The recovery and radiation of Early Jurassic ammonoids: morphologic versus palaeobiogeographical patterns

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Abstract

The recovery and radiation of the Early Jurassic ammonoid morphospace, as represented by nine morphologic groups identified in an earlier study, are traced through the first 36 subzones of the Hettangian to Domerian time interval. A quantitative survey of the dispersion of 436 species over 15 palaeogeographical areas reveals seven palaeobiogeographical patterns, each corresponding to an exclusive set of species exhibiting similar characteristics in terms of distribution and abundance. This study combines morphologic, chronostratigraphical, and palaeobiogeographical data in an attempt to investigate possible connections between morphologic recovery and radiation patterns and the history of ammonoid distribution on a global scale. Two out of nine morphologic groups are found to be prevalent in a single palaeobiogeographical pattern through the major part of the studied time interval, and a single morphologic group prevails in all the marine areas considered during Domerian times. All the other relationships identified are less tightly constrained in space and time and indicate loose ties over more limited periods and narrower distributions. The present results suggest that such complex relationships can be deciphered more successfully by using analytical palaeobiogeographical patterns as proposed here rather than classical palaeobiogeographical units (biochores). © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Ammonoidea; biodisparity; Early Jurassic; morphospace; palaeobiogeography

1. Introduction

Ammonoids narrowly escaped extinction on several occasions before they were finally wiped out at the KT boundary. Only the genus *Rhacophyllites* (or a small number of closely related genera) survived one such near-extinction at the Triassic–Jurassic boundary (Tozer, 1981;

Guex, 1982, 1987; Rakús, 1993; Guex et al., 1998). The ensuing dramatic radiation was the result of derivation from the survivor taxon (or taxa). An earlier paper demonstrated that the recovery and radiation of the morphodiversity of the Early Jurassic ammonites was a complex process occurring during the first three stages of the Jurassic (Hettangian, Sinemurian, Pliensbachian) (Dommergues et al., 1996). Multivariate analysis of 18 morphologic characters of 436 representative species shows that the whole range of morphodiversity falls into two main morphologic sets (I, II), subdivided into 4 (a–d) and 5 (e–i) morphologic

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subsets (Fig. 1). The distributions of these subsets define a continuous morphospace (Fig. 2) bounded by extreme morphologies (e.g. discoid, serpenticone, cadicone, and sphaerocone…). These latter

denominations, although commonly used in the literature, do not actually fit the morphologic subsets used here, which also encompass less extreme and less remarkable morphologies. The staggered pattern of morphological recovery and radiation through the 36 subzones can be depicted from the defined morphospace regardless of phyletic relationships.

The study of Dommergues et al. (1996) was a global approach with no reference to palaeobiogeography. However, palaeobiogeography may provide a new insight into the resurgence of the Early Jurassic ammonites. The aim of the present study is to match the morphological sets and subsets with the distributional patterns of Early Jurassic ammonites. The distribution of taxa is generally considered in adjacent or non-overlapping elementary regions (e.g. the Euro-Boreal Province versus the Mediterranean Province on either side of the Early Jurassic incipient Western Tethys), as defined by faunal data (mainly endemism), but also by tectonic and/or sedimentary arguments (Cariou et al., 1985). Nevertheless, ammonite species were commonly distributed over several such elementary palaeobiogeographical regions and cannot readily be fitted into this sort of conventional framework. We have chosen to define patterns by considering the distribution and abundance of species over these regions. Any one such pattern corresponds to a type of distribution that is common to a group of taxa and must be distinctive from all other patterns suggested by the analysis. Each species, particularly the non-endemic species, can be assigned to a pattern that is truly representative of its potentially complex distribution. By ascribing each species to a palaeobiogeographical pattern, as well as to a morphologic subset, and by considering its stratigraphical range, it is possible to investigate the relationships between palaeobiogeography and morphodiversity through time.

1.1. Temporal pattern of morphospace occupation

The pattern of morphologic recovery and radiation can be approached and quantified in several ways: by the distribution of species, labeled by subset, on two factorial axes; by the measurement of the occupied part of the morphospace (PMO)
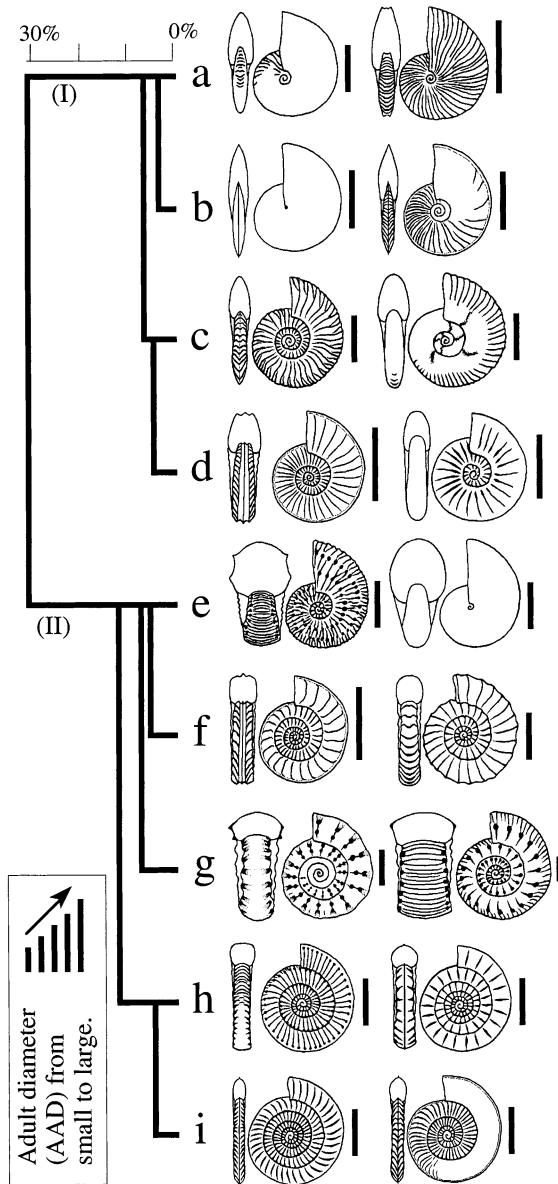

Fig. 1. Clustering of the ammonoid morphospace defines two clearly separate morphologic sets (I and II) composed of four (a–d) and five (e–i) morphologic subsets, respectively (from Dommergues et al., 1996).
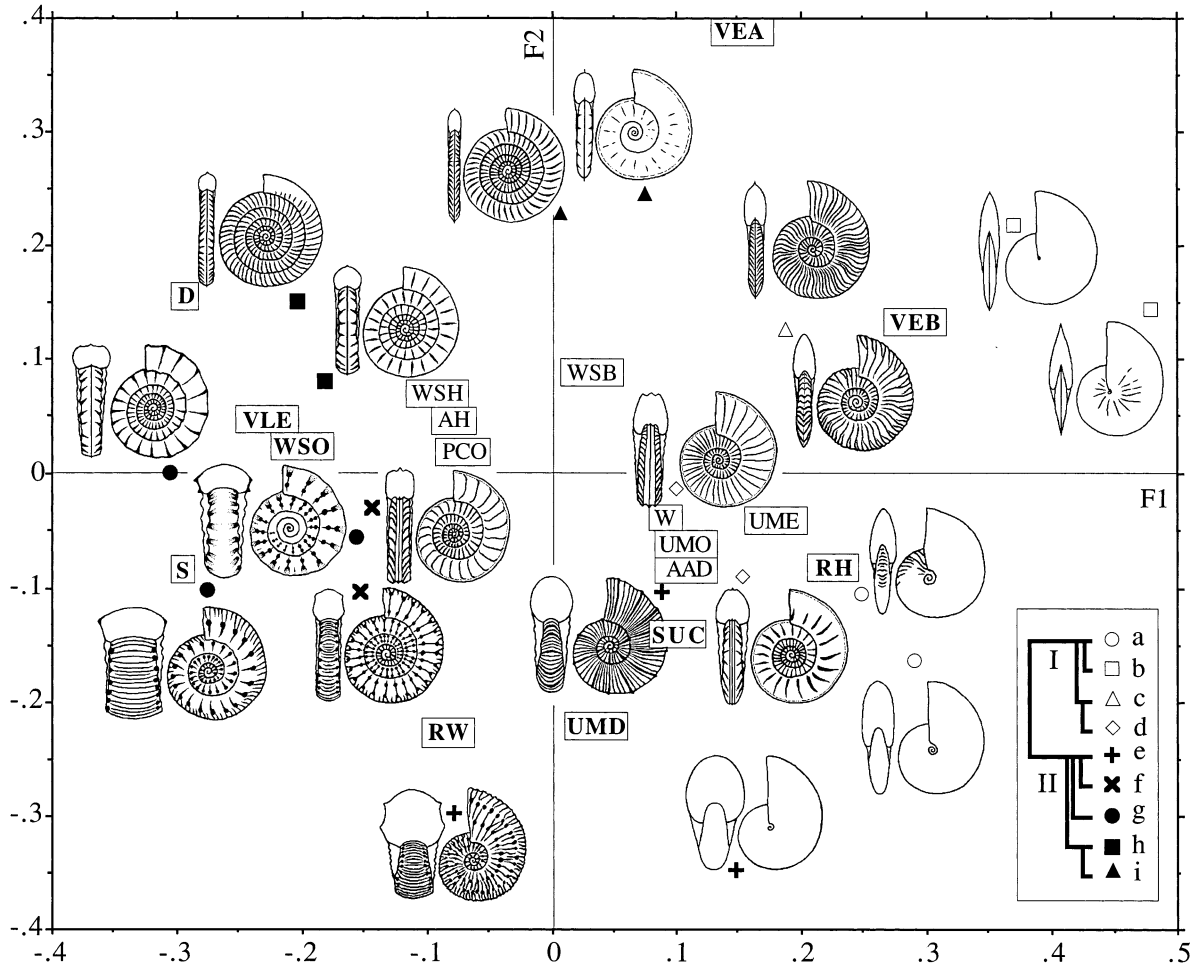
Fig. 2. Plot of some significant taxa for each morphologic subset on axes 1 and 2 of the analysis of correspondences of 18 variables (from Dommergues et al., 1996—see that paper for meanings of variables).

during a given subzone; by the variance around the origin on the first three factorial axes; by comparison, for each subzone, of the frequencies of species in each of the subsets, as weighted by a Shannon diversity index (SDI) (Dommergues et al., 1996). The variation of morphospace occupation through the 36 subzones may thus be depicted by looking at a selection of 12, which are considered particularly significant and which illustrate the major changes occurring through time (Figs. 3 and 4). From subzone 1 to 7, the initial increase in morphospace occupation is followed by a first decline mainly to the benefit of the outermost morphologies, resulting in a pattern with high variance in subzone 7. Then, from subzone 7 to 27, a progressive increase in morphospace occupation exhibits a brief reversal during subzone 16, related to the absence of subsets h and i. At the end of the series, from subzone 27 to 36, a new continuous decline in both PMO and SDI is observed. Rather than a process of diffusion, the Early Jurassic morphologic recovery and radiation consisted of a string of sequences of increasing morphodiversity, separated by episodes of morphospace decline. Moreover, the phases of growth or decline in morphospace involved different equilibria between the morphologic subsets.
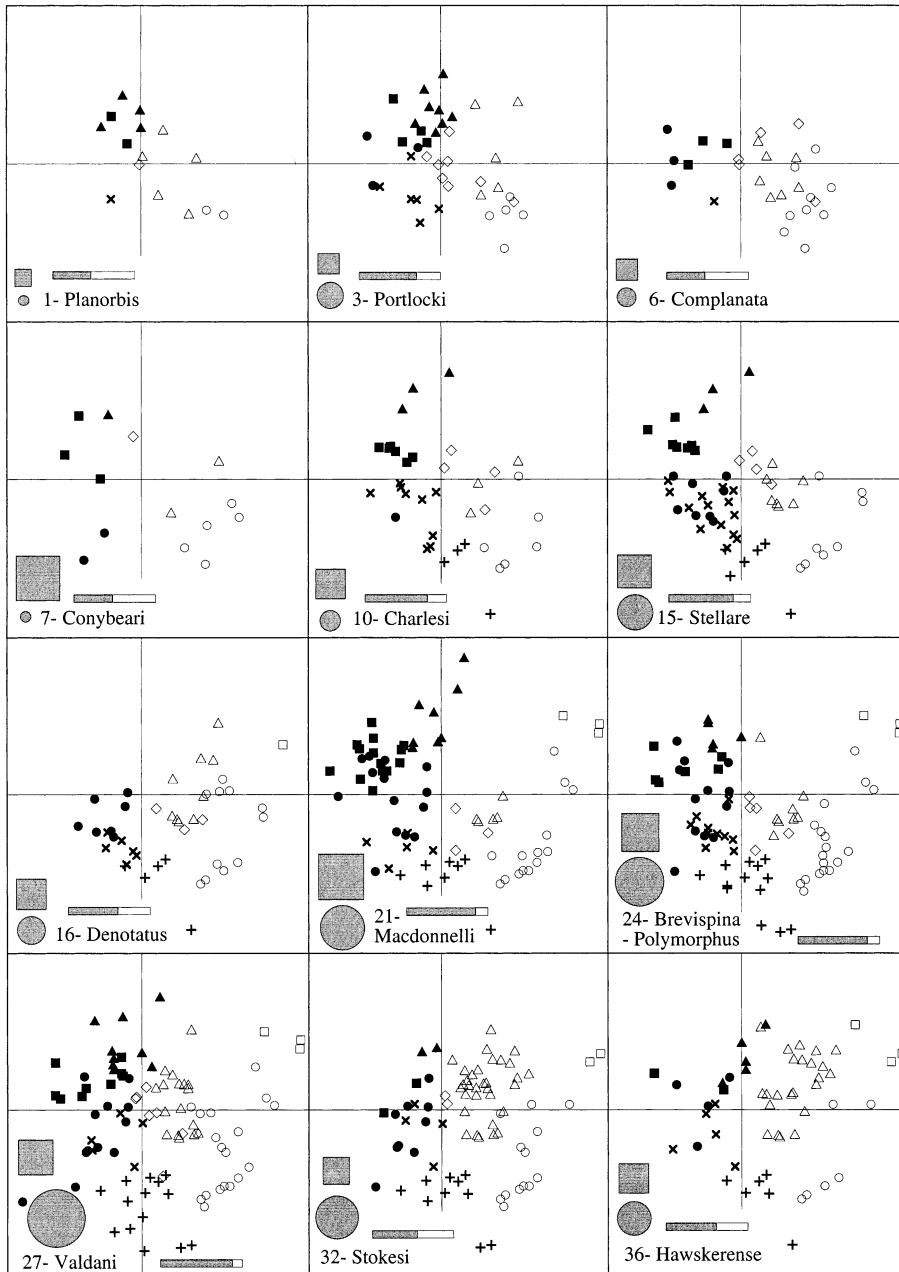
Fig. 3. Evolution of the Hettangian–Sinemurian ammonoid morphospace exemplified through nine significant steps. Size of the dark circle proportional to the PMO (percentage of morphospace occupation); size of the dark square proportional to the variance of the morphospace in the considered stratigraphical unit; gauge bar: value of the Shannon diversity index SDI [between 0.5 (entirely white) and 1 (entirely black)].

Previous studies have shown that the radiation began mainly with ubiquitous species and that it reached a phase of strong palaeobiogeographical differentiation resulting mainly in increased endemism (from species to family), with a maximum during the Early Pliensbachian (=Carixian),
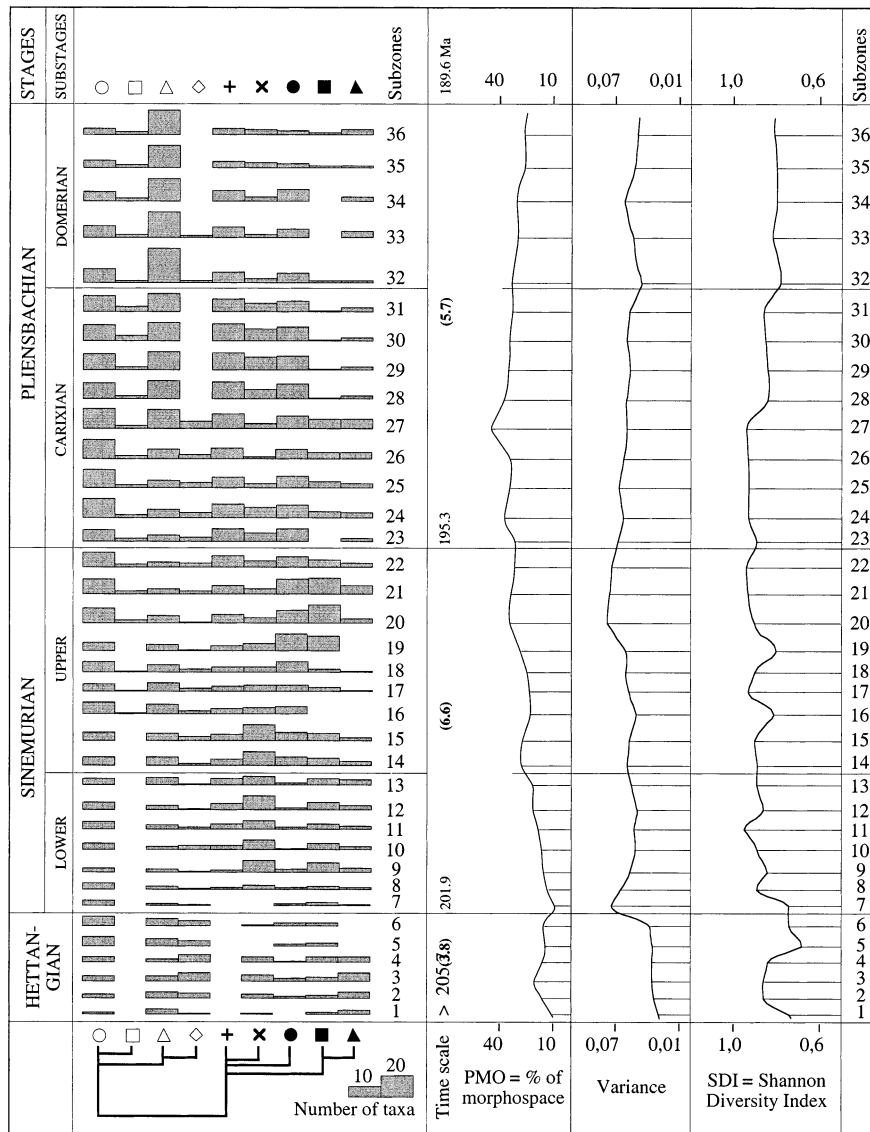
Fig. 4. Variation of the number of taxa in each morphologic subset through the 36 subzones, relative to the PMO, to the variance, and to SDI. Time scale from Gradstein et al. (1994).

followed by a decrease during the Late Pliensbachian (= Domerian) (Enay, 1980; Enay and Mangold, 1982; Mouterde and Elmi, 1993; Dommergues, 1994; Ferretti and Meister, 1994). The job in hand is therefore to explore and quantify the connections between this alleged taxonomic trend and the way morphodiversity is structured.

2. Material and methods

The 436 species used in this study are those used in the study of morphodiversity (Dommergues et al., 1996). The stratigraphical framework of the study covers the three first stages of the Early Jurassic.

2.1. Characterization of palaeobiogeographical patterns

In a conventional approach, the distribution of the studied ammonites can be described by reference to a framework of 15 elementary palaeobiogeographical regions (Fig. 5). These are defined by their fauna and geology s.l. Using a huge, world-wide database of almost all the Liassic ammonites illustrated in the literature, the distribution of each of the 436 species is estimated for each region, based on an evaluation of the relative abundance of each species: 0=absent, 1=only a few specimens, 2=rare, 3=common, 4=dominant. This evaluation is not a true quantification, but it is the only method applicable at the world-wide scale for processing the highly heterogeneous literature on ammonites. Although partly subjective, this method is sufficiently reliable to describe the principal trends in space and time. The data are processed by factor analysis of correspondences of the table of frequencies (0–4). The results are used to construct a dendrogram from which the palaeobiogeographical patterns can be identified. The number and significance of the patterns are estimated from their variances. The analyses are performed using the ANCORR, then the CAHVOR procedures of the ADDAD package (ADDAD, 1989). Thus, in this work, a palaeobiogeographical pattern is a particular type of distribution and abundance across the 15 elementary palaeobiogeographical regions shared by a set of species. Such a pattern can range from a restricted to an extensive part of the Early Jurassic seas and oceans.

Description of the elementary palaeobiogeographical regions:

1. Northern Mediterranean Threshold (A in Fig. 5): This includes all the allochthonous and autochthonous Alpine (*s.s.*) units belonging to the southern margin of the Western Tethys. Thus, it covers the whole of the southern Alpine and Austroalpine outcrops from Italy, Switzerland and Austria. Some Hungarian (e.g. Bakony Mountains) and Slovakian (e.g. Slovac Karst) localities are also included in the Northern Mediterranean Threshold. Although the faunas of this area are essentially constituted by
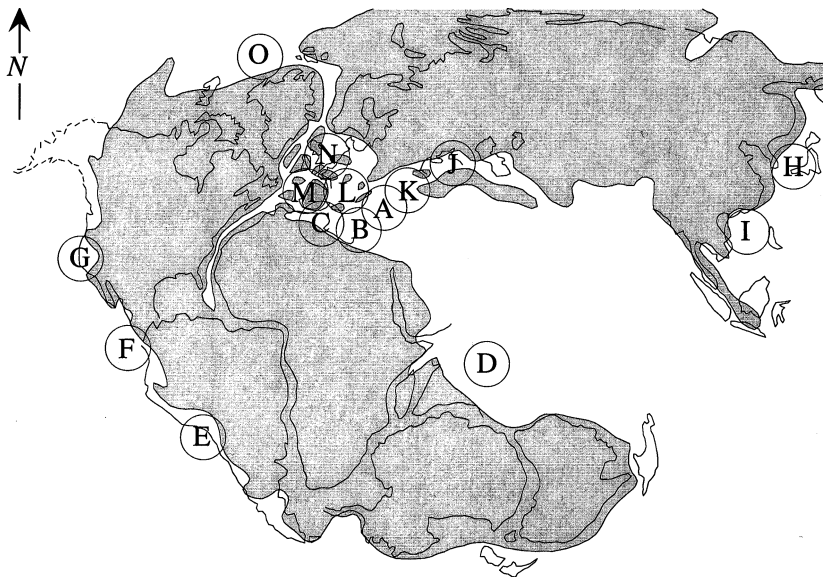

Fig. 5. Location of the 15 (A–O) elementary geographical regions. Ringed letters suggest the geographical position of the central part of each region. Some of them (D, E, G, O) cover very wide areas, and in these cases, the letter location gives only a rough indication. See the text for explanations about the exact contents and boundaries of the regions. Palinspastic reconstruction for the Early Jurassic modified from Owen (1983).

'Mediterranean' components, some conspicuous Celtic faunal ingressions can be observed locally (e.g. *Uptonia*, *Beaniceras*, *Aegoceras*…) (Dommergues et al., 1983; Dommergues and Meister, 1991). The fossil record is good (i.e. numerous specimens and rare stratigraphic gaps) for the Hettangian and Pliensbachian, but data are piecemeal for the Sinemurian. Northern Mediterranean Threshold endemic lineages are few in number.

2. Central Mediterranean Threshold (B in Fig. 5): This includes many of the classical Mediterranean fossiliferous localities. They are scattered over a wide, roughly central, part of the Western Tethys. Thus, from West to East, the Central Mediterranean Threshold includes the Algarve (Portugal), the Betic Range (Spain) the Calabro-Peloritan Sicilian sections (e.g. Taormina) as well as the Apennines (Italy) and the Hellenids (Greece). The Celtic faunal ingressions are either very rare (e.g. Late Pliensbachian in the Betic Range) or insignificant or even absent (e.g. Apennines or Hellenids). The fossils start to become frequent only from the Sinemurian (e.g. Semicostatum – Obtusum zones) (Dommergues et al., 1994). Before this time, data are usually rare and sparse (Braga et al., 1984). Endemic taxa are common in this area.

3. Southern Mediterranean Threshold (C in Fig. 5): All the sections considered here are from the North African Margin (Morocco, Algeria and Tunisia). They are either part of the North African Alpine Belt (e.g. Rif, Kabyle Range) or of the Atlas Ranges. Some Celtic faunal ingressions are known in the Moroccan and Algerian Late Pliensbachian (e.g. *Amaltheus*) (Cariou et al., 1985). As with the Central Mediterranean Threshold, the Hettangian and Early Sinemurian fossil record is also very incomplete here. It improves locally in the Late Sinemurian (e.g. Semicostatum–Obtusum zones) and becomes generally good from the Early Pliensbachian. By comparison with the Mediterranean Threshold as a whole, the Southern Mediterranean faunas include numerous endemic lineages, especially in Tunisia and in the Atlas localities and mainly at the generic level (Dommergues et al., 1986; El-Harriri et al., 1996).

4. North-eastern and Eastern Gondwana (D in Fig. 5): This wide and complex region includes some rare and scattered fossiliferous localities (e.g. Early Domerian in Baluchistan, Hettangian in New Caledonia) along the north-eastern and eastern margins of the Early Jurassic Gondwana remains (Pakistan, Western Africa, Australia, etc.). As a result, the North-eastern and Eastern Gondwana yield little information. Data are not significant for the quantitative analysis but help clarify a number of problems.

5. Western South America (E in Fig. 5): This palaeogeographical region covers the Andean localities, chiefly in Argentina and Chile, that sometimes yield abundant information. The Western South America region forms a broad, but fairly homogeneous, domain, at least as regards its endemic taxa (e.g. *Eoamaltheus*). It is reasonably well documented from the Early Hettangian to the Late Pliensbachian. It is characterized by several conspicuous endemic (Andean or West American) lineages. The presence of Mediterranean, Lusitanian or Celtic ammonites is doubtful, although it has been suggested by several authors (e.g. Hillebrandt, 1981).

6. Western Central America (F in Fig. 5): Unlike the rather continuously documented southern (Andean) and northern (mainly Athabascian) parts of the Western American Ranges, the Central American data are mainly confined to the Late Sinemurian. The fossiliferous successions situated in Mexico were deposited during a short transgressive episode. Geological data suggest that the Sinemurian gulfs connected up with the Pacific Ocean, and not with the Mediterranean and/or Lusitanian seas via a hypothetical 'Hispanic corridor' (Bassoulet et al., 1993). The Early Jurassic faunas of Mexico are mainly composed of ubiquitous taxa (e.g. *Arnioceras*, *Plesechioceras*), and they are of little weight in the data computation.

7. Western North America (G in Fig. 5): This region includes numerous, more or less allochthonous, terranes that are completely integrated at the present time in the highly complex North American Western Ranges (Rowley, 1992). Nevertheless, the north-eastern autochthonous units of these ranges (= Western Interior) are dominated by Arctic influences (Frebold, 1970; Poulton

et al., 1992) and are here excluded from Western North America area but analyzed with the Circum-Arctic area (cf. region O below). Throughout the period under study, the palaeontological data are usually plentiful and often of good quality. Western North America is one of the rare regions of the world to yield good information about the Early Hettangian (Guex, 1995). Taxa endemic to Western North America or West America are not rare in this region (Dommergues, 1994). Nevertheless, if viewed as a whole, Western North American faunas suggest Tethyan (*s.l.*) affinities. Although suggested by some authors (e.g. Smith et al., 1988; Thomson and Smith, 1992), the presence of Mediterranean or Lusitanian taxa (e.g. *Metaderoceras beirense* Mouterde, *Dayiceras* sp.) remains questionable. Conversely, there may have been Celtic and/or Boreal ingressions from a northerly direction (e.g. *Amaltheus*).

8. Japan (H in Fig. 5): Apart from some scarce Sinemurian ammonites, the Late Pliensbachian is the sole documented period for this area, which has mainly yielded Domerian Hildocerataceae and rare Amaltheidae (Sato et al., 1991). As a result, Japanese data are of little weight in the data computation as a whole. In spite of weak Circum-Arctic arrivals, the available material suggests prevalent Tethyan *s.l.* affinities, at least for the Late Pliensbachian.

9. South-eastern China, Indochina, Northern Borneo and Timor (I in Fig. 5): While highly complex in geological, geographical and palaeogeographical significance, this area includes scattered fossiliferous localities belonging either to the far eastern part of the northern margin of the Tethys, or associated with terranes suspected to have been close to that margin during Early Jurassic. Faunal data are also complex and often difficult to interpret because of the usual lack of good fossiliferous strata and the presence of several enigmatic endemic forms (Sato et al., 1991; Meister et al., 2000). Even so, this area yields interesting information about the Early Jurassic (mainly Sinemurian) ammonites of this distal part of the Tethys, but its influence remains of minor importance for the global analysis.

10. Pontic Range, Caucasus and Northern Iran (J in Fig. 5): This area is mainly documented by the fossiliferous localities of the Pontic Range (Northern Turkey), which yield plentiful and diversified Late Sinemurian and Early Pliensbachian ammonite faunas (Alkaya and Meister, 1995). Although they are less studied, ammonite faunas from the Caucasus and Northern Iran provide important complementary data (e.g. the Iranian Amaltheidae) (Pourmotamed and Motamed, 1976). The faunas of this Northern Tethyan Margin area display interesting endemic trends especially during the Early Pliensbachian, but viewed as a whole, they exhibit clear southern Celtic affinities versus weak Mediterranean ones.

11. Carpathians, Balkans and Northern Dobrogea (K in Fig. 5): This area includes fossiliferous localities in the Carpathians (Romania) and Balkans (Bulgaria) roughly ringing the Moesian platform. Data are chiefly available for the Sinemurian and Pliensbachian Stages, but the fossiliferous localities are usually scattered, and ammonites are seldom common (Dommergues et al., 1987; Popa and Patrulius, 1996). Although rather poorly documented, this area yields interesting data for the Northern Tethyan Margin and provides information about the transition patterns between the Northern Mediterranean Threshold and South Celtic areas on the one hand, and the Pontic Range, Caucasus and Northern Iran area on the other hand.

12. Southern Celtic (L in Fig. 5): This area, which is one of the best documented in the world, includes many classical regions such as Southern Germany, the Jura Mountains, Burgundy, the Paris Basin, the Causses Basin, the outer units of the Western Alps, and the Iberian Basin. The area also provides a wealth of data for all the three stages analyzed here. Together with the Northern Celtic area, this area is the cradle of biostratigraphical studies, where the North-West European zonal and subzonal standard scale for the Early Jurassic was first established. Moreover, and at least from the Early Domerian onwards, the Southern Celtic area records frequent Mediterranean ingressions and is thus a key area for establishing correlations between Celtic *s.l.* and Tethyan *s.l.* successions (Dommergues and Mouterde, 1980; Meister, 1987). Celtic biotic distinction (endemicity) was high principally during the Pliensbachian with the

acmes of the Liparoceratidae and Amaltheidae (Cariou et al., 1985).

13. Lusitanian Basin (M in Fig. 5): This Portuguese area is considered here as a distinct palaeobiogeographical unit although restricted to a narrow basin without ammonite faunas before the Late Sinemurian because of the numerous and remarkable Lusitanian endemic taxa (e.g. *Pompeckioceras*, *Dayiceras*), which dominated the assemblages during the Late Sinemurian and especially during the Early Pliensbachian (Dommergues and Mouterde, 1987). Nevertheless, and despite these dramatic endemic events and frequent Mediterranean ingressions since the Early Domerian, the Lusitanian Basin faunas express the closest affinities with the Celtic *s.l.* faunas. Although Lusitanian endemic taxa, chiefly the genus *Dayiceras*, are sometimes ranked among the Mediterranean faunas (Rakús, 1972; Faraoni et al., 1996), we consider that such references result from the presence of homoplasic taxa in the non-Lusitanian area. In fact, among *Dayiceras*, *D. polymorphoides* (Spath) is the only species that oversteps the Lusitanian Basin boundary and reaches northward to the Dorset Basin (Southern England).

14. Northern Celtic (N in Fig. 5): This area covers the numerous and very rich localities of the British Isles and Northern Germany, and the scarce and less fossiliferous outcrops of Southern Scandinavia. Northern Celtic faunas have, in many respects, a similar composition to those of the Southern Celtic area, but Mediterranean ingressions become scarcer northward, and the richness and diversity of the assemblages also decrease. In fact, Celtic endemic taxa (e.g. Polymorphitidae, Liparoceratidae, Amaltheidae) are usually clearly dominant among the Northern Celtic assemblages (Cariou et al., 1985).

15. Circum-Arctic (O in Fig. 5): This complex area includes fossiliferous deposits closely linked with the margin of the Early Jurassic Arctic Ocean (e.g. Northern Canada, Eastern Russia). Moreover, the Western Interior (cf. Western North-America) and East Greenland are also included within the Circum-Arctic area, in view of their affinities with the northernmost faunas. In fact, the Western Interior and East Greenland could also be viewed as transitional steps between the Circum-Arctic area (*s.s.*), and the Western North America and Northern Celtic regions. The Hettangian, Sinemurian and Late Pliensbachian faunas are fairly well documented in the Circum-Arctic area. Conversely, except for some very rare data from East Greenland (e.g. *Uptonia*, *Beaniceras*) (Rosenkrantz, 1934), the Early Pliensbachian faunas are unknown.

2.2. Relationships among morphology, palaeobiogeography and stratigraphy

The foregoing analyses ascribe to each species both a location in the morphospace and a palaeobiogeographical pattern as defined above (=a type of distribution and abundance across the 15 elementary palaeobiogeographical regions shared by a set of species). Moreover, the stratigraphical range of each species is defined on a subzonal scale. It is thus possible to look at the relationships among these three parameters.

This can be done in a table grouping the morphologic and palaeobiogeographical data into just 22 stratigraphical units defined from the 36 subzones. This simplification is possible because the previous analysis reveals successions of two to four subzones without any noticeable change in morphospace and palaeobiogeographical pattern. For each stratigraphical unit, the number of species of a given morphologic subset in a given palaeobiogeographical pattern constitutes the basic data of this next step of the analysis. This kind of three-entry table may be read by considering, through the stratigraphical units, the distribution of the palaeobiogeographical patterns in the morphologic subsets, and vice versa. The total table is processed by a factor analysis of correspondences with the morpho-subsets as columns (variables) and the palaeobiogeographical pattern through each stratigraphical unit as rows.

3. Results

The analysis of correspondences of the 436 species across the 15 elementary palaeobiogeographical regions and the 36 subzones, according

to their estimated abundances, produces factor scores that were processed by hierarchical clustering covering the first six factors (which account for 65% of the total variation). The resulting dendrogram reveals seven significant subsets of taxa representing the palaeobiogeographical patterns (1–7 in Fig. 6). The distribution of the variance on the dendrogram shows two well-separated groups and two intermediate groups. The first group (I) includes palaeobiogeographical patterns 1–3 (189 species), and the second group (II) includes patterns 6 and 7 (194 species). Almost equally spaced between these two groups, but also rather separate from one another, two minor groups (III, IV) correspond to palaeobiogeographical patterns 4 and 5, that contain just 29 and 24 species, respectively. Group I corresponds mainly to Mediterranean patterns, while Group II expresses a Celtic trend. Thus, each palaeobiogeographical pattern is characterised by a set of species, each species belonging to one, and only one, of these patterns. Each pattern may be ascribed palaeobiogeographical significance, based on the estimated abundance ($0=$ absent, $1=$ only a few specimens, $2=$ rare, $3=$ common, $4=$ dominant) of the species it includes, through the 15 (A–O) elementary plaeobiogeographical regions. For each pattern, the average abundance of all the species included in the set was calculated for each elementary paleobiogegraphical region. The average values (from 0 if the set is entirely absent in the region in question, to an observed maximum average of 3.1 if the species included in the set are common and sometimes dominant in the region) are ranked on a four-point graphic scale, from (α) to (δ), for rough and ready visualisation on Figs. 6–8. The palaeobiogeographical meaning of a pattern thus arises from the regions where the abundance of the set of species is represented by a large (δ) or at least a medium black dot (γ) on Figs. 6–8.
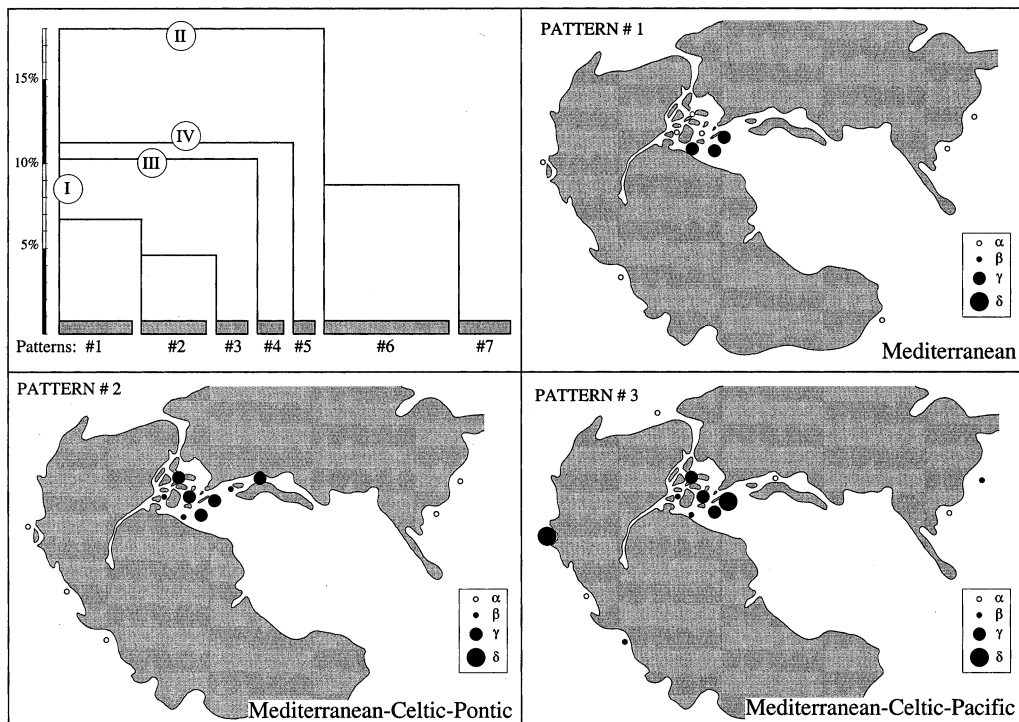

Fig. 6. Clustering of the species in seven palaeobiogeographical patterns, divided into four (I–IV) main groups and palaeobiogeographical patterns 1–3. Symbols α to δ (small ring to large black dot) correspond to a four-point graphic scale allowing a rapid visualisation of the average abundance, in an elementary palaeobiogeographical region, of all the species included in a given pattern.
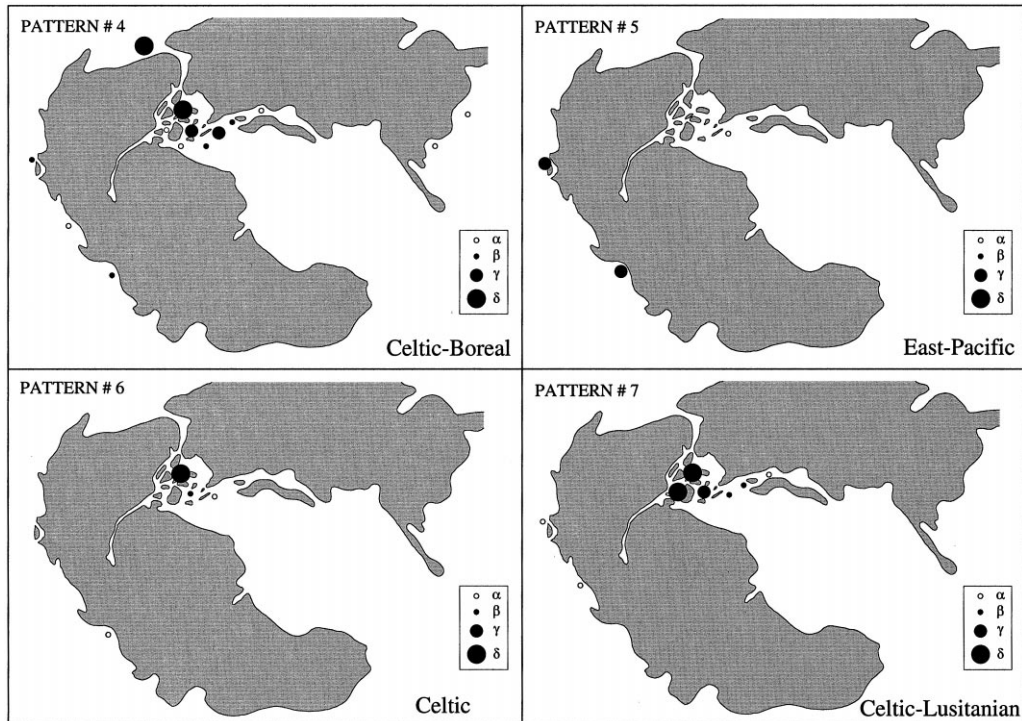
Fig. 7. Palaeobiogeographical patterns 4–7. Symbols α to δ (small ring to large black dot) correspond to a four-point graphic scale allowing a rapid visualisation of the average abundance, in an elementary palaeobiogeographical region, of all the species included in a given pattern.

3.1. Description of palaeobiogeographical patterns

1. Mediterranean pattern (Fig. 6): This pattern includes 82 taxa that share a distribution concentrated on the Mediterranean regions A, B and C (medium black dots, γ), where they are usually common but infrequently dominant. Outside these regions, species belonging to the Mediterranean pattern are rarely found (small ring, α), while they are never found in the Boreal area (O).

2. Mediterranean–Celtic–Pontic pattern (Fig. 6): The 72 species included in this pattern cover the main area of pattern 1 (regions A, B and C), but extend northward into regions L and N, and eastward into regions J and K. As suggested by small (β) or medium (γ) black dots, the significant species of the pattern are rare or common (evaluated abundance = 2 or 3) in these regions but are almost never dominant. Going deeper into the topology of the dendrogram, this pattern may be split into three

'sub-patterns' (2a–2c in Fig. 8). The sub-patterns express the same kind of geographical distribution, but with slight differences in average abundances. Thus, the Pontic area (J) appears in each sub-pattern either with a small ring (α) or with a medium black dot (γ). This example demonstrates the relevance of the pattern at the chosen level of significance.

3. Mediterranean–Celtic–Pacific pattern (Fig. 6): The 35 species belonging to this pattern share a fairly similar distribution to those of pattern 2, but also occur in the Western North-American region (G). Moreover, as suggested by the large black dots (δ), these wide ranging species are often dominant (evaluated abundance = 4) both on the Mediterranean Threshold and in Western North-America.

4. Celtic–Boreal pattern: This small pattern consists of 29 species that prevail as suggested by large black dots (δ) in both Boreal (O) and Celtic
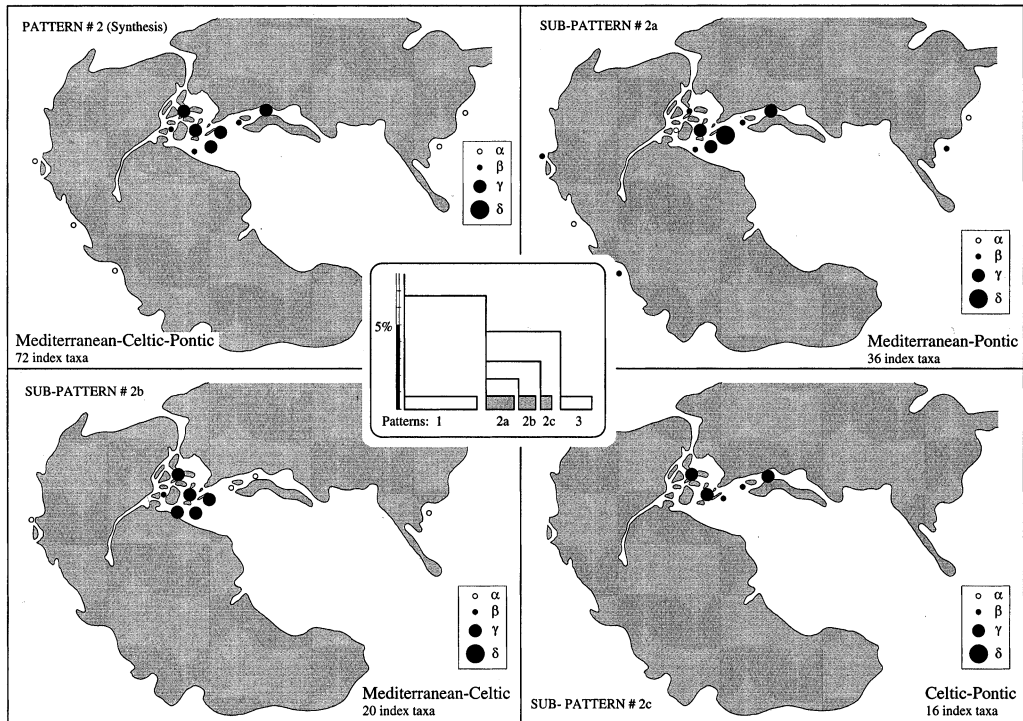
Fig. 8. Palaeobiogeographical pattern 2: break down into three sub-patterns (2a–2c) according to clustering within pattern 2 (grey boxes on partial cluster diagram) (symbols α to δ, small ring to large black dot) correspond to a four-point graphic scale indicating the average abundance, in an elementary palaeobiogeographical region, of all the species included in a given pattern.

(N) areas. This pattern exhibits a clear northern component, even if species are also observed in the Mediterranean or Western American areas.

5. East-Pacific pattern: The 24 species of this pattern are restricted to the Cordilleran and Andean Ranges (areas E–G) where they are usually common (evaluated abundance = 3) but infrequently dominant.

6. Celtic pattern: This pattern includes 135 species virtually endemic to the Celtic region (N). As reflected by the large black dot (δ), they are often common or dominant (evaluated abundance 3 or 4). This pattern is the most restricted in distribution, and contains the greatest number of taxa.

7. Celtic–Lusitanian pattern: This pattern consists of 59 species that usually prevail (evaluated abundance = 4) both in the Celtic (N) and in the Lusitanian (M) areas, but that also occur with lesser abundance in some adjacent Mediterranean regions.

It should be noticed that patterns 4 and 7 are not recorded in the Carixian and Hettangian–Early Sinemurian intervals, respectively (Fig. 9). This is due to the lack of any fossil record in the Arctic areas during the Carixian, and in the Lusitanian region during the Hettangian and Lower Sinemurian.

3.2. Relationships between morphologic and palaeobiogeographical patterns

Morphospace occupation varies over time at the global scale (Dommergues et al., 1996). Thus, the proportions of each morphologic subset can vary dramatically from one stratigraphical unit to another (Fig. 9 grey column). In such a framework, the null hypothesis about the distribution of a morphologic subset in the seven palaeobiogeographical patterns is that the proportions of each morphologic subset should be the same as in the global distribution in a given stratigraphical unit.
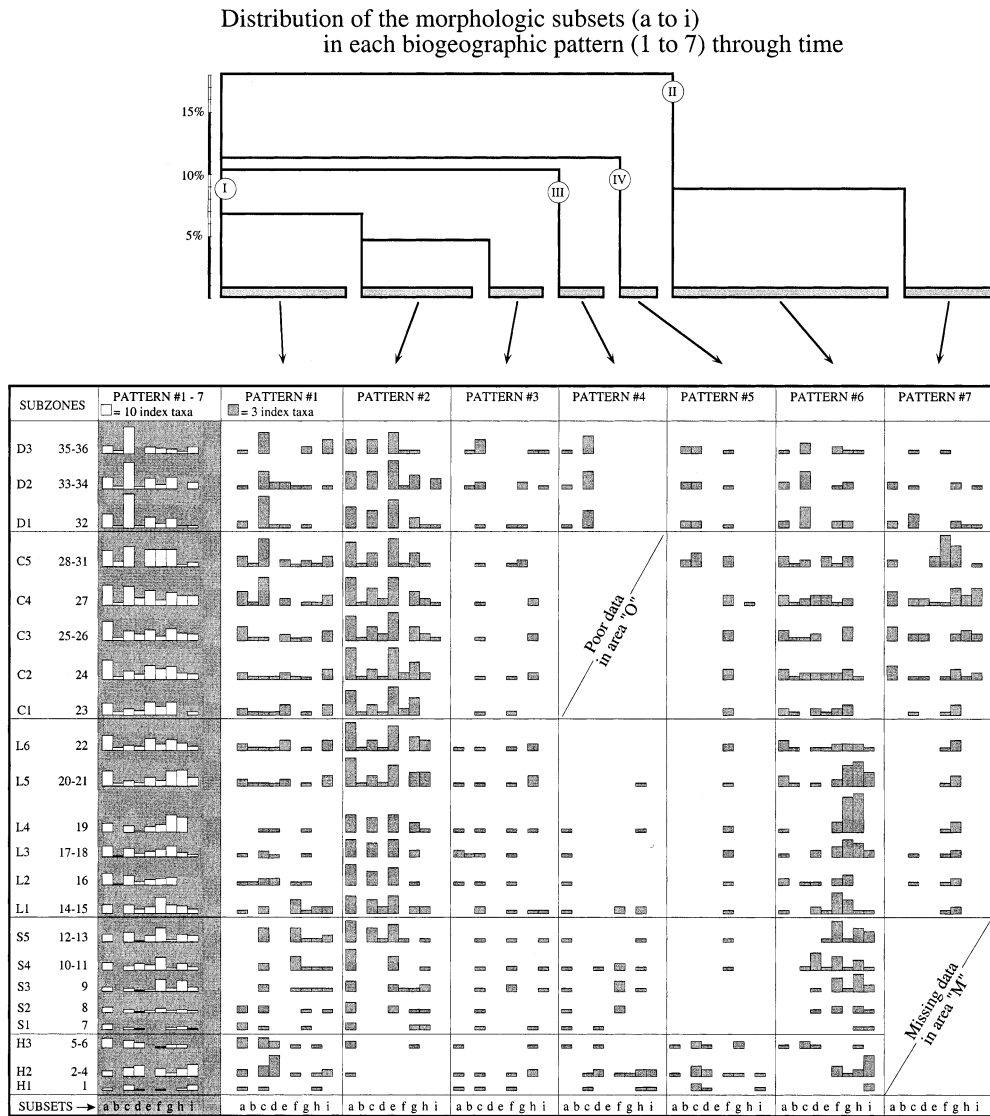
Fig. 9. Variation of number of taxa in each morphologic subset (a–i) through 22 stratigraphical units (covering sub-zones 1–36), for the whole set of taxa (grey column), and divided into palaeobiogeographical patterns #1–#7 (white columns).

This hypothesis would mean that no criteria, whether species phylogeny, geographical thresholds, or latitudinal distribution, influence the distribution of shape. The null hypothesis is clearly rejected by analysis of Fig. 9, which compares the global distribution and its subdivision into seven palaeobiogeographical patterns, and of the reciprocal Fig. 10 in which the distribution of each morphologic subset is considered by palaeobiogeo-

graphical patterns. Some features of the distribution of morphologies versus palaeobiogeographical patterns are noteworthy and can be described.

A clear discrepancy occurs between palaeobiogeographical patterns 1 (Mediterranean) and 2 (Mediterranean–Celtic–Pontic) (Fig. 9). In pattern 1, no obvious trend appears before the middle part of the Carixian (stratigraphical unit C4), after which, morphology c becomes predomi-
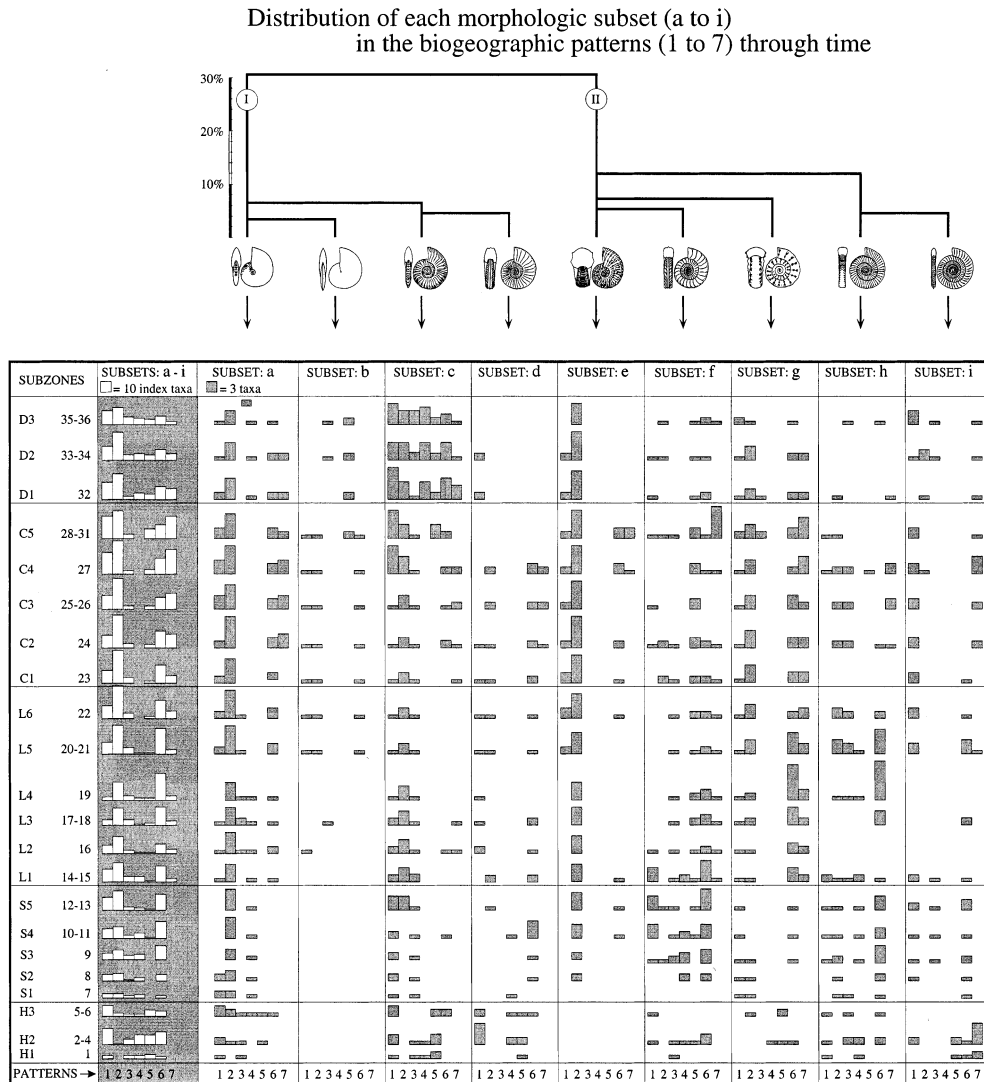
Fig. 10. Variation of number of taxa in each palaeobiogeographical pattern (#1–#7) through 22 stratigraphical units (covering subzones 1–36), for the whole set of taxa (grey column), and divided into morphologic subsets (a–i) (white columns).

nant. By contrast, in pattern 2, morphologies a and e become predominant as early as the Sinemurian, morphology c being significant, but less clearly expressed. those differences concern two very close Mediterranean palaeobiogeographical patterns: the Mediterranean area covered by pattern 1 being included in pattern 2. Despite this geographical similarity, the species grouped in pattern 2 occupy a constant particular part of the morphospace during the period in question, while

the species in pattern 1 do not express any sustained trend, except with morphology c at the end of the succession. Analysis of correspondences confirms these trends (Figs. 11–14). For pattern 1, the content of the stratigraphical units of the Early Sinemurian is clearly associated with morphologies f and i, and the samples from Late Carixian and Domerian are plotted near morphology c (b being totally absent in that pattern) (Fig. 11). On the plot of the closely focused pattern
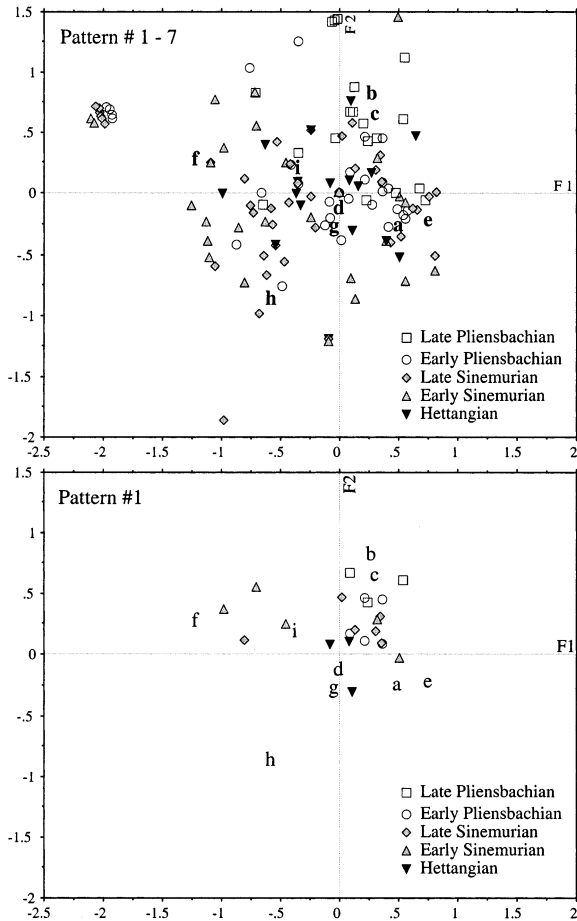
Fig. 11. Multivariate analysis of the data of Fig. 10 (white columns). Plots of the contents of each biostratigraphical unit in terms of number of taxa in each palaeobiogeographical pattern (symbols grouped by sub-stage) against the morphologic subsets (a–i). Top diagram: whole set of data; bottom diagram: detail of pattern #1.

Fig. 12. Plots of the contents of each biostratigraphical unit in terms of number of taxa in each palaeobiogeographical pattern (symbols grouped by sub-stage) against the morphologic subsets (a–i). Top diagram: detail of pattern #2; bottom diagram: detail of pattern #3.

2, many levels (from stratigraphical unit S5 to D3) are aggregated around morphologies a and e, with c being insignificant (Fig. 12).

Another pattern with significant variations through time is pattern 6 (Celtic), one of the best documented with the most taxa. From the Hettangian to the Late Sinemurian (L5), morphologies f, g, h are predominant (sometimes dramatically), while morphologies a–g occur in similar proportions during the Carixian. The Domerian is characterized by the prevalence of morphology c. This is well su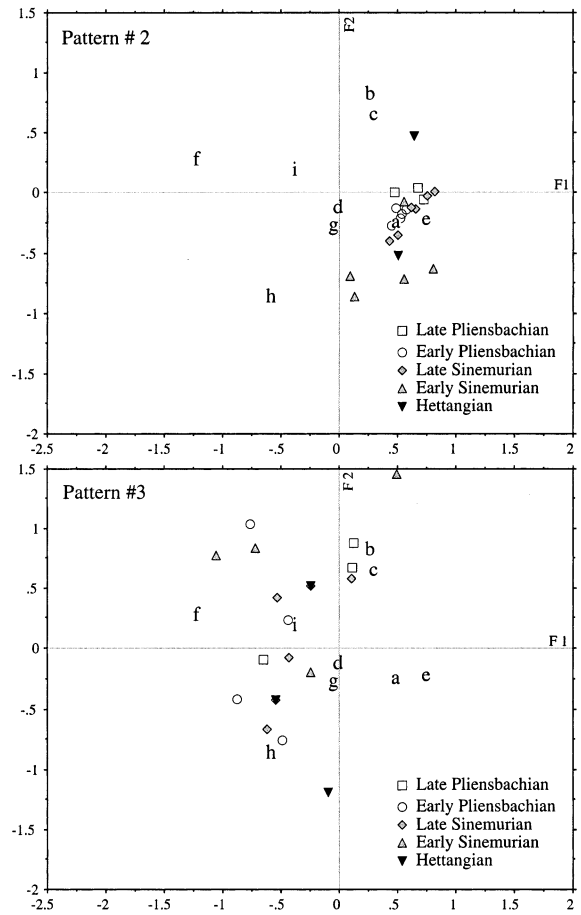pported by the graph of factorial axes (Fig. 14), where the Sinemurian levels are plotted in the triangle defined by morphologies f, g, and h. The Early Pliensbachian levels are located close to morphologies a, d, and e, and the Late Pliensbachian levels are close to morphology c (b being absent from that pattern).

The highly expanded pattern 3 (Mediterranean–Celtic–Pacific), with a small number of species, is represented by all the morphologies without any clearly expressed trend. Roughly, the distribution of morphologies over time seems random, as shown by the very unordered and scattered location of the levels on the factorial axes (Fig. 12).
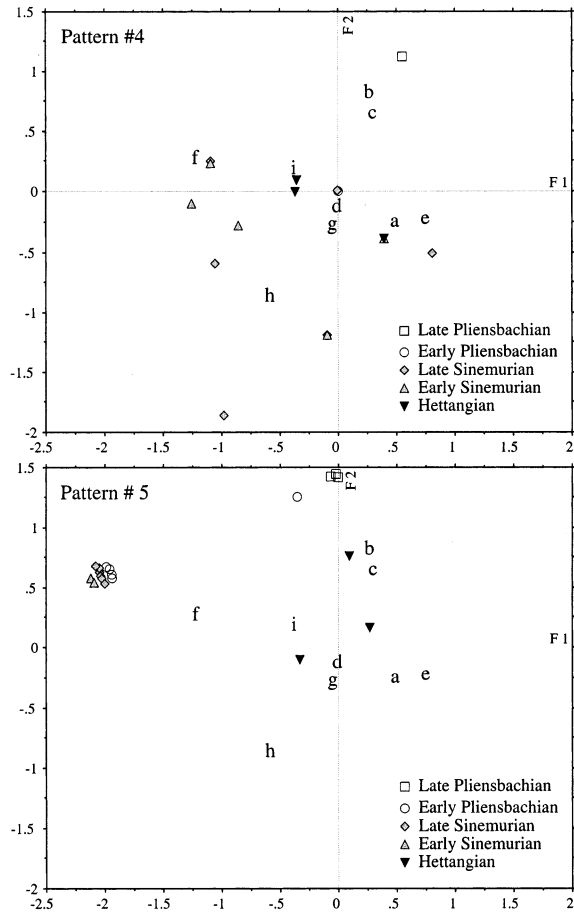
Fig. 13. Plots of the contents of each biostratigraphical unit in terms of number of taxa in each palaeobiogeographical pattern (symbols grouped by sub-stage) against the morphologic subsets (a–i). Top diagram: detail of pattern #4; bottom diagram: detail of pattern #5.
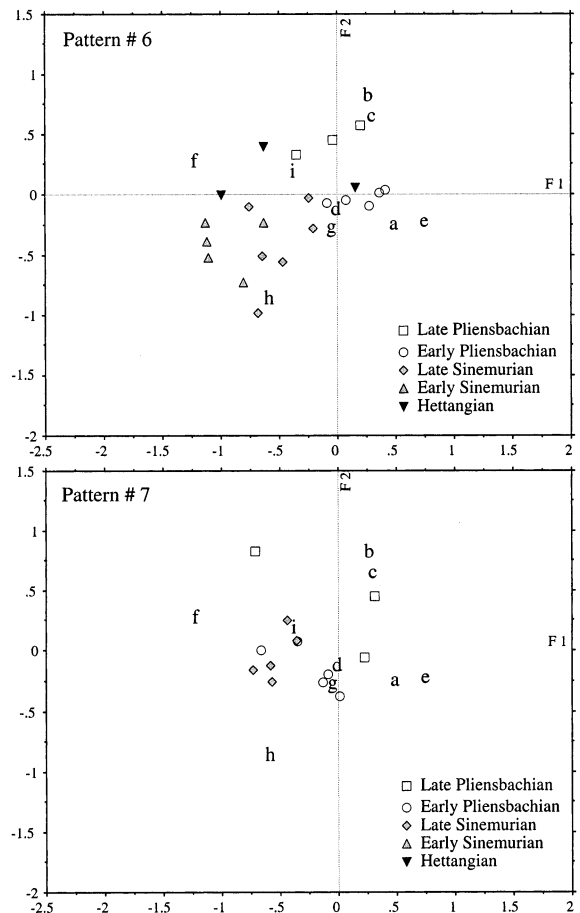

Fig. 14. Plots of the contents of each biostratigraphical unit in terms of number of taxa in each palaeobiogeographical pattern (symbols grouped by sub-stage) against the morphologic subsets (a–i). Top diagram: detail of pattern #6; bottom diagram: detail of pattern #7.

Although pattern 5 (East-Pacific) expresses various morphologies during the Hettangian, it later collapses except for morphology f until the end of the Carixian and then turns to morphologies b and c. On the scatter diagram of the multivariate analysis, the Sinemurian (except S1–S3) and Carixian levels (except C5) are plotted close to morphology f, while C5 and the Domerian levels are located near morphologies b and c (Fig. 13).

From the opposite standpoint (by morphologic subsets—Fig. 10), i.e. the occurrences of the seven patterns in each morphology, some significant cases can be pointed out. One of the most obvious

relationships concerns morphologic subset e, which is almost exclusively linked to pattern 2 from the Sinemurian onwards. This suggests that the unusual shapes with deep umbilicus, rounded whorl section, and highly complicated suture line constituting this group (e.g. Lytoceras *pro parte*, Phylloceras *pro parte*, Liparoceratidae *pro parte*) are found both in the Mediterranean area and in the neighbouring Northern Celtic area .

Morphologic subset a, including involute compressed ammonites with rounded venters, is also well expressed in pattern 2 (Mediterranean–Celtic–Lusitanian) from the Hettangian onwards. During

the Carixian, numerous taxa belonging to subset a also appear in endemic patterns 1 (Mediterranean) and 6 (Celtic), 7 (Celtic–Lusitanian), all patterns that are geographically included in pattern 2.

Morphologic subset c, expressed across the total stratigraphical range, corresponds to small platyconic ammonites. The distribution of this subset occurs in patterns 1, 3–6 during the Hettangian; subsequently, it is mainly reduced to mostly Mediterranean patterns 1, then 2 (S1–C3). It then becomes largely predominant in the same patterns in stratigraphical unit C4, with re-appearance or increase in other patterns. Mainly related to the Mediterranean and Mediterranean–Celtic–Pontic patterns, this trend subsequently achieves a generalized distribution through the seven patterns throughout the Domerian. This is a unique case where a morphology is simultaneously expressed with a relevant number of taxa in all the patterns: thus, the Domerian appears as the age of small platycone ammonites.

Morphologic subset f of broader, slightly evolute shells with deep umbilicus and arched venter, displays an almost generalized distribution during the Sinemurian (S3 to L1) with predominance in the Celtic pattern (6). Later, the number of taxa decreases in all the patterns, before becoming abundant again in the Late Carixian, with predominance, once again, in the Celtic–Lusitanian pattern.

4. Conclusions

A palaeobiogeographical pattern being defined as a set of species sharing the same kind of geographical distribution in similar proportions, the relationships between palaeobiogeographical patterns and morphologic subsets extend between two opposite situations. The first is a null hypothesis, completely non-constrained, of no correlation between the two parameters implying, for instance:

- the absence of any relation between shape and environment (the patterns being suspected of covering several kinds of environments);
- independence between shape and dispersion strategies (the same shapes might be achieved both in endemic and ubiquitous species);

- the absence of any correlation between shell shape and geographical distance because of the very high dispersive capacity of ammonites;
- the lack of phylogenetic constraints, allowing the same shapes to be produced, even if separate phyla are limited to separate patterns.

Another, but opposing and highly constrained, null hypothesis associates each pattern to one (or several) clearly defined morphologic subset. This implies, for instance:

- a strong adaptive relationship between shape and particular environments associated with particular patterns;
- characteristic shapes associated with widespread species, supposedly opportunistic, and with a high power of dispersion;
- strong phylogenetic constraints that limit the possibility of shape diversity in patterns characterised by endemic phyla.

Neither of these hypotheses can account for the observations described. All are intermediate situations that, moreover, vary over time. Nevertheless, some cases express arrangements falsifying either the non-constrained or the constrained null hypothesis.

During the first episode of recovery of disparity (Early and Middle Hettangian—H1 and H2), the situation appears as slightly constrained, most of the morphologic subsets being present in most of the patterns. Exceptions are the almost total lack of taxa in pattern 2, and a slight prevalence of morphologies a, c, d in pattern 1 versus a weak prevalence of morphologies f, g, h, i in pattern 6. Thus, the first phase of recovery appears as roughly homogeneous among the palaeobiogeographical patterns. Later, from the Early Sinemurian to Late Domerian, several divergent situations may be observed in the different palaeobiogeographical patterns as well as in the different stratigraphical units.

Among the cases suggesting strong and sustained constraints, the continuous prevalence of morphologies a and e within pattern 2 is noteworthy. Less expressed, the prevalences of morphologies f, g, h may be observed in the Celtic pattern (6) through the Sinemurian, then relayed during the Carixian in the Celtic–Lusitanian pattern (7). Thus, the evolute, coarsely costate shapes dominate the Celtic s.l. taxa during those times.

Some patterns suggest inconsistent constraints,

as in the widespread Mediterranean–Celtic–Pacific pattern 3, where all the morphologies (except d) are present throughout most of the stratigraphical column, without any clear sustained shape prevalence. A similar situation is observed in the Mediterranean pattern (1), except for some time-limited contrasted prevalences, e.g. morphology f from S4 to L1, and morphology c from C4 to D3.

This conspicuous and precocious prevalence of morphology c in pattern 1 heralds a wider phenomenon expressed during the Domerian. At this time, morphology c (small platycone) invaded all the palaeobiogeographical patterns, where the other morphologies drastically decreased, except for morphology e in pattern 2. The Domerian thus appears as particularly constrained, with one clearly prevalent morphology throughout the world. This might be linked implicitly either with the ability to cover a wide range of environments or with the expansion of a single type of environment at the global scale.

The most interesting results of that study lie in the fact that: (1) only one pattern (#2—Mediterranean–Celtic–Pontic) is associated throughout most of the period considered with constant morphologies (a and e); (2) only one morphology prevails throughout almost all the patterns but during a limited period (Domerian). Nevertheless, at the scale of the study, there is no general trend linking the recovery and the radiation of the ammonite morphospace within the whole space–time framework. Indeed, the various cases showing some links between morphospace and palaeobiogeographical patterns usually imply both short periods and narrow distributions. Such relations have to be deciphered for themselves, taking into account the various factors such as phylogeny, physical barriers, and environment distribution. However, those approaches would be improved by being grounded on combinatory palaeobiogeographical patterns rather than on a conventional palaeobiogeographical framework.

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