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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 $\approx$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) land-masses. 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