

## Ammonite Phenotypes and Ammonite Distributions. Notes and comments

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### RIASSUNTO

In questo lavoro sono commentati alcuni aspetti della distribuzione biogeografica delle ammoniti del Giurassico superiore nel contesto del modello proposto da Olóriz (1984/85). Sono analizzate alcune ipotesi recenti riguardanti i generi dell'Oxfordiano e del Kimmeridgiano-Titonico. Il modello applicato è infine paragonato ad altre recenti interpretazioni della biogeografia e dell'evoluzione delle ammoniti.

### ABSTRACT

In this paper some aspects of the biogeographical distribution of Upper Jurassic ammonites are commented upon within the context of the model proposed by Olóriz (1984/85). Some recent hypotheses concerning Oxfordian and Kimmeridgian-Tithonian genera are analysed. Lastly, the model applied is compared to other recent interpretations of ammonite biogeography and evolution.

### KEY WORDS

Ammonites. Biogeography, Migrations, Vicariance, Evolution, Upper Jurassic.

### INTRODUCTION

In September 1984, during our first meeting here in Pergola, I proposed some "outlines for a pattern" with the object of providing an hypothesis combining geological and paleontological information which might explain the underlying dynamics of the distributions of Upper Jurassic ammonite faunas (Olóriz 1984/85, with examples taken essentially from the Kimmeridgian and Tithonian). At the time of its presentation the pattern was only outlined in general terms, these being: a) the influence of the dynamics of the earth's crust on the environmental configuration and, consequently, on the ecological dynamics; b) the differentiation between two basic ecological environments; and c) the differentiation of two basic associations of ammonite faunas in correspondance with the above mentioned ecological environments. Using these criteria it was possible to put forward an hypothesis concerning the dynamics of the distribution of ammonites. Broadly speaking, this hypothesis is that a comparatively homogeneous and globally distributed *Distal Association* would have acted as a reserve of potential colonizers for any platform area. As a result of the colonization a *Proximal Association* of a comparatively heterogeneous nature would be established due to the necessary adaptation to more or less marginally restricted ecological conditions. Consequently<sup>(1)</sup> the

adaptation to particular ecological conditions would determine phenotypical expressions whose similarity would depend on the equivalence of the ecological context for any one particular group of ammonites. Thus vicariant faunas could be recognised in the analyses of dispersion patterns (s. Armstrong, 1977), an *bipolar distributions* should cease to surprise us. Using this approach, two questions take on particular relevance and provide an unequivocal identity for the proposed pattern: a) migrations, as they have traditionally been proposed would have to be reconsidered with regard to their significance, and b) the possibility of parallel developments could be admitted without further discussion. This possibility would be associated to the ecological context and, naturally, would have a variable evolutionary significance according to the case under examination. One final consideration made reference to the implications which the application of the model would have in systematics, since certain conceptual positions would be inherently affected.

### SOME RECENT DATA ON AMMONITE DISTRIBUTIONS AND RELATED QUESTIONS.

Let us examine some recent data. Since 1984 information on ammonites has continued to increase, but some studies in particular are of interest concerning the model proposed (Olóriz 1984/85), especially those by Marchand (1984), Donovan (1985), Bayer & McGhee (1984, 1985a, 1985b), and Marchand & Thierry (1986). In all of these studies importance is given to the influence of the environment in the phenotypical expression of ammonites. Environmental and faunistic changes are correlated on different levels. Of particular interest is the verification of phenotypical recurrence demonstrated by Bayer & McGhee (op. cit.). Although the hypotheses about the close dependence of ammonite phenotypes on the environment were revitalized by the work of Marchand (1982a, 1982b) and Tintant et al. (1982), the results obtained by Bayer & McGhee (op. cit.) broke down all resistance to the admission, in the final analysis, of the existence of parallel developments in relation to the influence of the environment by way of its dynamics throughout time. A recent precedent of interest are the conclusions of Brochwicz-Lewinski & Rozak (1975). At the present time Olóriz (in progress) has recognised recurrences in idoceroids from the Oxfordian and Kimmeridgian.

Although, whatever the environment may be, endemic genera and/or species will always be found as a result of an undeniable *in situ* evolution and, in accordance with

1 These aspects were voluntarily developed briefly in Olóriz 1984/85.

the foregoing, it would appear that at the present time there can be few objections to the acceptance of the idea that faunas affected by a process of vicariance and submitted to similar ecological conditions may follow more or less parallel evolutionary developments. A particularly extreme case is that of *bipolar distributions*. This all depends on the limitations for phenotypical expression in genetically integrated groups (Olóriz, in progress). Thus, isochronous or heterochronous homeomorphism, occurring in more or less widely separated areas, should be accepted as a frequent phenomenon. An example of this may be the record of *Pararassenia* in Mexico. This genus has been forced into a correlation with European forms, attributed a middle Kimmeridgian age (Ziegler, 1962) and is considered as the result of a supposed migration from Europe (Enay & Mangold 1982, Fig. 10), an opinion upheld by De Wewer *et al.* (1986). I, however, locate the record of *Pararassenia* in the terminal part of Burckhardt's "Couches à Idoceras" in Puerto Blanco, Mazapil area (1985, unpublished material), and I consider that, given the limited knowledge that we have of this genus, the possibility cannot be rejected of its being a simple case of a more or less heterochronous homeomorphism in relation to certain European Aulacostephaninae.

Although endemism has long been recognised and accepted as unequivocal evidence of *in situ* evolution, the cases of more or less isochronous morphological convergence in widely separated areas have given rise to the most varied *ad hoc* hypotheses, namely migrations. The mobilization of genera, species and, finally, more or less equivalent associations, seems to have been widely employed. This is the way in which explanations have traditionally been found for different ammonite distributions as deduced from the fossil record and it is on this important point that Olóriz's model (1984/85) offers a clear alternative, an example of which has recently been provided by the same author for the interpretation of the dynamics of "*Aspidoceras*" (Checa & Olóriz 1988). In this case it is easy to recognise the incidence of preconceived notions implied by the traditional, migrationist interpretation which lead aprioristically to the idea that populations were capable or incapable of producing descendency, according to whether they respectively occupy areas in the *Basin Ambitus* or the *Platform Ambitus*, despite the fact that they are phenotypically undistinguishable. Moreover, in this example the peculiarities of the stratigraphic record of the group examined are interpreted in accordance with the previsions of Olóriz's model (1984/85). Another example was presented by the author at the recent Symposium in Lisbon (Olóriz 1988 in lit.), through the analysis undertaken of the existing hypotheses about the interpretation of the geographical distribution of the genus *Idoceras* s. Burckhardt (1906), Ziegler (1959). On this occasion the consistency of the migratory routes proposed on the basis of the different authors' arguments was analysed and an alternative hypothesis offered, which takes into account, moreover, the polyphyletic character of the genus.

As might be expected, these are not the only cases of

traditional interpretation of ammonite biogeography, there being many others. Amongst the most recent studies which display a most complete information on Upper Jurassic ammonite biogeography I should like to point out those by Enay (1980a, 1980b, 1980c, 1985), Enay & Mangold (1982) and Cariou *et al.* (1985). I have chosen these studies since they contain interpretations of Kimmeridgian and Tithonian ammonite records, in other words, those belonging to the interval chosen as the basis for the development of my own pattern (Olóriz 1984/85), and also because they contain allusions to processes whose interpretation may be quite different if my pattern is applied. I shall later make brief reference to Oxfordian forms.

Enay (1980a) demonstrates the importance of bottom paleotopography in relation to shallowing (regressive) phases and their effects on ammonite distribution. According to his conclusions, although it is not presented as such, a clear process of vicariance affected the Anglo-Norman and French submediterranean associations. Some years later, the same author (Enay 1985), refers to *effets de seuil* which affect the faunistic exchanges between boreal and mesogean regions between the Middle Oxfordian and the Upper Kimmeridgian. If we take only the examples of the Upper Jurassic, what Enay suggests, correctly in my opinion, is the rôle of topographical barriers in platform areas. The interest of these examples derives from the comparatively reduced volume of the *Platform Ambitus* compared to the *Basin Ambitus* s. Olóriz (1984/85). Indeed, elevations of the sea-bottom, which become a determining factor of the greatest importance in ammonite distribution in the shelves, would be inoperative in the *Basin Ambitus*, which is today recognised in materials belonging to continental paleomargins. Consequently an *effet de seuil* in the *Basin Ambitus* would only be possible with regard to greater structural configurations of a continental or subcontinental order, and therefore would be fairly easy to recognise by means of geological data<sup>(2)</sup>. If this is the case, these would be phenomena of very diverse paleogeographical significance and, presumably, they would present marked differences with regard to their intensity and persistence as barriers. If the *effets de seuil* may have a local incidence of varying width in the platforms, in the *Basin Ambitus* the truly significant effects (caused by continental margins) act by broadly delimiting the periphery of this environment at all times and so do not subdivide it<sup>(3)</sup>. In accordance with this, the *Distal Association* which occupies the *Basin Ambitus* could with difficulty be confined by topographical barriers in its own environment, except as a result of greater paleogeographical events.

Other aspects of interest have to do with migratory routes and the direction in which they might have been used. Enay (1980b) acknowledges that "le sens des déplacements n'apparaît pas et n'est pas toujours évident". This author, as ever decidedly migrationist, later recognises (Enay 1985) that "le problème posé est celui du sens d'utilisation de ces voies. Cet aspect des voies d'échanges mériterait d'être développé". In their previ-

<sup>2</sup> See below bottom comments on the correlation of Alaska and Europe during the transition from Aalenian to Bajocian.

<sup>3</sup> Comparatively minor subdivisions can be expected on high and irregular outside shelves. In these cases minor deviations from the comparatively homogeneous standard composition of the *Distal Association* would be recognized.

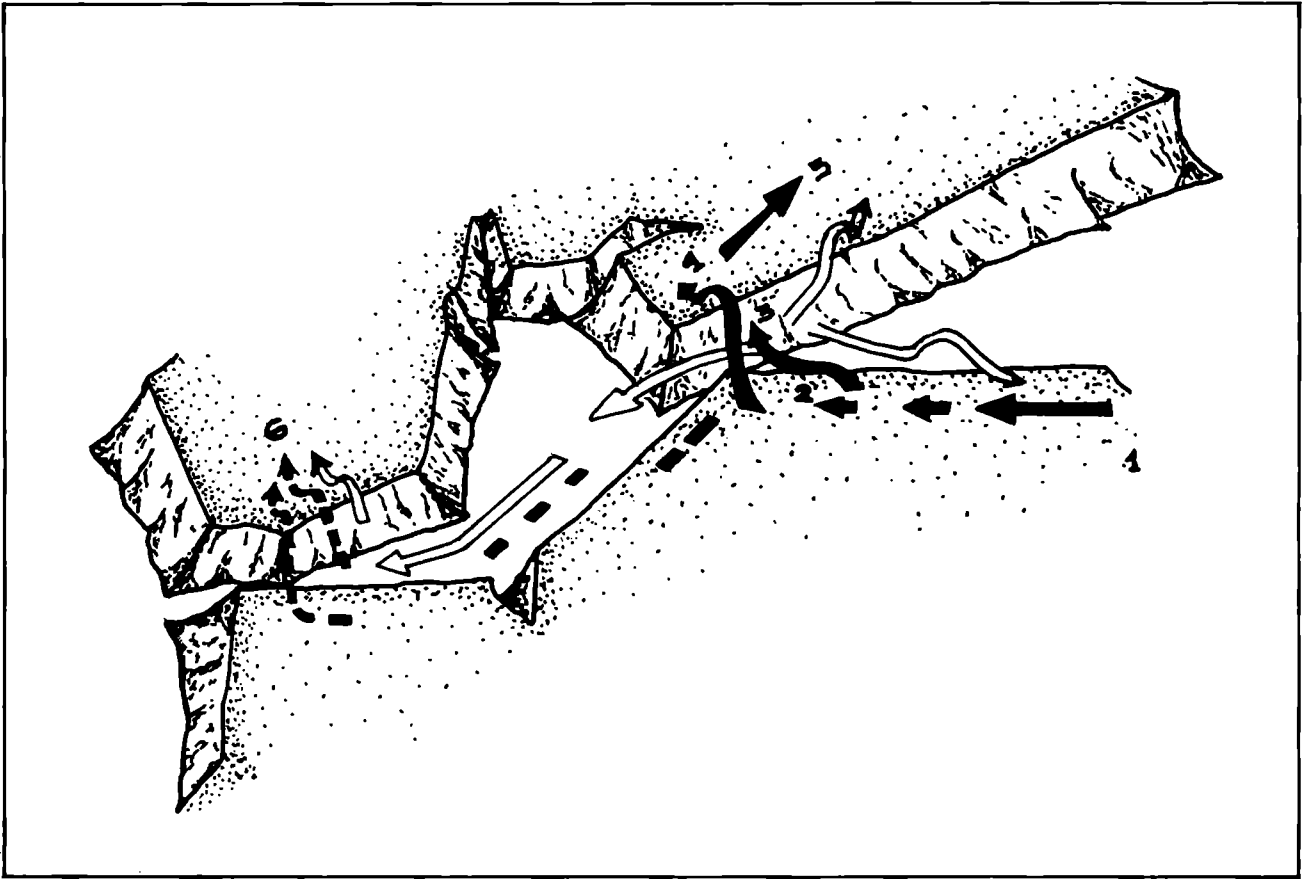



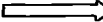



Fig. 1 - Schematization of migration routes proposed for *Hybonoticeras* according to hypotheses by Enay (1980b, c, 1985) and considering the author's own model (Olóriz 1984/85)

- |  |  |   |   |
|--|--|---|---|
|  | Basin Ambitus (ecological conditions outside shelves)      |  | Platform Ambitus (ecological conditions on shelves) |
|  | Hypothetical via of migration                              |  | migration vias deduced from Enay (1980b, c)         |
|  | migration vias deduced from Enay (in Cariou et al. - 1985) |   |   |
- 1: East Africa (Indo-Malgassy area), 2: North Africa (Marocco-Algeria), 3: Subbetic and lateral equivalents, 4: Iberia, 5: Submediterranean Europa, 6: Mexico.

ous analysis of the "Dynamique Biogéographique et Evolutive" Enay & Mangold (1982) saw a close relationship between the migratory routes and the "contiguïté, pour ne pas dire continuité, des grandes masses continentales et des plates-formes qui les bordent". These authors distinguish between epicontinental and "préocéaniques" routes, and recognise the barrier value of oceanic waters amongst other factors which I shall not refer to for the moment. Within the context of this conceptual framework, Enay makes reference in several studies to the biogeographical dynamics of the genus *Hybonoticeras* (Fig. 1). In 1980, (Enay 1980b) *Hybonoticeras* is understood to emanate from the East, although with certain reservations, and is used to characterise the East-West direction of the migrations in the Tethys. This interpretation is presented as firm later the same year (Enay 1980c), so that *Hybonoticeras* would be one of the Indo-Malgassy "immigrants" to Europe during the Kimmeridgian after passing through the preferential migratory route of the

Gibraltar sector. If in 1980 the East-West migratory route plays a primordial rôle in this author's interpretations, it later seems to disappear from his considerations with no further comment or explanation. Thus Enay (in Cariou et al., 1985)<sup>(4)</sup> changes his opinion in favour of a centre of evolution and dispersal in the western Tethys, from which point *Hybonoticeras* would have extended to the West (Mexico) and East (Kachchh and Madagascar). Accordingly, despite the direction of migratory routes being recognised as a problem worthy of consideration, one may change from an essentially unidirectional pattern to another, multidirectional-radiant one.

Nonetheless, in my opinion, and without agreeing strictly with Enay's latest hypothesis (Enay in Cariou et al. 1985)<sup>(5)</sup>, something important has indeed changed and this has not only to do with the direction in which *Hybonoticeras* may have extended. In this latest proposal Enay inverts the biogeographical dynamics of this genus which, according to my hypothesis (Olóriz 1984/85), is

4 This hypothesis may indeed be the work of Enay and Geysant who are the only researchers amongst those whose work is included in this paper to have studied the Tithonian. I personally feel that the idea belongs to Enay alone as he has referred to this problem in previous studies, as we have already seen.

5 Cf. footnote.

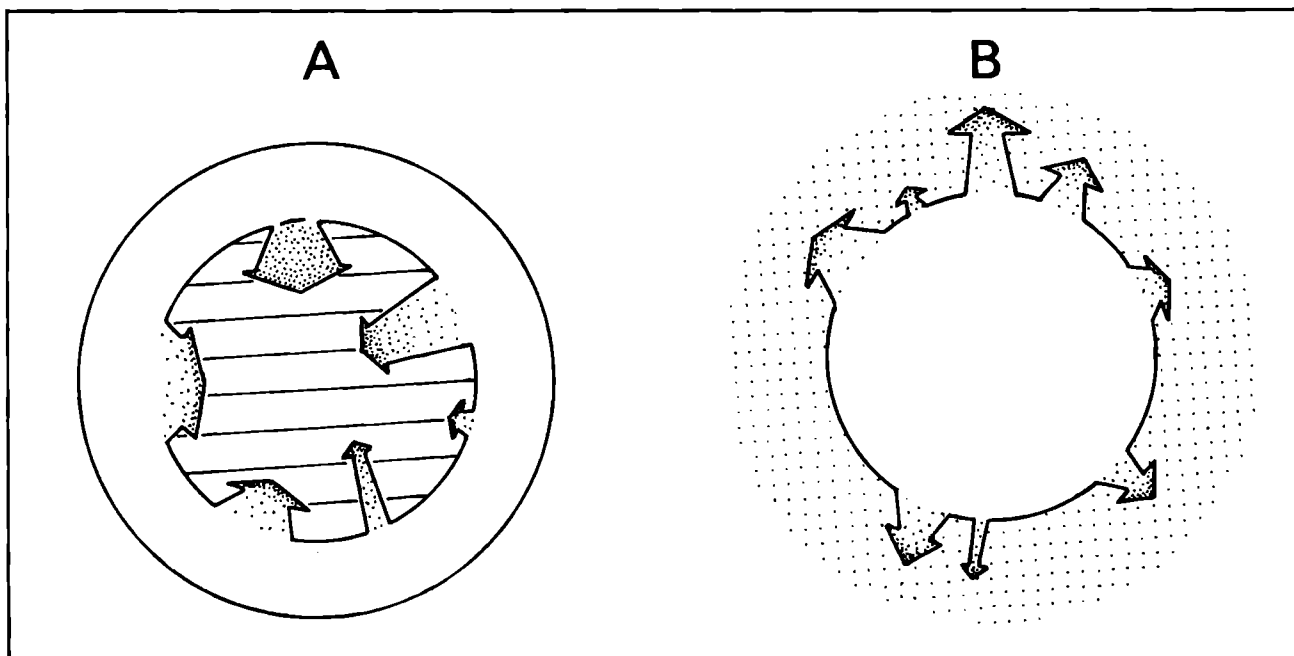


Fig. 2 - Ammonite distribution and biogeographical dynamics according the model of Olóriz (1984/85). The circular designs do not *per se* imply the concept of a single origin centre (this is better visualized in diagram A). The size, shape and location of the arrows refer to hypothetical characteristics and to the ecological significance of colonized areas on shelves.

Basin *Amnitus* (A = "Global", B = Regional)  

 emerged land and/or unfavourable proximal areas (A)  

 shelves (B)  

 available areas on shelves (*Platform Ambitus* in A and B). Darker stippling inside arrows: increasing *Platform Effect* (in A and B).  
 Diagram A: a more realistic case of main land masses surrounded by oceanic waters. A frame to understand "isochronous" records in separate areas can be recognized.

Diagram B: a more special case of a land-locked sea situation.

In diagram A two alternative hypotheses to the traditional interpretation of the biogeographical dynamics of *Hybonoticeras* can be considered according the model of Olóriz (1984/85 and cf. Olóriz in Checa & Olóriz 1988): a-only the genus *Hybonoticeras* is analyzed, and 1- the ancestral of the genus *Hybonoticeras* must also be analysed. In the latter hypothesis (b) *Hybonoticeras* could appear both in the *Platform Ambitus* and the *Basin Ambitus* without taking into account the possibilities of faunal movements related to environmental changes (sea-level fluctuations, marine currents...).

essentially seen as a process of adaptation to peripheral areas. In extreme locations, with regard to the western Tethys, the records would correspond to those of the colonizers of marginal platforms and in this way the process would be basically the same, although with the differences related to the peculiarities of each particular enclave. On the other hand, Enay's original hypothesis of an East-West route (with an Indo-Malagasy origin centre?) presupposed great ecological elasticity (tolerance) in *Hybonoticeras* which would have permitted its colonization of both the *Basin Ambitus* and different areas of the *Platform Ambitus*, all of this starting from forms developed on a platform in which the autoctonous *cachet* of ammonites is frequent. In this case the origin and dispersal centre would have to be clearly marginal or external in relation to its later distribution. If we consider the fossil record in western Mediterranean faunas *sensus stricto*, in my interpretation of the distribution of *Hybonoticeras* there is no need for migrations radiating from this sector because of the simple fact that this has traditionally been the only region of the *Basin Ambitus* for which we have

data, above all data concerning land outcrops. In principle, there can be no objection to a wider, even "global" <sup>(6)</sup>, distribution of *Hybonoticeras* in accordance with the possibilities for occupation of an "homogenous" *Basin Ambitus* (Olóriz in progress). Consequently the colonization of different shelves (Submediterranean, Indo-Malagasy, African and Mexican) would have taken place starting from the populations which occupied the most closely adjoining areas of the *Basin Ambitus* which could have been connected. Thus an origin centre in the western Tethys is not necessary to explain the record of *Hybonoticeras*. Indeed the limiting of the origin of this genus to one particular *ecological ambitus* should be demonstrated, above all if we consider the hypothesis of the existence of only one origin centre (Fig. 2).

Although the examples from the Kimmeridgian and the Tithonian are numerous, let us briefly examine one from the Oxfordian. Melendez *et al.* (1984) <sup>(7)</sup> offer an interesting study of Oxfordian fauna in the Iberian Chain and its paleo-biogeographical significance. Following the same lines as in the model of Pozariska & Brochwicz-

<sup>6</sup> To the extent of the foreseeable development of the geographical extension of continuous *Basin Ambitus* ecological conditions.

<sup>7</sup> I wish to express my thanks to the authors who provided me with both their own study and that of Pozariska & Brochwicz-Lewinski (1975), the latter being received by me on the 4/11/86.

Lewinski (1975) the interpretation of the association under examination agrees in broad terms with my own pattern. Another question is the paleogeographical significance of the area examined: "it was situated at or in close proximity of the *major migration routes*" (cf. Melendez *et al.*, 1984, p. 7 *My italics*). My own opinion is that it is exclusively on the basis of the geological data that the submediterranean character of the fauna could be deduced with a variable degree of mediterranean influence *sensus stricto*, at least as a null hypothesis. Of special interest is the interpretation these authors make of the Betic (S. Spain) and North-African records of *Dichotomoceras bifurcatus* (Quenstedt). They interpret, implicitly, a more northerly submediterranean origin (France, perhaps) and, explicitly, "migration across the Iberian Chain or adjoining areas" (ibid. p. 7). As is traditional, the context is clearly migrationist and within it attention must be drawn to the "problematic" lack of record of *Subdiscosphinctes* and *Subnebrodites*. Within the framework of Olóriz's pattern (1984/85) *Dichotomoceras bifurcatus* (Quenstedt) could have colonized Iberian and North-African platforms starting from the *Basin Ambitus*, and, indeed, not necessarily only these platforms; it could even have undergone parallel development on these shelves as long as its ancestor existed there, as it did in the *Basin Ambitus*. Consequently the origin does not necessarily have to be European-submediterranean.

The absence of *Subdiscosphinctes* and *Subnebrodites* requires comment. *Subdiscosphinctes* is considered by Melendez *et al.* (op. cit.) as a typical submediterranean genus of the northern Tethys and is to be found in mesogean regions and even through related forms in the Iberian Chain. In my opinion *Subdiscosphinctes* (just as in the case of *Pseudodiscosphinctes*, Olóriz 1976/78) represents a conservative microconch belonging to isocostate perisphinctids. At times it is undoubtedly found as a recurrent phenotype and as such should not be used as a paleobiogeographical index, and even less as a marker of supposed migratory routes, unless we are able to obtain much more complete and reliable information than that which is available at the moment. Its absence or scarcity in the Iberian Chain may be due, in the simplest of cases, to limitations of sampling since we cannot possibly consider the idea of a systematic inaccuracy, as the authors to whom I am referring are recognised experts in Oxfordian faunas. Other hypotheses would require, as I have already suggested, much more detailed information with regard to the composition of the populations and the existence of possible competitors or vicarious forms originating *in situ*. Their presence in Portugal may very likely be due to a parallel evolution such as has been recognised in other cases (Atrops & Marques 1986, Olóriz *et al.* 1987 in lit.). This could support the hypothesis of *in situ* evolutions for *Subdiscosphinctes* or its hypothetical substitutes<sup>(8)</sup> and, in any case, it constitutes a call for further research on these problems.

Concerning *Subnebrodites*, if it is considered in the sense in which I have interpreted the original diagnosis of Spath (1925) and following the recommendation of Cal-

lomon (1981), as do Atrops & Benest (1986), and Hantzpergue (1987), this genus does not appear to me to be unknown in the Iberian Chain, given the high number of existing references to it in the literature, (cf. Goy *et al.*, 1979/81, Sequeiros & Melendez 1979/81, Geyer & Pelledun 1979/81, Melendez *et al.* 1980), its unmistakable typology and the fact that I personally have identified it amongst material belonging to the uppermost Oxfordian of this region. In this same sense, moreover, *Subnebrodites* has been identified in adjoining regions of the south of Spain such as the Prebetic and Subbetic Zones (Behmel 1970, García Hernández *et al.* 1979/81, Olóriz 1976/78, Sequeiros & Olóriz 1979/81, Seyfried, 1978), in the North African area (Atrops & Benest 1984 and 1986), and, naturally, in the European-submediterranean platforms and even in North Aquitaine (Charente Maritime, France; Hantzpergue 1987). If there is a scarcity of *Subnebrodites* whose appearance is strictly equivalent to that of the European-submediterranean types, the reason must be connected with the relative local character of the Celtiberian forms, as is correspondent with an *in situ* evolution subjected to ecological conditioning factors which do not necessarily have to be identical in the different platforms. In the context of the Olóriz (1984/85) pattern, the Andean record of a *proteron-type* form is not in the least surprising because it was not found in the Iberian Chain and fits into a casuistry of convergences<sup>(9)</sup> similar to that of bipolar records and to which allusion was made at the beginning of this study in relation with vicariant processes. There is, therefore, no need for a selective migration at the level of genus or species.

As I briefly pointed out here in 1984 (Olóriz 1984/85), in Tübingen in 1985 (Olóriz in Checa & Olóriz 1988), and more extensively in Lisbon recently (Olóriz 1987 in lit.), my criticism of migrations does not necessarily imply the inexistence of dispersal, but, rather, I reject the treatment which these aspects receive in the study of ammonites. In particular, I consider valid those authentic expansions of fauna related to either regional effects of tilting/deepening or eustatic phenomena, such as those referred to by Wiedmann (1973), Johnson (1974), Hallam (1978), Enay (1980b), Enay & Mangold (1982), Gabilly *et al.* (1985), Hantzpergue (1985), Marchand (1982b, 1984), Marchand & Thierry (1986) among others. Another thing altogether are migratory routes used by ammonites, capriciously it would seem, at different moments and, occasionally, even by a single genus or species belonging to a specific association, with no regard for the ecological relation between the original environment and that colonized. In any case, I believe that the arguments brought to support the proposals about migratory routes and the directions in which they may have been should undergo a profound revision.

## NOTES FOR A BRIEF COMPARATIVE ANALYSIS

To conclude I think it of interest to proceed to a comparative analysis of other patterns proposed in the past few years for the interpretation of the biogeographi-

<sup>8</sup> The possibilities of the existence of microconchate *Larcheria* should be taken into consideration in this context.

<sup>9</sup> This term is here employed without special evolutionary significance since up to date the fossil record there is very poor, but the possibility of considering a case of parallel evolution could not be ruled out.

cal/evolutionary dynamics of ammonites by means of a selective comparison with my own pattern (Olóriz 1984/85, 1987 in lit., Olóriz in Checa & Olóriz 1988; and specific data taken from research in progress).

It is easy to see that, for some time now, practically all the factors which could foreseeably have influenced the geographical distribution of ammonites have been taken into consideration. Imlay (1965) presents an interesting revision of this. Naturally, opinions vary from author to author and the rôle of ecological factors changes. An example is the varying interpretation of the influence of temperature (Gordon 1974, 1976; Ziegler 1981 and Enay & Mangold 1982, *versus* Hallam 1969, Marchand 1984, Olóriz 1984/85 and Olóriz in progress). The same is true of other physical factors. For the moment we also lack paleobiological data of great interest which are the object of open discussion (e.g. the ecology of the early phases of ontogeny, rhythms of growth and reproduction, etc.). In the context of the available information, new hypotheses can only emerge from a clear differentiation of the theoretical base, since it is only in this way that new readings and interpretations of the existing (and new) data are possible.

The modern hypotheses concerning the interpretation of the geographical distribution of ammonites can be considered to be based mainly on the studies of Ziegler (1967) and Wiedmann (1973). In both of these studies the bases of the ecological behaviour of ammonites and their reactions to fluctuations in sea-level are established. Hallam (1978) makes an initial attempt on the level of eustatic fluctuations during the Jurassic. With regard to my own pattern, there is no equivalent to my *Distal Association* in Wiedmann (1973), Wiedmann's *Deep Faunas* refer only to leiostraceous, smooth oxycones, haploceratids, phylloceratids and lytoceratids, and they are subject to a very limited evolutionary dynamics. Although they are implicitly included (cf. Wiedmann, 1973, fig. 11) there is no commentary on cases of parallel evolution, except for sutures, and no explanation is given for certain limitations on descendency in platforms.

Ziegler (1981, p. 440) continues to attribute an important rôle to temperature and depth. This author makes no reference to the existence of a *Distal Association* connected to a dynamics comparable to that foreseen by me, and neither does he refer to parallel evolution even in those cases in which neither barriers nor facies seem to affect the distribution of certain *Glochiceras* (cf. Ziegler, 1981, p. 435).

The conclusions of Pozariska & Brochwic-Lewinski (1975) are particularly interesting. Using the ideas of Wiedmann (1973) and the pattern proposed by Johnson (1974) for shelf benthic faunas as a starting point, these authors come to attribute a dominant rôle to physical barriers, whether these be connected with climatic factors or not (e.g. Boreal trap v. endemisms in their Tethyan province). They conceive of stenotopical immigrants (as does Johnson 1974) and a distal-proximal platform gradient according to Wiedmann's predictions, although they present the problem of the reversion of ornamentation as an open question, which is, in itself, very interesting. Another aspect which contrasts with later hypotheses (Bayer & McGhee 1985a) is the slow nature of the migrations. As in previous cases, no consideration is given to a *Distal Association* nor to parallel evolution in separate

areas such as I have suggested. In addition, their biogeographical divisions imply a mixture of more than one ecological ambitus s. Olóriz (1984/85).

Both Lehmann (1976) and Kennedy & Cobban (1976) adopt Wiedmann's model (1973). Lehmann (1976) even quotes a precursor (Wedekind 1935) and suggests that the epibenthic character of ammonites would accentuate the effect of the fluctuations in sea-level; although he admits that the colonizations which give rise to later endemisms proceed from the Tethyan area, he does not admit the possibility of global distributions in spite of cases of wide geographical distribution. With regard to Wiedmann (1973) he recognises no selective character in the general evolutionary pattern of the suture (the ortoselective trend in Wiedmann op. cit.) and finds it to be merely informative of the phylogenetic moment.

Kennedy & Cobban (1976) give an exhaustive survey of the factors which determine the geographical distribution of ammonites, including the biological and taphonomic aspects, and they classify five types of distribution:

*Pandemic* = eurytopical and stenohaline ammonites. According to my pattern the northern and southern areas of abundance in this type of distribution would be the result of adaptations in marginal areas following strategy (e.g. *Pseudophyllites*).

*Latitudinally limited* = essentially Tethyan ammonites. In my pattern, for theoretical reasons, this would only be valid if on the basis of the *Basin Ambitus* record in high latitudes the existence of a clearly differentiated fauna were confirmed and no topographical barrier effect could be recognised.

*Endemic and provincial* = Ammonites differentiated latitudinally by the climate and longitudinally by barriers. These authors quote examples from Tithonian provinces (s. Enay 1973), from the Boreal Realm during the Jurassic-Cretaceous boundary, and in the West Interior during the Cretaceous. In the cases referred to no latitudinal trend can be observed, but rather marginal situations appear as opposed to those of the open marine environment.

*Disjunct* = In this case the authors find no explanation when the effects of continental mobilizations or errors in the bibliography or in the gathering of data in the field can be discounted (Kennedy & Cobban 1976, p. 64). In my pattern those cases with a reliable record can be explained as examples of convergences and/or parallel evolution in faunas subjected to similar ecological conditions.

*Post-mortem* = In my opinion this type can only be evaluated on the basis of taphonomic observations (facies, conservation, epizoa, etc.) and not directly deduced from a regional relation of ammonite frequencies. I am only aware of a few unequivocal cases in proximal sediments from the *Platform Ambitus*.

Tintant et al. (1982) provide an interesting pattern as a variation on the ideas of Ziegler (1967) and Wiedmann (1973), which is clearly connected with eustatic fluctuations as considered by Hallam (1978). Several aspects stand out in this interesting pattern: the ammonites had very limited horizontal movements, the complexity of the suture would be closely linked to the depth, the structuration of the shell would reflect the adaptation to the environment and, finally, their evolutionary development during the middle and Upper Jurassic would correspond

to an ecological dynamics of progressive subdivision of niches (as opposed to replacement linked with lower Jurassic transgressions). This stimulating integration of data requires some adjustments with regard to the significance of the complexity of the suture (Ward & Westermann 1985 offer a more realistic relation) and to the dynamics of the structuration of the shells during the process of adaptation. In the interval of time chosen for the argumentation of my pattern - Kimmeridgian-Tithonian - spherocoones can easily be identified which do not alter the structuration of the shell in the way predicted and platycoones are clearly present outside the platforms. Donovan (1985) also offers a somewhat more complex picture. The interpretation by Tintant *et al.* (1982) of the general course of evolution in the middle and Upper Jurassic is basically correct and, in my opinion, gives more weight to the hypothesis of vicariancy and parallel evolution, just as I have taken into account in my model (Olóriz 1984/85, Olóriz in Checa & Olóriz 1988, Olóriz *et al.* 1987 in litt., and research in progress). Tintant *et al.* (1982) do not present an hypothesis to explain the global distribution of ammonites on the basis of an "homogeneous" *Distal Association* of global distribution, even in the Upper Jurassic, subject to the dynamics contemplated by me. The course suggested by these authors for the structuration of the shell, in relation to the adaptation to the environment, proves to be much more rigid (schematic?) than that suggested by me as a reaction to the *Platform Effect* (Olóriz 1984/85, p. 7) <sup>(10)</sup>.

The hypotheses of Bayer & McGhee (1985a), published the year after my communication in Pergola, merit special attention. These authors refer to situations developed in small marginal basins and subject to a fluctuating environment in relation with minor fluctuations of sea-level. This dynamics implies regressive phases in which, generally speaking, the contraction and subdivision of the faunas takes place, followed by transgressive phases in which the initial situation is reformed. Given the narrow canalization of phenotypes, morphological recurrences take place and phenotypical sequences are repeated. This interesting study demonstrates, in essence, the dependence of ammonites on the environment they occupied, to the extreme of causing serious doubts as to the possibilities of differentiating the product of an *in situ* evolution from another due to ecological replacement. In the most complex model the relation between *speed of immigration* and the *time required for the manifestation of a process of natural selection* is seen as a determining factor.

Although Bayer & McGhee's models (1985a) were proposed for limited geographical areas, the authors reckon that the dynamic between basins at regional level are of the same type (cf. op. cit., p. 212) and I agree basically with their conclusions. Another question is the possibility of controlling the phenomena referred to by them within the *Basin Ambitus* (Olóriz 1984/85). Again Bayer & McGhee (op. cit.) reveal themselves to be clearly migrationist, as is appropriate for the cases studied by them

in "cul de sac" situations in platforms. Nonetheless, in the example analyzed by them at global level (the correlation between Europe and Alaska on the Aalenian-Bajocian boundary) their conclusions could be considered extremely hypothetical. The argumentation of the "paleogeographical event" pattern which arises out of the migration of faunas from the Pacific into Europe is not easy to conceive in the regressive context of the end of the Aalenian (cf. Hallam 1978, Jansa 1986 <sup>(11)</sup>) and neither does it seem appropriate to interpret a rapid appearance of *Sonninia* or of Stephanoceratids, in Europe, as evidence of immigration in this region. In general terms Bayer & McGhee's patterns (1985a) fit in easily with the pattern previously proposed by me (Olóriz 1984/85) representing a detailed analysis of marginal situations. These authors demonstrate the possibilities of ecologically induced morphological recurrence within a general dynamics of allopatry. Ecologically induced morphological recurrences are considered implicitly by me (Olóriz 1984/85, p. 7) when I refer to *vicariant faunas* as an explanation for *bipolar distributions*. In addition, this includes phenomena of parallel evolution on the basis of *in situ* evolution (see also Olóriz in Checa & Olóriz 1988). My pattern's context of vicariancy may also be recognised in the regressive phases of Bayer & McGhee's patterns (1985a). As I have recently suggested (Olóriz 1987 in litt.) it is also feasible to recognise vicariancy in phases of strictly peripheral or marginal differentiation, and transgressions favour this. Although the German authors foresee a possible application of their hypothesis at interregional level, I can find no direct allusion to the existence of a *Distal Association* with the characteristics suggested by me (Olóriz 1984/85). A detailed application of my model to the analysis of a specific group of Upper Jurassic ammonites, with references to the incidence of the pattern in the biostratigraphic record, may be found in Checa & Olóriz (1988).

Amongst other studies in which very valuable information is to be found are those of Enay & Mangold (1982) and Cariou *et al.* (1985). Basically these studies contain applications of the conclusions reached in studies considered here to be of great importance such as those by Imlay (1965), Ziegler (1967), Pozariska & Brochwicz-Lewinski (1975), Kennedy & Cobbam (1976), Hallam (1978) and Tintant *et al.* (1982). Naturally this implies a basic acceptance, which is not easy to evaluate, of the hypotheses of Wiedmann (1973), at least through Pozariska & Brochwicz-Lewinski (1975), as well as other more recent studies (Enay 1980) which modify those already mentioned in varying degrees. The context of both studies (Enay & Mangold 1982 and Cariou *et al.* 1985) is the same, i.e. what we may call "Migrationist-Platformists" with allopatry as the basic mechanism of differentiation.

Enay & Mangold (1982) are right in emphasizing the influence of eustatic events on platforms, and when they consider that "il est rare, pour ne pas dire exceptionnel, que l'évolution d'un phylum puisse être suivie totalement

<sup>10</sup> Point 2 in Olóriz (1984/85, p. 7) must be considered allusive to developing *extreme phenotypes*, because smoothing and/or ornamental simplification are not unfrequent (e.g. macroconchate Perisphinctoids). It could be implied in points 3 and 5 (final paragraph).

<sup>11</sup> Although the situation is not the same if the proposals of Vail *et al.* (1977) or Westermann (1984) are taken into account. All this is so as long as we accept the subordination of the biostratigraphical and chronostratigraphical divisions to the differing scales of absolute age, on which agreement has yet to be reached.

dans un même bassin ou une même région" (12) it is clear that they do not consider the situation in the *Basin Ambitus*, such as we know it in, for example, the paleomargins of the western Tethys (Olóriz 1984/85). Their analysis of the conditions which permit the migration of faunas are similar to those presented by Stevens (1971) for migrations in the Pacific during the Jurassic. Likewise, the French authors attribute particular importance to temperature among all the climatic factors which affected the geographical differentiation of ammonites. It is not surprising that, even having recognised a traditional case of parallel evolution (European Aulacostephanids) they should explain the record of *Parasenia* in Mexico by means of migrations.

In Cariou *et al.* (1985) a series of biogeographical maps are presented which permit "une nouvelle approche des aspects plus strictement paléontologiques de la paléobiogéographie: repartition, mouvement de faunes et/ou migrations, evolution" (cf. Cariou *et al.* 1985, p. 693). I agree with their treatment of Phylloceratina - "il s'agit plutôt d'un biome" (13) directement contrôlé par l'extension des influences océaniques au cours du Jurassique" (cf. Cariou *et al.* 1985, p. 694), but these are only one component of my ecologically controlled *Distal Association* (Olóriz 1984/85, p. 6). Their correct interpretation of the evolutionary sterility of boreal faunistic expansions, in connection with the restriction of these faunas to the platforms of the northern margin of the Tethys, even at times of maximum displacement to the south, allows for the conclusion that known boreal faunas have a character of a *Proximal Association* (s. Olóriz 1984/85). Thus the known boreal environment would belong to the *Platform Ambitus* as representative of a case of pronounced continentalization (which implies a high *Platform Effect* which would be recorded on the phenotypes) and it would not, in general, be very deep (compatible data and opinions were given by Hallam 1969, Kosygin & Parfenov 1975, Ziegler 1981, Marchand 1984 and Zakharov 1984, among others). As in Enay & Mangold (1982), the parallel evolution dynamics does not hold an important place in the hypotheses developed by these authors (Cariou *et al.* 1985), and therefore the interpretation of the Indo-Malagasy record of Proplanulitinae, the Malagasy record of *Larcheria*, or the difficulties of finding migratory routes for *Gravesia* (in particular for the colonization of the Russian platform) are clear examples of differences with regard to the pattern proposed by me. In addition, in the case of *Gravesia* the Mombasa record (14) (Verma & Westermann 1984) indicates without doubt a phenomenon of parallel evolution (15). The genus *Gravesia* can then be seen to be a *genre grade*, which could have developed in proximal environments of the *Platform Ambitus* and so, in accordance with the data available, considera-

bly reduces the importance of the supposed rôle of temperature in comparison with other climatic factors (Enay & Mangold 1982, p. 1025, p. 1042).

A final hypothesis which must be considered among recently proposed patterns is that of Gordon (1976). This author is probably one of the most determined defenders of the importance of the rôle of temperature, even though he admits that there were no particularly large latitudinal differences (Gordon 1976, p. 534). Gordon's study is especially outstanding as it represents an attempt to quantify the provincialism of ammonoids. The main limitations which I find in his interesting study are due to the consideration of insufficiently ecologically discriminated areas or regions. Although, with regard to those aspects concerning the rôle of temperature and biogeographical significance, Gordon's (1976) model and my own differ considerably, a previous study by this author (Gordon 1974) reveals interesting points of agreement in several aspects. In fact, when he concludes that "The circumglobal belt of the Tethys and the central Pacific was a favourable, relatively homogeneous and ecologically stable center from which successive outward waves of migration emanated" Gordon and I are indeed very close, but he also wrote: "Whatever the underlying cause, *observational data and theoretical considerations* both show that the Tethys Sea was the principal center for evolution and dispersal of successful new marine species and higher taxa during Mesozoic" (Gordon 1974, p. 145. My italics). *Theoretical considerations* are precisely the basic reason for not excluding the Pacific regions subject to a *Basin Ambitus* ecological situation from a rôle similar to those we know of in the Mediterranean Tethys. These regions would presumably have been connected with those of the Tethys Sea, forming part of a global system (16) which would not necessarily have been limited to the circumglobal belt of tropical Upper Jurassic as traditionally considered. In addition, *observational data* indicate that the sedimentary records of the Upper Jurassic in the Pacific area belong almost exclusively to more or less disconnected regions of the *Platform Ambitus* and, for this reason, information about them is fragmentary.

## SOME CONCLUDING COMMENTS

The geographical distributions of ammonites have generally been interpreted over the years in theoretical contexts coherent with the data available at the time. In the brief comparative analysis I have just presented, I have attempted to define my pattern's lines of argumentation and explanation (Olóriz 1984/85, Olóriz in Checa & Olóriz 1988) by examining the analogies and differences with the other patterns proposed which I have felt to be significant. It may be said that at the present mo-

12 To consider this expression *sensus stricto* is theoretically inappropriate because of the absolute character of some terms. We will probably never be able to know any phylum *totement* anywhere, but to compare the completeness of the fossil record with reference to significant traces of the evolutionary course of any one ammonite group in different regions is a reasonable proposition. As far as this is possible, it is in this sense that I refer to the comparative analysis of situations in the *Platform Ambitus* versus those in the *Basin Ambitus*.

13 The use of the term *Biome* requires specification, as can be deduced comparing with Valentine (1973)

14 A part of the material was revised personally by me (1985) in the R.O.M. (Toronto, Canada).

15 Although R. Enay does not accept the presence of *Gravesia* outside Europe (Erlangen 1984, oral communication).

16 "Global system" here refers to all the marine areas in a *Basin Ambitus* ecological situation which would basically be controlled by plate tectonics and other external geodynamic factors.



ment the inertia of neo-Darwinian influence still conditions the dominant paradigm, but it does not always provide reasonable or sufficiently reliable solutions and it tends to oversimplify interpretations of the paleobiological dynamics of ammonites. Although practically all the eco-evolutionary factors have been taken into consideration at one time or another, it is still possible to find new, theoretically based approaches, whose interpretations of the data offer new lines of research based on a scrupulous evaluation of the information and an openness even to conceptual refutation.

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