

THE ENDEMIC TRENDS OF LIASSIC AMMONITE FAUNAS OF PORTUGAL AS THE RESULT OF THE OPENING UP OF A NARROW EPICONTINENTAL BASIN

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Abstract

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During several stages the Sinemurian and Pliensbachian ammonite faunas of the Lusitanian Basin (coastal Portugal) have a pronounced endemic trend. These trends concern several lineages, without narrow phyletic relationship, belonging to Asteroceratinae (*Ptycharietites* and *Pompekioceras*), Phricodoceratinae (*Pseudophricodoceras* and *Epideroceras*), Polymorphitidae (*Dayiceras*), and Eoderoceratidae (*Metaderoceras*). Frequently the species most derived from these endemic lineages display a pronounced morphological convergence. These species possess an involute shell with rather slender ribbing. This converging trend is probably the result of a morphofunctional factor. The Lusitanian endemic trends can only be understood within their biogeographical framework.

The sequence of endemic events occurs during a critical phase in the geological history of the Lusitanian Basin: the settlement of a definite marine environment. Besides, this early extension of open marine conditions affects a narrow basin chopped up by several transform faults. It is within this particular paleogeographical framework that the main causes of these endemic events must be looked for.

Introduction

Endemic phenomena have always fascinated naturalists as they are the best witnesses of the close links between the history of the earth and life's history. The endemic nature of the Portuguese Liassic ammonite faunas (Late Sinemurian and Early Pliensbachian) has been known for a fairly long time but its significance has remained enigmatic; nowadays plate tectonic data give an insight into the phenomenon by placing and interpreting it within a dependable geological background.

Before studying the Lusitanian endemic trend it is useful to summarize briefly the main patterns of Liassic ammonite paleobiogeography; one will find a more complete treatise on this topic in a recent paper by Cariou et al. (1985). During the Early Liassic, from the Hettangian to Early Sinemurian, ammonite faunas become more and more ubiquitous. The *Arnioceras* fauna of the latest Early Sinemurian, widely spread in the world, is a good example of this tendency. From the Late Sinemurian and especially during the Pliensbachian the ammonite faunas display a note-

worthy provinciality which disappear from the Early Toarcian. During this faunal crisis one can recognize two main paleobiogeographical realms: on the one hand the Euro-boreal realm which includes the Arctic Ocean, the epicontinental seas of northern, northwestern and western Europe as well as the south margin of the Asiatic Continent at least to the Iranian areas; on the other hand the Tethyan realm which covers all the other parts of the Liassic seas and especially the Mediterranean areas including the Betic Ranges and areas to the south of the Ligurian rifting zone and the Gibraltar-Maghreb-Sicilia transform zone. In this paleogeographical framework, the whole

of the Lusitanian endemic ammonites are related with the Euro-boreal faunas.

During the Lias the Iberian passive margin was made up of a very narrow sedimentary basin which is only partly emergent today; at present only the southeastern edge is directly exposed as the richly fossiliferous outcrops on the coast of Portugal between Peniche in the South and Coimbra in the North (Fig.1).

These exposures and also many boreholes, commonly referred to as the "Lusitanian Basin", have produced abundant and stratigraphically well-located material, enabling the endemic intervals to be delimited within narrow chronostratigraphical limits, and be interpreted within their paleoecological context.

The Portuguese faunas have recently been the subject of a descriptive monograph including a richly illustrated atlas (Mouterde and Rocha, 1981; Mouterde et al., 1983). The most important of the endemic species are illustrated on Fig.2. Moreover, references to the plates in the "Atlas Portugais" will be systematically used after each species referred to.

The sequence of endemic events

Ptycharietites Spath (including *Pompeckioceras* Spath), ("Atlas", vol. 1; pl. 1, figs.11 and 14; pl. 2, fig.3); (in this paper Fig.2.A1, A2)

These forms are the earliest ammonites collected in the Lusitanian Basin. They still remain rare and are only to be found in an outcrop at Sao Pedro de Muel and in a borehole at Verride. These two closely related forms display in their rather involute internal whorls an odd ornamentation with slender striae which at a later stage in their growth become coarser ribbing like that of *Asteroceras*. In fact these Lusitanian ammonites resemble this latter genus more than any other Middle European species. It seems that, in spite of some superficial resemblance between *Ptycharietites* and both the Middle European *Aegasteroceras* and Arctic *Arctasteroceras*, it is not appropriate to link the groups, as these

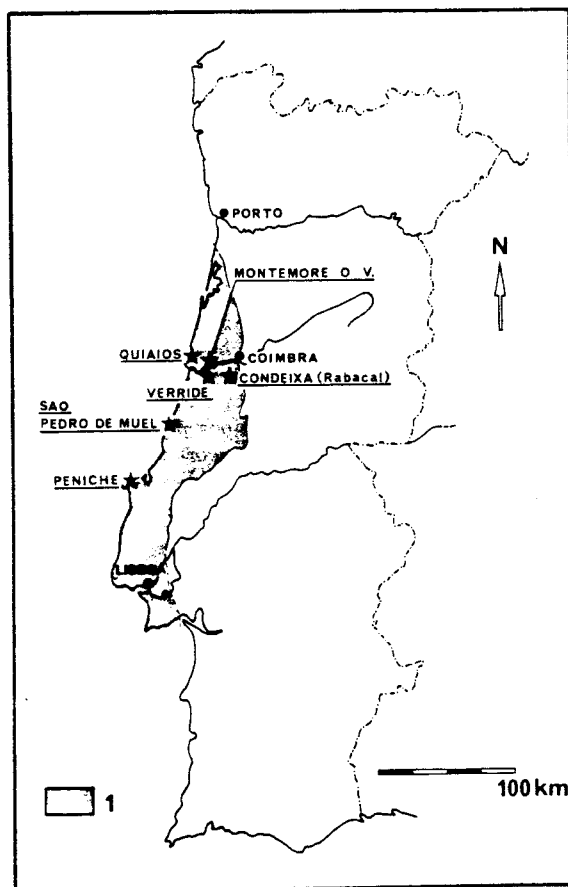


Fig.1. Location of the main exposures and boreholes in the Lusitanian Basin. 1=distribution of Jurassic rocks in outcrops or in subsurface.

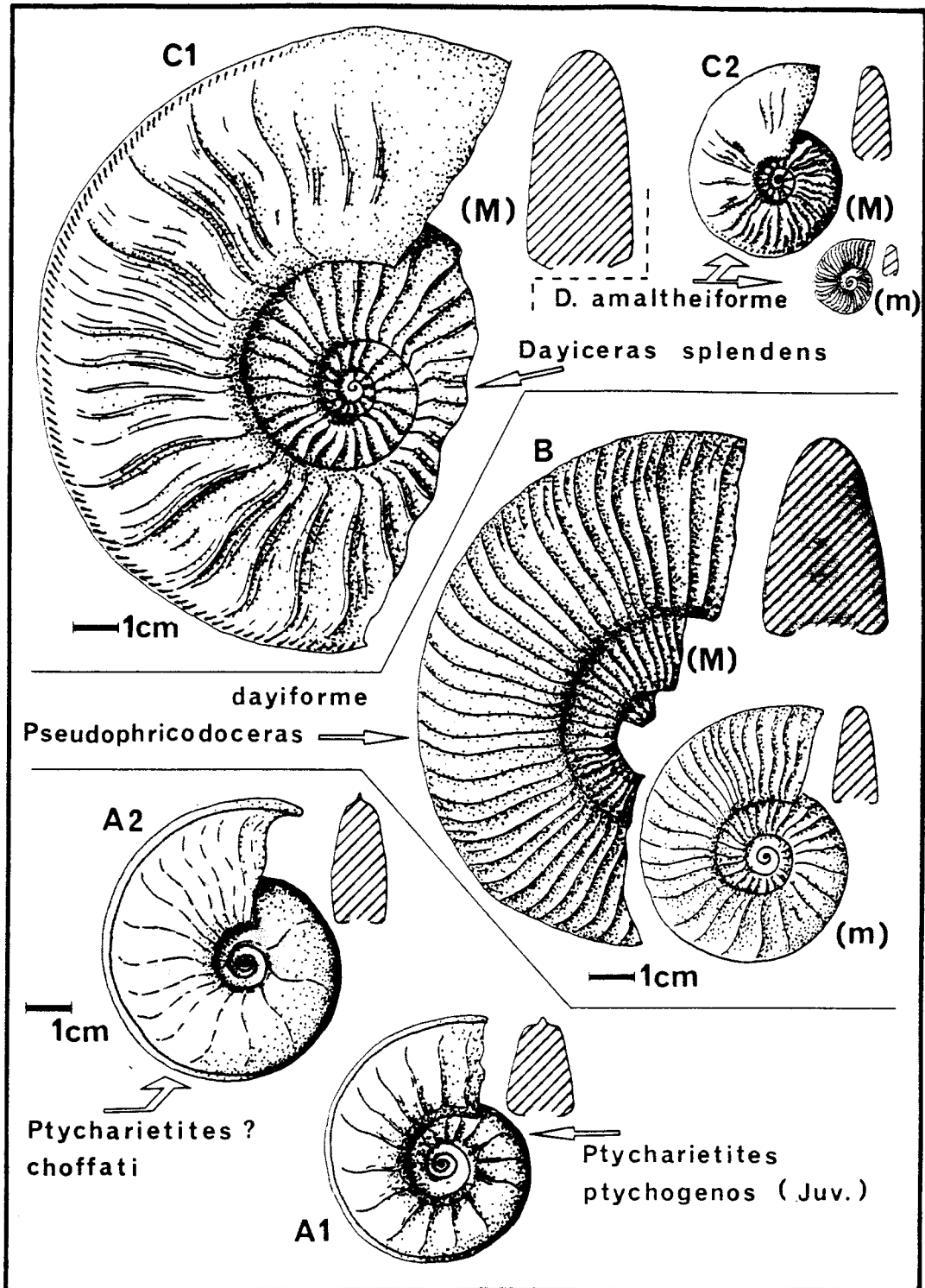


Fig.2. Convergent morphologies of the main Lusitanian endemic lineages (in stratigraphical sequence): (A1, A2) *Ptycharietites*, (B) *Pseudophricodoceras*, (C1, C2) involute *Dayiceras*; M = Macroconch, m = microconch.

latter possess very ornate inner whorls as opposed to the fine striae of *Ptycharietites*.

In other respects, the ventral region and the ornamentation with fine striae of "*Oxynoticeras*" *chofatti* Pompeckj (Fig.2. A2) are probably homologous to those of *Ptycharietites*: if these homologies are confirmed the Portuguese "*Oxynoticeras*" *chofatti* could be the result of the first Portuguese endemic lineage. Thus, an endemic trend appears as early as the first occurrence of Liassic ammonite faunas.

However, during the last part of the late Sinemurian, *Oxynoticeras* and *Echioceras* faunas (Fig.3) display a more ubiquitous complexion and can be related to Northwest European species, although as early as the Carixian substage (early Pliensbachian) the endemic trend can be observed once again with Phricodoceratinae.

Pseudophricodoceras Mouterde et al.:
P. caprariforme Mouterde et al. and
P. dayiforme Mouterde et al. ("Atlas", vol. 2;
pl. 1, figs.1-6, 9-10; pl. 2, figs.1-2); (in this
paper Fig.2.B).

These two species are strictly localised in the upper part of the Tylori subzone where they characterise two successive biostratigraphical horizons (Fig.3). They are only to be found in the axis of the Lusitanian Basin at Peniche, Sao Pedro de Muel and Quiaos. The more recent and the most divergent *P. dayiforme* would seem to be strictly confined to Portugal. The older, *P. caprariforme*, is perhaps less restricted in space because Hoffmann (1982, pl. 16, fig.3) quoted a specimen as *Epideroceras* in West Germany which seems very close to the Lusitanian species.

At first sight, *Pseudophricodoceras*, with their enigmatic morphology and ornamentation, is difficult to relate to any of the classical genera, whether it be European or Mediterranean. Nevertheless, it is with the Phricodoceratidae (including *Epideroceras* and *Phricodoceras*) that the Lusitanian genus seems the most closely related.

Epideroceras trigonale Mouterde et al.
("Atlas", vol. 2; pl. 2, figs.4-6; pl. 3, fig.2; pl.
4, figs.3-4).

This species from the basis of the Polymorphus subzone (Early Carixian) (Fig.3) has been collected at different points in Portugal, both in the axis of the basin and on its margins (Peniche, Sao Pedro de Muel, Quiaos, Montemor o Velho and Rabacal). It is unknown outside Portugal but is closely related to Northwest European *E. nodofissum* (Quenst.), being perhaps only a geographical subspecies morphologically differentiated.

Thus the endemic character of the first Carixian levels decreases at the base of the Polymorphus subzone and it becomes doubtful during the following two subzones (Brevispina and Jamesoni subzones). Only a few *Platypleuroceras* - *P. muellense* (Mouterde) and *P. acanthobronni* (Mouterde et al.) - display a certain originality but the genus is little known outside Portugal so it is difficult to conclude their endemism in the Lusitanian Basin.

The evolute *Dayiceras* of the *D. dayiceroides* (Mouterde) - *D. polymorphoides* Spath, lineage.

Whereas in Northwestern Europe the beginning of the Middle Carixian (Ibex zone) is marked by Acanthopleuroceratidae sharply replacing Polymorphitidae, in Portugal the latter continued to develop the prominent *Dayiceras* endemic lineage. From the latter *Uptonia* the genus *Dayicera* developed. Three species follow each other in time: *Dayiceras dayiceroides* (Mouterde) ("Atlas", vol. 2; pl. 7, fig.5; pl. 8, figs.1-9), *D. renzi* (Meister) ("Atlas", vol. 2; pl. 9, figs.4-8, 11) and *D. polymorphoides* Spath ("Atlas", vol. 2; pl. 9, figs.9-10, 14; pl. 10, fig.19).

Although these species, which are abundant all over the Lusitanian Basin, are mainly limited to Portugal, the youngest species *D. polymorphoides* is known outside Portugal, particularly in Southwest England (Spath, 1920) but it is also quoted in Northwest

Standard Sub - Stages	Standard Zones	Standard Sub - zones	Lusitanian Sub - zones	Lusitanian Horizons	<i>Ptycharietites</i>	<i>Pseudo - phricodoceras</i>	<i>Epideroceras trigonale</i>	<i>Daviceus</i> : ↓ evoilate species ↓ involute species	<i>Metatrocera bemense</i>	
C A R I X I A N	Dacoei	Fig.	Fig.	<i>Figulinum</i>						
				<i>Angulatum</i> pars.						
		Cap.	Cap.	<i>Dacoei</i>						
				<i>Crescens</i> pars.						
				<i>Capricornus</i>						
				<i>Rectiradiatum</i>						
		Mac.	Mac.	<i>Lataecosta</i>						
				<i>Maculatum</i>						
		Ibex	Lur.	Lur.						<i>Sparsicosta</i>
										<i>Luridum</i>
	<i>Crassum</i>									
	Valdani		Beir.	Renzi						<i>Rotundum</i>
										<i>Lepidum</i>
										<i>Beirense</i>
										<i>Amaltheiforme</i>
	Mass.									<i>Splendens</i>
										<i>Polymorphoides</i>
										<i>Renzi</i>
	Jamesoni	Jam.	Jam.	<i>Maugenesti</i>						
				<i>Dayiceroides</i>						
				<i>Carinatum</i>						
				<i>Uptonia</i> sp. nov.						
		Brev.	Brev.	Poly.						<i>Bronni - Lata</i>
										<i>Bronni - Jamesoni</i>
										<i>Acanthobronni</i>
										<i>Muellensis</i>
	Tayl.	Tayl.	Tayl.	<i>gr. costatus</i>						
				<i>Biruga</i>						
<i>Dayiforme</i>										
<i>Caprariforme</i>										
Obtusum	Raricos- tatum	Oxyndatum	<i>Taylori</i>							
			<i>Nodogigas</i>							
Obtusum	Raricos- tatum	Oxyndatum								
Obtusum	Raricos- tatum	Oxyndatum								

Fig.3. Stratigraphical occurrence of the endemic lineages; biostratigraphical scale from Mouterde et al. (1983).

Germany (Hoffmann, 1982, pp. 216–217, pl. 29, fig. 2B). Unfortunately the external view of the German example is not convincing. In addition, after Frebold (1970) and Imlay (1981) Smith (1983) recorded also *Dayiceras dayicero-ides* in western North America. All these American examples seem to belong to the genus *Dubariceras* Dommergues et al. It is a close relative to *Metaderoceras* which is clearly remote from the Polymorphitidae (Dommergues et al., 1984). This confirms the Lusitanian endemic complex of the evolute *Dayiceras*.

The involute *Dayiceras* of the *D. splendens* Mouterde – *D. amaltheiforme* Mouterde, lineage ("Atlas", vol. 2; pl. 10, figs. 4–17) (in this paper Fig. 2. C1, C2).

These late species which are characteristic of the two terminal horizons of the Renzi subzone (Mouterde et al., 1983) are strictly localised in the axis of the Lusitanian Basin (Sao Pedro de Muel and Peniche). They derive directly from the preceding group, but the new species display some important changes in their features. Involute shell and pronounced sexual dimorphism appear suddenly in the fossil record. The involute *Dayiceras* shows a very different morphology compared to their polymorphitid ancestors of the Early and Middle Carixian.

As the last member of Polymorphitidae, the involute *Dayiceras* provides one of the best illustrations of the Lusitanian endemic trend.

Metaderoceras beirense Mouterde ("Atlas", vol. 2, pl. 11, figs. 2–4)

This species is noteworthy because of its coarse and loose ribbing and its subquadrate whorl section. It occurs in the lowest horizon of the Beirense subzone all over the Lusitanian Basin. Although it has been cited elsewhere, for example by Géczy (1976) in Hungary, in reality it would seem to be strictly limited to the Lusitanian Basin. The close phyletic relationships of *M. beirense* are unfortunately misunderstood. It remains to be seen whether it is

related to the Northwest European *Metaderoceras* of *M. venarensis* (Op.) group or to the Mediterranean *M. gemmellaroi* (Levi) and *M. evolutum* (Fuc.). In Portugal the presence of some *Metaderoceras venarensis* in subjacent beds seems to support the former assumption.

With *M. beirense*, the Portuguese endemic trend seems to disappear and the Northwest European faunas become prevailing. It is only in the Early Domerian substage that a clear faunal spread of some Mediterranean components reaches the Lusitanian Basin. This faunal spread is known also in a major part of Northwestern Europe (Dommergues and Mouterde, 1980).

The peculiarity of the Portuguese endemic trend

From the early part of the Late Sinemurian to the Middle Carixian the Lusitanian ammonite faunas display several boldly expressed endemic episodes separated by periods of reversion to a strong Northwest European influence. For each endemic episode a distinct phyletic group is affected: these groups belong to clearly distinct families or superfamilies each time: Psiloceratacea (Asterooceratinae), Eoderoceratacea (Eoderoceratidae, Phricodoceratidae, Polymorphitidae). The morphology displayed by the most divergent endemic forms (*Ptycharietites*, *Pseudophricodoceras*, involute *Dayiceras*) is considerably different from the ancestral groups. It reveals an obvious convergence to platycone shell inclined to be involute, slender ribbing, narrow ventral area. It must be emphasized that these changes belong to rapid evolutive processes which never exceeded the duration of one subzone.

We do not know any other examples in the Jurassic system, and especially in the Lias, of such localised endemic phenomena resulting in such considerable and rapid morphological changes. Perhaps the Arctic or the Circumpacific regions can provide some? Only the Madagascan–Arabian endemic fauna can supply certain elements of comparison but the area covered by this fauna is much larger. Like

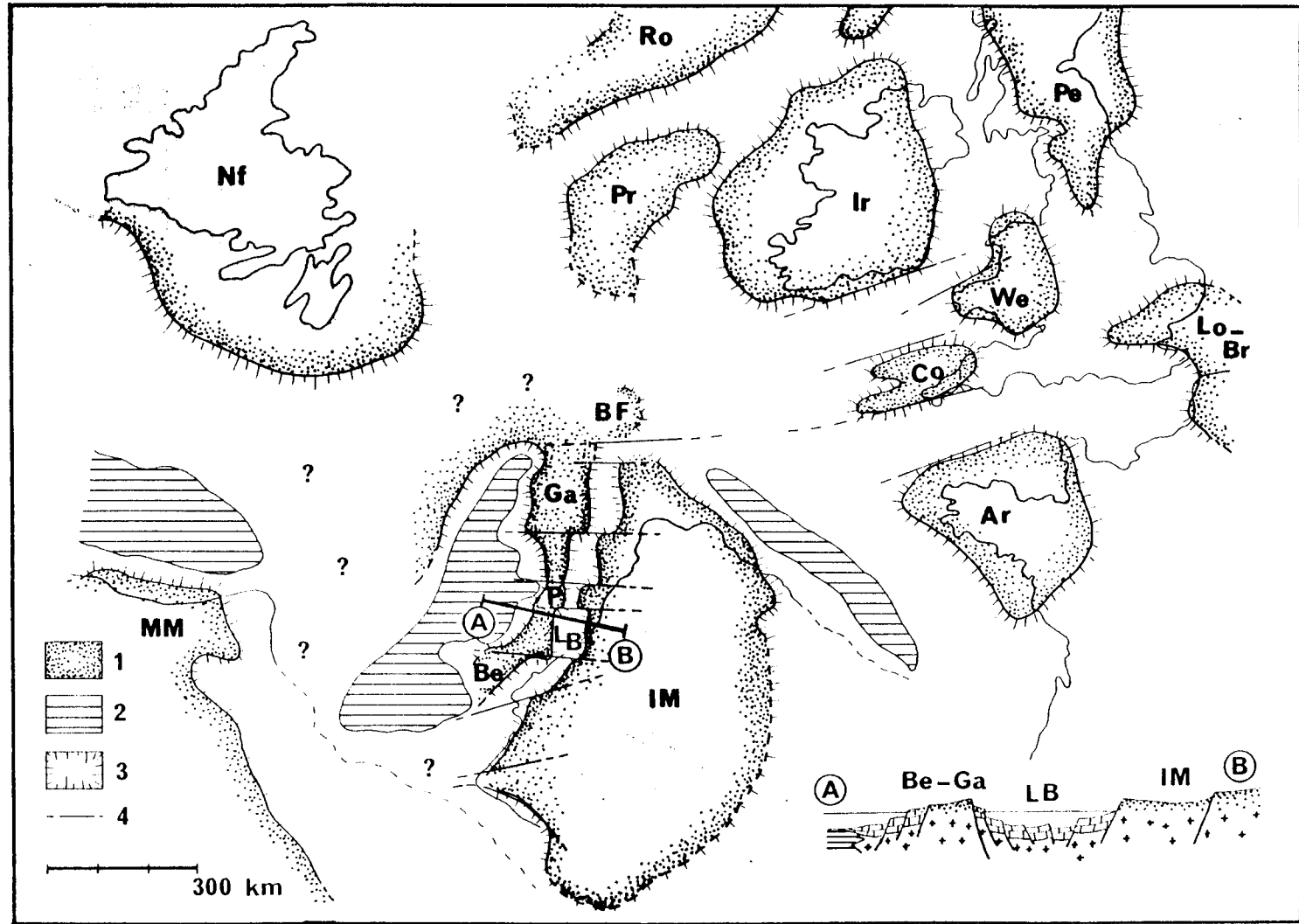


Fig.4. Tentative palinspastic sketch map for the Northern Atlantic confined to the Liassic times. Illustration of the paleogeographical significance of the Lusitanian Basin within this general framework (partly from Ziegler, 1982; Olivet et al., 1982; Guéry, 1984; Rat, 1984; Dercourt et al., 1985). 1 = probable land areas, 2 = hypothetical basaltic seafloor, 3 = continental boundary of the epicontinental basin, 4 = transform fault, LB = Lusitanian Basin, *Nf* = Newfoundland, *Ro* = Rockall, *Pe* = Pennin Massif, *Pr* = Porcupine Bank, *Ir* = Irish Massif, *W* = Welsh Massif, *Co* = Cornwall Massif, *Lo-Br* = London-Brabant Massif, *Ar* = Armorican Massif, *MM* = Moroccan Meseta, *BF* = Bonet-Flamand Bank, *Ga* = Galicia Bank, *P* = Porto Bank, *Be* = Berlinga Bank.

the endemic Lusitanian groups, the different lineages present in this area (*Bouleiceras*, *Nedjia*) display convergent morphologies and besides simplified suture lines (Arkell, 1952; Enay, 1980, Tintant et al., 1982). All this points to the unique nature of the Lusitanian endemic trend and leads us to look for its causes in the paleogeography of the period.

Conclusions

Most of the recent works on the evolution of the Iberian passive margin during the Jurassic (Jansa and Wade, 1975a, b; Mauferet et al., 1978; Boillot et al., 1979; Mougenot et al., 1979; Vanney and Mougenot, 1981; Guéry, 1984 agree about the existence of a very narrow west Iberian basin, roughly parallel to the existing coastline. This basin is bounded to the west by a string of horsts (tilted blocks) which probably mainly emerged during the Lias, including several undersea mounts: Galicia, Vigo, Porto, Berlingues, Camoes (Fig.4). It is chopped up by transform faults approximately WSW-ENE (Nazare, Tage, Oldamira-Avila) whose moving apart locally restricted faunal exchanges, probably from Liassic times, by shifting the axis of the basin.

Today, to the west of this string of tilted blocks partly emergent during the Jurassic, stretch the Iberian abyssal plains. Some authors (Olivet et al., 1982) think that an area of oceanic accretion existed as early as the Lias along these abyssal plains, at least to the south of the 41st parallel. Other authors, such as Gradstein and Sheridan (1983), think that sea floor spreading did not start until late Middle Jurassic times only in more southwestern areas.

For the Sinemurian and Pliensbachian, periods which concern us, the structural development of the Lusitanian Basin results from distinct stages of rifting: the early phase of "thermic tumescence", then the late phase of "thermic distumescence". On the whole there is agreement about this sequence of events although its actual timing is debated (Guéry, 1984). Generally the beginning of the late

phase of rifting is situated during the Late Lias or the Early Middle Jurassic; it could not have taken place before the Toarcian. For Guéry (1984) the beginning of this event would be even older, during the late part of the Sinemurian of the early part of the Pliensbachian. The actual building up of the intracontinental marine basin has succeeded an intracontinental rifting situated before Late Sinemurian times.

Thus, the endemic crisis which affects the ammonite faunas corresponds to a critical point in time: the setting up of a distinct marine environment within a structure of a narrow graben chopped up by transform faults. The ammonite faunas, which colonised this narrow basin during the Late Sinemurian and the Early Pliensbachian have their origins without doubt in Middle Europe. Before the beginning of the Late Pliensbachian there does not seem to be any communication of regular nature with the Mediterranean province.

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