middle Jurassic in the NW margin of Africa),

2) *distal regions of the margin*, in which, although the low areas (at times "gout-tieres") would foreseeably be clearly deeper than the epicontinental ones, the high ones (distal-pelagic-swells) were frequently found in the medium range of the depths reached on the platforms, and there would also be really shallow, and even emerged enclaves ("oceanic islands"). This abrupt bottom topography was induced by block tectonics which determined regional instability in the Subbetic Zone, including local emersions, both ephemeral and persistent, during the Upper Jurassic as admitted by, or deduced from, SEYFRIED (1978, 1979, 1980, 1981), COMPANY et al. (1982), MARTÍN-ALGARRA et al. (1983), VERA et al. (1984, 1988), GARCÍA-HERNÁNDEZ et al. (1986, 1988b), VERA (1988), VERA & MARTÍN-ALGARRA (1989) and RUÍZ-ORTIZ et al. (1990) among others. This is a well known feature in the Mediterranean Tethys; for Italy see, for example, FARINACCI et al. (1981), CECCA et al. (1981) and CECCA & SANT-ANTONIO (1986), and for regions in the North West African paleomargin see EL KADIRI et al. (1989). For comparisons with paleozoic equivalents see WENDT et al. (1984).

In this context, the major environmental differentiations were not directly or essentially related to the depth, but to the basic characteristics which define sea water types (*sensu* VALENTINE 1973). In response to this basic ecological differentiation on the continental margin and surrounding areas, the marine macro-invertebrate associations reacted with spectra of clearly differentiated composition (Figs. 2 and 3), both in the percentages, at the subfamily level (cf. OLÓRIZ et al. 1988), and even in the phenotypical expressions at the genus and/or species level, giving support, therefore, to the differentiation of the so-called Submediterranean and Mediterranean associations (SEQUEIROS 1974, OLÓRIZ 1978, GARCÍA-HERNÁNDEZ et al. 1979, MARQUES 1983) which are, respectively, examples of the *Proximal Association* and the *Distal Association sensu* OLÓRIZ (1985, 1987).

In this geo-biological context (geological configuration or physiography which imposes different eco-evolutionary scenarios), eustatic dynamics, in sporadic interactions with tectonic events, will determine the expansion-contraction of the ecospace, and will have a lesser ecological impact the greater the initial eco-sedimentary volume. An example in the ammonite faunas is the maintenance of conservative phenotypes in the perisphinctoids of the Mediterranean association *sensu stricto*, or *Distal Association sensu* OLÓRIZ (1985, 1987), during the Kimmeridgian phases of sedimentary progradation, during the Platynota Zone and the Hypselocyclum Zone, or during the middle Kimmeridgian (= upper Kimmeridgian *sensu gallico* below the Beckeri Zone, cf. OLÓRIZ & TAVERA 1981), in which significant eco-evolutionary processes took place in the associations occupying the platforms.

The parallelism of evolutionary sequences, with minor deviations, is particularly interesting in forms subjected to similar ecological trends on different platforms, as shown by sequence stratigraphy analyses. Thus, a regressive trend can be recognized on the Iberian shelves (Lusitanian Basin, Algarve, Prebetic Zone and Iberian Chain), S.E. France and Morocco during the lower Kimmeridgian, and the same evolutionary pattern is recorded for ammonite faunas (Ataxioceratinae) in the same areas, with only local and secondary deviations (GARCÍA-HERNÁNDEZ et al. 1979, ATROPS 1982, MAR-

QUES 1983, MOLINER & OLÓRIZ 1984, ATROPS & MARQUES 1986, OLÓRIZ et al. 1988, MARQUES & OLÓRIZ 1988a, 1988b, BENZAGGAGH 1988). It is open to discussion whether the record of the same general pattern in the evolution of ammonite faunas on different, and sometimes distant, areas is mainly the effect produced by migrations or whether this rather reveals parallel evolution phenomena, or both. As in the case referred to here (Ataxioceratinae of the lower Kimmeridgian), the record of both the ubiquitous ancestral *Orthosphinctes* and the same succession of genera in all the mentioned shelves is more parsimoniously interpreted as revealing parallel *in situ* evolution; migrations or faunal expansions being necessary when unfavourable phases for ammonites sporadically developed during the time interval in which the studied ammonite association existed.

The rôle played by the disconnections with regard to the open-sea waters of the Tethys, and which would presumably have been favoured during intervals of relative low sea level, is especially interesting. Figure 3 shows the intermediate composition of the association of the central sector of the Prebetic versus those of the Algarve (also belonging to epicontinental areas of the *Platform Ambitus*) and the Subbetic (distal-pelagic-swell areas belonging to the *Basin Ambitus*).

Second order: At a lower order, it is interesting to analyze the possible relations between the sedimentary trend induced by the relative sea level and the deviations of the associations. We are basically in agreement with BROCHWICZ-LEWINSKI & ROZAK (1981) that the observations at the stage level conceal the comprehension of the ecological dynamics typical of shorter intervals. However, at this level, data may be obtained on ecological behaviour at the level of supercycle or second order eustatic cycles in HAQ et al. (1987, 1988) and VAIL et al. (1987). In this case, the eustatic profile of reference will be the long term curve, to which the regional tectonic effects will have to be added.

If we therefore consider the LZA-4 supercycle of HAQ et al. (1987), which corresponds approximately to the Oxfordian-Kimmeridgian interval of increasing eustatic level (long term), we can observe (Fig. 8) the deviations in the associations in a particular ecological ambitus (*sensu* OLÓRIZ 1985). The basic ecological conditions which define the ecospace at this level should remain unaltered during the chosen interval of time. This is the case of the *Basin Ambitus* (distal-pelagic-swell areas of the South Iberian margin = Subbetic Zone). In this ecological ambitus, the spectra provided by SEQUEIROS & OLÓRIZ (1979), with a progressive increase of the Phylloceratidae, can be well related to the eustatic trend (long term) during the Oxfordian. Even at this level of a relatively long period, the quantifications can show deviations from the expected trend if only the eustatic factors were taken into account. This is the case of the Phylloceratidae in the total quantifications presented by OLÓRIZ & TAVERA (1981) for the Oxfordian-Kimmeridgian on a sample of more than 5.000 ammonites (see Fig. 8).

It is clear that for a correct interpretation of the deviations of the associations in relatively long intervals of time, it is most important to consider the evolutionary phase in which the group under consideration is found, in addition to the relative sea level, rather than the eustatic level alone. A good example of the application of these considerations is offered by the Taramelliceratinae for the same interval of time (Oxfordian-Kimmeridgian) in the Subbetic Zone according to the data by OLÓRIZ & TAVERA (1981).

Consequently, as recently suggested by MARQUES et al. (1989) for the eco-sedimentary evolution of the South Iberian margin during the Upper Jurassic, the rôle of the interactions between tectonics and eustatism is clear at this level of observation. In a relatively long interval of time (10–12 m.y.) with an increasing eustatic trend (long term), predominantly regressive situations cause deviations opposite to those expected at this level of reference, if only the eustatism is taken into account. An example belonging to the *Platform Ambitus* are the spectra obtained by MARQUES & OLÓRIZ (1988a) for the Middle Oxfordian-Lower Kimmeridgian in the Northern sector of the Algarve (Western South Iberian epicontinental margin) (see Fig. 8).

Third order: At a third order observational level (the depositional sequence level in HAQ et al. 1987), the information obtained locates the relation between the eco-sedimentary evolution and the deviation of the associations in eco-stratigraphic terms and allows the suggestion of eco-evolutionary interpretations between 1–4 m.y. (here within the LZA-4 supercycle in HAQ et al. 1987).

As we have suggested above, the limitations of outcrops in the South Iberian margin facilitate, in general, the recognition of *transgressive systems tracts* crowned by “*Progradational complexes*” (*sensu* MARQUES et al. 1989). This fact, which could actually be a fairly generalized situation in European epicontinental Jurassic outcrops, imposes, without tectonic disturbance, 3rd order depositional sequences with aggradational-transgressive trends in the lower part and progradational-regressive trends in the upper part. In these cases the *transgressive system tracts* have been proved to be useful for correlations and because they contain condensed levels with more or less significant hiatal surfaces related to marine flooding in wide areas, they could be considered to define depositional sequences other than those proposed by sequence stratigraphy *sensu* Exxon group (see GALLOWAY 1989) but easier to identify and correlate between distant regions.

In eco-sedimentary terms, the aforementioned sedimentary successions interpreted by sequence stratigraphy (*sensu* Exxon group) imply, in the simplest case, a pattern with intervals of progressive reductions of the ecospace punctuated periodically but irregularly by periods of recuperation of the ecological spaces. These dynamics should be reflected in the composition of the macro-invertebrate associations, if their configuration is ecologically controlled.

This type of analysis requires the previous obtainment of a stratigraphic scheme according to the methodology of the sequence stratigraphy (for the South Iberian margin cf. MARQUES et al. 1989). As can be seen from the scheme in Figure 9, a marked parallelism is revealed between the composition of the spectra of platform macro-invertebrates, their possible deviations and the situation of the samples in the sigmoid model proposed by the sequence stratigraphy (*sensu* Exxon group). This shows a close relation between the composition of the associations and the relative sea level, as is to be expected, which favours an increasing development of ecostratigraphic approaches. Figure 9 shows that the data are significant at different levels of resolution:

a) at substage and biozone level (Algarve cf. MARQUES & OLÓRIZ 1988a) they are “unrefined” data giving averages which cannot be used for levels of more detailed resolution.

b) at intra-biozone level the data obtained in the Prebetic Zone permit the comparison between the uppermost and lowermost parasequences belonging to a system

tract. At present the changes between consecutive parasequences within a system tract are under study. Finally, the eco-evolutionary behaviour at genus and species level is a problem which requires detailed analysis and will be the subject of a later paper.

One final question which we will look at here are the possible relations existing between the eco-evolutionary dynamics of the ammonites and the sedimentary breaks. MARQUES & OLÓRIZ (1988b) have presented the first considerations deduced from the

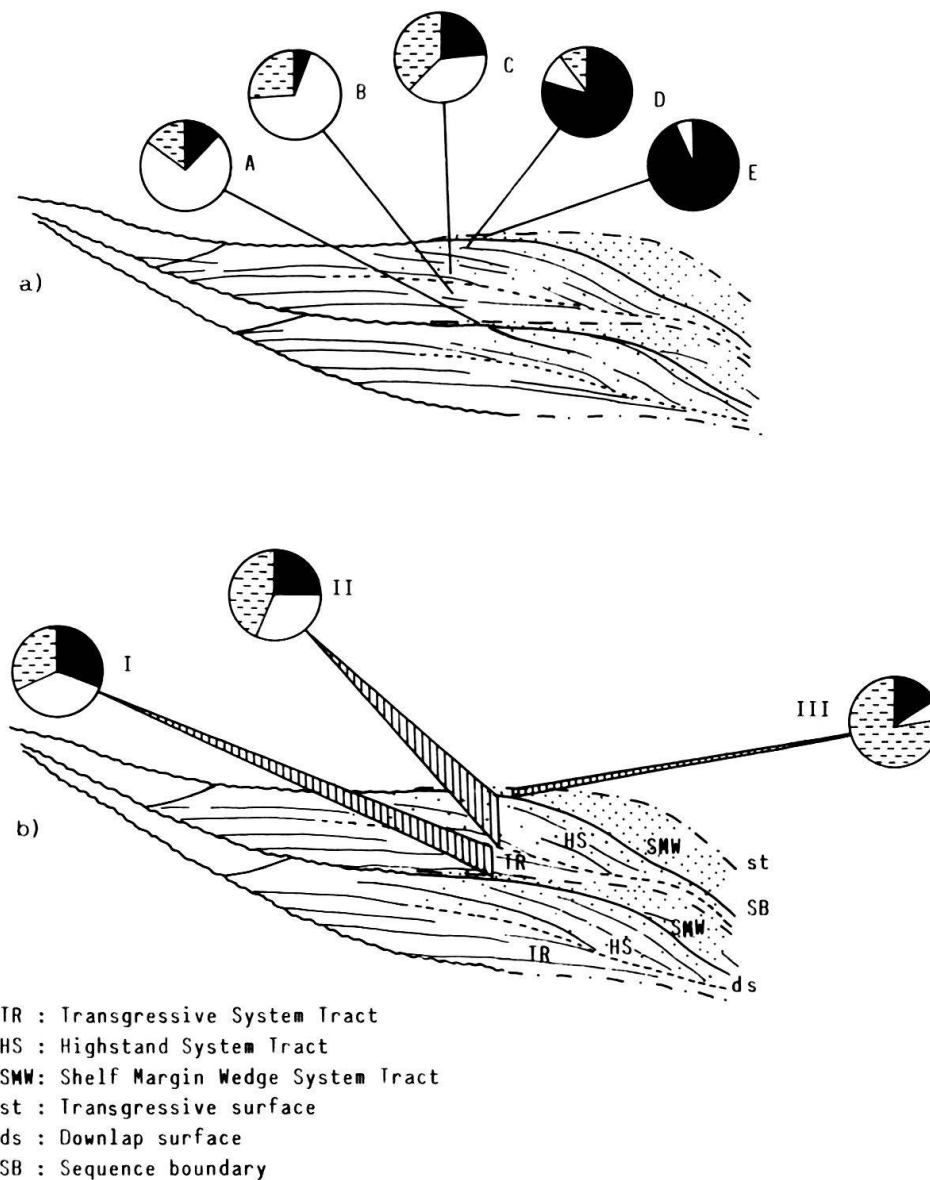


Fig. 9. Location of faunal spectra in the idealized depositional sequence model, as considered by the EXXON Group. Faunal spectra as type *a* diagrams in Fig. 3. Identification of Systems Tracts in 9b as usually quoted in sequence stratigraphy sensu EXXON Group. The amount of stippling refers to increase in the progradational trend.

9a) Data obtained from selected beds and outcrops in the Prebetic Zone by OLÓRIZ & SÁEZ (inedit: A, B) and OLÓRIZ & RODRÍGUEZ-TOVAR (inedit: C, D, E). A (Uppermost Bimammatum Zone), B (Uppermost Planula Zone), C (Lowermost Platynota Zone), D (Uppermost Platynota Zone) and E (Lowermost Hypselocyclum Zone).

9b) Average data obtained from selected outcrops in the Algarve by MARQUES & OLÓRIZ (1988a). I (Upper Oxfordian), II (Platynota Zone), III (Hypselocyclum Zone).

observations made in the western South Iberian epicontinental margin (northern sector of the Algarve). According to MARQUES & OLÓRIZ (1988b), the Middle Oxfordian-Lower Kimmeridgian (Hypselocyclum Zone *pro parte*) interval records a progressive increase in siliciclastic and marly sedimentation, which eventually deteriorates the conditions for benthic life in the basal Kimmeridgian and, moreover, can be related to a progressive imbalance in the ammonite associations. In this interval, these authors recognize 8 discontinuities (D2 to D9) correlatable with global eustatic events of variable significance. On the whole, the discontinuities can be divided into three main groups: those linked to eustatic falls or short term low sea levels (D5, D8 and D9); those which show evidence of tectonic pulses associated to the eustatic dynamics (D4, D6 and D7); and the discontinuity D3 may possibly represent a transgressive surface in an interval of tectonic quietude. D2 is as yet little known due to outcrop difficulties.

D3, at the base of a *transgressive interval* and with no important tectonic disturbances, precedes an interval of improvement in the conditions of life for cephalopods, and coincides with a faunal renovation which marks a zonal limit in the Middle Oxfordian.

Among the discontinuities linked to low or clearly falling eustatic levels according to the sea level curve proposed by HAQ et al. (1987), D5 is related to the precocious appearance of *Ardescia* and *Praeataxioceras*. These precocious records have also been detected in Portuguese Extremadura (Lusitanian Basin) according to ATROPS & MARQUES (1986). D8 corresponds with the accentuation of the progradational trend on the boundary of cycles 4.4–4.5 in HAQ et al. (1987) and also with a renovation of the Ataxioceratinae which can be used as the limit between the Platynota and Hypselocyclum Zones. D9 is related to the first traces revealing an environmental deterioration which will become generalized for the ammonites in the Algarve during the Middle Kimmeridgian (lower part of the Upper Kimmeridgian *sensu gallico*).

Among the discontinuities which show interactions between tectonics and eustatism, D4 is related to increases in the siliciclastic inflows which produce an ecological impact particularly on the benthic fauna. D6 may represent a flooding surface and even a pulse of instability on the boundary of a parasequence; it is probably involved in the disappearance of *Praeataxioceras* in the Algarve. D7 marks a phase of accentuated tectonic influence with generalized erosions which determine the significant record of siliciclastic deposits in the South Iberian margin; also a phase of increasing subsidence is known from the Prebetic coinciding with the greatest thickness at the biozone level (Platynota Zone). D7 is situated practically on the Oxfordian-Kimmeridgian boundary, but it does not have a great effect on the Ataxioceratinae at a lower taxonomic level, since the transition from one stage to another can only be established with regularity by the substitution of species (*galar-platynota*) in the cryptic genus *Sutneria*.

We may conclude from the foregoing that there is basically a relation between sedimentary breaks (discontinuities/unconformities as considered by MARQUES et al. 1989) and changes or substitutions among the ammonites, particularly in relation to the occurrence of the *transgressive systems tracts* and the increase of the progradational trend accompanying the development of the "Progradational complex" which on the shelves conclude with the development of the *shelf margin wedge systems tracts*. Nonetheless, it is important to note that there is not a simple relation between sedimentary

breaks and the dynamics of the morphological change in ammonites. In reality, some sedimentary breaks, which include tectonic and erosive processes which affected the sedimentary environment, do not seem to correlate with the major changes in the ammonites (e.g. D7 on the Oxfordian-Kimmeridgian boundary or D4, intra-Transversarium Zone). On the other hand, sedimentary breaks of comparatively subtle record and linked to limits of parasequences in a progradational regime (D5), to the establishment of aggradational trends (D6), or to the accentuation of progradation on the limits of sequences (D8), are related to the beginning or the end of phyletic lines or to important faunal renovations.

Consequently, it would seem reasonable to consider that the eco-evolutionary dynamics of the ammonites, which is without doubt related to the eco-sedimentary evolution, although in a complex way, is rather more closely related to the ecological effects of critical values of the ecospace and other associated factors. These effects may be of comparatively long period and coincide incidentally, but not essentially, with sedimentary breaks of eustatic origin.

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