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Endemism as a palaeobiogeographic parameter of basin history illustrated by early- and mid-Liassic peri-Tethyan ammonite faunas

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Abstract

Episodes of endemism during Sinemurian–Pliensbachian times are described from synthetic data (publications and unpublished collections) about ammonite faunas of the western reaches of the Tethys. The Lusitanian, Sub-Betic and High Atlas basins receive special attention. The study shows that (1) endemism occurs principally in the Lusitanian and High Atlas basins, which are the most confined palaeogeographic structures; (2) it tends to occur synchronously in different basins but involving different taxa, i.e. it is independent of phylogeny; (3) it is not obviously correlated with relative sea-level at any given time. However, the fact that episodes of endemism coincide with second-order regressive phases suggests some connection between sea-level falls, independently of the sea level, and the development of endemic faunas. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Endemic taxa are confined to clearly defined regions of the world although these may be of variable extent. They can be contrasted with (1) cosmopolitan taxa (also termed ubiquitous or pandemic taxa), which are found almost everywhere

in a given environment (among the ammonites it is the pelagic forms that tend to be cosmopolitan); (2) circumterrestrial taxa (e.g. circumpolar, circumtemperate, pan-tropical taxa), which occupy almost all of a given environment within certain latitudes and the distribution of which is governed more by major climatic factors than by palaeogeographic constraints. Therefore, a clear distinction must always be drawn between circumterrestrial and endemic distribution since, for the latter, the palaeogeographic setting is invariably important. As a corollary, endemism is always indicative of a confined palaeogeographic context. This study attempts to make use of this reciprocal

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property by using variations in endemic patterns within a given region as indicators of variations in the environment, in the broad sense, capable of affecting faunal dispersion.

The analytical stage of this study involves quantifying and localising episodes of endemism in time and space. These data may be read as signals providing direct information about the history of biodiversity and indirect information about the history of the basins that harboured that biodiversity. Special emphasis is placed on pinpointing periods when endemism tends to be synchronous but independent from phylogeny (different taxa are involved) in several geographically distinct basins. Only the occurrence of such episodes can demonstrate that endemism – rather than a mere palaeobiogeographical curiosity – is an indicator of trends affecting an entire region, here the western reaches of the Tethys.

2. The study framework

This study covers just the western reaches of the Tethys (Fig. 1) during part of the Sinemurian and the whole of the Pliensbachian. Although Northwest Europe is characterised from Hettangian times by shelves and shallow basins with rich ammonite faunas, neritic carbonate platforms inherited from the Triassic persisted throughout most Tethyan regions at least until the onset of the Sinemurian. These monotonous platforms were isolated from any pelagic influences and were not colonised by cephalopods. It was only with their break-up (Elmi, 1996), which began during the Sinemurian and was more or less directly related to rifting of the Ligurian–Piedmont Tethys, that ammonite faunas invaded and evolved in the newly formed basins. The Lusitanian, High Atlas and, to a lesser extent, Sub-Betic

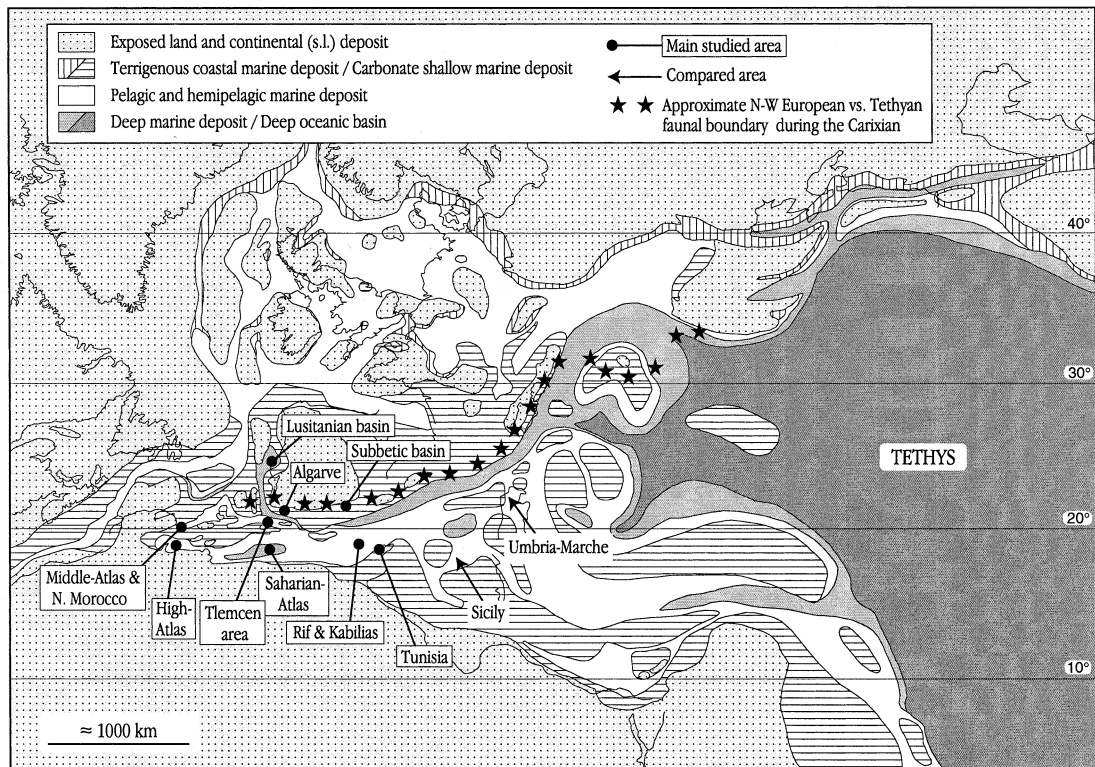


Fig. 1. Palaeogeographic reconstruction of the Western Tethys and its fringes (after Thierry et al., 2000, modified) and location of the main study sectors. The black stars mark the boundary between the Northwest European and Tethyan faunas, which was particularly sharp in Carixian times.

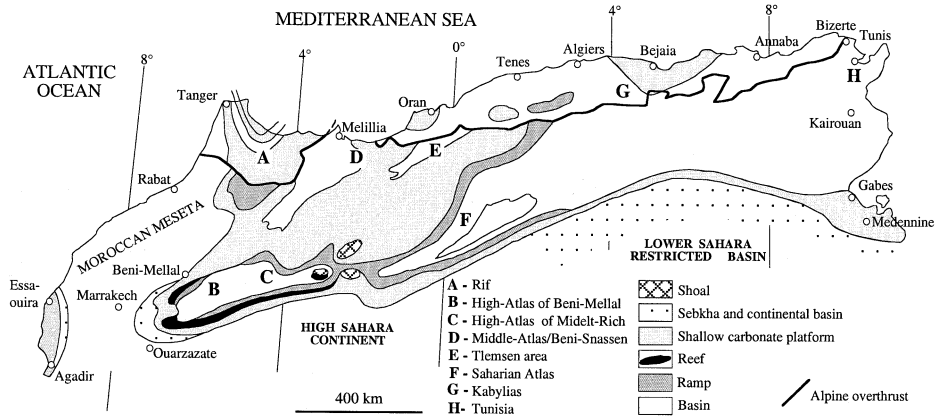


Fig. 2. Simplified palaeogeographic map of the North African basins and location of the study sectors (A–H).

basins were the most confined palaeogeographic structures within this highly complex setting (Figs. 1 and 2). In this palaeobiogeographic context, Tethyan and peri-Tethyan faunas prove exceptional material for analysing the chance establishment and evolution of tropical pelagic biodiversity on a vast regional scale of the order of several millions of square kilometres.

In the study region and on its fringes, sharp contrasts were found in ammonite distribution within two separate palaeobiogeographic entities (Hallam, 1973; Dommergues, 1987; Cariou et al., 1985; Dommergues and Meister, 1991):

(1) A northern fauna occupying primarily the shelves and shallow basins of Northwest Europe (Fig. 1) (e.g. Northern Iberia, France, Germany, the British Isles).

(2) A southern fauna associated mostly with basins formed by the break-up of Tethyan carbonate platforms (Fig. 1) (e.g. Greece, Italy, Southern Iberia, North Africa).

Viewed at lower resolution, Northwest European ammonites are the southernmost representatives of the Euro–Boreal faunas (sensu Dommergues, 1987) while the species herein designated as Tethyan taxa are the westernmost of the Tethyan (s.l.) faunas, a vast, largely pan-tropical, faunal group (Cariou et al., 1985; Dommergues, 1994). The boundary between Northwest European and Tethyan faunas (black stars in Fig. 1) is generally quite easy to trace (Dommergues and

Meister, 1991). This contrasted pattern probably results from complex interaction between palaeogeographic constraints (structuring of the European margin), palaeoecological factors in the broad sense (detrital influx, current directions, etc.) and the climatic gradient. Climate was probably a subsidiary factor, however, as the facies and faunal boundaries, running diagonally between 20° and 40° North, are largely independent of palaeolatitudes (Fig. 1).

Details apart, this palaeobiogeographical framework remains valid for the entire period under study. By reference to it, it is possible to identify:

(a) Widespread taxa (Fig. 3). These species (e.g. *Lytoceras* gr. *fimbriatum* (Sowerby); *Becheiceras* gr. *bechei* (Sowerby); *Protogrammoceras celebratum* (Fucini)) are found, at least in part, both in Northwest European and Tethyan regions. Only the distribution of species is considered and not that of the lineage to which they belong. Thus a widespread taxon may be part of a genus or even a family the other representatives of which are either Northwest European or Tethyan. An example is *Pleuroceras solare* (Phillips), which is found throughout Northwest Europe but is also reported in some Tethyan regions (e.g. the Sub-Betic Basin, northernmost Africa). Most other representatives of the Amaltheidae, the family to which *P. solare* belongs, are strictly Northwest European.

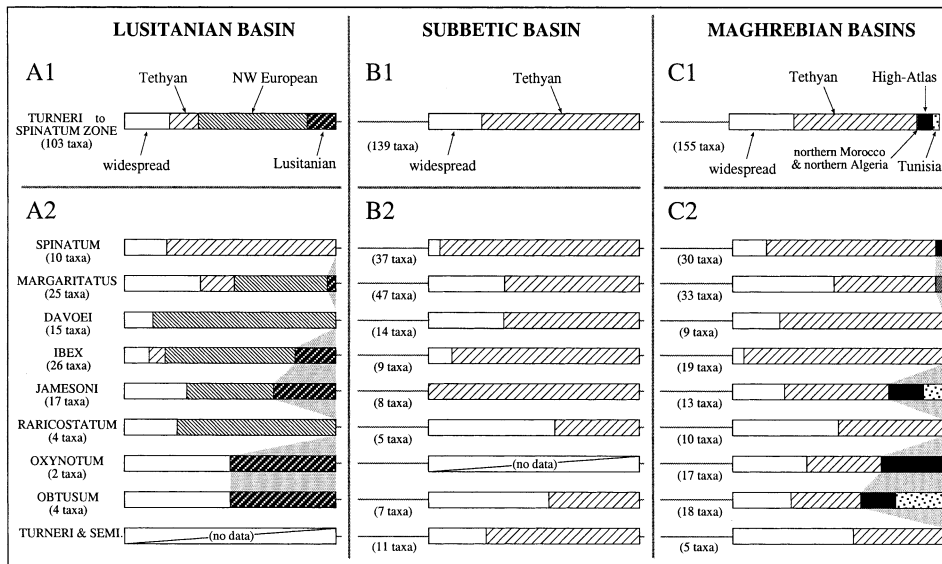


Fig. 3. Variations in the composition of ammonite faunas in three main regions on the western edges of the Tethys in the early and mid Liassic. Special emphasis is placed on micro-endemic taxa.

(b) Ammonites endemic to Northwest Europe. These species (e.g. *Tragophylloceras loscombi* (Sowerby); *Acanthopleuroceras valdani* (d'Orbigny); *Aegoceras maculatum* (Young and Bird)) occur in most basins and platforms of Northwest Europe but are absent or very rare elsewhere.

(c) Ammonites endemic to the Western Tethys. These species (e.g. *Adnethiceras adneticum* (Hauer); *Tropidoceras mediterraneum* (Gemmellaro); *Protogrammoceras dilectum* (Fucini)) are present in most basins of Mediterranean Europe and North Africa but do not occur in more northerly regions in any numbers.

(d) Micro-endemic ammonites reported only in restricted palaeogeographical areas. These are often, although not necessarily, long narrow, well-bounded basins such as the Lusitanian or High Atlas basins. These micro-endemic faunas include the following series of species. Firstly, Lusitanian species, e.g. *Pompekioceras onchocephalus* (Pompeckj), *Pseudophricodoceras dayiforme* (Mouterde, Dommergues and Rocha), and *Dayioceras splendens* (Mouterde). Secondly, Tunisian species (Northeast Tunisia), e.g. *Parasteroceras rakusi* (Dommergues, Faure and Peybernes) and *Arnioceras? fieldingiceroides* (Dommergues, Faure

and Peybernes). Thirdly, forms confined to North Morocco and North Algeria (peri-Rif folds, Rif, Béni-Snassen, Middle Atlas, Tlemcen area and Kabily), e.g. *Amaltheus idrissiensis nomen nudum* (Elmi and Faugère, 1973; Ouahhabi, 1994). Fourthly, taxa confined to the High Atlas Basin, e.g. *Gleviceras richei* (Rakus), *Miltoceras taguendoufi* (El Hariri et al.), and *Dudresnayiceras suesiforme* (Rakus).

3. Materials and methods

3.1. Chronological resolution

The aim is to quantify and situate in time and space the episodes of micro-endemism that characterised the Tethyan and peri-Tethyan basins during a period beginning with the Semicostatium zone (early Sinemurian) and ending with the Spinatum zone (end of the Pliensbachian). The ammonite zone was chosen as the basic biochronological unit for the analysis. Its mean duration of the order of a million years provides a pragmatic framework for correlations among all of the basins under study. The sharp faunal contrast be-

tween Northwest Europe and the Western Tethys and the frequency of micro-endemism in the Western Tethys preclude the use of higher-resolution biochronological divisions, such as divisions into sub-zones. Given that the period under consideration spans some 10 million yr, ammonite zones are sufficiently precise to bring out the main trends. Moreover, this level of resolution allows relevant comparison with second- and first-order cycles as used in sequence stratigraphy (Hardenbold et al., 1998; Souhel et al., 1998). Stratigraphical cycles are geological time intervals between two transgressions or regressions of similar order. Several orders of cyclicity are usually shown on the eustatic charts. According to Hardenbold et al. (1998), the average first-order cycle duration is about 40 Ma and the average second-order cycle duration is about 7 Ma.

3.2. Data

This study is based on analysis of publications on the Lusitanian Basin, Sub-Betic Basin and the various basins of North Africa. It also includes the scarce data available for the Algarve Basin. The Lusitanian Basin apart, the study therefore covers all the available data for the regions between the Iberian Meseta to the north and the Saharan basement to the south (Fig. 1). As a rule, only references with photographs or references to accessible collections were included, to ensure taxonomy was uniform. This information from the literature was supplemented by data on as yet unpublished material from North Africa in the collections of the Centre des Sciences de la Terre de l'Université de Bourgogne (France), the Laboratoire de Géologie des Facultés catholiques de Lyon (France) and the Département de Géologie de l'Université Cadi Ayyad de Marrakech (Morocco).

The following publications were analysed:

(a) for the whole of the Western Tethys and its fringes: Almeras and Elmi, 1982; Braga et al., 1988; Cariou et al., 1985; Dommergues, 1987, 1994; Dommergues and Meister, 1991; Dommergues and Mouterde, 1980; Meister, 1987.

(b) for the Lusitanian Basin: Dommergues, 1987; Dommergues and Mouterde, 1981, 1987;

Mouterde, 1955, 1970; Mouterde and Rocha, 1981a,b,c; Mouterde and Ruget, 1967; Mouterde et al., 1965, 1971, 1983; Phelps, 1985.

(c) for the Sub-Betic and Algarve Basins: Braga, 1983; Braga and Rivas, 1980, 1985; Braga et al., 1982, 1984a,b, 1985, 1987, 1988; Dommergues et al., 1984; Mouterde and Linares, 1979; Rocha, 1976; Rivas, 1977, 1979, 1983.

(d) for the North African basins: Deleau, 1948; Dommergues et al., 1986; Du Dresnay, 1963a,b, 1988; Dubar, 1943, 1948, 1961a,b; Dubar and Mouterde, 1978; El Hariri, 1998; El Hariri et al., 1996; Elmi, 1986; Elmi and Benshili, 1987; Elmi and Faugère, 1974; Elmi et al., 1974, 1998, 1999; Fallot, 1937; Faugères, 1978; Gelard, 1979; Griffon and Mouterde, 1961, 1964; Lachkar et al., 1998; Olivier and Mouterde, 1979; Ouahhabi, 1994; Mouterde, 1965; Mouterde et al., 1986; Rakus, 1972, 1973, 1979, 1991, 1994; Rakus and Biely, 1970; Rakus and Zitt, 1993; Raoult, 1974; Spath, 1913; Termier, 1933, 1936.

3.3. Gaps in the fossil record and limitations of the method

The main caveat when analysing endemism in palaeontology is that it is impossible to evaluate how representative the fossil record truly is (Janvier, 1986). Although we now have a clearer understanding of the significance of the presence or absence of fossil remains in some sedimentary strata in a given basin than formerly (Garcia, 1993; Garcia and Dromart, 1997; Kidwell, 1986; Kidwell and Flessa, 1996), it remains materially impossible to apply routine sampling protocols to fossils, as can be done, at least in theory, with Recent faunas. Palaeobiogeographic data are therefore potentially incomplete, often difficult to quantify, and invariably largely subject to the hazards of fossilisation and outcrop. Therefore, in palaeobiogeography, interpretation of an endemic pattern remains something of a lottery. This being the case, caution requires that only predominant trends, based on plentiful evidence, be considered, avoiding any temptation to generalise from one-off observations. It is this approach, confined to the consideration of trends, that is adopted here.

4. Results

4.1. The Lusitanian paradox

All of the palaeogeographic reconstructions, and particularly the summary one proposed by Thierry et al. (2000), interpret the Lusitanian Basin as a narrow inlet structure opening southwards towards the Tethyan regions (Fig. 1). This hypothesis depicts this basin as a peri-Tethyan appendix where one would expect to find faunas having southern affinities. However, this is only so from the end of Domerian times (Spinatum zone) (Fig. 3). For most of the period considered here the species are in the main widespread taxa, Northwest European taxa or endemic Lusitanian forms related to Northwest European taxa (Dommergues and Mouterde, 1987). Palaeogeographic reconstruction shows therefore that this is a basin opening towards the Tethyan domain but populated by fauna with Northwest European affinities. This paradox is useful to the present analysis as the Lusitanian Basin can be compared with the other peri-Tethyan basins independently of phylogeny. Comparison with the High Atlas Basin is particularly interesting as this, too, is a narrow inlet structure that can be supposed amenable to confinement of populations.

4.2. The nature of endemism

Endemism classically falls into two main categories. Be it palaeo-endemism (relic endemism) or neo-endemism (endemism by novation), the phenomenon is invariably interpreted as the result of confinement. Isolation may favour either the survival locally of relatively primitive taxa that were formerly much more widespread (palaeo-endemism) or the appearance of new forms which often develop remarkable adaptations to what may be highly specific local conditions (neo-endemism).

Most of the instances of micro-endemism analysed here can be interpreted as neo-endemism, with the appearance of a species or a small monophyletic group closely related to forms that were widespread at the same time outside the actual area of endemism. The clearest exception to this model is the spectacular development of the genus

Dayiceras in the Lusitanian Basin during the Ibex zone (mid Carixian). This is an atypical pattern between palaeo- and neo-endemism. While with the genus *Dayiceras*, we have in the course of the mid Carixian (Ibex zone) the localised persistence of the final representatives of the Polymorphitidae – a family that was spread widely throughout Northwest Europe during the early Carixian (Jamesoni zone) – the phenomenon is accompanied by astonishing evolutionary dynamism (Dommergues, 1987, 1990). Therefore, in this case it is impossible, at least at genus and species level, to speak of primitive forms and thus of relic endemism.

More generally, the peri-Tethyan micro-endemic lineages undergo active and rapid morphological differentiation. These lineages are short-lived, hardly exceeding the duration of an ammonite zone (approximately 1 Ma). Peri-Tethyan micro-endemism is apparently a phenomenon without lasting evolutionary consequences. With the exception of one species of *Dayiceras*, *D. polymorphoides* (Spath), which briefly became established in Southwest England (Spath, 1920; Phelps, 1985), none of the endemic taxa that appeared in the peri-Tethyan basins seems to have been able to sustain competition with more widespread forms. In short, while these observations confirm the evolutionary dynamism of marginal populations, they do not show the phenomenon as generating evolutionary innovations of interest at greater spatial and temporal scales.

4.3. Episodes of endemism

The data may be summarised in a figure showing the relative proportions of seven categories of taxa (widespread, Northwest European, Tethyan, Lusitanian, North Moroccan and North Algerian, Tunisian and High Atlas) in the main basins studied (Lusitanian, Sub-Betic and various North African basins). This can be done either by considering the whole of the period (upper part of Fig. 3) or by decomposing the signal into zones (lower part of Fig. 3).

Consideration of the period as a whole (upper part of Fig. 3) shows the following characteristics.

(A) A sharp contrast exists between the faunas

of the Lusitanian Basin (A1) – which are characterised primarily by Northwest European taxa and micro-endemic Lusitanian taxa the closest relatives of which are mainly Northwest European species – and those of the Sub-Betic Basin and the North African basins (B1 and C1), which are characterised above all by Tethyan taxa and by various micro-endemic taxa (North African basins only) the nearest relatives of which are generally Tethyan forms.

(B) A sharp distinction exists between Lusitanian and North African faunas (A1 and C1), on the one hand, with a remarkable proportion of micro-endemic taxa and the Sub-Betic faunas (B1), on the other hand, with no micro-endemic forms. Apart from the presence of many widespread taxa, the Sub-Betic fauna differs little from classic Tethyan populations as found, e.g., in the Apennines (Umbria–Marches) and in Sicily.

(C) Taxa specific to the High Atlas Basin (C1) are predominant among the micro-endemic forms of North Africa (s.l.).

These results can be refined by breaking down the palaeobiogeographic signal into zones thereby showing a clear temporal structure (lower part of Fig. 3). Chronologically, we observe the following.

(A) Lack of micro-endemism during the early Sinemurian (Semicostatum to Turneri zones). The ammonites involved in the early stages of colonisation of the Sub-Betic and North African basins are either widespread taxa or species spread throughout the Tethyan regions s.l. There were no ammonites at this time in the Lusitanian Basin.

(B) Development of the first, and the most marked, of the episodes of micro-endemism during the Obtusum and Oxynotum zones. This is a phenomenon found simultaneously in the Lusitanian Basin (A2) and in North Africa (C2) where micro-endemic taxa are reported in the High Atlas (Obtusum and Oxynotum zones) and in Tunisia (Obtusum zone only).

(C) Absence of micro-endemism in the Raricostatum zone.

(D) Development of a second episode of micro-endemism covering the Jamesoni and Ibex zones

in the Lusitanian Basin (A2) but restricted to the Jamesoni zone in North Africa (High Atlas and Tunisia) (C2). The endemic trend therefore vanishes earlier from the North African basins than from the Lusitanian Basin where the Ibex zone is marked by the remarkable development of the genus *Dayiceras*.

(E) Absence of micro-endemism in the Davoei zone.

(F) Appearance of a few micro-endemic taxa in the Margaritatus and Spinatum zones. During this period, micro-endemism became rare and short-lived and, consequently, difficult to interpret as major trends. There is some contrast though between the Margaritatus zone when micro-endemism is reported in the Lusitanian Basin (A2) and in North Africa (C2) and the Spinatum zone where the phenomenon is confined to the High Atlas (C2).

4.4. Endemism and sea-level changes

The simultaneity of phases of micro-endemism at the scale of the study region is a sufficiently well-marked pattern for it not to be ascribed to pure chance. Nor can it be determined by phyletic factors, since the taxa implied have affinities either with Northwest European forms in the Lusitanian Basin or with Tethyan forms in the North African basins. It was therefore probably an evolutionary – possibly adaptive – response (s.l.) to changes in one or more environmental factors (s.l.) affecting modes of exchange between ammonite populations almost simultaneously and throughout the study region. Of the possible factors, fluctuations in relative sea level are a priori the most likely to modify faunal confinement at regional scale. Any rise or fall in sea level is liable to alter the geometry of basins and more especially that of straits and shallows, thereby directly affecting the potential for faunal exchange. For the zone under study and considering only recent publications, we can refer to the synthesis by Hardenbold et al. (1998) proposing a sequence stratigraphy framework for all of Southwest Europe and its southern edges (including the Lusitanian Basin) and the sequence analysis established by Souhel et al. (1998) from data for the High Atlas of Béni-Mellal. Only sea-

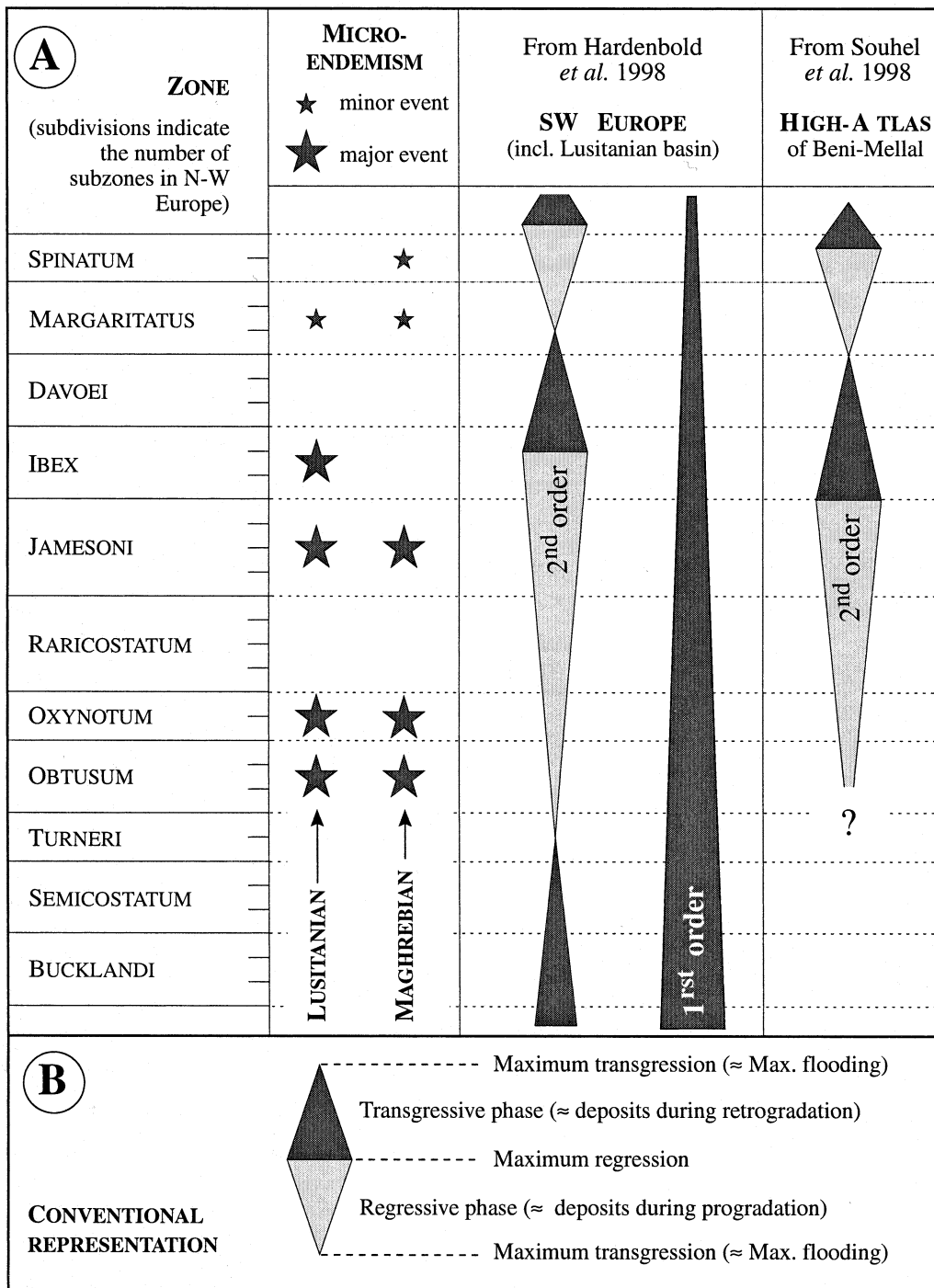


Fig. 4. (A) Comparison of endemic episodes with first- and second-order sea-level fluctuations proposed by Hardenbold et al. (1998) and Souhel et al. (1998). (B) Conventional representation of sea-level fluctuations in sequence stratigraphy.

level fluctuations corresponding to first- and second-order cycles are considered here as a breakdown into third-order cycles would include phenomena of shorter duration than the ammonite zone used here as the basic unit of correlation. Moreover, while local tectonism, e.g. tilted block dynamics, is often predominant at third-order scale, second-order cycles are often controlled by factors acting at larger spatial scales such as the region (Jacquin et al., 1991). Second-order cycles are therefore well adapted to the scale of the question considered here.

Fig. 4 provides a direct comparison of the chronology of episodes of micro-endemism with that of first- and second-order cycles (major transgressive–regressive cycles and transgressive–regressive facies cycles, respectively, in Hardenbold et al., 1998). Comparison shows that there is no obvious correlation between phases of micro-endemism and relative sea level at a given time. The first major episode (Obtusum and Oxynotum zones) corresponds to a relative highstand after a maximum transgression (second-order), whereas the second (Jamesoni and Ibex zones) marks a period of relative lowstand, preceding a maximum regression. There is, however, a degree of coincidence between the regressive trends of the second-order cycles and the episodes of endemism. If we accept such a correlation, the differences in the ages of reversal in trend proposed by the different authors seem consistent with the Carixian endemic episode being briefer in the High Atlas than in the Lusitanian Basin. For the High Atlas of Béni-Mellal, Souhel et al. (1998) propose a maximum regression at the base of the Ibex zone, whereas, working on data for Southwest Europe, Hardenbold et al. (1998) place the same phenomenon somewhat later, in the upper part of this zone. Moreover, the persistence of a first-order transgressive trend throughout the period under study is consistent with the weaker evidence of endemism over time and in particular during the second-order regressive phase of the Domerian. The only notable exception to the possible correlation between second-order regressive trends (R) and micro-endemism is in the Raricostatum zone. Although it falls clearly within a second-order

regressive phase, this period is marked by the total absence of micro-endemism in the study region.

5. Conclusions

Six main points arise from this study.

(1) Micro-endemism is localised preferentially in the more confined marginal basins such as the High Atlas Basin and the Lusitanian Basin. Therefore, basin geometry seems an essential factor in determining this type of endemism.

(2) There is a Lusitanian palaeogeographical paradox. Although palaeogeographic reconstructions portray this basin as a trough opening southwards towards the Tethyan basins, most of its characteristic taxa suggest on the contrary Northwest European faunal influences.

(3) Peri-Tethyan micro-endemism has no long-term evolutionary implications. The episodes are sometimes spectacular but invariably short-lived and localised. Endemic species seem unable to withstand competition for any sustained time from more widespread and probably more generalist species.

(4) A clear time structure can be detected in peri-Tethyan micro-endemism. Although it often affects lineages of separate phyletic origins (Northwest European versus Tethyan), the phenomenon often develops synchronously (e.g. *Obtusum*, *Oxynotum* or *Jamesoni* zones) in what are both structurally and faunally clearly separated palaeogeographic entities such as the Lusitanian Basin and High Atlas Basin.

(5) The phases of micro-endemism are not correlated with the relative sea level at a given time. The main episodes of micro-endemism occur during second-order highstands or lowstands indifferently.

(6) Episodes of micro-endemism tend to coincide with second-order regressive phases. While this correlation might be evidence of a causal link between a fall in relative sea level and the development of micro-endemism, this phenomenon is difficult to interpret as it is independent of sea level at a given moment.

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