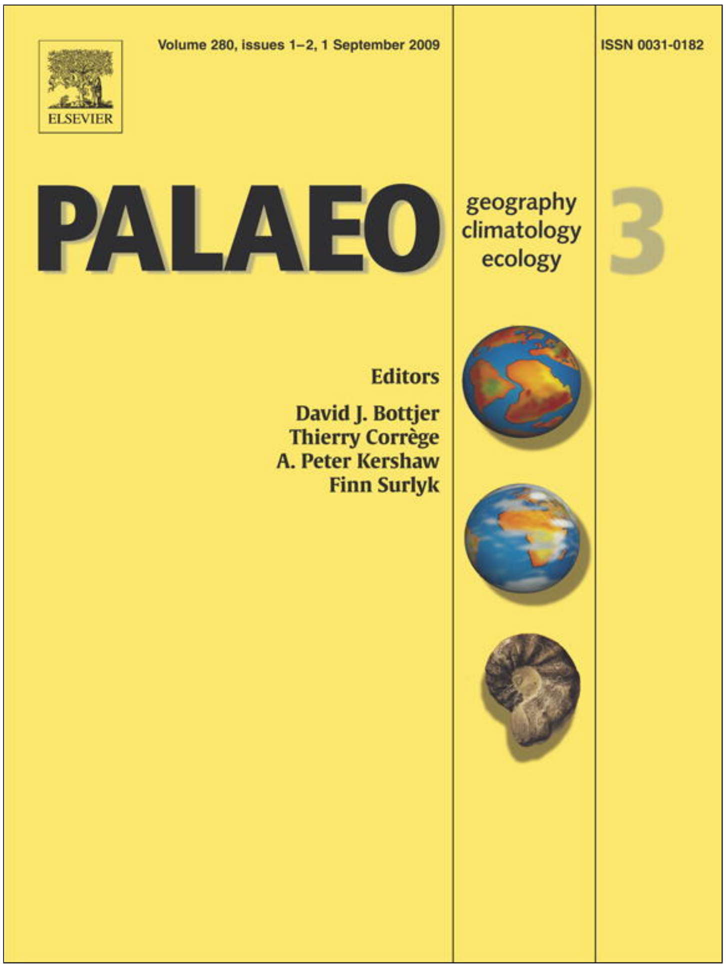
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Ammonite diversity and its palaeobiogeographical structure during the early Pliensbachian (Jurassic) in the western Tethys and adjacent areas

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ABSTRACT

The early Pliensbachian (Early Jurassic) is known as a time of marked provincialism in the marine realm, notably between the Mediterranean Tethys and North–West Europe. In order to test this observation quantitatively, we compiled 104 locality-level species lists from those areas based on a comprehensive revision of early Pliensbachian ammonites. With this dataset, we also explore the relationship between ammonite richness and biogeography at the scale of the sub-chronozone during the early Pliensbachian. Using various multivariate statistics and rarefaction techniques, we show that: (i) there is a sharp contrast between the NW European (NWE) and the Mediterranean (MED) provinces, although there is some mixing in Austroalpine and Pontic ammonite faunas; (ii) species richness in the MED province is about twice that in the NWE province for each chronozone; (iii) ammonite species richness tends to decrease during the early Pliensbachian, especially at the Ibex–Davoei transition; and (iv) the NWE and MED *sensu stricto* provinces both record the same pattern of variations in richness despite the fact that their taxonomic compositions have virtually nothing in common at the species level. We suggest that the low ammonite richness of the Davoei chronozone may be related to a coeval warming of seawaters, but that this was insufficient to affect the sharp palaeobiogeographic contrast between the two provinces. This persistent compartmentalisation probably reflects a major palaeogeographical structure, such as an emerged or near-emerged barrier running from the Betic range to the Briançonnais ridge. Overall, it seems that the diversity and distribution of early Pliensbachian ammonite species were simultaneously controlled by climate, palaeogeography and eustasy.

1. Introduction

Understanding biological diversity involves considering and quantifying its various aspects, such as species richness, abundance, body size distribution, morphology and intra-specific variance. It is crucial to combine some or all of these parameters if we are to decipher the processes underlying past and present biodiversity (e.g., Whittaker, 1975; Brown, 1995; Rosenzweig, 1995). In this perspective, palaeontologists explore quantitatively the diversity of various taxonomic groups, including Mesozoic ammonoids. For example, Dommergues et al. (2001) study the global-scale relations between palaeobiogeographical distribution and morphological disparity for Early Jurassic ammonites. Similarly, Cecca et al. (2005) and Brayard et al. (2006) analyse ammonoid palaeobiogeography and diversity worldwide. Such an approach necessarily leads to a low spatial, temporal and taxonomic resolution of the data because all these scales are inter-related. These major studies were based accordingly on faunal lists for ten to fifteen sedimentary basins and used a substage- or zone-based stratigraphic scale (mean durations of ≈1.5 My and ≈1.0 My, respectively) (Gradstein et al., 2004). The genus was therefore deemed an appropriate taxonomic level for practical reasons (Cecca et al., 2005; Brayard et al., 2006).

The present study supplements these works by using high-resolution data to investigate the richness of early Pliensbachian ammonites within two neighbouring major palaeobiogeographical provinces: the western or Mediterranean Tethys and North–West (NW) Europe. Since the works of Donovan (1967) and Sapunov (1974), these regions have usually been regarded as having clearly separate palaeobiogeographical entities during early Pliensbachian times. Here we first test this observation quantitatively and investigate its persistence within an interval during which Tethyan vs North–West European provincialism may have reached its maximum (Cariou et al., 1985; Meister and Stampfli, 2000). We also address the following questions: 1) Did any major change in ammonite diversity occur during the early Pliensbachian? 2) If so, how did it affect ammonite diversity and biogeography in these two faunal provinces?

Early Pliensbachian ammonites were chosen as a study case for several reasons. First, marine deposits of this age are widely exposed in Europe and North Africa, and their outstanding fossil record has been extensively studied since the nineteenth century. In many cases, recent revisions of major early Pliensbachian localities are available

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and many taxonomic groups are well-known from these marine deposits. Those groups include ammonites, which are of prime importance in biostratigraphy, as well as nautilids, belemnites, brachiopods, bivalves, and foraminifers. In turn, this should allow cross-comparisons to be made with various taxonomic groups.

Second, the temporal precision available for the Pliensbachian, with its total duration of about 6.6 My (Gradstein et al., 2004), is one of the best for the Lower Jurassic (Dommergues, 1997). In the most propitious cases (mostly NW Europe), some observations can be made at the resolution of the zonule, with its mean duration of about 0.2 My. Despite the conspicuous early Pliensbachian provincialism, the Austroalpine area and the southern Alps formed a restricted but remarkable area of mixed faunas, making it possible to establish robust correlations between western Tethyan and NW European faunas (Dommergues et al., 1983; Dommergues and Meister, 1991). As a result, a high temporal resolution is achievable up to the sub-chronozones (mean duration ≈0.45 My).

And third, it was possible to establish more than a hundred locality-level species lists based on a comprehensive critical revision of all the specimens illustrated in the vast literature on early Pliensbachian ammonites (see Appendix A). The resulting dataset is therefore a homogenous taxonomic thesaurus and not a mixture of data biased by the heterogeneity of the species concept in the literature.

In this context the analysis of early Pliensbachian ammonite biodiversity can be carried out with an unusual degree of detail. Diversity is assessed at the species level, the temporal scale is based on sub-chronozones, and more than a hundred localities are considered. As a consequence, we might expect to find patterns that are only retrievable at that degree of resolution. We also aim at getting as close as possible to station-level neontological analyses by using one of the best resolutions available to palaeontologists.

2. Geological and palaeontological settings

2.1. The spatial framework

During the early Pliensbachian, the studied area is characterised by a temporary but obvious palaeobiogeographical structuration with a strong faunal contrast between the Mediterranean and the NW European biotas. In fact, the Pliensbachian and particularly the early Pliensbachian is usually considered as a time of biotic crisis in the sense that an unusual number of faunal differentiation events occurred between the Tethyan and Euroboreal realms. These realms are represented in this study by the Mediterranean and by the NW European provinces, respectively. In historical terms, the Tethyan versus Boreal biotic differentiation, at least for Jurassic ammonites, has been known since the founding works of Neumayr (1872, 1883). While the Pliensbachian biotic crisis is outstanding and extensively documented for ammonites (e.g., Dubar, 1954; Donovan, 1967; Hallam, 1969; Geczy, 1973; Howarth, 1973; Sapunov, 1974; Enay, 1980; Dommergues, 1982; Enay and Mangold, 1982; Geczy, 1984; Cariou et al., 1985; Smith and Tipper, 1986; Dommergues, 1987; Dommergues and Meister, 1991; Dommergues, 1994; Meister and Stampfli, 2000), it is also identified and/or suspected for belemnites (Doyle, 1987, 1994), brachiopods (Ager, 1967, 1971, 1973; Vörös, 1977, 1984, 1993) and bivalves (Hallam, 1977). Furthermore, the Mediterranean province is usually divided into three parts of unequal importance. Indeed, it is possible to separate a Mediterranean s.s., an Austroalpine (including the South Alps) and a Pontic subprovince on the basis of their endemic taxa. The Austroalpine subprovince warrants special consideration because, although its diversified biota is usually dominated by Mediterranean taxa (species richness and abundance), it also includes a significant proportion of usually rare NW European taxa. This peculiarity is of major importance because it allows a convincing and accurate correlation framework to be established between the Mediterranean and NW European provinces (Dommergues et al., 1983, 1984; Dommergues and Meister, 1991; Meister, 1995). Unlike the complex Mediterranean province, the NW European province is considered as a more homogeneous and monotonous palaeobiogeographical entity, at least for the early Pliensbachian. The Lusitanian basin alone was a restricted but unambiguous centre of endemism within the NW European province (Dommergues and Mouterde, 1987; Dommergues and El Hariri, 2002). The presence of Mediterranean ammonites within NW European faunas is usually insignificant and the Austroalpine subprovince is the only area with mixed fauna in the studied area.

The present work is confined to the study of the Mediterranean and NW European peri-Tethyan marine areas and to some adjacent regions (East Greenland and the Pontids) (Fig. 1). Except for the Pontic and Austroalpine localities that are located on the Tethyan margins close to oceanic areas s.s., all the regions under consideration were epicontinental seas of variable depth and with numerous scattered islands (chiefly in NW Europe). The study area may be described as an intricate archipelago bounded to the north, east and south by the Fennosarmatian, Laurentian–Greenland and African (Saharan) landmasses. Today, the study localities lie in Europe, North Africa and Turkey (Fig. 2). Each locality is either a single fossiliferous outcrop or a set of abutting outcrops characterised by fairly similar geological traits. Here 104 localities are analysed: 64 of them are associated with NW European areas and 40 with Mediterranean ones (s.l.). The latter comprise 23 Mediterranean s.s., 12 Austroalpine and 5 Pontic localities (Fig. 2). The NW European areas are characterised mainly by barely tectonised basins and/or platforms with widespread ammonite-bearing facies, whereas the Mediterranean areas are usually highly tectonised and favourable facies are not so common. Accordingly, spatial sampling is evenly distributed across the NW European province but is more clustered in the Mediterranean province where many broad tracts are poorly documented with scarce condensed deposits. In fact, the Mediterranean faunas and their accurate stratigraphic successions are known mainly in Morocco, southern Spain, Italy and in the Austroalpine area.

The studied areas are among the best known in the world in terms of geology. Thus, it should be possible to compare and contrast the palaeoecological and palaeobiogeographical patterns with a rich assortment of proxies (e.g., sequence stratigraphy, geochemistry, isotopes, and mineralogy) providing valuable data about eustatic and/or climatic fluctuations (Graciansky et al., 1998; Hardenbol et al., 1998; Rosales et al., 2004; Van de Schootbrugge et al., 2005; Arias, 2007).

2.2. The temporal framework

The present work is confined strictly to the early Pliensbachian, which is clearly defined (Meister et al., 2006) and bounded at its base by a substantial global faunal renewal characterised mainly by the dramatic development of the Eoderoceratoidea and by a rapid intensification of provincialism. The lower boundary of the late Pliensbachian is not peculiar but it is clearly characterised, at least in NW Europe, by both the rapid evolutionary substitution of the abundant early Pliensbachian “Capricorn” Liparoceratidae by the Amaltheidae, and by a decline in provincialism (Dommergues and Mouterde, 1980).

The radio-isotopic ages proposed by Gradstein et al. (2004) for the whole Pliensbachian are 189.6 to 183 Ma (duration of 6.6 My). Thus, the duration of the early Pliensbachian can be estimated at 3 to 4 My.

The stratigraphical framework accepted in the present work is illustrated in Fig. 3. Two separate scales can be used to account for provincialism. They have distinct stratigraphical meanings. Indeed, although exploration of Mediterranean biostratigraphy (right part of the figure) is still in progress, knowledge of NW European biostratigraphy (left part of the figure) is much more advanced. Subsequently, the related NW European stratigraphical scheme achieves an excellent degree of stability at the zonal and subzonal levels, and a reasonably stable sequence of horizons or zonules is operational (Dommergues et al., 1997; Page, 2003). Moreover, while

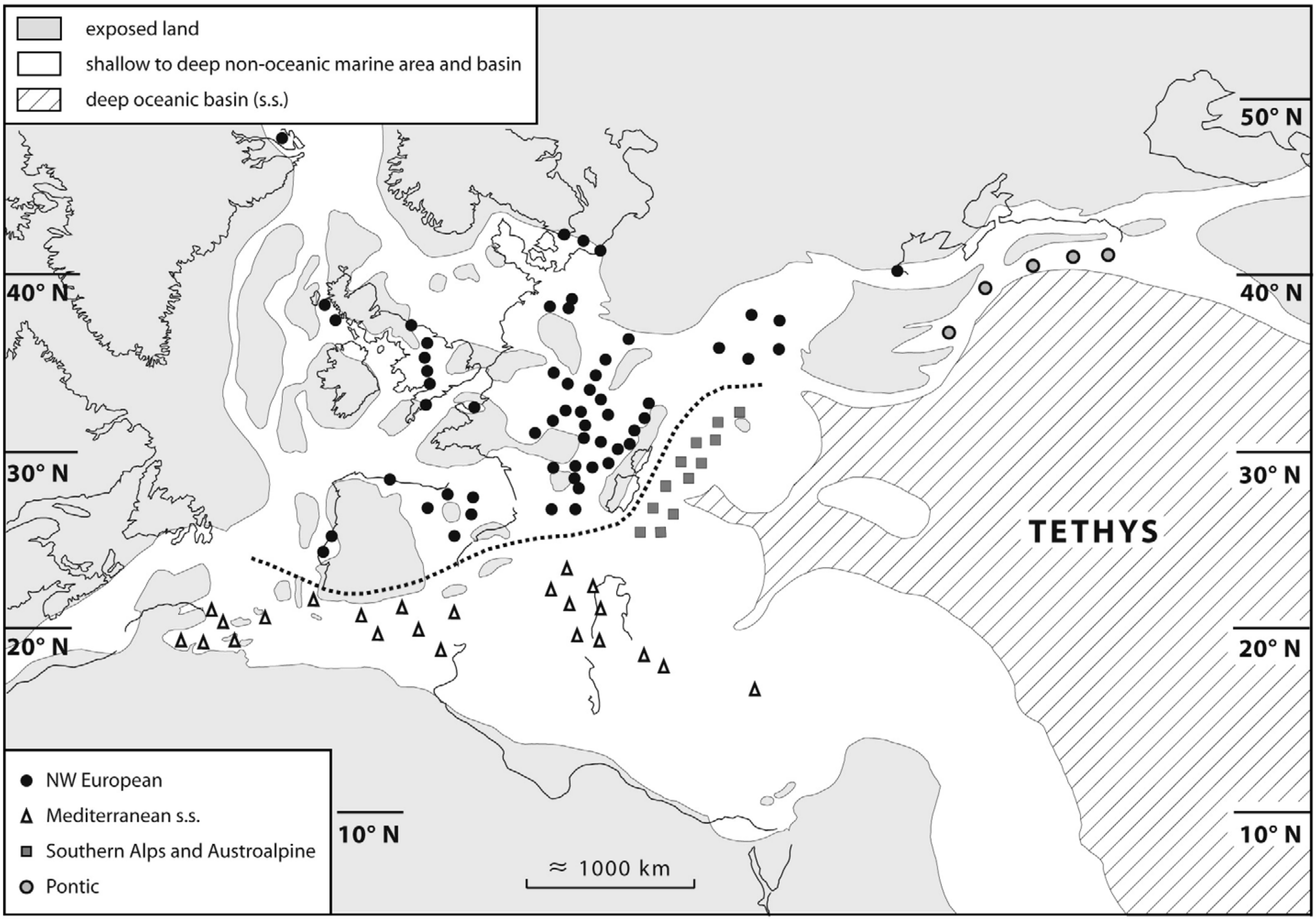


Fig. 1. Palaeogeographical reconstruction of the western Tethys and adjacent areas (from Thierry et al., 2000, modified) with indication of the 104 fossiliferous localities considered in the present paper. The NW European, Austroalpine, Mediterranean s.s. and Pontic localities are distinguished by symbols.

the Mediterranean stratigraphical units proposed for the Mediterranean province are clearly meaningful in terms of biostratigraphy (biozone, bioevent), those for NW Europe are of chronostratigraphic significance (chronozone, sub-chronozone, zonule). To avoid possible confusion, the chronostratigraphical units are not italicised by convention. The NW European scheme of chronostratigraphical units is also a standard against which the Mediterranean biozonal schemes are correlated. Moreover, because the obvious early Pliensbachian provincialism makes interprovincial correlations somewhat difficult, the sub-chronozone level is used as an acceptable compromise. To illustrate these difficulties, the boundaries of the Mediterranean biostratigraphic units are figured by dotted lines in Fig. 3, and the slant of the dividing lines between the bioevents roughly reflects the suspected magnitude of the uncertainties. Despite the uncertainties, though, the subzonal level is well suited to the degree of knowledge of the NW European and Mediterranean faunas. Indeed, the often short or very short stratigraphical ranges of taxa are now usually known (boundaries and duration) with the precision of the bioevent, zonule or sub-chronozone. Conversely a few taxa only, often with rather long ranges, are documented at the zonal or substage levels alone. In such cases, the range was converted to the corresponding sub-chronozones for the analyses (e.g., a taxon only known to occur in the Davoei chronozone was considered present in the Maculatum, Capricornus and Figulinum sub-chronozones).

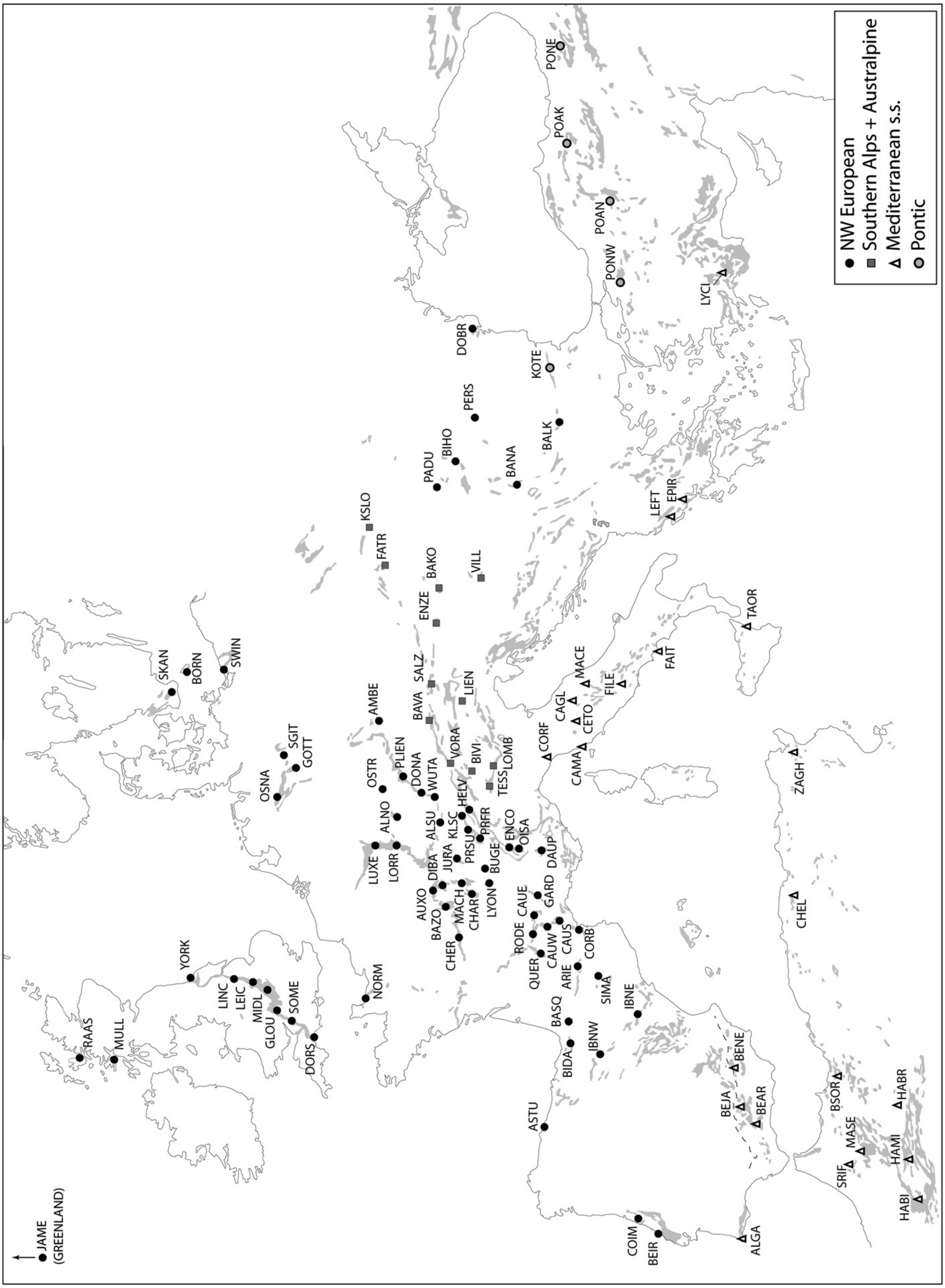
2.3. The taxonomic framework

Even if the species concept in ecology and biogeography is much debated (e.g., biological species concept [BSC] vs phylogenetic or diagnostic species concept [PSC]) (Isaac et al., 2004), species lists are the basis of nearly all studies of extant biodiversity. Moreover, and at least in the case of early Pliensbachian ammonites, the species level is often less complex than the genus level. For example, in the early Pliensbachian and in the lower part of the late Pliensbachian, the Hildoceratidae – a family of primary importance in the Mediterranean area – are represented by two genera (*Protogrammoceras* and *Fuciniceras*) that are both clearly polyphyletic. Conversely, the species are often clearly delineated (Neige and Dommergues, 1995; Dommergues et al., 2002). In addition, the use of the species level is well suited to, and consistent with, the spatio-temporal resolution of our study (locality and sub-chronozone).

In fact, and as far as early Pliensbachian ammonites are concerned, the only significant argument which could be put forward against the use of the species level is the significant number of unwarranted nominal species in the literature and consequently the need for a challenging preliminary revision.

The data base of the present work is founded on an assumed near-exhaustive taxonomic revision at the species level of the literature that includes illustrations (drawings and/or photographs)

Fig. 2. Location of the 104 localities considered in the present work. The NW European, Austroalpine, Mediterranean s.s. and Pontic localities are distinguished by symbols. The Early Jurassic outcrops or undifferentiated Jurassic outcrops in tectonised areas are indicated in grey. The meanings of the abbreviations are given in Appendix A (supplementary electronic material).


● NW European
■ Southern Alps + Australpine
▵ Mediterranean s.s.
○ Pontic
JAME (GREENLAND)
RAAS
MULL
YORK
LINC
LEIC
MIDL
GLOU
SOME
DORS
NORM
OSNA
SGIT
GOTT
SKAN
BORN
SWIN
AMBE
OSTR
PLIEN
DONA
WUTA
ALNO
LUXE
LORR
ALSU
DIBA
JURA
KLSC
HELV
PRSU
PRFR
BUGE
AUXO
BAZO
MACH
CHAR
LYON
CHER
ENCO
OISA
DAUP
CAUE
GARD
RODE
CAUW
CAUS
CORB
QUER
ARIE
SIMA
BASQ
IBNE
BIDA
IBNW
ASTU
COIM
BEIR
ALGA
BENE
BEJA
BEAR
SRIF
MASE
HABI
HAMI
BSOR
HABR
CHEL
ZAGH
BAVA
SALZ
VORA
BIVI
LIEN
TESS
LOMB
CORF
CAMA
CETO
CAGL
MACE
FILE
FAIT
TAOR
ENZE
BAKO
FATR
KSLO
VILL
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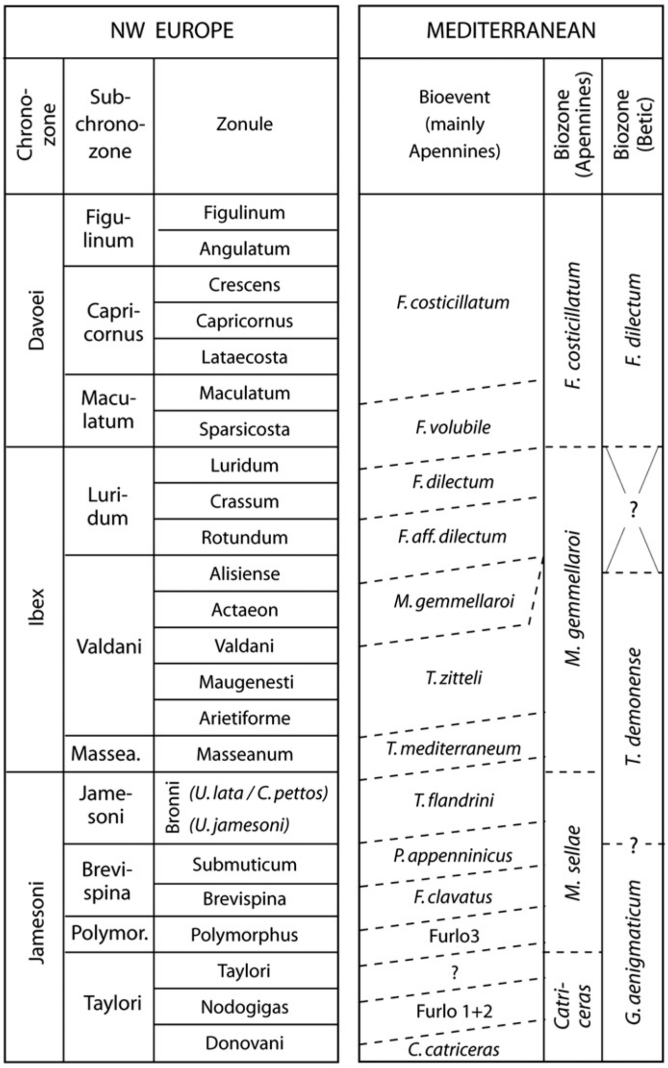

Fig. 3. The standard chronostratigraphic NW European (left) and the biostratigraphic Mediterranean (right) scales used in the present work. The NW European scheme at the subzonal level, materially formalised by Dean et al. (1961), is nowadays consensual. The minor differences between the NW European scale used here and the foregoing chronostratigraphic syntheses proposed by Dommergues et al. (1997) and Page (2003) concern the zonule level only. Conversely, the situation is complex for the Mediterranean scheme. At the zonal level two concurrent scales are commonly used. The first was established for the Betic ranges by Rivas (1981) and improved by Braga et al. (1982) and Braga and Rivas (1985). It lacks consistency for the zonal boundaries. The second one initiated by the works of Ferretti (1972, 1975), Faraoni et al. (1994) and Ferretti and Meister (1994) was first formalized by Faraoni et al. (1996) then improved and/or refined by Dommergues et al. (2004) and Venturi et al. (2005). This biostratigraphical scheme is characterised by fairly well defined zonal boundaries. It is supported by a convincing sequence of bioevents which is the basis for the tentative scale of Mediterranean bioevents proposed here.

of Mediterranean and/or NW European early Pliensbachian ammonites. This revision was fully and conjointly conducted by two of the authors (J.-L. D. and C. M.). Only properly illustrated specimens were taken into consideration and any taxa that were simply cited were ignored. Thus the taxonomic choices, and especially the appreciation of intra-specific variability, can be expected to be consistent and as homogenous as possible throughout the data base.

The rich literature analysed is a set of 273 distinct works illustrating almost two centuries of palaeontological investigations, from 1817 to 2008. Among those works, 49 are books, brochures or academic works (e.g., theses, reports). The other 224 are papers published in 111 different journals. These works were edited in 21 different countries and are written in 7 languages. Finally, and if one considers the 23 countries in which the ammonites were sampled, the pattern is well distributed in relation to the number, position, and significance of the localities. In palaeobiogeographical terms, 149 (55%) publications are wholly or mainly about NW European faunas and 124 (45%) about Mediterranean ones. Thus, and at least if one considers the number of publications, the study effort seems fairly comparable for both palaeobiogeographical areas.

The first step of the analysis was the creation of a catalogue of Non Revised Occurrences (NRO). Each of these NROs is a piece of information corresponding to an illustration or to a coherent set of illustrations of a nominal species from a given fossiliferous outcrop and illustrated in a given work. A total of 2862 NROs was extracted from the 273 works investigated.

The second step of the analysis was the taxonomic revision at the species scale of all NROs. Our taxonomic option is a compromise between the splitter and lumper cultures. It is essential to allow for intra-specific variability so as to ensure reasonable robustness of the taxonomic choices, but it is also crucial to maintain the ability to decipher and quantify the often subtle and complex patterns of endemism. Many endemic species, especially in intricate tropical environments (e.g., many Tethyan environments), are often very rare and highly restricted. In these cases, it is obviously impossible to appraise the intra-specific variability (e.g., some remarkable and clearly valid species are known only by a single or by very few specimens). The careful consideration of the palaeoecological and palaeogeographical frameworks is often the only mean to determine whether a rare nominal species can be understood as a valid one. In the present paper, only 214 (43%) of the 495 nominal species are kept as valid. To simplify, the valid species that form the taxonomic units of the analysis, are designated as species. The list is given in Table 1, together with the associated distribution into the NW European and Mediterranean provinces and subprovinces.

The third step was the elaboration of a catalogue of Revised Occurrences, hereafter designated as occurrences. Each of these occurrences is a synthesis taking into account both the revised taxonomic framework and the 104 localities. Thus, each occurrence is a piece of information that indicates the presence of one of the 214 species in one of the 104 localities, together with its age. Obviously, several NROs can be gathered as a single occurrence. Thus the initial set of 2862 NROs yields just 1765 (62%) occurrences.

3. Methods

We investigated faunal distinction – and therefore palaeobiogeographic patterns – for the entire early Pliensbachian substage using both Q-mode cluster and unconstrained ordination analyses. These techniques are complementary and their combined use is highly recommended (e.g., Williams and Lance, 1968; Sneath and Sokal, 1973; Shi, 1993; Legendre and Legendre, 1998; McGarigal et al., 2000; Fara et al., 2005). Only assemblages with more than four species were retained in the analyses.

Clustering was established by the UPGMA hierarchical agglomerative cluster algorithm applied to the early Pliensbachian similarity matrix. This matrix was computed for the incidence-based Raup–Crick coefficient (Raup and Crick, 1979). The robustness of the results was explored by using other usual coefficients, such as the Simpson, Jaccard, and Ochiai indices (e.g., see Magurran, 2004). To supplement this, we used three ordination techniques: nonmetric multidimensional scaling (NMDS) applied to a Raup–Crick similarity matrix; correspondence analysis (CA, Benzécri, 1973), and de-trended correspondence analysis (DCA, Hill and Gauch, 1980). Although these approaches rely on different assumptions – e.g., see Legendre and Legendre (1998) and McGarigal et al. (2000) for details – they yielded very similar results. Here we present the results of the de-trended correspondence analysis (DCA) because it is particularly

Table 1
List of species of ammonites and their distribution for the early Pliensbachian in the western Tethys and adjacent areas. NWE = NW European; MED = Mediterranean; MED AUST = Austroalpine; MED PONT = Pontic.

	NWE	MED s.s.	MED AUST	MED PONT
Acanthopleuroceras actaeon	x			
Acanthopleuroceras alisiense	x			
Acanthopleuroceras arietiforme	x		x	
Acanthopleuroceras carinatum	x		x	
A. maugenesti	x		x	
Acanthopleuroceras sp.1	x			
Acanthopleuroceras valdani	x		x	
A. ? sp. nov. 2	x			
Aegoceras artygyrus	x			
Aegoceras capricornus	x		x	
Aegoceras lataecosta	x		x	
Aegoceras maculatum	x		x	
Aegoceras sparsicosta	x		x	
Aegolytoceras varicosum		x	x	
Apoderoceras aculeatum	x		x	x
Audaxlytoceras audax		x	x	x
Baltzerites baltzeri		x		
Beaniceras crassum	x		x	
Beaniceras rotondum	x		x	
Beaniceras centaurus	x			
Beaniceras luridum	x			
Becheiceras bechei	x	x	x	x
Bettoniceras ? perisphinctoides		x		
Bettoniceras italicum		x	x	
Bifericeras donovani	x			
Calaiceras calais		x	x	x
Caleites calensis		x		
Calliphylloceras bicicolae	x	x	x	x
Capreoliceras asagensis			x	x
Castanayiceras canavarii		x	x	
Catriceras catriense		x	x	
Catriceras cf. *campiliense*		x		
Catriceras galaczi			x	
Coeloceras pettos sensu G		x	x	x
Coeloceras pettos	x			
Coeloderoceras ponticum	x		x	x
Coeloderoceras rugosa	x			
Coeloderoceras biruga	x			
Coeloderoceras micromphala				x
Cymbites ? sp. nov. *1*	x			
C. ? laevigatus sensu R&G		x		
Cymbites globosus	x		x	
Dayiceras amaltheiforme	x			
Dayiceras dayiceroides	x			
Dayiceras nanum	x			
Dayiceras polymorphoides	x			
Dayiceras renzi	x			
Dayiceras splendens	x			
Diaphorites vetulonius		x		
Dubariceras ? sp.		x		
Dubariceras inaequicosta		x	x	
Dubariceras dubari	x	x	x	
Eoderoceras ? lina	x			
Epideroceras ? cantianense		x		x
Epideroceras ? nodofissum	x			x
Epideroceras ? plumarius	x			
Epideroceras ? trigonale	x			
Eremiticeras evolutus		x		
Fieldingiceras sp. sensu V&F		x		
Foetterliceras salmojraghii		x	x	
Foetterliceras morogense	x			
Fuciniceras carixiense		x	x	
Fuciniceras dilectum		x	x	x
Fuciniceras elichense		x		
F. formosum sensu R&G		x		
Fuciniceras giennense		x		
Fuciniceras lycius		x		
Fuciniceras angulosum			x	
Fuciniceras balatonense			x	
Fuciniceras costicillatum		x	x	
Fuciniceras hungaricum		x	x	
Fuciniceras ionicum		x	x	
Fuciniceras mellahense		x	x	
Fuciniceras n. sp. A		x		
Fuciniceras nov. sp.*1*			x	
F. perplicatum sensu G&M			x	
Fuciniceras pseudodilectum	x			
Fuciniceras volubile	x	x	x	
Furlites involutus		x		
Galaticeras ? rosenbergi		x	x	
Galaticeras aegoceroides		x	x	
Galaticeras harpoceroides		x	x	
Galaticeras marianii		x		
Gemmellaroceras granuliferum		x	x	
G. ? gemmellaroi sensu M	x			
G. ? cortesi sensu B				x
G. ? gemmellaroi			x	
G. aenigmaticum	x	x	x	
G. circumcrispatum		x		
Gorgheiceras gorghense		x		
Harpophylloceras eximus		x	x	
Holcolytoceras nodostricum	x		x	
Holcolytoceras quadrijugum		x	x	
Hyperderoceras retusum	x		x	
Jamesonites ? spoliatus	x			
Jamesonites reticulatus	x			
Juraphyllites libertus		x	x	x
Juraphyllites nardii		x	x	x
Juraphyllites sp. A		x		
Leptonotoceras sp.	x			
Liparoceras cheltiense	x		x	
Liparoceras heptangulare	x		x	
Liparoceras lytoceroides	x			
Lytoceras altum			x	
Lytoceras fimbriatoides		x	x	
Lytoceras fimbriatum	x	x	x	x
Lytoceras fuggeri		x	x	
Lytoceras galatiforme		x		
Lytoceras kizilcius		x		
Lytoceras platypleura		x		
Lytoceras tortum	x		x	x
Metaderoceras ? pygmaeus	x			
Metaderoceras apertum		x	x	
Metaderoceras clavatus		x		
M. muticum sensu M&B			x	x
Metaderoceras beirense	x			
Metaderoceras gemmellaroi	x	x	x	
Metaderoceras muticum	x			
Metaderoceras pseudomuticum		x		
Metaderoceras venarense	x			
Miltoceras ? sp.		x		
Miltoceras furlense		x		
Miltoceras seguenzae		x	x	
Miltoceras sellae		x	x	
Miltoceras taguendoufi		x		
Oistoceras angulatus	x		x	
Oistoceras figulinum	x		x	
Platypleuroceras caprarium	x			
Paraderoceras picenum		x		
Paramicroderoceras birchoides	x			
P. aff. *birchiades*		x	x	
Paramicroderoceras fila	x			
P. tardecrescens				x
Paramorphites acutiventris		x		
Paratropidoceras numidianum		x	x	
Parinodiceras parinodus	x			
Partschiceras striatocostatum		x	x	x
Pelingoceras pseudocarinatum		x		
Peripleuroceras rotundicosta	x			
Phricodoceras taylori	x		x	
Phricodoceras taylori sensu H		x	x	x
Phricodoceras bettonii		x	x	
Phylloceras hebertinum	x	x	x	x
Platypleuroceras acanthobronni	x			
Platypleuroceras aff. *oblongum*				x
Platypleuroceras amplinatrix	x		x	
Platypleuroceras aureum	x			
Platypleuroceras brevispina	x		x	x
Platypleuroceras muellensis	x			
Platypleuroceras nodosum	x			

(*continued on next page*)

Table 1 (*continued*)

	NWE	MED s.s.	MED AUST	MED PONT
Polymorphites ? aff. bronni		x		
Polymorphites ? apenninicus		x		
Polymorphites ? bronni	x		x	
Polymorphites ? flexicostatus		x		
Polymorphites ? pseudodubari	x			
Polymorphites polymorphus	x			
Polymorphites rutilans	x			
Prodactylioceras aurigeriense	x			
Prodactylioceras davoei	x		x	
Prodactylioceras rectiradiatum	x			
Pseudophricodoceras caprariforme	x			
P. dayiforme	x			
Pseudoskirroceras mastodon		x	x	
Radstockiceras buvigneri	x		x	
Radstockiceras complanosum	x	x	x	x
R. pseudosaemanni	x			
Radstockiceras wiltshieri	x	x	x	
Reynesocoeloceras aegrum		x		
Reynesocoeloceras incertum	x	x	x	
Reynesocoeloceras indunense		x	x	
Reynesocoeloceras obesum	x	x	x	
R. praeincertum	x	x	x	
R. subcrassum		x	x	
Sinuiceras planulatum		x		
Sinuiceras sp. nov.		x		
Sphaenoacanthites costotuberculatum		x		
Spiniclaviceras spirale		x		
Tetraspidoceras evolutum	x		x	
Tetraspidoceras quadrarmatum	x		x	
Tragophylloceras carinatum	x			
Tragophylloceras loscombi	x			
Tragophylloceras ibex	x		x	
Tragophylloceras numismale	x		x	
Tragophylloceras undulatum	x			
Tropidoceras calliplocum		x	x	
Tropidoceras demonense		x	x	x
Tropidoceras densicosta	x		x	
Tropidoceras erythraeum		x	x	x
Tropidoceras flandrini	x	x	x	x
Tropidoceras masseanum	x		x	x
Tropidoceras mediterraneum		x	x	x
Tropidoceras obtusum	x			
Tropidoceras orientale				x
Tropidoceras semilaevis		x		x
Tropidoceras stahli	x		x	
Tropidoceras stahliforme		x		
Tropidoceras sulcatus		x		
Tropidoceras zitteli		x	x	
Tropidoceras zitteli sensu A&M				x
Tunisiceras insolitus		x		
Uptonia ? juraphyllitoides			x	
Uptonia ? sp. nov	x			
Uptonia confusa	x		x	x
Uptonia jamesoni	x		x	
Uptonia lata	x		x	x
Vicininodiceras gollingense		x	x	
Vicininodiceras simplicicosta	x		x	
Villania callomoni			x	
Villania densilobata	x		x	x
Zaghouanites arcanum		x	x	
Zamaiceras carinatum		x		
Zamaiceras mangoldi		x		
Zetoceras zetes		x	x	x
Z. iudicariense sensu G&M			x	

useful for describing trends in species composition. Indeed, Gauch (1982) noticed that de-trending by segments and re-scaling the axes nonlinearly confers an important property on DCA: the axes are scaled in units of the average standard deviation of species turnover. In other words, the length of the first DCA axis becomes an estimate of the underlying ecological gradient measured in species turnover units (Gauch, 1982; Legendre and Legendre, 1998).

In a second step, multivariate patterns observed in cluster and ordination analyses were tested for significance using one-way ANOSIM and NPMANOVA based on four binary similarity indices (Simpson, Jaccard, Ochiai, and Raup–Crick coefficients). These non-parametric techniques contrast the variation between clusters with variation within clusters due to sampling error and distributional patchiness (Clarke, 1993; Anderson, 2001; McArdle and Anderson, 2001). The null hypothesis is that there is no difference in species composition among the clusters previously identified. Computations were performed with PAST 1.81 (Hammer et al., 2001).

Occurrence and richness distributions were first explored with raw counts for the entire early Pliensbachian dataset, as well as for each chronozone. Temporal richness in ammonite species was not computed with the range-through method because the data are regional-to-provincial in scale (e.g., Fara, 2004). In order to compare the diversity of different regions at comparable levels of sampling efforts, we used sample-based rarefaction curves (sensu Gotelli and Colwell, 2001). These expected species accumulation curves and their associated 95% confidence intervals were constructed using EstimateS 8.0.0 (Colwell, 2006). The calculations are based on the analytical formulas of the moment-based estimator of richness τ (known as Mao Tau) and its confidence limits. See Colwell et al. (2004), Mao et al. (2005) and Colwell (2006) for details.

4. Results

Cluster analysis carried out for the entire early Pliensbachian shows a major division of the ammonite assemblages. One cluster corresponds almost exclusively to NW European (NWE) assemblages, whereas the other is composed of Mediterranean s.s., Pontic, and a majority of Austroalpine assemblages (Fig. 4). NW European samples form a homogeneous cluster, with the exception of Al-GOTT and Fr-OISA. The former is a peculiar, small assemblage that contains two species characterising the NWE province (*Beaniceras centaurus* and *Tragophylloceras carinatum*) and two NWE species also occurring in a few Austroalpine localities (*Liparoceras cheltiense* and *Tetraspidoceras quadrarmatum*). Fr-OISA is a small assemblage (just four ammonite species) that is also quite volatile between the NWE and MED clusters when other similarity indices are used. This is because it contains taxa present in both NW European and Austroalpine / Pontic sites (e.g., *Lytoceras tortum*, *Tropidoceras masseanum*, *Acanthopleuroceras carinatum*). The mixed nature of Austroalpine assemblages tends to scatter them across both NWE and MED clusters (Fig. 4). Such a case of intermediate faunal composition is best represented in an ordination plot.

Fig. 5 shows the results of the DCA applied to the same early Pliensbachian data matrix. The distinction between NWE and MED s.s. assemblages is also clear with this approach (Fig. 5A). More importantly, the mixed, intermediate composition of both the Austroalpine and Pontic faunas is evidenced by their position along axis 1. They form an interface between a Euroboreal and a Tethyan pole. Note the proximity of the above-mentioned NWE assemblage Fr-OISA with this transitional zone. The length of the first DCA axis, which is a measure of the largest compositional variation in the data set, is 4.86 standard deviation (SD) units. It testifies to the profound faunal difference characterising northwestern Tethyan ammonites during the early Pliensbachian. Indeed, along a regular environmental gradient, a complete species turnover occurs in about 4 SD units, whereas a 50% change in species composition occurs within about 1 to 1.4 SD units (Gauch, 1982; Legendre and Legendre, 1998). The first axis opposes a NWE extremity made up of Al-GOTT, Pl-SWIN and several British assemblages (low DCA scores) to a MED s.s. extremity formed essentially by Italian and Moroccan assemblages (DCA score between 4.5 and 4.86). The poles of axis 2 are formed mainly by the Bakony assemblages opposed to those of the Pontids. Fig. 5B shows the corresponding projection of ammonite species in the same DCA plot, illustrating some of the species with the most extreme scores on the first two DCA axes. They are typical representatives of the NW European, Mediterranean *sensu stricto*, Bakonian and Pontic poles

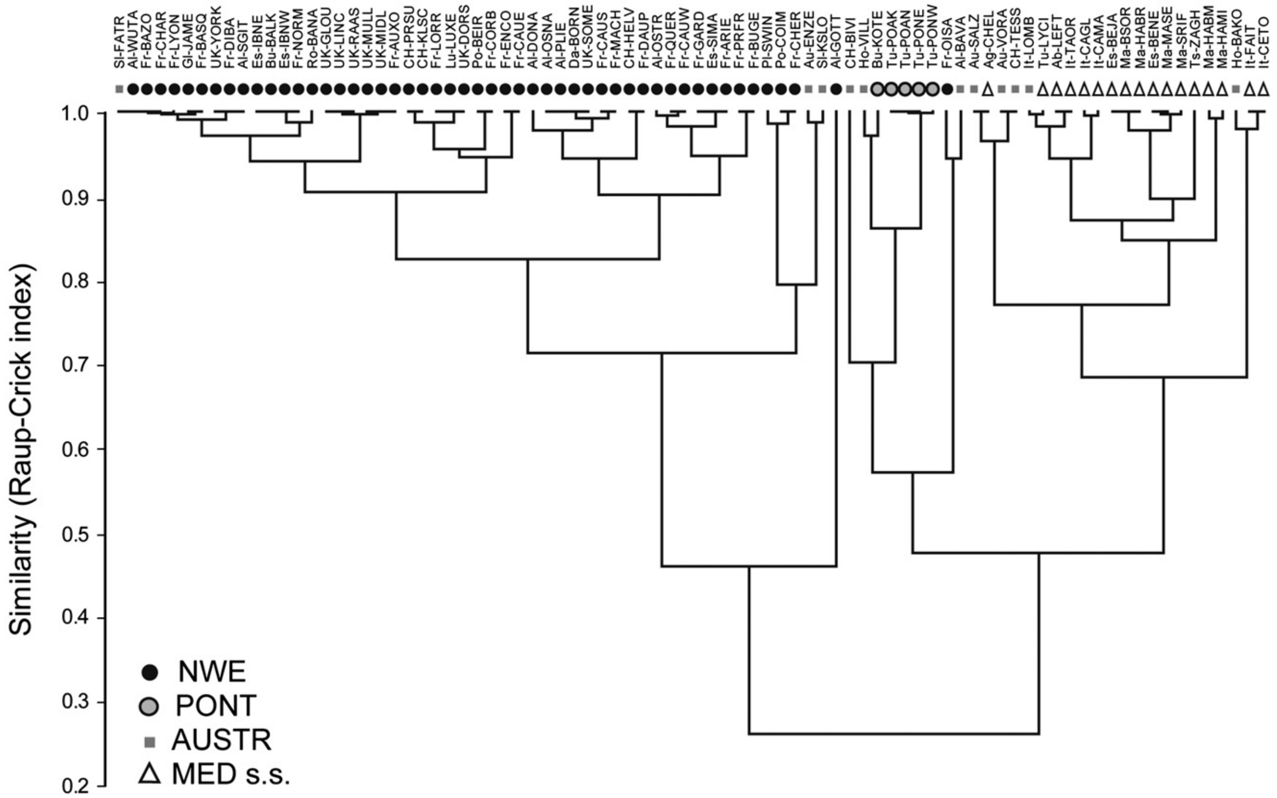

Fig. 4. Dendrogram resulting from a UPGMA cluster analysis of the early Pliensbachian ammonite assemblages containing at least four species. Faunal resemblance is measured by the Raup–Crick similarity index. Traditional palaeobiogeographic assignments are indicated with symbols. Abbreviations: NWE = Northwest European province; PONT = Mediterranean Pontic subprovince; AUSTR = Mediterranean Austroalpine subprovince; MED s.s. = Mediterranean subprovince *sensu stricto*.

among early Pliensbachian ammonites. Axis 3 is not described because it does not differentiate the provinces and subprovinces identified with axes 1 and 2. Note that the projections shown in Fig. 5 were established with the usual default value of 26 segments. Following the recommendations of Legendre and Legendre (1998), we tried various numbers of segments (from 10 to 39) for de-trending to see whether the observed patterns are affected by this methodological aspect. They are not.

One-way ANOSIM and NPMANOVA analyses confirm that the species compositions of NWE, MED s.s., PONT and AUSTR were significantly different altogether for the early Pliensbachian ($p<0.0001$ with both techniques and with the four similarity indices employed, see Methods), although pairwise comparisons show that PONT and AUSTR assemblages cannot be distinguished statistically in most cases. We also checked that the NWE vs MED s.s. distinction was present during the three chronozones of the early Pliensbachian substage. Matrix analyses for the Jamesoni, Ibex, and Davoei chronozones show that the overall pattern described here for the entire stage also prevailed during each of its chronozones. As a whole, the NWE and MED s.s. were completely different worlds during the early Pliensbachian, sharing only 6.6% of their ammonite species (13 out of 196).

Table 2 gives the distribution of localities, occurrences and raw richness for the entire early Pliensbachian dataset. It shows that Mediterranean localities are twice as rich in ammonites as their northwest European counterparts (R/L ratios), although their average numbers of occurrences per locality are similar (O/L ratios).

The species richness of the two provinces can be compared at a similar level of sampling effort using rarefaction curves. Fig. 6 illustrates several important patterns. First, Mediterranean species richness is about twice NW European richness for each chronozone. Second, the flattened NWE rarefaction curves suggest that the knowledge of early Pliensbachian ammonite diversity is rather complete, whereas it is not in the MED province. And third, there is a significant decrease in rarefied richness between the Ibex and Davoei chronozones in both provinces (Fig. 6). In order to explore this pattern further, we computed rarefaction curves for each sub-chronozone of the Ibex and Davoei chronozones. The results show that a large drop in richness did indeed occur at the boundary between these two chronozones (i.e., between the Luridum–Maculatum sub-chronozones). Furthermore, the resolution of the data for the NWE province enabled us to check that this pattern can be observed down to the zonule level (i.e., at the Luridum-Sparsicosta boundary).

Fig. 7 compares the temporal variation of rarefied richness during successive sub-chronozones in the Mediterranean and NW European provinces. The rarefaction level (that is, the number of localities used to compute the richness in each sub-chronozone) is determined by the sub-chronozone represented by the lowest number of localities. Here, the rarefaction level corresponds to 27 localities. The most striking pattern is that the two curves track each other very closely. Because such similarity could be due to the occurrence of identical species in both provinces, we re-computed rarefied richness after removing all the mixed assemblages, namely the Austroalpine and Pontic faunas. The pattern remains unchanged.

The Ibex–Davoei transition corresponds to a drop in species richness within the two provinces. The 95% confidence intervals show that this decrease is the only significant variation recorded in the Mediterranean province during the early Pliensbachian, and it seems to be an important breaking point between a high pre-Maculatum richness and a relatively low post-Luridum richness level (Fig. 7). The diversity drop is also present but less marked in NW Europe. As a whole, the general trend is a decrease in ammonite diversity during the early Pliensbachian, particularly in the Mediterranean province. As a result, the species richness in the two provinces tend to converge towards the end of the stage, although the Mediterranean province remains systematically and significantly richer. The Valdani sub-chronozone stands as an exception because its ammonite richness re-attained transitorily the Taylori sub-chronozone levels. This local

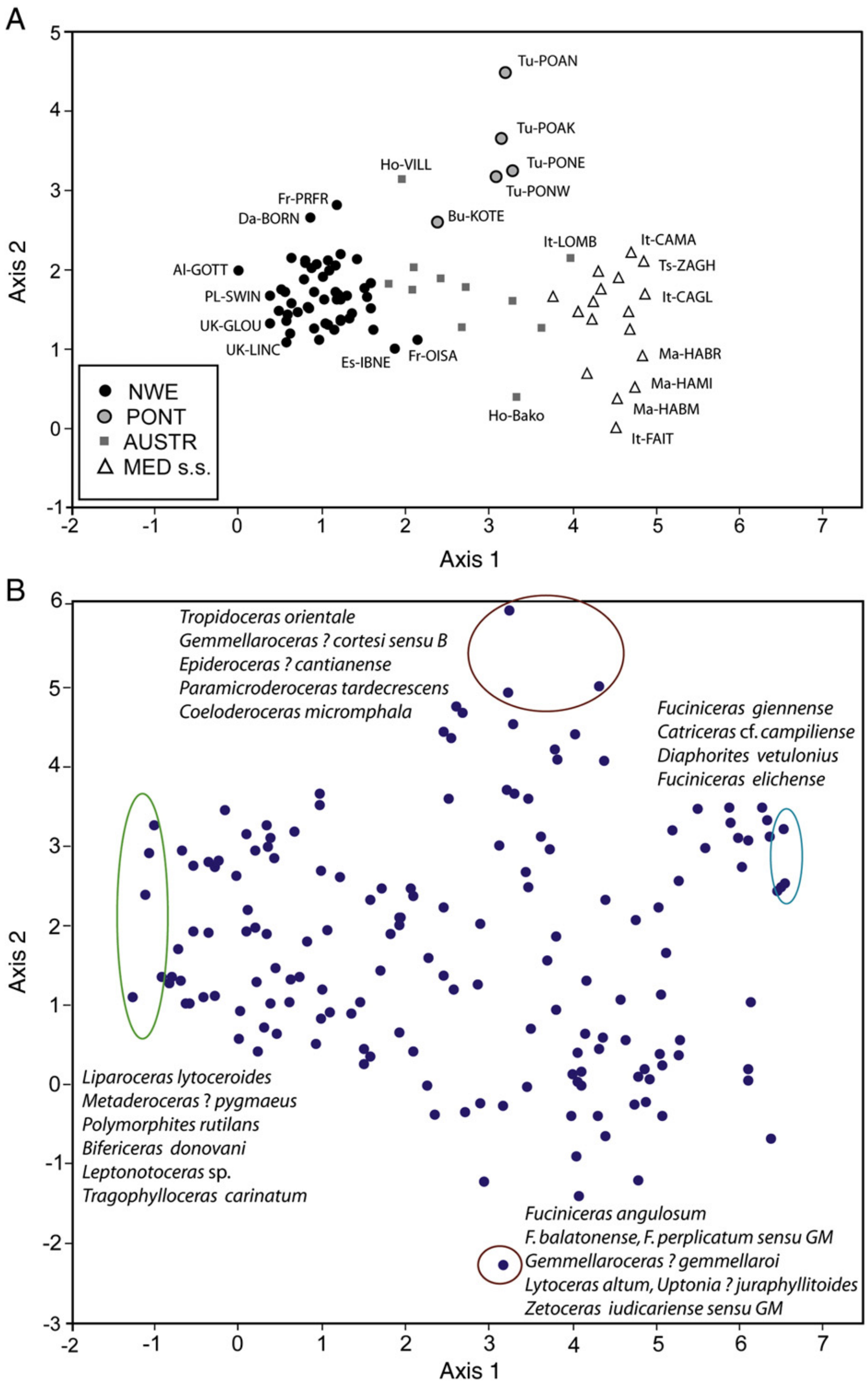

Fig. 5. Two-dimensional plots of the de-trended correspondence analysis applied to the early Pliensbachian data matrix. (A) Early Pliensbachian assemblages containing at least four species. For clarity, certain remarkable assemblages only have been labelled. Eigenvalue/gradient length are as follows: Axis 1: 0.77/4.86 SD; Axis 2: 0.34/4.45 SD; Axis 3 (not shown): 0.29/2.89 SD. Note the clear distinction between the NWE and MED s.s. assemblages, as well as the intermediate position of Pontic and Austroalpine samples along axis 1. (B) Corresponding projection of species for the same analysis. Only the groups of species with the most extreme DCA scores on axes 1 and 2 have been labelled and circled. Species names are ordered in decreasing score values.

maximum is the only significant value compared to the preceding and following sub-chronozones in NW Europe.

5. Discussion

The present quantitative study did not presuppose any palaeobiogeographical structuring of the ammonite faunas in the investigated area (i.e., the western Tethys and adjacent areas) throughout the early Pliensbachian. Thus, it is possible to falsify or to confirm objectively the pertinence of the major palaeobiogeographical units empirically defined and/or used by previous authors (e.g., Neumayr, 1872; Neumayr, 1883; Dubar, 1954; Donovan, 1967; Hallam, 1969; Geczy, 1973; Howarth, 1973; Sapunov, 1974; Enay, 1980; Dommergues, 1982; Geczy, 1984; Cariou et al., 1985; Smith and Tipper, 1986; Dommergues, 1987; Dommergues and Meister, 1991; Dommergues, 1994; Meister and Stampfli, 2000). Our quantitative analyses demonstrate that the

Table 2
Relation between the number of localities (L), the number of occurrences (O), and species richness (R) for early Pliensbachian ammonites.

Biogeographic units	L	O	R	O/L	R/L	O/R
MED PONT	5	87	37	17.40	7.40	2.35
MED AUSTR	12	293	108	24.42	9.00	2.71
MED MED s.s.	23	339	103	14.74	4.48	3.29
MED total	40	719	160	17.98	4.00	4.49
NWE total	64	1047	107	16.36	1.67	9.78
Total	104	1766	214	16.98	2.06	8.25

main palaeobiogeographical units (i.e., NW European and Mediterranean provinces) accepted by most authors are not artefacts. Thus, the palaeobiogeographical partitioning of the western Tethys and adjacent areas into a NW European and a Mediterranean province is an objective and sustained phenomenon. This pattern is certainly not a taxonomic artefact because the data base is founded on a taxonomic revision free of any palaeobiogeographical a priori, and because the species retained as valid are usually groupings of several nominal species. In fact, a moderate lumping option is preferred to a splitting one in order to avoid the artificial multiplication of hardly credible endemic species. Moreover, we show that the provincialism characterising the early Pliensbachian as a whole is also present in each of its chronozones (Jamesoni, Ibex and Davoei).

A similar palaeobiogeographical partitioning (i.e., NW European vs Mediterranean province) of the Early Jurassic Western Tethys and adjacent areas has been observed for other taxa. Among those are belemnites (Doyle, 1987, 1994), that are nektonic, but also benthic life forms such as brachiopods (e.g., Ager, 1967, 1971, 1973; Vörös, 1977, 1984, 1993), bivalves (Hallam, 1977) and ostracods (e.g., Bate, 1977; Lord, 1988; Arias and Whatley, 2005; Arias, 2007). Such a contrasted palaeobiogeographical pattern occurs most patently during the Pliensbachian, and more particularly during the early part of this stage. At that time faunal exchanges were scant and usually limited to the restricted Austroalpine and Pontic areas. This is in sharp contrast with the situation that preceded and followed that episode. Indeed, both Sinemurian and Toarcian faunas included much more ubiquitous taxa that considerably weakened ammonite provinciality. Endemic taxa are usually rare during the Sinemurian and early-middle Toarcian, and wide areas of mixed faunas suggest numerous and easy faunal exchanges during these stages.

During the early Pliensbachian palaeobiogeographical crisis, the NW European and the Mediterranean ammonite provinces can be characterised by both distinct richness and species proportions. These differences, that we quantify here, were noticed previously by Page (1996) and by Meister and Stampfli (2000). Such dissimilarity between the NW European and Mediterranean ammonite faunas is probably genuine. Indeed, if the number of publications is used as a proxy for the pressure of study, it appears that NW European and Mediterranean provinces are comparable, with 55% and 45% of the publications analysed, respectively. Moreover, sampling heterogeneity is controlled for by the use of rarefied richness.

In the present work, ammonite richness and the proportion of species within faunas are quantified for the entire early Pliensbachian, but their temporal variations are also monitored at the chronozonal and/or sub-chronozonal levels. Surprisingly, at all these levels, the NW European and Mediterranean provinces record almost the same pattern of variation in ammonite species richness despite the fact that their taxonomic compositions at the species level have virtually nothing in common (Fig. 7). As previously suggested by the raw data given by Meister and Stampfli (2000), the overall tendency is a decrease in species richness during the substage. Nevertheless, and as far as the sub-chronozonal level is concerned, this trend is briefly interrupted during the Valdani sub-chronozone, where a peak in species richness is observed in both NW European and Mediterranean provinces (Fig. 7). This pattern stems in part from the occurrence of several ubiquitous taxa that temporarily increase locality-level diversity. Interestingly, this phenomenon is coeval with a major change in ammonite morphological disparity. Indeed, Dommergues et al. (2001) show that the maximum of morphospace occupation at the global scale during the three first stages of the Jurassic occurs during the Valdani sub-chronozone. This curious synchronism remains difficult to explain, but it can be emphasised that: 1) Haq et al. (1987) indicate an especially high global sea level during the Valdani sub-chronozone, 2) the diversification of the Harpoceratinae subfamily begins in the Mediterranean province approximately at the same time (Meister and Stampfli, 2000; Venturi and Ferri, 2001). Further investigations will be necessary to say whether these phenomena are related to each other and how.

The present study shows that the main decline in species richness occurs after the Valdani sub-chronozone (especially between the Luridum and Maculatum sub-chronozones) and in both the NW European and Mediterranean provinces (Fig. 7). We think that this striking parallelism in species richness in the two provinces is a genuine pattern at both the chronozonal and sub-chronozonal levels. Indeed, although correlations between the NW European and Mediterranean provinces are often difficult or unfeasible at the zonule and/or bioevent level, they become credible at the sub-chronozonal and chronozonal levels (Page, 2003). This is why we often voluntarily downgraded our dataset from the zonule/bioevent levels down to this resolution in order to establish robust correlations between the NW European and Mediterranean provinces. It is thus remarkable that

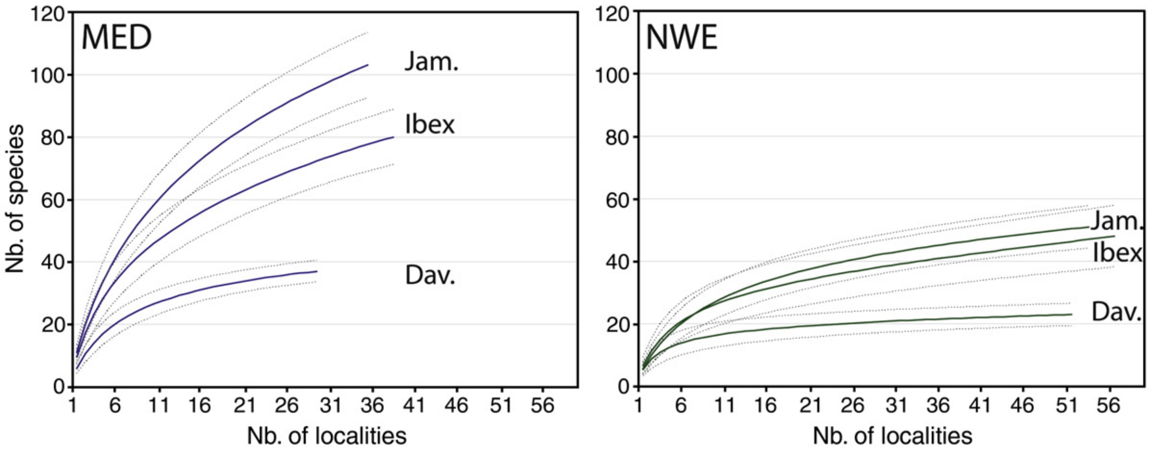

Fig. 6. Sample-based rarefaction curves for ammonites in the Mediterranean (MED) and NW European (NWE) provinces. Each curve corresponds to an early Pliensbachian chronozone (Jam. = Jamesoni chronozone; Ibex = Ibex chronozone; Dav. = Davoei chronozone). Note the significant decrease in species richness between the Ibex and Davoei chronozones in both provinces.

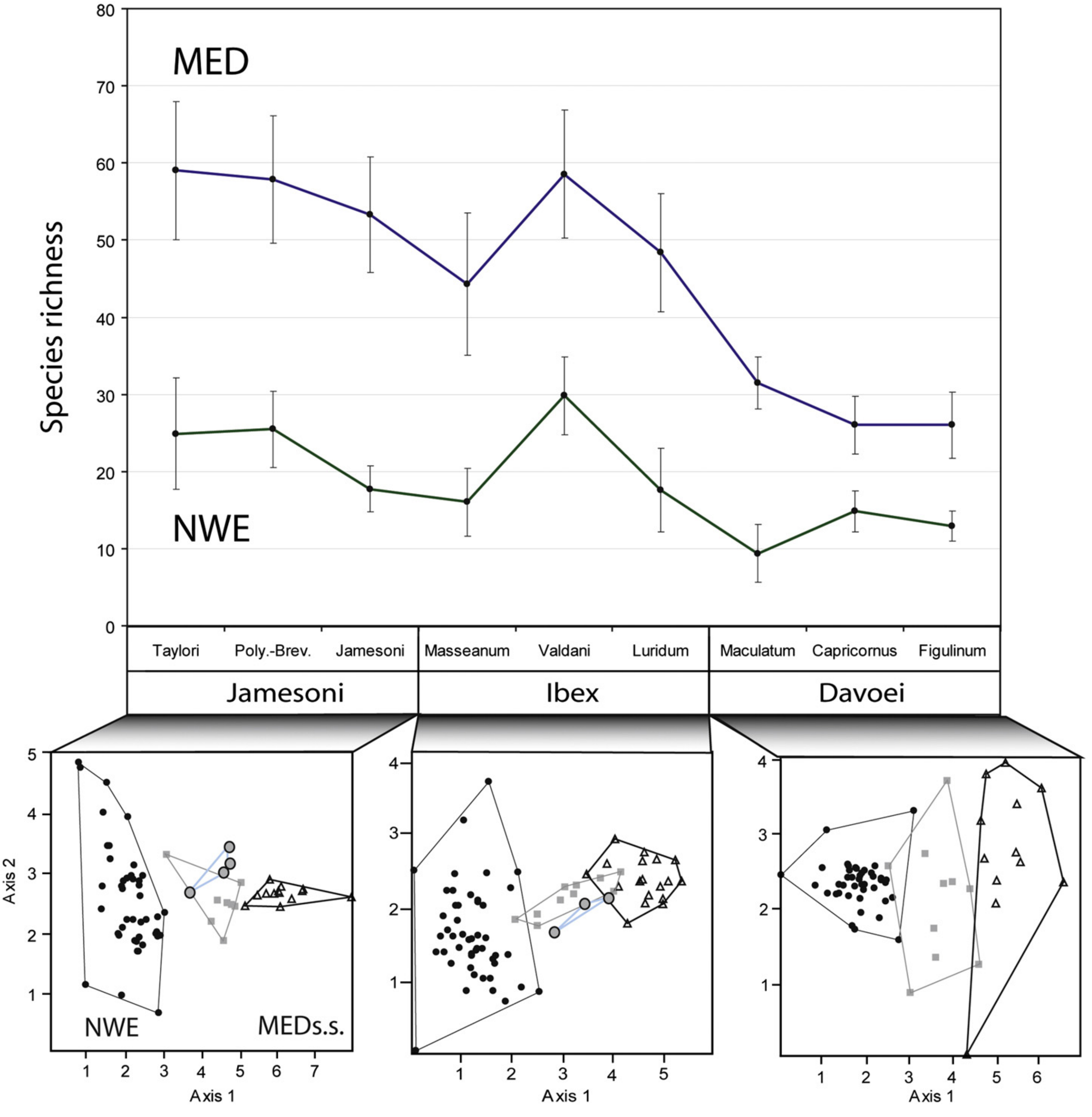

Fig. 7. Rarefied species richness of early Pliensbachian ammonites plotted for successive sub-chronozones in the Mediterranean (MED) and NW European (NWE) provinces. The richness is rarefied to 27 localities within each sub-chronozone to allow for comparison. Error bars represent 95% confidence intervals computed using the analytical formula of the Mao Tau (see Methods). The lower part of the figure shows the corresponding DCA two-dimensional plots of the assemblages for each chronozone. Note that the NWE and the MED s. s. assemblages remained distinct in the successive chronozones. Symbols as in previous figures.

ammonite diversity changed similarly and contemporaneously in these two provinces despite the scarcity of faunal exchanges between them. In contrast, Brayard et al. (2006, 2007) show that variations in taxonomic richness for Early Triassic ammonites are often related to significant changes in the palaeobiogeographical framework (e.g., cosmopolitan vs latitudinally restricted distributions). For example, low taxonomic richness at the global scale was clearly associated with episodes of barely structured provincialism during the Early Triassic. On the contrary, our study shows that variations in species richness (notably its fall prior to the Maculatum sub-chronozone) did not affect the palaeobiogeographical compartmentalisation characterising early Pliensbachian times. The causes of such a conservative palaeobiogeographical framework throughout the early Pliensbachian are difficult to disentangle, but at least three, more or less interconnected, factors can be considered: climate, eustasy and palaeogeography.

5.1. Climate

The propensity of ammonite faunas to be influenced by climatic variations has been considered by many authors (e.g., Enay, 1980;

Taylor et al., 1984; Smith, 1989; Cecca et al., 2005). For example, the pioneering work of Neumayr (1883) already regarded climate as the major determinant of global palaeobiogeographical patterns for ammonites. Recent advances in isotopic geochemistry (e.g., $\delta^{18}O$) and clay analysis now allow the relationship between ammonite biodiversity and palaeoclimate to be objectively addressed (e.g., Cecca et al., 2005; Brayard et al., 2006, 2007). The Early Jurassic is commonly known as an episode of a regular and warm climate associated with a very low gradient of sea surface temperatures. As such, the influence of climate on Early Jurassic palaeobiological patterns is usually deemed insignificant (Enay, 1980; Hallam, 1987; Dommergues and Meister, 1991). Nevertheless, some works report that significant climatic changes did occur during the Early Jurassic (e.g., Brandt, 1986; Zakharov, 1994; Bailey et al., 2003; Rosales et al., 2004; Van de Schootbrugge et al., 2005; Metodiev and Koleva-Rekalova, 2006; McArthur et al., 2007; Gómez et al., 2008; Suan et al., 2008; Dera et al., 2009). For instance, $\delta^{18}O$ values of belemnite rostra and/or clay assemblages indicate that seawater temperatures were significantly warmer (about 4 °C) during the Davoei chronozone than during the preceding Jamesoni and Ibex chronozones (Rosales et al., 2004; Dera et al., 2009). As a hypothesis, we presume that the low species richness of the Davoei chronozone may be related to this warming of seawaters. If not permanent, the relationship between warm seawaters and low ammonite species richness seems at least to be a recurrent and probably frequent phenomenon (see for example Brayard et al. (2006, 2007) for Early Triassic ammonites). However, and in contrast to the results of Brayard et al. (2006, 2007), our results show that the warming of the seawaters did not cancel out the stark palaeobiogeographic contrast between the NW European and Mediterranean provinces during early Pliensbachian times. This is consistent with the proposal by Doyle (1994) that climate was not a paramount controlling factor for the distribution of Early Jurassic belemnites. Cecca et al. (2005) do not rule out that climatic fluctuations may have influenced the palaeobiogeographical patterns of Late Jurassic ammonites (e.g., provincialism, steepness of diversity gradients), but they think that the role of palaeogeography, possibly combined with eustasy, was of greater importance.

5.2. Eustasy and palaeogeography

Dommergues (1982, 1987), Cariou et al. (1985), Dercourt et al. (1985), Dommergues and Meister (1991) and Meister and Stampfli (2000) show that during the early Pliensbachian, the NW European and Mediterranean provinces were for the most part abruptly separated by a narrow chain of emerged or shallow areas. This SW–NE oriented barrier ran roughly along the southern margin of the European plate, from the Betic range in southern Spain to the Briançonnais ridge (Fig. 1).

Furthermore, the prevailing facies are clearly distinct on both sides of this mostly emerged boundary. In NW European areas, the usually fossiliferous hemipelagic facies (e.g., greyish limestone–marl alternations) are more common than the facies from carbonate platforms (e.g., pale massive limestone deposits). The latter are widespread in the Mediterranean province and the fossiliferous localities are unevenly distributed and often limited to some remote restricted basins. East of the Briançonnais ridge, the border line between the main palaeobiogeographical entities is difficult to define in palaeogeographical terms. This is probably why the boundary was not a true barrier but rather a selective filter in that region. It allowed some faunal ingressions of NW European taxa into the Austroalpine and Pontic areas, which are consequently characterised by mixed ammonite faunas (Dommergues and Meister, 1991; Meister and Stampfli, 2000). Despites the uncertainties concerning its eastern part, the boundary between the main provinces was therefore essentially concomitant with a major palaeogeographical structure that operated as a durable emerged or near-emerged barrier throughout the early Pliensbachian. Moreover, facies distribution indicates that both environmental and tectonic constraints were clearly distinct in the NW European and Mediterranean areas. In this context, and as suggested by Page (1996, 2003) and Cecca et al. (2005), palaeogeography appears as a paramount factor structuring the distribution of NW European and Mediterranean ammonites during the early Pliensbachian. Clearly, the functioning of such a palaeogeographical barrier can be associated with eustatic fluctuations (e.g., a sea level rise could drown some previously emerged part of the barrier). That was apparently not the case for the early Pliensbachian because the main palaeobiogeographical pattern went unchanged throughout the substage.

The recognition of the extrinsic factors controlling ammonite distribution is hampered by the fact that biotas also have their own inertia due to intrinsic features. Interspecies competition can superpose itself on a strictly palaeogeographical cause and so confuse the relation between palaeobiogeographical patterns and environmental constraints in space and time (Ager, 1973; Dommergues and Meister, 1991). For example, Cariou et al. (1985) suggest that the distribution of Phylloceratina is simply linked to their pelagic mode of life (biome-dependent distribution), whereas Ammonitina preferred shallower epicontinental seas for which the geographic provincialism is clearer (palaeogeography-dependent distribution).

6. Conclusion

Our study confirms with quantitative arguments the existence of a marked palaeobiogeographical differentiation between the western (= Mediterranean) Tethyan areas and the adjacent NW European ones during the early Pliensbachian. It is difficult to prove what caused such a phenomenon, but it is cogent to suspect the primary or at least significant influence of a chain of emerged and/or shallow areas forming a barrier between the main two palaeogeographic entities. In any event, the Mediterranean Tethyan and the NW European faunas shared very few ammonite species during the early Pliensbachian.

The somewhat restricted Austroalpine s.l. areas were the only significant faunal interface. Austroalpine faunas are of major importance because they provide a framework for correlating Mediterranean and NW European faunas at the sub-chronozone or zonule levels. We show here that NW European faunas are rather poor, monotonous and fairly well-known, whereas Mediterranean ones are rich and contain many rare taxa that are still undersampled. Thus, in addition to their strikingly distinct taxonomic compositions, the NW European and Mediterranean faunas are characterised by their clearly dissimilar structure of ammonite diversity. It is remarkable, then, that the fluctuations in species richness in these two palaeobiogeographical units should track each other as they do. In particular, in both provinces, the species richness of the Davoei chronozone is clearly lower than in the preceding Jamesoni and Ibex chronozones. This parallel impoverishment of both Mediterranean and NW European faunas can be tentatively correlated with an episode of seawater warming during the Davoei chronozone. Several studies have shown that, during the Early Triassic at least, the decline in ammonite taxonomic richness induced by seawater warmings are systematically associated with a clear reduction in the palaeobiogeographical contrast. Surprisingly, the palaeobiogeographical structure of early Pliensbachian ammonites remained unchanged, and such an original response provides a good opportunity to explore further the link between biodiversity and palaeobiogeography.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2009.06.005.

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